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Post-dispersal seed predation in relation to selection on seed size in *Dithyrea californica*

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ABSTRACT

Question: We asked whether a desert ant population and a community of heteromyid rodents select *Dithyrea californica* seeds in relation to their size, frequency of seed sizes, and absolute density and thus have the capacity to influence natural selection on seed size.

Hypothesis: Following the predictions of optimal diet theory, we hypothesized that seed predators will prefer to prey upon larger seeds, that seed selection should be frequency independent, and that only variation in the absolute density of the preferred seeds will influence predator behaviour by lowering their preference for larger seeds.

Organisms: A colony of the desert harvester ant *Pogonomyrmex rugosus* and a community of heteromyid rodents (*Dipodomys merriami* and *Dipodomys desertii*).

Site of experiments: Reserva de la Biósfera El Pinacate y Gran Desierto de Altar and Hermosillo, Sonora, México.

Methods: We conducted two preference experiments in which we offered *D. californica* seeds that varied in size, relative frequency of sizes, and absolute density of seeds to a population of the harvester ant and to the community of heteromyid rodents of the Sonoran Desert.

Results: We found that ants had a preference for larger seeds whereas rodents had an equal preference for large and small seeds, despite variation in seed frequency and density. In accordance with optimal diet theory, seed predation was frequency independent. Contrary to our predictions, neither changes in absolute density of larger seeds nor of smaller seeds had a significant influence on predator behaviour.

Conclusion: Our results suggest that only *Pogonomyrmex rugosus* influenced selection on seed size, which it does by preferring larger seeds and counteracting the competitive effect of larger seeds in other life stages. Selection via seed predation conflicts with post-germination selection on seed size, when encountered by ants but not rodents.

Keywords: density, desert rodents, harvester ants, optimal diet theory, post-dispersal seed predation, preference, selection on seed size.

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INTRODUCTION

Seed size is a key trait that can influence offspring fitness throughout the life cycle (Moles and Westoby, 2004, 2006; Moles *et al.*, 2005; Larios *et al.*, 2014). The strength and direction of selection on seed size might differ between the various life stages of a plant because interactions with the environment change with the plant's development. For instance, water availability and competition might influence selection on seed size post-germination (Leishman and Westoby, 1994b; Larios *et al.*, 2014). Selection on seed size can also be affected by other selective pressures during the plant's life cycle that might create a selective conflict post-germination, such as seed predation (Alcantara and Rey, 2003; Gomez, 2004) and seed dispersal (Martinez *et al.*, 2007).

Post-dispersal seed predation is an important selective force that potentially shapes plant demography and the evolution of seed traits such as seed size (Geritz, 1998; Hulme, 1998). Seed consumption by predators has strong negative fitness consequences for plant populations because consuming seeds always translates directly into demographic losses. It is therefore a selective force that will affect seed size through survival selection. For annual plants, the impact of seed predation on fitness is even stronger given that annual plants exist most of their life as seeds. This makes them vulnerable to predation for longer periods relative to their life cycle. Post-dispersal seed predation can affect selection on seed size when predators display a preference for differently sized seeds (Mitchell, 1977; Herrera, 1984; Jordano, 1984, 1995; Reader, 1993). Post-dispersal seed predation has been found to create a selective conflict with selection on seed size post-germination because plants originating from larger seeds tend to have higher fitness but seed predators are known to prefer larger seeds (Alcantara and Rey, 2003; Gomez, 2004). However, resource availability and phenotypic variation in seed size can also influence predator behaviour via the functional response of the predators.

