

Frequency-dependent seed predation by rodents on Sonoran Desert winter annual plants

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Abstract. Numerous mechanisms may allow species to coexist. We tested for frequency-dependent predation, a mechanism predicted by theory and established as a foraging behavior for many types of animals. Our field test included multiple prey species exposed in situ to multiple predator species and individuals to determine whether the prey species experienced predation patterns that were frequency dependent. The prey were seeds of three species of Sonoran Desert winter annual plants while the predator species were a guild of nocturnal seed foraging heteromyid and murid rodents that co-occur naturally in the same community as the desert annuals at Tumamoc Hill near Tucson. Seeds of one species were much preferred over the other two. Nonetheless, we found the net effect of rodent foraging to be positively frequency dependent (the preference for each species is higher when it is common than when it is uncommon) as has been previously hypothesized. This frequency-dependent predation should function as a species coexistence promoting mechanism in concert with the storage effect that has been previously demonstrated for this system.

Key words: *foraging theory; frequency dependence; predator switching; seed predation; Sonoran Desert; species coexistence; winter annual plants.*

INTRODUCTION

Most models of species coexistence require a mechanism that allows species to recover from periods of rarity (Chesson 2000). Community ecologists have produced a large body of theory describing how these mechanisms might operate. These mechanisms are not mutually exclusive but can interact with each other in various ways (Chesson 2000). Some coexistence mechanisms, especially resource partitioning, have been empirically investigated extensively (Lemen and Rosenzweig 1978, Price and Waser 1985, Price and Reichman 1987, Angert et al. 2009), while other mechanisms including frequency-dependent predation (FDP) have not received as much attention.

Predator responses to changes in the relative frequency of alternative prey types has been proposed as a mechanism for maintaining intraspecific color polymorphisms and interspecific coexistence among prey guilds (Clarke 1962, Manly et al. 1972, Krivan 2003, Krivan and Eisner 2003, Chesson and Kuang 2010, Kuang and Chesson 2010). There is a well-established theoretical literature showing how FDP may lead to coexistence of prey and suggesting that it can be a powerful driver (Murdoch 1973, Murdoch and Oaten 1975, Oaten and Murdoch 1975, Chesson and Kuang 2010). “Switching,” has been defined as a change in the level of preference for a single species that is disproportionate to its change in relative abundance (Murdoch 1969). However, most

empirical research on frequency-dependent predation (switching) has been predator focused, asking questions relating to optimal foraging, the foraging behavior of single predators, or to predator regulation of prey populations instead of specifically studying the effects that FDP or switching may have on the interspecific coexistence of prey populations (Manly et al. 1972, Ayala and Campbell 1974, May 1977, Gendron 1987, Hughes and Croy 1993, Krivan 1996, Abrams and Matsuda 2004, Warburton and Thomson 2006).

Frequency-dependent predation has been proposed as one consequence of a number of foraging strategies within optimal foraging theory (Murdoch 1969, Rapport 1971, Hubbard et al. 1982, Staddon and Gendron 1983, Brown and Mitchell 1989, Krivan and Eisner 2003). Per-capita predation on a particular prey species or type can either increase (positive FDP) or decrease (negative FDP) in response to an increase in the frequency of that prey type among the total prey population (Chandra and Williams 1983, Gendron 1987, Celis-Diez et al. 2004). Formation of a search image or a decrease in handling time learned through repeated exposure to a particular prey would enhance a predator’s capacity to harvest and consume the more frequent prey efficiently and lead to positive FDP (Tinbergen 1960). Independent of the specific behavioral mechanism involved, the idea that predators potentially stabilize prey populations through positive FDP has been accepted in the literature for many years though without much empirical support (Murdoch 1969). In contrast, negative FDP could occur if, for example, prey at high frequency provide merged cues making detection of an individual or fixing its location difficult. This would make selection of rare prey

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types more profitable (Greenwood 1984). Negative FDP destabilizes a prey community and can lead to the eventual extinction of a rare prey type (Hulme and Hunt 1999). Frequency-dependent predation has been shown across a wide range of predator types, including protozoa, arthropods, birds, and mammals (Allen and Clarke 1968, Landenberger 1968, Maskell et al. 1977, Akre and Johnson 1979, Hulme and Hunt 1999).

