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Promotion of exotic weed establishment by endangered giant kangaroo rats (*Dipodomys ingens*) in a California grassland

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Giant kangaroo rats (*Dipodomys ingens*) continually modify their burrow precincts by digging tunnels, clipping plants, and other activities. In the valley grasslands of the Carrizo Plain Natural Area (San Luis Obispo County, California), this chronic disturbance to soil and vegetation promoted the establishment of exotic ruderal and early successional plant species. *Erodium cicutarium*, *Bromus madritensis* ssp. *rubens*, and other Mediterranean annuals were found to constitute a very large proportion of the vegetation on giant kangaroo rat precincts. When vegetation on precincts was compared with the vegetation in less disturbed intermediate areas located between precincts, species richness, cover and frequency of exotic plants were significantly greater on precincts. The reverse was found for native species. In addition, exotic species encountered in this study had significantly larger seeds than did native species, suggesting that these granivorous kangaroo rats preferentially cache large weed seeds on their precincts. Since the kangaroo rats depend on exotic plants for food and the exotic plants depend upon the kangaroo rats to disturb their habitat continually, the weed–kangaroo rat relationship is mutualistic. This strong relationship may also inhibit population growth of native grassland plants which occupy disturbed habitats but have difficulty competing with exotic weeds for resources. From a conservation perspective, this mutualism presents an intractable management dilemma. Restoration of valley grasslands where endangered giant kangaroo rats occur, to conditions where native species dominate, may be impossible.

Keywords: kangaroo rat; grassland; disturbance; introduced species; endangered species; restoration

Introduction

Exotic plants began colonizing the valley grasslands of California in the 18th century (Jackson, 1985; Sauer, 1988). Mostly ruderal and early successional annuals from the Mediterranean region, these exotic species displaced native species and soon dominated this community (Baker, 1978; Jackson, 1985; Heady, 1988; Sauer, 1988; Keeley, 1990; Blumler, 1992; D'Antonio and Vitousek, 1992). Now, much of the 5 300 000 ha originally occupied by grasslands (Barbour and Major, 1988) have been replaced by agriculture, such that grassland vegetation covers only a very small fraction of the original area (Wester, 1981; Heady, 1988; Keeley, 1990). The presence of exotic species in California's few remaining valley grasslands poses serious restoration and management problems because very little is known about species composition, disturbance frequencies, or ecosystem dynamics of the original grasslands (Baker, 1978; Wester, 1981;

Jackson, 1985; Heady, 1988; Sauer, 1988; Menke, 1990; Edwards, 1990; Blumler, 1992). For example, relationships between vegetation and native vertebrates, and the effects of displacement of native plants by exotics on these relationships are very poorly understood.

The giant kangaroo rat (*Dipodomys ingens* Merriam) is one of the animals which would have been affected by the floristic shift to dominance by exotic species. A mostly granivorous animal, it is endemic to the arid grasslands of California's western San Joaquin Valley region (Williams and Kilburn, 1991; Williams, 1992). As a result of habitat loss in this region caused by widespread conversion of grassland to agriculture and the use of rodenticides, the giant kangaroo rat is a state and federally listed endangered species (Williams *et al.*, 1993). Currently, this species' habitat covers only 1.5–17.6% of its historic range (Williams, 1992).

Studies have shown that some small burrowing grassland mammals (e.g. prairie voles, pocket gophers, prairie dogs) chronically disturb soil and vegetation and often have a strong influence on plant community composition (Platt, 1975; Mielke, 1977; Coppock *et al.*, 1983; Tilman, 1983; Hobbs and Mooney, 1985; Reichman and Smith, 1985; Koide *et al.*, 1987; Gibson, 1989; Brown and Heske, 1990; Kalisz and Davis, 1992; Reichman *et al.*, 1993). Giant kangaroo rats also continually modify the soil and vegetation in the vicinity of their burrows (burrow 'precincts'; Grinnell, 1932) by extending tunnels, adding new entrance holes, clipping plants, harvesting and caching seeds, and dust bathing (Braun, 1985; Williams and Kilburn, 1991; Williams, 1992). These activities may promote the establishment of exotic weeds and may have actually contributed to the shift from native to exotic dominance in California's valley grasslands.

