



Seed removal by small mammals, birds and ants in semi-arid Chile, and comparison with other systems

Douglas A. Kelt^{1*}, Peter L. Meserve² and Julio R. Gutiérrez³

¹Department of Wildlife, Fish, & Conservation Biology and Graduate Group in Ecology, University of California, CA, ²Department of Biological Sciences, Northern Illinois University, DeKalb, IL, USA and ³Departamento de Biología and Centro de Estudios Avanzados en Zonas Áridas, Universidad de La Serena, Casilla, La Serena, Chile

ABSTRACT

Aim This study aims to evaluate the relative importance of birds, small mammals, and ants as seed predators at a semi-arid site in northern Chile.

Location Northern Chile, in Parque Nacional Bosque Fray Jorge (30°41' N, 71°40' W, c. 80 m elevation).

Methods We studied the relative abilities of birds, small mammals, and ants to find and remove millet seeds either singly (i.e. background seed removal) or in bulk. Single seeds were set in shallow depressions in Plexiglas trays which were established in long and arbitrary transects, and were available either to birds (diurnally) or small mammals (nocturnally) or were covered by hardware cloth and therefore available only to ants. Bulk removal was evaluated with seeds in Petri dishes that also were established in long and arbitrary transects, and trays were either open diurnally (birds) or nocturnally (small mammals); a third set of trays was covered with hardware cloth cages to excluded vertebrates, and ants were given access to Petri dishes with twigs that were arranged across the edge of the dishes. All experiments lasted four days and nights, and trays and dishes were checked and replenished as needed in the morning and evening. In the former study vertebrate consumption was determined as the mean number of seeds removed from trays (within a given transect) minus the number removed from ant-only trays. Because ants were rarely seen in vertebrate access Petri dishes, however, we did not correct consumption there. Treatments were compared using repeated measures mixed model analysis of variance. In addition to evaluating patterns within this community, we compared our results against those obtained in similar studies in various arid regions.

Results Diurnal seed consumption was significantly greater than nocturnal seed consumption, which in turn was significantly greater than consumption by ants. Diurnal consumption was highly seasonal, evidently corresponding to the seasonal arrival and departure of migratory birds. In general, South American sites exhibit much lower levels of seed predation than sites in the northern hemisphere, but removal at our site appears to be much greater and more strongly avian-dominated than at other sites in South America. Our results are consistent with predictions based on a hypothesis relating precipitation to seed predictability.

Main conclusions Both birds and small mammals were much more important seed consumers at our site than elsewhere in South America, whereas ants have been relatively unimportant at all South American sites studied to date. Although the dominant seed consumers differ across sites, overall levels of seed removal appear similar in South America and Australia, and substantially lower than reported from sites in the northern hemisphere and Africa.

Keywords

Granivory, deserts, South America, mammals, birds, ants, seed trays.

*Correspondence: Douglas A. Kelt, Associate Professor of Wildlife Biology, Department of Wildlife, Fish, & Conservation Biology, University of California, Davis One Shields Avenue Davis, CA 95616, USA.
E-mail: dakelt@ucdavis.edu

RESUMEN

Objetivo El objetivo de este estudio es evaluar la importancia relativa de aves, pequeños mamíferos y hormigas como depredadores de semillas en un sitio semiarido del norte de Chile.

Localidad En el norte de Chile, en el Parque Nacional Bosque Fray Jorge (30° 41' N, 71° 40' W, 80 m.s.n.m.).

Métodos Estudiamos las capacidades relativas de aves, pequeños mamíferos y hormigas para encontrar y remover semillas de mijo tanto individualmente (es decir, remoción de la semilla del fondo) como en paquetes. Las semillas individuales se fijaron en depresiones superficiales en bandejas de Plexiglás que fueron puestas en transectos largos y arbitrarios, y que estaban disponibles para las aves (en el día) o los pequeños mamíferos (en la noche), o fueron cubiertas por una malla tipo harnero y por lo tanto disponibles solamente para las hormigas. La remoción de paquetes fue evaluado con semillas en placas Petri que también fueron establecidas en transectos largos y arbitrarios, y las bandejas fueron abiertas durante el día (para aves) o durante la noche (para pequeños mamíferos); un tercer grupo de bandejas se cubrió con jaulas de malla tipo harnero para excluir a los vertebrados, y a las hormigas se les dió acceso a las placas Petri con ramitas que se pusieron en los bordes de las placas. Todos los experimentos duraron cuatro días y cuatro noches, y las bandejas y las placas se revisaron y reabastecieron de acuerdo a lo necesario en la mañana y la tarde. En el estudio anterior el consumo por los vertebrados se determinó como el número promedio de las semillas removidas de las bandejas (dentro de un transecto) menos el número removido de las bandejas con acceso a las hormigas solamente. Debido a que las hormigas fueron raramente vistas en las placas Petri con acceso a los vertebrados, sin embargo, no corregimos el consumo allí. Los tratamientos se compararon usando el modelo mixto de análisis de varianza para medidas repetidas. Además, para evaluar los patrones dentro de esta comunidad, comparamos nuestros resultados con otros obtenidos en estudios similares en varias regiones áridas.

Resultados El consumo de semillas durante el día era significativamente mayor que el de la noche, lo que en cambio fue significativamente mayor que el consumo por las hormigas. El consumo diurno fue altamente estacional, lo que evidentemente corresponde a la llegada y salida estacional de aves migratorias. En general, las localidades sudamericanas exhiben niveles de depredación de semillas que son mucho más bajas que en sitios del hemisferio norte, pero la remoción en nuestro sitio parece ser mucho mayor y dominado por aves que en otras localidades de América del sur. Nuestros resultados son consistentes con las predicciones basadas en una hipótesis que relaciona la precipitación con la predicción de semillas.

