RESEARCH ARTICLE

Selection for seed size: The unexpected effects of water availability and density

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Abstract

1. Seed size is a functional trait with important fitness consequences that potentially extend throughout the life cycle of plants. *Dithyrea californica* experiences selection for larger seeds in postgermination stages but it is still uncertain how environmental factors mediate the strength and the direction of natural selection on seed size.

2. *Dithyrea californica* represents a unique opportunity to investigate selection on seed size in natural conditions due to a persistent seed ring that stays attached to the root throughout the plant's life. This makes it possible to unearth plants at any stage and measure the size of the seed from which they originated.

3. We conducted a factorial experiment manipulating water availability and intraspecific competition using plants that naturally germinated in the wild.

4. Selection on seed size via survivorship was nil because all individuals survived to reproduce. The strength and the direction of selection on seed size via fecundity depended on water availability and conspecific density.

5. Contrary to our predictions, increasing conspecific density relaxed directional selection favouring larger seeds, but only in the wettest conditions and an increase in water availability strengthened it, but only at low density. A possible explanation of these counter-intuitive results relies on the observed absence of survival selection and increased plant growth rates under high water and low density.

6. Larger seeds require more resources to construct, and when this cost is taken into account, there is no overall fitness increase with seed size. This nicely follows the life-history theory predictions for optimal seed size. At the evolutionary equilibrium, if seeds could be larger, per seed fitness would still increase, which is what we observed, but cost-corrected fitness should be flat. Maternal fitness equals per seed fitness times seed number, so any increase to per seed fitness of making a bigger seed is balanced by the resulting cost to seed number. Our results indicate flat cost-corrected fitness of seed size as theory predicts.

KEYWORDS
density, intraspecific competition, natural selection in the wild, selection on seed size, water availability

1 | INTRODUCTION

Seed size is a functional trait that affects offspring fitness and is therefore under selective pressure. The effects of seed size are not only important in early stages of offspring development, that is seedling survival and establishment (Dalling & Hubbell, 2002; Moles & Westoby, 2004a,b), but can also be important to adulthood affecting fecundity (Halpern, 2005; Larios, Burquez, Becerra, & Venable, 2014; Mojonnier, 1998; Simons & Johnston, 2000; Stanton, 1984; Susko & Cavers, 2008). In *Dithyrea californica,* there is selection for larger seeds in postgermination stages (plants originating from larger seeds survive longer and produce more seeds) but it is still uncertain how environmental factors such as water availability and intraspecific competition mediate the strength of selection on seed size and whether these effects operate consistently throughout the life cycle (Larios et al., 2014).

Selection on seed size depends upon limiting resources. In deserts, water is limiting and thus selection on seed size is expected to be strongly affected by water availability (Baker, 1972; Hallett, Standish, & Hobbs, 2011; Leishman & Westoby, 1994b). Increased water availability is hypothesized to relax natural selection on traits such as seed size that help overcome stressful circumstances. In water-limited environments, increased water availability boosts plant growth and increases the probability of survival at the seedling stage, regardless of seed size (Noy-Meir, 1973). Water availability is mediated by the amount of precipitation, which varies year to year and therefore should influence the dynamics of selection on seed size (Larios et al., 2014; Leishman & Westoby, 1994b).

Intraspecific competition is another selective force hypothesized to influence selection on seed size. Competition for limiting resources in plants creates very strong selective pressures that might influence all components of fitness: growth, survival and fecundity (Grace, 1990). Competition is mainly thought to affect selection on seed size through seedling mortality although the evidence that supports this idea is sparse (reviewed by Moles & Westoby, 2004b). In a previous study of *Dithyrea californica* in which a range of natural densities was used as a covariate to investigate survival selection on seed size, we found no evidence of mortality induced by competition (Larios et al., 2014). Furthermore, the evidence that competition might be influencing selection on seed size via fecundity (the number of seeds produced) is very scarce. Despite the lack of evidence of the influence of competition on selection on seed size, competition by definition is a negative interaction that should impact survival and fecundity in a negative way. Increased competition should strengthen selection on traits such as seed size that help overcome resource stress.

Water availability and competition are not independent in nature, and greater water availability may often increase competition. Depending on their relative strength, water availability and intraspecific competition could enhance, diminish or even cancel out the effects of seed size on fitness. For example, if water availability is positively correlated with competition, the selective effects on seed size may be opposing, resulting in uncertain net outcomes.

