INDIRECT FACILITATION OF GRANIVOROUS BIRDS BY DESERT RODENTS: EXPERIMENTAL EVIDENCE FROM FORAGING PATTERNS

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Abstract. In order to quantify the response of birds to experimental manipulations of seed availability and densities of granivorous rodents and ants, we counted granivorous birds and measured diurnal and nocturnal seed removal on 24 plots during winter months in the Chihuahuan Desert. Removal of single, widely spaced millet seeds provided a reliable measure of bird and rodent foraging activity.

Avian foraging activity increased in response to supplemental seeds, but decreased in response to long-term removal of all rodents and all ants. Although birds potentially compete for seeds with rodents and ants, these results suggest that, in the long term, indirect facilitation dominates the interactions among all three taxa. The positive effect of the other granivores on birds may be mediated through changes in habitat structure (e.g., reduction in the density of annual plants). The increase of avian foraging in response to seed addition and the high spatial and temporal variance in the patterns of seed removal by birds indicate that in desert habitats granivorous birds use their mobility to find and exploit high concentrations of seeds. Thus, birds may reduce the spatial variation in seed abundance and reduce the densities of seeds available to other granivores. The foraging behavior of birds and rodents revealed by these experiments clarifies the response of granivores to experimental manipulations reported earlier, such as the lack of biomass compensation by rodents in response to seed addition.

Key words: ants; birds; community; competition; desert; experiment; foraging; granivory; microhabitat; rodents.

INTRODUCTION

Extensive studies of North American desert granivorous rodents (reviewed in Brown et al. 1979, 1986, Price 1986, Kotler and Brown 1988), granivorous ants (Davidson 1977, 1980, Davidson et al. 1984, Rissing 1986), and seed-producing plants (Inouye et al. 1980, Reichman 1984, Davidson et al. 1985, Price and Reichman 1987) have contributed to our understanding of ecological processes. These studies have elucidated a surprisingly complex network of direct and indirect interactions among distantly related taxa, especially given the superficial simplicity of the resource base of annual and perennial seeds. So far these studies have not addressed the interactions of birds with desert granivores and plants, despite the potential importance of avian granivores (Raitt and Pimm 1976, Brown et al. 1979, Dunning and Brown 1982).

In this paper we address the role of seed-eating birds in the Chihuahuan desert community studied by Brown, Davidson, and collaborators (Davidson et al. 1984, 1985, Brown and Munger 1985, Brown et al. 1986, Bowers et al. 1987). We report 6 yr of bird population estimates and measurements of seed-foraging patterns. We used the rate of removal of single millet seeds, dispersed across 24 0.25-ha plots, to quantify the foraging of birds in relation to experimental treatments and to microhabitat. In particular, we focused on the responses of birds to removal of various combinations of granivorous rodents and ants and to addition of seeds on replicated 0.25-ha experimental plots. For comparative purposes, we also measured the rate of removal of single millet seeds by nocturnal rodents. These observations enabled us to determine the patterns of foraging behavior of granivorous birds and to assess the extent to which they interact directly and indirectly with other granivores in the community.
From the results of other studies of avian granivores (e.g., Pulliam and Brand 1975, Raitt and Pimm 1976, Pulliam and Parker 1979, Dunning and Brown 1982, Parmenter et al. 1984), we expected that flocking finches would use visual cues and high mobility to exploit ephemeral patches of high resource abundance. Therefore, we predicted that birds would rapidly detect and exploit local concentrations of seeds made available by experimental addition of millet seed and removal of competing granivores on different treatment plots.

In studies of competition between desert rodents and ants (Brown and Davidson 1977, Brown et al. 1986) it has been suggested that these granivores may compete directly with birds. However, predicting the response to long-term “press” experiments (continuous removal of potentially competing taxa) is not straightforward (Bender et al. 1984, Brown and Munger 1985, Brown et al. 1986). In addition to direct effects, experimental manipulations of this desert community have demonstrated indirect effects of granivore exclusion that are mediated through plants. These indirect effects are often positive in sign and have been comparable in magnitude to the direct negative effects of competition and predation (Inouye 1981, Davidson et al. 1984, 1985, Brown et al. 1986; see also Vandermeer 1980, Boucher et al. 1982). For example, there is an indirect positive influence of granivorous rodents on populations of granivorous ants. Rodents apparently consume seeds of large-seeded plants that otherwise would competitively reduce the abundance of the small-seeded plants that ants prefer (Davidson et al. 1984). Given the potential complexity of the interactions among birds, rodents, and ants, we predicted that although bird populations should exhibit an initial response to the removal of rodents and ants that would indicate a direct negative effect, the long-term response could include a direct or indirect negative effect or an indirect positive effect of rodent and ant taxa on birds.

**Methods**

**Study site**

The experiments were conducted on a desert bajada 6.5 km east and 2 km north of Portal, Cochise County, Arizona at an elevation of 1330 m. The relatively flat bajada (alluvial fan) is covered with a mixture of Chihuahuan desert shrubs, desert annuals, and perennial grasses (Davidson et al. 1985). Three dry watercourses that dissect the study site are lined by dense stands of tree-shrubs (Acacia, Prosopis, Mimosa, and Chilopsis). The entire 20-ha study site is surrounded by a barbed wire fence that has protected the area from livestock grazing since July 1977.

**Experimental design**

Perturbations of the desert granivore community were conducted on 24 0.25-ha plots (for details of the experimental protocol and an aerial photograph see Brown and Munger 1985). In June 1977, each 50 × 50 m plot was fenced with 6-mm wire mesh that extended 60 cm above the ground and 20 cm below the ground. A 15-cm band of aluminum flashing at the top of the fences prevented rodents from climbing over. Rodent access to plots was controlled by a set of 16 evenly spaced holes (gates) of varying size cut in the fence at ground level.

