

## The Particular Maternal Effect of Propagule Size, Especially Egg Size: Patterns, Models, Quality of Evidence and Interpretations<sup>1</sup>

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**SYNOPSIS.** Propagule size is perhaps the most widely recognized and studied maternal effect in ecology, yet its evolution is not well-understood. The large body of extant optimality theory treats parental investment solely as an ecological problem, largely from the perspective of progeny. This approach has had limited success explaining the ubiquitous variation in propagule size within and among natural populations at most temporal and spatial scales. This problem aside, an unassailable gap in propagule size theory is that it pays little heed to the fact that offspring size is a joint phenotype of two individuals— the offspring and its mother. Hence, the ecology of mothers is decidedly as important in shaping the evolution of propagule size phenotypes. There are two reasons to suspect that this gap may account for the lack of success of optimality theory to explain variation in nature. The first is that optimality models of propagule size make no allowance for, nor can they explain, widespread, multivariate correlations between maternal characters and clutch parameters, namely the positive phenotypic covariances of maternal age, size, fecundity, and per-propagule investment found in many organisms. If per-propagule investment is optimized by selection based on the expectation of offspring fitness, then why should that phenotype be a function of maternal age or size when the ecological circumstances of progeny are not changing as a function of maternal age or size? The second gap in current theory is that, like all optimization theory, it is patently non-genetic in that it is assumed that the phenotypes optimized are evolutionarily accessible. Recent maternal effects theory indicates that traits subject to maternal influence behave in unanticipated ways. Specifically, there may be time lags in response to selection, and hence, selection away from the optimum phenotype. This paper explores a suite of issues pertaining to the evolution of propagule size from the broader perspective of propagule size as a maternal effect (PSME) with a goal of widening the lens through which propagule size is viewed by evolutionary ecologists. Two themes are developed. First, I suggest that, to understand egg size variance and its implications for both maternal and offspring fitness, it is necessary to consider explicitly the ecological context in which a mother is producing eggs, not just that into which offspring will enter. I argue that some of the variables that have only been incorporated in pairwise fashion (or not at all) into studies of propagule size might account for the lack of agreement about how this important life history feature evolves. Further, I suggest that failure to consider other sources of selection on maternal phenotypes, driven by a narrow adaptationist view that has historically been taken of PSMEs, has obfuscated many interesting questions surrounding their coevolution with maternal characters. Thus, the second theme is that it is necessary to consider other explanations for why prop-

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agule size varies apart from those pertaining to offspring fitness *per sé*. Based on a detailed review of the empirical literature, I conclude that the concept of an optimal propagule size is not only an insufficient construct to explain the evolution of propagule size, but that continued reliance on an optimization approach is likely to stifle development of more realistic and predictive theory for the evolution of this key life history trait. Novel theory should incorporate realities from physiology, development and genetics and should accommodate the dynamic nature of the selective environments in which propagule size evolves, all of which have been shown by empiricists to play a role in determining propagule size phenotypes. A key feature of this theory should be the explicit treatment of propagule size as a maternal effect.

“Even life itself is an exercise in exceptions.”  
(Picard, 1988).

Propagule size is both evolutionarily and ecologically significant because the amount of resource packaged in propagules (per-offspring investment, POI) affects both maternal and offspring fitness. Moreover, there are diverse kinds and avenues of selection on propagules acting via both parental and progeny fitness. This complex web of selection has competing outcomes which cause conflicts (tradeoffs) within the parental organism, and between the parent and offspring. A large theoretical and empirical literature has resulted from exploration of discrete parts of *the propagule size problem*.

The first source of conflict that affects propagule size occurs within the female organism: the amount of resource she can provide her progeny is limited because of resource garnering ability and her other needs for assimilated energy, including maintenance (Dunham *et al.*, 1989). Because of this finite quantity of resource available for investment in progeny and the costs of that investment to the parent, much life history theory has explored how levels of total effort and clutch size should evolve. Far less work has explored how per-offspring investment should evolve as a function of total effort (but see Winkler and Wallin, 1987).

The second tradeoff arises directly from the first: if parental resources are limited, increasing allocation of resource to one propagule means that other propagules must be either smaller or fewer in number. This

intuitive tradeoff between propagule size and number has also received a great deal of theoretical and empirical study.

The third tradeoff derives from the contrasting effects of increasing investment in individual progeny on female and offspring fitness. Increases in offspring fitness accrue more directly via further parental investment in propagules, whereas once propagules are large enough to make likely offspring survival to independence, parental fitness is enhanced by producing additional, rather than larger, propagules. Thus, there is conflicting selection (parent-offspring conflict, POC) in relation to POI, which is not widely explored theoretically or empirically.

While evolution of propagule size must respond to these three sources of competing selection—the parent’s competing demands for resources, the intrinsic tradeoff between propagule size and number, and the conflict between parents and offspring over per-offspring investment—environmental effects further complicate the evolutionary dynamics of propagule size. This is because the propagule size phenotype a mother produces, and the relative fitness that it confers to her developing progeny, both depend on the distinct environmental contexts in which these activities occur. In mother’s case, local resource availability affects her condition, energy reserves, and maintenance demand. In the case of her progeny, spatio-temporal variation in local environments alters the shape and position of the function that relates propagule size to progeny fitness (PSPF function).

The constant through these levels of conflicting supply and demand for resources is the maternal organism and her own phenotype, which is shaped by other functional demands besides those relating to reproduction. My main argument in this paper is that our understanding of how propagule size evolves is far from complete, and that this is because theoretical effort dedicated to this problem over the last two decades has not considered the role of maternal phenotypes—and the myriad sources of environmental variation and selection which affect them—as a source of variation in propagule size. Consequently, we lack a conceptual framework that can both accommodate the striking existing diversity of propagule size within populations, and make reliable predictions about how propagule size should vary in the short term, and evolve in the long term. The extent and reasons for such discrepancies are a subject of this paper.

