

Can competitive asymmetries maintain offspring size variation? A manipulative field test

Hayley Cameron^{1,2} and Dustin J. Marshall¹

¹Centre for Geometric Biology, School of Biological Sciences, Monash University, Melbourne, Victoria 3800, Australia

²E-mail: Hayley.cameron@monash.edu

Received March 20, 2019

Accepted May 16, 2019

Offspring sizes vary within populations but the reasons are unclear. Game-theoretic models predict that selection will maintain offspring-size variation when large offspring are superior competitors (i.e., competition is asymmetric), but small offspring are superior colonizers. Empirical tests are equivocal, however, and typically rely on interspecific comparisons, whereas explicit intraspecific tests are rare. In a field study, we test whether offspring size affects competitive asymmetries using the sessile marine invertebrate, *Bugula neritina*. Surprisingly, we show that offspring size determines whether interactions are competitive or facilitative—large neighbors strongly facilitated small offspring, but also strongly competed with large offspring. These findings contradict the assumptions of classic theory—that is, large offspring were not superior competitors. Instead, smaller offspring actually benefit from interactions with large offspring—suggesting that asymmetric facilitation, rather than asymmetric competition, operates in our system. We argue that facilitation of small offspring may be more widespread than currently appreciated, and may maintain variation in offspring size via negative frequency-dependent selection. Offspring size theory has classically viewed offspring interactions through the lens of competition alone, yet our results and those of others suggest that theory should accommodate positive interactions in explorations of offspring-size variation.

KEY WORDS: Egg size, facilitation, frequency dependence, larval size, life-history theory, seed size.

For most organisms, parental care is restricted to the provisioning of offspring before they must fend for themselves. The size of offspring at independence from their parents reflects this provisioning—larger offspring receive more parental resources than smaller offspring (reviewed in Bernardo 1996; Marshall et al. 2018b; Mousseau and Dingle 1991). Offspring vary remarkably in size across time and space, and all scales of organization (reviewed in Krist 2011; Leishman et al. 2000; Marshall et al. 2018b). For example, two offspring can differ fivefold in the resources they receive from the same parent (Lips 2001; Turnbull et al. 2006). Offspring size strongly determines performance—larger offspring typically have higher survival, growth, and reproduction than smaller offspring (Krist 2011; Marshall et al. 2018b). Links between offspring size and performance are particularly evident early in the life history, but can persist at later stages and may even affect subsequent generations (Benton et al. 2005;

Krist 2011; Marshall et al. 2018b). Overall then, offspring-size effects are ubiquitous, pervasive, and of fundamental interest to life-history theory.

Nevertheless, life-history theory has struggled to explain variation in offspring size within populations of the same species (Marshall et al. 2018b; Stearns 1992). Classic optimality theory predicts that for a given environment (or population), a single offspring size will maximize maternal fitness—in other words, selection on offspring size is stabilizing (Smith and Fretwell 1974). A fundamental assumption of this model is that mothers trade-off the size and number of their offspring—larger offspring perform better, but smaller offspring are cheaper so mothers make them in larger numbers. Mothers, therefore, balance the relative benefits of better performing offspring with those of increased fecundity, and this balance depends on the relationship between offspring size and performance. Empirical parameterizations of the

Smith–Fretwell model can reliably predict mean values of offspring size, and even variation among populations (Einum and Fleming 2000; Marshall and Keough 2008). Yet this classic theory cannot account for the striking variation observed within populations.

Elaborations to the Smith–Fretwell model applied game-theory to incorporate small-scale, density-, and frequency-dependent interactions among offspring (Geritz 1995; Geritz et al. 1999). In these models, the trade-off between offspring size and number generates a competition–colonization trade-off that favors larger and smaller offspring, respectively. Larger offspring are competitively superior and win contests over smaller offspring, but smaller offspring frequently colonize unoccupied sites because they are the most abundant propagule. These models predict that under asymmetric competition, where larger offspring disproportionately acquire resources relative to their size (Weiner 1990), no single offspring size is evolutionarily stable and variation is maintained. Conversely, if competition is symmetric and all offspring receive the same resources (Weiner 1990), a single offspring size is optimal and will exclude all other sizes (Geritz 1995; Geritz et al. 1999). Importantly, a qualitative prediction of these models is that competition must be *strongly* asymmetric to overcome the colonization advantage of smaller offspring—that is, the degree of asymmetry is crucial for the maintenance of offspring-size variation (Geritz et al. 1999). Analogous models predict the coexistence of species with different seed sizes (Rees and Westoby 1997). Although optimality theory cannot account for offspring-size variation within populations, game-theoretic models suggest competitive asymmetries and positive frequency-dependent selection drive this variation.

So do competitive asymmetries maintain offspring-size variation in natural populations? There are good reasons to expect that larger offspring will win contests over smaller offspring. For instance, larger offspring are provisioned with more energy reserves, and use proportionally less of these reserves during development—thus, larger offspring have more energy for growth, survival and reproduction (Leishman et al. 2000; Pettersen et al. 2015, 2017). Greater reserves can also increase the resistance of larger offspring to starvation and their capacity to withstand low resource environments—although these advantages are not universal (Allen et al. 2008; Bashey 2008; Berven and Chandra 1988; Fisher et al. 2007; Freckleton and Watkinson 2001). Once feeding commences, larger offspring typically access more resources than smaller offspring (Leishman 2001; Martin and Pfennig 2010; Stanton 1984), though it is unclear whether they access disproportionately more resources (Marshall et al. 2018b)—a requirement of asymmetric competition (Weiner 1990). Furthermore, while larger individuals acquire more resources, smaller individuals often have lower resource requirements and may tolerate resource depletion better than their larger neighbors (Persson 1985).

Overall then, while some studies support the assumption that competitive asymmetries favor larger offspring, others provide instances where these assumptions may be violated—although direct empirical tests are rare.

