LONG-TERM EXPERIMENTAL STUDY OF A CHIHUAHUAN DESERT RODENT COMMUNITY: 13 YEARS OF COMPETITION

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Abstract. An experimental study of competition between kangaroo rats (Dipodomys spp.) and other sympatric desert rodents using exclosures with "semipermeable" fences has been continuously maintained at a site in the northern Chihuahuan Desert since 1977. A new set of experimental manipulations begun in 1988 at the same site repeated this study.

As reported previously for this community, exclusion of three species of Dipodomys from both original and new experimental plots resulted in greater abundances of five species of small granivorous rodents (Chaetodipus penicillatus, Perognathus flavus, Peromyscus eremicus, P. maniculatus, Reithrodontomys megalotis) on these plots relative to controls. In contrast, there were no significant treatment effects on the abundances of insectivorous grasshopper mice (Onychomys spp.). The long time lag before the response by small granivores to Dipodomys removal observed in the original experiment was not repeated in the experiment begun in 1988.

Long-term (10 yr) exclusion of kangaroo rats from experimental plots has resulted in changes in vegetative cover, particularly increased grassiness, on these plots relative to controls. We used the repetition of the Dipodomys exclusion experiment in 1988 to evaluate the importance of this potential indirect effect of kangaroo rats on other rodents in this community. By examining differences in rodent capture numbers on the original and new sets of Dipodomys exclusion plots, we could identify four species (C. penicillatus, Perognathus flavus, Peromyscus eremicus, P. maniculatus) whose responses to kangaroo rat removal reflected direct competition from kangaroo rats, one species (R. megalotis) whose response reflected both direct and indirect (via vegetation changes and habitat selection) effects, and two species (Sigmodon hispidus, S. fulviventer) whose responses reflected only vegetation-mediated effects.

The continuous presence of competition between small granivores and kangaroo rats over the 13-yr study despite large, species-specific fluctuations in abundances suggests that competition is pervasive within this community.

Key words: Chihuahuan Desert; community; competition; desert rodents; Dipodomys; experiments; indirect effects; long-term study; replication.

INTRODUCTION

Studies of interspecific competition have played an important role in the development of theoretical and empirical community ecology (Salt 1983, Strong et al. 1984, Diamond and Case 1986). Most experimental studies have concentrated on pairwise interactions and assumed that the mechanism involved was interference or exploitative competition. In recent years, attention has been attracted to interactions between species that are mediated through a third species or trophic group (Schmitt 1987, Wootton 1992, 1993); these interactions are generally termed indirect interactions (reviewed in Strauss 1991). At present, however, few studies have evaluated the relative importance of direct vs. indirect effects in structuring communities. This is for good reason. There are several problems in detecting indirect effects, and in assessing their full magnitude. First, unless all species (or at least all functional groups of organisms) are monitored, it is likely that indirect pathways will be overlooked, and their consequences will be confused with the results of direct interactions. Second, long-term press experiments (Bender et al. 1984) may be required for the consequences of perturbations to play out over indirect pathways with long time lags (Brown et al. 1986, Brown and Heske 1990a). Finally, the magnitude of indirect pathways may fluctuate over time, because each indirect pathway involves at least one intervening species that may be influenced by extrinsic environmental variation.

The granivore-dominated desert rodent communities of southwestern North America have served as a model system for the study of competition and community structure (Brown et al. 1986, Reichman 1990). Studies of these rodents have not only produced experimental evidence that interspecific competition occurs, but have also provided many insights into the mechanisms of resource partitioning and competitive

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A long-term experimental study of interactions among desert granivores and between these seed-eaters and the ephemeral plants that provide their primary food was initiated in 1977 by J. H. Brown, D. W. Davidson, and their colleagues (Brown et al. 1986). Thus far, these experiments have documented several effects of granivorous rodents or ants on the abundances and species diversity of desert plants (Davidson et al. 1985, Brown et al. 1986, Brown and Heske 1990a, Samson et al. 1992, Heske et al., *in press*), diffuse competition among granivorous ants (Davidson 1985), and an unexpected indirect mutualism between granivorous rodents and ants (Davidson et al. 1984, Brown et al. 1986) and between rodents and birds (Thompson et al. 1991). Initial results of an experiment to detect competition among granivorous rodents were reported in Munger and Brown (1981); results of the first 5 yr were reported more comprehensively in Brown and Munger (1985). Numbers of five species of small granivorous and omnivorous rodents (Chaetodipus penicillatus, Perognathus flavus, Peromyscus eremicus, P. maniculatus, Reithrodontomys megalotis) increased significantly on plots where three species of kangaroo rats (Dipodomys spectabilis, D. ordii, D. merriami) had been removed, but only after a long time lag.