Two replicates of 11 different treatments plus a control were established on randomly chosen plots. The experimental treatments are of four kinds. (1) **Seed addition.** There were four treatments of supplemental millet seed in three size classes with two regimes of application. LARGE (whole), MIXED (one-half whole/one-half cracked), and SMALL (cracked) millet seeds were added at a constant rate of 8 kg per 0.25-ha plot per month (96 kg/yr). For the PULSE treatment, 96 kg per year of mixed seed was added in one period (September–October) that coincided with the peak seed production of the summer annuals. (2) **Rodent removal.** Different combinations of rodent species were excluded by a combination of trapping and selective control of immigration onto the plots through gates of different sizes. In one treatment, –DIPO, *Dipodomys spectabilis*, *D. merriami*, and *D. ordii* were removed. The smaller granivorous rodents (*Chaetodipus penicillatus*, *Perognathus flavus*, *Reithrodontomys megalotis*, *T. eremicus*, and *P. maniculatus*) could enter the plots via the gates. In a second treatment, –D. SPECT, only *D. spectabilis*, the largest granivorous species, was excluded. In the third rodent treatment, –ROD, all rodent species were removed. (3) **Ant removal.** Ant colonies were removed by careful application of a localized poison. In one treatment, –POGO, all colonies of the large harvester ants *Pogonomyrmex rugosus* and *P. barbatus* were removed. In the other treatment, –ANT, all granivorous ants were removed (Davidson et al. 1985). (4) **Rodent and Ant removal.** In one treatment, –DIPO –POGO, *Dipodomys* spp. and *Pogonomyrmex* spp. were removed. In the other treatment, –ROD –ANT, all species of granivorous ants and rodents were removed.

All of the manipulations were initiated by late summer 1977 and were continued throughout the period of this study. Human disturbance was restricted to a set of permanent paths.

**Bird census**

The number of individuals per species per plot was recorded in 28 census periods from September to February, 1980–1985. Each census was conducted between sunrise and 0900 or between 1600 and sunset. One to three observers walked slowly through all 24 plots for a total of 60–90 observer minutes per census. The sequence of plots visited was altered regularly and birds flushed from one plot were watched to determine their destination and then not counted on the plot where they settled.
Measurement of seed consumption rates

Nine seed removal experiments were conducted in 1981 to 1985 from November to February when temperature was low and granivorous ants were inactive. Diurnal rodents were also virtually absent (they occurred along one dry watercourse but not on the plots). Thus, we were able to attribute seed removal during daylight hours to consumption by birds.

Forty-nine stakes, arranged in a $7 \times 7$ grid (6.5 m apart), were placed in each plot to mark rodent trapping sites. Clear plexiglass squares (1 cm × 1 cm × 4 mm), each with a small depression containing a single millet seed, were placed flush with the soil surface at randomly chosen positions within a 1 m radius of each grid stake. A single millet seed was put at each of the 1176 stakes on the 24 plots at sunrise or sunset. Each grid point was checked at sunrise and sunset and missing seeds were recorded and replaced. This allowed us to determine diurnal and nocturnal seed removal for 24 consecutive hours. Since rain and wind sometimes knocked seeds out of the squares, the data analyzed here are for the seven experiments in which there was no adverse weather.

To normalize the data in all analyses, we used an arcsine square-root transformation (Sokal and Rohlf 1981) of the proportion of the seeds removed per grid point in the seven experiments. (Tables contain values that have been transformed back to a proportion.) In Fig. 2, the cumulative number of seeds removed at each grid point over the seven test periods was used to quantify diurnal seed removal.

Measurement of microhabitat variables

Perennial vegetation was measured in 1978, 1981, and 1983. Since the measurements from the first 2 yr were incomplete and there was no significant variation over years, the 1983 data were used for this analysis (Bowers et al. 1987). Soil particle size was estimated by determining the percentage of the surface area that was covered by sand, gravel, and stones within a 2 m radius of each grid point. Area percentages were measured by visual comparison to cardboard reference disks that were 2.5, 5, 10, and 25% of the 2 m radius circle. The identity and percentage cover of all perennial plants within a 2 m radius of each grid point was also recorded. The common plants were *Flourensia cernua*, *Gutierrezia sarothrae*, *Ephedra trifurca*, *Lycium palidum*, *Atriplex canescens*, and *Haplopappus heterophyllus*. Perennial grasses were combined into a single category. In all analyses of habitat variables, we used an arcsine square-root transformation of the percentage cover (Sokal and Rohlf 1981) to normalize the data. (Tables contain values that have been transformed back to percent cover.)

In September and October 1987, we measured the area at each grid point that was covered with litter, annual plants (any species), or bare ground (<5% cover of annuals and <5% cover of litter). Two perpendicular transects, each with 21 contiguous 2-cm$^2$ squares (40 squares total; center square omitted), were centered at each grid point, and each of the 2-cm$^2$ squares was assigned to one of the categories above. The number of squares in each category was converted to a proportion of the 40 total squares and arcsine square-root transformed for analysis.

Statistical analysis

Because bird foraging was influenced by microhabitat, the confounding effect of microhabitat heterogeneity on foraging patterns within and among treatments was removed by analysis of covariance (ANCOVA). Stepwise multiple regression (SAS 1988) of microhabitat variables against single seed consumption measured at each grid point for all plots was used to determine the microhabitat variables to enter into the ANCOVA. Linear and quadratic terms for all of the soil particle size and vegetation variables were tested in the stepwise regression. Variables were added to the model if the $F$ statistic for their contribution to the model had a $P \leq .10$, and were deleted if at any later step $P \geq .10$. Microhabitat variables were only weakly intercorrelated; analyses that used principal components as covariates in an ANCOVA, similar in other respects to the ANCOVA described below, gave identical results.

A nested, mixed-model ANCOVA of diurnal seed consumption was used to test the significance of variation among treatments (fixed effect) and variation among plots nested within treatments (random effect) after the influence of the microhabitat covariates was removed. After assessing the overall treatment effect (tested over the mean square of plot [nested within treatment]), we used a series of planned orthogonal contrasts (type IV) as adjusted for covariates) to compare the adjusted means of treatments to the control while controlling experimentwise error (Sokal and Rohlf 1981). There were 11 1-df a priori contrasts in each analysis (tested over plot [treatment] MS). Nine of these contrasts compared a treatment mean to the control (with the exception of PULSE and SMALL) and the remaining contrasts compared the combined seed addition treatments to the control and the combined mixed and large seed additions (PULSE, MIXED, and LARGE) to the SMALL seed addition.