For the few studies that directly estimate competitive asymmetries, evidence is equivocal. So far, most tests have used comparisons of competitive abilities among plant species with different seed sizes. In general, larger-seeded species tend to out-compete smaller-seeded species (Freckleton and Watkinson 2001; Leishman 2001; Turnbull et al. 2004), although there are exceptions (Ben-Hur and Kadmon 2015; Eriksson 2005). Furthermore, studies that report asymmetric competition coefficients suggest these asymmetries are not sufficiently strong to compensate for the colonization advantage of smaller-seeded species (Coomes and Grubb 2003; Rees and Westoby 1997; Turnbull et al. 2004). As such, the validity of competitive asymmetries as drivers of multispecies coexistence have been questioned (Coomes and Grubb 2003).

Although undoubtedly informative from a community perspective, interspecific comparisons cannot predict the processes that generate offspring-size variation within species. Most intraspecific studies focus on competitive asymmetries generated by body size and/or ontogenetic stage (Bassar et al. 2016; de Roos and Persson 2003), but few have explicitly explored asymmetries among newly independent offspring to test the validity of game-theoretic models of offspring size (Geritz 1995; Geritz et al. 1999). Although rare, some intraspecific tests suggest that larger offspring outcompete smaller offspring (Gribbin and Thompson 1990; Marshall et al. 2006; Rodriguez-Girones et al. 2003). For example, in laboratory studies, small damselfly larvae grow less and develop more slowly due to interference competition from larger larvae, but are unaffected by other small larvae (Gribbin and Thompson 1990). Other intraspecific studies suggest that variation in offspring size mediates interactions via mechanisms other than competition. For example, in tadpoles and marine invertebrates, offspring size can promote resource partitioning that may reduce competitive inequalities (Cameron et al. 2017; Martin and Pfennig 2010). Interactions among offspring may even be beneficial—for instance, high densities of neighbors facilitate offspring of certain sizes across a range of systems (e.g., in birds: Russell et al. 2007; marine invertebrates: Cameron et al. 2016; and plants: Zepeda and Martorell 2019). Given the limited number of studies that manipulate the sizes of interacting offspring, however, generalizations about offspring size-mediated competition appear premature.

In a manipulative field experiment, we tested the assumption that offspring size generates intraspecific competitive asymmetries using the sessile marine invertebrate, *Bugula neritina*. We used a trait-specific, response-surface design to manipulate the size differences between offspring involved in pairwise

interactions. We then measured the outcomes of these interactions by comparing the performance (survival, growth, and reproduction) of different-sized offspring in the presence and absence of neighbors under field conditions across their lifetime.

Materials and Methods

STUDY SPECIES

Bugula neritina (hereafter *Bugula*) is a bryozoan common to sessile marine communities worldwide. *Bugula* grows by asexual budding of zooids to form branched colonies. Colonies are simultaneous hermaphrodites and fertilization is internal; colonies cast sperm into the water column, but retain the eggs and developing larvae. Colonies brood the larvae in external reproductive structures (ovicells) for up to one week before the fully developed, nonfeeding larvae are released.

Within populations, offspring (larval) size varies up to four-fold both among and within females. Larval size determines post-settlement performance—larger offspring typically survive, grow, and reproduce more than smaller offspring (Marshall et al. 2018a). Larger offspring appear to cope better with competition, although this can be context dependent (Allen et al. 2008; Cameron et al. 2016). Importantly, these previous studies manipulated the size of focal offspring, but only the densities (and not the phenotypes) of neighboring offspring. In contrast, our current study manipulates the size differences between interacting offspring to address competitive asymmetries explicitly.

EXPERIMENTAL METHODS

We conducted our experiments at Blairgowrie Yacht Squadron, Victoria, Australia (38°21'20.2"S, 144°46'22.8"E) from March to June 2016. To obtain larvae for our experiments, we collected mature colonies from the field and held them within dark, aerated aquaria at 17°C for two days. We induced the colonies to spawn their brooded larvae by exposing them to bright light and measured these larvae using standard techniques (Cameron et al. 2017). We settled all larvae (after measurement) onto preroughened, biofilmed acetate squares. For each experimental run, we measured between 250 and 350 larvae that we pooled from ~30 parental colonies.

In a field experiment, we tested whether offspring size mediates the outcomes of pairwise interactions using a trait-specific, response-surface design (Inouye 2001). For our manipulations, we used the continuous range of larval sizes from our source population (5.65–15.29 μg) to generate pairwise combinations of offspring (absolute size difference range: –7.83 to 7.83 μg ; relative size ratio range: 0.43–2.35; Fig. 1). To create our treatments, we glued the acetate squares bearing the offspring onto PVC plates (5.5 \times 5.5 cm) at a distance of 1 cm from each other. We treated both these offspring as the focal and neighbor

simultaneously to test for reciprocal interactions (Inouye 2001). We also estimated the baseline relationship between offspring size and performance by gluing a blank acetate square 1 cm from focal settlers of various sizes (neighbor-free controls; Fig. 1A). We circled all experimental settlers and noted their position on the plates so we could distinguish them from field recruits and monitor their performance over time.

We deployed our experiment in the field by attaching the plates (bearing the settlers) to PVC backing panels (55 \times 55 cm) that hung 1 m below the water surface. We replicated the experiment across three runs that we deployed into the field at one-week intervals. Runs one and two had five panels, and run three had four panels. Each backing panel received 14 plates that represented the full range of focal and neighbor size pairings (i.e., covariate ranges overlapped). Overall, the experiment included 196 plates deployed across 14 backing panels, and we measured the performance of 336 individuals of known offspring size.