It is hypothesized that predator foraging behaviour is shaped by natural selection resulting in foragers that maximize their fitness by making optimal foraging decisions (Schoener, 1971; Pyke *et al.*, 1977; Pyke, 1984). Standard optimal diet theory predicts that predators should prefer larger seeds if foraging for them does not incur a higher cost of handling time or searching time than foraging for smaller seeds, thus maximizing energy acquisition per unit effort (E/h) (Davies *et al.*, 2012). This is because larger seeds provide more energy in a single package, thus maximizing foraging efficiency (Smith, 1970; Orians and Pearson, 1979; Abramsky, 1983; Bailey and Polis, 1987). A less explored but equally important idea is that predators could select their prey in a frequency- or density-dependent manner by displaying a switching behaviour (Murdoch and Oaten, 1975; Chesson, 1984; Greenwood, 1985; Allen, 1988). When predators look for seeds as individual prey items, they are typically confronted with phenotypic variation in prey sizes. Predators could adjust their foraging decisions in order to maximize their own fitness by switching their preference to the more valued item (Murdoch, 1969). A seed predator may also prey upon seeds based on the relative frequency of seed sizes, a phenomenon known as switching or apostatic selection. When predators select the most common phenotype, they confer a selective advantage for the rare phenotypes; this is called pro-apostatic selection (*sensu* Greenwood, 1985) or positive switching (*sensu* Chesson, 1984). The opposite occurs when predators select the rarest phenotype, and this is known as anti-apostatic selection (*sensu* Greenwood, 1985) or negative switching (*sensu* Chesson, 1984). Another source of apostatic selection comes at the population level even if individual predators do not show switching behaviour, but vary greatly, one from another, in their preferences (Chesson, 1984). The theory of switching behaviour at the population level in the presence of such between-individual variation in preference predicts anti-apostatic selection.

Despite the expected prevalence of frequency-dependent seed-size predation, only two studies have addressed this phenomenon. In the first, predators of *Cryptocarya alba* preferentially ate large seeds in an anti-apostatic manner (Celis-Diez *et al.*, 2004) by selecting larger seeds more when scarce than when common. These results contradicted the predictions of optimal foraging theory in the sense that predators are expected to switch from the most profitable phenotype to foraging for both prey types only when the absolute density of the most profitable phenotype falls to a threshold level where the fitness gain is lower (Hubbard *et al.*, 1982). In a second study, Celis-Diez and Bustamante (2005) investigated frequency-dependent seed-size predation on the same species but manipulated absolute seed density. They hypothesized that at low density, seed consumption should be pro-apostatic whereas at high density, seed consumption should switch to anti-apostatic. Celis-Diez and Bustamante found that larger seeds were always preferred irrespective of frequency and absolute seed density. Contrary to their hypotheses, predation at high density was frequency independent while at low density it was anti-apostatic, which corresponds with their previous results when they did not manipulate seed density (Celis-Diez *et al.*, 2004). They argued that selective responses to seed predation need to be assessed with short-term experiments because in their study most of the responses were concentrated at the beginning of the experiment, and hence pointed to strong density-dependent effects. It is most likely that, above a certain threshold, seed depletion made the patch unattractive.

In this study, we ask whether two different but functionally similar granivores (the harvester ant *Pogonomyrmex rugosus* and a community of heteromyid rodents) of the Sonoran Desert exert selective pressure on seed size in *Dithyrea californica*. If granivores prefer to consume larger rather than smaller seeds, there will be selective conflict selection in the post-germination stages because, post-germination, selection on seed size tends to benefit larger seeds in *D. californica*. This is because plants originating from larger seeds survive more days and also produce more seeds (Larios *et al.*, 2014). We address three questions related to the removal of seeds by granivores in relation to seed size. First, do granivores prefer to consume larger rather than smaller seeds? We hypothesize that both ants (H1) and rodents (H2) will prefer larger seeds because large seeds are the most profitable phenotype that maximizes foraging efficiency. Second, do granivores display switching behaviour when confronted with the problem of selecting differently sized seeds that vary in relative frequency? We hypothesize that both granivores will prey upon the most profitable phenotype regardless of their relative frequency in the environment. In other words, neither ants (H3) nor rodents (H4) will be influenced by relative frequency of seed sizes as posited by optimal diet theory (Hubbard *et al.*, 1982). Finally, does absolute seed density affect the foraging decisions of granivores? We hypothesize that a preference for large seeds will only decrease when the absolute density of large seeds diminishes (ants: H5 and rodents: H6). Alternatively, when the absolute density of small seeds increases, the preference for large seeds will not change (ants: H7 and rodents: H8).

MATERIALS AND METHODS

Study species

Dithyrea californica Harvey (Brassicaceae) is a winter annual native to the sand dune areas of the Lower Colorado subdivision of the Sonoran Desert. For the first few months after fall or winter germination, *D. californica* grows as a basal rosette. Then it bolts and reproduces, usually in February and March, dying by early April. The rest of the year *D. californica* exists as a population of seeds in the soil seed bank until the following germination-inducing winter rains, which may occur at any time between October and January. During this period, seeds experience high predation, especially those seeds that do not get buried in the dunes early and become part of the soil seed bank (Price and Joyner, 1997).