The purpose of this study was to assess whether the establishment of introduced weeds was enhanced by giant kangaroo rat activity. If kangaroo rats promoted exotic weed establishment, vegetation on burrow precincts would have greater exotic cover, frequency, and species richness than vegetation in less disturbed intermediate areas located between precincts. If the behaviour of these endangered small mammals does encourage exotic species in California valley grasslands, weed eradication and restoration of vegetation to conditions resembling the original community may be very difficult to achieve.

Methods

Study sites

Two annual grassland sites in the Carrizo Plain Natural Area (San Luis Obispo County, California) were selected for sampling. The Carrizo Plain, one of only a few areas supporting significant giant kangaroo rat populations (Williams and Kilburn, 1991; Williams, 1992), is a 81 000 ha preserve managed jointly by the United States Bureau of Land Management, California Department of Fish and Game, and The Nature Conservancy (Holing, 1988). An arid valley, it has a climate typical of valley grasslands in California (Keeley, 1991). Temperatures average 9°C in January and 29°C in July. Precipitation, which occurs almost exclusively as winter rain, averages about 14.5 cm annually (National Oceanic and Atmospheric Administration, 1989).

The research sites, located 25 km apart, exhibited evidence of giant kangaroo rat population activity. The regularly spaced, roughly circular burrow precincts were 1.8–7.7

m in diameter; vertical and diagonal burrow holes had openings 57–89 mm in diameter and were surrounded by aprons of disturbed soil and clipped vegetation; seeds were deposited in surface pit caches and clipped infructescences were piled into 'hay stack' caches in late spring (Grinnell, 1932; Shaw, 1934; Hawbecker, 1951; Braun, 1985; Williams and Kilburn, 1991; Williams, 1992; Williams *et al.*, 1993). The elevation of Site 1 was 588 m, and Site 2 was 648 m. Both were relatively flat ($<2°$ slope). Although neither site was grazed by livestock at the time of the study (3–8 April, 1993), both had been grazed (primarily by cattle) prior to January 1990.

Sampling and data analysis

At each site, 50 clearly identifiable active burrow precincts were selected at random. Fifty less disturbed intermediate areas, located between precincts, were also arbitrarily selected. At each sampling location (precinct and intermediate area), a 2 m transect was positioned at a randomly determined compass direction. Pins were dropped at 20 cm intervals along this transect and plant species (or bare ground) covering each pin point were noted (Barbour *et al.*, 1987).

To determine whether the seeds of species found primarily on precincts differed in size when compared to seeds of species found primarily in intermediate areas, seed length (mm) data were extracted from Hickman (1993) and Munz (1959). When a range of seed sizes was provided for a particular species, the median of that range was used. Since these sources did not include seed lengths for grass species, seeds of specimens stored in the Herbarium at California State University–Northridge were measured.

Cover and frequency percentages were determined for each species sampled along the precinct and intermediate area transects (Barbour *et al.*, 1987). In addition, the species were classified as either 'exotic' or 'native' as indicated by Hickman (1993). Mean exotic and native species richnesses and mean exotic and native vegetation covers were then determined for each site. Statistical methods (1-tailed 2 sample *t*-test and 1-tailed Mann–Whitney *U*-test) were used to test for vegetational and seed size differences between precincts and intermediate areas. In addition, 2×2 χ^2-tests were used to test for relationships between vegetation composition and kangaroo rat activity.