We measured several fitness components for all experimental colonies weekly. For survival, we scored the colonies as alive if they were present on the plates or dead if they were absent. We measured growth as the number of times the colonies had branched (bifurcated)—a good proxy for colony biomass (Keough and Chernoff 1987). We measured fecundity as the number of ovicells on the colonies each week to give a cumulative value of reproductive output for each colony (Pettersen et al. 2016). At each census, we removed nonexperimental settlers (both *Bugula* and other species) from the plates to eliminate competition from other organisms and randomized the plates within the backing panels. We ended the experiment after 11 weeks because by this time most plates had only a single survivor.

STATISTICAL ANALYSES

We tested for size-mediated interactions among settlers of known larval size using generalized linear models (GLMs). For these models, we included the size-specific performance of offspring in neighbor-free conditions (i.e., controls) by setting their corresponding value for neighbor size to zero (unless otherwise specified). For survival, we used a binomial GLM with a logit-link function, where focal and neighbor offspring sizes were continuous fixed effects and experimental run was a categorical fixed effect. For growth, we analyzed the size (bifurcations) of the focal colonies after 11 weeks using a Gaussian GLM with the same model structure as above.

We also tested whether the size of focal and neighbor offspring affected the probability that focal colonies reproduced using a binomial GLM with a logit-link function and the same model structure above. Here, our binary response variable described whether colonies had reproduced (assigned a value of 1) or had not reproduced (assigned a value of 0) after 11 weeks in the field. Because neighbor size did not affect the probability that

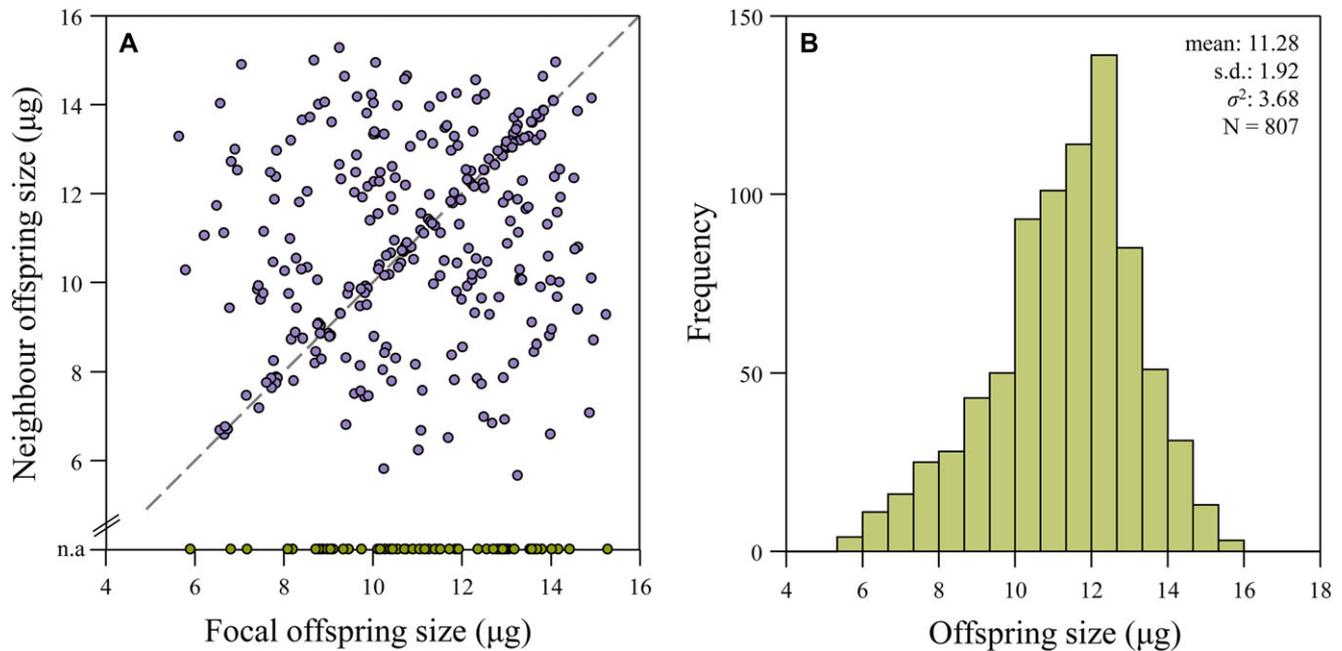


Figure 1. (A) Schematic of the trait-specific, response-surface design used to test the effects of offspring size on pairwise interactions between *Bugula neritina* settlers. The purple points show the combinations of focal and neighbor sizes used in pairwise interactions ($N = 330$), the green points show the sizes of offspring grown without neighbors (neighbor-free controls; $N = 56$). The gray-dotted line indicates size equivalence between focal and neighbor offspring. (B) The natural frequency distribution of offspring-sizes in our source population (Blairgowrie Marina) obtained by measuring >800 larvae that were spawned from ~ 90 randomly collected colonies.

focal colonies reproduced (see Results section), we again analyzed our binary response for reproduction in a binomial GLM, but this time we included neighbor presence/absence and backing panel as categorical fixed effects and focal offspring size as a continuous fixed effect. For those individuals that survived to reproduce, we also analyzed cumulative reproductive output (fecundity) after 11 weeks in the field using a quasi-Poisson GLM with a log-link function and the same model structure described above. For all analyses, we first fit full models and reduced these where appropriate by removing nonsignificant interactions (assessed from log-likelihood ratio tests (binomial GLMs) or F -ratio tests (Gaussian and quasi-Poisson GLMs) where $\alpha > 0.05$).