Granivorous species

The community of heteromyid rodents used in the preference experiments was first sampled in order to determine the number of species and their abundances at the site. We used a mark-recapture technique that assumes a constant capture probability and also that the population is closed to emigration, immigration, births, and deaths (Schnabel, 1938). On three consecutive nights, we captured rodents with Sherman traps (H.B. Sherman Traps, Inc., Tallahassee, FL) arranged in two 7 × 7 quadrats with traps placed 15 m apart (for a summary of species and estimated densities, see Table A1: www.evolutionary-ecology.com/data/3098Appendix.pdf). There were three species of heteromyid rodents in the site (*Dipodomys desertii*, *Dipodomys merriami*, and *Chaetodipus penicillatus*) and one species of murid rodent (*Peromyscus eremicus*). Murid rodents are not seed specialists and although they could have visited our trays, their abundance was very low. *Dipodomys desertii* and *D. merriami* are kangaroo rats that forage for seeds in open spaces, while *C. penicillatus* is a pocket mouse that forages under shrubs (Phillips *et al.*, 2000). By placing our trays in the open, we largely excluded *C. penicillatus* from the experiment and left the two species of kangaroo rats to forage our experimental treatments. We also corroborated the presence of kangaroo rats by studying tracks in the sand in the morning before recovering the sand (Fig. B1, 3098Appendix.pdf). Kangaroo rats leave easily recognizable tracks on the sand from which their hind legs and long tails can be readily identified.

The ant *Pogonomyrmex rugosus* is a seed specialist and a central place foraging ant species that carries single seeds from the foraging patch to the nest. We minimized the effect of distance from the patch to the nest by offering the experimental treatments just outside their nests.

Preference experiments

In order to test our hypotheses that (1) desert granivores will prefer larger seeds and (2) prey upon larger seeds of *D. californica* regardless of relative frequency, and that (3) larger seed absolute density will make predators display a switching behaviour, we set up two preference experiments (one for rodents and one for ants) in which we manipulated seed size and frequency of large to small seeds at two densities.

Rodent preference experiment

This experiment was performed on 28 and 29 May 2015 in semi-stabilized dunes of Gran Desierto within Reserva de la Biósfera el Pinacate y Gran Desierto de Altar (31°49′20″N, 113°43′08″W). We offered seeds in 47 cm × 36 cm plastic trays filled with local sand placed outside rodent burrows. Sand was sieved with a 1-mm Archeology sieve (Stoney Knoll Inc., Stockton Springs, ME) in order to remove any *D. californica* or other seeds. Large seeds were added at high frequency (3 : 1 ratio) to half of the trays and at low frequency (1 : 3 ratio) to the other half. In the laboratory, we designated two seed size categories representing the extreme quartiles of the natural distribution of seed size. Small seeds ranged from around 2 mm to 3.36 mm (standard sieve #6) and large seeds ranged from 4.76 mm to around 6 mm (standard sieve #4). We also manipulated the absolute number of seeds so that trays with high seed density contained 100 seeds per tray and trays with low seed density had 28 seeds per tray. Therefore, the high-density treatments had trays with 75:25 or 25:75 large to small seeds, and the low-density treatments had trays with 21:7 or 7:21 large to small seeds. We offered all four treatments simultaneously at each burrow in a randomized block design replicated 16 times. We used a randomized block design instead of a fully randomized one tray per burrow because of the low number of burrows in the site. The rodent preference experiment was set at dusk and left overnight for rodents to forage. Sand and the remaining seeds were recovered before dawn. The recovered sand and seeds were placed in heavy-duty plastic bags and analysed in the laboratory. Prior to initiating this experiment, we acclimated the rodent community to trays with food by setting them out for a week with a mixture of commercial birdseed (sunflower and millet seeds) previously sterilized in a microwave oven.

