

Seed predation by birds and small mammals in semiarid Chile

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We studied spatial and temporal patterns in foraging activity among diurnal birds and nocturnal mammals at a semiarid site in northern Chile using artificial foraging trays. Small mammals foraged more extensively under shrubs than in open microhabitats, but birds showed no such selection. Moreover, avian foraging was more extensive than that by small mammals in all seasons and both microhabitats. Avian foraging was highly seasonal, as many birds at our site migrate to the Andean prepuna or to Patagonia during the austral summer. Birds have tended to be overshadowed by small mammals and ants in studies of granivory, but this study suggests that their importance may be underestimated in some systems.

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Foraging animals must obtain sufficient nutrients for survival and reproduction while avoiding being eaten by other foraging animals (predators). Additionally, they must compete with both conspecifics and allopecifics, including both closely and distantly related taxa. In arid ecosystems, seeds may lie dormant for extended periods and therefore constitute a potentially abundant food source. Consumers of seeds include truly granivorous species such as many harvester ants, kangaroo rats, etc., as well as omnivorous taxa that consume seeds opportunistically when available (Whitford 2002). Desert regions of the world include large numbers of taxa that consume seeds either as principal dietary items or as part of a broader trophic strategy. In particular, many ants, small mammals, and birds (especially fringillid passerines) consume seeds and may compete for them (Brown et al. 1979, Kotler and Brown 1988, Whitford 2002).

Extensive research in North America has documented foraging patterns among granivorous taxa, including small mammals (Brown et al. 1979), birds (Bent 1968, Thompson et al. 1991), and ants (MacMahon et

al. 2000). In particular, small mammals and ants have been reported to be the dominant granivores in North American deserts, with asymmetric reciprocal effects on each other via exploitative competition (Brown et al. 1986, Valone et al. 1994). Birds also consume seeds, and may have important impacts on local seed consumption (Thompson et al. 1991). Their high vagility allows birds greater flexibility to respond to regional patterns of seed availability at larger spatial scales than small mammals or ants, so evidence of competitive interactions between birds and other granivores have been difficult to document (Wiens 1989), and indeed, Thompson et al. (1991) argued for facilitation between small mammals and birds in SE Arizona. At the same site, Guo et al. (1995) documented differential impacts of birds and small mammals on plant community structure, reporting important roles for both vertebrate groups. Studies elsewhere have both supported and questioned the generality of results based on North American deserts. Limited evidence from Israel supports a role of mammals as principal seed consumers there, but studies from the southern hemisphere have

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allocated much less ecological influence to seed-eating mammals, and proportionally more (albeit not necessarily absolutely more) to ants (Kerley 1991, Predavec 1997, Lopez de Casenave et al. 1998), and recent work in Argentina (Lopez de Casenave et al. 1998, Marone et al. 2000) indicates that birds may be more important than previously believed.

One tool in the arsenal of ecologists studying co-existence of potentially competing seed consumers is experimental measurement of foraging decisions. Artificial foraging stations allow researchers to quantify the amount of seed that consumers take. By provisioning stations with a known density of seed in a specified matrix (e.g. sand, pebbles, etc.), one can quantify the density of seed at which foragers “give up” and move on to forage elsewhere. If tracks are readily distinguished (Brown et al. 1997, Kotler and Brown 1999) or sub-sets of the fauna can be provided with differential access to such trays (Yunger et al. 2002, Kelt et al. in press), then taxon-specific “giving up densities” (GUDs) are a useful metric to compare foraging efficiency by different taxa. For GUDs to be insightful, the ratio of matrix to food must be rather high. Otherwise, the mass of remaining seed is likely to continue to decline over time. Quantitatively, if the harvest rate, $H = C + P + MOC$ (where C is the foragers cost due to competition, P due to threat of predation, and MOC the missed opportunity cost associated with failing to forage elsewhere), interpretation of GUDs is based on the assumption that H should decline to zero at some point (but see Price and Correll 2001). Fortunately, it is possible to obtain insights into community processes using foraging tray studies that do not yield GUDs. Specifically, differences in foraging activity across microhabitats, seasons, or among taxa in a community all yield insights into the means by which communities are structured and the mechanisms by which species are able to co-exist.