Results

Species composition

χ^2-tests indicated that frequencies of exotic and native species were very strongly linked to whether vegetation occurred on precincts or in intermediate areas ($p = 0.018$, d.f. = 1 at Site 1 and $p < 0.001$, d.f. = 1 at Site 2). Exotic species occurred in significantly greater numbers on precincts than they did in the intermediate areas (Fig. 1a). The reverse was found for native species. Intermediate areas supported more native species than did the precincts (Fig. 1b). These tendencies were especially distinctive at Site 2 where, on average, precincts had more than twice as many exotic species as the intermediate areas. Moreover, the intermediate areas at Site 2 averaged more than twice as many native species as precincts.

Erodium cicutarium and *Bromus madritensis* ssp. *rubens* (botanical nomenclature

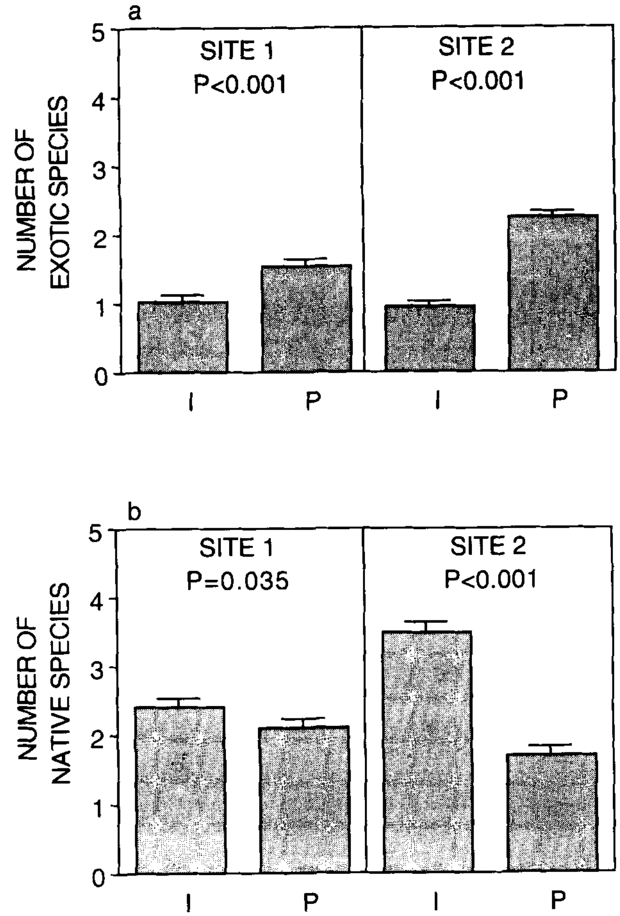

Figure 1. Mean number of (a) exotic and (b) native species ($\pm$SE) on giant kangaroo rat burrow precincts (P) and in intermediate areas (I) at Sites 1 and 2. *p* values refer to 1-tailed two-sample *t*-tests. Sample size for each mean = 50.

follows Hickman (1993)) were the exotic species most frequently encountered in this study (Table 1). *E. cicutarium* was identified in 74% of the samples at Site 1 and 87% of the samples at Site 2. Twenty-seven percent of the samples at Site 1 and 46% of the samples at Site 2 contained *B. madritensis*. These two exotic annuals were most widespread on precincts, but did also occur with less frequency in intermediate areas at each site. The giant kangaroo rat precincts examined by Grinnell (1932) also supported more *E. cicutarium* than did adjacent intermediate areas. The three other less common exotic species, *Hordeum murinum* ssp. *leporinum*, *Medicago polymorpha*, and *Schismus barbatus* were also all more frequent on precincts than in intermediate areas.

