EVOLUTIONARY ECOLOGY OF PROGENY SIZE IN ARTHROPODS

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■ **Abstract**   Most models of optimal progeny size assume that there is a trade-off between progeny size and number, and that progeny fitness increases with increasing investment per young. We find that both assumptions are supported by empirical studies but that the trade-off is less apparent when organisms are iteroparous, use adult-acquired resources for reproduction, or provide parental care. We then review patterns of variation in progeny size among species, among populations within species, among individuals within populations, and among progeny produced by a single female. We argue that much of the variation in progeny size among species, and among populations within species, is likely due to variation in natural selection. However, few studies have manipulated progeny environments and demonstrated that the relationship between progeny size and fitness actually differs among environments, and fewer still have demonstrated why selection favors different sized progeny in different environments. We argue that much of the variation in progeny size among females within populations, and among progeny produced by a single female, is probably nonadaptive. However, some species of arthropods exhibit plasticity in progeny size in response to several environmental factors, and much of this plasticity is likely adaptive. We conclude that advances in theory have substantially outpaced empirical data. We hope that this review will stimulate researchers to examine the specific factors that result in variation in selection on progeny size within and among populations, and how this variation in selection influences the evolution of the patterns we observe.

INTRODUCTION

Progeny size is an especially interesting life history trait because it is simultaneously a maternal and progeny character—mothers make eggs and determine egg size, but egg size can have substantial fitness effects for progeny. Thus, progeny size is subject to selection in both the parental and progeny generations. This selection often varies in direction and/or magnitude among generations (parental versus offspring), among environments, and even among siblings within

a family, such that understanding the factors that influence the evolution of progeny size can become quite a challenge. In this review, we focus on understanding the causes and consequences of egg and progeny size variation in arthropods. Although most arthropods lay eggs, many crustaceans brood their eggs and studies of progeny size in crustaceans measure progeny after eggs hatch and are released by the parent. We thus use the phrases "egg size" or "progeny size" interchangeably. We also acknowledge that eggs and progeny often vary in ways other than size (e.g. egg composition) and that this variation may be ecologically and evolutionarily as important as variation in size (17). However, due to space constraints we limit our discussion to progeny size.

We begin with a brief discussion of the optimality model developed by Smith & Fretwell that laid the foundation for how we think about the evolution of progeny size (197). We focus on empirical studies that examine the two primary assumptions of this model. Next, we explore patterns of variation in progeny size among species and among populations within species. Lastly, we review the sources of variation in progeny size within populations and discuss proposed explanations for this variation.

CONCEPTUAL FRAMEWORK

Christopher Smith and Steven Fretwell (197) offered the first mathematical analysis of optimal progeny size. They asked "what size progeny should a female produce to maximize her total number of grandprogeny?" The number of grandprogeny a female will produce depends on both the number of progeny she produces and the fitness of those progeny. To model this, Smith & Fretwell started with two assumptions: *(a)* progeny fitness (W_{Young}) increases with increasing parental investment per offspring (I_{Young}) (i.e. larger progeny will have higher fitness), and *(b)* for any fixed amount of parental investment into reproduction (I_{Total}), a female can produce $N = I_{Total} / I_{Young}$ progeny. In other words, there is a trade-off between the number of progeny a female can make and the amount of resources allocated to each of those progeny. If a female makes larger progeny, I_{Young} increases and N decreases. To increase N, a female must either decrease I_{Young} or increase I_{Total}. Smith & Fretwell assumed that I_{Total} is a constant. Maternal fitness, $W_{Parent} = N \times (W_{Young}) = (I_{Total} / I_{Young}) \times (W_{Young})$, the product of the number of progeny that she produces times the fitness of each of those progeny. The value of I_{Young} that results in the highest parental fitness is the value that maximizes $(I_{Total} / I_{Young}) \times (W_{Young})$. Maternal fitness thus increases as W_{Young} increases, but also increases as (I_{Total} / I_{Young}) increases (i.e. fecundity increases). The constraint here is that for any fixed amount of resources (I_{Total}), females can increase W_{Young} only by increasing I_{Young}, which necessarily results in a decrease in fecundity (I_{Total} / I_{Young}).

This model illustrates three points that have become the subject of much empirical and theoretical exploration. First, for any fixed parental allocation to repro-

duction, progeny size is under balancing selection; large progeny are favored because W_{Young} increases as I_{Young} increases, and small progeny are favored because N increases as I_{Young} decreases. Second, there is a conflict of interest between parents and their progeny. Because progeny fitness (W_{Young}) increases with increasing investment per progeny (I_{Young}), the value of I_{Young} that maximizes progeny fitness is larger than the value that maximizes parental fitness. Third, any environmental variable that affects the relationship between investment per progeny and progeny fitness (i.e. between I_{Young} and W_{Young}) can result in a change in the optimal progeny size and thus a change in the size of progeny that should evolve in a population. The first and third of these points will be discussed in this paper. The consequences of conflicts of interest between parents and their offspring has been reviewed extensively elsewhere and will not be discussed here.

Since the original development of the Smith-Fretwell model, more complex models have been developed to examine optimal progeny size under more specific conditions (46, 182). It is not the objective of this paper to review the various models and their specific assumptions (see 17). However, most of these models start with the same basic assumptions that Smith & Fretwell started with, that *(a)* there is a trade-off between progeny size and number, and *(b)* progeny fitness (W_{Young}) increases with increasing parental investment per offspring. We thus focus first on these two assumptions.