QUALITY OF EVIDENCE:  
 INTERSPECIFIC PATTERNS AS TESTS OF  
 PHENOMENA OPERATIONALLY DEFINED AT  
 THE WITHIN-POPULATION LEVEL

There is a diverse and abundant literature from both plants and animals demonstrating that propagule size is variable along three continua of complexity: space, time and phylogenetic relatedness, sometimes simultaneously (reviews: Roach and Wulf, 1987; McGinley *et al.*, 1987; Roff, 1992; Stearns, 1992). Although a comprehensive review of propagule size patterns and effects in animals is lacking, attempts have been made to discover general patterns of variation in propagule size, and explain them as the product of logical kinds of selection on offspring performance. A key underlying assumption of this approach is that similar phenotypic patterns among different species belie common evolutionary causes, at least insofar as the kinds of selection that are thought to mold the traits being studied.

Patterns in life history, at least as they are typically studied by biologists, often take the form of bivariate correlations. Propagule size, at a minimum, is part of a three variable relationship involving maternal phenotype (size, age, lipid reserves, etc.), clutch size, and propagule size. Even

the casual observer might suspect that the large body of bivariate theory about propagule size in which maternal phenotypes are not included is at best, wanting. Nevertheless, the bivariate approach to studying propagule size shares with other bivariate characterizations of life history problems the advantage of being studied with correlations.

The first step in attempting to generalize from this rich literature is to ask, At what scale is a particular pattern evident? Comparisons have been made across closely related to unrelated species to seek general patterns, and less fruitfully among populations or races of a single species, among females within populations within years, among years within populations, among populations within years, among clutches within females in a lifetime, and so on. It is imperative to distinguish these kinds of variation because they have different meanings (Chambers, 1993).

Correlations involving propagule size are easily perceived when based on comparisons among species. There is evidence from many such studies for particular correlations such as the propagule size/number tradeoff, or correlations between maternal size and propagule size (*insects*: Berrigan, 1991; Blackburn, 1991; García-Barros 1994; *fish*: Marshall, 1953; Hutchings and Morris, 1985; Sargent *et al.*, 1987; Elgar, 1990; *amphibians*: Salthe, 1969; Salthe and Duellman, 1973; Kaplan and Salthe, 1979; *reptiles*: Elgar and Heaphy, 1989; Iverson *et al.*, 1993; van Buskirk and Crowder, 1994; *birds*: Olsen and Cockburn, 1993; but see Rowher, 1988; *mammals*: Martin and MacLarnon, 1985; Gordon, 1989; Read and Harvey, 1989; Pontier *et al.*, 1993).

Citing apparent agreement between correlations so constructed and the relationships predicted from bivariate functions that form the basis of life history models (*e.g.*, propagule size/number tradeoff), some workers have concluded that the evolutionary molding of many life history phenomena has been sufficiently elucidated because interspecific correlations make sense. But for nearly a half century cautious life historians from Lack (1954, pp. 40, 52) to Charlesworth (1994, p. 243) have noted that

the trends revealed from interspecific comparisons, typically used in "tests" of life history theory, are often elusive when comparisons are made within species. Many empirical papers that assess within population variation make similar observations (e.g., Crump, 1984; Marsh, 1984, 1986). Indeed, examination of studies made at the intraspecific level shows great diversity of "patterns." Consider for instance the striking variation that may occur within a single clutch laid by a single female, a component of variation that some models say should not exist (McGinley *et al.*, 1987): egg size within a clutch may show no particular pattern (Nilsson and Svensson, 1993; Roosenburg, 1996), there may be a temporal pattern such that first laid eggs are largest (Takahashi and Iwasawa, 1988), the largest eggs may be those laid in the middle of a laying sequence (Leblanc, 1987; Williams *et al.*, 1993a, b), or the last-laid eggs are the largest (Potti, 1993). Comparisons of among-clutch egg size from different clutches laid throughout a particular season may show no temporal pattern of variation (Selcer, 1990; Roosenburg, 1996), egg size in early season clutches may be largest with a continual decline in egg size (Karlsson and Wiklund, 1984, 1985), or eggs produced in late season clutches are the largest (Green, 1966; Kerfoot, 1974; Nussbaum, 1981; Ferguson *et al.*, 1982; Lessios, 1987). It is hard to imagine a single theoretical schema that can account for this diversity, yet these different patterns certainly have implications for both parental and offspring fitness.

Moreover, fitness is operationally defined as a population-genetic, and not a phylogenetic, parameter (Sober, 1984). The ecological and evolutionary implications of variation in propagule size are evaluated by selection and modeled by theoreticians as a within-population variance component. The lack of concordance between the level at which evolution is operationally defined and modeled and the level at which tests for an evolutionary effect are made can be explained because the two comparisons involve different variance components. It matters little in a discussion about how egg size affects offspring performance (a key is-

sue in optimal propagule size theory) that different species of birds of different size in different places produce different sized eggs because so many factors covary at these higher levels (phylogenetic divergence, selective mileaus, as well as organismal features such as body shape and patterns of resource use which also may evolve). The ecological contexts in which those two bird species' eggs are being evaluated by selection are just as likely very different but are confounded with other variables. These problems are less severe in interpopulational comparisons. The essential message is that fitness arguments are by definition, not about comparing apples and oranges. While it is easy to distinguish between the flavors of apples and oranges, this comparison yields little insight into what kind of apples make the best pie, or which oranges are best for juice (what the optimal phenotype is for a given context).