The original kangaroo rat exclosure and control plots have now been continuously maintained for over 13 yr. In January 1988 a new set of rodent manipulations was begun on eight other plots that were initially used for other manipulations. This new series of kangaroo rat exclosures and controls provided additional replication of the original competition experiment in space, on new plots, and repeated the experiment in time, a decade later. Thus, this study is unique in both the length of time that the manipulations have been maintained and monitored, and in its repetition at a much later time.

Following Brown and Munger (1985), we used numbers of grasshopper mice (genus *Orychomys*) on kangaroo rat removals and controls as an additional test of the competition hypothesis. Grasshopper mice are primarily insectivorous (although they do consume some seeds, especially in winter when insect abundance is low), and thus are not likely to compete for food with kangaroo rats during most of the year. Grasshopper mice are also similar in size to many of the small granivores, and we assume that they are similarly susceptible to predation by large snakes that might be present on control plots but differentially excluded from plots with small gates. Finally, grasshopper mice are aggressive and readily attack kangaroo rats when placed together with them in small arenas (J. H. Brown, *personal observation*); they are therefore not likely to be aggressively excluded from study plots by kangaroo rats (see also Rebar and Conley 1983). Thus, a lack of response by the two species of grasshopper mice to the kangaroo rat removal would lend further support to the interpretation that a positive response by the five species of small granivores is the result of competitive release.

We also used the repetition of the *Dipodomys* removal treatment 10 yr after the original experiment to assess the relative contributions of direct competition (aggressive interactions and exploitation of food resources) and indirect interactions (responses to kangaroo rat mediated vegetation changes) on the distribution of captures of rodent species at our study site by comparing data for the original kangaroo rat removal plots, where grass cover has increased dramatically (Brown and Heske 1990a, Heske et al., *in press*) and the new kangaroo rat removal plots, where these vegetation changes have not yet occurred. We predicted that (1) small granivore/omnivore species characteristic of desert scrub habitat (*Perognathus flavus, C. penicillatus, Peromyscus eremicus, P. maniculatus*) would respond only to the direct competitive effect (show approximately equal abundances on original and new kangaroo rat removal plots, with both greater than on their respective control plots), (2) small granivore/omnivore species more typically associated with grassland habitat (*R. megalotis*) would respond to both direct competition and indirect pathways mediated through vegetation changes (thus, should have even greater abundances on original kangaroo rat removal plots than on the new ones), and (3) folivorous typical of grassland (cotton rats: *Sigmodon hispidus, S. fulviventris*) would respond only to the indirect, vegetation-mediated pathway (and be abundant only on original kangaroo rat removal, or at least grassy, plots).

**METHODS**

**Study site and experimental treatments**

The study was conducted on the Cave Creek Bajada (bajada = an alluvial fan), 6.5 km east and 2 km north of Portal, Coconino County, Arizona, USA, at an elevation of 1330 m. The habitat is transitional between arid grassland and upper elevation Chihuahuan Desert scrub (Brown 1982), and varies from open, sometimes grassy patches to areas dominated by shrubs (primarily *Gutierrezia sarothrae, Flourensia cernua, Ephedra trifurcata, Lycium torreyi*, and *Prosopis glandulosa*) to dense stands of arborescent shrubs (primarily *Acacia*...
greggi, Acacia neoverrcosa, and P. glandulosa) along the usually dry watercourses that dissect the study site in several places. The soil is a mixture of alluvial boulders mixed with and overlain by finer particles. The entire 20-ha study site has been enclosed since July 1977 with a barbed-wire fence to exclude domestic livestock.