Results

Bird flock composition and foraging patterns

The major species of granivorous birds at the study site were Black-throated Sparrow (BTSP, *Amphispiza bilineata*), Brewer’s Sparrow (BRSP, *Spizella breweri*), Vesper Sparrow (VESP, *Pooecetes gramineus*), White-crowned Sparrow (WSCP, *Zonotrichia leucophrys*), Lark Bunting (LABU, *Calamospiza melanocorys*), Mourning Dove (MODO, *Zenaida macroura*), and Scaled
Quail (SCQU, Callipepla squamata). Of these, Black-throated Sparrows and Scaled Quail were the only species that nested on the site and were resident all year. Cactus Wrens (Campylorhynchus brunneicapillus) and Brown Towhees (Pipilo fuscus) were sometimes present but never abundant. The largest populations of combined granivorous bird species were present between September and March (Fig. 1). The winter migrants, mainly Brewer’s Sparrow, Vesper Sparrow, and Lark Bunting, arrived in late August or early September and left at different times after March (Fig. 1).

The birds moved in flocks of varying species composition. With the exception of September 1980, when flocks of 80–500 Lark Buntings were common, the largest flocks each year were composed primarily of Brewer’s Sparrows (5–350 birds, \( \bar{X} = 38.8, n = 72 \)). From the mean number of each species observed in these flocks, the average composition was: 57.6% Brewer’s Sparrow, 22.8% Vesper Sparrow, 18.5% Black-throated Sparrow, and 1.1% White-crowned Sparrow. Occasionally the flocks contained 1–5 Lark Buntings, but, if there were larger numbers of Lark Buntings elsewhere on the site, they always formed single-species flocks that were independent of the small sparrow flocks.

With the exception of Mourning Dove and Scaled Quail, most birds rested in the shrubs that bordered the three washes that crossed the study site. The experimental plots were located on high ground between the three washes. Despite the observation that bird flocks flew from these perching sites to the adjacent high ground to forage, there was no relationship between bird foraging activity and distance from the washes. A correlation of mean diurnal seed removal per plot with distance (in metres) to the nearest wash was not significant \( (r = 0.08, df = 22, P > .30) \).

Direct observations \( (n = 9) \) of mixed flocks of Brewer’s Sparrow and Black-throated Sparrow, independent of the census periods, led to the following generalizations. In approaching a given foraging site, birds flew low to the ground and landed in shrubs in a localized area (<20% were observed to land directly on the ground). After landing, birds hopped to the ground and began to forage. Birds tended to maintain a 1–1.5 m separation while alternately moving along the ground and scanning for seeds. Residency times of a flock within a plot ranged from 50 s to 114 min, with a mean of 18 min.

**Bird microhabitat use**

Multiple stepwise regression (see Methods: Statistical analysis) was used to identify the microhabitat variables that explained variation in avian seed consumption and that could be used as covariates in the analysis of treatment effects. There were significant positive linear relationships between the proportion of single millet seeds removed per grid point and cover of the smallest soil particle size category (sand, \( B = \text{regression coefficient} = 0.158, R^2 = 0.146 \)) and cover of two perennial plant species (Flourensia, \( B = 0.262, R^2 = 0.04 \); Gutierrezia, \( B = 0.087, R^2 = 0.015 \)), and negative relationships for cover of two other perennial species (grass spp., \( B = -0.113, R^2 = 0.008 \); Lycium, \( B = -0.001, R^2 = 0.005 \)). Quadratic terms for each variable were entered, but only the linear terms listed above were retained by the stepwise procedure. In all, the five microhabitat variables explained 21.4% of the variation in the dependent variable. Although there were relationships between diurnal seed removal and percent cover of several perennial shrub species, a composite variable of total shrub cover was not significant.

To determine if the microhabitat variables were correlated with one another, we performed a principal components analysis on the 10 microhabitat variables. With the exception of the expected negative correlations among the three soil particle size variables, the microhabitat variables were not strongly intercorrelated (elements of the correlation matrix ranged from -0.19 to 0.21). Thus, an ANCOVA of diurnal seed consumption with the 10 principal component covariates as independent variables was significant. The percent cover of sand per plot is the covariate.

**Table 1. Summary of ANCOVA of the mean number of granivorous birds of seven species (Total, Table 2) sighted on each plot in 28 sample periods between September and March, 1980–1985. The percent cover of sand per plot is the covariate.**

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>ss</th>
<th>( F )</th>
<th>( P )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Treatment</td>
<td>11</td>
<td>5597.9 (5547.9)*</td>
<td>2.69†</td>
<td>.05</td>
</tr>
<tr>
<td>Plot (Treatment)</td>
<td>12</td>
<td>3746.5 (2241.6)*</td>
<td>0.65</td>
<td>.82</td>
</tr>
<tr>
<td>Sand</td>
<td>1</td>
<td>2031.9</td>
<td>7.05</td>
<td>.008</td>
</tr>
<tr>
<td>Within</td>
<td>647</td>
<td>186 753.6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>671</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* The \( F \) tests of Treatment and Plot(Treatment) are calculated with type IV ss (in parentheses), adjusted for the covariate.† \( F \) test using Plot(Treatment) ms as error term.
Table 2. Mean number of birds sighted per 0.25-ha plot and means adjusted for percent cover of sand per plot in an ANCOVA of winter bird samples on 12 treatments. Total finch is the sum of the densities of BTSP, BRSP, VESP, LABU, and WCSP.* Total is the sum of the densities of all granivorous species (all finch species plus MODO and SCQU).