Most lab trials have used symmetrically preferred prey types, that is, prey that are equally preferred when presented at equal abundances. This is sometimes accomplished by changing the color of otherwise identical artificial prey items (Allen and Clarke 1968). However, in nature, asymmetrical preferences are common. Some species are highly preferred regardless of frequency and continue to be highly preferred even when rare (Greenwood 1985, Samson et al. 1992). Alternatively, some species may be unpalatable or toxic and generally ignored even when common (Hulme 1998). It is unclear how strongly FDP operates in such systems. The greater the asymmetry of preference, the greater the need for a stabilizing mechanism, such as positive FDP, to prevent exclusion of the preferred prey from the community.

Sonoran Desert winter-annual plant communities have been used as a model system both for refining coexistence theory and for testing proposed coexistence mechanisms (Sears and Chesson 2007, Angert et al. 2009). Most winter annuals exist longer as seeds (five months to many years) than as vegetative growing plants (one to six months; Venable and Pake 1999, Moriuchi et al. 2000). Granivorous rodents, ants, and birds are known to be important consumers of desert annual seeds (Chew and Chew 1970, Price and Brown 1983, Parmenter et al. 1984) and seeds of winter-annual plants comprise a significant portion of the diet of desert rodents (Reichman 1975). Predation at the seed stage is thus a significant component of plant fitness (Inouye et al. 1980). The granivorous rodents that prey on these seeds are also a model system and their foraging behavior has been well studied (Brown et al. 1975, Reichman and Fay 1983, Price 1984, Price et al. 1984, Price and Waser 1985, Price and Jenkins 1986, Reichman and Price 1993, Curtin et al. 2000, Sullivan et al. 2001). In lab trials, species closely related to the species in our experiment have shown positive frequency-dependent foraging patterns (Drickamer 1972). While Kuang and Chesson (2010) have modeled how positive FDP by granivorous rodents can operate as a coexistence mechanism utilizing the same winter annual plant system as our field experiment as a heuristic, until now, there have been no empirical field-tests of frequency-dependent foraging on winter-annual seeds nor by granivorous desert rodents.

Our objective was to empirically test for frequency-dependent predation in a system where its potential population-level effects have been modeled. We designed a multi-prey species, aggregate-predator species experiment to test whether a community of winter-annual plants experience frequency-dependent seed predation by

nocturnal rodents. Based on the results of lab trials using closely related predators, we hypothesized that seeds would experience positive FDP patterns. A secondary goal was to determine the level of seed preference asymmetry among the three common prey species chosen for the experiment.

METHODS

To test whether winter annual seeds experience positive frequency-dependent predation at the community level, we designed a field experiment using three species of winter annuals that have been common at our field site, the Desert Laboratory at Tumamoc Hill, Tucson, Arizona (32.223799°, -111.009263°; Venable and Kimball 2011). The Desert Laboratory is a 350-ha ecological reserve that has been fenced to exclude livestock since 1906, creating a generally undisturbed habitat for the winter annual community. Our native experimental species, *Pectocarya recurvata* I.M. Johnst. (PERE), *Erodium texanum* A. Gray (ERTE), and *Plantago insularis* Eastw. (PLIN; now *Plantago ovata* Forssk.), grow on creosote flats dominated by *Larrea tridentata*, *Opuntia* spp., and *Acacia* spp. Average seed masses (\pm SD) for the experimental species of seeds gathered in 2008 are PERE, 0.54 ± 0.12 mg; ERTE, 1.46 ± 0.32 mg; and PLIN, 0.99 ± 0.20 mg. We collected seeds for the experiment as they ripened in May and stored them outdoors at the field site in shelters that protected them from rain and predation. Seeds were presented as they normally are at the time of dispersal, i.e., in the forms that predators would likely encounter them (Fig. 1). PERE occurs as a single nutlet, as well as in a group of four nutlets. PLIN occurs as a single seed. ERTE occurs, usually, with a large corkscrew-shaped awn. All are known to be eaten by nocturnal heteromyid and murid rodents in this region (Tevis 1958, Reichman 1976, Price 1983). Cactus