Besides their being an inappropriate test of trait dynamics within populations, interspecific comparisons and the overgeneralizations they invite also have the unfortunate effect of obscuring outliers. The very existence of exceptions indicates a different functional relationship between variables than that which a model predicts, a different kind of selection than that envisioned in the general case, or a different evolutionary response to the same kind of selection. Given the counterintuitive evolutionary dynamics of traits subject to maternal inheritance and selection (Riska *et al.*, 1985; Kirkpatrick and Lande, 1989; Lande and Kirkpatrick, 1990; review: Arnold, 1994; Bernardo, 1996), it is feasible if not likely that some of the noise in generalizations about propagule size reflect some of these evolutionary compromises.

Exceptions also reveal salient assumptions involved in interpreting apparently reasonable correlations. If a correlation fits a presumed mechanism, the concordance is often interpreted as evidence for the presumed mechanism. Correlational approaches contain no objective means of determining whether goodness of fit is due to the hypothesized mechanism, or to some other, equally plausible mechanism. Exceptional observations provide opportunities to dis-

cover such alternatives. An example is the “safe harbor” hypothesis advanced by Shine (1978) to explain an interspecific correlation between propagule size and parental care. He suggested that parental care evolves in response to increased per-propagule investment, that in turn evolves if the propagule stage is a relatively benign part of the life cycle with respect to extrinsic mortality. Nussbaum (1985, 1987) used exceptional examples that did not conform to the mechanisms outlined by Shine (1978) to suggest that the opposite causal pathway was as reasonable an explanation of the observed interspecific correlation. Subsequently, Nussbaum and Schultz (1989) suggested a third explanation for the correlation, that parental care and propagule size coevolve. Shine (1989) noted the fourth possibility, that these two life history features may be correlated through a third variable. He also pointed out that opportunity for evolution of parental care itself depends on parental phenotypes and environments, not just on whether parental care would enhance offspring fitness.

Several lessons may be taken from this exchange. First, a phenotypic correlation observed between two variables, in this case between propagule size and parental care, is *perforce* devoid of directionality—cause and effect between the variables may exist in either or both directions. Second, as a consequence, there may exist multiple and non-exclusive causes of a particular phenotypic pattern depending on the taxa involved and their ecologies. Lastly, propagule size does not evolve due purely to direct selection involving other traits in pairwise fashion, but rather via correlational selection on other variables as well. This last point means that propagule size evolution is a complex problem that cannot be understood by pairwise analysis of traits (Rausher, 1992).

It is at the within- to among-population (intraspecific) level that we should seek evidence of the ecological role and evolutionary dynamics of propagule size and their relationships to parental phenotypes. In the following section I review such data to evaluate the assumptions that form the basis of current propagule size theory.

#### PROPAGULE SIZE THEORY DEVELOPED IN A LIFE-HISTORY VACUUM

Evolution of propagule size has attracted substantial theoretical attention (Pianka, 1974, 1976; Smith and Fretwell, 1974; Brockleman, 1975; Wilbur, 1977; Itô, 1980; Kaplan and Cooper, 1984; Parker and Begon, 1986; Schultz, 1986, 1991; Temme, 1986; Lloyd, 1987; McGinley *et al.*, 1987; Morris, 1987; Winkler and Wallin, 1987; McGinley and Charnov, 1988; McGinley, 1989; LaLonde, 1991). My goal here is not to review these models (see Schultz, 1986; Heins and Baker, 1987; Congdon and Gibbons, 1990), but to identify and examine the validity of key assumptions.

This exercise has several goals. Models should stand the test of unbiased empirical scrutiny; failing such tests, models should either be made more realistic or abandoned, because models based on false mechanisms hinder the development of models involving accurate mechanisms (Bernardo, 1994a). Hence, the first goal is to examine whether the key assumptions of the optimization approach (and elaborations upon it) are reasonable. In conjunction, I explore implications of these assumptions for model predictions. The second purpose is to use data from empirical studies with which optimal propagule size models are inconsistent to identify possible reasons for discrepancies. Maternal phenotypes are likely candidate causes. The final goal of this exercise is to evaluate the logic for the continued use of optimal propagule size models.

#### *Assumptions of models of propagule size evolution and quality of evidence*

Two key premises underlie theory of propagule size evolution: first, that offspring fitness increases as a function of per-offspring investment, and second, that the amount of resources allocated to the propagule come at the cost to the parent of decreased fecundity, and hence fitness.

It is self-evident that, given some defined set of environmental conditions (productivity, competitive and predatory environments, biophysical environments), there exists some phenotype that produces higher fitness than all others. Smith and Fretwell

(1974) (see also Pianka, 1974, 1976) formalized this intuitive notion in an influential graphical analysis which made elegantly simple predictions about the evolution of egg size. As elegant as the model is, so, too, are its assumptions simplistic. While models constructed to explain in general terms how propagule size evolves obviously must make simplifying assumptions, the validity of assumptions, their impact upon model predictions, and the success of the ultimate model must all be examined. Many of these assumptions are implicit and have been identified by students of the models. Assumptions (see Schultz, 1986; McGinley and Charnov, 1988; Heins and Baker, 1987) include that 1) a finite resource pool is available for reproduction; 2) this finite resource pool is *the* proximate constraint determining clutch phenotypes; 3) POI and total parental investment are negatively correlated; 4) offspring fitness is determined solely by parental investment; 5) the form of the function relating offspring fitness to POI is monotonic and asymptotic; 6) there is a minimum POI for viability; and 7) optimal phenotypes are evolutionarily accessible.