Results

After 11 weeks in the field, we found that focals from larger offspring survived better than those from smaller offspring ($\chi^2 = 7.961$, $df = 1$, $P = 0.005$; Fig. 2A), and this was not affected by the offspring size of their neighbors (neighbor size: $\chi^2 = 0.593$, $df = 1$, $P = 0.441$; focal \times neighbor size: $\chi^2 = 0.450$, $df = 1$, $P = 0.503$). Larger offspring also grew into larger colonies ($F_{1,105} = 7.590$, $P = 0.007$), but again the growth of the focals was not affected by their neighbor's size (neighbor size: $F_{1,217} = 1.023$, $P = 0.314$; focal \times neighbor size interaction: $F_{1,104} = 0.895$, $P = 0.346$). Larger focal offspring had a higher proba-

bility of reproducing than smaller offspring ($\chi^2 = 13.644$, $df = 1$, $P = <0.001$), irrespective of neighbor size (neighbor size: $\chi^2 = 0.12$, $df = 1$, $P = 0.663$; focal \times neighbor size: $\chi^2 = 0.001$, $df = 1$, $P = 0.974$). Interestingly, however, the probability that the focal colonies reproduced tended to be lower in the presence of neighbors (ignoring neighbor size) relative to neighbor-free conditions ($\chi^2 = 3.865$, $df = 1$, $P = 0.049$), and this was consistent across focal sizes (focal size \times neighbor presence: $\chi^2 = 0.37$, $df = 1$, $P = 0.541$).

For the focal colonies that reproduced, both their own offspring size and that of their neighbor interactively affected their reproductive output ($F_{1,133} = 4.511$, $P = 0.036$; Fig. 2B). When offspring occurred in isolation, larger offspring had five times the reproductive output of smaller offspring. In pairwise interactions, however, the offspring size of the focals determined their response to neighbors—neighbors increased the fecundities of smaller offspring, but diminished the fecundities of larger offspring (relative to neighbor-free conditions). In other words, neighbors facilitated smaller offspring but competed with larger offspring. Interestingly, the offspring size of neighbors determined the strength of these interactions. Most surprisingly, facilitation increased with neighbor size—the largest neighbors were the strongest facilitators of small focals ($\sim 350\%$ increase in fecundity relative to neighbor-free conditions), whereas large offspring competed most strongly with each other ($\sim 50\%$ decrease in performance

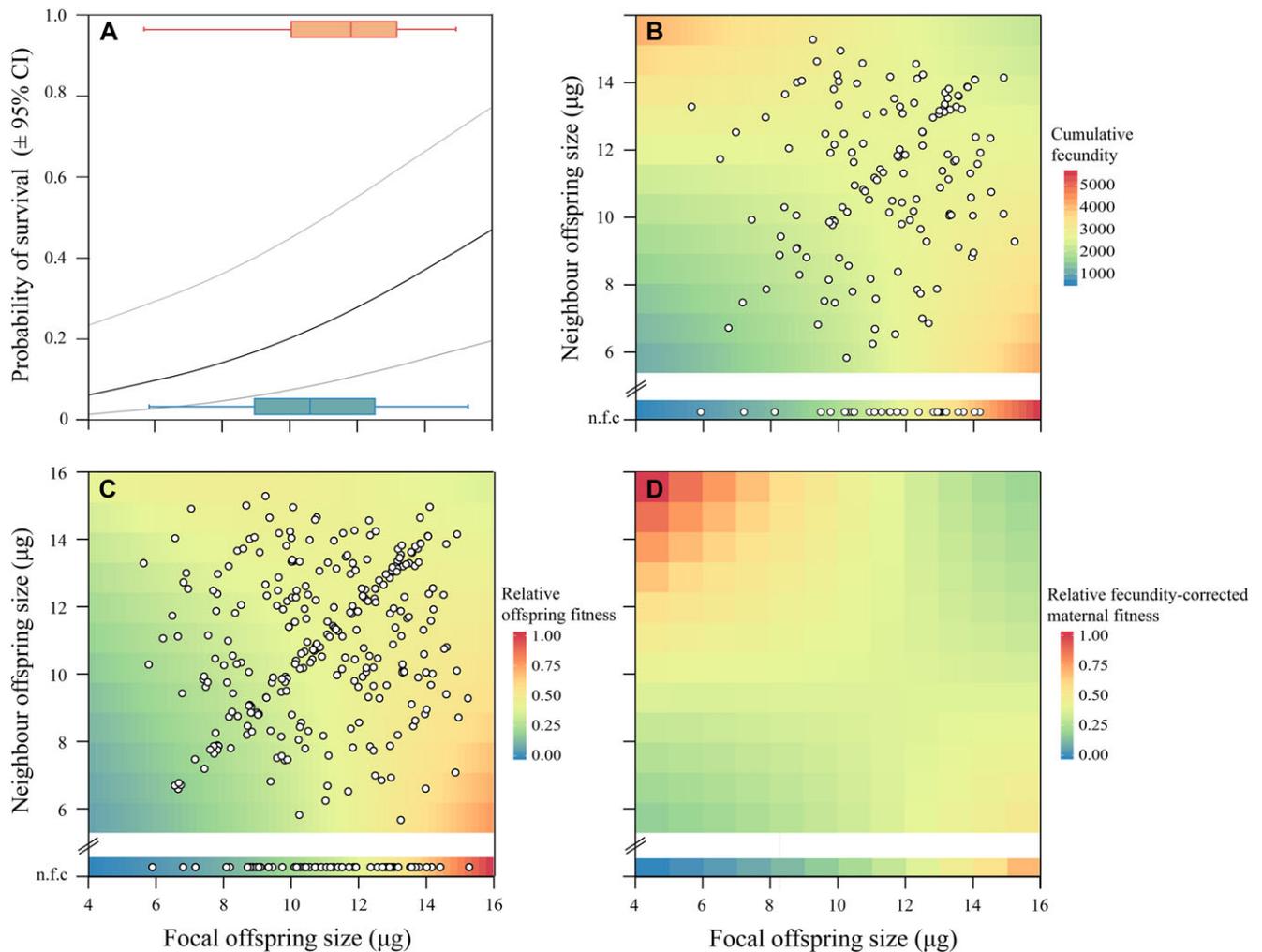


Figure 2. The effects of focal and neighbor offspring size on (A) the probability of survival ($\pm 95\%$ CI); (B) the cumulative reproductive output (no. of ovicells); and (C) predicted offspring fitness (probability of reproduction \times fecundity) of *Bugula neritina* colonies after 11 weeks in the field. (D) The relative predicted fitness of mothers that produce a certain offspring size accounting for a trade-off between offspring size and number is shown. Boxplots in (A) show the distribution of offspring that survived (red) or died (blue). White dots in (B) and (C) show the underlying data points. N.f.c., neighbor-free controls.

relative to neighbor-free conditions). It is also worth noting that offspring around the population mean size (11–12 μg ; Fig. 1B) were unaffected by neighbor identity (both similar and dissimilar phenotypes; Fig. 2B).

