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LINKING ORGANISMAL FUNCTIONS, LIFE HISTORY STRATEGIES AND POPULATION PERFORMANCE

A global synthesis of offspring size variation, its eco-evolutionary causes and consequences

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Abstract

1. Offspring size is a key functional trait that can affect all phases of the life history, from birth to reproduction, and is common to all the Metazoa. Despite its ubiquity, reviews of this trait tend to be taxon-specific. We explored the causes and consequences of offspring size variation across plants, invertebrates and vertebrates.
2. We find that offspring size shows clear latitudinal patterns among species: fish, amphibians, invertebrates and birds show a positive covariation in offspring size with latitude; plants and turtles show a negative covariation with latitude. We highlight the developmental window hypothesis as an explanation for why plants and turtles show negative covariance with latitude. Meanwhile, we find evidence for stronger, positive selection on offspring size at higher latitudes for most animals.
3. Offspring size also varies at all scales of organization, from populations through to broods from the same female. We explore the reasons for this variation and suspect that much of this variation is adaptive, but in many cases, there are too few tests to generalize.
4. We show that larger offspring lose relatively less energy during development to independence such that larger offspring may have greater net energy budgets than smaller offspring. Larger offspring therefore enter the independent phase with relatively more energy reserves than smaller offspring. This may explain why larger offspring tend to outperform smaller offspring but more work on how offspring size affects energy acquisition is needed.
5. While life-history theorists have been fascinated by offspring size for over a century, key knowledge gaps remain. One important next step is to estimate the true energy costs of producing offspring of different sizes and numbers.

KEYWORDS
egg size, maternal investment, propagule size, seed size

1 | INTRODUCTION—OFFSPRING SIZE, A UNIVERSAL FUNCTIONAL TRAIT?

There are few life-history features or functional traits that are more ubiquitous across the metazoa than size, and offspring size is perhaps the most interesting. While sexual mode (clonal/parthenogenesis/sexual), developmental mode (direct/indirect) and life history (complex/simple), all vary enormously across species, common to all metazoan life is the necessity to allocate resources to offspring, so they can complete development. But this allocation is fraught. Inevitably, allocating resources to one offspring comes at the expense of other fitness-enhancing activities, such as allocation to other offspring, current performance or future reproduction. Intuitively, we expect larger offspring, those that receive more parental resources, to have higher fitness than smaller offspring, and indeed, this has been demonstrated repeatedly. Thus, at some level, parents face a universal trade-off between producing many, poorer performing offspring and fewer, better performing offspring. This offspring size-number trade-off was first modelled formally by Vance (1973), but is better known from Smith and Fretwell (1974), and forms the lens through which the evolutionary ecology of offspring size is viewed.

Because the offspring size-number trade-off is common to all metazoans, we are afforded the rare opportunity to gain insights from comparisons across the entire tree of multicellular life. Yet remarkably, such comparisons are lacking—much of the offspring size literature remains taxon-specific, with too little exchange among say, the seed literature (Moles & Westoby, 2003), the bird-egg literature (Krist, 2011) and even between the marine fish and invertebrate literature (Kamler, 1992; Marshall, Krug, Kupriyanova, Byrne, & Emlet, 2012). Broad synthetic efforts that span the major phylogenetic groups are largely lacking, despite the commonality of ideas. Indeed, most offspring size reviews are taxon-specific; the most recent general review was over 20 years ago (Bernardo, 1996). While these taxon-specific reviews have been excellent for advancing the field, their capacity for identifying patterns and contrasts among broad taxonomic groups is intrinsically limited.

Here, we seek to unify our understanding of offspring size by working across taxonomic boundaries to make what generalizations are now possible, and identify both commonalities and contrasts among groups. Such an approach is not without risk (as we stray beyond our taxonomic expertise) and downsides (we must be briefer than we would prefer). For instance, we prioritize empirical studies over theoretical ones, but we recognize theoretical approaches are essential. We review the concept of offspring size as a functional trait and explore patterns in offspring size variation at all levels of biological organization, from among species to within clutches from the same parent. Next, we examine how offspring size covaries with offspring fitness and why offspring size affects fitness, using energy as a common currency that applies across all taxa. Finally, we identify and prioritize the key questions that remain outstanding with regard to offspring size.

Offspring size is only one axis on which parental investment can vary but we believe it is the most useful. Offspring size at independence from parents is the perhaps the best and simplest metric by which to measure per offspring investment for most organisms that lack post-parturition care if it captures the majority of energy investment a parent makes in each offspring. Across species, larger offspring have more energy than smaller offspring. Across a wide variety of marine invertebrates (Marshall, Reitzel, & McAlister, 2017), plants (Leishman, Wright, Moles, & Westoby, 2000), birds (Williams, 1994), fish (Wootton & Smith, 2015) and insects (Fox & Czesak, 2000), larger offspring have greater dry weights, protein and energy contents than smaller offspring, although this relationship is imperfect and composition can vary.