Conclusiones principales Tanto las aves como los pequeños mamíferos fueron consumidores de semillas mucho más importantes en nuestro sitio que en otros sitios de Sudamérica, mientras que las hormigas han sido relativamente poco importantes en todos los sitios sudamericanos estudiados hasta la fecha. Aunque los consumidores de semillas dominantes difieren entre sitios, los niveles totales de remoción de semillas parecen similares en América del Sur y Australia, y substancialmente más bajos que los documentados para sitios del hemisferio norte y África.

INTRODUCTION

Seeds are key food resources for many animals, especially ants, birds (e.g. finches and sparrows), and small mammals. Numerous studies have documented post-dispersal seed predation by these taxa (Janzen, 1971; Louda, 1989; Crawley, 1992; Hulme, 1998), and several have documented substantial impacts on plant communities. Seed consumption by rodents can limit regeneration (Hoffmann *et al.*, 1995; Hulme, 1996; Campbell & Atkinson, 1999; Edwards & Crawley, 1999; Maron & Simms, 2001) and have important effects of plant community composition and structure (e.g. Brown & Heske, 1990; Campbell & Atkinson, 1999; Howe & Brown, 2000, 2001). Ants may be important consumers or dispersers of seeds as well (e.g. Andersen & Ashton, 1985; Bond & Breytenbach, 1985; Andrew, 1986), and in some regions appear to rival small mammals as seed predators (Holmes, 1990), although their actions often result in secondary dispersal rather than predation (Hulme, 1998). Fewer studies have documented important effects of birds on post-dispersal seed consumption (Hulme, 1998), although in some instances their activities have been shown to be substantial (e.g. Genard & Lescourret, 1985; Okamoto, 1994; Guo *et al.*, 1995; Marone *et al.*, 2000), and recent work has suggested indirect facilitation among these three foraging groups in the Chihuahuan Desert of Arizona (Thompson *et al.*, 1991).

Early studies in North America showed ants and small mammals, especially heteromyid rodents, to be the principal seed consumers (Brown & Davidson, 1977; Brown *et al.*, 1979, 1986). In contrast, Mares & Rosenzweig (1978) reported ants to be the dominant seed predators in Argentina, where they found no wholly granivorous mammals. Although patterns in Israel were similar to those observed in North America (Abramsky, 1983), such was not the case in South Africa (Kerley, 1991) and Australia (Morton, 1985; Predavec, 1997). Early conclusions were that granivory in Northern Hemisphere deserts was dominated by small mammals, whereas in Southern Hemisphere deserts this role was occupied by ants; birds were thought to be relatively unimportant in desert systems globally (Mares & Rosenzweig, 1978; Abramsky, 1983; Morton, 1985; Kerley, 1991; Kerley & Whitford, 1994).

Recent work has questioned this paradigm, however. Birds are at least as energetically important as small mammals in the Chihuahuan Desert on North America (Parmenter *et al.*, 1984), and investigations in the Southern Hemisphere have suggested that birds are more important than previously believed. In temperate Africa, birds in miombo habitat dominated seed removal from Petri dishes, followed by ants and then small mammals (Linzey & Washok, 2000). At the Ñacuñán Biosphere Reserve in Argentina, ants were trivial granivores in winter but were significantly more important than mammals or birds during summer (Lopez de Casenave *et al.*, 1998). Under shrub canopies, ants were more important than birds, which in turn were more substantial seed predators than small mammals; away from shrub cover, however, all

three taxa were similar in their ability to find and capitalize on artificial seed resources. Further south, however, Folgarait & Sala (2002) reported that Patagonian birds were much less effective than insects or small mammals at capitalizing on artificial seed provisions. In central (Mediterranean) Chile the relative impact of ants, birds, and small mammals differed by habitat (Vásquez *et al.*, 1995). In dense matorral these authors reported similar results to Lopez de Casenave *et al.* (1998), with seed removal greatest by ants, then birds, and least by small mammals. In sparse matorral, however, birds and ants removed similar amounts of seed, and both were superior to small mammals. Finally, the ant faunas in the Monte Desert have more species and broader foraging periods than those in Chile (Medel & Vásquez, 1994). Importantly, seed removal in the Monte Desert was *c.* four times that in Chilean sites, suggesting that ants are relatively unimportant seed consumers in Chilean arid regions.

We have been studying the ecology of a semi-arid site in northern Chile for the past 14 years, emphasizing the relative importance of biotic (e.g. competition vs. predation) and abiotic effects on ecological processes. Our site is strongly influenced by El Niño Southern Oscillation (ENSO) events, which greatly increase precipitation in northern Chile about every 4–6 years (Jaksic, 2001). Although this site occurs south of the hyperarid Atacama Desert, annual variation in rainfall is high (CV = 10.2 at La Serena *c.* 100 km from our site) and mean precipitation is low ($X = 110$ mm). Most herbaceous plants at our study site produce very small seeds (Gutiérrez & Meserve, 2003). Perhaps reflecting the limited energy source provided by small seeds, there is only one granivorous rodent in northern Chile (*Oligoryzomys longicaudatus*) and it exhibits irruptive population dynamics that correspond with El Niño events (Meserve & Le Boulengé, 1987; Meserve *et al.*, 2003; see also Murúa *et al.*, 2003). Consequently, we predicted that seed consumption at our site would be dominated by birds and possibly ants, with mammals being relatively less important. We studied the role of these three groups of seed predators over multiple years and seasons, and under shrub cover as well as in open microhabitats. This constitutes the first such work for this region, only the second in South America, and was designed to be comparable with similar research being pursued in Argentina (Marone *et al.*, 2000).

