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Control of a Desert-Grassland Transition by a Keystone Rodent Guild

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Twelve years after three species of kangaroo rats (*Dipodomys* spp.) were removed from plots of Chihuahuan Desert shrub habitat, density of tall perennial and annual grasses had increased approximately threefold and rodent species typical of arid grassland had colonized. These were just the most recent and dramatic in a series of changes in plants and animals caused by experimental exclusion of *Dipodomys*. In this ecosystem kangaroo rats are a keystone guild: through seed predation and soil disturbance they have major effects on biological diversity and biogeochemical processes.

THE BIOLOGICAL DIVERSITY AND biogeochemical processes that characterize an ecosystem depend on interactions of the organisms with each other and with their abiotic environment. The presence or absence of certain kinds of organisms, called "keystone species" (*1*), can dramatically alter the structure and dynamics of ecological systems. In most ecosystems, vertebrate animals account for only a small fraction of the biomass and energy flow (*2*), but through predator-prey, competitive, and mutualistic interactions with other species and by causing physical disturbance they can have disproportionately large effects on habitat structure, species composition, and biogeochemical processes (*2, 3*). We show that long-term experimental removal of a guild of three kangaroo rat species from a desert ecosystem initiated changes that have led to the conversion of the habitat from shrubland to grassland.

In 1977, experiments were begun on an alluvial outwash plain with diverse desert shrub vegetation in the Chihuahuan Desert of southeastern Arizona (*4, 5*). Twenty-four plots, each 0.25 ha in area (50 by 50 m), were fenced with fine wire mesh and assigned at random to experimental manipulations. Treatments included removal of some or all rodent or ant species and addition of millet seeds (Table 1). Access of different rodent species to appropriate plots was controlled by cutting holes of different sizes at ground level in the fences surrounding the plots. Populations of rodents, ants, birds, and plants were monitored systematically at a grid of permanent sample sites within each plot. Between 4 and 16 September 1989, in order to better characterize plant cover inside and immediately outside each plot, all plant species were counted at 10-cm intervals along eight 25-m transect lines: four inside transects began 8 m from the center of the plot and ran outward toward each corner; after a gap of 2 m on either side of the fence, the other four transects continued for another 25 m outside the fence.

In ten plots, one of three different combinations of desert rodent species was excluded (Table 1): all rodents; three species of kangaroo rats, *Dipodomys spectabilis, D. ordii,* and *D. merriami;* or just the largest and behaviorally dominant kangaroo rat, *D. spectabilis.* An initial analysis of variance (ANOVA), with plots as the sample units to avoid "pseudoreplication" (*6*), showed that treatments in which all rodents or all kangaroo rats had been removed were similar to each other in the plant variables analyzed below. They differed significantly from all other treatments, except *D. spectabilis* removal. In addition, there were no detectable effects of ant removal or seed addition treatments on these plant variables. Therefore, the eight plots where all kangaroo rats were absent were compared to the 14 plots where all kangaroo rats were present in the following analyses. The two plots from which just *D. spectabilis* had been removed were excluded from the analyses, because the vegetation parameters were often intermediate between the two treatment classes and the limited replication did not permit statistical resolution.

Long-term removal of kangaroo rats caused a dramatic change in habitat, from desert shrubland to grassland (Fig. 1). Effects of *Dipodomys* on vegetation were analyzed by ANOVA, not only comparing plots where kangaroo rats had been removed to plots where kangaroo rats were present, but also comparing transects inside and immediately outside the plots where kangaroo rats had been removed (Fig. 2). Tall-statured perennial and annual grasses colonized the open spaces between the shrubs and increased approximately threefold in the absence of kangaroo rats. Much of this response can be attributed to two species: the perennial *Eragrostris lehmanniana,* which increased more than 20-fold, and the annual *Aristida adscensionis,* which increased approximately threefold. There were complementary changes in two species of short

Table 1. Schematic representation of the experimental treatments (*4*). All plots with kangaroo rats removed (−) were compared to all other plots (+), except those with *D. spectabilis* removed.

Treatment	Number of plots
Unmanipulated control	2 (+)
All rodents removed	2 (−)
All rodents and all ants removed	2 (−)
Kangaroo rats removed	2 (−)
Kangaroo rats and *Pogonomyrmex* ants removed	2 (−)
Dipodomys spectabilis removed	2
All ants removed	2 (+)
Pogonomyrmex ants removed	2 (+)
Seed addition	8 (+)

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annual grasses (*Bouteloua aristidoides* and *B. barbata*); these were significantly less abundant where kangaroo rats had been removed. *Tridens pulchella,* a short-statured species and the only perennial grass that was common on the site when the experiments were begun, was the only abundant species that did not show a significant response to kangaroo rat removal. The net result of excluding either all rodents or all three *Dipodomys* species for 12 years was a dramatic increase in the cover of tall grasses.