1.1 | Offspring size and the duration of development

In 1973, Vance brilliantly intuited that offspring size must affect the duration of the developmental period. Vance assumed that larger embryos take longer to reach the same developmental stage as smaller embryos. This assumption has intuitive appeal—if rates of cell cleavage are relatively constant across species, then inevitably larger eggs take longer to become embryos. While well known to marine invertebrate biologists, Vance's models are less appreciated by those working in other groups. Very early studies also supported the idea that larger eggs take longer to become larvae (Morgulis, 1909), and as Vance's pioneering models, it has become increasingly apparent that embryos from larger-egged species take longer to develop than embryos from smaller-egged species. In birds, insects, fish and plants, offspring size strongly affects among-species patterns in time to hatching or germination (Maino, Pirtle, & Kearney, 2017; Moles & Westoby, 2003; Pauly & Pullin, 1988; Rahn & Ar, 1974). Similar effects are observed in mammals with regard to gestation (Blueweiss et al., 1978). In marine invertebrates, where development is complicated by larval feeding in some groups, larger embryos take longer to hatch more generally, although the total larval period may not be longer overall (Marshall & Keough, 2008; Marshall et al., 2017)—similar effects have been noted in frogs (Morgulis, 1909). As discussed later, the effect of offspring size on developmental duration may be a key driver of latitudinal patterns in offspring size across species.

Within species, the effects of offspring size on development are far less clear. For some groups, intraspecific patterns mirror interspecific patterns (Kamler, 1992), whereby larger eggs take longer to develop, but the converse is also true (Marshall & Keough, 2008; Schenk & Sondgerath, 2005). Why these effects seem so consistent among species, but so variable within species is unclear—although could simply be driven by effect size and statistical power (there is more offspring size variation among species than within). Resolving this question is important, however, because size and developmental duration can critically affect dispersal distances of offspring, such that mothers may alter the dispersal potential of their offspring through maternal provisioning. Such effects are particularly important for plants and sedentary marine invertebrates (Leishman et al., 2000; Marshall & Keough, 2008; Wang & Ives, 2017), where the early life-history stages are also the most dispersive, but offspring size also affects dispersal in groups with highly mobile adults (such as fish; Einum et al., 2011; Kamler, 1992).

1.2 | Biogeographical patterns in offspring size

Spatial patterns in offspring size among species are often striking. For example, marine life-history theoreticians noted a strong relationship between offspring size and latitude in the 1930s (Thorson, 1936). Such patterns have only become more apparent as studies accumulate; across taxa, offspring size covaries with latitude but remarkably, no broad syntheses of these patterns exists. We compiled these taxon-specific syntheses of biogeographic variation in offspring size to yield the largest and broadest database of offspring size ever compiled (see Supporting Information for details).

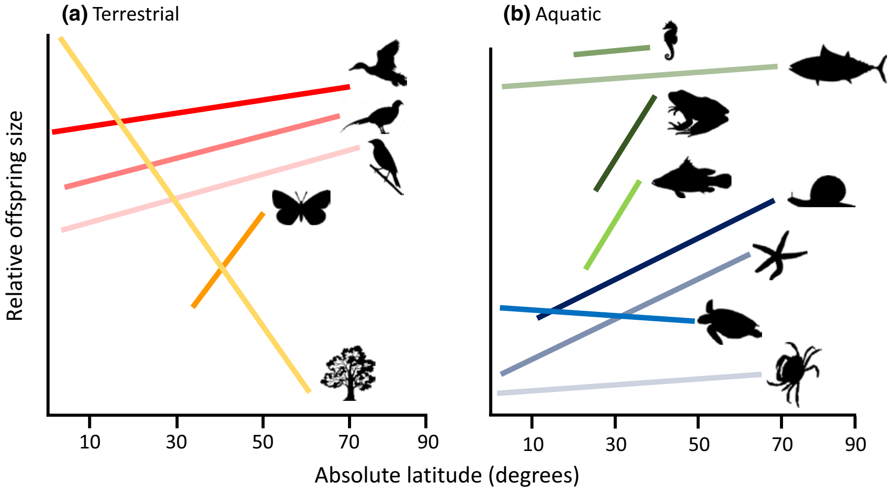

FIGURE 1 Spatial patterns in relative offspring size across latitude for different (a) terrestrial species—including different groups of birds, butterflies and plants, and (b) aquatic species—including different groups of marine and freshwater fish, turtles and marine invertebrates with different developmental modes (for the marine invertebrates, many phyla are included in each developmental mode and the snail, seastar and crab represent species with direct development, non-feeding larvae and feeding larvae, respectively). Note that these lines do not represent absolute offspring sizes, nor are their relative positions on the *y* axis representative. Rather the lines show the slope of the relationship between offspring size and latitude for each group, as well as the latitudinal extent of the underlying data. Importantly, the slope of the line for plants is extremely underestimated relative to the other studies because this group shows much higher levels of variation (4 orders of magnitude) in offspring size across the latitudinal gradient)

