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Maternal adjustment of offspring provisioning and the consequences for dispersal

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Abstract. Phenotypic plasticity in seed provisioning is a widespread phenomenon in plant populations that is often manifested as environmentally induced maternal effects. Environmental maternal effects can be beneficial if they influence population dynamic functions of seeds in a way that increases fitness, such as escaping from crowding. Using the winter annual plant, *Dithyrea californica*, we studied the response of seed provisioning to the maternal competitive environment and the associated seed dispersal consequences. We measured the average size of seeds produced by plants experiencing different competitive environments in order to test the hypothesis that mother plants respond to crowding by providing fewer resources to each offspring. We also hypothesized that smaller seeds produced by crowded mothers would benefit from greater dispersal away from their high-density natal habitat. We marked seeds with fluorescent paint while still attached to the mother plant, recorded seed diameter, and followed them for nine months after dispersal, recording the distance they moved from the mother plant. Plants that experienced more competition produced smaller seeds that dispersed farther from their mother plant. Larger seed diameter was previously shown to be associated with greater competitive ability in *D. californica*. Thus the production of smaller seeds in more competitive environments implies a possible trade-off between competitive ability and dispersal arising from an environmentally driven aspect of phenotype. Fitness consequences of this trade-off in the context of the year-to-year variation in rainfall and density are uncertain.

Key words: competition; crowding; environmental maternal effects; heritability of seed size; seed dispersal; seed size.

INTRODUCTION

Environmental maternal effects are a particular form of phenotypic plasticity that occurs when the functional dynamics of the mother influences offspring phenotype in a way that is independent of offspring genotype. Maternal effects in plants can act during seed provisioning via maternal manipulation of the embryo or endosperm and the tissues surrounding the embryo and endosperm including the seed coat and sometimes fruit tissues. Maternal effects can vary depending on the environment experienced by the mother plant during growth and development, such as the competitive environment caused by crowding. Their consequences for offspring fitness can be beneficial (adaptive maternal effects; Galloway and Etterson 2007), but they can also be detrimental (Schuler and Orrock 2012). Environmental maternal effects can have ecological and evolutionary consequences as they may constrain or amplify the evolutionary response to selection and can alter offspring gene expression and selective environment

(Kirkpatrick and Lande 1989, Lande and Kirkpatrick 1990, Rasanen and Kruuk 2007, Donohue 2009).

Environmental maternal effects might result from plant size-dependent seed provisioning. They are expected to evolve in the context of ontogenetic constraints on plant function that enhance the fitness of the mother rather than that of the offspring per se (Marshall and Uller 2007). When the predictability of a variable offspring environment is high, maternal fitness can be enhanced by anticipating the offspring environment and modifying the offspring phenotype to improve offspring fitness and thereby increase maternal fitness. For example, competition experienced in the parental stage of an annual plant may be highly predictive of a high-density environment for non-dispersing offspring. Phenotypic plasticity in seed provisioning has been argued to be one of the main causes of seed size variation in natural plant populations (Schaal 1984). Considering that seed size is under strong selection and thus expected to have low genetic variability (Mousseau and Roff 1987, Charmantier and Garant 2005, Visscher et al. 2008), environmental variance is likely to be driving phenotypic variation in seed size in natural populations. In fact, studies of heritability of seed size in natural populations often show very low genetic variation (Winn 1988, Kalisz 1989, Schmid and Dolt 1994, Wolfe 1995, Mojonier 1998, Galloway et al. 2009).

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Competition can be a strong determinant of a plant's fitness since finite resources available for plant growth and reproduction have to be shared with neighbors in a patch. Yet, surprisingly, there are very few studies of the effects of competition on offspring provisioning. Plant species modify seed provisioning in response to competition in different ways. Some species manipulate the size of their offspring in response to competition either by producing larger offspring (Miao et al. 1991), or by making offspring size more variable (Violle et al. 2009). Violle et al. (2009) suggested that both enlarging and varying the size of the offspring are adaptive responses when facing competition ("adaptive response hypothesis") because bigger seed size confers higher competitive ability and variation in seed size reduces risk in variable environments. Violle and colleagues also proposed that a reduction in offspring size and number (passive response hypothesis) would be a maladaptive response because having less seed reserves would only exacerbate the negative effects of competition.