Trade-Offs Between Progeny Size and Number

The concept of trade-offs is an integral part of life history theory (182). If an individual has a fixed amount of resources available, those resources can be divided into three basic functions—growth, somatic maintenance, or reproduction. Resources directed to reproduction can subsequently be divided into either many small progeny or a few larger progeny. Thus, for a fixed amount of resources allocated to reproduction it necessarily follows that there is a trade-off between the number and size of progeny

Phenotypic correlations between egg size and number *(a)* among species (18, 19, 33, 42, 65, 84, 86, 127, 129, 139, 143, 175, 177, 193, 204, 217), *(b)* among populations within species (2, 56, 127, 230) and *(c)* among individuals within populations (Table 1) generally indicate a trade-off between egg size and number. Most of these studies examine only phenotypic correlations between egg size and number, but a genetically based trade-off has been demonstrated for *Daphnia* (57, 140).

In general, trade-offs have been detected in most studies of relatively semel-parous arthropods that use larval-acquired resources for egg production and exhibit no parental care (Table 1). In studies of more complex systems (especially vertebrates), in which females are iteroparous, use adult-acquired resources for reproduction (e.g. shrimp, mosquitoes), or exhibit parental care (e.g. birds), a trade-off has been more difficult to demonstrate (87), leading some authors to suggest that such a trade-off is not universal (e.g. 17). Failure to demonstrate

TABLE 1 Evidence for (or against) a trade-off between egg/progeny size and number, based on variation among females within a population (number of species)

Taxon	Trade-off	No Trade-off	Reference (trade-off)	Reference (no trade-off)
Crustacea (cladoceran)	7	1	15[2], 22, 45, 87[1], 140, 153, 213	15[2]
Crustacea (copepod)	2	0	2, 93	
Crustacea (shrimp)	0	4		42
Crustacea (isopod)	2	1	135, 230	50
Orthoptera	5	0	39, 68[3]	
Heteroptera	3	0	132, 154, 198	
Lepidoptera	3	3	66[2], 136, 180	16, 26, 146[4]
Coleoptera	3	0	81, 94, 219	
Diptera	3	2	4[2,5], 138	4[2], 29

[1]Varied with age of the female (iteroparous organism)
[2]Based on variation in egg size through the season
[3]Confounded with maternal age
[4]Did not control for female size
[5]Varied among studies

trade-offs probably has less to do with their absence than with the complexity of the system. For a trade-off between egg size and number to be evident, we must assume that the quantity of resources allocated to reproduction (I_{Total}) is constant. Yet I_{Total} is often not constant. For example, variation in larval growth can produce substantial variation in body size at maturation, which generally corresponds closely to total reproductive effort (within a population). Thus, larger individuals generally lay both more and larger eggs, leading to a positive correlation between egg size and number. In this case, the relationship between egg size and number will be negative only when body size is controlled (e.g. 16, 40, 81, 154).

Other sources of variation in reproductive effort are less easily quantified and controlled, including variation in adult feeding rates, the proportion of adult-acquired resources allocated to reproduction, degree of parental care, etc. Our conclusion is that the assumption of a trade-off between egg size and number is generally supported by empirical studies in arthropods; studies that have failed to detect such a trade-off have generally been on animals in which there may be substantial variation in reproductive effort obscuring the patterns.

We suggest that rather than testing for the presence or absence of trade-offs between progeny size and number, future research should focus on two general issues. First, we know of little empirical data on the shape of the relationship between progeny size and number, although theoretical predictions often depend on an assumed shape (but see 40a). Smith & Fretwell (197) originally proposed that the number of offspring produced by a female is a simple function of I_{Total} and I_{Young}; the female can produce I_{Total}/I_{Young} progeny. However, it is likely that,

due to inefficiencies in resource allocation, allocating I_{Total} resources to reproduction does not allow for the production of I_{Total} / I_{Young} progeny of size I_{Young}; dividing resources among progeny may not be as simple as dividing a pie into pieces. Second, we have little understanding of how changes in reproductive effort affect the relationship between progeny size, progeny number, and maternal fitness (230a). Reproductive effort may evolve as a result of changes in female survival probabilities, changes in resource availability, or due to selection on progeny size or fecundity (e.g. 182). Smith & Fretwell (197) and most models since have assumed that total reproductive effort is constant (but see 230a). More theoretical and empirical exploration of these two issues is needed.

Fitness Consequences of Progeny Size

Many studies have examined the relationship between egg size and fitness components of progeny. They often demonstrate that smaller eggs hatch more quickly (7, 72) or are brooded for a shorter time (231), but are less likely to hatch (7, 48, 69, 70, 154; but see 93, 146, 214). Progeny hatching from smaller eggs tend to be smaller hatchlings (7, 9, 27, 31, 38, 46a, 92–94, 130, 132, 161, 178, 187, 225) that grow into smaller-than-normal later instars (118, 132, 135, 219) and have lower juvenile survivorship (27, 36, 38, 40, 70, 78, 81, 110, 119, 168, 214, 219; but see 49, 72, 202).