<table>
<thead>
<tr>
<th>Treatment*</th>
<th>BTSP</th>
<th>BRSP</th>
<th>VESP</th>
<th>Total finch</th>
<th>Adjust. finch</th>
<th>Total</th>
<th>Adjust. total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>0.71</td>
<td>1.70</td>
<td>1.00</td>
<td>3.54</td>
<td>2.08</td>
<td>5.42</td>
<td>3.63</td>
</tr>
<tr>
<td>Seed pulse</td>
<td>1.77</td>
<td>3.23</td>
<td>1.66</td>
<td>6.75</td>
<td>6.16</td>
<td>11.01</td>
<td>10.29</td>
</tr>
<tr>
<td>Large seed</td>
<td>1.56</td>
<td>2.23</td>
<td>2.00</td>
<td>5.80</td>
<td>5.64</td>
<td>6.38</td>
<td>6.18</td>
</tr>
<tr>
<td>Mixed seed</td>
<td>1.52</td>
<td>4.14</td>
<td>2.27</td>
<td>8.07</td>
<td>6.94</td>
<td>12.55</td>
<td>11.16</td>
</tr>
<tr>
<td>Small seed</td>
<td>1.14</td>
<td>2.71</td>
<td>1.41</td>
<td>5.30</td>
<td>7.47</td>
<td>9.14</td>
<td>11.80</td>
</tr>
<tr>
<td>-POGO</td>
<td>1.30</td>
<td>3.36</td>
<td>1.09</td>
<td>5.95</td>
<td>5.06</td>
<td>6.61</td>
<td>5.51</td>
</tr>
<tr>
<td>-ANT</td>
<td>0.30</td>
<td>1.32</td>
<td>0.51</td>
<td>1.55</td>
<td>2.68</td>
<td>2.68</td>
<td>4.06</td>
</tr>
<tr>
<td>-D. SPECT</td>
<td>0.80</td>
<td>2.14</td>
<td>0.80</td>
<td>3.96</td>
<td>3.29</td>
<td>4.96</td>
<td>4.13</td>
</tr>
<tr>
<td>-DIPO</td>
<td>0.66</td>
<td>1.43</td>
<td>1.14</td>
<td>3.25</td>
<td>5.47</td>
<td>5.17</td>
<td>7.91</td>
</tr>
<tr>
<td>-DIPO-POGO</td>
<td>0.89</td>
<td>1.71</td>
<td>1.09</td>
<td>3.73</td>
<td>3.60</td>
<td>7.30</td>
<td>5.95</td>
</tr>
<tr>
<td>-ROD</td>
<td>0.45</td>
<td>1.00</td>
<td>0.89</td>
<td>2.79</td>
<td>2.05</td>
<td>3.64</td>
<td>2.74</td>
</tr>
<tr>
<td>-ROD-ANT</td>
<td>0.45</td>
<td>1.00</td>
<td>0.95</td>
<td>2.39</td>
<td>3.60</td>
<td>3.80</td>
<td>5.29</td>
</tr>
</tbody>
</table>

* BTSP = Black-throated Sparrow (Amphispiza bilineata), BRSP = Brewer's Sparrow (Spizella breweri), VESP = Vesper Sparrow (Poecetes gramineus), LABU = Lark Bunting (Calamospiza melanocorys), WCSP = White-crowned Sparrow (Zonotrichia leucophrys), MODO = Mourning Dove (Zenaida macroura), and SCQU =Scaled Quail (Callipepla squamata). -POGO = all Pogonomyrmex rugosus and P. barbatus colonies were removed. -ANT = all colonies of granivorous ants removed. -D. SPECT = only Dipodomys spectabilis removed. -DIPO = D. spectabilis, D. merriami, and D. ordii removed. -ROD = all rodent species removed.

† A priori comparison of the combined Seed Addition treatments to the Control, P = .05

The effect of soil particle size on bird foraging was also apparent in the analysis of winter bird population censuses (Table 1). Regression analysis revealed that the mean number of individuals of seven migrant species (Table 2, Total) observed on each plot from 1980-1985 was positively associated with the mean percentage cover of sand per plot (Table 1, B = 0.24, P = .008). The other habitat variables were not significantly associated with bird population censuses.

Bird response to seed addition and granivore removal

Diurnal seed consumption.—The confounding effects of microhabitat variation among plots were removed by analysis of covariance (Table 3). The assumptions of ANCOVA were met since there were no significant treatment × covariate interactions and a plot of the residuals revealed no deviations from the expectations of homoscedasticity. Because there was significant plot (treatment) variation (Table 3), the statistical power to detect differences among the adjusted treatment means in the nested ANCOVA was low (1 - P = .06-.42, depending on the method of estimation, for α = .05; Cohen 1988). As a means of compensating for the low statistical power inherent in an experiment of this size, we have relaxed the Type I error and use α = .10 in F tests ([1 - β] = .12-.61, depending on the method of estimation, for α = .10). Thus, the overall treatment effect was significant (Table 3, P = .06).

1. Seed addition.—The adjusted means of seed consumption by birds were higher on two of the seed addition plots, LARGE and MIXED, than on controls and SMALL, although these differences were not significant (Table 4; a priori contrast of combined mixed and large seed additions to SMALL, P = .43). Seed addition may not have had an effect on single seed removal (a priori contrast of combined seed addition to control, P = .38) because seeds were quickly depleted in an ephemeral response that could not be detected, particularly because our single seed experiments never coincided with the monthly application of seeds to addition plots. Indeed, large flocks of Mourning Doves were attracted to the PULSE plots in the days and weeks immediately following application of the 96 kg of seeds and many birds were attracted to the other seed addition plots (see Bird census, below) when seeds were added in the winter months (particularly September to December).

2. Rodent removal.—There was a graded response of bird foraging to removal of various combinations
of rodents. The greatest response was the more than twofold reduction of seed consumption on rodent removal plots (−ROD) in comparison to CONTROL (Table 4; \(P = .04\)). Although the removal of only the three species of Dipodomys (−DIPO) and the removal of the largest species of Dipodomys (−D. SPECT) slightly reduced the adjusted mean seed consumption by birds, these responses were not significant (Table 4). Since avian foraging decreased rather than increased in response to rodent removal, we have rejected the hypothesis of long-term direct competition between birds and rodents. The alternative hypothesis of indirect facilitation of birds by rodents was not rejected.