It should be noted that despite the importance of exotic species, especially on burrow precincts, native species richness was considerably higher than exotic species richness at each site. Thirteen native and four exotic species were identified at Site 1, and five exotic and 24 native species were found at Site 2 (Table 1). However, many of the native

Table 1. Frequencies and seed lengths of exotic and native species encountered at Sites 1 and 2 (frequency is the percentage of 50 precinct or 50 intermediate area transects in which each species occurred)

Species	Origin	Form	Frequency				Seed length (mm)
			Site 1		Site 2		
			Precincts	Intermediate areas	Precincts	Intermediate areas	
Bromus madritensis ssp. *rubens*	E	AG	32	22	90	2	8.5[b]
Erodium cicutarium	E	AF	84	64	96	78	5.5
Hordeum murinum ssp. *leporinum*	E	AG	18	16	12		6.0[b]
Medicago polymorpha	E	AF	20		4		5.0[a]
Schismus barbatus	E	AG			22	14	1.0[b]
Amsinckia menziesii	N	AF			8		2.75
Amsinckia tessellata	N	AF	24	2	10		3.25
Astragalus didymocarpus	N	AF	12	6		2	3.0
Calandrinia ciliata	N	AF			8		1.75
Castilleja exserta	N	AF	4	2		10	1.5
Chaenactis glabriuscula	N	AF			2	4	6.0
Crassula connata	N	AF		2		16	<1.0
Dichelostemma capitatum	N	PH				6	3.25
Guillenia lasiophylla	N	AF			2		1.0
Lasthenia californica	N	AF	20	58	14	50	2.25[a]
Lasthenia minor	N	AF			4		2.6
Layia platyglossa	N	AF	2				4.75

Table 1. Continued

Species	Origin	Form	Frequency				Seed length (mm)
			Site 1		Site 2		
			Precincts	Intermediate areas	Precincts	Intermediate areas	
Lepidium nitidum	N	AF	20	36	42	70	3.25
Linanthus dichotamus	N	AF				4	0.7[a]
Lotus humistratus	N	AF			4	30	1.75[a]
Lupinus microcarpus	N	AF				4	3.0
Malacothrix coulteri	N	AF	2		4		2.4
Malacothrix glabrata	N	AF	6	4	4	4	2.65
Pectocarya pencillata	N	AF				6	1.55
Plantago ovata	N	AF				2	2.25
Platystemon californicus	N	AF	4			2	1.0
Poa secunda	N	PG			4	30	2.0[b]
Trifolium gracilentum	N	AF		28	4	20	5.0
Tropidocarpum gracile	N	AF	24	8	4	4	1.3[a]
Vulpia microstachys	N	AG	90	92	52	80	4.0[b]

E = exotic, N = native, AG = annual grass, AF = annual forb, PG = perennial grass, PH = perennial herb.
[a] Indicates seed lengths from Munz (1959).
[b] Indicates seed lengths determined from herbarium specimens. All other seed lengths were from Hickman (1993).

species were scattered and relatively uncommon. For example, 46% of the native species at Site 1 and 71% of the native species at Site 2 occurred in 10% or fewer of the samples collected. Moreover, most native species were largely restricted to intermediate areas (Table 1).

The three native species most frequently encountered at both sites were *Vulpia microstachys*, *Lasthenia californica*, and *Lepidium nitidum*. These annuals occurred in 91%, 39%, and 28%, respectively, of the samples collected at Site 1, and 66%, 32%, and 56%, respectively, of samples at Site 2. These three native species were most often found in intermediate areas, but did occur in precinct samples as well (Table 1). Grinnell (1932) also noted that *L. californica* and *L. nitidum* occurred predominantly in the intermediate areas located between giant kangaroo rat precincts.