FIG. 1. Seeds as used in the experiment. From left: PERE as a single nutlet; PERE as a whole fruit composed of four nutlets; PLIN; ERTE with awn. Species names are provided in *Methods*.

mice, *Peromyscus eremicus*; desert, rock, and Bailey's pocket mice, *Chaetodipus penicillatus*, *C. intermedius*, and *C. baileyi*; and the white-throated wood rat, *Neotoma albigula*, have all been trapped at the field site (K. R. Keck and D. L. Venable, unpublished data), and Merriam's kangaroo rat, *Dipodomys merriami*, tracks were recorded in the seed trays during this study. These species are expected to form the majority of the local nocturnal rodent population based on elevation, location, soil characteristics, and dominant vegetation (M. Nachman, personal communication; M. Price, personal communication). The experiment was conducted in early October, a time of high rodent activity but low ambient seed availability.

We selected 18 sites, each 1 m away from what appeared to be an active rodent burrow. Trays were placed 15–20 m from each other in zig-zag fashion along a 190-m transect. At each site, we placed a seed tray, an aluminum baking tray 62 × 42 × 3 cm, on the ground adjacent to but outside the canopy of a *Larrea tridentata* shrub with the long edge of the tray following the canopy border. This equalized tray accessibility to the resident rodent species, some of which prefer to forage in the open areas between shrubs and some of which prefer to forage under the shelter of a shrub canopy (Rosenzweig 1973, Price 1978).

We trained the rodents to the trays for seven days. During this week, the sand-filled trays were stocked each evening just before sundown with a "handful" of rodent-preferred exotic seeds: sorghum (*Sorghum bicolor*), millet (*Panicum millaceum*), and sunflower (*Helianthus annuus*), which were rendered non-viable in a microwave oven to prevent establishment of exotic species on the research site. Training was done with exotic seed species so that rodent foragers would not have prior experience with any of any the three test species in trays. Trays were loaded with 3 L of 120-grit silica sand (0.102 × 0.102 mm) that approximates the soil matrix naturally occurring in this part of the Desert Laboratory and is much smaller than any of the seeds used. The difference between sand size and seed size permitted a rapid foraging rate, as well as eased the recovery and counting of non-foraged seeds (Price and Heinz 1984) using a size 25 standard soil sieve. In contrast to many rodent foraging experiments, where seeds are buried or mixed into the soil matrix, we spread seeds in a haphazard manner on top of the sand tray. This presentation more accurately mimicked recently dispersed seeds, which predominate in rodent diets (Price and Joyner 1997). This contrasts to the mixed approach used in some experiments to prevent bird predation on the seeds (Veech 2001, Veech and Jenkins 2005) or to gauge a giving up density within a patch (Price and Correll 2001).

For the experiment, conditions and methods were the same as during training with the exception of the seeds presented. Our experimental treatment (using PERE, PLIN, and ERTE) consisted of presenting two of the species at low frequency, 25 seeds per tray, and one species at high frequency, 100 seeds per tray. The total seed number was held constant at 150 seeds per tray. The ratio of seeds presented was in the same range as those used in

other frequency-dependence trials (Murdoch 1969) and represented a density of seeds that is within the normal range found at the research site (Venable and Kimball 2011). Each night, the treatment (high vs. low frequency) for each of the 18 sites was randomly reassigned with the constraint that each species had six high-frequency trays. The trays remained in place for the duration of the experiment, the nights of 8–10 October 2009.