Our synthesis found that biogeographical patterns in offspring size fell into two broad groups (Figure 1): those that show a negative relationship between offspring size and latitude; and those that show a positive relationship between offspring size and latitude. Plants show the most reliable and strongest covariation between latitude and offspring (seed) size. Moving from the tropics to the poles, seeds become much smaller. Turtles also show a negative relationship between latitude and offspring size. In contrast, offspring size for all other animal groups positively covary with latitude. We note, however, that for one group (minnows), there was no indication of a relationship. For this group, all but one species came from the same 10° latitudinal band, suggesting limited power to detect any differences.

Some generalizations seem possible based on our compilation. Plants generally show a consistent negative relationship between seed size and latitude. In contrast, it is clear that most animals (except turtles) show strong positive covariance between offspring size and latitude. Why turtles show the opposite pattern is unclear—this group shows the standard Bergmann size cline whereby lower latitude species tend to be smaller adults (Ashton & Feldman, 2003), and so maternal body size constraints are unlikely to drive the pattern. We suspect that both turtles and plants show different patterns to most other animals because of the way offspring size and temperature affects development across all of these groups.

1.3 | Developmental windows as a driver of latitudinal offspring size variation

Plant and animal life-history theorists have tended to invoke different factors when considering biogeographical patterns in offspring size. Nevertheless, we suspect there is some newfound potential for unifying explanations. Discussions of latitude–seed size relationships have traditionally focused on biotic factors that covary with latitude such as herbivory and competition (Leishman et al., 2000; Moles, Warton, Stevens, & Westoby, 2004; Moles & Westoby, 2003). More recently, however, explanations of latitude–seed size relationships have focused on scope for growth and development (Moles & Westoby, 2003). Temperature strongly affects development rates in all organisms—small increases in temperature yield massive increases in developmental rate (Gillooly, Charnov, West, Savage, & Brown, 2002). Higher latitudes have far fewer warmer days and therefore provide shorter windows for rapid seed development (de Casas et al., 2017). Seed size, among species at least, positively covaries with development time and so it is argued that large seeds simply cannot complete development at higher latitudes (Moles & Westoby, 2003). Interestingly, the same argument has been invoked independently for turtles (Iverson, Balgooyen, Byrd, & Lyddan, 1993). Larger turtle eggs take longer to develop (Iverson et al., 1993), and as turtle eggs are largely at the mercy of ambient temperature regimes, large eggs may simply fail to complete development in the shorter warm periods of high latitudes.

But if developmental windows drive offspring size covariance patterns with latitude, why do birds and other animals produce larger offspring at higher latitudes, while plants and turtles show the converse? A key difference between birds and turtles of course is that birds typically incubate their eggs such that environmental temperature would more strongly affect development for turtles relative to birds. Other reptiles (e.g., squamates, crocodiles) that show limited thermoregulation of their nests would represent a key group in which to test the developmental window hypothesis, yet compilations of egg size variation in these groups are lacking.

Biogeographic patterns in offspring size for non-avian animals other than turtles, however, appear to contradict the developmental window hypothesis. Certainly, egg size positively covaries with developmental time among species of both invertebrates and fish (Gillooly et al., 2002; Pauly & Pullin, 1988; Pepin, 1991), so we would expect these ectotherms to follow the same patterns as turtles. One speculative explanation is that because eggs are typically much smaller in fish, amphibians and invertebrates relative to other vertebrates and the seeds of plants, developmental windows might be less severe in fish and invertebrates. We predict that once developmental window constraints are removed, all else being equal, selection for larger offspring may be stronger at higher latitudes, potentially explaining the production of larger offspring towards the poles in these groups. In the next section, we formally test whether there are any apparent geographic patterns in selection on offspring size.