3. Ant removal.—There was also a trend toward a graded response to removal of ants. The apparent decrease in seed removal in response to removal of Pogonomyrmex spp. (−POGO) was not significant. However, removal of all ants (−ANT) almost halved diurnal seed consumption relative to control, although this effect was not significant (Table 4; \(P = .18\)). Because avian foraging did not increase in response to ant removal, however, we also reject the hypothesis of long-term direct competition between birds and ants.

4. Rodent and ant removal.—Despite the responses to removal of each taxon independently, there was no additive effect of the joint removal of rodents and ants (−ROD −ANT) on the consumption of single seeds by birds. There was a substantial reduction in single seed consumption on rodent/ant removal plots in comparison to controls (Table 4; \(P = .09\)) but the adjusted mean seed consumption was intermediate between the means of the rodent removal and ant removal plots. The combined removal of two species of Pogonomyrmex and three species of Dipodomys (−DIPO −POGO) did not significantly alter diurnal seed consumption. Thus, the indirect positive effect of the presence of ants and rodents on bird foraging was not an additive function of the number of taxa present.

Bird census.—The bird censuses provide a different measure of avian responses to the experimental manipulations. In addition to seasonal variation, there was year-to-year fluctuation in total bird population sizes but no significant long-term trend across years. Therefore, we combined years in a nested ANCOVA of mean numbers per plot using percent cover of sand, the only significant microhabitat variable, as a covariate (Table 1). The assumptions of ANCOVA were met since there was no treatment \(\times\) covariate interaction and no indication of heteroscedasticity. The overall treatment effect was significant and there was no significant plot (treatment) variation (Table 1). A priori contrasts of the adjusted means revealed significantly higher mean densities of two species, Black-throated Sparrow and Brewer’s Sparrow, on all seed addition plots combined than on controls (Table 2; \(P = .05\)). In a priori tests of the mean population sizes of all species combined (Table 2; Adjusted Total) and of all finch species (Table 2; Adjusted Finch), comparisons of the control against all seed addition plots were significant (\(P = .05\)).

Although the treatments, other than those mentioned above, were not significantly different from the control (\(P > .10\)), the values for the adjusted and unadjusted treatment means of total finch numbers (Table 2) show qualitative trends that parallel the adjusted means.
and unadjusted treatment means of diurnal seed consumption (Table 4). This trend is evident in the product–moment correlation ($r = 0.637, P = .001$) between mean number of birds (Total Finch) and mean diurnal seed consumption per 0.25 ha across the 24 plots (Fig. 2). Both measures of avian foraging reveal similar responses of birds to the experimental manipulations.

**Rodent microhabitat use**

Rodent seed consumption was measured to determine the degree of overlap in the locations of rodent and avian foraging. The influence of soil particle size and perennial plant cover on nocturnal seed consumption by rodents was determined, as for birds, by multiple stepwise regression. Although there were significant positive relationships for one soil particle size category and two perennial plant species and significant negative relationships for three other perennial plants ($P < .02$), the variables only accounted for 7.3% of the variation in nocturnal seed consumption. We have analyzed nocturnal foraging in an ANOVA since it yields the same results as an ANCOVA. Microhabitat explained little of the variation in overall rodent foraging because rodents foraged at most of the grid points.

**Nocturnal seed consumption**

The ANOVA of nocturnal seed consumption revealed significant plot (treatment) variation (Table 5). As with the ANCOVA of bird foraging, the nested analysis had low statistical power ($|1 - \beta| = .05-.36$, depending on the method of estimation, for $\alpha = .05$). Thus, we again use $\alpha = .10$ in $F$ tests. The overall treatment effect was significant (Table 5, $P = .06$).

1. **Seed addition**.—The adjusted means of nocturnal seed consumption on seed addition plots were individually not significant, and the combined seed addition means were not significantly different from the control (a priori comparison; $P = .43$). We infer that enhancement of seed resources did not lead to increased rodent consumption of single seeds, because only the largest rodent species, *D. spectabilis*, increased in abundance on these plots (Brown and Munger 1985).

Individuals of *D. spectabilis* did not harvest single millet seeds, even when single seeds were placed adjacent to their burrows/mounds. The smaller rodent species that did harvest single millet seeds (see below) either remained the same or decreased in abundance on seed addition plots (Brown and Munger 1985).

2. **Ant removal**.—The adjusted means for -POGO and -ANT were lower than that of CONTROL, but these differences were not significant (Table 6). The numbers of rodents captured on the ant removals were also not different from the control (Brown and Munger 1985).

3. **Rodent removal**.—The removal of some rodent taxa produced changes in seed consumption. The highest rates of nocturnal seed removal were recorded on -D. SPECT plots (Table 6; $P = .43$). This was the only treatment that had higher nocturnal feeding rates than CONTROL and, at times, all of the single seeds available in one night were consumed. Although it was not significant, we attribute this increase in seed consumption to the numerical increase of *D. merriami* and *D. ordii* that occurred in response to removal of *D. spectabilis* (Brown and Munger 1985). Bowers et al. (1987) have demonstrated that increased seed harvesting on -D. SPECT plots occurred in microhabitat sites with low vegetative cover, the sites where *D. spectabilis* is most active when it is present.

The adjusted mean nocturnal seed consumption on plots from which all *Dipodomys* species had been removed (-DIPO) was significantly lower than CONTROL (Table 6; $P = .06$) as was -DIPO -POGO ($P = .01$). However, the seed consumption rates on these plots were still 60% or more of CONTROL. This indicates that a large portion of the single seeds were harvested by the remaining five species of small granivorous rodents. These species were significantly more numerous on -DIPO and -DIPO -POGO treatments than on other plots (Brown and Munger 1985).

**Effect of background seed density**.—If granivores exhibited a functional response to seed abundance, the probability of encounter and consumption of single millet seeds could have been affected by the background seed density. As seed density increased, there may have been an initial, concomitant increase in foraging activity; but the probability that a given seed was harvested might have declined if foraging activity peaked and seed density continued to increase. If so, some treatments with low measurements of single seed consumption might actually have had high foraging activity that was not detected because of enhanced background seed densities.