Ant preference experiment

This experiment was performed on 19 and 20 June 2015, 10 km southwest of Hermosillo, Sonora, Mexico (29°00′27″N, 111°02′09″W) with a population of a harvester ant *Pogonomyrmex rugosus*. We offered seeds to ants in 8.5-cm diameter petri dishes filled with the same sieved sand from the rodent preference experiments. Half of the dishes had large seeds at high frequency (3:1 ratio) and the other half at low frequency (1:3 ratio). We also chose two seed size categories from the extreme quartiles of the natural distribution of seed sizes of the species as with the rodent experiment. The high- and low-density petri dishes contained 40 and 12 seeds per dish respectively. Therefore, the high-density treatments had 30:10 or 10:30 large to small seeds, and the low-density treatments had 9:3 or 3:9 large to small seeds. We also offered all four treatments simultaneously per ant mound in a randomized block design replicated around 20 ant mounds. The ant preference experiment was set at dawn and left for 4 hours, i.e. during the morning period of ant activity. We did not perform any acclimation for ants but they responded readily to the presence of seeds of *D. californica* without it.

Data analysis

Preference estimation

Preference was calculated using the maximum likelihood estimator for the case where initial food densities become depleted without replacement:

$$\hat{\alpha}_i = \frac{\ln[(n_{i0} - r_i)/n_{i0}]}{\sum_{j-1}^{m} \ln[(n_{j0} - r_j)/n_{j0}]}, \qquad i = 1, \ldots, m \tag{1}$$

where n_{i0} is the number of seeds of type i at the beginning of the experiment and r_i is the number of seeds of type i removed (Chesson, 1983). The resulting preference estimates are proportions summing to 1. Since our experiment used only two phenotypes, a preference for small seeds is complementary to a preference for large seeds (i.e. when preference for large seeds is 1, preference for small seeds is 0), and so we only analysed preference for large seeds, as analyses of small seeds would be redundant. We applied a bias correction to our preference estimates using a quadratic approximation (eq. 10 in Appendix C, 3098Appendix.pdf) because the estimates are non-linear functions of the data, by formula (1). This means that bias occurs in small samples due to Jensen's inequality (Needham, 1993).

Model selection

Because the experiments were performed on two consecutive days in a randomized block design, we first used linear mixed-effect models with bias-corrected alpha estimates as a function of frequency, density, and granivore identity as fixed effects, and date within block and block as random effects for each hypothesis test. We then performed a likelihood ratio test to determine whether the models with or without random block and date effects fitted the data better. In all cases the test was non-significant, so for all analyses we used the simpler model without block and date effects. We also logit-transformed preference as suggested by Warton and Hui (2011). We then compared the AIC of models of preference for large seeds with and without the logit transformation. In all cases, the model without transformation gave a better fit, so we present all analyses below using untransformed preference values.

Seed size preference

For all analyses, we used the bias-corrected preference for large seeds as the response variable. In order to test hypotheses 1 and 2 (H1 and H2), whether granivores prefer to consume large seeds rather than small seeds, we used a two-tailed Student's *t*-test for each treatment combination in order to compare whether the mean preference for large seeds ($\alpha_{\mathbf{large}}$) was significantly higher or lower than 0.5, separately for rodents and ants (Chesson, 1983). We used the function *t.test* from the R package *stats* (R Development Core Team, 2008).

Preference in relation to relative frequency

To test hypotheses 3 and 4 (H3 and H4), whether granivores prey upon seeds of different sizes in a frequency-independent manner when confronted with different relative frequencies of seed sizes, we analysed preference for larger seeds as a function of relative frequency and absolute density with ordinary least squares.

Preference in relation to absolute density of large and small seeds

We tested hypotheses 5 and 6 (H5 and H6), whether granivores' preference for large seeds will change when absolute density of large seeds changes, using preference for large seeds as our response variable and absolute large-seed density as our explanatory variable. In this hypothesis test, we only compared those treatments that differed most in large-seed absolute density (for ants: 30:10 vs. 3:9 large to small seeds; for rodents: 75:25 vs. 7:21 large to small seeds). This way we were able to contrast only the change in absolute density of large seeds. To test hypotheses 7 and 8 (H7 and H8), whether preference for large seeds will change when absolute density of small seeds changes, we used preference for large seeds as our response variable and absolute small-seed density and granivore identity as our explanatory variables. Similar to the previous hypothesis test, we only compared the two treatments that differed most in small-seed absolute density (for ants: 10:30 vs. 9:3 large to small seeds; for rodents: 25:75 vs. 21:7 large to small seeds).