*Assumption 1: Resources must be limiting and this influences POI*

Resources available to mothers affect propagule phenotypes, and these resources may be locally abundant, or derived from storage (review: Reznick and Braun, 1987), and so not limiting at the time of allocation to propagules (Williams *et al.*, 1993b); it cannot be taken for granted that resources are limiting. Further there is no evidence that local resource availability has predictable influences on POI, even within a single genus or family. Compared to their counterparts in resource-poor environments, mothers in food rich environments can produce smaller (*Daphnia*: Taylor, 1985; Glazier, 1992; Gliwicz and Guisande, 1992; *polychaetes*: Qian and Chia, 1991; *isopods*: Brody and Lawlor, 1984; *poeciliid fish*: Reznick and Yang, 1993; Reznick *et al.*, 1996), larger (*echinoderms*: George, 1990; *Daphnia*: Tessier and Consolatti, 1991; Glazier, 1992; *poeciliid fish*: Reznick *et al.*, 1996), or same-sized propagules (*fish*:

Wootton, 1973; *salamanders*: Bernardo, unpublished data; *snakes*: Ford and Seigel, 1989a) (see also Table 10.8 in Roff, 1992). Mothers can also increase egg (clutch frequency) with no change in egg size (Checkley, 1980). Finally, all of these parameters may change as a function of maternal diet (Qian and Chia, 1991). Variation in maternal local resource environments has diverse effects on POI, making it difficult to state with generality how resource availability affects POI.

*Assumption 2: The proximate constraint on total investment in a reproductive bout is resource-based*

A key assumption is that resources available to mothers at the time at which they are provisioning their young is *the only* limiting factor that determines reproductive phenotypes (clutch properties). In other words, no other factor ever limits the magnitude of a female's total reproductive investment. But it is easy to imagine just such circumstances, most of which involve variation in maternal phenotypes. Implicit in this assumption is that parental fitness is determined by POI. However, it is possible that the optimal POI is itself a function of total effort. This means that if other variables constrain total investment, the way in which POI affects parental fitness may not be predictable as it is in optimal propagule size theory. Some authors have explored how total investment and POI should co-evolve (Winkler and Wallin, 1987) but no theory exists concerning how constrained total investment should affect POI. This assumption also depends on the idea that POI affects parent fitness solely via offspring performance, but propagule size affects parental fitness in other ways. For example, Levitan (1993) has shown that propagule size directly influences both gametic dispersal and fertilization success in sea urchins.

*Morphological constraints.* Maternal phenotypes affect offspring size in other ways. Anatomical constraints imposed by female size can limit the maximum size of propagule that she can produce. Congdon and Gibbons (1987) document such apparent constraints with convincing data from

several turtle species. They found that in two species egg size increases with female age and size and maximum egg width was just slightly narrower than the width of the pelvic aperture. Further, this relationship plateaued as females became larger (older). Emlet (1989) makes parallel arguments for sea urchins, in which genital pores 1) are positively correlated with egg size and maternal size, 2) are sexually dimorphic with larger pores in females, and 3) increase in size as females grow.

Another form of morphological constraint might influence a mother's capacity to simply store or deliver a larger egg than she does. In cylindrical organisms (lizards, snakes, salamanders, many fish), maternal body volume and ovarian volume increase non-linearly with female size. Yet in small individuals of such species, oviducts may be linear and tubelike, limiting the packing of ova into linear arrays of a restricted diameter (Ford and Seigel, 1989*b*; Bernardo, unpublished). Only in larger females are ovaries and oviducts sufficiently voluminous to allow for the packing of larger individual ova. Other more subtle examples of female size effects on egg size or shape have been reported (van Noordwijk *et al.*, 1981; Werner, 1989; Rowe, 1994). More subtle constraints might be imposed by locomotory or other activities. For example, it has been argued based on comparative analyses that relative clutch mass (mass of clutch relative to mass of parent) and embryo packing evolve in conjunction with functional demands that influence female body size and shape (Vitt and Congdon, 1978).

*Variation in the interval between when maternal investment is made and when propagules enter the population.* The conditions during which a mother accrues and allocates resources for reproduction may be uncorrelated with the conditions that her offspring will experience. In short-lived organisms with multiple generations in a season such as cladocera (Tessier and Consolatti, 1991; Glazier, 1992; Ebert, 1993), small live-bearing fish (Reznick and Yang, 1993; Reznick *et al.*, 1996) or many small lizards (Nussbaum, 1981; Ferguson *et al.*, 1982), females yolk eggs in environments

close to the time and place at which their offspring are born; in these cases, females could tailor offspring size to local environmental conditions. In contrast, many mothers provision their progeny in an environment far-removed in time (and often space) from that which their offspring will experience. For instance, many female amphibians and anadromous fishes accumulate reproductive resources in habitats different from those in which eggs will be laid.

There are other problems with this assumption. Current models implicitly assume that fecundity is unconstrained except within the context of partitioning a given amount of investment within a reproductive bout (that is, that fecundity is not pre-determined by follicle recruitment well before resources for reproduction have been accrued). Schultz (1986) models this problem and discusses this assumption for fish. Plethodontid salamanders yolk eggs for up to one year before oviposition. In some species, embryonic development lasts an additional year (Collazo, 1996), meaning that offspring experience an environment two seasons removed from that in which mothers provisioned them. Many plants and invertebrates produce eggs that lie dormant for one or more years after mother allocated resources to them. Such pronounced differences between maternal and offspring environments common in many animal species make it unlikely that many females can anticipate offspring environments and provision their progeny in an adaptive way with that information.