However, reducing seed size in the presence of competition might not be maladaptive if smaller seeds are more dispersive and thus able to escape competition (Muller-Landau 2010). Smaller seeds might be better able to travel longer distances by virtue of being lighter in mass, although this has mostly been studied in wind-dispersed species (Greene and Johnson 1986, Ezoe 1998). Nonetheless, this increased dispersal may come at the cost of competitive ability (Skarpaas et al. 2011). Theoretical formulations on the evolution of dispersal suggest that dispersing a fraction of the offspring is always adaptive even in constant environments due to avoidance of sibling interactions (Hamilton and May 1977). Spatiotemporal environmental heterogeneity will further favor the evolution of greater dispersal for two reasons. First because dispersal typically puts seeds in lower density sites on average, and also because dispersal may reduce variance of parent fitness due to averaging over variable unpredictable environments (Levin et al. 1984). The optimal dispersed fraction depends on the costs associated with dispersal such as the risk of predation by the seed disperser, landing in a crowded or unsuitable site, or lower probability of establishment due to diminished seed size (Venable and Brown 1993). When the cost of dispersing is zero, models suggest that it is adaptive to disperse all propagules (Hamilton and May 1977, Levin et al. 1984).

The objective of this paper is to determine whether or not crowding induced maternal effects on offspring provisioning can increase seed dispersal in a desert annual herb, *Dithyrea californica*. We ask the following questions: (1) What is the effect of competition on the average offspring seed diameter? (2) Are smaller seeds able to disperse farther than larger seeds? (3) Is there heritable variation in seed diameter? We predicted that mother plants that experience more competition would be smaller and produce smaller seeds, and that smaller seeds would disperse farther. We also predicted that

variation in seed size among plants would mostly be a plastic response to the environment rather than due to additive genetic variation.

MATERIALS AND METHODS

Study species

Dithyrea californica Harvey (Brassicaceae) is a winter annual plant from the Sonoran Desert that typically germinates from October to early January depending on the occurrence of the fall and winter rains. It grows as a basal rosette during the first few months after germination, eventually bolting and reproducing, usually in February and March. It subsequently dies, leaving only seeds in the soil to carry over until the next germination season or to form a persistent soil seed bank like most annual plants in the desert (Venable 1989, Philippi 1993, Pake and Venable 1996). The flat round seeds of *Dithyrea californica* disperse from their mother plant by wind and gravity, mostly falling around their mother. Once on the soil surface, seeds may subsequently be blown farther along with other debris consisting mostly dead plant matter. Seeds and debris tend to accumulate in dune depressions. Seeds of *D. californica* have an unusual feature that allows us to relate vital rates such as survival and fecundity to the size of the seed the plant originated from. Each fruit usually produces two mericarps, each mericarp consisting of a single seed plus associated ovarian tissue that individually dehisces from the mother plant and functions ecologically as a dispersal unit. Each mericarp (which we will call a "seed") has a persistent ring (an induration of the pericarp on its rim) that stays attached to the root for the life of the plant (Larios et al. 2014). Using the persistent seed ring, we can keep track of the seed size of undisturbed individual plants that naturally germinate, allowing easy measurement of parental seed (mericarp) size in the wild (see Appendix B). Seed ring diameter is a good predictor of seed mass (Larios et al. 2014). *D. californica* plants originating from larger seeds have been shown to have higher germination, survival, and fecundity rates than plants originating from smaller seeds especially in competitive environments (Larios et al. 2014).

Maternal provisioning as a function of crowding and plant mass

In two years, we gathered data on the average diameter of the seeds produced by plants, as well as dry mass of mother plants that experienced different amounts of competition. We used data from two desert populations: Sierra del Rosario, Sonora, Mexico (32°9'57.85" N, 114°7'15.46" W) in 2010, and Coachella Valley Preserve, California, USA (33°48'35.60" N, 116°19'56.45" W) in 2011. In order to measure the effect of competition on offspring provisioning, we marked seedlings at the cotyledon stage and counted the number of neighbors less than ten cm away from the base of each seedling. We followed individuals through

the whole growing season, and collected 87 plants with seeds still attached at the time of seed set from the two populations. Aboveground biomass was measured to the nearest 0.001 g using an analytical balance (Mettler Toledo Excellence XS105; Mettler Toledo, Columbus, Ohio, USA) after oven drying at 60°C to constant mass. Average offspring seed diameters were estimated from measuring a sample of seeds on each plant (from 30 to 50 seeds) using digital calipers. Separately for each population, we analyzed the effect of competition and plant mass on the average offspring seed diameters produced by individual mother plants with a path analysis using PROC CALIS in SAS (SAS Institute 2004). Path analysis allowed us to partition the total, direct, and indirect effects of competition and plant mass on the average size of seeds produced (see Fig. 1a). We also performed an ANCOVA with the *lm* function in R statistical package *stats* (R Development Core Team 2008), to test for differences between the two populations in the average offspring diameter as a function of the number of neighbors and plant mass.