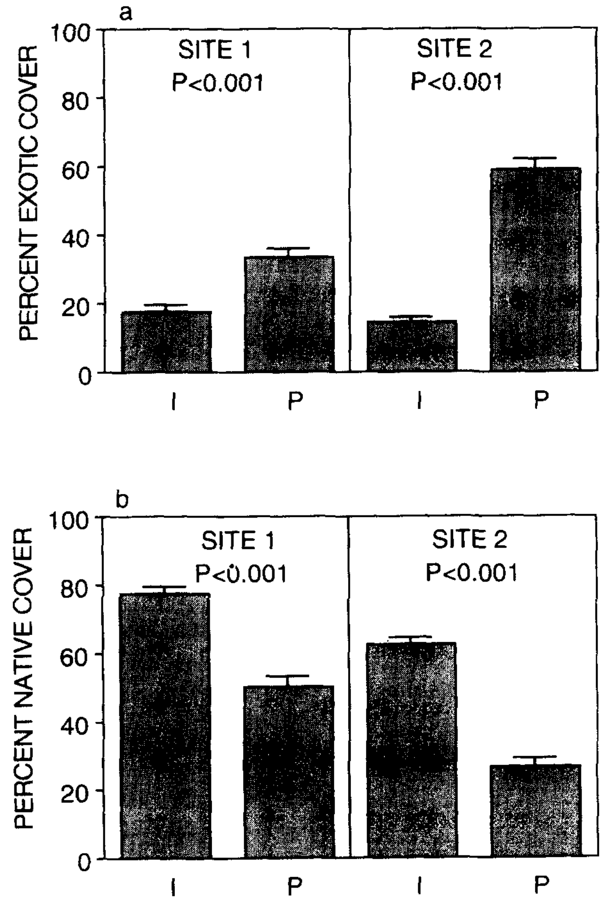

Figure 2. Mean percent cover of (a) exotic and (b) native vegetation (±SE) on giant kangaroo rat burrow precincts (P) and in intermediate areas (I) at Sites 1 and 2. *p* values refer to 1-tailed two-sample *t*-tests. Sample size for each mean = 50.

Vegetation cover

As with species composition, trends in vegetation cover were quite similar at Sites 1 and 2. At each site, mean exotic vegetation cover on burrow precincts was significantly greater than in intermediate areas (Fig. 2a). This was especially true at Site 2, where exotic cover on precincts was more than 300% greater than in intermediate areas. The opposite pattern was found for native vegetation. Mean cover of native vegetation in intermediate areas exceeded that of precincts by 54% at Site 1 and 135% at Site 2 (Fig.