In addition to the direct influence of seed size on fitness, seed size is thought to evolve in the context of a life-history trade-off with the number of seeds that a maternal plant can produce (Smith & Fretwell, 1974). For a given amount of resources available to a parent plant, seed size and number constrain one another and this affects fitness (Shaanker, Ganeshaiah, & Bawa, 1988). The life-history theory of seed size evolution recognizes that increasing seed size has an allocation cost to the maternal plant that is usually framed in terms of reduction in the number of the larger seeds that can be produced for the same amount of resources available to make seeds (Smith & Fretwell, 1974). A plant gains fitness through both seed size and number, thus selection on seed size must balance the fitness costs and benefits of a change in seed size. As selection on seed size is usually modelled from the parental point of view, it will be influenced by any change in seed number required to compensate for a change in seed size. Thus, the fitness consequences of a change in seed size need to be corrected to account for the associated allocation cost on fitness. Seed size and variation in seed size are also thought to be bet hedging traits that can evolve in response to environmental variation (Olofsson, Ripa, & Jonzén, 2009; but see Rees, Jessica, Metcalf, & Childs, 2010).

In this study, we ask: What are the independent effects of competition and water availability on natural selection for seed size, and do they interact? Also, how does the answer differ when the cost of changing seed size is taken into account? To answer this, we performed a factorial experiment where we independently varied water availability and conspecific density, to disentangle their potentially opposing effects on seed size selection. To increase realism, the experiment was conducted in a natural population with naturally germinated plants. We measured selection on seed size operating via survivorship and fecundity during the whole postgermination stage of *Dithyrea californica's* life cycle. Water additions were used to simulate potential precipitation variation across years and thinning simulated natural variation in density. In unmanipulated conditions, conspecific density has been found to have a negative impact on fecundity (number of seeds produced and the average size of seeds produced) in *Dithyrea californica* (Larios & Venable, 2015; Larios et al., 2014), but not on seed size selection. While there are many advantages of measuring selection in natural and unmanipulated conditions, it is difficult to disentangle the multiplicity of environmental factors that could be affecting fitness (Primack & Kang, 1989). By independently manipulating water and density, we can measure the effect of competition under different moisture scenarios.

The hypotheses for this study concern to two main components of selection: selection operating through survivorship and through fecundity. We hypothesized that H1: plants originating from larger seeds will have higher probability of surviving to reproduce and will produce more seeds than plants originating from smaller seeds, regardless of water and competition levels. H2: Increased water levels will be beneficial for plant performance and therefore will increase the probability of survival to reproduction and the number of seeds produced. In consequence, an increase in moisture should relax directional selection for larger seeds, and H3: increased competition

will be detrimental to plant performance and hence will decrease the probability of survival to reproduction and the number of seeds produced. We expect that an increase in the number of conspecific neighbours should strengthen directional selection for larger seeds. Finally, H4: any overall advantage of larger seeds should disappear when the cost of making larger seeds is accounted for (i.e. seed size is at an optimum).

2 | MATERIALS AND METHODS

2.1 | Study species

Dithyrea californica is a widespread winter annual plant of dune habitats in the Lower Colorado River Subdivision of the Sonoran Desert (Felger, 2000). It has a special feature which makes it ideal for investigating the ecology of seed size: a seed "ring" that persists on the taproot through the life of the plant providing a permanent record of the size of the seed from which the plant originated. Each fruit usually produces two disc-shaped mericarps deployed side by side, reminiscent of eyeglasses (hence the common name, Spectacle pod mustard). Each mericarp, consisting of a single seed plus associated ovarian tissue, individually dehisces from the mother plant and functions ecologically as a dispersal unit. Each mericarp (which we call a seed) has a persistent ring (an induration of the pericarp on the rim of each disc) that stays attached to the root for the life of the plant. Using the diameter of the persistent seed ring, we can keep track of the seed size of undisturbed individual plants that germinate naturally. This has allowed us to easily measure natural selection on seed size in the wild and provides a good retrospective measure of seed mass (See Supporting Information Figure S1 in Larios et al., 2014). *Dithyrea californica* typically germinates in response to late fall or early winter rains in the Sonoran Desert. Germination of this species, along with the rest of the community of dune desert annuals, responds to as little as 10 mm of rain (Bowers, 1996, also E. Larios, personal observation). However, seedlings germinating with so little rain would require additional rain to survive and reproduce. Once germinated, *D. californica* grows as a basal rosette for approximately two months, eventually bolting and reproducing, usually from late February to early April.