The above analyses indicate that larger offspring have both a survival advantage and a higher chance of reproducing, but that smaller offspring that survive to reproduce have higher reproductive outputs relative to larger offspring in the presence of neighbors. We therefore visualized composite fitness by multiplying our estimates of fecundity and the probability of reproducing (which includes both survival to maturity and whether or not the survivors reproduced) to fully integrate the benefits of offspring size on offspring performance (Fig. 2C). Although neighbors reduced the probability that focal colonies reproduced, their

positive effects on the fecundities of smaller offspring outweighed this negative effect—thus overall, neighbors facilitated smaller offspring.

Nevertheless, larger offspring in isolation or pairwise interactions with smaller offspring had the highest performance overall, although this advantage was not disproportionate to their size (Fig. 2C). To illustrate, consider pairwise interactions between offspring of 5 and 15 μg . Although the smaller offspring is one-third the size of the larger offspring, their performance is over half that of the larger offspring. Importantly, when we account for the fecundity costs of making larger offspring, we find that mothers receive higher fitness returns if they make more numerous, smaller offspring relative to fewer, larger offspring when these offspring interact (Fig. 2D).

Discussion

Our study contradicts a key assumption of game-theoretic models—that strong competitive asymmetries favor larger offspring (Geritz 1995; Geritz et al. 1999). Rather, we found that offspring size altered the strength and direction of pairwise interactions. Focal offspring size determined whether interactions were positive or negative—neighbors facilitated smaller offspring but competed with larger offspring. Meanwhile, the offspring size of neighbors determined the strength of these interactions—neighbors from larger offspring were both the strongest facilitators and competitors of small and large focals, respectively. These findings are indicative of absolute, or antagonistic, asymmetric facilitation (Lin et al. 2012; Schob et al. 2014)—that is, small offspring receive benefits from larger offspring, but large offspring only experience competition (i.e., reciprocal interactions are $+/-$). Our study is the first to show that asymmetric facilitation can occur between offspring of different sizes. This raises two important questions: (1) How widespread is asymmetric facilitation among offspring? and (2) What are the eco-evolutionary consequences for variation in offspring size?

Our finding that larger offspring facilitate smaller offspring contradicts previous studies—most studies find larger offspring outcompete smaller offspring (Freckleton and Watkinson 2001; Gribbin and Thompson 1990; Leishman 2001; Rodriguez-Girones et al. 2003; Turnbull et al. 2004; Marshall et al. 2006). Nevertheless, tests that manipulate size differences among offspring at the intraspecific level are rare (but see Gribbin and Thompson 1990; Marshall et al. 2006; Rodriguez-Girones et al. 2003). Thus far, most tests of offspring competitive ability manipulate focal size across different densities of conspecifics, but not the sizes of these neighbors (Allen et al. 2008; Bashey 2008; Berven and Chadra 1988; Cameron et al. 2016). In contrast, our study investigates pairwise interactions between offspring of different sizes, but interactions obviously occur across a range of densities in nature. Density alters the mode of competition (symmetric vs. asymmetric) across ontogenetic stages of offspring (Cameron et al. 2007). An important next step, therefore, would be orthogonal manipulations of both the density *and* frequency of contemporary offspring that differ in size. Such an approach would allow direct parameterizations of ESS models to determine whether facilitative and (or) competitive asymmetries are expected to maintain offspring-size variation within populations.

One way that asymmetric facilitation may arise in our study is through correlations between offspring size and other traits that determine resource supply and demand. In aquatic systems (including our own), the physical structure of organisms can disrupt boundary currents and increase the entrainment of resources—resulting in facilitation (Cameron et al. 2016; Cardinale et al. 2002). In our study, larger offspring grew into larger colonies that may disproportionately disrupt

flow and increase resources. Meanwhile, smaller offspring likely benefit most from resource amelioration because they form smaller colonies that are less efficient at resource capture, especially in high flow environments (Cameron et al. 2016; Okamura 1984). Conversely, larger colonies acquire resources more efficiently (even in high flows: Okamura 1984), such that larger offspring may receive less resources when neighbors are present and so experience competition (Cameron et al. 2016). Competition was particularly intense between large offspring, suggesting their combined resource requirements exceed the resources they entrain. This highlights an important point—in our study, asymmetric facilitation is the net outcome of interactions, while it is unclear how competition and facilitation truly scale with offspring size (or related traits: e.g. adult size, metabolism). Identifying size-scaling relationships for competition and facilitation is challenging, but would inform the development of more explicit models of offspring interactions.