This possibility was evaluated for rodents on 16–17 September 1983 by comparing single seed removal rates on the night preceding and the night following the application of 0, 8.8, 17.6, or 35.2 kg of millet seed to seed addition plots (during the time that seeds were normally added to these plots; Fig. 3). The proportional reduction in single seed consumption on the night fol-

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**Table 6.** Mean nocturnal (i.e., rodent) single seed consumption per grid point and coefficient of variation in an ANOVA of 10 treatments. *P* is the significance of an a priori contrast with Control.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>$\hat{X} \pm SD$</th>
<th>CV</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>0.62 ± 0.017</td>
<td>27.2</td>
<td>...</td>
</tr>
<tr>
<td>Seed pulse</td>
<td>0.59 ± 0.017</td>
<td>33.4</td>
<td>...</td>
</tr>
<tr>
<td>Large seed</td>
<td>0.55 ± 0.018</td>
<td>37.6</td>
<td>.39</td>
</tr>
<tr>
<td>Mixed seed</td>
<td>0.64 ± 0.018</td>
<td>26.1</td>
<td>.88</td>
</tr>
<tr>
<td>Small seed</td>
<td>0.49 ± 0.018</td>
<td>40.7</td>
<td>...</td>
</tr>
<tr>
<td>-POGO</td>
<td>0.54 ± 0.018</td>
<td>39.6</td>
<td>.30</td>
</tr>
<tr>
<td>-ANT</td>
<td>0.55 ± 0.018</td>
<td>31.3</td>
<td>.34</td>
</tr>
<tr>
<td>-D. SPECT</td>
<td>0.68 ± 0.017</td>
<td>20.9</td>
<td>.43</td>
</tr>
<tr>
<td>-DIPO</td>
<td>0.46 ± 0.018</td>
<td>30.0</td>
<td>.06</td>
</tr>
<tr>
<td>-DIPO-POGO</td>
<td>0.38 ± 0.018</td>
<td>80.2</td>
<td>.01</td>
</tr>
</tbody>
</table>
following application of the seeds (after/before) was arcsine square-root transformed and analyzed by ANOVA. There was a highly significant reduction in single seed consumption in response to the treatments ($F_{3,6} = 13.51, P = .005$). Tukey’s pairwise comparisons held at an experimentwise error rate ($\alpha = .05$) revealed that the addition of 8.8 kg of millet seed per 0.25 ha did not decrease the rate of single seed consumption relative to control plots ($P > .05$), but that addition of 17.6 and 35.2 kg caused a significant, progressive reduction in seed consumption rates ($P < .05$) relative to control and 8.8-kg plots (Fig. 3). Thus, background seed densities could be increased by at least 8.8 kg per 0.25-ha plot without causing a short-term decline in the measured single seed consumption. These results indicate that, for rodents, the absence of enhanced seed consumption rates on treatments, such as seed additions and ant removals, was not due to the direct effects of enhanced background seed densities on foraging rates.

Comparison of bird and rodent foraging

A comparison of diurnal (Table 4) and nocturnal seed consumption rates (Table 6) indicates that birds were 38.4–64.5% as effective as rodents in removing single millet seeds. The degree of overlap in use of foraging sites between birds and rodents, estimated with a product–moment correlation of the seeds consumed per grid point during diurnal and nocturnal seed grid experiments, was positive ($r = 0.405, df = 12, P = .0001$ for seed addition, ant removal, and control plots). When −DIPO, −DIP0, and −DIPPO plots were added, the correlation was slightly lower ($r = 0.339, df = 18, P = .0001$). Thus, there was a consistently high degree of overlap between the two taxa in their use of microhabitats and, presumably, resources, since correlations within each plot revealed similar relationships and there was no discernable effect of specific treatments on these correlations.

A major difference in the foraging patterns of birds and rodents was evident in comparisons of variation in grid-point-specific single seed consumption rates (Tables 4 and 6). The coefficient of variation for birds was at least twice that of rodents on all treatments except −DIPO −POGO. We infer from this that, in winter months when these measurements were made, birds foraged in flocks that moved over large areas in a spatially and temporally patchy fashion. In contrast, rodents were dispersed on individual home ranges and harvested seeds more uniformly in space and time.

**Discussion**

*Indirect facilitation of birds*

The results of the seed grid experiments demonstrate that although birds are important seed consumers in this desert community and although they overlap extensively with rodents in both resource and microhabitat use, their long-term interactions with rodents and ants are mutualistic or at least commensalistic rather than competitive. Avian activity and foraging were lower on plots where either rodents, ants, or both were experimentally removed than on unmanipulated plots where intact assemblages of these taxa were present. These findings are similar to the long-term decrease in ant activity observed on plots where rodents were removed (Davidson et al. 1984, Brown et al. 1986). Verifications of mutualistic, as opposed to commensalistic, interaction await reciprocal tests of the effects of bird removal on rodents and ants.

The positive effects of rodents and ants on birds were unexpected because there is good evidence that seed resources limit all three kinds of granivores (Brown et al. 1979, 1986, Brown and Munger 1985). In our experiments, wintering finches increased in density (immigration) in response to seed addition treatments. In addition, results of other studies indicate that densities...
of winter finches in arid environments are positively correlated with precipitation and, presumably, with seed production during the previous growing season (Raitt and Pimm 1976, Pulliam and Parker 1979, Dunning and Brown 1982). Given this evidence of resource limitation and the high degree of overlap in bird and rodent microhabitat use observed on every plot, there is the potential for substantial direct competition among these taxa.

If birds compete directly with the other granivores, we would expect them to increase local foraging activity in response to removal of rodents and ants. Although this predicted response was not detected, a short-term increase in bird foraging could have occurred on granivore removal plots. We did not monitor bird responses until 1981, 4 yr after granivores were removed. If a short-term increase in bird activity did occur, by 1981 it was counteracted by a decrease in avian foraging that has persisted for at least 6 yr.