Within the livestock exclusion are 24 study plots, each 50 x 50 m (0.25 ha) in area and surrounded by a fence of 6-mm wire mesh topped with 15 cm of aluminum flashing (Munger and Brown 1981, Brown and Munger 1985). All plots were potentially rodent proof, but holes (gates) of different sizes provide access to selected plots by rodents of different species. Sixteen gates are equally spaced (four per side) at ground level around these plots; large gates (3.7 x 5.7 cm) allow access by all rodent species, whereas small gates (1.9 x 1.9 cm) exclude the larger kangaroo rats but allow access by several species of smaller rodents. To facilitate the location and use of the small gates by rodents, wire-mesh baffles (15 x 15 cm) are placed perpendicular to the fences on either side at gate sites. Baffles were not needed at the large gates, because well-worn runways leading through most of these gates on non-removal plots indicated that they are easily found and readily used by rodents.

Plots were randomly assigned to various experimental treatments, and manipulations were initiated in September 1977 following a 3-mo pretreatment census period. Initial treatments included removal of some or all rodent and ant species in a 2 x 2 factorial design, or addition of millet seeds (see Brown and Munger 1985 for plot assignments and details of the manipulations). An additional treatment, removal of only the largest species of kangaroo rat (Dipodomys spectabilis) and its continued exclusion via medium-sized (2.6 x 3.0 cm) gates, was begun in July 1979 on one plot, and replicated in February 1980 on a second. Results of the seed additions were discussed in Brown and Munger (1985) and will not be considered here. Ant removals did not affect rodent numbers at this site (Davidson et al. 1984, Brown and Munger 1985). Because the factorial design of the experimental treatments allows us to focus attention just on the manipulations of the rodent community, ant removals will also not be considered further. We follow Brown and Munger (1985) in using four plots (two with all Dipodomys excluded, and two with both Dipodomys and Pogonomyrmex rugosus harvester ants removed) as the original kangaroo rat exclusion treatment, and four plots (two unmanipulated and two with Pogonomyrmex rugosus harvester ants removed) as the original controls.

In January 1988, six plots that had formerly been seed additions and two plots that were ant removals were reassigned in a 2 x 2 factorial, stratified-random (treatments equally divided between north and south sides of the study area) design as new replicates and controls of the kangaroo rat and ant removal experiment. Thus, a new set of four kangaroo rat removal (two Dipodomys removal and two Dipodomys plus ant removal) and four control (two unmanipulated and two ant removal) treatments was established. Gate size was adjusted on the plots selected for kangaroo rat exclusion, and removals were begun during the January rodent census.

Rodents were censused on all 24 plots approximately once each month over a period of 2-3 consecutive nights near the time of the new moon. Each plot was live-trapped for one night by setting a single Sherman live trap baited with either mixed bird seed or millet at each of 49 permanent grid stakes spaced 6.25 m apart. Gates were closed at the time traps were set to insure that only individuals residing on the plots at the time of each census were captured. Individuals were marked either by toe-clipping (Chaetodipus, Perognathus prior to 1987) or ear-tagging with monel fingerling tags (all other species, Reithrodontomys after 1987). Species, sex, mass, and reproductive condition were recorded for all captured animals before their release at the capture site.

**Statistical analyses**

We used repeated-measures analysis of variance (rmANOVA; PROC ANOVA, SAS 1988) to test for differences in numbers of captures of rodents of various categories on experimental vs. control plots. For the original set of four kangaroo rat removal and four control plots, a series of 155 census periods was used for the analysis (September 1977-January 1991). For the new set of four kangaroo rat removal and four control plots initiated in 1988, this series was divided into a premanipulation series of 118 census periods (September 1977-January 1988), and a postmanipulation series of 37 periods (February 1988-January 1991). There is less statistical power when these shorter series are used compared to results obtained from the full 155 periods, thus increasing the risk of a Type II statistical error. However, this makes the test more conservative when positive results are obtained. We used the combined densities of five species of small granivores on experimental or control plots in these analyses because the experimental design does not allow us to control for possible interactions among these species, but we also used rmANOVA to assess the responses of the individual species.

To evaluate the relative influence of direct and indirect effects of kangaroo rat removal on numbers of small granivores, we compared abundances, using rmANOVA, of all small granivores and each species individually on the original and new sets of experimental and control plots for the 3 yr following the start of the new experiment (February 1988-January 1991). All analyses used the basic model statement CENSUS TREATMENT CENSUS x TREATMENT, with TREATMENT representing the blocking variable and CENSUS representing the repeated measure. Signifi-
The presence or absence of kangaroo rats was an important factor affecting the abundance and distribution of small granivorous rodents on the experimental plots. Fig. 1A illustrates that the exclusion fences were very successful at excluding kangaroo rats from Dipodomys removal plots, while allowing them access to control plots. Combined capture numbers of five species of small granivores were significantly higher on the four experimental plots from which Dipodomys have been excluded since 1977 than on control plots (rmANOVA, $P = .005$, Fig. 1B). In contrast, numbers of grasshopper mouse captures did not differ significantly between original control vs. original Dipodomys removal plots (rmANOVA, $P = .59$, Fig. 1C).