Each morning, just before dawn, we collected the sand and remaining seeds from each of the trays and noted whether tracks were present in the sand. We sieved any remaining seeds from the sand and recorded the number of non-harvested seeds of each species by tray. If any species was completely harvested, we scored the number of seeds remaining as 0.5 to avoid undefined logarithms in the preference equation (Eq. 1).

To demonstrate whether the different seed types are symmetrically or asymmetrically preferred (if there is an innate likelihood that predators will harvest one species more extensively if presented with all seeds in the same frequency) we calculated their probability of harvest (POH). The POH values for each species were calculated as the proportion of seeds of that species removed from each replicate, i.e., each tray × day combination (Price and Jenkins 1986). Across the entire experiment, the total number of seeds of each species presented was equal. We conducted an ANOVA using PROC MIXED, SAS 9.3 (SAS Institute, Cary, North Carolina, USA) on the arcsine-square-root-transformed POH using the independent variable, species, to designate to which species the POH value belonged. The species in question, the species at high frequency, and their interaction were modeled as fixed effects and night was modeled as a random effect (the model with night as a random effect gave a better fit than models with tray (location), tray and night, or no random effect. Frequency treatment and its interaction with species were not significant and the model with frequency treatment and the interaction did not give a significantly better fit than the model with just species (likelihood ratio test, $P = 0.08$), so we report result for the simpler model. Pairwise comparison of the means for the three frequency treatments used P values with Tukey adjustment for multiple comparisons.

We calculated preference values, α , for each species within a replicate using the equation

$$\alpha_i = \frac{\ln((n_{i0} - r_i)/n_{i0})}{\sum_{j=1}^m \ln(n_{j0} - r_j)/n_{j0}}, i = 1, \dots, m \quad (1)$$

where n_{i0} is the number of seeds of species i at the beginning of the experiment and r_i is the number of seeds of species i consumed (Chesson 1983). This equation assumes that as the experiment progresses the available food is not replenished; that is, the ratio of food types available is constantly changing. These preference values compare the average depletion rates of each prey type for the duration of the feeding trial. Within each replicate (tray) the preference values of the three species sum

to 1. Multiple diet choice strategies for desert rodent foragers have been modeled and tested under scenarios of heavy patch depletion (Brown and Mitchell 1989). Each of those strategies predict a positive FDP signal when considered from the prey perspective leading to our a priori prediction of positive FDP.

We used a MANOVA (PROC GLM, SAS 9.3; SAS Institute) to test for differences in preferences at different seed frequencies because preferences sum to one, so are not independent. Thus, three separate ANOVAs would not be appropriate for these data because the tests would not be independent and one would be completely redundant. The MANOVA tested if the vector of preference values of ERTE and PERE differed between the three frequency treatments (because the preference for PLIN is completely determined by that of the first two species, we do not have degrees of freedom necessary test all three as a multivariate dependent vector). We then partitioned the frequency treatment effect into two a priori linear contrasts between high frequency and low frequency: one for ERTE and one for PERE. Then we also did a profile analysis, which used a compound variable of the two dependent variables: the difference between the preference for ERTE and for PERE. We compared this difference in preference across the three frequency treatments. Finally, we compared this difference in preference for ERTE and PERE with the a priori linear contrasts of high vs. low frequency of ERTE and high vs. low frequency of PERE. The linear contrasts were evaluated with one-tailed tests because our a priori hypothesis was that each species will be more preferred when it is common than when it is rare.

RESULTS

By the end of the training period, rodents were visiting all trays each night, indicating that they were both accustomed to the trays and were likely to visit the location as a reliable food source. During this phase of the experiment, trays were left out during the day as well and the tracks of other diurnal seed predators, including birds and harvester ants, were easily distinguishable in the sand.