2 | OFFSPRING SIZE–FITNESS RELATIONSHIPS

Offspring size affects fitness. While this seems straightforward, there are remarkably few formal compilations of the relationship between offspring size and fitness (but see Rollinson & Rowe, 2015). We expanded the dataset of Rollinson and Rowe (2015) to examine the spatial patterns in linear selection across latitudes and conducted a phylogenetically controlled analysis using weighted regression (see Supporting Information for details). As expected, selection on offspring size is generally (though not invariably) positive with an average standardized selection gradient of 0.125 and an average selection differential of 0.145 across all studies. We found that the strength of selection on offspring size increases with latitude; although this pattern is only apparent for selection differentials, but not selection gradients (Figure 2). Overall, stronger positive selection tends to favour larger offspring at higher latitudes relative to lower latitudes, providing some support for our suggestion that biogeographic patterns in selection may drive latitudinal patterns in offspring size observed in some groups (discussed above). Nevertheless, our results are very preliminary as there are few formal estimates of selection on offspring size generally, and we encourage future studies of offspring size effects to provide such estimates.

The mechanisms mediating latitudinal variation in selection are unclear. It is always tempting to invoke differences in mean conditions across latitude as drivers of latitudinal patterns. For example, earlier in this review, we invoked mean temperature and its effect on development as a driver of latitudinal patterns in offspring size. However, recent studies remind us that latitudes differ in ways beyond mean conditions. For example, the seasonality and predictability of conditions also differ dramatically across latitude, and both mediate selection on, and shape spatial patterns in, offspring size (Marshall & Burgess, 2015).

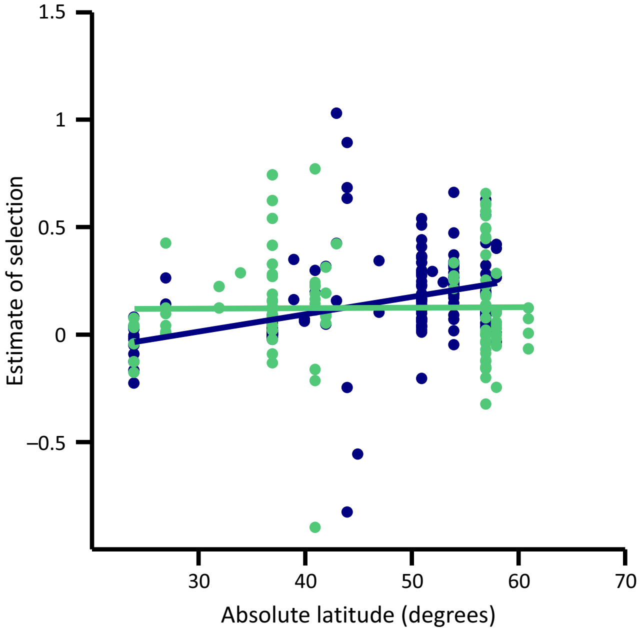

FIGURE 2 Spatial patterns in linear selection on offspring size across latitude. Each point is a single estimate of selection and selection differentials are shown in green, while selection gradients are shown in blue

3 | INTRASPECIFIC VARIATION IN OFFSPRING SIZE

In this section, we consider variation among populations, mothers and siblings. We consider two different drivers of variation in offspring size: extrinsic or environmental sources and intrinsic sources. These distinctions are largely artificial and simply for convenience—in reality, environmental factors such as food availability can quickly translate into intrinsic factors such as maternal phenotype. Nevertheless, we would argue that the field has progressed in its understanding of external, rather than internal drivers of variation in offspring size, and so we make these distinctions here.

3.1 | Environmental sources of variation

Life-history theoreticians have long known that offspring size varies with environmental conditions such as temperature, local food regimes, competitors and stressors. Traditionally, there was a tendency to simply assume that poor quality maternal conditions would translate to the production of poor quality (i.e., smaller) offspring, otherwise known as a transmissive maternal effect (Marshall & Uller, 2007). Pioneering work by Chuck Fox and others overturned these assumptions, showing that often, the opposite was the case: mothers in poor quality environments often produce larger offspring (Fox, Thakar, & Mosseau, 1997). Increasingly, it seems that much of this variation is driven by adaptive transgenerational plasticity on the part of parents whereby mothers anticipate the environment their offspring are likely to experience and provision their offspring accordingly (Allen, Buckley, & Marshall, 2008). Mothers often produce larger offspring when competition is more intense or food availability/quality is lower (Bashey, 2008; Plaistow, Lapsley, & Benton, 2006). Such anticipatory maternal effects can work both ways—mothers can also reduce the size of their offspring when conditions are benign. A beautiful meta-analysis by Swanson et al. (2016) showed that, across many species of butterfly, mothers decrease the size of their eggs when laying on higher quality food sources, allowing them to lay more eggs overall. Thus, offspring size is typically the functional trait by which mothers buffer their offspring from harsher environments or maximize fecundity in more benign environments. Such anticipatory maternal effects are particularly likely when the environment affects resource availability and the maternal environment is a good predictor of the offspring environment (Burgess & Marshall, 2014). Importantly, a recent meta-analysis of parental effects found they were often not adaptive (Uller, Nakagawa, & English, 2013). We suspect that this meta-analytical result reflects the nature of the tests that have been made so far—most have manipulated maternal environment without formally considering whether such manipulations are meaningful in that they provide reliable cues to mothers about their offspring's likely environment. Maternal effects are no panacea, but we believe that more careful consideration of the reliability and predictability of parental environments as cues for offspring provisioning decisions should result in better estimates of the prevalence of adaptive parental effects.