Heritability of seed diameter

Heritability of seed diameter was estimated using measurements of seed diameters of parent–offspring pairs and mother plant dry mass from the same individuals used to measure maternal provisioning as a function of crowding in a natural field setting in the winters of 2010 in Sierra del Rosario and 2011 in Coachella Valley. Parent–offspring pairs in the wild can be measured in this species due to the unusual feature of seeds described in *Study species*. We estimated the heritability of seed diameter in each population separately with path analysis using the PROC CALIS in SAS software (SAS Institute 2004). Fig. 2a shows a path diagram with our hypothesized causal arrows. We assume that the maternal seed diameter effect operating on the average offspring seed diameter through plant mass is allometric rather than genetic, so we only used the direct effect of the maternal seed diameter on the average offspring seed diameter to estimate heritability. Since *Dithyrea californica* is self-incompatible, our regressions are for one parent–offspring regression, which should estimate one-half of the heritability (Falconer 1960). Finally, in order to detect population differences in heritability (maternal seed diameter \times population interaction), we analyzed the average offspring seed diameter as a function of maternal seed diameter and plant mass for the two populations with an ANCOVA with the *lm* function in R statistical package *stats*.

Seed dispersal as a function of seed diameter

In February of 2012, we spray-painted seeds still attached to mother plants with four differently colored fluorescent paints and pushed a numbered flag into the ground at the base of each plant to indicate the exact position of each mother especially after death. Because we had four different colors of fluorescent spray paint, we used groups of four plants naturally occurring in the

field and isolated from other groups by approximately 25 m. Each of the four plants within a group was assigned a different color of paint (fluorescent orange, yellow, pink and green) and all of its seeds were painted. Groups were isolated from each other also by a topographic change in the landform of the dune such that different groups of plants were either on the leeward or the windward sides of the dune. That ensured no overlapping dispersal between seeds of the same color from different plants. After all plants had dispersed their seeds and died, we came back in May, July, and November of 2012, to look for fluorescent seeds at night using an ultraviolet flash light. We searched for seeds in all directions up to 10 m from each mother plant using a measuring tape to record the dispersal distance. We also measured the diameter of each located seed with a pair of digital calipers. Each measured seed was then relocated at the same spot so it could continue to disperse. To make sure we did not lose the spot where the seed was initially located, we replaced the seed with a small coin while we were measuring its diameter. In order to determine whether smaller seeds dispersed farther than larger seeds, we analyzed dispersal distance as a function of seed diameter, date of sampling, and mother plant. Dispersal distance was log transformed in order to normalize the residual error. Because seeds were nested within different mother plants we used a linear mixed model with the *lme* function in the R package *nlme*, with seed diameter and date as fixed effects and the mother plant as a random effect. We performed likelihood ratio tests between the mixed model and a null linear model to determine the significance of the random effects and between random models with random intercept only and random intercept and slopes in order to determine the best random effect structure.

RESULTS

Maternal provisioning as a function of crowding and plant mass

In both Rosario and Coachella, the total effects of the number of neighbors were related negatively to the average diameter of seeds produced by mother plants (total path coefficients; Rosario = -0.493 , $P = 0.0001$, Fig. 1b; Coachella = -0.411 , $P = 0.0005$, Fig. 1c; Appendix A: Table A1). For every unit of increase in number of neighbors, average offspring seed diameter decreased 0.037 mm and 0.044 mm for Rosario and Coachella, respectively. The number of neighbors was also negatively related to $\ln(\text{plant mass})$ (path coefficients; Rosario = -0.729 , $P = 0.0001$; Coachella = -0.388 , $P = 0.001$; Table A1). For every unit of increase in the number of neighbors, $\ln(\text{plant mass})$ decreased 0.084 and 0.047 in Rosario and Coachella, respectively. Plant mass was positively related to average offspring seed diameter only in the Coachella population (path coefficients, Rosario = 0.297 , $P = 0.15$; Coachella = 0.476 , $P = 0.0001$; Table A1), so that for every unit increase in $\ln(\text{plant mass})$, offspring seed diameter