METHODS

We conducted our research at Parque Nacional Bosque Fray Jorge, a *c.* 10,000 ha park located on the coast of northern Chile, *c.* 400 km N Santiago and 100 km S La Serena (30°41' N, 71°40' W, *c.* 80 m elevation). Descriptions of the park may be found in Meserve *et al.* (1996, 1999, 2003). Summers are warm and dry, winters mild. Our work was conducted in the Quebrada de las Vacas, which is dominated by coastal and forested steppe chaparral ('matorral estepario costero' and 'matorral estepario boscoso'; Gajardo, 1993); major shrub species are *Porlieria chilensis*, *Proustia pungens*, and *Adesmia bedwellii* (Gutiérrez *et al.*, 1993).

The small mammal community includes ten species representing two orders, three families, and a diverse array of trophic strategies. Only a subset of these is sufficiently common to be well studied. The degu [*Octodon degus* (Molina, 1782); herbivore], Darwin's leaf-eared mouse [*Phyllotis darwini* (Waterhouse, 1837); herbivore-granivore], and the didelphid elegant fat-tailed opossum [*Thylamys elegans* (Waterhouse, 1839); insectivorous] persist in the thorn scrub habitat through all years of study. The olive grass mouse [*Akodon olivaceus* (Waterhouse, 1837); omnivore] generally is present but exhibits strong oscillations during and following El Niño events. Some species disappear from thorn scrub habitat in dry years; these include the long-tailed pygmy rice rat [*Oligoryzomys longicaudatus* (Bennett, 1832); granivore] and the long-haired grass mouse [*Abrothrix longipilis* (Waterhouse, 1837); insectivore]. Two other species, Bennett's chinchilla rat (*Abrocoma bennetti* Waterhouse, 1837; herbivore) and the moon-toothed degu (*Octodon lunatus* Osgood, 1943; herbivore), are not commonly captured and are not considered here.

The avifauna at Fray Jorge is moderately diverse but remains poorly studied ecologically (but see Cornelius *et al.*, 2000). Of relevance to the present study, it includes a number of primarily granivorous taxa (Table 1), the most abundant of which are the rufous-collared sparrow [*Zonotrichia capensis* (Statius Muller) 1776] and the common diuca finch [*Diuca diuca* (Molina) 1782]. Considered to be 'the most conspicuous granivorous birds of the Chilean Mediterranean scrubland' (Lopez-Calleja, 1995), these birds are highly granivorous, and

both species were observed to be the most common visitors to our feeding trays. While *Zonotrichia* appears to feed opportunistically on the most abundant seeds and insects, *Diuca* is an obligate granivore (Lopez-Calleja, 1995).

The Andes may be an important barrier to dispersal by ants, as faunas on either side of this range are notably different. In particular, the fauna of northern Chile is much less diverse than that of Argentina (Medel & Vásquez, 1994; Medel, 1995). Although a dozen or more species may occur in the vicinity of the park (based on maps in Snelling & Hunt, 1975), Medel & Vásquez (1994) reported only three species (*Araucomyrmex goetshi*, *Brachomyrmex giardii*, and *Solenopsis gayi*) from the region, and our observations failed to add any taxa.

In 1989 we established a series of biotic exclosures at Fray Jorge. Some of these excluded all predators, whereas others excluded only the degu, a dominant and relatively abundant rodent. Most of the research reported herein was conducted outside of these experimental plots. Because degus are diurnal, however, we placed some experimental foraging stations in degu exclosures to confirm that diurnal seed removal was predominantly by birds (see below).

We applied two approaches to evaluate the relative importance of birds, ants, and terrestrial small mammals as seed predators at our site. We repeated each of these experiments in summer and winter over multiple years, and evaluated both spatial and temporal patterns in seed consumption. Additionally, small mammal numbers changed dramatically during the course of this research; they were low in 1999, very low in 2000, and then high in 2001 (Meserve *et al.*, 2003).

Taxon		Ñacuñan	Fray Jorge
Tinamiformes, Tinamidae			
<i>Eudromia elegans</i>	Elegant crested tinamou	Yes	
<i>Nothoprocta perdicaria</i>	Chilean tinamou		Yes
Galliformes, Odontophoridae			
<i>Callipepla californica</i>	California quail		Yes
Columbiformes, Columbidae			
<i>Colombia livia</i>	Rock dove	Yes	
<i>Colombia maculosa</i>	Spot-winged pigeon	Yes	
<i>Columba araucana</i>	Chilean pigeon		Yes
<i>Columbina picui</i>	Picui ground dove		Yes
<i>Zenaida auriculata</i>	Eared dove	Yes	Yes
Passeriformes, Fringillidae			
<i>Diuca diuca</i>	Common diuca-finch	Yes	Yes
<i>Phrygilus alaudinus</i>	Band-tailed Sierra-finch		Yes
<i>Phrygilus carbonarius</i>	Carbonated Sierra-finch	Yes	
<i>Phrygilus fruticeti</i>	Mourning Sierra-finch		Yes
<i>Phrygilus gayi</i>	Gray-hooded Sierra-finch		Yes
<i>Poozpiza torquata</i>	Ringed warbling-finch	Yes	
<i>Poozpiza ornata</i>	Cinnamon warbling-finch	Yes	
<i>Salatricula multicolor</i>	Many-colored chaco-finch	Yes	
<i>Sicalis luteola</i>	Grassland yellow-finch	Yes	
<i>Zonotrichia capensis</i>	Rufous-collared sparrow	Yes	Yes
<i>Carduelis barbata</i>	Black-chinned siskin		Yes
<i>Carduelis magellanica</i>	Hooded siskin	Yes	