Our study is the first to demonstrate asymmetric facilitation among offspring, but we suspect this phenomenon may be more widespread. For example, smaller-seeded plant species experience both the strongest facilitation *and* competition from high densities of heterospecifics (Zepeda and Martorell 2019). Although we are unaware of other intraspecific studies similar to ours, we suspect these effects occur in other systems. For example, larger seeds produce greater root biomass and form larger seedlings (Leishman 2001; Stanton 1984) that may disproportionately ameliorate unstable sediments, soil water loss, or UV radiation for more vulnerable, smaller seeds. Smaller offspring also perform as well, if not better, than larger offspring when resources are abundant, and these effects can persist at high densities (e.g., in birds: Russell et al. 2007; marine invertebrates: Allen and Marshall 2013; Cameron et al. 2016; Cameron et al. 2017; and plants: Larios and Venable 2018). Although asymmetric facilitation appears most applicable for sessile organisms, many mobile species show remarkable variation in offspring size and have sedentary juvenile stages where siblings interact in size-specific ways (e.g., in mobile invertebrates: Kamel et al. 2010; Kudo 2006; frogs: Martin and Pfennig 2010; and birds: Krist 2011). That facilitation occurs via different modes (e.g., symmetric, asymmetric) is a relatively new concept in ecology (Lin et al. 2012; Lin et al. 2016; Schob et al. 2014). We, therefore, encourage further empirical tests to determine the extent to which asymmetric facilitation occurs, its links with offspring size, and its eco-evolutionary consequences.

Given the potential for asymmetric facilitation to be widespread, how might such interactions affect variation in offspring size? One possibility is that size-mediated facilitation generates negative frequency-dependent selection on offspring size (Day and Young 2004). In our study, large offspring performed best in isolation, suggesting they are advantageous when

population densities are low and large phenotypes are rare. As the frequency of large offspring increases, however, their performance will decrease due to intraphenotypic competition, whereas smaller offspring will initially proliferate due to facilitation, but decline again as large offspring become less abundant. Frequency-dependent selection may thus generate cycles in the abundance of offspring sizes—but neither large nor small offspring will be competitively excluded, and ultimately both will remain rare. Certainly, frequency-dependent selection generates predictable oscillations in egg sizes in lizards—although asymmetric facilitation was not the driver in this instance (Sinervo et al. 2000). In our study population, small and large offspring were the rarest phenotypes, providing support for our prediction that asymmetric facilitation and frequency dependence shape offspring-size distributions in nature (Fig. 1B). Based on this distribution of offspring sizes, and assuming that offspring settle in pairs at random, we predict that ~40% of the offspring size pairings in the field would yield facilitative outcomes (Table S1). Thus, asymmetric facilitation may be an important driver of offspring-size variation in natural populations.

Game-theoretic models of offspring size were an important step that presciently anticipated frequency-dependent consequences of offspring size (Geritz 1995; Geritz et al. 1999). Given our findings, however, several assumptions of these models warrant modification. First, these models exclusively explore the modes of competition, but not the modes of facilitation. Second, our data suggest that resources may vary with the local sizes and densities of offspring (via asymmetric facilitation), while these models do not consider this possibility (Geritz 1995; Geritz et al. 1999). That offspring size generates small-scale heterogeneity in resources (or other stress) also applies to alternative models of offspring size (D'Andrea et al. 2013; Muller-Landau 2010). In these models, larger offspring are more stress tolerant (c.f. competitively superior; Geritz, 1995) and so win more stressful sites, whereas smaller offspring are more abundant and so win less stressful sites. We provide some support for these models—smaller offspring were advantageous when stress was reduced (albeit through facilitation, rather than fecundity), whereas larger offspring won when stress was not ameliorated (i.e., neighbor-free conditions). Surprisingly, stress-tolerance models do not consider that facilitation may create spatial heterogeneity in stress for propagules (D'Andrea et al. 2013; Muller-Landau 2010), despite well-established links between facilitation and stress tolerance more generally (Liancourt et al. 2005; Zhang and Tielbörger 2019). Given our findings, explicit exploration of positive interactions may greatly extend these theories.

Although ecologists have long recognized the importance of positive and negative interactions for natural populations and communities (Bruno et al. 2003; Gross 2008), life-history theory has traditionally viewed offspring interactions through the lens of

competition (Geritz 1995; Geritz et al. 1999; Parker and Begon 1986; Rees and Westoby 1997; Venable 1992). To our knowledge, a single model investigates positive interactions among offspring (McGinley 1989), while no theory explicitly considers size-dependent competition and facilitation—but some models could accommodate these assumptions (Venable 1992). In light of our findings, we propose a novel mechanism that may maintain offspring size variation in natural populations—that is, asymmetric facilitation generates negative frequency-dependent selection on offspring size (Day and Young 2004). Given offspring size mediates facilitation in other systems (Zepeda and Martorell 2019), these ideas warrant further empirical and theoretical exploration.

AUTHOR CONTRIBUTIONS

HC and DJM designed and analyzed the experiment, HC collected the data and wrote the first draft of the manuscript, and all authors contributed to manuscript revisions.

ACKNOWLEDGMENTS

We are grateful to Blairgowrie Yacht Squadron for access to our field site. We thank M. Amor, A. Guillaume, R. Lange, K. Monro, and others for assistance in the field and laboratory. We thank M. Malerba, M. Alvarez Noriega, D. Hall, S. Immler, and two anonymous reviewers for providing insightful comments that greatly improved the manuscript.

DATA ARCHIVING

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.2jg0d2m>

LITERATURE CITED

- Allen, R. M., and D. J. Marshall. 2013. Phenotypic links among life-history stages are complex and context-dependent in a marine invertebrate: interactions among offspring size, larval nutrition and postmetamorphic density. *Funct. Ecol.* 27:1358–1366.
- Allen, R. M., Y. M. Buckley, and D. J. Marshall. 2008. Offspring size plasticity in response to intraspecific competition: an adaptive maternal effect across life-history stages. *Am. Nat.* 171:225–237.
- Bashey, F. 2008. Competition as a selective mechanism for larger offspring size in guppies. *Oikos* 117:104–113.
- Bassar, R. D., D. Z. Childs, M. Rees, S. Tuljapurkar, D. N. Reznick, and T. Coulson. 2016. The effects of asymmetric competition on the life history of *Trinidadian guppies*. *Ecol. Lett.* 19:268–278.
- Ben-Hur, E., and R. Kadmon. 2015. An experimental test of the relationship between seed size and competitive ability in annual plants. *Oikos* 124:1346–1353.
- Benton, T. G., S. J. Plaistow, A. P. Beckerman, C. T. Lapsley, and S. Littlejohns. 2005. Changes in maternal investment in eggs can affect population dynamics. *Proc. Roy. Soc. B.* 272: 1351–1356
- Bernardo, J. 1996. The particular maternal effect of propagule size, especially egg size: patterns, models, quality of evidence and interpretations. *Am. Zool.* 36:216–236.
- Berven, K. A., and B. G. Chandra. 1988. The relationship among egg size, density and food level on larval development in the wood frog (*Rana sylvatica*). *Oecologia* 75:67–72.
- Bruno, J. F., J. J. Stachowicz, and M. D. Bertness. 2003. Inclusion of facilitation into ecological theory. *Trends Ecol. Evol.* 18:119–125.