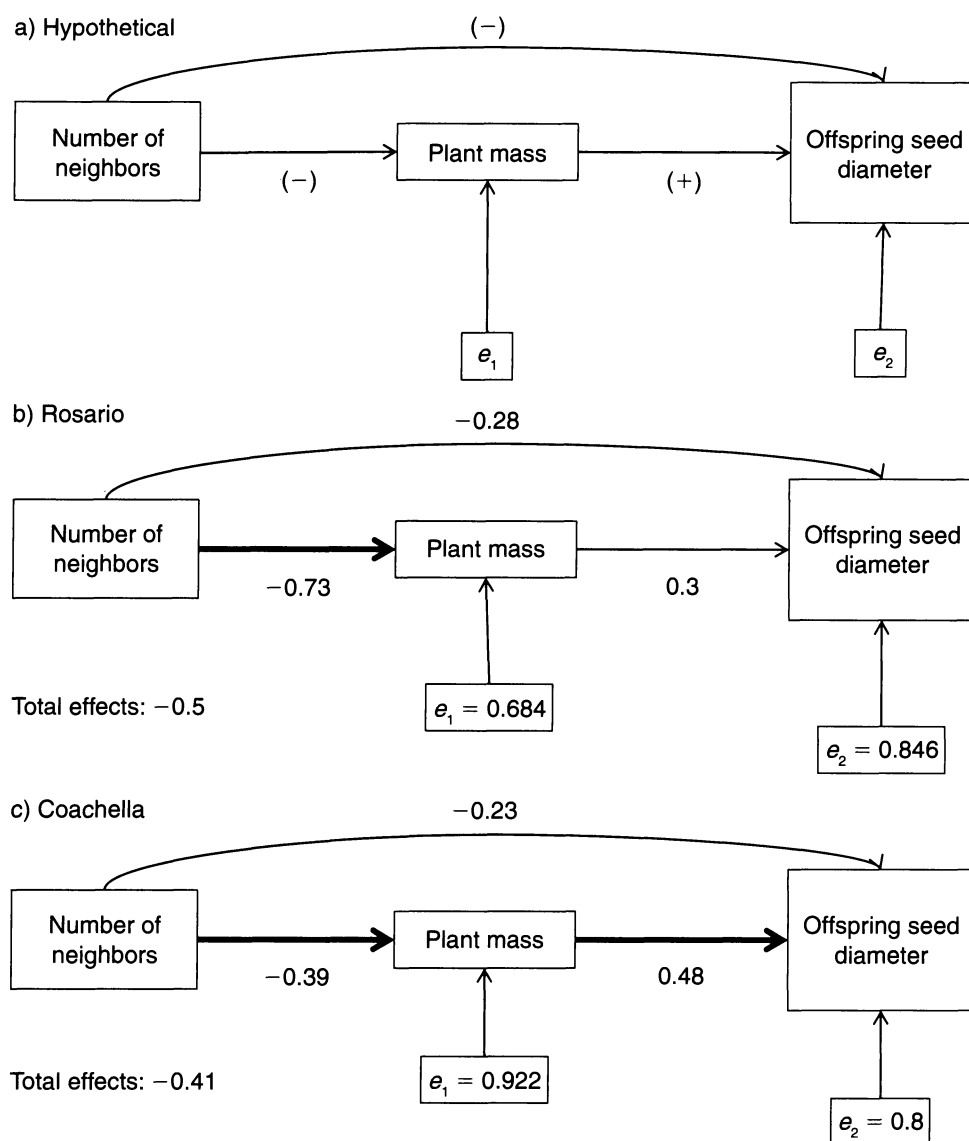


FIG. 1. Path diagrams showing (a) the hypothetical relationship between the number of neighbors within a patch, plant mass, and the average size of seeds produced by mother plants. Arrows indicate hypothesized causal pathways. Signs on each arrow indicate the hypothesized direction of the relationship (+ positive or - negative); (b) results for Rosario population; and (c) results for Coachella population. Heavy arrows and boldface type indicate a statistically significant relationship ($P < 0.05$). Numbers next to arrows indicate the magnitude and direction of the relationship in terms of standardized coefficients. Total effects for each population are indicated on the bottom left corner of each diagram. Error terms for endogenous variables are indicated with e_1 for plant mass and e_2 for offspring seed diameter. $N = 88$ samples.

increased by 0.194 mm and 0.307 mm in Rosario and Coachella, respectively. Finally, there was no significant difference between the two populations in the effect of density on seed diameter. (number of neighbors \times population interaction, $P = 0.7$; Fig. 3).

Heritability of seed diameter

In the Rosario population, a positive direct effect of parental seed diameter on the average offspring seed diameter was only marginally significant (direct path coefficient = 0.276, $P = 0.07$, Table A2). Every 1 mm

increase in maternal seed diameter translates in to 0.53 mm increase in offspring seed diameter due to genetic effects. However, total and indirect effects (through $\ln(\text{plant mass})$) were positively correlated to average offspring seed diameter (total path coefficient = 0.446, $P = 0.0009$; indirect standardized regression coefficient = 0.17, $P = 0.04$, Table A2). For every 1 mm increase in maternal seed diameter, a 0.857 mm increase in average offspring seed diameter is explained by \ln plant mass and genetic effects while a 0.327 mm increase is explained by the indirect effects operating on average offspring seed diameter