2.2 | Water/density experiment

We carried out a fully factorial field experiment where we randomly selected 134 naturally germinated *Dithyrea californica* seedlings and assigned them randomly to three water treatments and three densities. The experiment was conducted in the sand dunes at Sierra Blanca within the Reserva de la Biósfera El Pinacate y Gran Desierto de Altar, Sonora, México, (31°34′21.04″N, 113°29′27.96″W) during the winter of 2012. Mean annual precipitation at Sierra Blanca is approximately of 75 mm per year (Lancaster, Greeley, & Christensen, 1987). The plants studied in this experiment were from a single cohort which germinated after a 93-mm precipitation event that occurred from 4 November to 31 November 2011. This was the only

cohort of plants that germinated because this was the only precipitation event during 2011–2012 growing season. The amount of precipitation was determined at a local weather station managed by the Pinacate reserve (Texas Electronics TR-525I tipping bucket rain gauge). Water treatments consisted of two levels of artificial irrigation (Wet and Medium) and a control without any irrigation. Individual focal plants in the wet watering treatment were watered twice a week for a half an hour, totalling 3.78 L (one gallon) per week per plant and in the medium watering treatment were watered once a week for a half an hour, totalling 1.89 L (0.5 gallons) per week per plant. Artificial irrigation was set up with a 2,500-L tank (Rotoplas, Mexico) connected to a diaphragm pump (Pentair/ShurFlo, Costa Mesa, CA, USA) and a drip irrigation system (Supporting Information Figure S1). The irrigation system consisted of polyethylene tubing and one gallon-per-hour drippers (DIG Corporation, Vista, CA, USA). Drippers were placed next to each of the focal plants in each of the two water addition treatments (Supporting Information Figure S2). Water was applied for fourteen weeks from 6 December 2011 to 10 March 2012. 3.78 L per week of water poured in the soil is equivalent to 113 mm of rain per week (Martin & Baretto, 2011). However, artificial irrigation is less effective than natural precipitation in terms of plant responses due to soil evapotranspiration and diffusion into surrounding dry soil. Natural precipitation events are associated with changes in humidity, temperature and light levels, which also influence evapotranspiration and plant physiology. Targeted individual irrigation is very effective in sandy soil because water penetrates to the individual root system with no runoff so water will only reach target plants and their nearby competitors. Competitive neighbourhoods were defined as a circle with a 10 cm radius around a focal plant. This is the approximate area of resource depletion for *D. californica* and the area used in a previous observational study of density effects (Larios et al., 2014).

Density was manipulated by thinning high-density patches of *D. californica* once watering treatments were established. Selected seedlings of *D. californica* and all seedlings of other species were carefully thinned out with scissors at ground level without disturbing the soil or the remaining seedlings in the patch. Conspecific density treatments were high density (5 to 10 conspecific neighbours), medium density (two to four conspecific neighbours) and low density (no neighbours). Intraspecific competition has been shown to depress fecundity in this species (Larios et al., 2014). Intraspecific competition has also been found to be more predictive of *D. californica* performance than interspecific competition at our field sites. Density treatments were randomly distributed among watering treatments. As interspecific competition is low in this system, we removed all interspecific competitors for simplicity of design and interpretation. When plants died or started showing signs of senescence, we collected them and recorded whether or not they survived to reproduce. When individual focal plants reproduced naturally, we counted the number of seeds produced as a measure of fecundity. The final plant collection was done on 10 March 2012, before plants started showing signs of senescence and about the time when *D. californica* usually disperses its seeds.

2.3 | Data analysis

Our analysis of survivorship selection was simple: no plants died before reproducing so there was no variation in survival to reproduction hence no survivorship selection on seed size.

To analyse how selection acted on seed size through fecundity, we estimated relative fitness by dividing the numbers of seeds produced by each germinating plant by the population mean. As no plant in this experiment died before producing seeds, this per germinant fecundity is the same as the number of seeds per plant surviving to reproduce. We also standardized seed size by subtracting individual values from the population mean and dividing by the standard deviation as described by Lande and Arnold (1983). We then calculated selection on phenotypes using standard selection gradient analysis (e.g. see (Linnen & Hoekstra, 2009). Specifically, we regressed relative fitness as a function of standardized seed size, water, density and the two- and three-way interactions using a restricted maximum-likelihood procedure (sas 9.4 proc mixed). The coefficient of selection on seed size equals the slope of the regression of relative fitness on standardized seed size. The interaction of this slope with water and density describes the environmental dependencies of seed size selection that test our hypotheses.

While the analysis outlined above measures selection on seed size per se, to include consideration of the size-number trade-off, we conducted a second selection analysis on per germinant fecundity per unit seed cost, estimated as seed mass. This is equivalent to measuring fitness with seed size and number, assuming the cost of larger seed size is absorbed by a reduction in seed number. We first converted seed diameter to seed mass with the allometric equation reported in Larios et al. (2014). We then divided each seed mass by the population mean to get a seed cost correction factor with an average of 1. We then calculated fitness by dividing the number of seeds produced, by the seed cost correction factor. With this procedure, we are adjusting the fitness of a particular seed size by its cost which is traditionally thought of in terms of seed number. We then analysed this cost-corrected relative fitness as a function of standardized seed size, water, density and the two- and three-way interactions as described for the previous analysis.