Table 1 Granivorous bird species recorded from two sites in southern South America. Ñacuñan Biosphere Reserve (34°02' S) is located in Mendoza Province, in the Monte Desert. Parque Nacional Bosque Fray Jorge is located at a similar latitude (30°38' S) in the semi-arid region just south of the Atacama Desert. Only *Diuca diuca* and *Zonotrichia capensis* were observed to forage from our experimental trays

Experiment 1 – bulk seed removal

To estimate the relative abilities of birds, ants, and small mammals to find and remove dense seed resources, we established arbitrary transects (e.g. having neither a fixed starting point, fixed inter-station distances, or an *a priori* bearing to follow) with experimental stations placed every 5–10 m. At each station we provisioned two plastic Petri dishes (60 mm diameter \times 15 mm height) with 5 g of millet seed [measured to 0.01 g with a portable field balance (Ohaus Navigator Model N12120, Ohaus Corporation, Pine Brook, NJ, USA)]. Additional packets of 5 g of millet were added as existing stores were depleted. One Petri dish in each set was left open at night but closed during the day, allowing access by nocturnal ants and small mammals but not birds, while the second was closed at night and open during the day, providing access to diurnal ants and to birds, but not to nocturnal mammals. Ant consumption initially was evaluated with a third dish enclosed in a box made of hardware cloth to exclude birds and small mammals, but these proved ineffective at excluding vertebrates. We subsequently evaluated the influence of ants with larger cages that we placed over Petri dishes to exclude birds and small mammals. These ant exclusions were very effective, but were employed only during the winter and summer of 2001, whereas bird and mammal accessible trays were studied over five seasons from winter 1999 through winter 2001. Ant-only dishes were provisioned with small sticks to allow ready access to ants. We rarely observed ants in open Petri dishes and those that were encountered generally were walking in circles and appeared unable to escape the Petri dish. Consequently we do not correct for seed removal by ants when evaluating bird and rodent trays.

Experiments were conducted for four consecutive days and nights. Trays that were disrupted by animals or wind were cleaned and re-provisioned with 5 g of seed; these trays consequently were operational for fewer than four days and nights, although all trays were present in the field for the same duration. We summed the mass of seed that was consumed across the experiment and divided by the number of 12-h periods that the tray was open to obtain a mass consumed per 12-h period.

Because we had varying numbers of field assistants in different seasons, the number of stations we could establish also varied; we placed a line of thirty-five stations (two dishes per station) in winter 1999, two lines of ninety stations in summer 2000, two lines of 120 stations in winter 2000 (including twenty stations in degu exclusions), two lines of 138 stations in summer 2000 (including eleven stations in degu exclusions), and one line of 145 stations in winter 2001 (including twenty-five stations in degu exclusions).

We analysed ant-only trays separately from open trays. We compared seasonal foraging by ants with a *t*-test assuming unequal variances. We tested for the influence of diurnal degus in open trays by placing a subset of trays in degu enclosures. Consumption in these grids was compared with that in control (degu access) trays using a nested analysis of variance with

season, time of day, degu access, and plot (i.e. degu enclosures, nested within degu access to account for any differences between enclosures) as independent variables and mean 12-h consumption the dependent variable. Although overall seed consumption was not significantly different in degu access and degu exclusion trays ($MS = 0.29$, $F = 0.08$, $P > 0.80$), the pattern of nocturnal to diurnal consumption was reversed in these treatments, with greater consumption diurnally in control trays (1.66 ± 0.04 g vs. 1.54 ± 0.04 g), but nocturnally in degu exclusions (1.59 ± 0.13 g vs. 1.75 ± 0.13 g). While this interaction was not significant ($MS = 1.15$, $F = 1.05$, $P > 0.55$), this trend for greater nocturnal consumption in the absence of degus likely reflects compensatory feeding by *Akodon* and *Phyllotis*, which are more abundant in degu exclusion plots than in controls; because of this difference in nocturnal foragers, we analysed only control trays hereafter. Nocturnal and diurnal equal-access trays were compared with a three-way mixed-model analysis of variance, with year, season, and time of day treated as independent variables and mean 12-h consumption the dependent variable. Stations (with one nocturnal and one diurnal Petri dish) were treated as random effects, nested within year and season. A season \times time of day interaction would be particularly interesting, as diurnal consumption likely reflected foraging by birds, and the avifauna at our site changes markedly between summer and winter (pers. obs.). Data were square root transformed to meet assumptions of normality.

Experiment 2 – estimation of background seed removal

Because bulk seed removal may be subject to a variety of local contingencies and consequently may provide a very coarse estimator of seed consumption rates in nature, we also evaluated the ability of seed predators to find isolated seeds in the environment. To do this, we set single millet seeds in shallow depressions drilled in small (*c.* 1×4 cm) Plexiglas trays. These trays were established in pairs; one tray was covered by hardware cloth to exclude birds and small mammals, while the second tray was open and accessible by all potential seed consumers. Trays were placed in the field in long transects with 3–10 m separation between trays, and checked at dawn and dusk for four consecutive days. Transects were established from arbitrary points in the study region, and not according to any *a priori* distribution, and trays were placed either under shrubs or in the open. Because of the density of vegetation, however, most trays were under or adjacent to shrubs; all trays were readily accessible, however, by all taxa under study. Seeds were replaced as needed, and the number of seeds removed per transect per 12-h time period (square-root transformed) was recorded. As with other analyses, consumption from undisturbed ant-only trays was assumed to be by ants, and from undisturbed from open trays by either mammals (nocturnal) or birds (diurnal); because the latter also were accessible to ants, however, we subtracting the number of seed removed from ant-only trays to estimate seed

removal by vertebrates alone. Disturbed trays were re-provisioned as needed.