Smaller-than-average young have three developmental options: *(a)* mature at a smaller-than-average size (27, 36, 38, 79, 90, 109, 118, 130, 154, 202; but see 9, 49, 179, 180), *(b)* extend development to fully or partially compensate for their small starting size (7, 27, 56, 70, 72, 73, 76, 94, 101, 137, 154, 179, 184, 190, 202, 214; but see 9, 118, 219, 229), or *(c)* increase their rate of growth to mature at a normal size. Most arthropods exhibit some degree of developmental plasticity by which progeny partially compensate for their small hatchling/birth size by extending development time (72, 73). Few studies have examined the influence of juvenile size on growth rates in arthropods (but see 7). Progeny hatching from larger eggs can often better withstand environmental stresses such as larval competition (7), starvation (38, 89, 145, 199, 212), desiccation (201), oxygen stress (97), cold stress (36, 105), nutritional stress (27, 74, 78, 219), and environmental toxins (62). Some studies have failed to detect fitness advantages of hatching from large eggs; most of these studies have raised progeny in high-quality environments (e.g. 118, 228, 229), suggesting that selection is generally weak in high-quality environments but favors larger eggs in lower-quality environments (74, 189).

Most of the studies cited here are correlational studies that confound relationships between egg size and progeny fitness with genetic correlations between morphological and life history characters (194). For example, larger females generally lay larger eggs and produce progeny that mature at a larger size (because body size is generally heritable) such that there is a positive correlation between egg size and progeny size at maturation (71). Experimental approaches were thus developed to study the consequences of, and selection on, egg size variation (194).

By manipulating egg size physically or physiologically we can quantify effects of egg size variation on progeny fitness. A few studies have manipulated egg size in invertebrates (61, 100, 195) including one insect species (72). They have generally demonstrated that progeny hatching from larger eggs do indeed have higher fitness or improved performance (but see 99).

Time Limitation, Parental Care, Clutch Size, and Constraints on Progeny Size

Smith & Fretwell assumed that all eggs of size I_{young} have the same influence on a female's fitness such that maternal fitness is the product of the average fitness of her offspring times the number of progeny produced (197). However, this model assumes that females can actually lay all of their matured eggs. In many parasitic insects (e.g. herbivores and parasitoids) females may be incapable of finding enough hosts to lay all their eggs, relaxing selection for increased fecundity (177, 228) and potentially shifting the optimal egg size to a larger value than predicted by the Smith-Fretwell model (86). Thus, shifts in the abundance of hosts may result in a change in optimal egg size, even without changes in the relationship between egg size and progeny fitness (183).

The Smith-Fretwell model also assumes that maternal fecundity influences progeny fitness only by affecting progeny size. However, for organisms that exhibit parental care, large clutches may be less easily tended/defended than smaller clutches, such that progeny survivorship decreases with increasing maternal fecundity even if progeny size is constant. Similarly, progeny within larger clutches may experience increased competition or conflict that decreases progeny fitness (169). Thus, both parental care and sibling competition can select against large clutches (but see 193), resulting in a change in optimal progeny size without a change in the relationship between progeny size and progeny fitness.

Finally, there may be morphological and physiological constraints on the ability of females to make especially large or small eggs. For example, the necessity for progeny to fit into the brood pouch of a female may constrain the evolution of large progeny in *Daphnia* (181), even when large progeny are favored by environmental conditions. Unfortunately, although some physical and physiological constraints on progeny size have been studied in vertebrates (17, 46, 182), constraints have been little examined in arthropods.

VARIATION IN PROGENY SIZE AMONG SPECIES AND AMONG POPULATIONS WITHIN SPECIES

Selection on Progeny Size Varies Across Space and Time

When environmental conditions vary, the relationship between progeny size and progeny fitness is likely to vary, resulting in different optimal progeny sizes in different environments. However, few studies have manipulated progeny envi-

ronments and quantified the relationship between egg size and progeny growth or survival in each environment. These studies have demonstrated that selection on egg size varies across environments (27, 40, 74, 78, 154, 180). In general, it appears that the fitness difference between progeny hatching from large vs. small eggs is greatest in lower quality or more stressful environments (27, 74, 78).

Climatic conditions vary substantially across space and time and may result in substantial variation in selection on progeny size (6, 180). In some insects, selection on egg size may depend on whether progeny need to overwinter before hatching (39, 66, 105, 125, 131, 178). Variation in season length or the amount of time left before winter may impose variable selection on development time, in which selection for rapid development of progeny produced late in the season (or progeny living in areas with short or cool summers) favors progeny hatching from large eggs (8, 169).

Selection on egg size can vary with the depth at which eggs are laid in the soil (crickets, 39) and the host species upon which eggs are laid (herbivores, 27, 74, 78, 161). Population density can affect the amount of competition for food that progeny will encounter, which may affect selection on egg size (169). At low population densities, sperm limitation becomes important for free-spawning arthropods, and selection may favor the evolution of large eggs that are more likely to be fertilized (206). Egg size may affect the ability and tendency of larvae to disperse (9, 16), such that variation in the need to disperse will influence selection on egg size.

Size-specific predation may represent an important source of selection on progeny size (128) either by influencing the demographic environment or because smaller progeny may be less susceptible to visual predators (30, 123, 139). For terrestrial insects size-selective egg predators and parasites impose selection on egg size that will vary with predation intensity. When predation on immature stages is high, selection may favor progeny that spend less time as juveniles, thus favoring progeny that start life larger (188). Egg size of predators may be constrained by the minimum size at which hatchlings can capture prey (204) such that selection intensity varies with prey size (1, 129; but see 204). Also, larger eggs may be favored at low prey densities to protect against periods of starvation encountered after egg hatch (129, 209).