3 | RESULTS

Plants produced an average of 202 (*SD* ± 176.6) seeds. The average seed diameter was 4.45 (*SD* ± 0.69) mm. Results from the analysis of selection on seed size through fecundity (uncorrected for the size/number trade-off) indicated statistically significant effects on relative fitness of standardized seed size, water, density, the two-way interaction between standardized seed size and water, the two-way interaction between standardized seed size and density, and the three-way interaction between standardized seed size, water and density (see Table 1). In the wettest conditions, the benefit of larger seed size for relative fitness increased as density decreased

(Figure 1, upper row graphs: WH, WM and WS). Thus, in the wettest conditions, higher density relaxed seed size selection rather than showing the predicted increase in selection for larger seeds. At medium and low density, adding more water increased the benefit of larger seed size to relative fitness, again contrary to our prediction (Figure 1, column graphs: WM, MM, DM; WS, MS, DS). Significant two-way interactions between standardized seed size and water, and standardized seed size and density, and the three-way interaction between standardized seed size, water and density provide statistical support for these patterns (Table 1).

This analysis shows the direct fitness benefits of seed size. When the allocation costs of larger seed size are included in the selection analysis, the benefits of larger seeds are reduced as reflected in less positive (or more negative) fitness/seed size regressions (Figure 2). The slopes are generally flatter and statistical interactions between density and water with seed size are less significant than the analysis of the fitness benefits of seed size (Table 2). The main effect of seed size is flat and nonsignificant. Density still affects seed size selection with flat or positive slopes becoming more negative as density increases. In the wettest condition, an increase in density appears to lead to a relaxation and a change in direction of the selection gradients (Figure 2, column graphs: WH, WM and WS) although the three-way interaction of water, density and seed size was not quite significant (Table 2).

4 | DISCUSSION

In this study, we showed that under experimental conditions, the strength and the direction of selection on seed size in *Dithyrea californica* were influenced by water availability and intraspecific competition that acted only via fecundity selection and not through survival selection. This is surprising as most studies of seed size selection show that larger seeds improve survival under stressful environments such as drought, shade or high density; especially during early stages (Bonfil, 1998; Dalling & Hubbell, 2002; Leishman & Westoby, 1994a,b; Lloret, Casanovas, & Penuelas, 1999; Moles & Westoby, 2004a). In our study, 93 mm of natural precipitation in one

TABLE 1 Three-way ANOVA showing the significance of standardized seed size, water and density on relative fitness of seeds

Parameter	NDF	DDF	*F*	*p*
Seed size	1	112	11.63	0.0009
Water	2	112	10.40	<0.0001
Density	2	112	3.91	0.0227
Seed size × Water	2	112	4.96	0.0086
Seed size × Density	2	112	7.77	0.0007
Water × Density	4	112	1.70	0.1550
Seed size × Water × Density	4	112	2.91	0.0247

Note. NDF, numerator degrees of freedom; DDF, denominator degrees of freedom; *F*, *F* statistic; *p*, *p* value.

week in November (~20% more than the average annual precipitation) was enough to result in 100% survival to reproductive maturity, even in the control treatment with no water added. Universal survival to reproduction following a large germination inducing rainfall event with no follow-up rain for the rest of the season is not surprising given the high water-use efficiency of Sonoran Desert annuals (Smith, Monson, & Anderson, 1997).

While the effect of seed size on fitness tended to be positive overall (e.g. the positive main effect of seed size on fitness was highly significant), when the allocation cost of making larger seeds was accounted for, it tended to cancel out the benefits of seed size, as can be seen in the nonsignificant main effect of seed size on cost-corrected fitness. This is an interesting result that is congruent with life-history theory on offspring size/number evolution. Theory predicts that at the fitness-maximizing seed size, seeds would still benefit from an increment in size, but for a maternal plant, that offspring benefit is cancelled by the associated increase in the cost of making each seed and the consequent fitness decline from reduced seed number (Smith & Fretwell, 1974). Our finding of positive selection on seed size but flat cost-corrected selection on seed size matches these predictions nicely.

We hypothesized that an increase in competition would strengthen selection for larger seeds, but it relaxed it. Similarly, we predicted that increased water availability would relax selection for larger seeds, yet the effect of competition on selection for seed size was strongest when water availability was at the highest level (Figures 1 and 2). For seed size, increasing density erased the fitness benefit of larger seeds. When selection for larger seed size was corrected for the associated allocation cost, selection in the wettest treatment goes from favouring larger seeds at low density to favouring smaller seeds at high density.