*Corollary: There must exist a tradeoff between propagule size and number (assumption 3).* A propagule size/number tradeoff is intuitive given assumptions 1 and 2, and it remains a basic tenet of most life history theory concerning the evolution of clutch parameters. Is there, in general, evidence for the tradeoff? Reviews (Roff, 1992; Stearns, 1992) of empirical studies reach opposite conclusions about whether a tradeoff exists (Bernardo, 1994*a*). Neither author provides a comprehensive review, but Roff found that there is general support for tradeoffs (considering only within-species data in his tables 9.5 and 10.4:13 species show no correlation, 2 show a positive

correlation, and 22 show a negative correlation). Stearns reviewed fewer studies finding a tradeoff in only 8 of 15 species he examined; he concluded that there is no general pattern. Other examples not cited by these authors in which tradeoffs were not observed include Semlitsch, 1985; Marsh, 1986; Lessios, 1987 (multiple urchin species); Woodward, 1987*a, b*; Rohwer, 1988 [twelve species were examined for intraspecific tradeoffs, but none was found]; Lessells *et al.*, 1989; Glazier, 1992; and Ebert, 1993. There are three possible explanations for this disagreement: one reviewer is wrong and the other is right, both are right, or both are wrong.

Obviously, both conclusions are correct. It is clear from the literature that for many taxa, no tradeoff exists. There are also many cases in which a positive correlation exists between these variables (see below). This lack of consensus about such a widely studied problem indicates that generalizations are masking intriguing diversity. In light of this gap, perhaps we can at least now ask a more thoughtful question: Why doesn't egg size tradeoff with clutch size in so many species? A comprehensive, unbiased review of available data is needed; it would illuminate how often phenotypic tradeoffs really exist. Such a review should clearly distinguish the kinds of data (intra- or interspecific) being used to evaluate the tradeoff hypothesis.

*Assumption 4: Offspring fitness is determined solely by parental investment*

*Environmental contingency of effect of propagule size on fitness and its implications in varying environments.* There is abundant evidence that the impact of a propagule size phenotype on offspring performance (growth, survival, etc.) is contingent on larval environments (general discussion in Bernardo, 1996): variation in prey availability, conspecific density, and temperature have been shown to modify egg size effects (Richards and Myers, 1980; Marsh, 1986; Ferguson *et al.*, 1982; Ferguson and Fox, 1984; Berven and Chadra, 1988; Semlitsch and Gibbons, 1990; Parichy and Kaplan, 1992; Ebert, 1993; and others). For example, Tessier and Goulden

(1987) showed that smaller rather than larger *Daphnia* neonates were competitively superior under food scarcity.

The impacts of such effects are illustrated by the model of Parker and Begon (1986). In modeling how clutch size, egg size and maternal phenotypes covary, they examined a variety of cases in which offspring fitness is mediated by sib competition and foraging efficiency of larvae. They show that depending on the ecological conditions that juveniles experience, the "optimal" parental allocation to per-offspring investment varies considerably, causing very different correlations among maternal size, egg size, and clutch size. This model deserves careful study by empiricists.

*Assumption 5: Monotonically increasing and asymptotic PSPF function*

Because fecundity contributes directly to fitness, diminished fecundity is not an evolutionarily stable strategy unless it is accompanied by increased per-propagule fitness. The obvious path to increase per-offspring fitness is to increase POI. While intuitive, this hypothesis still requires testing. Does increasing POI always enhance fitness? As Bagenal (1969) put it:

"... it has been repeatedly stated that the more fecund parents produce smaller eggs ... Svardson argued that if larger eggs had greater survival, this would compensate for their smaller number. Many authors have assumed that there would be greater mortality among the progeny of smaller eggs and this has been taken as too obvious to require further comment. However it is not obvious and cannot be taken for granted for all species."

Svardson's premise—that there should exist directional selection for larger eggs—persists in most models of offspring size and number.

Indeed, offspring from large compared to small propagules have often been found to have higher fitness. Relatively few studies that have shown that such effects have identified the specific mechanisms by which propagule size is transduced into fitness differences. Those studies that have postulated



or demonstrated particular mechanisms reveal that this effect arises in many ways: Larger propagules may provide post-hatching energetic reserves (Kraeuter *et al.*, 1982; Troyer, 1983; Beacham *et al.*, 1985; Goulden *et al.*, 1987; Chambers *et al.*, 1989; Congdon and Gibbons, 1990; and papers cited therein), one result of which is that offspring can grow without incurring any risks that foraging might entail. Larger propagules often yield larger progeny that have enhanced locomotory ability (Sinervo and Adolph, 1989; van Damme *et al.*, 1992) which in turn might enhance survival or foraging success. Larger offspring may have a competitive advantage (Bagenal, 1969; Ferguson *et al.*, 1982). Larger offspring might be able to exploit a larger prey resource spectrum (larger sizes, greater diversity) than their smaller counterparts (Wilson, 1975). Larger offspring may be less susceptible to size-limited predators (Reznick *et al.*, 1990), or simply, they may have to spend less time in life cycle phases or habitats subject to high mortality (Ferguson and Fox, 1984), such as in the plankton (*e.g.*, as pelagic larvae: George, 1990; Qian and Chia, 1991). Larger offspring may simply be able to withstand harsh environments (*e.g.*, low food) better than small offspring (Barnes and Barnes, 1965; Tessier *et al.*, 1983; Marsh, 1986; Gliwicz and Guisande, 1992). In general these patterns suggest directional selection for larger propagule size, an almost universal assumption, often implicit, of models of parental investment. Concomitantly, most models of propagule size evolution implicitly assume that there is nothing intrinsically maladaptive about large propagules. Hence, offspring fitness is modeled to increase monotonically with propagule size.

*Quality of evidence.* Although much current life history theory is divorced from physiology, genetics, and development (Bernardo, 1993, 1994a), these features of organismal biology may modify if not reverse the relationship between propagule size and fitness from those expected on the basis of very general models, dramatically altering the allowable phenotypic space in which propagule size can exist for a given species.