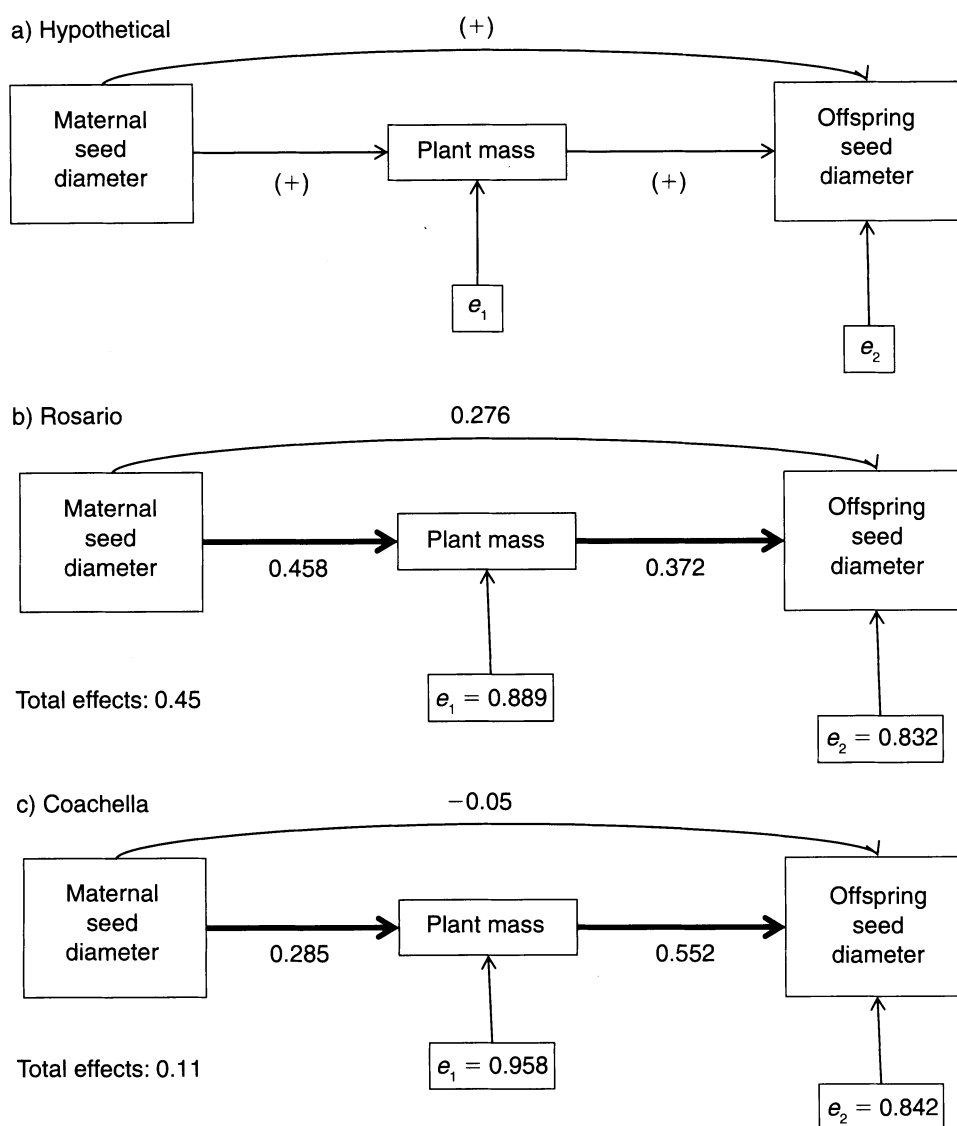


FIG. 2. Path diagrams showing (a) the hypothetical relationship between the maternal seed diameter, plant mass, and the average size of seeds produced by mother plants. Arrows indicate hypothesized causal pathways. Signs on each arrow indicate the hypothesized direction of the relationship (+ positive or - negative); (b) results for Rosario population; and (c) results for Coachella population. Heavy arrows and boldface type indicate a statistically significant relationship ($P < 0.05$). The numbers next to arrows indicate the magnitude and direction of the relationship in terms of standardized coefficients. Total effects for each population are indicated on the bottom left corner of each diagram. Error terms for endogenous variables are indicated e_1 for plant mass and e_2 for offspring seed diameter. $N = 88$ samples.

through $\ln(\text{plant mass})$. In Coachella, direct effects of maternal seed diameter on average offspring seed diameter were not significant (direct path coefficient = -0.05 , $P = 0.7$, Table A2). However, indirect effects operating through \ln plant mass were marginally significant and positively related to average offspring seed diameter (indirect path coefficient = 0.157 , $P = 0.057$; Table A2). Every 1 mm increase in maternal seed diameter results in a 0.178 mm increase in average offspring seed diameter due to the indirect effect operating through $\ln(\text{plant mass})$. Total effects were nonsignificant (total standardized

coefficient = 0.106 , $P = 0.46$; Table A2). There were no significant differences in heritability between sites (ANCOVA, $P = 0.137$; parental seed diameter \times population interaction, Fig. 4), when $\ln(\text{plant mass})$ was included in the model.