RESULTS

Seed size preference

In support of hypothesis 1, *Pogonomyrmex rugosus* showed a mean preference for larger seeds of 0.695 (± 0.085); *P. rugosus* preferred to consume larger seeds in all treatment combinations except when larger seeds were more common at low absolute density (Table 1; Fig. D1, 3098Appendix.pdf). Mean bias-corrected preference values with confidence intervals for each treatment combination are presented in Table 1.

Heteromyid rodents showed a mean preference for larger seeds of 0.49 (± 0.084), failing to reject null hypothesis 2 that preference values differ from 0.5. Heteromyid rodents also did not show a marked preference for seed size except when larger seeds were more common at low absolute density where preference for larger seeds was marginally non-significant ($P = 0.058$, Fig. 2; and Table D2, 3098Appendix.pdf).

Preference in relation to relative frequency

As posited by hypothesis 3, there was no indication that preference for large seeds of *Pogonomyrmex rugosus* was influenced by the relative frequency of seed sizes present in the experiment ($P = 0.58$, Fig. 1a, Table 2). Neither absolute density of seeds ($P = 0.235$, Fig. 1a, Table 2) nor the interaction between frequency and absolute density ($P = 0.17$, Fig. 1a, Table 2) had a significant influence on preference. As proposed by hypothesis 4, heteromyid rodent preference for large seeds was not significantly influenced by the relative frequency of seed sizes ($P = 0.8$, Fig. 1b, Table 2). Absolute density of seeds did not have a significant influence on this relationship ($P = 0.16$, Fig. 1b, Table 2); however, the interaction between frequency and density was marginally non-significant ($P = 0.07$, Fig. 1b, Table 2), and the significant three-way interaction (Appendix E, 3098Appendix.pdf) implies that rodents and ants show different density–frequency interactions. However, none of these results provide strong evidence of frequency- or density-dependent foraging behaviour in ants or rodents.

Table 1. Results of Student's *t*-tests of the bias-corrected preference for seed size for all treatment combinations

Granivore	Treatment	Mean	CI	*t*	*df*	*P*
Ants	Large 75% – High density	0.733	(0.597, 0.869)	3.749	12	0.002
	Large 75% – Low density	0.579	(0.262, 0.896)	0.594	7	0.5706
	Small 75% – High density	0.67	(0.538, 0.803)	2.842	11	0.01602
	Small 75% – Low density	0.76	(0.534, 0.985)	2.57	10	0.02775
Rodents	Large 75% – High density	0.507	(0.375, 0.638)	0.11	14	0.9104
	Large 75% – Low density	0.70	(0.489, 0.911)	2.44	5	0.05848
	Small 75% – High density	0.482	(0.322, 0.642)	–0.23	16	0.8166
	Small 75% – Low density	0.353	(0.121, 0.586)	–1.42	9	0.1884

Note: Mean preference values > 0.5 represent a preference for larger seeds while mean values < 0.5 represent a preference for smaller seeds. CI represents confidence intervals of mean preference values.