After the switch to using native seeds at different frequencies, the number of seeds harvested overnight from a single tray by rodents ranged from 2.0% to 55.3% of

the 150 seeds available. Trays showed tracks from both large and small quadrupedal rodents as well as bipedal kangaroo rats. Neither ants nor birds left any tracks in the trays at night.

Some seed species were more likely to be harvested than others (ANOVA, main effect of species, $F_{2,98} = 30.24$, $P < 0.0001$). Specifically, ERTE had a higher POH than either PERE or PLIN (for both, Tukey adjusted $P < 0.0001$), but PERE and PLIN did not differ ($P > 0.72$; Table 1). Even at low frequency, ERTE had higher POH values than did either PERE or PLIN at high frequency, and over the course of the experiment, almost twice as many ERTE seeds were harvested as of the other two species combined (Table 1).

The vector of species preferences differed across treatments (the three seed frequencies), i.e., preference values showed frequency dependence (Fig. 2; MANOVA, Wilks' Lambda = 0.74, $P = 0.0468$ and Pillai's Trace = 0.28, $P = 0.0431$). Independent contrasts showed that preferences for ERTE and PERE were higher when each was common (ERTE high vs. low, Wilks' Lambda = 0.83 and Pillai's Trace = 0.17, both $P = 0.0481$; PERE high vs. low, Wilks' Lambda = 0.83 and Pillai's Trace = 0.17, both $P = 0.0508$). The profile analysis showed that the difference in preference between ERTE and PERE depended on which of the three species was most frequent (Wilks' Lambda = 0.82 and Pillai's Trace = 0.13, both $P = 0.0345$). As predicted, the preference for ERTE over PERE was greater when ERTE was at high frequency (the difference in preference was tested using a contrast between high vs. low ERTE frequency; Wilks' Lambda = 0.83 and Pillai's Trace = 0.17, both $P < 0.006$). Likewise the preference for ERTE over PERE was lower when PERE was at high frequency, also as predicted (difference in preference tested using a contrast between high vs. low PERE frequency, Wilks' Lambda = 0.89 and Pillai's Trace = 0.011, both $P = 0.03$). Taken together, these analyses show that in this experiment predation on these three species occurred in a positive frequency-dependent manner.

DISCUSSION

It is well known that predation can have large effects on species abundance (Schoener et al. 2002, Salo et al. 2007, Campbell et al. 2012). Furthermore, specific kinds of predation can promote species coexistence of prey.

TABLE 1. Probability of harvest.

Species	Probability of harvest			
	All species	High-frequency species		
		ERTE	PERE	PLIN
ERTE	0.363 ± 0.055	0.364 ± 0.097	0.356 ± 0.091	0.367 ± 0.101
PERE	0.066 ± 0.018	0.020 ± 0.013	0.065 ± 0.027	0.113 ± 0.041
PLIN	0.034 ± 0.010	0.020 ± 0.011	0.024 ± 0.011	0.056 ± 0.025

Note: Values are the mean proportion of seeds of each species harvested overall and by treatment (±SE).