Seed dispersal as a function of seed diameter

Random effects of mother plants were statistically significant when compared with a linear model without mother plant (likelihood ratio test, $df = 6$, likelihood ratio = 15.32 , $P = 0.0001$) so we decided to analyze the

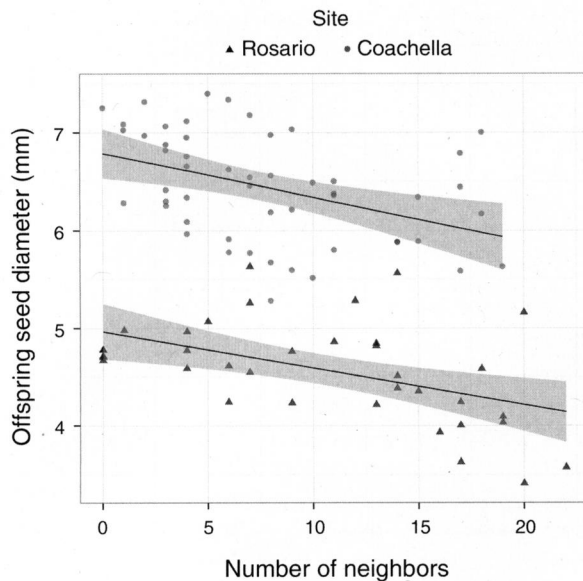


FIG. 3. Average seed diameter produced in relation to the number of competing plants that mother plants experienced in a 10 cm radius neighborhood for two populations, Coachella in gray circles and Rosario in black triangles. Data were analyzed with ANCOVA. Shaded areas represent standard errors. $N = 88$ samples.

data including the random effects of mother plant. The model with random slopes and intercepts was not statistically different from the model with random intercepts only (likelihood ratio test, $df = 6$, likelihood ratio < 0.0007 , $P = 1$) so we used the random structure with random intercepts only. There was a negative relationship between the distance traveled from the mother plant and the diameter of seeds, i.e., smaller seeds tended to disperse farther (linear mixed model, $P = 0.01$; Table 1, Fig. 5, see Appendix C). For every 1 mm increase in seed diameter, dispersal distance decreased by 19.74%. Dispersal distances were higher in July than in May ($P = 0.007$) but not significantly different between July and November ($P = 0.48$).

DISCUSSION

We show how environmental maternal effects can have ecological consequences in *Dithyrea californica* by adjusting the size of offspring in response to crowding. Plants with more neighbors grow to be smaller, and tend to make smaller seeds that are better able to disperse away from the mother plant, thus potentially avoiding competition with other seeds, which are likely to be abundant near the mother in the next growing season. This reduced offspring size with competition might occur as the direct result of reduced plant size if adult plant size constrains the size of the offspring. Experiments on the effect of competition on the mean and the variance of seed size in individual plants are scarce. Some studies have measured total reproductive allocation in annual plants and found a decrease in

reproductive mass with increased competition (Waite and Hutchings 1982, Miao et al. 1991). However, they did not measure the means and variances of individual seed size. Other studies that measured seeds individually, have found evidence for maternal effects on seed number to be more important than on seed size (Sultan 1996), or effects on the variance in seed size with increased competition (Violle et al. 2009). Other studies supported the idea that seed size is not plastic (Marshall et al. 1986). Alternatively, diminished seed size as a result of competition for resources might be caused by allometric constraints on seed size via plant size or twig size (Aarssen 2005, Chen et al. 2009). Most of the evidence in the literature does not support the hypothesis that the size of the offspring is constrained by resources (i.e., by plant size; Moles et al. 2004, Venable and Rees 2009). Moles et al. (2004) showed in a meta-analysis that seed mass and plant size correlate more strongly across species than within species. So the evidence for within-species allometric scaling laws for seed size is weak, suggesting that attention should be directed towards other possible explanations for the observed seed size shifts in *D. californica*.

Diminishing the size of offspring produced as the result of competition might be adaptive if it increases average fitness through other correlated mechanisms such as dormancy or dispersal (Venable and Brown 1988). A previous study of seed size selection in this species showed that seed size positively influences fecundity (the number of seeds produced), but that

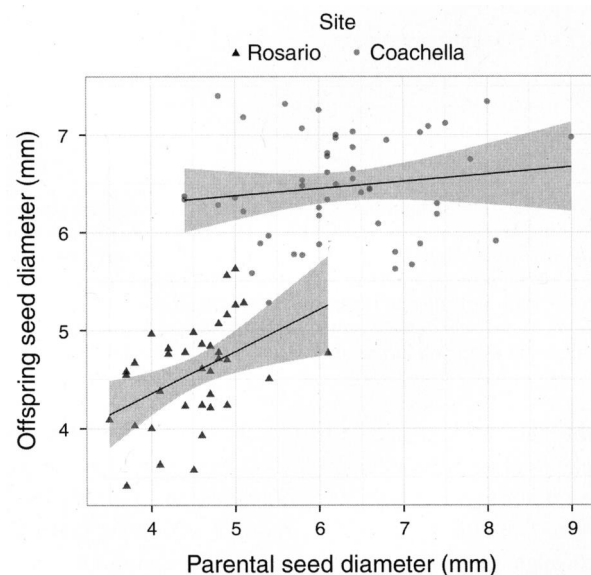


FIG. 4. Parent-offspring regression of seed diameter. Parental seed diameter is the diameter of the seed that a plant germinated from, and offspring seed diameter is the average offspring seed diameter produced by the same plant. Coachella is represented by gray circles and Rosario by black triangles. Data were analyzed with ANCOVA. Shaded areas represent standard errors. $N = 88$ samples.