Selection may also vary among progeny produced by a single female due to small-scale environmental variation. For example, selection on egg size varies among trees in the seed beetle *Stator limbatus*. Theoretical models predict that increased variability in selection on progeny size within populations will result in selection for larger progeny than predicted by the Smith-Fretwell model (67). Alternatively, variation in selection can result in the evolution of increased variance in progeny size (115, 174) or plasticity in progeny size (46, 182).

Variation in Progeny Size Among Species

Within genera or families, females of larger species generally lay larger eggs than females of smaller species (3, 18, 19, 33, 84–86, 90, 108, 139, 176, 204, 223), suggesting morphological constraints on egg size. However, in many taxa vari-

ation in female body size does not explain among-species variation in egg size (28, 64, 65, 129, 175, 176, 211, 228) and, even when female body size is correlated with egg size, there is generally substantial variation around the regression line (85, 124, 181, 193). Although females of larger-bodied species generally lay larger eggs, they often allocate a smaller proportion of their resources to each egg (3, 18, 85, 139, 147, 181; but see 223).

Few studies have examined the causes of variation in egg size among species. In many crustaceans, marine- and brackish-water species differ from inland species in both the size and number of eggs laid (98, 144). Higher-latitude shrimp (42) and satyrid (84) species generally lay larger eggs than lower-latitude species, while higher-latitude cladoceran species on average lay smaller eggs (175; but see 176), suggesting climate-mediated adaptive differentiation. Mode of parasitism explains some of the interspecific variation in egg size among parasitic cladocerans (175). Variation in relative egg size among species of cladocerans (in which smaller species produce proportionately larger eggs; 181) may be due in part to size-specific predation on progeny (139); small cladoceran species may minimize juvenile mortality by producing relatively larger progeny that quickly attain adult body size and reproduce before they are subject to predation. However, this pattern of negative allometry is observed in many other arthropods for which size-selective predation is not likely a source of selection (see above).

Marine arthropods with planktotrophic larvae produce smaller eggs than species with direct developing larvae (41, 100). Host plant toughness may influence the evolution of skipper (hesperiid) egg sizes; species that oviposit on hosts with tougher leaves lay larger eggs (160; see also 178; but see 85). In stored-products insects, the relationship between body size and egg size is different for semelparous versus iteroparous species; semelparous insects produce smaller eggs (relative to body size) and the slope of the relationship between egg size and body size (among species) is less steep, but the explanation for this pattern is unclear (108).

In ponerine ants, selection for large colony size appears to explain among-species variation in egg size (small eggs in species that produce large colonies; 217). Egg size of carabids varies among species according to prey type (219), and in some herbivore taxa specialist feeders lay larger eggs than generalist feeders (64, 86; but see 178), possibly as a result of relaxed selection on fecundity due to difficulty finding enough hosts (183). In Lepidoptera, species that overwinter as eggs tend to lay larger eggs than species that overwinter in other stages (178; but see 85).

Variation in Progeny Size Among Populations Within Species

Within species, females from larger-bodied populations tend to lay larger eggs (13, 228). However, variation in body size alone cannot account for the substantial geographic variation observed in many arthropods (43, 55, 83, 199, 230). Egg size often follows a cline in latitude (6, 13, 20, 43, 44, 91, 103), altitude (13, 98,

158), or, for crustaceans, habitat predictability (permanent versus temporary pools; 13, 158), from coastal to inland waterways (149, 150, 163, 165, 220) or from deep-sea benthic to shallow coastal waters (165). Some of these clines are known to be genetically based (6, 103, 151). Most cannot be explained entirely by clines in female body size (6, 13, 44, 103).

Most intraspecific latitudinal clines go from smaller eggs produced at lower latitudes to larger eggs at higher latitudes (6, 13, 43, 44, 91, 99, 103; see also 2, 21, 199), although some insects exhibit the opposite pattern (3, 20, 83). The commonness of these latitudinal clines is often interpreted as evidence that large eggs are selectively favored at low temperatures. However, environmental effects of temperature on egg size often mimic the geographic clines observed in nature (larger eggs at lower temperatures; see below).

Only one study (by Azevedo et al.) has experimentally demonstrated that eggs evolve to be larger when populations are reared at low temperatures; *Drosophila* maintained for nine years at 16.5° C evolved larger egg sizes than flies maintained at 25° C (6). However, it is unclear why larger eggs are favored at lower temperatures (6, 63, 180; see below). For some insects, short growing seasons may constrain fecundity of females in northern latitudes, relaxing selection for small eggs (228), but this hypothesis does not explain the results of Azevedo et al (6). Egg size clines in aquatic crustaceans have been argued to be due to variation in water temperature (165) or salinity (98). However, clines vary substantially in form and direction among species (148, 150, 151, 163, 165), suggesting alternative explanations.

Other explanations have been proposed to account for latitudinal clines. For example, food availability in polar environments may select for relatively K-selected life history strategies, including the production of a small number of highly competitive progeny, a pattern typical of polar benthic organisms (42). Variation in food availability has also been proposed to explain coastal-to-inland clines (149) and altitudinal clines (98) in crustacean egg size.