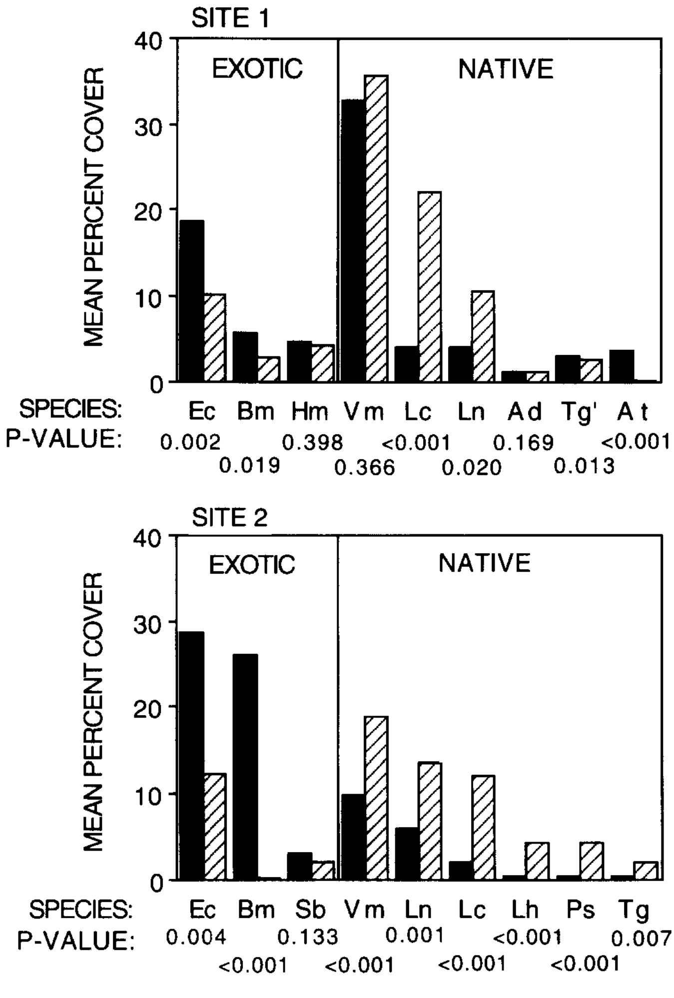

Figure 3. Mean percent cover of exotic and native species on giant kangaroo rat burrow precincts (■) and in intermediate areas (▨) at Sites 1 and 2. Only species with cover $\geq 2\%$ at one or both sides are included. *p* values refer to 1-tailed Mann–Whitney *U*-tests. Sample size for each mean = 50. Species abbreviations: Ad = *Astragalus didymocarpus*, At = *Amsinckia tessellata*, Bm = *Bromus madritensis* ssp. *rubens*, Ec = *Erodium cicutarium*, Hm = *Hordeum murinum* ssp. *leporinum*, Lc = *Lasthenia californica*, Lh = *Lotus humistratus*, Ln = *Lepidium nitidum*, Ps = *Poa secunda*, Sb = *Schismus barbatus*, Tg = *Trifolium gracilentum*, *Tg'* = *Tropidocarpum gracile*, Vm = *Vulpia microstachys*.

2b). These differences in native cover between precincts and intermediate areas were also highly statistically significant.

E. cicutarium and *B. madritensis*, the most widespread exotic species at each site, had significantly greater mean percentage cover on precincts than in intermediate areas (Fig. 3). The other exotic species found at these sites (*H. murinum*, *S. barbatus*, and *M. polymorpha*) also had higher mean covers on precincts than intermediate areas, but these differences were either not significant ($p > 0.05$) or could not be tested statistically.

In comparison, the three most important native species, *V. microstachys*, *L. californica* and *L. nitidum*, all had greater cover in intermediate areas rather than precincts. In all cases except one (*V. microstachys* at Site 1), these differences were statistically significant (Fig. 3). Moreover, at Site 2, three other native species (*Lotus humistratus*, *Poa secunda*, and *Trifolium gracilentum*) had statistically greater cover in intermediate areas than on precincts. Interestingly, the percentage cover of the annual species *Tropidocarpum gracile* and *Amsinckia tessellata* were significantly higher on precincts at Site 1.

Seed size

Seeds of exotic species encountered in this study were, on average, much larger (in length) than seeds of native species (exotic mean = 5.20 mm, SE = 1.21, $n = 5$; native mean = 2.81 mm, SE = 0.38, $n = 25$; $p = 0.031$; Table 1). When the comparison was restricted to only those species with statistically significant precinct/intermediate area cover differences (at Site 1 and/or Site 2), the discrepancy in mean seed size between exotics and natives was even greater (exotic mean = 7.00 mm, SE = 1.50, $n = 2$; native mean = 2.85 mm, SE = 0.44, $n = 8$; $p = 0.018$; Table 1). Baker (1972) also noted that exotic herb species in California valley grasslands had larger (heavier) seeds than native herb species.

Discussion

Burrow precinct vegetation

The clear differences in vegetation cover and species composition between burrow precincts and adjacent intermediate areas indicated that the giant kangaroo rat was an important determinant of vegetation composition in the Carrizo Plain grasslands. Because of this, it should probably be considered a 'keystone species' (Brown and Heske, 1990; Davidson, 1993; Lodge, 1993; cf. Mills *et al.*, 1993; Richardson and Cowling, 1993). Kangaroo rat precincts, which were chronically disturbed by burrowing and other activities (Grinnell, 1932; Williams and Kilburn, 1991; Williams, 1992; Williams *et al.*, 1993), served as habitat patches for exotic annual weeds, including two of the most widespread exotic weeds in California's valley grasslands, *Erodium cicutarium* and *Bromus madritensis* ssp. *rubens* (Wester, 1981; Jackson, 1985; Heady, 1988; Sauer, 1988; Keeley, 1990; Blumler, 1992). While exotic species also occurred off precincts, in the less disturbed intermediate areas, their importance in those areas, relative to native species, was considerably less. By regularly disturbing precincts, the giant kangaroo rat maintained large proportions of exotic ruderal and early successional species in this community.