TABLE 1. Linear mixed model for the dispersal distance traveled by offspring (cm) as a function of seed diameter (mm) and dates when dispersal was measured (fixed effects), and mother plants (random effects).

Dispersal distance	Estimate	SE	Intercept	Residual	<i>t</i>	<i>P</i>
Fixed effects						
Seed diameter (mm)	-0.22	0.0856			-2.5886	0.01
Date (May)	0.35	0.1314			2.6993	0.007
Date (Nov)	-0.11	0.1642			-0.7048	0.48
Random effects						
Mother			0.358	0.921		

Notes: Date effects were calculated as differences from July. Random effects are reported in terms of standard deviations from the mean. *N* = 383 samples, nested in 32 mother plants.

competition has a negative effect (Larios et al. 2014). Thus, the fact that smaller seeds of *D. californica* are more dispersive than larger seeds might produce a trade-off between the benefit of large seeds for making large plants in a more competitive environment and the benefit of small seeds for dispersal to escape competition (Ganeshaiah and Shaanker 1991, Venable and Brown 1993). If the benefits of dispersal outweigh the growth costs of reduced seed size, dispersing smaller but more numerous seeds in response to competition could be adaptive.

Studies from other taxa (especially marine invertebrates and fish) have proposed that offspring provisioning is maternally controlled by phenotypic plasticity and that optimal provisioning depends on the competitive environment mothers experienced during egg develop-

ment (Leips et al. 2009, Marshall and Keough 2009). In marine environments, to increase offspring dispersal, it is adaptive to increase the size of the offspring at the expense of number since larger larvae are better able to swim away from their parental site. For plants the process is different, and a decrease in offspring size is a better way for seeds to achieve higher ability to disperse (Skarpaas et al. 2011).

A recent contribution to the study of seed dispersal by Thomson et al. (2011) has shown that plant height is a more important factor influencing seed dispersal distances than seed mass. However, another recent study looking at plant traits as predictors for maximum dispersal distances working with a large data set of plant species found that including seed mass increased predictive power (Tamme et al. 2014). Plants of *D.*

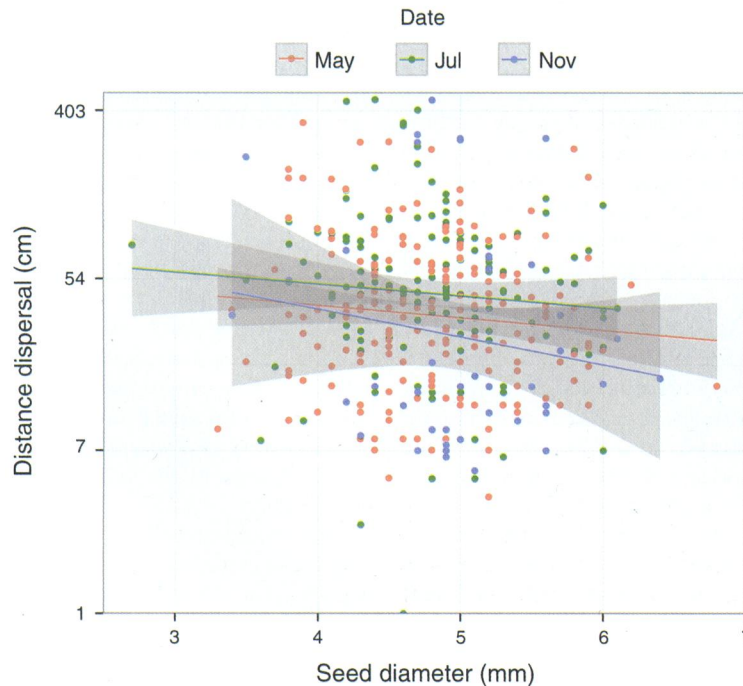


FIG. 5. Distance traveled (cm) by offspring in relation to their seed diameter at three dates of sampling. May is represented by red circles, July is represented by green circles, and November is represented by blue circles. Dispersal distance was ln-transformed for analysis, then back-transformed and shown on a ln-scale in this figure. *N* = 383 samples, nested in 32 mother plants.

californica grow as basal rosettes very close to the ground until reproduction when vertical reproductive stems bolt and produce flowers arranged in a raceme. As plants face more competition, plants tend to grow smaller with fewer and shorter reproductive stems rather than investing in greater height. *D. californica* seeds do not have obvious dispersal structures such as wings, a fleshy pulp, or a conspicuous attractive color. They dehisce and initially fall near the mother plant. Once on the soil, they are blown along with sand, debris, and seeds of other co-occurring species. Thus plant height may be a less important determinant of dispersal distance in *D. californica* than in some other species.