Despite variation among the replicate plots, the most important responses to experimental treatment, a decrease in bird single seed consumption on rodent removal plots and an increase in bird population density on seed addition plots, were statistically significant with \( \alpha = .05 \). Responses of birds to ant, combined rodent/ant, and Dipodomys removal treatments were not significant at this level, although they were in a direction consistent with indirect facilitation. These weak treatment effects may reflect weak indirect interactions among birds, ants, and large species of rodents that can only be detected with more extensive replication.

We offer two general hypotheses for the observed long-term positive influence of rodents, and perhaps ants, on birds. Both involve indirect pathways through plants. First, like the indirect facilitation of ants by rodents (Davidson et al. 1984), the positive effects of other granivores may be mediated by competition among seed plants for which the different kinds of granivores have distinct preferences. If seeds of some plant species are preferred by rodents or ants and avoided by birds, and these plants compete with those preferred by birds, then the rodents and ants may indirectly facilitate birds if they decrease the abundance of plants that are less palatable to birds. There is no evidence to support this hypothesis. Although there are differences in the attributes and species of seeds preferred by birds, rodents, and ants (Pulliam and Brand 1975, Brown et al. 1979, Davidson et al. 1984), the largest differences appear to be between seeds harvested mostly by ants and those preferred by the two classes of vertebrate granivores. While there were large changes in the vegetation in response to rodent removal and smaller ones in response to ant removal at the study site (Davidson et al. 1984, 1985), most of the annual and perennial plant species that have increased in abundance produce seeds that appear to be readily taken by birds.

Alternatively, the primary effect of rodents and ants on birds may be mediated through the physical structure of the vegetation, and perhaps to a lesser extent through the structure of the soil. Through their foraging activities, rodents and ants decrease the densities of annual plants, make trails through the standing dead annuals, and create areas of bare soil devoid of litter. Because foraging birds run along the ground and scan visually for seeds, dense cover of standing dead plants would interfere with movements and organic litter would conceal seeds from view. Thus, even though rodent and ant removal plots may have contained more seeds, birds might have used them less than controls if absence of the physical effects of other granivores sufficiently reduced the profitability of foraging.

As unlikely as this hypothesis may seem at first, it is consistent with a number of observations. Dense stands of Eriogonum abertianum and other annuals occur on ant removal plots (Davidson et al. 1985), and perennial grasses and standing dead annuals cover many of the rodent removal plots (J. H. Brown, unpublished data). Foraging finches were often observed hopping along rodent trails through the dense vegetation and pecking in areas of bare soil. If birds are benefiting from rodent physical disturbance, the activities of the small rodents (Chaetodipus, Peromyscus, and Reithrodontomys) must cause sufficient disturbance, because the large reduction in bird foraging was observed only on complete rodent removals and not on Dipodomys removals.

In 1987, after documenting the indirect facilitation of birds by other granivores, we measured the amount of bare ground, litter, and annual cover at each grid point (Table 7). These data provide an a posteriori test of the hypothesis that the activities of rodents and ants decrease the amount of litter and standing annual cover and, in turn, enhance the suitability of microhabitats to bird foraging. The results reveal less bare ground at grid points on −POGO, −ANT, and MIXED treatments and a nearly one-third reduction in bare ground on −ROD, −ROD −ANT treatments relative to

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Bare</th>
<th>Annuals</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>( \bar{X} )</td>
<td>( P )</td>
</tr>
<tr>
<td>Control</td>
<td>0.35</td>
<td>0.06</td>
</tr>
<tr>
<td>Seed pulse</td>
<td>0.54</td>
<td>...</td>
</tr>
<tr>
<td>Large seed</td>
<td>0.37</td>
<td>0.06</td>
</tr>
<tr>
<td>Mixed seed</td>
<td>0.28</td>
<td>0.08</td>
</tr>
<tr>
<td>Small seed</td>
<td>0.24</td>
<td>0.05</td>
</tr>
<tr>
<td>−POGO</td>
<td>0.19</td>
<td>0.10</td>
</tr>
<tr>
<td>−ANT</td>
<td>0.19</td>
<td>0.07</td>
</tr>
<tr>
<td>−D. SPECT</td>
<td>0.39</td>
<td>0.07</td>
</tr>
<tr>
<td>−DIPO</td>
<td>0.27</td>
<td>0.07</td>
</tr>
<tr>
<td>−DIPO − POGO</td>
<td>0.33</td>
<td>0.05</td>
</tr>
<tr>
<td>−ROD</td>
<td>0.23</td>
<td>0.09</td>
</tr>
<tr>
<td>−ROD − ANT</td>
<td>0.16</td>
<td>0.08</td>
</tr>
</tbody>
</table>
CONTROL. In addition, −POGO, −ROD, −ROD−ANT, and MIXED treatments have higher standing cover than controls (Table 7). Although these responses are not significant due to plot(treatment) variation, the directions of the responses are consistent with the hypothesis that the indirect influence of ants and rodents on birds is mediated by physical alteration of microhabitats.

In another test of the mechanism underlying the indirect interaction, we used a stepwise regression of diurnal seed consumption residuals (after removing the effects of the microhabitat variables in Table 3) against the bare ground, litter, and annuals measured at each grid point on all plots. The analysis revealed a positive relationship for bare ground ($B = 0.29, P = .0001$) and a negative, but not significant, relationship for annual cover. The positive relationship between seed consumption and bare ground was also present within plots for all treatments. These results confirm that birds are affected by variation in the amount of open space that is available for foraging. Further research is clearly needed to fully elucidate this potentially important pathway of indirect interaction.

Although the mechanism is still uncertain, this is another case in which taxa that would be predicted to interact competitively, actually interact positively in the long term (Davidson et al. 1984, Brown et al. 1986). Three points are of general interest. First, in comparison to direct interactions, the effects of indirect interactions may often be opposite in sign and equal or greater in magnitude. Second, these kinds of indirect relationships potentially promote stability in community structure and dynamics (Vandermeer 1980, Brown et al. 1986, Pianka 1987). Not only do the positive indirect interactions tend to promote the coexistence of species whose direct interactions are negative, but they also tend to prevent particular species or functional groups from dominating the community. Third, the indirect interactions may be mediated by effects that are not directly related to resource abundance or interference per se, but rather, to other aspects of the biology of interacting organisms. If our hypothesis of the cause of the indirect facilitation of birds is valid, the important factor in the indirect interaction is microhabitat structure, not strict seed abundance.