We conducted a preliminary study in 1999 to evaluate the impact of biotic exclusions (control, degu and/or predator exclusion) on single seed removal. These data were analysed with a nested mixed-model ANOVA using the number of seeds removed per transect per 12-h time period as the dependent variable, and biotic treatments and time of day as independent variables. Treatment plots ($N = 2$ for each treatment, eight plots total) were nested within biotic treatments. These analyses showed that significantly fewer seeds were removed from control plots than from any of the three biotic treatments (mean \pm SD, Control = 0.27 ± 0.38 ; Degu = 0.40 ± 0.57 ; Predators = 0.63 ± 1.36 ; Predators and Degus = 0.49 ± 0.64 ; MS = 0.18, $F = 6.65$, $P < 0.03$), in contrast to the higher expectation if degus were consuming these seeds. Moreover, nocturnal consumption was greater than diurnal consumption ($0.18 + 0.32$ vs. $0.74 + 1.13$; MS = 0.79, $F = 16$, $P < 0.005$), suggesting that compensatory foraging by *Akodon* and *Phyllotis* (see also Yunker *et al.*, 2002; Kelt *et al.*, 2004) was responsible for this difference. Consequently, as with the Petri dish studies described above, we analysed only control data hereafter.

Subsequent experiments were conducted in 2000 and 2001, and analysed with a mixed model analysis of variance with year, season, time of day, transect (e.g. a given line of trays), and foraging group (ants vs. birds or small mammals) as independent variables, and mean 12-h consumption the dependent variable. Because plexiglass trays within transect are not independent we nested lines within year and season. Finally, all independent variables were treated as fixed, whereas plexiglass transects were treated as a random variable. Because higher-level interactions are difficult to interpret, we only pursued second and third order interactions among independent variables.

Reflecting differing numbers of field assistants, the number of plexiglass stations varied across the four seasons studied: we placed three lines of seventy-four, seventy-five, and seventy-five stations in summer 2000, five lines of sixty-four, sixty-six (including fifty in degu exclusions), sixty-seven, seventy-three, and seventy-five stations in winter 2000, four lines of seventy-five stations in summer 2001 (one line included twenty-six stations in degu exclusions), and three lines of seventy-five stations in winter 2001 (one line included thirty-nine stations in degu exclusions).

RESULTS

Bulk removal study

Foraging was greatest in the final year of study (1.70 ± 0.03 g) and lowest in the second year (0.90 ± 0.03 g), and was more extensive in winter than summer (1.41 ± 0.04 vs. 1.38 ± 0.04 g), and during the day than at night (1.58 ± 0.04 vs. 1.22 ± 0.04 g; Table 2). The discrepancy between nocturnal and diurnal foraging declined over time, being marked and significant in 1999 and 2000 ($P < 0.0001$ in both years,

Table 2 Results of mixed model analysis of variance on seed removal from Petri dishes, comparing nocturnal (small mammal) and diurnal (primarily avian) consumption (g/12-h period) in summer and winter across 3 years from control (+D) trays. This analysis does not include ant-only trays

Source	d.f.	MS	<i>F</i>	<i>P</i> > <i>F</i>
Model	475	1.13	2.86	< 0.0001
Year	2	68.17	163.52	< 0.0001
Season	1	7.99	19.17	< 0.0001
Time of day	1	78.51	197.84	< 0.0001
Station (year \times season)	466	0.42	1.05	0.2971
Year \times time of day	2	24.79	62.48	< 0.0001
Season \times time of day	1	54.73	137.93	< 0.0001
Year \times season \times time of day	1	0.59	1.49	0.2230

Significant results ($P < 0.05$) are highlighted with bold font.

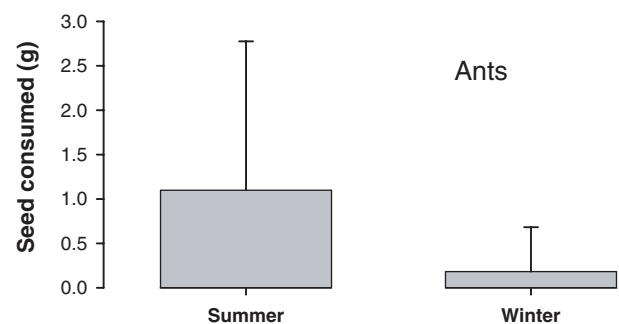


Figure 1 Mean 12-h removal of seed from Petri dishes in summer and winter, separated by foraging period (night vs. day).

one-way ANOVA) and effectively extinguished in 2001 (1.70 g in both time periods; $P > 0.97$, one-way ANOVA). Additionally, nocturnal foraging exceeded diurnal foraging in summer ($P < 0.0004$, one-way ANOVA) whereas the reverse was true in winter ($P < 0.0001$, one-way ANOVA). This seasonal change in diurnal foraging corresponded to periods when migratory finches and sparrows were present, most notably the common diuca finch (*D. diuca*) and rufous-collared sparrow (*Z. capensis*), which constituted the bulk of avian visits to our trays (pers. obs.). These patterns are similar to those being exposed at Ñacuñán Biosphere Reserve, where autumn and winter seed removal also appears to be dominated by birds (Marone *et al.*, 2000; L. Marone, pers. comm.).