In addition, the results of this study supported the hypothesis that kangaroo rats aided in the displacement of native species by Mediterranean annuals in the western San

Joaquin Valley region. Giant kangaroo rat precincts can be as large as 7.7 m in diameter and occur in densities up to 69 precincts per ha (Williams and Kilburn, 1991). Therefore, vegetation directly affected by giant kangaroo rats could occupy as much as 32% of a grassland's total area (this estimate assumes that precincts are circular and it excludes the corridors of disturbed vegetation that interconnect precincts). Grasslands with such large areas of chronically disturbed soil and vegetation would have been prime locations for colonization by exotic ruderal and early successional species.

Significant modifications of soil and vegetation by burrowing animals have been observed in other North American grasslands as well (e.g. Platt, 1975; Mielke, 1977; Coppock *et al.*, 1983; Tilman, 1983; Hobbs and Mooney, 1985; Reichman and Smith, 1985; Koide *et al.*, 1987; Gibson, 1989; Brown and Heske, 1990; Kalisz and Davis, 1992; Reichman *et al.*, 1993). Relationships between exotic weed establishment and small mammal burrowing activity were not noted in these other grasslands, however. Although Hobbs and Mooney (1985) did find that disturbance of serpentine California grassland soils by western pocket gophers (*Thomomys bottae* Mewa) promoted the establishment of *Bromus hordeaceus* (an exotic annual grass), several native species (including *V. microstachys* and *L. californica*) also responded somewhat positively to gopher disturbance.

Giant kangaroo rats and exotic seeds

This absence of similar relationships between disturbance by other burrowing mammals and exotic weeds suggested that the enhancement of exotic weeds by giant kangaroo rats was attributable to something more than just chronic disturbance to soil and vegetation. Unlike most other small burrowing mammals in North American grasslands, the giant kangaroo rat is granivorous. The finding that the seeds of exotic species, which dominated giant kangaroo rat precincts, were larger than seeds of native species, which dominated intermediate areas, suggested that the kangaroo rats modified precinct vegetation composition by preferentially caching fruits and infructescences of exotic weeds with large seeds. Some seeds cached on precincts would have escaped predation, subsequently germinated and grown into mature plants. Other researchers (Brown and Lieberman, 1973; Mares and Williams, 1977; Reichman and Oberstein, 1977; Hutto, 1978) have noted that large heteromyid species tend to collect large seeds or clusters of seeds. Since the giant kangaroo rat is the largest *Dipodomys* species (Williams and Kilburn, 1991), it would be expected to collect mostly large seeds, which, in this grassland, were produced by exotic plants. By selecting and caching large exotic seeds, kangaroo rats could have rapidly altered grassland composition once exotics were introduced.

There are a few probable explanations for the apparent preference for large weed seeds by giant kangaroo rats. First, large seeds would be expected to have relatively high moisture levels and caloric contents (Reichman, 1976). Because the kangaroo rats obtain virtually all of their required water and calories from seeds (Williams and Kilburn, 1991), it makes sense, in terms of foraging energetics, to collect the largest seeds available (Brown and Lieberman, 1973; Mares and Williams, 1977; Hutto, 1978). In addition, many of the exotic species that currently dominate California's grasslands were derived from cultivated grains and forage crops with long histories of selection for large seed size and palatability (Baker, 1972; Sauer, 1988). Moreover, in contrast to the exotics, some of the important native plant species in this grassland had pungent odours (e.g. *Lasthenia* spp.) or flavours (e.g. *Lepidium nitidum*) which could discourage herbivory.