Foraging trays (usually using GUDs) have been successfully employed in many of the world’s arid regions (e.g. North America, Brown 1988, 1989, Meyer and Valone 1999; Israel, Kotler 1992, Kotler et al. 2001; South Africa, Hughes and Ward 1993; Hughes et al. 1994, 1995; Australia, Kotler et al. 1998, Haythornthwaite and Dickman 2000; South America, Yunger et al. 2002). Nonetheless, to date only one research group has applied this approach to questions of local co-existence of birds and small mammals. Brown et al. (1997) and Garb et al. (2000) tested several mechanisms of co-existence between two species of gerbil (*G. pyramidum* and *G. allenbyi*) and crested larks (*Galerida cristata*) in the Negev Desert of Israel (Kotler and Brown 1999). They found that gerbils foraged more intensively (= lower GUDs) than larks in both microhabitats studied, in both sand habitats, and in every month of study (Brown et al. 1997). These results were supported when different seed sizes were offered (Garb et al. 2000).

Evidently the mechanism(s) of co-existence between these species operates at larger spatial scales than studied by these researchers, perhaps underscoring the importance of avian vagility.

Kotler and Brown (1999) extended these results by evaluating GUDs for crested larks, Allenby’s gerbil (*G. allenbyi*, and Wagner’s gerbil (*G. dasyurus*) in three substrates (sand, loess, cobble) and with three food types (millet seed, alfalfa pellets, and insects). They also evaluated the role of substrate outside foraging trays (“escape substrate”). Gerbils in this study segregated by habitat, with *G. allenbyi* in sand habitat and *G. dasyurus* in loess and rock. Kotler and Brown (1999) found larks to be inferior to gerbils on all substrates in sandy habitats, but superior on all substrates in rock and loess habitats. Finally, on sand habitat larks were inferior to gerbils when foraging on seeds or alfalfa pellets, but were similar when foraging on insects. In rock and loess habitat, larks were superior to gerbils for seeds and insects, but these species were similar in their ability to extract alfalfa pellets from foraging trays. The superiority of Allenby’s gerbil on sand was attributed to their well-haired hind feet, providing traction on sandy substrates and allowing for effective escape from predators. Larks foraged more effectively in loess and rock habitats largely because of diligence rather than particular foraging efficiency.

The only other study we are aware of that compared small mammals and birds with foraging trays was Kotler et al. (1998), who used foraging trays to evaluate the effects of water availability on patch use by Australian ravens (*Corvus coronoides*) and sandy inland mice (*Pseudomys hermannsburgensis*). The latter was a preliminary study, however, and did not address mechanisms of co-existence between these species.

We studied the foraging ecology of the assemblage of seed-eating species at a semiarid site in northern Chile. Our objectives were to evaluate the relative importance of nocturnal seed predation by small mammals and diurnal consumption by birds. We used experimental foraging trays and quantified the amount of seed remaining after all-night (small mammals) or all-day (birds) foraging bouts in two microhabitats, at two seasons, under two lunar phases, and across three years of study. Although the mammal fauna at our site is very well known (see below), the birds have received relatively little attention (but see Cornelius et al. 2000, Kelt 2000, Kelt et al. in press). We interpret our results in the context of what is known about mammalian and avian granivory in this and other arid regions.

Methods

We conducted our studies at Parque Nacional Bosque Fray Jorge (“Fray Jorge”), a ca 10000 ha park located

on the coast of northern Chile ca 400 km N Santiago and 100 km S La Serena (30° 41'N, 71° 40'W, ca 80 m elevation). The habitat is classified as coastal steppe chaparral (Gajardo 1993) and is characterized by dense shrubs covering ca 50–60% of the ground (Gutiérrez et al. 1993). Dominant plant species are *Porlieria chilensis*, *Proustia pungens* and *Adesmia bedwellii*.

This study capitalizes on long-term biotic manipulations that were initiated in the austral winter of 1989 when we established 16 experimental plots (75 × 75 m) at Fray Jorge. These plots were designed to exclude either: 1) terrestrial and aerial predators (N = 4); 2) a large, social, diurnal rodent, the degu (*Octodon degas*; N = 4); 3) or both predators and degus (N = 4); a final set of four control grids include low fences with holes to provide access by all residents of the park (Meserve et al. 1993, 1996, 2003).