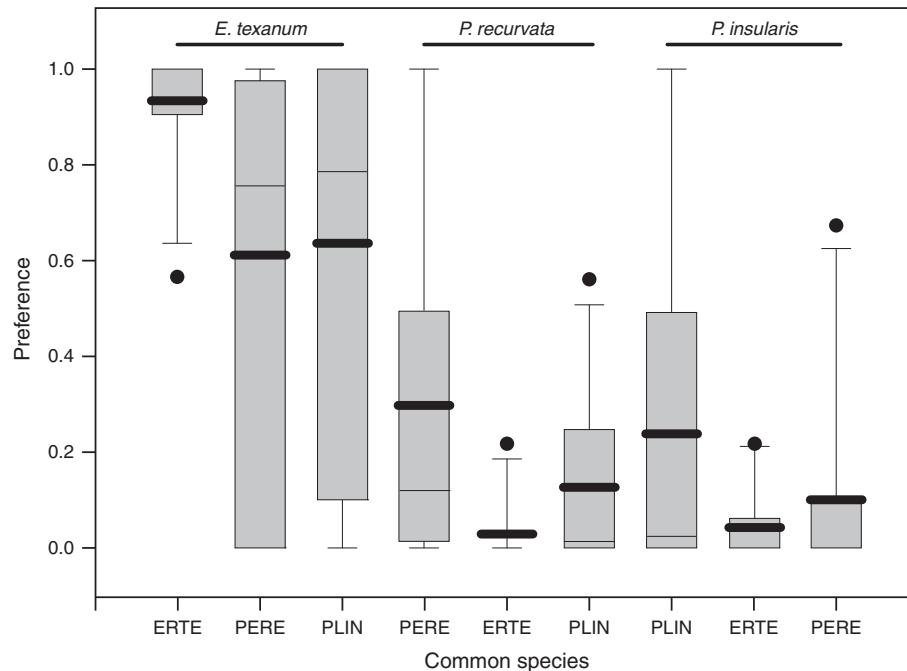


FIG. 2. Preference values, α , for each species for each frequency treatment. The three frequency treatments consisted of one common species and two less common species in a ratio of 4:1:1. The thick horizontal line represents the median, thin line the mean, gray bars extend from the 25% to 75% quantiles, whiskers extend from 10% to 90% quantiles, and dots indicate outliers.

For example, the Janzen–Connell mechanism can promote the coexistence of many species when each species has its own specialized predator (Janzen 1970, Connell 1971, Stump and Chesson 2015). More generalized predation can promote species coexistence as well. When predators act as general disturbance agents in a patchy way, they can promote coexistence via colonization/competition trade-offs (Paine 1966, Levin and Paine 1974). Alternatively, generalized predators whose preferences switch based on relative abundance of prey species can be important agents of prey species coexistence. This scenario is especially feasible for desert annual plants fed upon by generalized seed-feeding rodents (Kuang and Chesson 2010).

In our field experiment, we found clear evidence of positive frequency dependence in the foraging patterns of granivorous rodents on winter annual seeds at this field site in the Sonoran Desert, even though one species, *Erodium texanum*, was highly preferred (Fig. 2). Similar tests in deciduous woodlands have found frequency-independent foraging and speculated that switching was mostly likely to occur when seeds had low palatability (Hulme and Hunt 1999), though our experiment shows switching even with a highly palatable species. While Paine and Beck (2007) report finding frequency-dependent seed and seedling predation by small mammals for tropical trees, they base their definition of frequency on the numbers of adult individuals of the prey species present and presented seeds of each species in equal ratios per replicate, making their test not reflect community-level results of FDP as usually defined. Our results provide the first

field experimental evidence of positive frequency-dependent seed foraging for annual plants.

The foraging behavior of predator species may affect the strength of frequency dependence. When ERTE was common, PERE was harvested in only two trays (3 of 25 seeds taken) and PLIN was only harvested in three trays (1, 2, or 3 of 25 seeds). Because PERE dehisces in groups of up to four joined single-seeded nutlets, there could have been as little as one harvesting event. It seems possible that these few harvests could have been “mistakes” in the search for the common species. Heteromyids sometimes forage in a semi-systematic way across seed trays by raking through the sand with their paws (Price and Correll 2001). With tactile foraging, and the large linear-dimension difference between experimental species (Fig. 1), ERTE would have been much easier to discover than the rest. Since we found that seeds of ERTE are highly preferred by rodents and that their seeds are readily encountered, it seems possible that upon encountering an ERTE seed in a tray the individual forager may have immediately switched to search specifically for these large seeds, only taking the other species opportunistically. This could be considered a tactile analog to Tinbergen’s search image (Tinbergen 1960). By spreading their digits farther apart as they rake through the sand, a foraging rodent could increase its efficiency in foraging for ERTE. This behavioral modification would also decrease the discovery rate for the other two species, especially for PLIN or PERE seeds that occurred individually, as they could fit in the gaps between the spread digits.