In fact, in many taxa, offspring fitness does not increase monotonically with propagule size. Biologists have amassed substantial evidence that increases in egg size carry potential disadvantages, after a point: increasing egg size does not always yield larger offspring (Mire and Millett, 1994; Lagomarsino *et al.*, 1988; Reid and Boersma, 1990) or enhance juvenile growth or survival (Zonova, 1973; Wiklund and Persson, 1983; Karlsson and Wiklund, 1984, 1985; Chambers *et al.*, 1989; Reid and Boersma, 1990; Tessier and Consolatti, 1991; Williams *et al.*, 1993a, b). Intriguing studies by Kaplan (1992) suggest that when larger eggs of frogs (*Bombina orientalis*) develop in warmer natural ponds, their morphology is maladaptive compared to individuals from smaller eggs, or compared to large eggs that develop in cooler ponds. Although it has never been shown that females having larger eggs actually oviposit in the warmer ponds (frogs have been shown to have the ability to discriminate adaptively among potential oviposition sites; Resetarits, 1996), this study calls into question the assumption that PSPF functions are monotonically increasing and asymptotic.

*Egg size affects development.* Another reason to suspect that the PSPF function is neither monotonic nor asymptotic is that there is substantial evidence from diverse taxa (marine invertebrates, amphibians, fish) that development time is affected by egg size; larger eggs prolong development within species of molluscs, echinoderms, amphibians, and lizards (reviews: Steele, 1977; see also Spight, 1975; Bradford, 1990; Elinson, 1987). In other taxa, the opposite correlation is observed (Berven and Chadra, 1988; George, 1990; Rossiter, 1991) and in still others, no effects of egg size on development are seen (Beacham *et al.*, 1985; Hutchings, 1991; Mire and Millett, 1994). This disparity is evident within amphibia and marine invertebrates in which surface area to volume ratios affect egg respiration rates (Seymour, 1984; Seymour and Bradford, 1995; Strathmann and Chaffee, 1984), limiting the upper size at which eggs may develop.

If development is extended as POI in-

creases, fitness could decline due to mortality during embryogenesis. The propagule stage is often subject to substantial mortality (Darwin, 1859, 1871); the longer its duration, the greater the cumulative susceptibility of propagules to parasites, predators, pathogens, or desiccation during embryogenesis. These issues are further exacerbated where parental brooding behavior has evolved. Parents that brood their young do so at additional risk: the attentive parent may be subject to increased mortality risk due to predation, desiccation or starvation, and the cumulative risk increases with the duration of brooding (*e.g.*, Hom *et al.*, 1990). It is even possible that the degree of extrinsic mortality to which parents are exposed during brooding could affect the evolution of propagule size via the effects of egg size on duration of development, and hence, the length of risk that parents can tolerate (Bernardo, 1994b).

Evidence is accumulating from a variety of taxa that egg size also influences developmental pattern. Evolutionary transitions in egg size and cleavage pattern have been demonstrated in marine invertebrates, fish and amphibians (Ellinson, 1989; Collazo, 1996). Thus, in addition to possibly extending development time, proximate increases in egg size might change developmental pattern and possibly, ecology of early life history stages, thereby altering the PSPF function. Such developmental shifts within species are poorly studied, but have been shown experimentally within species of marine invertebrates (review: McEdward, 1996).

*Assumption 7: Optimal propagule size phenotypes are evolutionarily accessible*

Most models implicitly assume that the propagule size phenotype is wholly a consequence of selection on offspring fitness. An extension of this reasoning is that the propagule size observed in a particular habitat must reflect selection resulting from features of that habitat (*e.g.*, large eggs are produced where juvenile mortality is high [Reznick 1982a; Reznick *et al.*, 1990]) that will interact with egg size to determine what part of the phenotypic distribution of egg size actually results in successful prog-

eny. A subtle but distracting result of this argument is the implicit assumption, evident in the majority of published papers on egg size variation, that correlations between egg size and maternal size always reflect the effects of direct selection on egg size.

Several lines of evidence suggest that this is unlikely. First, abundant empirical evidence shows that the effect of propagule size on offspring fitness depends on environmental conditions (above). Thus, selection will not always sort offspring phenotypes cleanly with respect to propagule size. Second, paternal genetic contributions to offspring size are one generation removed in their expression (Reznick, 1981, 1982b). Hence, the impact of selection on those genetic contributions is diffuse. Third, quantitative genetic models (Kirkpatrick and Lande, 1989; Lande and Kirkpatrick, 1990; review: Arnold, 1994, Bernardo, 1996) show that selection on traits subject to maternal effects can introduce lags in phenotypic response, meaning that not only is propagule size a moving target in spatio-temporally varying environments, but that the aim of selection is also unsteady. In a 12 year study of egg size in geese (*Anser caerulescens*), Williams *et al.* (1993b) could find little evidence for directional or stabilizing selection on egg size. Finally, propagule size phenotypes are correlated with multiple other phenotypes such as clutch size, maternal traits, and so on. Positive covariances among female age, size, fecundity and POI observed in many taxa, including invertebrates (*e.g.*, ontogenetic increase in total parental investment due to changing female phenotype: Semlitsch 1985; Lessios, 1987; Resetarits and Aldridge, 1988; Congdon and Gibbons, 1987; review: Schultz, 1986) mean that selection on any of these other traits will impact propagule size if there are genetic correlations between propagule size and any other trait.

*Other issues: Propagule size is the relevant variable affecting offspring fitness*

Is egg size a reasonable estimate of egg quality? Egg size (usually as diameter) has long been used as a proxy for "amount of parental investment" in both theoretical and

empirical research. Evidence is mounting that this assumption is not met for many eggs. Rossiter (1991) found that in gypsy moths (*Lymantria dispar*), the biochemical composition of mother's diet affected offspring attributes such as growth rate, even after having accounted for effects of egg size. Bridges (1993) found correlations between embryo size and both nitrogen and carbon content within several polychaete worms (genus *Streblospio*), but embryo size explained a small proportion of the variance in parental investment as measured by elemental concentrations. McEdward and Coulter (1987) showed that egg size and energetic content were not correlated between sibling starfish (*Pteraster tessellatus*). Other studies (Kuznetsov, 1973; Tessier *et al.*, 1983; McEdward and Carson, 1987; Chambers *et al.*, 1989) have shown a lack of correlation between egg mass and quality.