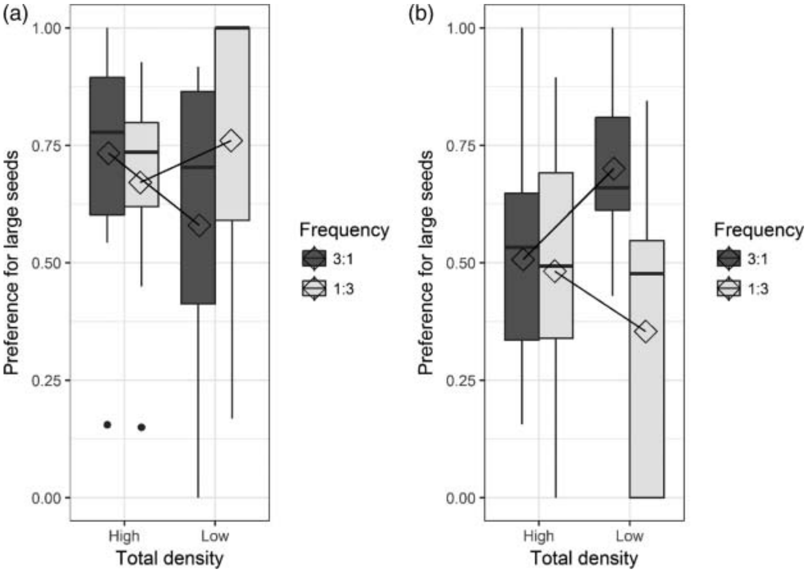

Fig. 1. Preference for large seeds (α_i) as a function of absolute density and relative frequency (large : small) of seed sizes: (a) *Pogonomyrmex rugosus* ($n = 47$), (b) heteromyid rodents ($n = 48$). Upper and lower box limits correspond to the first and third quartiles (the 25th and 75th percentiles). Diamonds represent means; dots represent outliers.

Table 2. Results of two-way ANOVA of the bias-corrected preference for larger seeds as a function of frequency of seed sizes (3 : 1 and 1 : 3) and absolute seed density (12 and 40 for *Pogonomyrmex rugosus*, 28 and 100 for heteromyid rodents)

Granivore	Parameter	SS	*df*	*F*	*P*
Ants	Density	0.1169	1	1.456	0.235
	Frequency	0.0244	1	0.3037	0.585
	Frequency × Density	0.1569	1	1.9535	0.170
	Residuals	3.2123	40		
Rodents	Density	0.1607	1	2.0286	0.1614
	Frequency	0.0049	1	0.0619	0.8047
	Frequency × Density	0.2644	1	3.337	0.0745
	Residuals	3.4865	44		

Preference in relation to absolute density of large and small seeds

Contrary to the predictions of hypotheses 5 and 6, preference for larger seeds was not affected by changes in the absolute density of large seeds (*Pogonomyrmex rugosus*, $P = 0.82$, Fig. 2a; heteromyid rodents, $P = 0.185$, Fig. 2a). Hypotheses 7 and 8 were supported by our data because there were no significant differences in preference for large seeds when absolute density of smaller seeds was varied (*Pogonomyrmex rugosus*, $P = 0.496$, Fig. 2b; heteromyid rodents, $P = 0.126$, Fig. 2b), in line with the predictions of optimal diet theory.

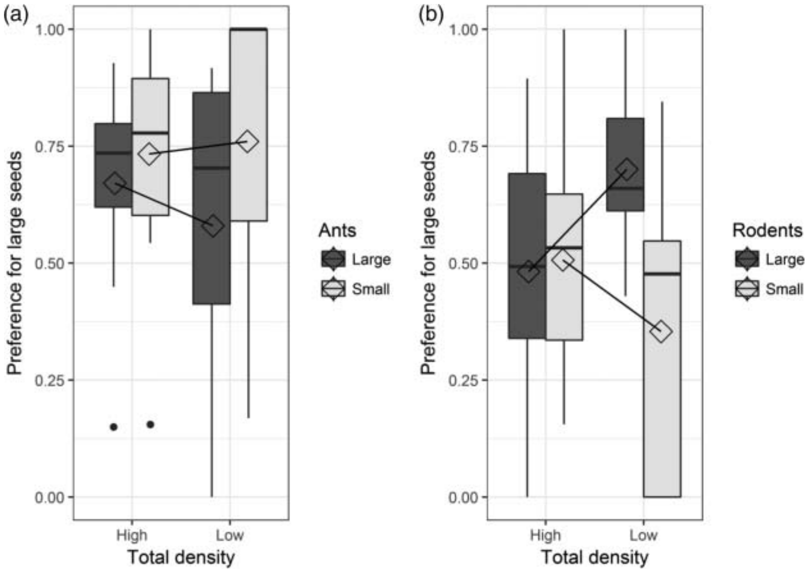

Fig. 2. Preference for large seeds (α_i) as a function of changes in absolute density of large and small seeds: (a) *Pogonomyrmex rugosus* ($n = 47$), (b) heteromyid rodents ($n = 48$). Dark boxes represent changes in absolute density of large seeds and lighter boxes represent changes in absolute density of small seeds. Upper and lower box limits correspond to the first and third quartiles (the 25th and 75th percentiles). Diamonds represent means; dots represent outliers.