Why the discrepancy with expectations? Much of the work suggesting that larger seed size is advantageous under high density or water stress has focused on seedling survival (Black, 1958; Bonfil, 1998; Cideciyan & Andrew, 1982; Dalling & Hubbell, 2002; Lloret et al., 1999; Lönnberg & Eriksson, 2013; Moles & Westoby, 2004a; Pitelka, Thayer, & Hansen, 1983; Schaal, 1980). Yet, this was not relevant in our field experiment in which 100% of seedlings survived to reproduce. Hence, any selection on seed size in our study operated through the seldom studied growth and reproductive phases of the life cycle. It seems likely that removing competition and adding water strengthened fecundity selection
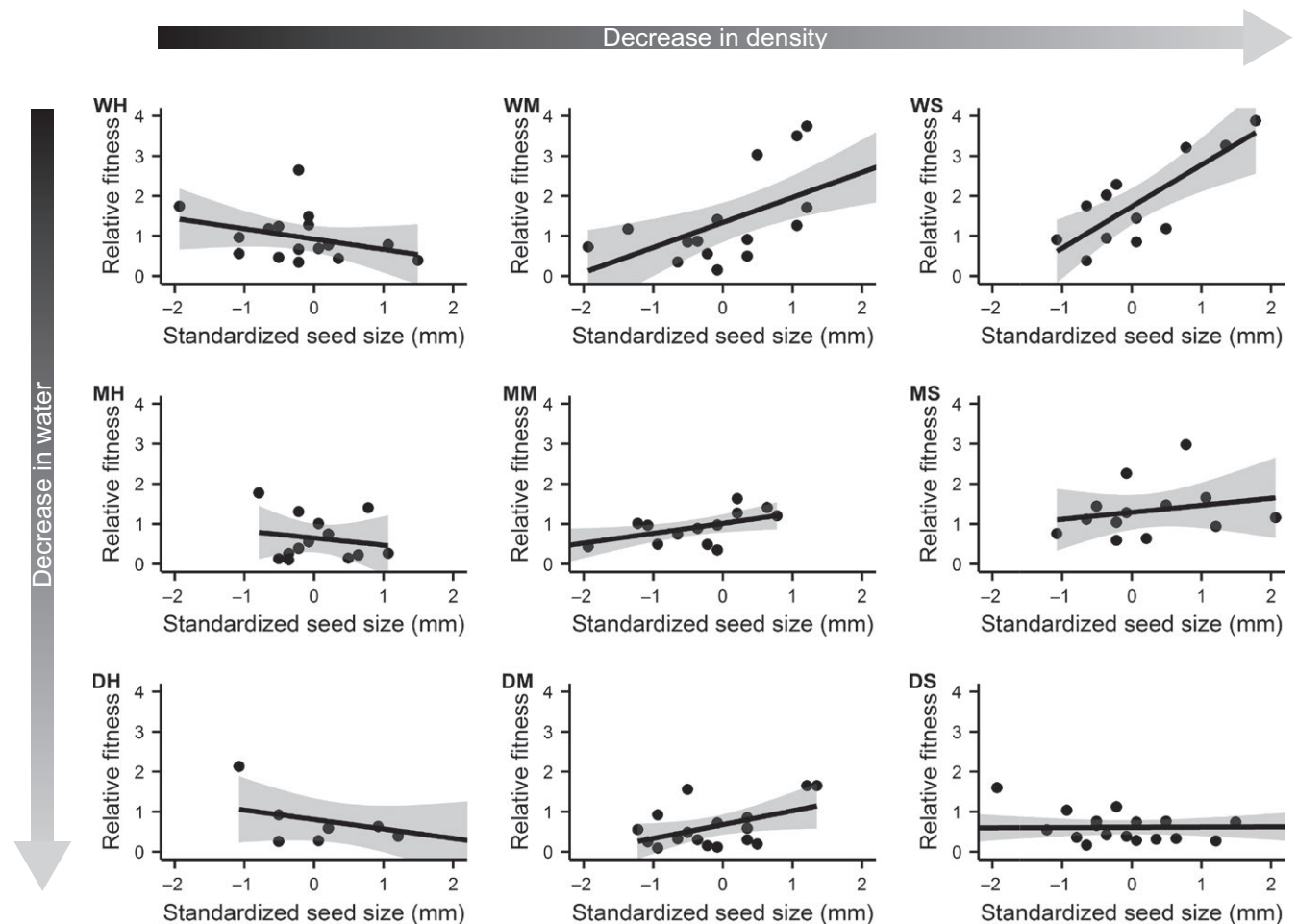