Evidence to date that egg dimensions or mass do not reflect resource content is biased toward studies of the very small eggs of insects, marine invertebrates and some fish. Is it possible that in the large, yolky eggs of birds, reptiles and amphibians and some invertebrates, such egg quality differences are of minor importance, so that egg size remains an adequate surrogate for parental investment? Although these eggs have not been well-studied in the context of ecology or life history (*i.e.*, to determine if there is a correlation between egg mass, nutrient content or composition), there is growing evidence for variation in the nutritional quality of bird and reptile eggs, including as a function of maternal diet (review: White, 1991); clearly, reptile and bird eggs are far from generalized packets of fat and protein (White, 1991; Noble, 1991). This means that the potential for small nutritional differences among mothers (micronutrients: see White 1991) could be reflected in their eggs, and that these effects on offspring survival or growth could be large (Lance *et al.*, 1983). Arnold (1992) found differences in protein, lipid and water content in eggs of yellow-headed blackbirds (*Xanthocephalus xanthocephalus*), some of which were correlated with egg size and others of which were not. Meathrel *et al.*

(1993) found similar results in shearwaters (*Puffinus tenuirostris*)—slight compositional differences among eggs of different sizes. They also found that egg size had no discernible impact upon hatching success. Selcer (1990) found no correlation of egg size with female size in a lizard (*Hemidactylus turcicus*); he did find a correlation between lipid content of eggs and female size, indicating that the composition, though not the size, of eggs varied among females. Thus, despite limited effort to analyze egg content of reptile or bird eggs in an ecological context, evidence for variation among eggs in nutrient composition and content is accumulating.

It is difficult to judge how similar or different these levels of variation are between the very small eggs of insects and marine invertebrates, for example, and the large yolky eggs of birds and reptiles. A small absolute difference in, say, yolk lipid between two tiny eggs of a sea urchin is a large proportional difference, for total egg size is small, meaning that those two eggs are compositionally very different from each other. In contrast, a small absolute difference in yolk lipid between two bird eggs is a small proportional difference simply because total yolk mass is so much greater in magnitude, meaning that these two eggs are not so different from each other. For example, Meathrel *et al.* (1993) found nearly 40% variation in egg mass, but variation in the most variable egg component, albumen protein, was only 16%. It is safe to conclude from this brief survey that the description of egg composition of macrolethal eggs is a pressing empirical problem that needs to be tackled more vigorously by life history workers interested in egg size and parental investment.

An alarming implication (besides those for empiricists) of the finding that egg size is not always the proper phenotype to study in analysis of parental investment is that theoretical models of fecundity and optimal propagule size, and the ways in which these variables interact, do not at all capture information about how parental investment evolves if the focal variable in the models is not that being seen by natural selection. Theoreticians have extended propagule al-

location models to the case of two resources being allocated simultaneously to propagules (McGinley and Charnov, 1988). Not surprisingly, variation in the relative sizes of the resource pools available for propagule investment can produce counter-intuitive results that differ strikingly from the univariate construct that dominates most other propagule size theory. This promising model has not yet been generalized to multiple resources, or to animal eggs, nor have these ideas penetrated empirical work on animals. Such theoretical and empirical extensions of McGinley and Charnov's approach seem relevant to the study of animal eggs, given the abundant evidence for variation in both their size and composition. Furthermore, manipulations of egg size *per se* (Sinervo, 1990; Sinervo and Huey, 1990; Sinervo and Licht, 1991), while having great potential to elucidate some issues surrounding the evolution of parental investment (reviewed by Bernardo, 1991) have limited utility if the manipulations affect egg composition, or if egg size and composition covary unpredictably.

*How variable is it?* It would seem a trivial question to ask how variable propagule size or composition is, but many papers provide no means of answering it. Some oft-cited studies characterize egg size of a species based upon a single or just a few clutches laid at one time or in one place (e.g., Crump, 1981; Crump and Kaplan, 1979). A surprisingly large proportion of papers lack distributional statistics: sample size, ranges, variances, standard deviation or coefficients of variation. Other studies, some of which are seldom cited in discussions of variable propagule size, provide much of this detail (e.g., Kuramoto, 1978; Crump, 1984). To facilitate comparisons and greater understanding of the concept of variation in both egg size and egg composition, it would be invaluable for authors to compute and include statistical measures of variability when reporting their data. Congdon and Gibbons (1990) present a thoughtful, detailed discussion about the issues attendant to any analysis of egg composition that should be read by anyone undertaking such an analysis.

#### IS THE OPTIMAL EGG SIZE CONCEPT TRACTABLE OR USEFUL?

(It is) "necessary to account for enormous variation among species in offspring size that is currently begging for explanation in both the plant and animal kingdoms." (Lloyd, 1987).

Abundant unexplained variation in propagule size at many hierarchical levels in nature remains the greatest challenge to optimal propagule size theory. Numerous authors of empirical studies have commented on the great complexity of variation in propagule size that is routinely observed within natural populations, and many have questioned the value of the concept of optimal propagule size (Marsh, 1984, 1986; Semlitsch, 1985; Congdon and Gibbons, 1987; Semlitsch and Gibbons, 1990; Chambers and Leggett, 1996; see discussion in Berven and Chadra, 1988). Even theoreticians have had to provide lengthy verbal explanations for the lack of explanatory power of their models (e.g., McGinley *et al.*, 1987).