Exotic weed – endangered kangaroo rat mutualism

The dominance of precincts by exotic plants and the evident dependence of giant kangaroo rats upon exotic weed seeds for a large proportion of their diet (as indicated in May 1993 by large haystack caches of *B. madritensis* infructescences and *E. cicutarium* fruits, personal observation) pointed to a probable mutualistic relationship between the giant kangaroo rat and exotic weeds. The exotics would benefit from the continual disturbance of the substrate and inhibition of succession in their precinct habitats. The kangaroo rats would benefit from the high level of food availability associated with the high reproductive levels of exotic annuals (Heady, 1988).

The strong exotic weed–giant kangaroo rat relationship that developed in these grasslands probably inhibited population growth of native plant species which had difficulty competing with exotics for resources (Heady, 1988; Keeley, 1988; Sauer, 1988). *Caulanthus californicus*, a federally listed endangered plant species, may have been negatively affected in this way. Recently, other researchers found that *C. californicus* was significantly more likely to occur on precincts than at other locations in grasslands of the Carrizo Plain Natural Area (E. Cypher, personal communication). *C. californicus* was probably one of the native species that originally dominated precincts and was almost driven to extinction when the strong mutualistic weed–kangaroo rat relationship developed.

Of course, this weed–kangaroo rat relationship did not always exist. Prior to the introductions of Mediterranean exotics, early successional native species would have occupied kangaroo rat precincts and other chronically disturbed areas in valley grasslands. Unfortunately, very little is known about California's original grassland vegetation (Baker, 1978; Wester, 1981; Heady, 1988; Keeley, 1990), and it is not known which native species dominated precinct vegetation. In this study, two native annual forbs, *Amsinckia tessellata* and *Tropidocarpum gracile* had significantly greater covers on precincts than in intermediate areas at Site 2. Perhaps these species were among the natives that dominated precinct vegetation before the widespread displacement of natives by exotics.

Management and restoration implications

From a conservation perspective, this mutualism between exotic weeds and the endangered giant kangaroo rat is a distressing finding and indicates an intractable management dilemma. In valley grasslands where giant kangaroo rats occur, such as the Carrizo Plain Natural Area, restoration to conditions where native species dominate is likely to be impossible. Because giant kangaroo rats have become dependent upon exotic seeds for food, eradication of exotic plants would probably have a significant negative impact on populations of this endangered species. Furthermore, the data also suggest that enhancement of giant kangaroo rat populations would result in increases in exotic plant cover and diversity. Lubchenco *et al.* (1991) stated that 'the importance of introduced species . . . cannot be overlooked, whether we are restoring ecosystems, creating new ones, or trying to predict changes in existing systems'. This is certainly true of California's valley grasslands, particularly those in which giant kangaroo rats occur.

There are many examples of introduced species which have altered natural areas and imperilled native species (Mooney and Drake, 1986; Lodge, 1993). I am unaware, however, of other mutualistic relationships between exotic and endangered native species. Still, given the widespread importance of invasive organisms in many of the world's ecosystems, it is probable that similar mutualisms have developed in other ecosystems which have experienced large-scale compositional change (e.g. 'derived' neotropical grasslands occupying previously forested areas that now include many African and Middle Eastern grasses; Baker, 1978).

It seems likely that the absence of evidence of other similar mutualisms is due in part to an emphasis on autecological studies of endangered species. While autecological approaches are clearly important to understanding these organisms, they would tend to overlook important community-level relationships. The unusual and disturbing mutualism between giant kangaroo rats and exotic weeds discussed here points to the critical importance of undertaking higher ecological scale studies. The development of effective management plans for many endangered species may be dependent upon such research (Vitousek, 1986; Lodge, 1993).

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