Comparing nocturnal and diurnal consumption in ant-only trays, variances were not equal (Folded $F_{22,29} = 11.28$, $P < 0.0001$) and consumption was significantly different in summer and winter ($t_{25} = 2.52$, $P < 0.02$). Ants consumed more seed in summer than winter, but this was highly variable from tray to tray (Fig. 1; note the high SD),

Background seed removal study

Although foraging was higher in 2001 than 2000, this was not statistically significant when other factors were accounted for in the model (Table 3, Fig. 2a). Similarly, more seed was

Table 3 Results of analysis of variance on removal of single seeds from plexiglass trays. Data are from 2000 and 2001

Source	d.f.	MS	F-value	P > F
Model	59	0.26	22.69	< 0.0001
Year	1	0.39	3.45	0.0903
Season	1	0.52	4.63	0.0545
Year × season	1	5.31 × 10 ⁻⁴	0.00	0.9465
Transect (year × season)	11	0.11	0.78	0.6588
Time of day	1	3.30	64.14	< 0.0001
Year × time of day	1	0.57	11.10	0.0067
Season × time of day	1	0.50	9.64	0.0100
Year × season × time of day	1	0.06	1.22	0.2924
Time of day × transect (year × season)	11	0.05	0.57	0.8196
AntTrt × transect (year × season)	11	0.18	2.01	0.1223
AntTrt	1	0.56	3.07	0.1073
Year × AntTrt	1	1.38 × 10 ⁻⁷	0.00	0.9993
Season × AntTrt	1	0.53	2.90	0.1166
Time of day × AntTrt	1	1.01	11.42	0.0054
Year × season × AntTrt	1	0.32	1.75	0.2131
Year × time of day × AntTrt	1	0.50	5.50	0.0370
Season × time of day × AntTrt	1	0.10	1.06	0.3236
Time of day × AntTrt × transect (year × season)	12	0.09	8.14	< 0.0001
Error	204	0.01		

Significant results ($P < 0.05$) are highlighted with bold font.

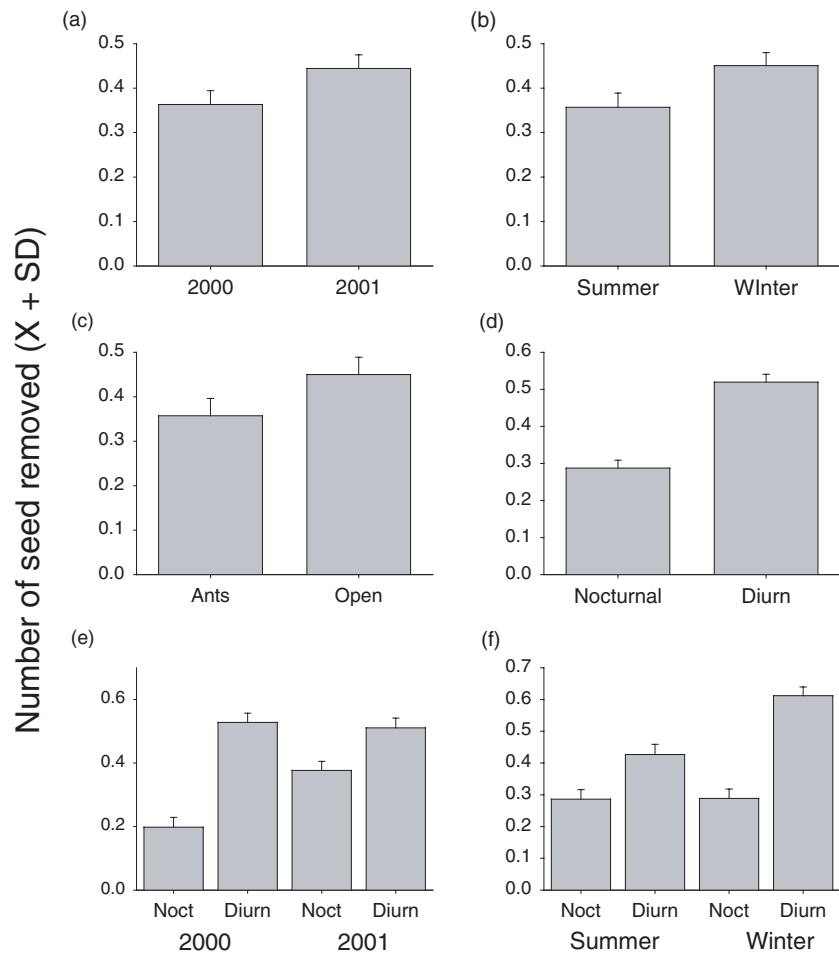


Figure 2 Mean (± 1 SD) 12-h number of seeds removed from plexiglass trays.

removed from open dishes than from ant-only dishes, but this was not significant (Table 3, Fig. 2c). There was a trend for greater seed removal in winter than summer, but this was not significant. Diurnal removal was greater than nocturnal removal (Fig. 2d), and this held in both years and both seasons, although nocturnal seed removal increased in 2001 (Fig. 2e) and nocturnal removal, but not diurnal removal, increased in winter (Fig. 2f).

DISCUSSION

Because of the limited number of strictly granivorous small mammals in northern Chile, we predicted that birds and possibly ants would be dominant seed predators at our site, followed by small mammals. In part, our predictions were supported. Most seed removal was diurnal, and this was greater in winter than summer, paralleling seasonal changes in the avifauna at our site. Mammals were less important than birds at this site, but in contrast to our predictions, ants were the least important foragers at Fray Jorge, although extensive removal of seed from some trays suggests that they may have an influence at very local scales. Ants and nocturnal mammals were equally poor at locating single seeds (compare Figs. 2b,d), although results from the bulk removal study suggest that mammalian granivory was greater at our site than at any other South American aridland that has been studied (Fig. 3).

The extent of seed predation by birds and ants also varied seasonally in other parts of South America. Research at Ñacuñan Biosphere Reserve in the Monte Desert of Argentina has uncovered important roles for ants, birds, and small mammals, but the importance of these varies seasonally; ants were particularly important in summer, whereas birds and, to a lesser extent, small mammals, were most influential in the autumn (Lopez de Casenave *et al.*, 1998). In Patagonian Argentina, seed removal from trays was significantly less in summer than in spring, primarily reflecting a decrease in

consumption by birds and, to a lesser extent, small mammals (Folgarait & Sala, 2002). In Mediterranean Chile, ants were the most important group of granivores overall, followed by birds and then mammals, but the role of ants was trivial in winter (Vásquez *et al.*, 1995).