Some studies of seed dispersal of desert plants conclude that desert seeds do not usually travel long distances or even have dispersal adaptations (Ellner and Shmida 1981, Venable et al. 2008). On the contrary, desert seeds sometimes evolve antitelechory (anti-dispersal) mechanisms hypothesized to be due to the limited occurrence of suitable sites for success in deserts. Most *D. californica* seeds tend to stay close to the mother plant, but a few reach at least a 5-m dispersal distance. Seed dispersal in space has been shown to be less important than dispersal in time via delayed germination for some other annuals from the Sonoran Desert (Venable et al. 2008). Theoretical work on the correlated evolution of seed size, seed dormancy, and seed dispersal suggests that these three seed traits evolve in coordination to reduce risk in variable environments, escape crowding, and avoiding kin interactions (Venable and Brown 1988, 1993). In this study, we focused on elucidating the mechanisms involved in the coordinated evolution of seed dispersal and seed size in order to escape crowding.

One must also consider the correlated effects of dormancy on the optimal dispersal fraction, as dormancy and dispersal are both solutions for escaping current local conditions so the expectation is that either will often reduce the need for the other (Levin et al. 1984). Seed size and dormancy are also negatively correlated in *D. californica*, as demonstrated by previous germination experiments in the lab, which showed that time to germination is shorter in larger seeds than smaller seeds across a range of temperature and water potential combinations (E. Larios, Z. Huang, and D. L. Venable unpublished data). As a result, larger seeds dominate the germinated fraction (Larios et al. 2014). Thus, there is a relationship between seed size, dormancy, and dispersal, such that the colonization of new safe sites involves a coordinated plastic reduction in seed size with a potential increase in dormancy. It remains an open question whether the dispersal benefits of small seeds can outweigh the survival, reproductive, and potential germination benefits of larger seeds and thus constitute an adaptation. With regard to the temporal dynamics of seed dispersal of *D. californica*, we found that the average distance of seeds from the mother decreased with time since dispersal. This could be the result of seed

loss due to predation or burial. For example, with a dispersal curve such as exponential decay, removal of a constant number of seeds at all dispersal distances would reduce the apparent average dispersal distance.

Our results from path analysis on heritability showed that there is no additive genetic variation for seed diameter in either Rosario or Coachella populations. The absence of genetic variation in these populations supports our prediction of very low genetic variance due to strong selective pressures on seed size. Additive genetic variance can change with environmental conditions. The general trend found by a meta-analysis studying heritability as a function of environmental quality in wild populations is that additive genetic variance tends to decrease with unfavorable environmental conditions (Charmantier and Garant 2005). That study only considered animals and the trend was found for morphological traits (i.e., growth rate, body mass) but not life history traits (i.e., survival and reproductive effort). Alternatively, lack of additive genetic variance in seed size in *D. californica* might be related to the germination process. Differential germination in relation to seed size in this species was shown to mediate the strength of seed size selection operating through survival by determining phenotypic variance in seed size in the germinated fraction (E. Larios, Z. Huang, and D. L. Venable, unpublished data). Thus, drier years might also decrease additive genetic variance if only a fraction of the seed sizes germinate.

Some caution is needed regarding the interpretation of our heritability results. Our estimate of parent-offspring seed size relations was conducted using the seed diameter of the mother so there are potential maternal effects transmitted to the offspring that are possibly not accounted for in our path analysis. To control for this, we assumed that maternal effects were reflected in the plant size that the mother attained. Thus, by including plant mass in our path analysis, we separated the direct effects that parental seed diameter had on offspring seed diameter from the indirect effects operating through plant mass. The direct effect should contain the additive genetic effect but could also contain some maternal effects not linearly related to plant size. Another caveat is the possibility that correlated parental and offspring environments, not manifested in plant size, and could give a false signal of genetic variation. Alternatively we could be underestimating genetic effects if some of the indirect effects through plant size are genetic.

This study sheds light on the importance of environmental maternal effects on offspring provisioning and shows how offspring can take advantage of the detrimental effects of competition by dispersing away from the mother plant and potentially gaining fitness by avoiding crowded conditions. We hypothesize that propagules benefit from higher dispersal as a mechanism to escape the mother's competitive environment, however, a measure of the fitness consequences of smaller

seeds with higher dispersal ability in terms of survival and reproductive success is still needed.

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A–C are available online: <http://dx.doi.org/10.1890/14-1565.1.sm>