The diverse vertebrate community at Fray Jorge has been the subject of numerous studies (Meserve et al. 2003). The small mammal community of this habitat includes ten species, which have been the subject of extensive demographic and community-level studies (Meserve et al. 1999, 2003). Birds are abundant at Fray Jorge but have been studied relatively little (Cornelius et al. 2000, Kelt et al. in press), although the park hosts a diverse avifauna that includes a number of insectivorous and granivorous species. Granivores include a tinamou (*Nothoprocta perdicaria*), three pigeons and doves, and half a dozen fringiblid passerines (Kelt et al. in press). Of the ca 11 granivorous taxa, the most abundant are rufous-collared sparrow (*Zonotrichia capensis*) and common diuca finch (*Diuca diuca*), both of which are widespread and abundant throughout much of Chile (Lopez-Calleja 1995, De la Peña and Rumboll 1998). The latter species is a seed specialist (Lopez-Calleja 1995).

Foraging was quantified with artificial foraging trays (22 × 28 × 5 cm aluminum cooking pans), provisioned with 630 cc of finely sifted soil and 30 g of non-hulled oat seed (weighed to the nearest 0.01 g with a portable electronic balance; Ohaus Navigator Model N12120), autoclaved to prevent germination. The density of seed used in trials was extrapolated from earlier work (Yunger et al. 2002) that was based on observed seed density at the park. Although oats are not native to this system, they were readily consumed by both birds and small mammals at our site (pers. obs.). Trays were placed under shrubs and in open microhabitats ≥ 1 m from the nearest shrub. Trays were established in sets of two and referred to as “caged” and “uncaged” trays. The former was placed in a hardware cloth cage to exclude birds; mammals were provided access via a 50 cm long Ø4 cm L-shaped section of PVC pipe (we recorded only two instances of birds in these trays, and believe that these were otherwise effective in limiting entry to mammals; (Kelt et al. in press). We established trays in sets of two (one caged tray and one uncaged

tray) that were separated by ≤ 2 m. Sets of trays were paired such that groups of 4 trays included one set placed either under the canopy of shrubs or in open microhabitat ≥ 1 m from shrub cover; sets within groups generally were ≥ 4 m apart. Finally, these groups of trays were established both inside and outside of each of 8 study plots (4 degu exclosures and 4 control plots); groups inside and outside study plots were separated by ≥ 20–30 m. Most analyses here use only the 16 “uncaged” trays located outside of degu exclosures. The presence of a diurnal rodent potentially confounded our interpretations of avian (e.g. diurnal) foraging. To evaluate the potential importance of degus as diurnal seed predators we compared seed consumption inside and outside of degu exclosures using all 32 “caged” and 32 “uncaged” trays (e.g. those inside as well as outside of degu exclosures). All experiments were run for three consecutive days and nights (except in the final season, when rain forced us to close the trays for one night) under the peak of both the new and full moon, in summer and winter, for 2 and 1/2 years (winter 1999 through winter 2001). Experiments were initiated prior to dawn, and at dusk and dawn we sieved the soil to remove the remaining seed, which was returned to our field station to be air-dried and weighed on a portable balance to the nearest 0.01 g. After the seeds were sieved, trays were re-provisioned with 30 g of seed.

The metric we used to quantify foraging was the density of seed in foraging trays when animals stopped foraging. Although this is similar to the giving-up densities used by many researchers, we do not interpret our results in this rigid conceptual framework because the seeds we used are relatively large and they were presented in a relatively high density. As a result it is not clear that trays left in the field for longer periods would not be further depleted, violating a basic premise underscoring the use of GUDs (B. Kotler in litt.). Nonetheless, seeds were largely obscured by the sand matrix in which they were presented. Because all trays were in the field for the same diurnal or nocturnal period they were comparable measures of consumption, and allowed for rigorous comparisons of foraging in different microhabitats, seasons, and across years.

At our study site, the focal taxa were sufficiently similar in size that we could not distinguish them on the basis of tracks. Consequently in this study we distinguish only between “birds” and “small mammals.”

Because seeds absorbed moisture during the night we placed one additional tray in each set to estimate moisture uptake. These trays were enclosed in mesh cages lacking any entrance holes, effectively excluding all vertebrates. Ants are trivial consumers at our site (Kelt et al. in press), and did not influence results in foraging trays. Full exclosure seed samples were treated identical to those from experimental trays, and the

proportional change from 30 g was used to adjust the final mass of experimental seed samples in the same set.