FIGURE 1 The relationship between relative fitness and standardized seed size for each of the nine treatment combinations. WH = high water with high density, WM = high water with medium density, WS = high water with no neighbours; MH, MM, MS = medium water with high, medium or low density; DH, DM, and DS = low water with high, medium or low density
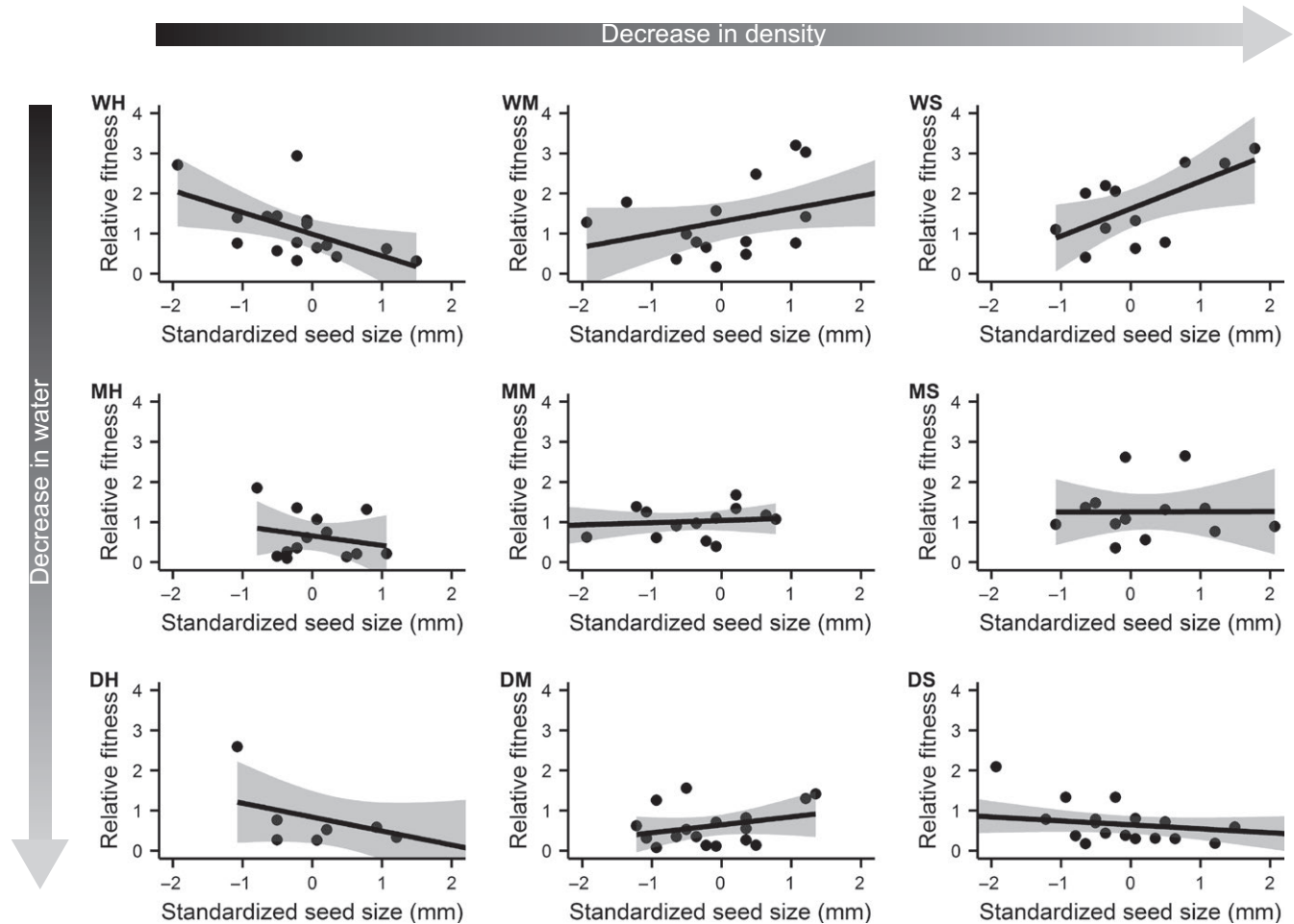
FIGURE 2 Relationship between relative fitness corrected by the size/number trade-off and standardized seed size of each of the nine treatments in the experiment. WH = high water with high density, WM = high water with medium density, WS = high water with no neighbours; MH, MM, MS = medium water with high, medium or low density; DH, DM, and DS = low water with high, medium or low density

for larger seeds by removing impediments to higher plant growth rates. These higher growth rates amplified initial plant size differences and ultimately seed production differences, creating steeper slopes of fitness vs. seed size (Figure 3). Under this interpretation, the special conditions that resulted in the counterintuitive effects of competition and water availability are, first, a huge seedling survival-enhancing rainfall event which moved any selective effects of seed size from survival to the growth and reproductive stages. Second, the absence of any subsequent rain meant that water addition, especially when combined with thinning, enhanced plant growth rate substantially. Having zero or little seedling mortality is not that likely for most plants, but may occur now and then with favourable conditions for annual plants of open habitats. When it does happen, any selective effects of seed size will occur during the growth and reproductive phases of the plant life cycle. When this occurs, selection on seed size is likely to be stronger when water availability is high and competition is low permitting faster plant growth rates (Figure 3). How likely are the different combinations of water and density in desert annual habitats? Given the high fluctuations in density of desert annuals, all combinations are likely to occur now and then.