Temperature has also long been recognized to covary with intraspecific variation in offspring size in ectotherms. Mirroring interspecific patterns discussed above with regard to latitude, in animals at least, warmer mothers tend to produce smaller offspring than cooler mothers across a range of animal taxa (Atkinson, Morley, Weetman, & Hughes, 2001). While some have speculated that this pattern is a product of physiological processes (Van der Have & de Jong, 1996), we suspect it is actually an adaptive response to differences in the costs of development at different temperatures (Kamler, 1992). Interestingly, in both vertebrates and invertebrates (Bownds, Wilson, & Marshall, 2010; Burgess & Marshall, 2011; Fischer, Bot, Brakefield, & Zwaan, 2003), smaller offspring tend to perform better in higher temperatures and vice versa when both parental and offspring environmental temperatures are manipulated, indicating that temperature-mediated changes in offspring size are likely to be adaptive.

It is worth noting that maternal manipulations of offspring in response to environmental changes are unlikely to be perfect, and that particular attention should be paid to changes in the offspring size fitness function across environments, and whether it is biologically likely for mothers to anticipate such changes (Burgess & Marshall, 2014). In some instances, the environment might be so bad that no amount of provisioning will increase offspring fitness (Allen et al., 2008). In these instances, mothers appear to change the size of their offspring, not so the offspring can perform better in the local environment, but so the offspring can escape that environment. Because offspring size affects development time, dispersal probability or dormancy duration (de Casas et al., 2017; Marshall & Keough, 2008; Wang & Ives, 2017), mothers may alter the dispersal potential or dormancy of their offspring by manipulating offspring size. Thus, maternal effects on offspring size insulate offspring from particularly bad local environments by facilitating dispersal out of that environment, or delaying development such that the environment is likely to improve.

3.2 | Intrinsic sources of variation

Mothers that experience the same environment may still produce offspring of very different sizes and much of this variation seems correlated with maternal phenotype—particularly maternal size and age (Marshall, Heppell, Munch, & Warner, 2010). Within a wide range of taxa, larger mothers produce larger offspring (Lim, Senior, & Nakagawa, 2014). Rollinson and Rowe (2016) recently provided an excellent summary of this topic, and we share their view that non-adaptive, constraint-based arguments regarding maternal size–offspring size (MSOS) correlations are unlikely to be broadly applicable. In their review, Rollinson and Rowe highlight two schools of thought for why MSOS correlations might be adaptive. Briefly, one school of theory assumes that because larger mothers are more fecund or select different habitats than smaller mothers, the offspring from larger mothers have a different offspring size fitness function than the offspring of smaller mothers (Marshall et al., 2010; Rollinson & Hutchings, 2011). Thus, larger mothers place their offspring in environments that select for larger optimal offspring sizes, and so produce larger offspring. Rowe and Rollinson are somewhat dismissive of such explanations, but we believe there is insufficient evidence to discount these ideas, and direct tests of the theory are still rare (Cameron, Monro, Malerba, Munch, & Marshall, 2016; Plaistow et al., 2006; Rollinson & Hutchings, 2010). We therefore encourage more empirical work along this line.

The second school of thought proposes that maternal size alters the costs of producing offspring independently of the offspring size fitness function. This theory was pioneered by Sakai and Harada (2001), with subsequent iterations and modifications (Filin, 2015). Essentially, these theories predict that if larger mothers can mobilize more nutritional resources more quickly, and offspring use resources while being provisioned, then larger mothers are able to produce larger offspring more cheaply than smaller mothers. While the key assumptions of these models seem reasonable, empiricism again lags behind, with very few direct tests.

Rollinson and Rowe suggest that maternal nutritional status, rather than maternal size per se, drives MSOS correlations. While nutritional status and maternal size are highly correlated in some species, we suspect that in others, mothers might be larger because of greater accumulated size from previous periods but can still have poor nutritional status in the current reproductive round. As Rollinson and Rowe suggest, a straightforward test would be to manipulate maternal size and current food regime orthogonally and examine the relationship between maternal size and offspring size.

In addition to varying with maternal size, offspring size also covaries with maternal age. In some instances, this covariance appears to be driven by the fact that maternal age is a reliable predictor of offspring environment (Plaistow et al., 2006), but in others, it is unclear whether size or age is the driver. While theory has explored these issues specifically and sought to disentangle size and age (Kindsvater, Alonzo, Mangel, & Bonsall, 2010), too few empirical studies have sought to disentangle these factors (Green, 2008).