For many arthropods, variation in egg size among populations does not appear to be clinal. In many crustaceans, egg size varies among lakes or bays (12, 25, 56, 127, 142, 155, 205). In some herbivores, egg size varies among populations using different host plants (27, 78). Variation in egg size among populations may be due to variation in the need to resist desiccation (201; but see 200) or compete with conspecifics for food (169). Each of these studies suggests adaptive differentiation of egg size among populations, but in most cases the explanation for the differentiation is unclear or untested.

VARIATION IN PROGENY SIZE AMONG FEMALES WITHIN POPULATIONS

Female Size

Within populations, larger females tend to lay larger eggs (Table 2), suggesting some morphological constraints on egg size. However, there are many exceptions to this pattern: In some butterflies larger females lay smaller eggs, and in most

TABLE 2 Phenotypic correlations between maternal size and egg/progeny size, within populations (number of species)

Taxon	Positive	Negative	Variable or No Relationship	Reference
Crustacea (cladoceran)	9	0	0	Positive (22, 87, 88, 90, 97, 123, 130, 153, 172, 181)
Crustacea (copepod)	1	0	0	Positive (101, 155)
Crustacea (shrimp)	1	0	6[1], 1[2]	Positive (220); Variable (12, 13); None (158, 165)
Crustacea (isopod)	2	0	5[1], 1[2], 1[5]	Positive (211, 230); Variable (43); None (49, 50, 135, 211)
Crustacea (lobster)	0	0	1[1]	None (203)
Ephemeroptera	0	0	1[1]	None (46a)
Orthoptera	4	0	6[1]	Positive (38, 131); None (35 40, 68)
Heteroptera	5	0	2[1], 1[4]	Positive (52, 53, 132, 154, 162); Variable (208); None (110, 199)
Lepidoptera	6	2	3[1]	Positive (16, 26, 107, 116, 117, 146, 164); Negative (102, 113); None (21, 180, 207)
Coleoptera	5	0	1[1], 1[5]	Positive (69, 71, 94, 112, 122, 134, 168); Variable (81); None (114)
Diptera	2	0	5[1]	Positive (202, 224); None (29, 65, 99, 138)
Hymenoptera	7	0	0	Positive (133, 166)

[1]No relationship
[2]Varied among populations
[3]Varied among clones
[4]Varied among wing morphs
[5]Varied among studies

isopods and orthopterans there is no relationship between progeny size and female size (Table 2). Even when the relationship between female size and progeny size is positive, it is generally weak (e.g. 81), and larger females generally allocate a smaller proportion of their resources to each egg. Numerous authors have advanced adaptive explanations for why egg size should increase with female size within populations (24, 46, 152). We suggest that an equally interesting question is why (physiologically and evolutionarily) the proportion of a female's resources allocated to each egg generally decreases with increasing body size. It is likely that the degree to which egg size varies with body size is in part influenced by where resources come from during egg maturation. For insects that obtain most resources for egg production from adult feeding, the size of eggs laid by females may be more dependent on female diet than female size (202), while the reverse may be true if mostly larval-derived resources are used.

Maternal Diet/Food Availability

Maternal diet influences egg size in many arthropods. Generally, unfed or food-stressed females lay smaller eggs than well-fed females (28, 69, 104, 117, 124, 141, 159, 202, 219). However, there are many examples in which maternal diet does not affect egg size (63, 96, 99, 107), has only a small effect on egg size (106), or affects egg size only when females are extremely food stressed (104).

Theoretical models generally predict that, as food availability decreases, and thus progeny mortality increases, females should shift to laying larger eggs (46, 189). In some crustaceans females produce larger progeny at low food concentrations (Daphnia: 23, 24, 34, 58, 87–89, 92, 153, 173, 179; *Euterpina:* 93; and one isopod: 32), although progeny size may decrease at very low food levels (22, 213, 215). This increased progeny size often results in higher survivorship under food stress (89; references in 22). In some *Daphnia* the response to food concentration varies among clones (60, 87, 88, 213), indicating the potential for adaptive evolution of egg size plasticity. The environmental cues to which females respond, and the physiological mechanisms by which they respond, are still unknown (88).

Oviposition Host

Some insects modify egg size in response to the host plant upon which they mature eggs (81, 136). For the seed beetle *Stator limbatus,* hosts vary in the degree to which their seeds are defended against larvae. On well-defended hosts larval mortality is high and selection favors females that lay large eggs (74, 78, 81, 82). On undefended hosts larval mortality is low and selection favors females that lay small eggs (and thus have high fecundity; 78, 81). Apparently in response to this variation in selection, females have evolved egg size plasticity—they lay large eggs on seeds of the well-defended host and small eggs on seeds of undefended hosts (81, 82). The degree of plasticity exhibited by females is genetically variable within populations (75). Interestingly, this plasticity appears to mediate a diet shift by *S. limbatus* onto an exotic legume (80).

Maternal Density

Females reared at high densities often lay eggs that are smaller than those of females reared at low density (73, 76, 79, 154; but see 65, 185), likely due to effects of competition on female size or nutritional status. In some cladocerans, females respond to increased population density by producing larger progeny (173), which can better tolerate periods of starvation (45, 89) and may compete better for food. This plasticity may be mediated by sensitivity to the chemical (e.g. waste products) or physical cues emitted by other individuals (34), or by effects of density on food availability. Similar egg size plasticity in response to perceived larval competition has been reported for a seed beetle (122).