The relative inefficiency of small mammals at removing seeds at our site is not surprising given the trophic diversity of the mammal fauna there (Meserve, 1981). The only true granivore (*Oligoryzomys*) exhibits irruptive population dynamics; relegated to moist habitats in most years, this species rapidly invades all habitats of the park when ENSO events lead to increased seed production. *Oligoryzomys* ranges to southern Chile, where it is a common inhabitant of temperate rainforests (Meserve *et al.*, 1991a,b) and one of the most abundant taxa in forest remnants (Kelt, 2000). It likely is more successful in these environments because the greater moisture leads to greater seed productivity.

Although seed removal at our site is lower than that observed in North America or Israel, it was substantially greater than other sites in South America, and vertebrate seed predation was greater than that reported for Australia (Morton, 1985; Predavec, 1997). Thus, our site may be somewhat of an anomaly even within South America. This may reflect the environment at Fray Jorge, which is very different than the other South American regions that have been studied; our site is coastal and has cooler summer temperatures and greater cloud cover than sites studied by Vásquez *et al.* (1995); Marone *et al.* (2000), or Folgarait & Sala (2002). In warm deserts in North America, Brown (1975) reported that ants rivalled small mammals in terms of their ability to find seed resources, but they were much less efficient at consuming these resources. Comparative data from more inland sites in semi-arid Chile could be highly informative.

The importance of birds as seed consumers parallels recent research in east Africa and Argentina. Birds removed over 50% more seed than mammals, and roughly 4 1/2 times as much as

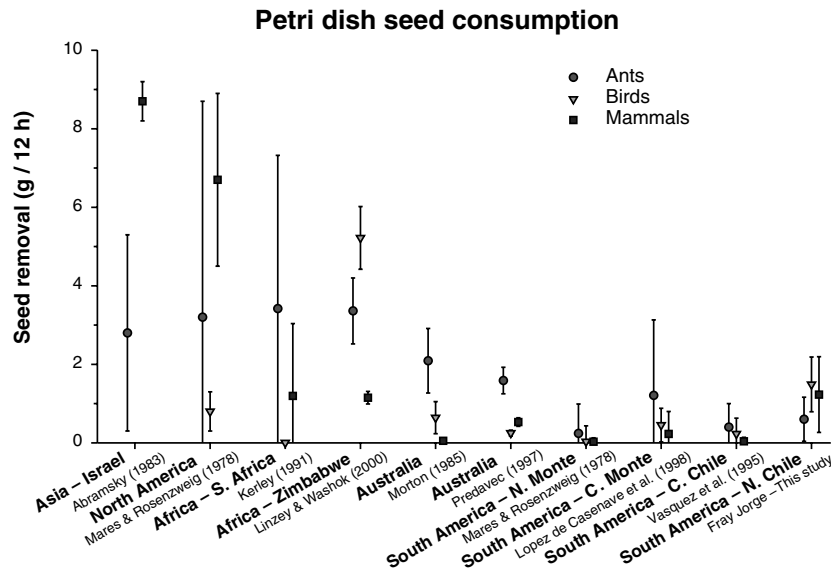


Figure 3 Mean (± 1 SD) rates of seed removal in several desert regions. Except for Fray Jorge (this study) and the central Monte Desert (data provided by J. Lopez de Casenave), data are from Predavec (1997); Linzey & Washok (2000), or redrawn from Lopez de Casenave *et al.* (1998) and Kerley & Whitford (1994). Fray Jorge data are averaged across seasons.

ants, from experimental trays in miombo habitat in Zimbabwe (Linzey & Washok, 2000). Birds evidently are important seed predators in central Argentina as well. Many of the taxa in the Monte Desert are closely related to those found at Fray Jorge (Table 1); both sites have a tinamou, three doves or pigeons, and six or eight fringillid passerines. Fray Jorge also has an introduced quail and three tapaculos (Rhinocryptidae), which may take seeds when available. The dominant granivorous birds at Fray Jorge are the common diuca finch (*D. diuca* (Molina) 1782) and the rufous-collared sparrow (*Z. capensis* (Statius Muller) 1776; D. A. Kelt pers. obs.); both of these species are widely distributed, highly granivorous (Lopez-Calleja, 1995), and occur also at Ñacuñan (Marone *et al.*, 1997). Not all sites in temperate South America are bird-dominated, however; work in Patagonia (Folgarait & Sala, 2002) suggests that insects and small mammals are more important seed consumers, although the infamous winds of Patagonia forced these authors to place seed trays inside large mesh enclosures; while these enclosures were open at the top to provide access to birds, it is not clear that avian foraging would be similar inside of such enclosures.

When data on bulk seed removal from our site are compared with similar data from other studies (Fig. 3), two interesting points emerge. First, South American sites exhibit much lower levels of seed predation than arid regions in the Northern Hemisphere (see also Folgarait *et al.*, 1998; Marone *et al.*, 2000). Secondly, however, removal of seeds at our site is very high relative to other sites in South America. Although consumption by ants is comparable with work in Argentina and central Chile, our values for both birds and small mammals are much greater than observed at these other temperate Neotropical sites, and our site is more strongly dominated by avian seed predation (albeit seasonally) than other South American sites.