Determining the drivers of MSOS correlations is particularly important given that many harvested species suffer shifts in mean body size (Hixon, Johnson, & Sogard, 2014). If larger mothers produce offspring of different quality than smaller offspring, then removing larger mothers will have disproportionate impacts beyond any fecundity effects alone (Hixon et al., 2014). Crucially, the two schools of thought regarding the drivers of MSOS correlations have different consequences for offspring quality—one implies that offspring quality (irrespective of offspring size) is unchanged across maternal sizes, the other does not (Marshall et al., 2010). Thus, resolving this issue is not only important to life-history theory, it is also crucial for the management of harvested species.

3.3 | Offspring size variation within mothers

Offspring from a single reproductive bout are never perfectly uniform in size, although this variability is often underestimated (Turnbull, Santamaria, Martorell, Rallo, & Hector, 2006). Indeed in some groups, offspring size variation within a clutch exceeds the variation observed among mothers (Kamler, 1992; Marshall, Bonduriansky, & Bussiere, 2008). Although widespread, offspring size variation within broods (or clutches, litters, etc.) has received less empirical attention than at other scales. As such, the causes and consequences of within-brood variation remain unclear. Some authors suggest physiological constraints (Fox & Czesak, 2000) or family conflict (Kamel & Williams, 2017) may limit the capacity of mothers to equally provision their offspring. But given that mothers can adaptively alter the mean size of their offspring (discussed above), we suspect that mothers may adaptively control variance, at least to some degree. We review the adaptive explanations proposed to maintain within-brood variation, which generally fit into two categories: (1) bet-hedging hypotheses, and (2) sibling competition hypotheses.

3.4 | Within-brood variation as a bet-hedging strategy

As previously discussed, when mothers can anticipate the environment their offspring will face, they should produce offspring of a single, optimal size. But what if mothers cannot accurately predict the offspring environment? Theory predicts that in unpredictable environments, mothers “hedge their bets” by producing variable clutches to ensure that at least some offspring survive the prevailing conditions. In unpredictable environments, mothers that unequally provision their offspring therefore trade-off arithmetic mean fitness for reduced variation in fitness across generations, increasing long-run (geometric mean) fitness (Philippi & Seger, 1989). Within-brood variation is most commonly attributed to bet-hedging, but evidence remains equivocal. Theory supports this idea when the offspring size fitness function is modelled as dome-shaped (Marshall et al., 2008), but not when offspring fitness is a positive function of offspring size (Einum & Fleming, 2004; McGinley, Temme, & Geber, 1987). Correlative studies suggest a positive relationship between environmental predictably and the level of offspring size variation within broods (Morrongiello, Bond, Crook, & Wong, 2012), but few studies have manipulated the offspring environment to explore maternal bet-hedging responses (but see Barbosa et al., 2015).

3.5 | Within-brood variation mediates sibling competition

In many systems, siblings can co-occur across small spatial scales for some of the life history, and can interact to alter one another’s fitness. Theory suggests, within-brood variation may be adaptive if competition among different-sized siblings is asymmetric. In birds, hatching asynchrony may create competitive hierarchies where older, larger siblings out-compete later-hatched, smaller siblings for parentally supplied resources (Lack, 1947). Analogous theory in plants predicts within-brood variation is maintained by small-scale variation in seed density and asymmetric competition in favour of larger seeds (Geritz, van der Meijden, & Metz, 1999). A key assumption of these models is a colonization/competition trade-off in favour of smaller and larger seeds, respectively. Again, empirical support for these theories are rare. In contrast to competitive asymmetry hypotheses, novel evidence suggests that within-brood variation mediates facilitation in a sessile marine invertebrate. Cameron, Monro, and Marshall (2017) found that within-brood variation increases not only the collective performance of broods, but also the performance of individual offspring, irrespective of their size. These authors speculate that their results may be driven by food-resource partitioning among different-sized siblings, and is supported by evidence in frogs (Martin & Pfennig, 2010).

4 | WHY DOES OFFSPRING SIZE AFFECT FITNESS? A FUNCTIONAL TRAIT APPROACH

The vast majority of studies measuring the consequences of offspring size variation have focussed on the nature of the offspring size fitness function, where “fitness” may pertain to survival, growth rate, longevity or reproductive output (Bernardo, 1996). These phenomenological approaches provide strong evidence that offspring size covaries with fitness (Ronget et al., 2017). However, it is surprising that in most cases, the mechanism by which offspring size affects fitness remains unknown. While many species-specific explanations have been proposed, general mechanisms that apply across taxa are surprisingly limited. Given that the fitness benefits of having a larger size early in the life history are ubiquitous among species, we might expect to see general mechanisms driving this response.