- Cameron, H., K. Monro, M. Malerba, S. Munch, and D. Marshall. 2016. Why do larger mothers produce larger offspring? A test of classic theory. *Ecology* 97:3452–3459.
- Cameron, H., K. Monro, and D. J. Marshall. 2017. Should mothers provision their offspring equally? A manipulative field test. *Ecol. Lett.* 20:1025–1033.
- Cameron, T. C., H. J. Wearing, P. Rohani, and S. M. Sait. 2007. Two-species asymmetric competition: effects of age structure on intra- and interspecific interactions. *J. Anim. Ecol.* 76:83–93.
- Cardinale, B. J., M. A. Palmer, and S. L. Collins. 2002. Species diversity enhances ecosystem functioning through interspecific facilitation. *Nature* 415:426–429.
- Coomes, D. A., and P. J. Grubb. 2003. Colonization, tolerance, competition and seed-size variation within functional groups. *Trends Ecol. Evol.* 18:283–291.
- D'Andrea, R., G. Barabás, and A. Ostling. 2013. Revising the tolerance-fecundity trade-off; or, on the consequences of discontinuous resource use for limiting similarity, species diversity, and trait dispersion. *Am. Nat.* 181:E91–E101.
- Day, T., and K. A. Young. 2004. Competitive and facilitative evolutionary diversification. *Bioscience* 54:101–109.
- de Roos, A. M., and L. Persson. 2003. Competition in size-structured populations: mechanisms inducing cohort formation and population cycles. *Theor. Popul. Biol.* 63:1–16.
- Einum, S., and I. A. Fleming. 2000. Highly fecund mothers sacrifice offspring survival to maximize fitness. *Nature* 405:565–567.
- Eriksson, O. 2005. Game theory provides no explanation for seed size variation in grasslands. *Oecologia* 144:98–105.
- Fisher, R., S. M. Sogard, and S. A. Berkeley. 2007. Trade-offs between size and energy reserves reflect alternative strategies for optimizing larval survival potential in rockfish. *Mar. Ecol. Prog. Ser.* 344:257–270.
- Freckleton, R. P., and A. R. Watkinson. 2001. Predicting competition coefficients for plant mixtures: reciprocity, transitivity and correlations with life-history traits. *Ecol. Lett.* 4:348–357.
- Geritz, S. A. H. 1995. Evolutionarily stable seed polymorphism and small-scale spatial variation in seedling density. *Am. Nat.* 146:685–707.
- Geritz, S. A. H., E. van der Meijden, and J. A. J. Metz. 1999. Evolutionary dynamics of seed size and seedling competitive ability. *Theor. Popul. Biol.* 55:324–343.
- Gribbin, S. D. and D. J. Thompson. 1990. Asymmetric intraspecific competition among larvae of the damselfly *Ischnura elegans* (Zygoptera: Coenagrionidae). *Ecol. Entomol.* 15:37–42.
- Gross, K. 2008. Positive interactions among competitors can produce species-rich communities. *Ecol. Lett.* 11:929–936.
- Inouye, B. D. 2001. Response surface experimental designs for investigating interspecific competition. *Ecology* 82:2696–2706.
- Kamel, S. J., R. K. Grosberg, and D. J. Marshall. 2010. Family conflicts in the sea. *Trends Ecol. Evol.* 25:442–449.
- Keough, M. J., and H. Chernoff. 1987. Dispersal and population variation in the bryozoan *Bugula neritina*. *Ecology* 68:199–210.
- Krist, M. 2011. Egg size and offspring quality: a meta-analysis in birds. *Biol. Rev.* 86:692–716.
- Kudo, S. I. 2006. Within-clutch egg-size variation in a subsocial bug: the positional effect hypothesis. *Canad. J. Zool.* 84:1540–1544.
- Larios, E., and D. L. Venable. 2018. Selection for seed size: the unexpected effects of water availability and density. *Funct. Ecol.* 32:2216–2224.
- Leishman, M., I. J. Wright, A. Moles, and M. Westoby. 2000. The evolutionary ecology of seed size. Pp. 31–57 in M. Fenner, ed. *Seeds: The ecology of regeneration in plant communities*. CABI International, Oxon, U. K.
- Leishman, M. R. 2001. Does the seed size/number trade-off model determine plant community structure? An assessment of the model mechanisms and their generality. *Oikos* 93:294–302.
- Liancourt, P., R. M. Callaway, and R. Michalet. 2005. Stress tolerance and competitive-response ability determine the outcome of biotic interactions. *Ecology* 86:1611–1618.
- Lin, Y., U. Berger, V. Grimm, and Q.-R. Ji. 2012. Differences between symmetric and asymmetric facilitation matter: exploring the interplay between modes of positive and negative plant interactions. *J. Ecol.* 100:1482–1491.
- Lin, Y., U. Berger, M. Yue, and V. Grimm. 2016. Asymmetric facilitation can reduce size inequality in plant populations resulting in delayed density-dependent mortality. *Oikos* 125:1153–1161.
- Lips, K. R. 2001. Reproductive trade-offs and bet-hedging in *Hyla calypsa*, a neotropical treefrog. *Oecologia* 128:509–518.
- Marshall, D. J., and M. J. Keough. 2008. The relationship between offspring size and performance in the sea. *Am. Nat.* 171:214–224.
- Marshall, D. J., C. N. Cook, and R. B. Emlet. 2006. Offspring size effects mediate competitive interactions in a colonial marine invertebrate. *Ecology* 87:214–225.
- Marshall, D. J., J. S. McAlister, and A. M. Reitzel. 2018a. Evolutionary ecology of parental investment and larval diversity. Pp. 34–49 in T. J. Carrier, A. M. Reitzel, and A. Heyland, eds. *Evolutionary ecology of marine invertebrate larvae*. Oxford Univ. Press, Oxford, U.K.
- Marshall, D. J., A. K. Pettersen, and H. Cameron. 2018b. A global synthesis of offspring size variation, its eco-evolutionary causes and consequences. *Funct. Ecol.* 32:1436–1446.
- Martin, R. A., and D. W. Pfennig. 2010. Maternal investment influences expression of resource polymorphism in amphibians: implications for the evolution of novel resource-use phenotypes. *PLoS One* 5:e9117.
- McGinley, M. 1989. The influence of a positive correlation between clutch size and offspring fitness on the optimal offspring size. *Evol. Ecol.* 3:150–156.
- Mousseau, T. A., and H. Dingle. 1991. Maternal effects in insect life histories. *Ann. Rev. Entomol.* 36:511–534.
- Muller-Landau, H. C. 2010. The tolerance–fecundity trade-off and the maintenance of diversity in seed size. *Proc. Natl. Acad. Sci. USA* 107:4242–4247.
- Okamura, B. 1984. The effects of ambient flow velocity, colony size, and upstream colonies on the feeding success of Bryozoa. 1. *Bugula stolonifera* Ryland, an arborescent species. *J. Exp. Mar. Biol. Ecol.* 83:179–193.
- Parker, G. A., and M. Begon. 1986. Optimal egg size and clutch size: effects of environment and maternal phenotype. *Am. Nat.* 128:573–592.
- Persson, L. 1985. Asymmetrical competition: are larger animals competitively superior? *Am. Nat.* 126:261–266.
- Pettersen, A. K., C. R. White, and D. J. Marshall. 2015. Why does offspring size affect performance? Integrating metabolic scaling with life-history theory. *Proc. R. Soc. B: Biol. Sci.* 282. <https://doi.org/10.1098/rspb.2015.1946>
- . 2016. Metabolic rate covaries with fitness and the pace of the life history in the field. *Proc. R. Soc. B Biol. Sci.* 283. <https://doi.org/10.1098/rspb.2016.0323>
- Pettersen, A. K., C. R. White, R. J. Bryson-Richardson, and D. J. Marshall. 2017. Does the cost of development scale allometrically with offspring size? *Funct. Ecol.* 32:762–772.
- Rees, M. and M. Westoby. 1997. Game-theoretical evolution of seed mass in multi-species ecological models. *Oikos* 78:116–126.
- Rodriguez-Girones, M. A., H. Sandsten, and L. Santamaría. 2003. Asymmetric competition and the evolution of propagule size. *J. Ecol.* 91:554–562.