Prior to January 1988 there was no significant difference in the number of kangaroo rats captured on the plots designated to become new sets of experimental removals and controls (rmANOVA, $P = .09$), but the modified gates and removal program were highly effective in excluding Dipodomys from experimental plots after this time (rmANOVA, $P = .01$; Fig. 2A). Similarly, there was no significant difference in the number of small granivores captured on plots designated as Dipodomys removals or controls up to January 1988 (rmANOVA, $P = .66$), but a significant difference was present during the postmanipulation period (rmANOVA, $P = .009$, Fig. 2B). Again, there was no significant difference in numbers of Onychomys captured on Dipodomys removal vs. control plots either before (rmANOVA, $P = .22$) or after the manipulation (rmANOVA, $P = .35$, Fig. 2C).

Numbers of small granivores were much higher at our study site in 1988–1990 than 1978–1980 (Figs. 1A–B).
Fig. 3. Mean number of captures per census period of five species of small granivorous rodents (species considered independently) on either the four control and four kangaroo rat exclusion plots from the experiment initiated in September 1977 (original) or the four control and four kangaroo rat exclusion plots initiated in January 1988 (new) during the years indicated. Note differences in scale of vertical axis. Significant differences between original and new Dipodomys removal plots in 1988-1990 indicate an indirect effect: 1978-1980 data for original plots are included for comparative purposes only and to illustrate the effect of competition on these plots in their first 3 yr postmanipulation (see also Munger and Brown 1981).

and 2). Small granivores were slow in responding to the removal of kangaroo rats in the original experiment (Fig. 1B), and numbers of captures of small granivores on kangaroo rat exclusion plots did not consistently exceed those on control plots until well over a year after the original manipulation. In contrast, a competition response was immediately obvious in the new experiment (Fig. 2B), and numbers of captures of small granivores were consistently greater on kangaroo rat exclusion plots beginning with the month after the new manipulation.

Although the total number of small granivores captured in 1988–1990 was slightly higher on the original set of kangaroo rat exclusion plots than on the new set, the difference was not significant (rmANOVA, $P = .53$). When each species was examined individually, however, the most grassland-prefering of the five small granivore species, Reithrodontomys megalotis, did show significantly more captures on the original than on the new kangaroo rat exclusion plots (rmANOVA, $P = .04$.

Fig. 3E). $R. megalotis$ was about twice as abundant on new kangaroo rat exclusion plots as on controls, but 3 times as abundant on the original kangaroo rat exclusion plots as on controls. The other four species of small granivores all were more abundant on both sets of kangaroo rat exclusions than controls as predicted by the competition hypothesis (rmANOVA, all $P$ values $< .05$), but differences between the new and original exclusion plots were not significant (Fig. 3A–D). In contrast, cotton rats, Sigmodon hispidus and $S. fulvescens$, were captured only on the four original kangaroo rat exclusion plots and on two each of the original and new control plots. All captures of cotton rats occurred in grassy areas on these plots, although not all plots with grassy areas yielded captures of cotton rats (E. J. Heske, personal observation). Because grasses were patchily distributed at our site, $Sigmodon$ were captured on four out of eight control plots as well as all four original kangaroo rat exclusion plots, but none of the new kangaroo rat exclusion plots. Thus, cotton rats were captured significantly more often on the original than on the new kangaroo rat exclusion plots during this period (68 vs. 0 captures; rmANOVA, $P = .05$), whereas numbers of captures on original and new control plots were not significantly different (25 vs. 18 captures; rmANOVA, $P = .73$).

**DISCUSSION**

Our data clearly show that interspecific competition with kangaroo rats affected the abundance and local distribution of five species of small granivorous rodents at our study site. Numbers of small granivores averaged twofold higher on the set of experimental plots from which kangaroo rats had been continuously excluded since 1977 than on control plots (see also Brown and Munger 1985). This response was observed again when a second set of kangaroo rat exclosures and controls was initiated in 1988. There was no difference between removal and control plots in the numbers of insectivorous grasshopper mice in either the original or new kangaroo rat removal experiments.