Here we discuss potential drivers of the offspring size-performance relationship.

4.1 | Energy acquisition and energy loss

All organisms uptake, transform and expend energy. The amount of energy available for key biological processes is thought to be closely linked to fitness. Because offspring often need to undergo some development before they can begin to feed, or cannot access the full range of nutritional resources available to adults, offspring are particularly reliant on parentally derived resources. As discussed earlier, the best predictor of parental energy investment seems to be offspring size for most taxa. Increased energy reserves may be a potential advantage to producing larger offspring, but it is also possible that there are higher costs associated with originating from a larger offspring size. In order for larger offspring sizes to carry an energy advantage, larger offspring must also possess or gain more energy relative to the costs of maintaining a larger size. In other words, for energy acquisition/use to provide a general mechanism for the offspring size–performance relationship, larger offspring size should have higher net energy available for fitness-enhancing functions than smaller offspring (Leishman et al., 2000). These benefits can arise via two non-mutually exclusive ways: (1) bigger offspring *acquire* proportionally more energy, or (2) bigger offspring *use* proportionally less energy.

It seems that larger offspring often access more energy resources than smaller offspring. In spadefoot toads, larger tadpoles originating from larger eggs can access a more nutrient-rich carnivorous diet, and thus potentially out-compete smaller, omnivorous tadpoles (Martin & Pfennig, 2010). Similarly, larger gape sizes at birth allow for more efficient energy acquisition and growth in some snakes and fish (Aubret, 2012; Kamler, 1992; Knutsen & Tilseth, 1985). In filter-feeding marine invertebrates, larger offspring initially produce more, or larger, feeding structures (Marshall et al., 2017).

In plants, seed size likely affects photosynthetic capacity (energy intake) by affecting the size of leaves that are produced by the seedling (Leishman et al., 2000). Numerous interspecific studies find that species with larger seeds typically produce seedlings with greater initial leaf mass (Moles et al., 2004), but intraspecific studies (which we are necessarily interested in when exploring mechanism) are rarer. Classic studies show that larger seeds produce larger cotyledons and have greater leaf surface area (Moegenburg, 1996; Stanton, 1984). Though rare, other intraspecific studies show seed size affects the size of the root mass, another way in which plants access essential resources (Bonfil, 1998).

While these studies imply that larger offspring can take in more energy than smaller offspring—it is unclear whether they can take in *disproportionately* more than smaller offspring (i.e., energy intake scales hyperallometrically). At this point, we think it is reasonable to assume that energy intake scales at least isometrically with offspring size, although we encourage formal tests. Such patterns of isometry takes on new significance when we also consider size-dependent energy use in offspring.

Energy use (metabolism) is likely to scale allometrically with offspring size. In most, if not all metazoans, metabolic rates scale to mass with an exponent less than 1—larger organisms have lower mass-specific metabolic rates (Pettersen, White, Bryson-Richardson, & Marshall, 2017). Thus, larger offspring should expend relatively less energy than smaller offspring and should complete any costly developmental stage with a higher proportion of their initial energy reserves. This developmental allometry is particularly crucial for offspring during non-feeding phases. There is direct evidence for allometric scaling in marine invertebrates and fish where a doubling in offspring size can yield a reduction in mass-specific metabolic rates of *c.* 40% (Pettersen, White, & Marshall, 2015; Pettersen et al., 2017). Similar ideas were raised by Kamler (1992) where she argued that the relative costs of development should decrease with increased offspring size when metabolism scales allometrically. There is also indirect evidence for development being more metabolically efficient in birds and fish (Duarte & Alcaraz, 1989; Williams, 1994). Williams (1994) showed that hatchlings from larger eggs did not necessarily emerge with a greater size (measured as wing length), but they did emerge with a higher mass and higher proportion of yolk reserves, as one might expect if larger offspring completed development more efficiently. An analysis of the data in Duarte and Alcaraz (1989) shows that fish larvae from larger eggs are disproportionately larger than larvae from smaller eggs (our analysis of their data included both intra- and interspecific variation). Interestingly, some studies also suggest larger offspring (particularly in fish) are more resistant to starvation than smaller offspring (Kamler, 1992; Marshall & Keough, 2008). Such an effect would not occur if larger offspring had the same mass-specific metabolic demands as smaller offspring. Given the ubiquity of allometric scaling, we suggest developmental allometry is a potentially universal explanation for why larger offspring perform relatively better than smaller offspring.