DISCUSSION

In this study, we have shown that harvester ants and heteromyid rodents use different strategies when foraging and therefore exert different selective pressures on seed size in *Dithyrea californica.* Seed predation by the harvester ant *Pogonomyrmex rugosus* can result in selection on seed size in the opposite direction from selection in the post-germination stages because *P. rugosus* will benefit smaller seeds by preferring to consume larger seeds independently of their relative frequency and absolute seed density. This outcome represents a selective conflict because we have previously shown that large seeds have higher fitness post-germination (Larios *et al.*, 2014). Preference for larger seeds in *P. rugosus* was not significantly influenced either by the relative frequency of seed sizes or by the absolute density of seeds in the environment. Experiments with *Pogonomyrmex occidentalis* from the Great Basin Desert showed that larger seed size constrains seed removal rather than predicts it (Crist and MacMahon, 1991). On the other hand, a study on the foraging behaviour of *P. rugosus* in the Chihuahuan Desert showed that its foraging behaviour is mostly influenced by absolute density of those plant species that produce large quantities of seeds (Morehead and Feener, 1998). While most studies have focused on seed selectivity between species of seeds, no study has measured how relative frequency of seed sizes and absolute density influence behaviour towards different seed phenotypes. The community of heteromyid rodents did not demonstrate a general preference for differently sized *Dithyrea* seeds, but seed size selection might occur through other mechanisms. However, there is a weak but inconclusive suggestion that when absolute seed density is low, rodents display positive switching behaviour.

Selective conflicts on seed size between seed predation and other life stages have also been reported in other systems. Seed predation in *Crataegus monogyna* created a selective conflict with seed size selection during dispersal when frugivorous birds dispersed larger seeds more than smaller ones and seed predators (rodents) also preferred to consume the larger seeds (Martinez *et al.*, 2007). A fitness advantage of dispersing farther was assumed but not empirically verified in this study. A study on *Quercus ilex* found conflicting selective pressures on seed size between seed predation and post-germination selection on seed size as in the present study. During seedling establishment in *Q. ilex*, larger acorns have an advantage in terms of germination, emergence, and survivorship but also are highly preferred by wild boar and wood mice, thus cancelling those advantages (Gomez, 2004). This study, like many studies of the fitness consequences of seed size, only looked at the early stages (Marshall, 1986; Leishman and Westoby, 1994a, 1994b; Benard and Toft, 2007) of a plant without considering the effects of seed size into adulthood (Larios *et al.*, 2014).

Dithyrea californica has several advantages for a study of seed size in relation to fitness. It bears single seeded fruits (mericarps) that do not have any complex resource-demanding dispersal adaptations. Therefore, the evolution of seed size is not confounded by such things as the evolution of pulp content or nutrition in relation to dispersal. Also, seed predators make their foraging decisions upon individual *D. californica* seeds rather than groups of seeds within a fruit, so selective pressures operate directly on seed size rather than fruit size. Heteromyid rodents may prey upon multiple seeds in one foraging trip because they gather seeds into their cheek pouches; however, when selecting their prey they make their foraging decisions on individual seeds. Another advantage of this study is that *D. californica* is an annual plant. This makes the measurement of fitness (survival selection in this case) an easier task given that we are studying the fitness consequences of seed size in relation to seed predation throughout the life cycle of *D. californica*.

Differences in size and foraging behaviour of ants and rodents might explain why ants prefer to prey upon larger seeds and rodents do not. For an ant, variation in size of *D. californica* seeds might be more significant in relation to the allometric relationship between predator body size and prey mass, which is larger for ants than for rodents (Nakazawa *et al.*, 2013). Both rodents and ants are central place foragers so that they make repeated trips from their nest to the foraging patches (Orians and Pearson, 1979). However, a big difference is that ants forage individual seeds from patch to nest while rodents tend to accumulate seeds in their cheek pouches. So it might also be that for rodents, the total seed biomass is more important than individual seed size as an optimal foraging strategy.

It might be that different ecological circumstances lead to the evolution of predator behaviour that makes seeds experience frequency dependence of different strength and direction. Conflicting seed-size selection between seed predation and post-germination seed-size selection in the desert could then occur either in years where there is low seed production or in years where the seed bank becomes depleted after several years of drought. This work has highlighted that the behaviour of seed predators varies between taxa and that multiple selective pressures act in concert to determine the evolution of seed size in arid environments.

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