- Russell, A. F., N. E. Langmore, A. Cockburn, L. B. Astheimer, and R. M. Kilner. 2007. Reduced egg investment can conceal helper effects in cooperatively breeding birds. *Science* 317:941–944.
- Schob, C., R. Michalet, L. A. Cavieres, F. I. Pugnaire, R. W. Brooker, B. J. Butterfield, B. J. Cook, Z. Kikvidze, C. J. Lortie, S. Xiao, et al. 2014. A global analysis of bidirectional interactions in alpine plant communities shows facilitators experiencing strong reciprocal fitness costs. *New Phytol.* 202:95–105.
- Sinervo, B., E. Svensson, and T. Comendant. 2000. Density cycles and an offspring quantity and quality game driven by natural selection. *Nature* 406:985–988.
- Smith, C. C., and S. D. Fretwell. 1974. Optimal balance between size and number of offspring. *Am. Nat.* 108:499–506.
- Stanton, M. L. 1984. Seed variation in wild radish: effect of seed size on components of seedling and adult fitness. *Ecology* 65:1105–1112.
- Stearns, S. C. 1992. *The evolution of life histories*. Oxford Univ. Press, Oxford, U.K.
- Turnbull, L. A., D. Coomes, A. Hector, and M. Rees. 2004. Seed mass and the competition/colonization trade-off: competitive interactions and spatial patterns in a guild of annual plants. *J. Ecol.* 92:97–109.
- Turnbull, L. A., L. Santamaria, T. Martorell, J. Rallo, and A. Hector. 2006. Seed size variability: from carob to carats. *Biol. Lett.* 2:397–400.
- Venable, D. L. 1992. Size-number trade-offs and the variation of seed size with plant resource status. *Am. Nat.* 140:287–304.
- Weiner, J. 1990. Asymmetric competition in plant populations. *Trends Ecol. Evol.* 5:360–364.
- Zepeda, V., and C. Martorell. 2019. Seed mass equalises the strength of positive and negative plant–plant interactions in a semi-arid grassland. *Oecologia*. doi: 10.1007/s00442-018-04326-4
- Zhang, R., and K. Tielbörger. 2019. Facilitation from an intraspecific perspective—stress tolerance determines facilitative effect and response in plants. *New Phytol.* 221:2203–2212.

Associate Editor: S. Immler
Handling Editor: D. W. Hall

Supporting Information

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

Table S1. The expected frequency (%) of pairwise interactions in the field among *Bugula neritina* offspring of different sizes (μg) given their relative proportion (shaded in gray) in the population.