Combining the effects of offspring size on energy acquisition and loss, it seems likely that a key mechanism underlying offspring size effects on offspring performance is net energy acquisition. Larger offspring are likely to access more, and expend proportionally less, energy during key early life-history stages than smaller offspring, and thus larger offspring should have comparatively more energy for fitness-enhancing processes such as growth and reproduction.

5 | OUTSTANDING QUESTIONS

5.1 | Whose fitness is it?

A number of outstanding questions regarding offspring size remain. First among these is the assignment of fitness. As Wolf and Wade (2001) brilliantly show, life-history theoreticians think about offspring size differently to classic quantitative geneticists. Life-history theoreticians typically assign fitness returns of different maternal investment strategies to mothers. In this sense, offspring size is an odd trait because it affects the fitness of both mothers and offspring, but life-history theoreticians assume that selection maximizes maternal fitness (Smith & Fretwell, 1974; Stearns, 1992). This assumption arises because otherwise, it is hard to explain why selection would favour an offspring receiving less than perfect provisioning from the mother. Yet, the view that offspring sizes are the product of selection on mothers, is at odds with standard quantitative genetic theory that assigns fitness strictly to the organism bearing the trait (Wolf & Wade, 2001). From this perspective, given offspring size affects offspring fitness, selection should act on offspring size to maximize offspring fitness. Given the ubiquity of directional selection for increased offspring size (Rollinson & Rowe, 2015), under this framework then, we should expect larger offspring to be favoured, regardless of the trade-off mothers might face.

Wolf and Wade provided a clear reconciliation of this issue—they showed that neither view (life-history theory or the strict quantitative genetics view) was completely correct. Instead, it appears that the assignment of fitness will depend on the genetic covariance between offspring size in one generation and the next. We strongly recommend those interested read the paper in detail as it provides a clear path for resolving this issue. In the meantime, studies in model systems suggest that mothers generally win the parent–offspring conflict, with gene knockout studies revealing that maternal genes limit offspring size in both *Drosophila* and *Arabidopsis* (Dani & Kodandaramaiah, 2017).

5.2 | Offspring size-number trade-off

Models of offspring size inevitably assume a size-number trade-off, but such trade-offs are not likely to be observed within or among species for reasons elegantly described by Stearns (1992, p. 80). Nevertheless, the true costs of producing offspring of different numbers and size are poorly resolved. For example, while the energy allocated to each offspring is non-trivial and reflected by size, there are other costs associated with producing offspring of different sizes or number. For example, if there are specialized reproductive structures for each offspring, then it might be more costly to produce multiple offspring than fewer offspring (Filin, 2015). If offspring use resources while being provisioned, that may alter the relative costs of offspring sizes (Sakai & Harada, 2001). If male gametes are limited, there are several reasons why making smaller, more numerous offspring will be costly and wasteful (Marshall et al., 2017). Unfortunately, the energy costs of brooding offspring, or the per capita costs of making reproductive structures are largely unknown and so a true energy budget of offspring, beyond the simple energy content of those offspring, remains unknown.

5.3 | Offspring size and predation

Offspring size may affect fitness simply because a physically larger offspring is fitter, regardless of energy considerations. For example, physical size may affect predation—this idea has been important to fish offspring size discussions for over 50 years (Kamler, 1992). If predators are size-limited, then larger offspring may simply be less susceptible to predation (Reznick, Callahan, & Llauredo, 1996). Larger offspring can also have greater locomotory abilities, allowing them to better escape predators (Kamler, 1992). In some cases, however, larger offspring can actually be more attractive to predators in both plants (Gómez & Husband, 2004; Moegenburg, 1996; Wang & Ives, 2017) and animals (Donelan & Trussell, 2018; Gosler, Greenwood, & Perrins, 1995), but further tests are needed more generally. Similarly, larger offspring may actually make more effective predators/consumers (Martin & Pfennig, 2010; Palmer, 1990), but again there have been exceedingly few tests.

6 | CONCLUSIONS

Offspring size is a fascinating functional trait that shows predictable global patterns among species. Offspring size affects every part of an organism's life, from birth to reproduction and selection tends to favour larger offspring, although the strength of selection varies in space and time. We suggest that the negative relationship between offspring size and absolute latitude observed for some groups (large-egged clades that cannot insulate their offspring) is explained by the developmental window hypothesis. For other groups (birds and invertebrates), latitudinal patterns in selection appear to shape global patterns in offspring size, but more data are required for more robust tests of this prediction. We suggest that a major way in which offspring size affects subsequent offspring fitness is by altering the relative energy costs of development and subsequent energy intake at independence.

AUTHORS' CONTRIBUTIONS

All three authors wrote the first draft and contributed to subsequent revisions.

DATA ACCESSIBILITY

No new data are contained in this manuscript other than summary data provided in Supporting Information.

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