That kangaroo rats are a keystone guild in this ecosystem is further demonstrated by other changes that occurred on plots where they were removed. During the first 10 years after initiation of the experiments, large-seeded winter annual plant species had increased (Fig. 1), some by as much as several thousand times, and small-seeded winter annuals decreased on plots with rodents and kangaroo rats removed (*5, 7*). During this same period, seed-eating birds decreased their foraging on plots with rodents removed in comparison with plots where kangaroo rats were present (*8*). This was associated with an increase in herbaceous (both grass and forb) vegetation and a decrease in the amount of bare ground, conditions that made it more difficult for the birds to harvest the available seeds. Six to 12 years after the experiment was begun, and in response to the increase in grass cover documented above, six species of rodents that are characteristic of arid grasslands differentially colonized the grassy plots where kangaroo rats had been removed (Fig. 3). Finally, we have noted, but not quantified, greatly increased accumulation of litter and longer persistence of snow on the plots where kangaroo rats were absent.

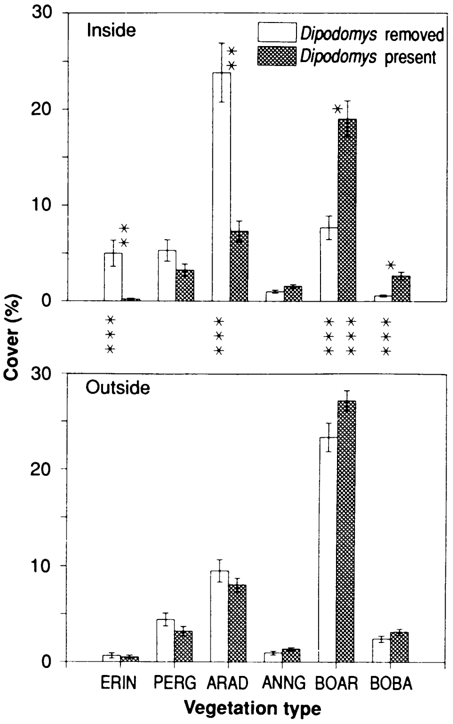

Fig. 2. Effects of removing kangaroo rats (*Dipodomys*) on densities of perennial and annual grasses. Plotted are mean values (±SE) of the percentage of cover for *Eragrostris lehmanniana* (ERLE), all other tall perennial grass species (PERG), *Aristida adscensionis* (ARAD), all other tall annual grasses (ANNG), and the short annual grasses *Bouteloua aristidoides* (BOAR) and *B. barbata* (BOBA). (**Top**) Data from transects inside plots where kangaroo rats were either present or removed; asterisks indicate significant differences between kangaroo rat removal and other plots. (**Bottom**) Data from transects immediately outside these plots. Asterisks indicate statistically significant differences between transects inside and outside plots where kangaroo rats were present or absent. (ANOVA, with plots as units of replication; $*P < 0.05$, $**P < 0.01$, $***P < 0.001$.)

Fig. 1. Photographs across the fences surrounding plots from which kangaroo rats were removed (left side of fence). (**Top**) Increase of the yellow-flowered, large-seeded annual, *Lesquerella gordonii,* 5 years after kangaroo rat removal. (**Bottom**) Increase in tall-statured annual and perennial grasses 13 years after kangaroo removal.

Two processes, seed predation and soil disturbance, appear to be responsible for the changes in this desert ecosystem that were caused by removing kangaroo rats. Selective foraging by kangaroo rats for large seeds is sufficient to explain the shorter-term responses to our experiments (*5, 9*). Large-seeded winter annual plants increased in response to their release from rodent predation, and asymmetrical competition from these dominant large-seeded species then caused the decrease in the small-seeded winter annuals. Increased availability of seeds and reduced competition from kangaroo rats may account, at least in part, for the colonization of kangaroo rat removal plots by the granivorous *Reithrodontomys* rodents (Fig. 3). Physical disturbance appears to have played the major role in the longer-term responses to removal of kangaroo rats. During their foraging, food caching, and burrowing activities, kangaroo rats make runways through the vegetation and move large quantities of soil, creating many shallow pits and little mounds. This disturbance