Statistical analysis

We analyzed these data with a mixed model repeated measures analyses of variance (rmANOVA) in which plot (a covariate) was treated as a random effect, and lunar phase (full vs new), season (summer vs winter), microhabitat (shrub vs open), time of day (diurnal vs nocturnal), and year (1999, 2000, 2001) were treated as fixed effects. Because initial analyses (see Results) indicated that patterns of seed removal were significantly different diurnally and nocturnally, subsequent analyses excluded the time of day effect. Error terms and associated degrees of freedom were estimated using the RANDOM option in PROC GLM (SAS Institute Inc. 1999; Littell et al. 2002) because these are complex functions of dependent variables they often are not simple integers. All inference employed Type III sums of squares. We limited interactions in our analyses to 2nd and 3rd order, and we discounted statistically significant results that appear to carry little biological information (evaluated by the relative magnitude of the sums of squares).

Nocturnal seed removal is interpreted as reflecting activities of small mammals, and diurnal seed removal is interpreted as avian consumption (but see “Effects of diurnal degus” below). After an initial analysis to evaluate overall patterns of foraging (e.g. diurnal vs nocturnal consumption), we conducted separate mixed model ANOVAs on avian (diurnal) and mammalian (nocturnal) seed consumption.

Effects of diurnal degus

One of the dominant species of small mammal at our site is the degu (*Octodon degus*), a moderately large (120–150 g) diurnal hystricognath rodent. Degus generally are folivorous (Meserve 1981) and were not expected to forage in our trays. To confirm that they were not influencing the diurnal patterns attributed to birds we placed a sub-set of trays in experimental degu exclusion plots that had been maintained since 1989 (10 years from the beginning of this study, Meserve et al. 1993, 1995, 1996, 2003). A rmANOVA on these data showed that diurnal foraging was similar in control and degu exclusion trays (11.71 vs 11.73 g remaining; $MS = 13.07$, $F_{1,3} = 0.18$, $P > 0.70$). We interpret this to mean that birds, which had access to all foraging trays, depleted seed resources to lower levels than degus. We tested this with the “caged” foraging trays from which birds were excluded as described above. If birds consistently deplete resources to lower levels than degus we would expect the statistical interaction between tray

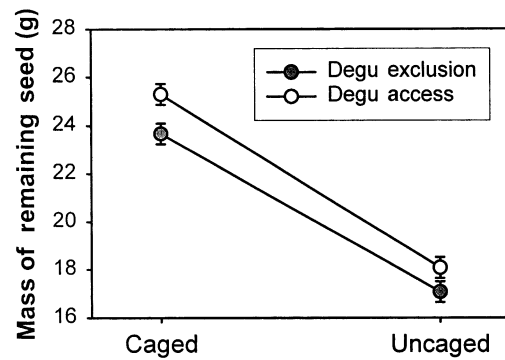


Fig. 1. Comparison of foraging efficiency by small mammals (caged trays) and small mammals plus birds (uncaged trays) where degus are present versus where they have been excluded. These data represent only diurnal foraging efforts. The parallel relationship ($P > 0.31$) indicates that the presence or absence of degus has little effect on foraging.

type (caged vs uncaged) and degu treatment (present vs absent) to be non-significant, and this was the case ($MS = 37.32$, $F_{1,56} = 1.21$, $P > 0.31$; Fig. 1; power to detect a difference of 1 was > 0.96 , calculated using the University of Iowa Java script power calculator (www.stat.uiowa.edu/~rienth/Power/index.htm/). Indeed, seed removal from caged trays was low both at sites with and without degus, suggesting that these folivorous rodents did not forage for seed in these trays. The greater removal of seed from caged trays in the exclusion of degus likely was from other small mammals, which forage more extensively when degus have been removed (Kelt et al. in press). Thus, we interpret diurnal seed removal as representing avian activity, and nocturnal seed removal as that of small mammals. Although degu exclusion does not impact foraging levels overall, trays in degu exclusions are subject to greater levels of nocturnal foraging (Kelt et al. in press), so we exclude these from subsequent analyses.