Paternal Effects

In most arthropods, nutrients and other substances are transferred to females during mating and provide a pool of resources for females to use during egg maturation (216). These contributions may affect female egg size by being incorporated directly into eggs or by changing female energy budgets. Many studies have examined how male contributions affect female survivorship or fecundity (216), but few have examined whether they affect the size or composition of eggs. Female insects sometimes lay larger eggs when they receive more (95, 96, 164, 192) or larger spermatophores (96), although the effect is sometimes seen only late in a female's life (69, 222). Some insects lay larger eggs when they mate with larger males (154, 225), possibly as a result of paternal investment or because males manipulate female allocation to the eggs they have fertilized (167).

Other studies have failed to find effects of female mating frequency (35, 207), spermatophore size, or male size (76, 79, 186) on egg size. Some authors have suggested that effects of male-derived nutrients on female reproduction may be detectable only when females are food stressed (but see 69). The relative influence of male-derived nutrients on egg size is still unclear.

Rearing and Oviposition Temperature

Many studies show that females lay larger eggs when reared (104) or ovipositing (4, 5, 63, 101) at lower temperatures (232), although some arthropods lay larger eggs when reared at intermediate temperatures (10), lay larger eggs at high temperatures (110), exhibit variable responses to temperature depending on other environmental conditions (e.g. food availability, 153), or show no response to temperature (221). Unfortunately, many studies do not distinguish between the effects of rearing versus oviposition temperature (10, 30, 47, 172, 181, 187). Interestingly, the temperature at which *D. melanogaster* males are reared affects the size of eggs laid by their daughters (47), but the mechanism and adaptive significance for this environmentally-based paternal effect is unknown.

The rate of oocyte production relative to the rate of oocyte growth (vitellogenesis) may change with temperature, affecting both the size and number of eggs (63). If so, the temperature at which vitellogenesis occurs should affect egg size (218), and an increase in egg size should be accompanied by a decrease in fecundity, as generally observed. The size of a female's fat body may be affected by temperature (but see 63) and may in turn affect the rate of vitellogenin uptake. This hypothesis predicts that only temperatures experienced during fat deposition (prior to oviposition) should affect egg size, and that both egg size and fecundity should be affected similarly by temperature (both increase or decrease), neither of which is generally observed.

Temperatures experienced by adults may affect the metabolic rate of females (4): If low temperature reduces the cost of somatic maintenance, a greater proportion of the female's resources may be shunted to vitellogenesis. Some arthro-

pods mature at a larger body size when reared at lower temperature (e.g. most cladocerans; 156), potentially resulting in an increase in egg size (e.g. Table 2). However, females of many species respond to oviposition temperature independent of rearing temperature (4, 5, 63, 101), indicating that a change in body size is not a general explanation (see also 172).

Other arthropods delay oviposition at lower temperatures (e.g. *Drosophila;* 111), potentially resulting in increased vitellogenesis. This hypothesis predicts that egg size should vary with manipulations of oviposition rate independent of temperature. In some insects, delaying oviposition or changing oviposition rate affects egg size (219; references in 4), but in other insects, females forced to delay oviposition do not lay larger eggs (e.g. 81). Also, in some insects the production of larger eggs does not result in an increase in the period of oogenesis or delayed oviposition (54).

Increasing egg size at low temperatures may represent an adaptive response to temperature (232). For example, at lower temperatures growth is slower, so selection may favor the production of larger progeny that mature sooner, reducing their exposure to sources of mortality (232) or simply decreasing generation time (91, 172). Few other adaptive hypotheses have been proposed (see 181, 232) and none have been tested.

Seasonal Variation

In many arthropods, progeny size varies throughout the year (4, 5, 28, 32, 46a, 50, 63, 66, 110, 125, 161). In some cases this is due to aging of females in the population and corresponding changes in egg size (Table 3). However, seasonal variation sometimes reflects variation among generations (27, 28, 161), and maternal age cannot explain some of the patterns observed within generations (46a, 63).

Most species of crustaceans that exhibit seasonal variation in progeny size produce larger progeny in winter (15, 30, 33, 93, 123, 130, 155, 187, 196, 231), although some species produce larger progeny in summer (15), and others show some other seasonal pattern (15). In some species, females may be responding primarily to temperature, but it is unclear whether the responses are adaptations to temperature itself, non-adaptive physiological responses to temperature, or whether temperature is used as a cue to predict some other environmental condition. However, temperature cannot explain the seasonal pattern observed in some other species (93, 123, 155).

Seasonal variation in progeny size often reflects variation in female size (30, 123, 155) although it is unclear whether this reflects a cause-and-effect relationship or whether body size and egg size are influenced by the same external factors. In some crustaceans seasonal differences in body size cannot explain all of the variation in egg size (230). Seasonal changes in cladoceran progeny size often correspond to changes in predator abundance, suggesting an adaptive response to variation in size-specific predation (22, 30, 123, 130). Alternatively, seasonal variation may reflect a plastic response to variation in food availability (91; but

TABLE 3   Change in egg or progeny size as females age (number of species)