Morton (1993) hypothesized that the limited granivory among Australian small mammals reflected the extreme unpredictability of precipitation, which in turn reduced the predictability of a seed crop; this was later extended to explain termite abundance and myrmecophory in lizards and mammals (Abensberg-Traun, 1994). Although Kelt *et al.* (1996) noted that the number of granivorous small mammal taxa did not correlate significantly with mean annual precipitation or the coefficient of variation of mean annual precipitation, it is evident (Fig. 4) that precipitation at many sites in the hyper-arid Sechura and Atacama Deserts of western South America is at least as limited and unpredictable as in Australia. One important difference between these regions is that much of Australia experiences similarly high CVs regardless of mean annual precipitation, whereas in South America, sites on either side of the Andes Mountains are very different in this regard (Fig. 4). Sites in Argentina's Monte Desert range from very dry to relatively mesic, and generally have levels of variability similar to North America, Africa, and the Middle East; in contrast, sites in Peru and northern Chile have uniformly low precipitation, but regionally variable CVs in mean annual precipitation.

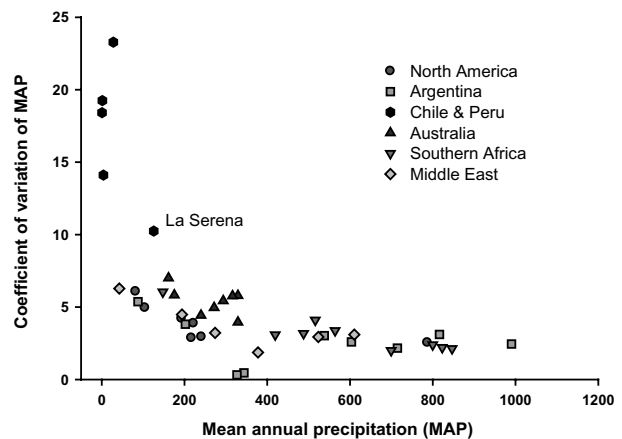


Figure 4 Mean annual precipitation plotted against the coefficient of variation in mean annual precipitation for forty-six sites in six desert regions. Most deserts exhibit a range of mean precipitation, with relatively low coefficients of variation. The Atacama and Sechura Deserts, along the coast of Peru and Chile, exhibit uniformly low mean precipitation, generally with very high variation from year to year; the town of La Serena is c. 100 km north of our study site. The variation in annual precipitation observed in Atacama and Sechura sites reflects the influence of ENSO events, which lead to very high levels of precipitation in ENSO years (data from World Weatherdisc, WeatherDisc Associates, Inc., 1994, Seattle, WA).

Additionally, 70–90% of seeds in the soil at Fray Jorge were < 1 mg in mass (Gutiérrez & Meserve, 2003), possibly too small to support granivorous mammals. Some authors have argued that plants produce smaller seeds in environments with high risk of drought during germination and seedling establishment (e.g. Salisbury, 1942; Baker, 1972). The underlying logic is that plants producing smaller seeds are able to produce more seeds, increasing the probability that some will find suitable sites for germination and establishment. The generality of this pattern, however, and hence the validity of this as an explanation of seed size and, by extension, of granivory at Fray Jorge, has been called into question (Westoby *et al.*, 1992, 1996). Further work aimed at understanding why seeds in this region are so small, however, would be informative.

Folgarait *et al.* (1998) presented an alternative explanation for the global distribution of granivory. They noted that the proportion of granivory across seven desert regions was best explained by high 'continentality' (land/ocean ratio) and annual thermal range (difference between extreme annual mean temperatures). They proposed that granivory is favoured in thermally stressful environments because seeds, unlike most other foods, can be stored under such conditions without rapid degradation. These authors did not emphasize the benefit in terms of water deficit that is accrued in water-limited environments by eating seeds, which are predominantly comprised of starches; whereas lipids have more free water than starches or proteins, the cost of metabolizing lipids requires more oxygen (and therefore increased respiratory water loss) than do starches (Schmidt-Nielsen, 1964). Thus,

environments that are water limited are likely to yield relatively stronger selection for granivory than are more mesic regions. Given the fact that faunas on both the east and west side of the Andes have similarly low levels of granivory, but dramatically different levels and predictability of precipitation, the argument presented by Folgarait *et al.* (1998) may be the best explanation to date for the global distribution of granivory. Moreover, many of the species found in arid Chile are derived from more mesic regions of Chile (Osgood, 1943; Meserve & Kelt, 1990) where numerous alternative foods are available, further reducing any selective advantage to granivory.

As other authors have noted, North America and Israel appear to stand out in terms of the importance of small mammals as seed predators; no other desert that has been studied shows a substantial role for small mammals. Ants are moderately important in several systems, including Israel, North America, Australia, and South Africa (where they appear to be the dominant seed predators; Kerley, 1991). Ants are also important in covered habitats at Ñacuñan, although their influence there is somewhat unpredictable.

In contrast, birds are not highly important in most desert regions. They were the dominant granivores, however, in Zimbabwe miombo (Linzey & Washok, 2000) as well as at our site, where their activities were strongly seasonal.

Recent studies (e.g. Marone *et al.*, 2000) have demonstrated that granivory in South America is more important than initially reported by Mares & Rosenzweig (1978). Our data underscore that even within South America there is great variation in patterns of granivory. Nonetheless, the magnitude of this mechanism clearly is less important than in North America. The roles played by different taxonomic groups, and the degree to which this varies geographically, remain fertile ground for further work.

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BIOSKETCHES

Douglas Kelt is an associate professor at the University of California, Davis, where he studies community and conservation ecology as well as biogeography and macroecology, emphasizing small terrestrial mammals.

Peter Meserve is a Distinguished Research Professor in the Department of Biological Sciences, Northern Illinois University. His research interests emphasize vertebrate community ecology and biogeography, and include over 30 years experience with Chilean ecosystems.

Julio R. Gutiérrez is a professor in the Department of Biology, Universidad de La Serena, La Serena, Chile. He has been working for over two decades in plant ecology, arid and semi-arid systems, and the impact of long-term ecological phenomena such as El Niño Southern Oscillation events.