Results

An analysis with all data demonstrated that seed removal was significantly greater diurnally than nocturnally ($F_{1,3} = 231$, $P < 0.0006$; Fig. 2). Interactions between time of day and season ($F_{1,3} = 196$, $P < 0.0008$) further emphasized the distinction between these two foraging periods; this likely reflected seasonal changes in avian populations, which increase substantially at our site with the arrival of winter migrants (pers. obs.). Consequently we analyzed these two time periods separately in all subsequent analyses.

Patterns of nocturnal seed removal in uncaged trays (Table 1) were similar to those reported elsewhere (Kelt

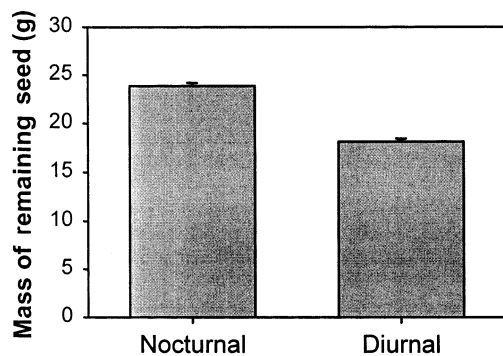


Fig. 2. Comparison of foraging efficiency by nocturnal and diurnal foragers. Significantly more seed are removed during the day than at night.

et al. in press). Seed removal changed significantly across 2 and 1/2 years of study (Fig. 3a), generally tracking population sizes (Kelt et al. in press). Diurnal seed removal was significantly greater in winter than summer (Fig. 3c), although this difference was not large (mean 22.9 vs 24.2 g seed remaining). Seed removal was not significantly influenced by lunar phase (Fig. 3e), although it was affected by shrub cover (Fig. 3g); diurnal consumers removed on average 20% more seed under shrubs than in open microhabitats, although this was presented only in the third year of study (Fig. 4e) when small mammal numbers were highest (Kelt et al. in press).

Diurnal seed removal also varied across years (Fig. 3b), although the pattern deviated from that observed nocturnally. Both diurnal and nocturnal seed removal was lowest in 2000, but whereas nocturnal removal was greatest in 2001, diurnal seed removal was much greater in 1999 than any other year. In other respects as well, patterns of diurnal consumption were quite different from those observed nocturnally. Unlike the latter,

diurnal consumption was highly seasonal ($MS = 29719$, $F_{1,3} = 410$, $P < 0.0003$), with over 2 and 1/2 times as much seed removal in the winter than in summer (Fig. 3d). Somewhat inexplicably, diurnal consumers displayed a trend towards greater foraging during the new lunar phase (Fig. 3f; $MS = 501$, $F_{1,23} = 14$, $P < 0.06$), although this was only true in 1999 (Fig. 4b). More surprising was the significant interaction between season and lunar phase (Fig. 4d; $MS = 1909.43$, $F_{1,3} = 50.05$, $P < 0.006$); diurnal seed removal was greater during the full lunar phase in summer, but in winter this was greatest under the new lunar phase. Finally, diurnal consumers displayed no preference for shrub or open microhabitat (Fig. 3h; $MS = 6.16$, $F_{1,0.14} = 32.5$, $P > 0.62$). As with nocturnal consumption, diurnal foragers elicited no readily interpreted and biologically important 3-way interactions.

In summary, three major patterns stand out in these analyses. First, seed removal was consistently greater diurnally than nocturnally. This was true in all seasons and all years. Second, although both diurnal and nocturnal seed removal was greater in winter, the magnitude of this change was substantially greater diurnally. Finally, diurnal consumers were not greatly affected by microhabitat, whereas nocturnal consumers clearly preferred protected (shrub) sites.

Discussion

Although research has emphasized the role of small mammals as seed predators in most arid regions, birds are at least seasonally important in the Monte Desert of Argentina (Lopez de Casenave et al. 1998), and may be more important overall than has been generally recognized. Our results suggest a much greater role for diurnal than nocturnal seed consumers at Fray Jorge (Kelt et al. in press), although the former are highly

Table 1. Results of separate repeated measures mixed-model analysis of variance on small mammals and birds at Fray Jorge, Chile. Analyses for each taxon were identical, so the salient results are presented simultaneously to simplify comparison.