While we have shown that seed patches can be exploited in a positive frequency-dependent fashion, there is an additional layer of complexity involved in relating this to plant species coexistence. Only a small fraction of seeds harvested by heteromyid rodents are eaten at the time of harvest (Price and Jenkins 1986, Leaver and Daly 1998, Price et al. 2000). Those that are not consumed are often placed in “scatterhoards” (Leaver and Daly 2001), depots of seeds buried 0.5–3.0 cm below the soil surface (Vander Wall 1990). Scatterhoarded caches are exploited both by the individual who made them and by thieving neighbors (Behrends et al. 1986, Daly et al. 1992, Price et al. 2000, Price and Mittler 2003, 2006). However, some caches elude exploitation. An interesting side effect of germination in unrecovered caches is an increase in the local density of seedlings, especially in the case of species-segregated caches (Monson and Kessler 1940, Vander Wall 1990). This tends to increase intraspecific competition (McMurray et al. 1997), which may promote coexistence by reducing the per capita population growth rates of common species. This possibility warrants further study of the germination and growth patterns from seeds cached in scatterhoards. It will be important to elucidate the levels of competition and frequency dependence that result from caching and to determine the effect this has on demographic patterns and coexistence.

Theory has shown that multiple coexistence mechanisms can interact with each other both positively and negatively (Chesson and Kuang 2008). Previous studies have shown that the storage effect, a fluctuation-dependent coexistence mechanism, plays an important role within this community (Angert et al. 2007) and other similar arid communities (Chesson et al. 2004). The storage effect requires covariance between the environment and competition for common species: as the environment improves for a particular common species, competition also increases. However, positive FDP reduces the density of the common species to a greater extent than would frequency-independent predation. This decreases the intensity of intraspecific competition between individuals of the common species in a good environment resulting in a reduction to the strength of the storage effect. While positive FDP and the storage effect interact negatively, the interaction can still promote coexistence, albeit at a level lower than the effect of the stronger mechanism in isolation (Chesson and Kuang 2010, Kuang and Chesson 2010). Quantifying the relative importance of each mechanism for maintaining diversity in a variable environment within this community is an important goal for future research.

While models have shown that predation weakens the storage effect, and that frequency-dependent predation does so in an intensified way, it is unclear whether predation in this guild of plants lowers densities to a point that the effects of competition are substantially reduced. Seed and seedling densities at germination are often very high, up to 56,043/m² (Venable and Kimball 2011). Even

restricted to the size class likely to be eaten by rodents, those larger than 0.4 mg, densities are frequently in the range of 1,000–20,000/m², and strong competitive effects have been documented for this system both in the greenhouse (Gremer et al. 2013) and in under ambient predation levels in natural field sites (Pantastico-Caldas and Venable 1993).

By demonstrating frequency-dependent seed predation, this work represents an important first step toward determining the relative importance of multiple coexistence mechanisms in desert annuals. We used seed frequencies and densities that fall within the normal range of what is found at our field site (Venable and Kimball 2011). Thirty years of monitoring winter annuals at this field site have shown extreme inter-annual variability in both density and frequency of species (Angert et al. 2007, Venable and Kimball 2011). To determine the varying levels of coexistence-mediating power that FDP might confer on this system, future work must explore preference values under the wider range of frequencies and densities that occur in the system. To achieve a full understanding of coexistence mechanisms as they operate within this system, a future synthesis will be required to delineate the power of each coexistence mechanism within the widely varied population levels that occur naturally.

This work demonstrates frequency dependent seed predation for a previously unstudied life form (annuals) and biome (deserts) and provides the first evidence that frequency-dependent predation can be important even in a system with highly asymmetric preference values.

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