One difference between results from the original experimental treatments begun in 1977 and the new treatments begun in 1988 is the presence of a long time lag in the former. In the original experiment, there was a delay of $\approx 1$ yr before any differences between small granivore numbers on kangaroo rat exclusion and control plots were detected. In the new experiment, a response to the removal of kangaroo rats was apparent immediately.

Brown and Munger (1985) suggested that the long time lag before the response by small granivores to the original kangaroo rat removals might be due either to the fact that seed crops are episodic and at least some species appear to rely heavily on seeds stored in caches, or to the fact that reproduction is episodic and dispersal may occur primarily by juveniles. Thus, a new seed crop or new cohort of rodents might have been required...
before population responses to the manipulation would occur. However, the original manipulations were also started following an extended severe drought, when the small granivorous rodents were at low density. The new series was started when the abundance of small granivores was at a record high, in part because it followed an El Niño year of high precipitation and seed production (Brown and Heske 1990b). We now believe that the delayed responses to the original manipulations occurred because at that time there were simply not many individuals of the small granivore species to detect and move into the favorable habitat patches created by removing kangaroo rats. The extended drought during and preceding this period may also have reduced resources to low levels throughout the area, so that differences in resource abundance between kangaroo rat exclosures and controls were not as detectable as in 1988. This difference underscores the value of repeating ecological studies under as many different conditions as possible. Our 1988 findings demonstrate that a long time lag before a response is not a general property of this system.

After the initial time lag in 1977–1978, the response of small granivores to the removal of competing kangaroo rats was highly consistent over 13 yr of monitoring. There was no indication that competition only occurred during “ecological crunches” when resources were scarce (Wiens 1977). Rather, a negative influence of kangaroo rats on the abundance and local distribution of small granivores appears to be a strikingly consistent feature of the rodent community at our site in spite of much year-to-year variation in precipitation, primary production, and population densities of rodent species (J. H. Brown et al., unpublished manuscript).

This relative constancy of competition poses an apparent paradox when we consider patterns of community dynamics at our site (Brown and Heske 1990b). On the one hand, kangaroo rats have a consistent negative impact on the local distribution of the small granivores (Munger and Brown 1981, Brown and Munger 1985, this study). On the other hand, species in this community tend to exhibit highly individualistic patterns of population dynamics, the relative proportions of species in the community have varied over time in a manner not explainable by a simplistic competition model, and many species that we have demonstrated or suspect to be competing strongly show positively correlated temporal variation in abundance (Brown and Heske 1990b). How do we reconcile the apparently deterministic outcome of competition with the observed Gleasonian independence of species in this community?

One solution may be to consider the processes that govern population dynamics. The long-term temporal fluctuations in rodent abundance reflect the influence of environmental conditions within the local region (that includes a much larger area than just our study area) on the birth and death rates of the populations of the different species. We observe highly individualistic, species-specific patterns of temporal variation in abundance, both seasonally and year to year (Brown and Zeng 1989, Brown and Heske 1990b). While we have not yet identified all of the environmental variables causing these fluctuations, the available evidence suggests that they reflect the interaction between the unique resource requirements and environmental tolerances of each species and the temporal variation in weather, food supply, vegetative cover, predators, and so on. Thus, it is not surprising that species that tend to have positively correlated population dynamics are often ones that compete strongly; the requirements for similar conditions and resources that cause similar population fluctuations also tend to cause these species to compete intensely.

In contrast, the differential responses of the small granivores to the presence or absence of kangaroo rats reflect the influence of small patches of habitat (patches within our study site created by our experimental manipulations) on the habitat selection and movements of individual rodents (see also Brown and Munger 1985). The experimental study plots at our site are relatively small (0.25 ha), and individuals of the small granivore species were often captured on more than one plot. Therefore, differences in small granivore abundance among plots apparently reflected primarily habitat selection by individual rodents. Such small-scale habitat selection has been demonstrated in other studies of desert rodents (e.g., Rosenzweig 1973, M’Closkey 1978, Price 1978, Wondolleck 1978). Other studies have demonstrated that use of the shrub/open space mosaic of microhabitats by small granivores is affected by the presence of kangaroo rats (Price 1978, Bowers et al. 1987). Our data indicate that small granivores also select habitat patches on a slightly larger scale, i.e., study plots with or without kangaroo rats. Regardless of the other variables that are driving the population dynamics of the rodents in the community, patches of habitat that are similar in every respect except for the absence of kangaroo rats are always more favorable for small granivores to reside and forage in. The scale(s) at which interactions between individuals become translated into the dynamics of populations and metapopulations rather than just patch selection by a few individuals is an important area for future research.