Source	Mammals				Birds		
	DF	MS	F value	Pr < CF	MS	F value	Pr < CF
Year	2	7845.13	156.59	<0.0001	1900.01	13.93	0.0053
Season	1	1113.06	19.68	0.0205	29719.00	410.23	0.0003
Moon	1	7.07	0.67	0.5372	501.21	14.02	0.0519
Microhabitat	1	1718.92	59.72	0.0042	6.16	32.54	0.6290
Year × Season	1	363.51	2.58	0.2066	1155.31	4.88	0.1141
Year × Moon	2	42.38	1.59	0.2790	1799.08	27.71	0.0009
Season × Moon	1	1264.29	36.75	0.0088	1909.43	50.05	0.0058
Year × Microhabitat	2	1567.64	26.46	0.0009	60.52	1.65	0.2631
Season × Microhabitat	1	88.28	1.50	0.3079	0.89	0.07	0.8067
Moon × Microhabitat	1	3.44	0.19	0.6643	8.42	0.32	0.5832
Year × Season × Moon	1	1077.68	44.76	<0.0001	527.53	22.03	<0.0001
Year × Season × Microhabitat	1	43.92	1.82	0.1775	6.51	0.27	0.6024
Year × Moon × Microhabitat	2	48.46	2.01	0.1348	68.73	2.87	0.0578
Season × Moon × Microhabitat	1	266.42	11.07	0.0009	37.32	1.56	0.2126

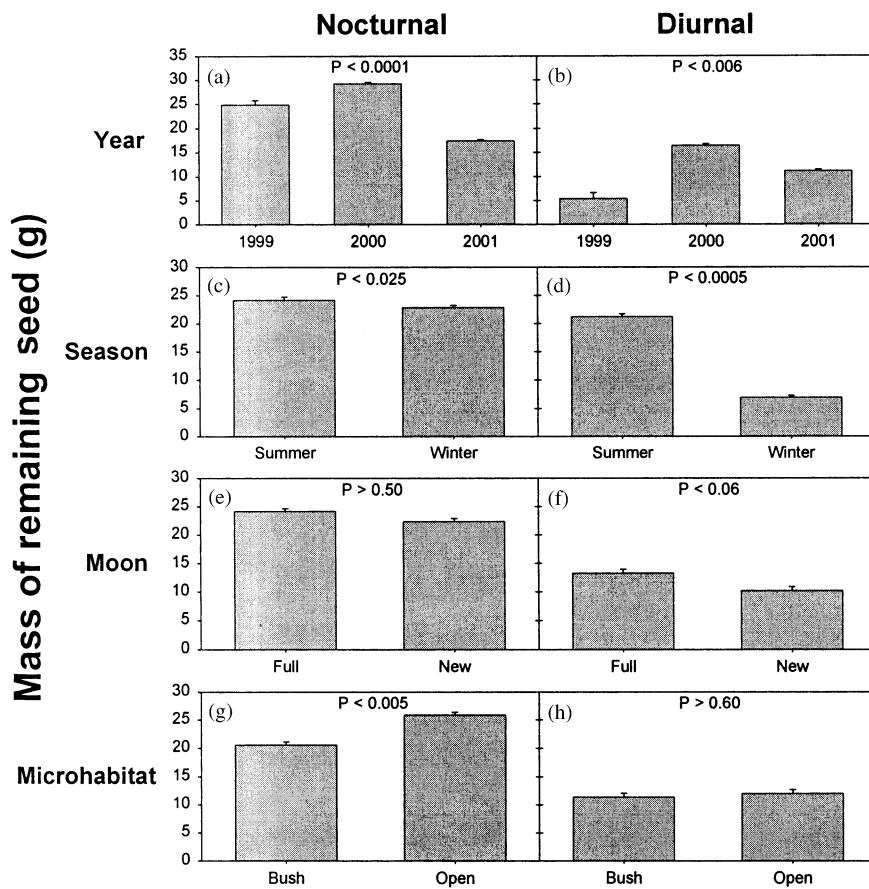


Fig. 3. Seed removal by nocturnal (left panels) and diurnal (right panels) consumers for all main effects. Probability values (Table 1) are provided to simplify comparison across taxa.