TABLE 2 Three-way ANOVA showing the significance of standardized seed size, water and density on relative cost-corrected fitness

Parameter	NDF	DDF	F	p
Seed size	1	112	0.00	0.9569
Water	2	112	8.62	0.0003
Density	2	112	2.73	0.0695
Seed size × Water	2	112	1.39	0.2533
Seed size × Density	2	112	6.10	0.0031
Water × Density	4	112	1.56	0.1907
Seed size × Water × Density	4	112	2.04	0.0932

Note. NDF, numerator degrees of freedom; DDF, denominator degrees of freedom; *F*, *F* statistic; *p*, *p* value.

For example, high water, low-density conditions might occur in a wet year after several years of seed bank depletion due to good germination conditions followed by bad growth and reproductive conditions.

Previous studies of selection on seed size and competition that followed the fate of plants through reproduction are rare, confined
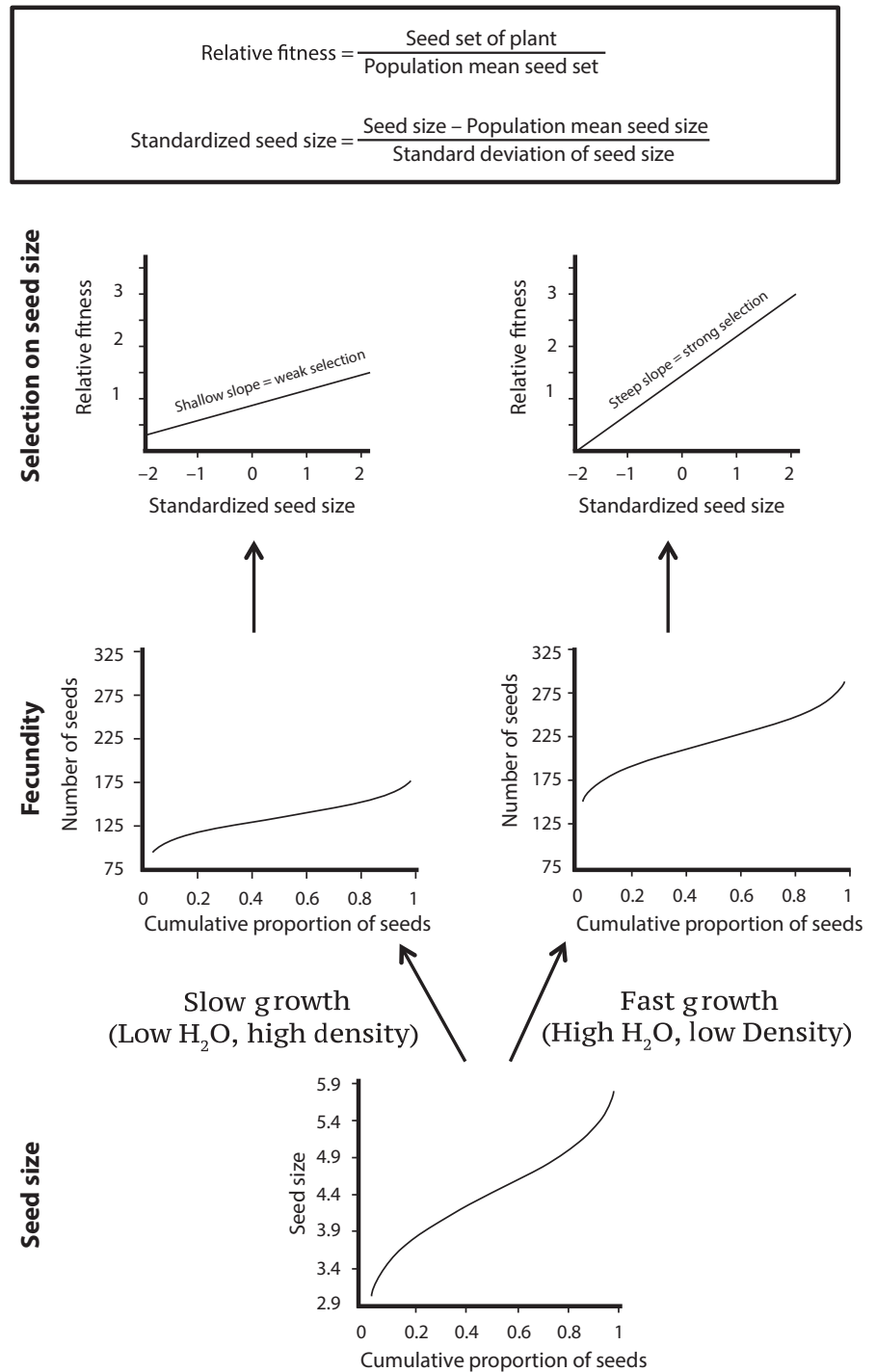
$$\text{Relative fitness} = \frac{\text{Seed set of plant}}{\text{Population mean seed set}}$$

$$\text{Standardized seed size} = \frac{\text{Seed size} - \text{Population mean seed size}}{\text{Standard deviation of seed size}}$$