The long-term maintenance and monitoring of our experiments, along with the repetition of the kangaroo rat exclusion treatment 10 yr after initiation of the original experiment, provide a unique opportunity to evaluate the importance of an indirect mechanism by which the absence of kangaroo rats can influence the distribution of small granivores in this rodent community. Exclusion of kangaroo rats from study plots at our site produced dramatic changes in the relative abundances of several species of ephemeral plants (Davidson et al. 1985, Brown et al. 1986, Samson et al.
1992) and later caused major changes in vegetative cover, particularly that of certain grasses (Brown and Heske 1990a, Heske et al., in press). Because these differences in grass cover took many years to develop, we can use differences between capture numbers of small granivores on the original long-term kangaroo rat exclosures and the new kangaroo rat exclosures where such vegetation changes have not yet had time to take place to measure the additional influence of these vegetation changes on the abundance and distribution of several rodent species.

The relative importance of direct and indirect effects of kangaroo rats on the local distribution of rodents varied among species in a way predictable by their general habitat associations. Four out of five species of small granivores were not significantly more abundant on the original kangaroo rat exclusion plots than on the new exclusion plots. These are species typical of desert scrub, or, in the case of Peromyscus maniculatus, not strongly associated with either desert scrub or grassland. The effect of kangaroo rats on these species appears to be primarily through direct competition, by some combination of aggressive behavioral interactions (Frye 1983) and resource depletion. R. megalotis, the one of the five species most typically associated with grasslands, however, was captured significantly more often on the original than on the new kangaroo rat exclosures. This difference reflects an additional contribution of an indirect effect of the long-term changes in vegetation induced by the absence of kangaroo rats and the differential selection of grassy habitats by Reithrodontomys (Brown and Heske 1990a). The distribution of harvest mice at our site was therefore affected by kangaroo rats through both direct competition and indirect pathways.

Two other species, Sigmodon hispidus and S. fulviflenter, responded only to characteristics of the vegetation (Brown and Heske 1990a), and hence only to indirect effects. Cotton rats are as large or larger than kangaroo rats, primarily folivorous, and grassland specialists. Therefore, we expect that they are not intimidated behaviorally by Dipodomys, do not compete significantly with kangaroo rats for food, and prefer habitats with high grass cover. Captures of both Sigmodon spp. and R. megalotis are significantly correlated with grass cover on study plots at our site (Brown and Heske 1990a), whereas captures of the other common species of rodents at our site are not (E. J. Heske et al., unpublished data). Further, cotton rats have only become regular inhabitants of our study site since 1987; only seven captures of Sigmodon were made in the preceding 10 yr even though they are regularly found in other grassy sites within the San Simon Valley (E. J. Heske, unpublished data). As expected, cotton rats were significantly more abundant on the original than on the new kangaroo rat exclosures. There was no consistent treatment effect in the distribution of cotton rats other than that explainable by their positive cor-

relation with grass cover, indicating that direct interactions between cotton rats and kangaroo rats were minimal.

The relative importance of direct vs. indirect effects on community structure is unknown, and will probably be found to vary among taxa and systems. One of the mechanisms that we have considered a direct effect (exploitative competition) could, in fact, technically be considered an indirect effect because it also involves other organisms (the seeds that the rodents consume). Our distinction between direct and indirect pathways is really between competitive mechanisms and non-competitive mechanisms involving other kinds of organisms. Our approach of repeating an experiment in time is a useful way to assess the nature and importance of indirect effects because interactions involving indirect pathways are expected to play out with longer time lags than direct interactions (Bender et al. 1984). The indirect effect of kangaroo rats on other rodents via changes in grass cover was not apparent until ≈10 yr after kangaroo rat removal was begun. Obviously, it would not have been detected by the typical short-term experiment. For this reason, indirect effects are probably more widespread and important than is currently appreciated.

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