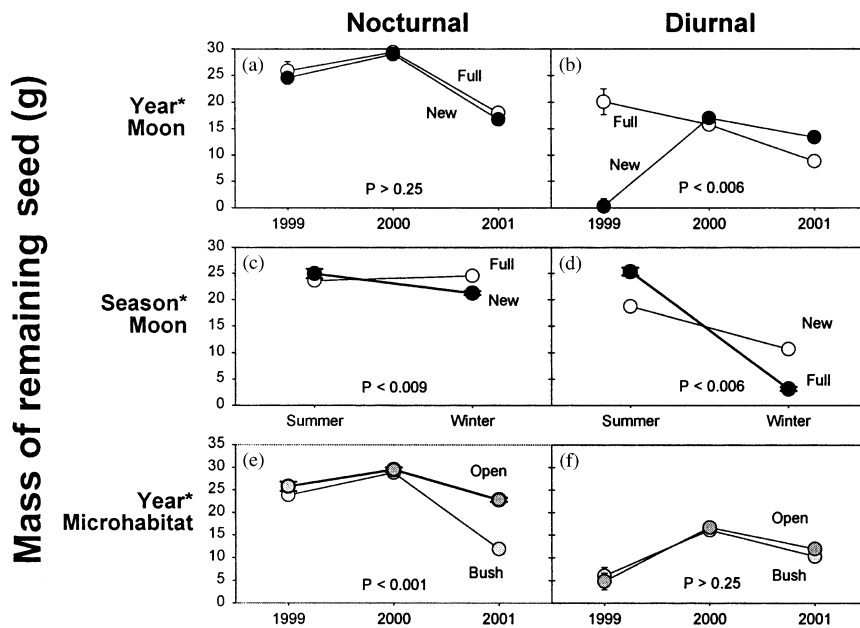


Fig. 4. Foraging efficiency for small nocturnal (left panels) and diurnal (right panels) seed consumers. Presented is the mass of seed remaining after a foraging period for each two-way interaction for which at least one taxon was statistically significant (Table 1). Probability values are presented for ease of comparison across taxa.

seasonal. Because small mammals at Fray Jorge are largely nocturnal (degus are an exception, but were shown to be unimportant seed consumers) we believe that the diurnal foraging recorded here was largely by birds. The seasonality of this pattern supports this interpretation; many of the birds at our site leave in the warmer summer months, which they spend in the Andean prepuna or in Patagonia. Fray Jorge boasts a relatively diverse avifauna, but from roughly a dozen granivorous species only a few consistently foraged from our trays, most notably *Diuca* and *Zonotrichia*.

Birds were superior (i.e. removed more seed) in all habitats and in all seasons; we observed both *Diuca diuca* and *Zonotrichia capensis* to forage extensively in experimental trays. Small mammals that utilized trays included primarily *Akodon ollivaceus* and *Phyllotis darwini* both species were abundant on the grids during these studies, based on live trapping that was conducted in these grids (unpubl.). These results are dramatically different from those reported by Brown et al. (1997) for the Negev Desert, and Parmenter et al. (1984) in North American deserts. In the Negev, nocturnal small mammals (gerbils) were more efficient foragers (lower GUDs) than crested larks in every habitat and month studied. As in our study, gerbils in the Negev foraged more intensively under shrub cover than in the open. Larks, however, displayed the opposite pattern to our birds, with more efficient foraging in open microhabitats. Brown et al. (1997) explained this with reference to Lima's (1992, 1993) reviews of escape tactics in birds, suggesting that shrub cover might constrain escape opportunities. Birds at Fray Jorge evidently were not similarly constrained. In North America, Parmenter et al. (1984) applied two approaches to measuring granivory by rodents, birds, and ants. Salient results were that rodents were energetically more important than birds in three desert regions (Sonoran, Mojave, Intermountain), but birds were equally or more important in the fourth (Chihuahuan). Thus, regional variation in the relative importance of these two groups might be expected, and further studies in Chile and elsewhere in South America may uncover similar heterogeneity.

These results beg a number of interesting ecological questions. Are these observations real or do they reflect some underlying bias inherent to our study design? Why are birds such effective granivores at our site? If seeds are so readily consumed by birds, why have small mammals generally failed to assume a granivorous trophic strategy? What characteristic of these birds makes them particularly adept at finding and consuming food resources? Why aren't birds at our site responding to shrub cover?