Taxon	Increase	Decrease	Varied or no change	Reference
Crustacea (cladoceran)	2	0	0	Increase (14, 24, 62, 87, 130, 153)
Crustacea (isopod)	1	0	0	Increase (32)
Orthoptera	2	4	1^1, 3^2	Increase (35, 131); Decrease (40, 68, 131); No change (131); Varied (37, 40)
Heteroptera	6	2	$2^{2,3}$	Increase (51, 52, 120, 154, 162); Decrease (110, 132); Varied (155a, 198)
Lepidoptera	0	20	2^1, 1^4; 1^5, 1^6	Decrease (26, 28, 36, 83, 102, 107, 113, 116, 118, 119, 126, 136, 137, 164, 180, 185, 207, 210, 226, 227, 229); No change (16, 146); Varied (28, 106, 157, 159)
Coleoptera	0	2	1^4	Decrease (69, 77, 219, 222); Varied (81)
Diptera	0	0	1^1	No change (221)

[1]No change
[2]Varied among females
[3]Varied among morphs
[4]Varied among treatments
[5]Varied among seasons
[6]Varied among studies

see 30) or clonal replacement, in which natural selection results in the replacement of large-egg clones with small-egg clones in warmer seasons (130).

In terrestrial arthropods, no consistent seasonal patterns are apparent, so temperature is not a general explanation for seasonal variation. In some insects, seasonal changes in body size correspond to changes in egg size (27). Eggs laid by second-generation females of a tortricid moth (which enter diapause) may be larger to ensure overwinter survivorship of diapausing eggs (66; see also 125, 131). In some herbivores selection on egg size varies among host plants and a seasonal change in egg size may be an adaptation to changes in host plants availability (27, 161). In isopods, seasonal variation in egg size may reflect a response to food availability (32).

Responses to Predation Risk

Some cladocerans exhibit plasticity in progeny size in response to predator-associated chemical cues (97, 179). Populations of *Daphnia magna*, and clones within populations, vary in their responses to fish kairomones, with clones from lakes with fish generally more sensitive (25). Other arthropods may also respond to predation risk by varying egg size. For example, females of the shield bug

Elasmucha ferrugata lay smaller eggs at the periphery of their clutch where the eggs are most susceptible to predation (145) and thus have lower reproductive value.

Other Environmental Sources of Variation

Many insects exhibit complex polymorphisms in suites of morphological and life history characters, and egg size often differs substantially among morphs. For example, macropterous individuals of both *Lygaeus equestris* and *Orgyia thyellina* lay smaller (and more) eggs than brachypterous individuals, possibly as a result of selection for rapid population increase (and thus high fecundity) on females that colonize new habitats, and selection for producing large, competitive progeny on females that stay in established populations (125, 198). However, the opposite pattern is observed in *Jadera aeola* (208). Alatae of polymorphic aphids generally produce smaller offspring than apterae (52, 162). This pattern has been attributed to competition between gonads and flight muscles for limited resources (162). Obligate asexual clones of *Daphnia* produce larger progeny than sexual clones (232), but parthenogenetic eggs do not differ in size from fertilized eggs in a stick insect (37).

Genetic Variation

There are surprisingly few data available on genetic variation in egg size within populations of arthropods. Estimates of the heritability of egg size, and its genetic correlations with other life history traits, are even fewer. In two seed beetles, egg size is highly heritable (range of $h^2 = 0.22$ to 0.91; h^2 varies among hosts and populations; 71, 75). Likewise, variation in egg size is heritable in spruce budworm (104). Comparisons of clones of *Daphnia* indicate substantial genetic variation in both progeny size (25, 56, 59, 87, 140) and egg size plasticity (25, 60, 87) within populations. Laboratory selection experiments have also demonstrated that egg size is heritable (7, 38, 170, 186a, 221) and is genetically correlated with body size. Selection on other life history characters, such as development rate (8) and resistance to desiccation (200) have also resulted in the evolution of egg size, indicating genetic correlations between egg size and these traits.

Little is understood about the genetic basis of among-species or among population differences in egg size. Crosses among strains of *D. melanogaster* (221) suggest that at least one autosomal and one sex-linked gene affect the variation in egg size (among strains). Egg size variation among species of *Choristoneura* (36) and among strains of silkworms (121) is also partially sex linked.

VARIATION AMONG EGGS AND PROGENY PRODUCED BY A SINGLE FEMALE

For many arthropods, the variation in size among progeny produced by a single female may be as large as or larger than the variation among females within a

population. Much of this variation is an effect of maternal age (below), but in many arthropods there is substantial variation in egg size within individual clutches of eggs. Variation in egg size within and among clutches may be selected for as a diversified bet-hedging strategy to minimize variation in fitness (174; see 67a for a related adaptive explanation). Alternatively, physiological limitations in the ability to make identically sized eggs may explain much of the egg size variation within clutches.

Female Age/Egg Order

Most life-history models posit the production of uniform-sized progeny through-out a female's life (e.g. 197). In most arthropods, however, progeny size decreases with maternal age (Table 3), although an increase is commonly observed in orthopterans and heteropterans (Table 3). Only a few insects exhibit no change in egg size (16, 40, 146). An increase in progeny size is commonly observed in cladocerans (24; Table 3), but this is because females continue to grow after beginning reproduction; the ratio of progeny size to maternal size actually decreases with age (153). In some insects, maternal age effects are not observable until females near their last clutch (157). The variance in egg size sometimes also increases as mothers age (171), but too few studies present estimates of variance to allow generalization.