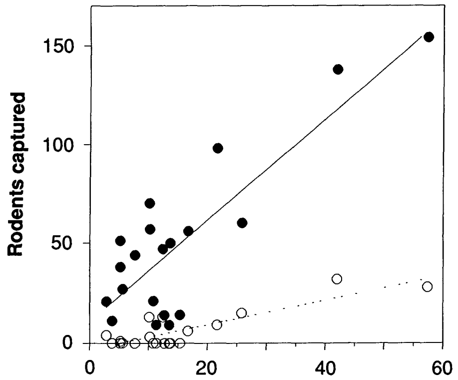

Fig. 3. Number captured per plot since 1983 of rodent species typical of grassland habitat as a function of mean percentage of cover of all tall perennial grasses plus *Aristida adscensionis*. Unshaded symbols represent only the most specialized grassland species, *Sigmodon hispidus*, *S. fulviventer*, and *Baiomys taylori*; shaded symbols represent the above species plus *Reithrodontomys* spp. Least-squared regression lines are fitted, and both are statistically significant ($P < 0.0001$).

may facilitate decomposition of litter, establishment of many annuals, and foraging of birds (*8*). Conversely, the reduction in soil disturbance following exclusion of kangaroo rats promoted the establishment and persistence of tall grasses, and this in turn favored colonization by specialized grassland rodent species.

Although kangaroo rats presumably cause size-selective seed predation and extensive soil disturbance wherever they are abundant, the kind and magnitude of changes reported here would probably not be duplicated if kangaroo rats were removed from different kinds of desert habitats. Our experimental site is near the zone of natural transition from desert to grassland, so that certain abiotic conditions or the presence or absence of keystone species can cause a shift between alternative vegetation types. Elsewhere in the southwestern United States grazing by domestic livestock is known to cause degradation of arid grassland to desert shrubland (*10*). At our site, however, the effects on vegetation of the exclusion of kangaroo rats in combination with livestock exclusion were much greater than those produced by the exclusion of cattle and horses alone. Grazing livestock were excluded from our entire 20-ha site since 1977, but no significant change in vegetation has yet been detected across the fenceline (*11*).

In the present case the "keystone" organism whose removal caused large changes in ecosystem structure and dynamics was not a single species, but a guild of three taxonomically related and ecologically similar kangaroo rat species. Removal of the largest and behaviorally dominant of these (*D. spectabilis*) had significant effects on the abundance and distribution of other desert rodents (*4, 12*), but it required the removal of all three species to cause wholesale changes in vegetation. On the other hand, the eight common and several rare species of desert rodents that remained after kangaroo rats had been removed clearly did not play the same keystone role and were not able to prevent the conversion of desert to grassland.

Twenty-five years after the concept of "keystone species" was first introduced, examples have been found in a number of taxonomic groups and habitat types (*1, 3*). It remains, however, to develop a general conceptual framework that will predict which kinds of organisms play key roles in different kinds of ecosystems. Native species are increasingly being eliminated from local habitats and larger regions as a result of human activities. It is critical to develop a theoretical basis for assessing the effects of these species on ecosystems so that, if extirpation of keystone organisms cannot be avoided, their roles can be replaced by other native or exotic species or by active ecosystem management.

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Characterization of "Peak E," a Novel Amino Acid Associated with Eosinophilia-Myalgia Syndrome

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Epidemiologic studies strongly associate eosinophilia-myalgia syndrome (EMS) with ingestion of tryptophan containing a contaminant ("peak E"). Prior reports have suggested that peak E is the di-tryptophan Nα-aminal of acetaldehyde. Spectral and chemical studies now demonstrate that peak E is 1,1′-ethylidenebis[tryptophan]. This novel amino acid may be the etiological agent responsible for EMS, or it may be a marker of a still unidentified causal agent.

As of August 1990, EMS was linked to 27 deaths and over 1500 cases (*1*). Epidemiological studies (*2, 3*) have associated EMS with the ingestion of L-tryptophan (Trp) produced by a single manufacturer, suggesting that a contaminant is responsible for EMS. Recently we reported the discovery of a contaminant (peak E) in the Trp samples consumed by EMS patients that was absent in the Trp consumed by asymptomatic controls (*3*). A significant association exists between the presence of peak E and EMS-associated Trp (*3, 4*). Two groups have previously reported that peak E is the di-tryptophan Nα-aminal of acetaldehyde (*4, 5*). We present chemical and spectral data which show that peak E is actually the isomeric 1,1′-ethylidenebis[tryptophan] (1).

Peak E was isolated by high-performance liquid chromatography (HPLC) (*3*). Fast atom bombardment–mass spectrometry (FAB-MS) revealed peaks at mass-to-charge ratios (*m/z*) of 157, 231 (base peak), and 435 ($[M + H]^+$). High-resolution FAB-MS gave a mass of 435.2041, consistent with the molecular formula $C_{24}H_{27}N_4O_4$.

The proton nuclear magnetic resonance (^{1}H NMR) spectrum of peak E in D_2O (*6*) was similar to that of Trp in terms of