We believe these observations reflect real differences in foraging tactics by birds and small mammals at our study site. A detailed analysis of diet in small mammals from this site (Meserve 1981) documented only two

species to be largely granivorous (*Oligoryzomys* and *Phyllotis*), and *Phyllotis* now is understood to be much more omnivorous than initially believed (P. L. Meserve, pers. obs.). Thus, the Chilean mammal fauna simply lacks an assemblage of seed specialists, and the one that is present (*Oligoryzomys*) exhibits irruptive population dynamics in response to moisture pulses (e.g. El Niño; Meserve and Le Boulengé 1987). This species was not present at our study site in 1999 or 2000, and was not common in 2001. In contrast, the birds that occur here include two of "the most conspicuous granivorous birds" of mediterranean Chilean shrublands (*Zonotrichia capensis* and *Diuca diuca*, Lopez-Calleja 1995:73), as well as a number of other species that are at least opportunistically granivorous, such as ground doves (e.g. *Columbina picui*), Sierra finches (e.g. *Phrygilus alaudinus*, *P. fruticeti*, *P. gayi*) a tinamou (*Nothoprocta perdicaria*), and introduced quail (*Callipepla californica*) (Kelt et al. in press).

Why have birds opted for a granivorous trophic strategy in northern Chile, and why have mammals not done so? Stafford Smith and Morton (1990) argued that regional predictability of precipitation could lead to a cascade of ecological effects in arid systems. Where precipitation is not predictable from year to year, plants respond by producing large numbers of small seeds. In contrast, where precipitation is predictable from year to year the likelihood of a given seed finding a good site for germination is greater, and plants can opt to produce smaller numbers of larger seeds. In the former scenario, we would not expect mammals to emphasize granivory, as small seeds are costly to handle relative to the energetic return. Birds, on the other hand, are much more vagile and can adopt a nomadic strategy of capitalizing on local pulses of seeds. Additionally, handling costs may be lower for birds than for small mammals foraging on seed; the former generally crack the hull in their mouth and extract the seed, but the latter have to physically manipulate the seed as they chew through the hull. Consequently, in deserts with unpredictable precipitation we would expect greater levels of granivory by birds than mammals. We have argued (Kelt et al. in press) that this explanation pertains well to the coastal deserts of Chile and Peru, where mean annual precipitation is very low and much more unpredictable than most other deserts (Kelt et al. in press).

Finally, why are seed-eating birds not influenced by shrub cover at our site? Foraging in both microhabitats was remarkably similar, indicating that the potential cost relative to the energetic return was not greatly different in these habitats. It is possible that different species are foraging under shrubs and in open habitats, and further work aimed at quantifying habitat use (sensu Pulliam and Mills 1977) would be useful in this system. Our observations of *Zonotrichia* and *Diuca* foraging both under shrubs and in open microhabitats,

however, would undermine an argument that shrub and open foraging were by different taxa. North American seed-eating sparrows evidently co-exist by segregating either by microhabitat or distance from cover (Pulliam and Mills 1977), and Lima (1992, 1993, Lima et al. 1987) has argued that possibility of escape from attack may be as important in microhabitat selection by birds as is avoidance of attack. Birds face different threats of predation in shrub and open habitats, with terrestrial predators (e.g. foxes, felids) in the former and aerial predators (e.g. raptors) in the latter. At Fray Jorge the aerial predator guild is much more diverse than the terrestrial guild (Jaksic et al. 1997). Common aerial predators include three species of owls (burrowing owl (*Speotyto cunicularia*), great-horned owl (*Bubo virginianus*), barn owl (*Tyto alba*), and two species of hawk (bay-winged hawk (*Parabuteo unicinctus*), and red-backed hawk (= Harris' hawk; *Buteo polyosoma*). In contrast, common terrestrial predators include only the culpeo fox (*Pseudalopex culpaeus*). Consequently, foraging in open sites would appear to be more dangerous than under shrubs. On the other hand, Fray Jorge lacks highly agile aerial predators such as accipiter hawks, and the existing aerial predator guild may not be as threatening to small birds as that in North American aridlands. Thus, the threat of predation might be relatively low at our site; at the least, it may not differ in open and shrub microhabitats. Understanding microhabitat selection and behavioral responses to predation would be particularly useful for interpreting foraging activities in this avifauna. Finally, the limited microhabitat selection could reflect the high energetic return associated with foraging in these artificial trays, either due to the concentration of seeds in trays or the large size of oat seeds relative to other seeds in this system (Brown et al. 1997, Garb et al. 2000). Either factor could lead birds to forage more extensively than they otherwise might, and further research to evaluate the influence of seed type and size, as well as starting density, would be highly informative.

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