The effect of age often varies substantially among females (37, 102, 131, 119, 228, 229) but the degree to which variation among females reflects genetic differences is unclear. At least some of the variation is environmentally based. For example, the direction or magnitude of the maternal age effect can differ among host plants (81), between macropterous and brachypterous bugs (198), and between alatae and apterae of aphids (51). The maternal effect may also vary with maternal diet (28; but see 107), with the decrease generally steepest for food-stressed mothers (69, 159) or for females that had been food stressed as larvae (102).

A decrease in progeny size with increasing age is often attributed to a depletion of the female's resources (36, 180, 210, 228). Studies in which maternal diet is manipulated (69, 159) support this hypothesis. Alternatively, decreasing progeny size with increasing maternal age may be adaptive when female clutch size is constrained (11); young females should allocate a larger proportion of their resources to reproduction when their chances of surviving to lay the next clutch are lower. However, this hypothesis assumes that age-specific fecundity does not evolve, an assumption that is unlikely to be realistic.

Maternal age effects on progeny size may reflect a bet-hedging strategy (174); selection favors variation among progeny to ensure that at least some progeny are well suited for future environmental conditions. However, this raises the question of why females do not simply produce the full range of offspring sizes within each clutch or age class. That changes in egg size are sometimes non-adaptive is suggested by the observation that female *Daphnia* produce the size offspring that maximized maternal fitness when they were youngest (24).

In general, eggs laid by older females are less likely to hatch (68, 69, 77, 229) and progeny hatching from these eggs have higher mortality (69, 75, 110, 222; but see 102), produce smaller nymphs/larvae (132), and take longer to reach maturity (69, 77, 137, 222; but see 180) or longer to pupate (102). Sometimes progeny produced by older mothers mature smaller (110, 185) but more often they mature at normal size (69, 77, 102, 180, 222), generally by increasing development time. The sex ratio of progeny may also change as females age (102). These effects on progeny are probably in part mediated by the changes in egg size. However, egg composition (e.g. proportion yolk) also often changes with maternal age (210), such that maternal age effects on progeny cannot be attributed to a decrease in egg size without more careful and creative experimentation.

CONCLUSIONS

Arthropods exhibit substantial variation in progeny size among species, among individuals within species, and sometimes even among progeny produced by a single female. Many theoretical models have been developed to explain some of this variation, but most start with the same two assumptions as Smith & Fretwell (197)—they assume that progeny fitness increases with increasing progeny size, and that there is a trade-off between progeny size and number. We find that these two assumptions are generally supported by data but that the trade-off between progeny size and number is less apparent when organisms are iteroparous, use adult-acquired resources for reproduction, or provide parental care. This is because variation in total reproductive effort is difficult to quantify for these species. Most models solve for optimal progeny size by assuming that total reproductive effort is constant. However, reproductive effort may vary substantially among individuals and may evolve in response to natural selection. Thus, selection for increased progeny size may lead to increased reproductive effort rather than a decrease in fecundity. This possibility has been examined theoretically but needs to be explored empirically.

Much of the variation in progeny size among species, and among populations within species, appears to have evolved in response to differences in natural selection among environments. Many environmental factors covary with variation in progeny size, and these factors may be the cause of the species or population differences. However, few studies have manipulated progeny environments and demonstrated that the relationship between progeny size and fitness actually differs among environments, and fewer still have demonstrated why selection favors different sized progeny in different environments (e.g. why does selection favor larger eggs at lower temperatures?). Understanding the evolution of intra- and interspecific variation in progeny size will require more empirical studies that identify sources of natural selection within environments and that demonstrate how selection varies among environments.

Much of the variation in progeny size within populations appears to be non-adaptive. For example, smaller females generally lay smaller eggs as an inevitable consequence of phenotypic and genetic correlations between body size and egg size (due to morphological or physiological constraints). However, maternal body size explains a surprisingly small amount of the variation in progeny size within and among populations of many species. Much of the remaining variance is probably also nonadaptive, due to variation in factors such as maternal diet (e.g. food-stressed females generally produce smaller progeny). Yet some species of arthropods, especially crustaceans but also a few insects, exhibit plasticity in progeny size in response to several environmental factors, and much of this plasticity is likely adaptive. Unfortunately, few studies have examined the fitness consequences of plasticity in progeny size, and results of these studies are not always consistent (e.g. comparisons among *Daphnia* studies). The evolution of life history plasticity, including adaptive plasticity in progeny size, is one of the most exciting topics in the study of life histories. We thus suggest that substantially more research effort should be dedicated to understanding the evolution of reaction norms for progeny size.

Variation in size of progeny produced by a single female has been more difficult to explain than variation among females or among populations. Most theoretical models predict that females should produce progeny of a single size. Yet progeny size sometimes varies greatly within families (e.g. changes with female age). We suggest that much of the variation within families is probably nonadaptive. However, some authors have suggested that at least some of the variation within families is an adaptive response to living in a variable environment. At this time, however, there are few experimental studies and too little theoretical work to generalize.

The evolution of progeny size has been extensively modeled by theoretical evolutionary ecologists. However, advances in theory have substantially outpaced empirical data—few empirical studies have progressed much beyond documenting patterns of variation in progeny size within or among population, measuring phenotypic correlations between progeny size and maternal fecundity, or quantifying the relationship between progeny size and a few components of progeny fitness in one environment. We hope that this review will stimulate researchers to examine the specific factors that result in variation in selection on progeny size within and among populations, and how this variation in selection influences the evolution of the patterns that we observe.

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