FIGURE 3 Conceptual framework for the unexpected effects of water availability and density on natural selection on seed size in the desert annual *Dithyrea californica*. Bottom graph: a population of seeds with normally distributed seed sizes. Middle graphs: final fecundity distribution is determined by final plant size after slow vs. fast exponential growth of plants from seeds of different sizes. If all plants survive to reproduce, fitness differences will be due to these fecundity differences. Top graphs: the selection coefficient is given by the slope of the regression of relative fitness on standardized seed size. This slope is steeper (= stronger selection on seed size) for plants that experienced high water and low density. Relative fitness and standardized seed size are defined in the box at the top following Lande and Arnold (1983)

to pot experiments in glasshouses and tend to show different patterns from ours. In *Thlaspi arvense*, larger seeds had a biomass advantage in a low nutrient environment regardless of plant densities but in a high nutrient environment plants originating from larger seeds were bigger only at high density (Susko & Cavers, 2008). The effect of seed size on reproduction for *Desmodium paniculatum* was studied by Wulff (1986) who found no difference in total seed weight produced by plants from large and small seeds grown in isolation but higher total seed weight for plants from large when grown in competition against plants derived from small seeds. In both of these experiments, plant growth was constrained by limited soil volume in pots. This removed the dynamic we suggest gave rise to our contrary result: the enhancement of fecundity selection by the removal of constraints to higher plant growth rates which amplify initial plant size differences.

One additional component of fitness in relation to seed size that we did not measure in this experiment is the seed to seedling transition. As *D. californica*, like other desert annual plants, often has a persistent seed bank, a single cohort of seeds of this species would emerge in multiple years, making the measurements of the

seed to seedling transition very difficult. However, previous studies on this system have provided evidence regarding this demographic transition. In an observational study in field conditions, larger seeds had a higher probability of germination, and germination probabilities were significantly different from year to year, suggesting that water availability and seed size influence the germination dynamics of these seeds (Larios et al., 2014). Furthermore, in a growth chamber experiment where we germinated *D. californica* seeds of varying seed sizes in Petri dishes with different water potentials and temperatures, larger seeds germinated faster than smaller seeds. Also, water potential influenced germination speed positively without interacting with seed size (E. Larios, unpublished data). Together, these results suggest that seed size affects germination and that the size of precipitation pulses might also influence the frequency of seed sizes of germinated plants. Presumably with little or no rain, very few seeds would germinate and differential germination by seed size would be minimal. With an intermediate amount of rain resulting in approximately 50% germination, there would be maximal seed size-dependent germination. With the high germination rain measured in this experiment, most viable seeds will germinate, again reducing the potential for differential germination of seeds of different sizes.

Seed size in *Dithyrea californica* is known to be affected by the competitive environment maternal plants experience in a given year and exhibits very low genetic variation as shown by parent–offspring regressions (Larios & Venable, 2015). This same study showed that genetic variance in *D. californica* seems to vary between populations and years. Genetic variation can vary between years in the same population because it can be influenced by the environment (Mazer & Wolfe, 1992; Miller & Weiner, 1989). Genetic variation in seed size is very low in general (Antonovics & Schmitt, 1986; Biere, 1991; Montalvo & Shaw, 1994; Platenkamp & Shaw, 1993) with some exceptions where genetic variance is high (Mazer & Wolfe, 1992; Zas & Sampedro, 2014). It is still unknown whether precipitation or competition is able to influence genetic variation in seed size in *D. californica*. It is also not known whether conditions exist to favour the evolution of seed size through the evolution of plasticity of seed size. A controlled experiment with a quantitative genetics component using plants from different populations cultivated under a range of water availability and competition treatments could address these questions.

This investigation has helped to elucidate the effects of the environment on the selective dynamics of seed size in *Dithyrea californica*. Contrary to our predictions, increased conspecific density reduced the strength of selection on seed size. A large precipitation event ensured that water availability was high enough under all treatment levels so that seed size did not impact the probability of survival (all seedlings survived to reproduce) and allowed us to examine the effect of seed size on fecundity. These results demonstrate the importance of separating fitness into individual components because selective pressures might not operate equally at all life-history stages. They also highlight the value of estimating the independent and interacting effects of alternative environmental conditions on the strength and direction of natural selection of fitness-related traits.

AUTHORS' CONTRIBUTIONS

E.L. and D.L.V. conceived ideas, designed the experiment and analysed its data; E.L. collected data and led the writing of the manuscript. Both authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

A dataset for the selection experiment is available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.5vp4vs3 (Larios & Venable, 2018).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.