**Foraging patterns of birds**

Our results support the suggestion that granivorous birds act as “cream skimmers” (Brown 1986) since they are much more mobile than ants and rodents and, thus, are able to find and exploit highly concentrated seed patches that are variable in space and time. Although, like rodents, they have high per individual energy demands, birds do not store seeds, and hence, must meet daily energy demands by continuous foraging in areas of high seed abundance (Pulliam and Brand 1975, Pulliam 1983). To the degree that they rapidly consume large, high-density patches of seeds, the main impact of birds in the granivore community may be to reduce the spatial and temporal variance in seed resources. Consequently, other granivores do not encounter the high concentrations of seeds that could accumulate in the absence of birds.

The ability of birds to locate and exploit rich seed patches is evident in the high bird densities and high rates of diurnal seed consumption measured on seed addition plots. The harvesting of supplemental millet seeds on seed addition plots by birds explains, at least in part, the low degree of rodent biomass increase measured in response to these manipulations (Brown and Munger 1985). Because the consumption of single millet seeds by birds was >50% of the removal rate by the entire rodent community (Table 4 and 6), birds depleted a substantial proportion of the supplemental seeds that would otherwise have been available to rodents. In fact, the birds probably consumed more than this estimated proportion, since we observed large flocks moving onto the plots within hours after seed addition. Although bird foraging can account for the lack of rodent biomass compensation on seed addition plots, there is no evidence that enhanced bird foraging on the various granivore removal plots accounted for the lack of biomass compensation in either rodents or ants, as suggested by Davidson et al. (1985), Brown and Munger (1985), and Brown et al. (1986). Birds actually foraged less on these treatments than on control plots.

An additional aspect of avian foraging consistent with “cream skimming” is the high spatial and temporal variance in seed consumption measured in the seed-grid experiments. The overall spatial (among grid points) coefficients of variation of seed removal were 64.7 for birds and 31.8 for rodents. The overall temporal (among winter census periods) coefficients of variation were 34.7 for birds and 25.8 for rodents. The variance in avian foraging was probably even greater than we have estimated, because none of the seed grid experiments coincided with the periods when the largest flocks of Lark Buntings and Brewer’s Sparrows were observed on the study site.

The high spatial and temporal variation in seed removal by birds illustrates another aspect of this desert granivore association that does not fit standard concepts of population interaction. If seeds are a limiting resource, and birds directly or indirectly alter their availability to other granivores, the population densities of rodents and ants should increase or decrease due to changes in birth and death rates. In contrast, because birds are migratory and highly mobile, alteration of seed availability by rodents and ants should mainly result in bird immigration or emigration and a shift in the location of bird foraging. Changes in bird population birth and death rates should be controlled by the availability of resources in entire summer breeding and winter migration areas rather than by interactions in any local granivore assemblage (Pulliam and Parker 1979). Thus, there is an asymmetry in the pop-
ulation interactions of the granivores that arises from discrepancies in the spatial scales of movement of individuals. The scale of the asymmetry and its impact on direct and indirect interactions among granivorous taxa are important issues that warrant further investigation regardless of whether the interactions are short-term negative or long-term positive in their effects.

Our estimates of the importance of birds in determining the fate of desert seeds are greater than those reported in other studies (Brown et al. 1975, Mares and Rosenzweig 1978; but see Parmenter et al. 1984). These other studies were based on the removal of seeds from small dishes that contained 5 g or more of commercial seeds. Parmenter et al. (1984) addressed several reasons why seed dish experiments underestimate avian granivory, since they censused high densities of seed-eating birds at a Chihuahuan Desert site but measured low rates of diurnal seed removal from dishes. Our method of measuring avian foraging activity using single seeds spread over a large area overcomes many of the problems discussed by Parmenter et al. (1984) and probably provides a more accurate estimate of avian granivory.

Foraging patterns of rodents

Although this paper is primarily about the foraging of birds, two aspects of nocturnal seed removal by rodents are of interest. The rodent community as a whole foraged in all microhabitats, even though traps placed at the same grid stakes as the single millet seeds revealed differential capture of different species in each of the different vegetative microhabitats (Bowers et al. 1987).

In addition, although nocturnal seed removal was highest on plots where D. spectabilis alone had been removed, it was only moderately reduced on plots from which all three species of Dipodomys had been removed (Table 6). This indicates that the five species of small seed-eating rodents that remained after kangaroo rats had been experimentally excluded were capable collectively of harvesting a large fraction of the available millet seeds from most of the microhabitats. Thus, even though these rodents showed <10% compensation in density and biomass for the absent kangaroo rats (Brown and Munger 1985), they exhibited much greater compensation in their harvesting of the single millet seeds. Because millet seeds are much larger (6 mg) than the vast majority of native seeds, the small seed-eating rodents appear to be able to forage economically for millet, but not to the same extent for the native seeds that should have accumulated in the absence of kangaroo rats.

In summary, our results have revealed an indirect facilitation of granivorous birds by rodents and ants that is apparently mediated by microhabitat structure and soil surface disturbance, rather than directly by resources per se. The long-term effect of this indirect interaction on the foraging activities of birds is probably found. Taken together, the occurrence of minimal compensation in rodent and ant biomass in response to removal of the other taxon, and the low levels of bird foraging activity in response to rodent and ant removal, underscore the observation that there is no overall accumulation of seed resources that can be effectively utilized by one class of granivores when the other granivores are removed.

Acknowledgments

We are indebted to B. Harney, M. Kurzius, J. Munger, M. Bowers, D. Gori and many others for assistance at the study site. P. Nicoletto helped prepare the figures. The manuscript was greatly improved by numerous insightful comments from B. Parmenter on an early version of the manuscript and by the critical comments of M. Price, G. Mittelbach, and two anonymous reviewers. The research has been supported by National Science Foundation grants BSR-8021535, BSR-8506729, and BSR-8718139 to J. H. Brown.

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