Many potent challenges to optimal propagule size theory derive from features of organismal biology not included in the models. As in many areas of life history research, most theoretical attention has focused on the consequences of variation in propagule size, and far less effort has been directed at understanding the sources of this variation. Although there are many theoretical and empirical studies of propagule size evolution from the narrower perspective of how it affects offspring fitness, this body of work and many generalizations that have arisen from it are at best incomplete because it ignores the impact of other sources of selection on maternal phenotypes.

Perhaps the largest gap in propagule size theory is that it does not involve maternal phenotypes, nor is it obvious how maternal characters could be incorporated. It has been understood from genetic models for several decades that traits subject to maternal effects do not evolve as predictably as less complexly determined traits (review: Arnold, 1994). Further, maternal phenotypes are subject to environmental effects

and other kinds of selection apart from selection on reproduction.

The complexity of maternal phenotypes, and the diverse kinds of forces acting on them, are amply illustrated in the diversity of correlations between propagule size and maternal age and size. Even closely related taxa may show differing patterns. As mothers age, egg size may increase (Wilson and Millemann, 1969; Zonova, 1973; Thomas, 1983; Semlitsch, 1985; Congdon and Gibbons, 1987; Kasule, 1991; Glazier, 1992), decrease (Capinera, 1979; Richards and Myers, 1980; Wiklund and Karlsson, 1984; Potti, 1993; and others; see also Cavers and Steel, 1984; review: Begon and Parker 1986; but see Moore and Singer, 1987), or not change (Congdon and Gibbons, 1987; Marshall, 1990). The correlation between maternal size and egg size can be positive (*e.g.*, Wilson and Millemann, 1969; Glazier, 1992; Potti, 1993; Bernardo, unpublished), negative (*e.g.*, Iguchi and Yamaguchi, 1994), or zero (Marsh, 1984; Lessios, 1987; Woodward, 1987*a, b*; Brody and Ducie, 1989; Dangerfield and Telford, 1990; Mire and Millett, 1994). Marshall (1990) found that larger female moths (*Parapediasia teterrella*) laid more and larger eggs than smaller females of the same age. Kuznetsov (1973) showed that both egg mass and diameter increase with female age and size, but egg lipid content declines as females grow and age (see also Table 10.3 in Roff, 1992). This small sample of papers suggests that it is potentially misleading to make generalizations about how maternal phenotypes are related to egg size, even within a single genus.

To date, few theoretical models of propagule size evolution have started without the optimal propagule size premise. Many authors have noted that a key difficulty of optimality models is that they assume what they demonstrate, namely that there must exist an optimal trait value that results via the process of adaptation. This leaves the optimality modeler, and the army of empiricists trying to put their work into a conceptual context, with the onerous task of having to explain away variation that is universally observed. This is often accomplished by arguing that temporal and spatial

heterogeneity, genetic variation, or other factors cause this optimum to shift in time and space. Such observations beg the question. Given that there is intense selection on propagules (Darwin, 1859) and that parental investment must surely play a role in determining offspring fitness, why is propagule size not a more canalized trait?

One explanation is that POI, like many evolutionarily significant life history phenotypes, is a plastic character whose reaction norm is the target of stabilizing selection. Propagule size has not traditionally been viewed as a character that has evolved principally via selection on its reaction norm. I do not mean to suggest that plasticity of propagule size has not been acknowledged, but rather, that too much emphasis has been placed on understanding evolution of the character mean, and little has been targeted at understanding its variance. This narrow view traces directly to the explanatory momentum associated with an optimizing view of natural selection in general in life history research, and the optimal propagule size construct in particular. A view of propagule size as a plastic character whose reaction norm adaptively evolves immediately provides a framework for beginning to understand how the joint influences of local resource environments and maternal characters have effected evolution of propagule size.

Some theoreticians have chastised arguments that variation in propagule size itself might be a target of selection. In particular, McGinley *et al.* (1987, p. 381) trivially dismiss suggestions by Capinera, Janzen, Crump, and Kaplan and Cooper: "Researchers who have argued that environmental variation favors offspring size variation either have not made a formal analysis of their argument or have relied on what we consider inappropriate assumptions about the relationships of offspring size to offspring fitness and environmental quality." This polemic is troubling for several reasons. First, verbal models do need to be formally analyzed, but verbal arguments should not be dismissed because they have not yet been so studied; verbal arguments and models have been of fundamental import to evolutionary biology (*e.g.*, Darwin,

1859, 1871). Verbal arguments about propagule size variation continue to be made because many thoughtful, well-informed and careful workers do not find optimal propagule size theory useful in explaining the ubiquitous variation in natural populations. Second, McGinley *et al.* (1987) assert that the PSPF fitness function proposed by Kaplan and Cooper is “inappropriate.” This is not surprising, since McGinley *et al.* actively ignore in their data review a rich literature that is inconsistent with their assumption. Further, although Kaplan and Cooper’s model may not be the most appropriate approach to analyzing propagule size variation, their model and Capinera (1979) and Janzen’s (1977) arguments do highlight that predictions about “optimal propagule size” are extremely sensitive to assumptions about the form of the PSPF function and how it varies in relation to environmental variability. A third difficulty with McGinley *et al.*’s reasoning is their dogmatic assumption that, if a mathematical model does not support a particular result, that the result and not the model or its assumptions, is responsible, a common philosophy in life history work (Bernardo, 1993, 1994a). This attitude arises from the determinism inherent in the optimality approach, which in turn views variation as failure to attain the optimal trait. Finally, McGinley *et al.*’s objection to verbal arguments applies as much to their model as it does to other ideas in the literature: they spent the bulk of their discussion trying to explain why their model cannot explain the ubiquitous variation in propagule size within natural populations.

#### SYNTHESIS AND PROSPECTUS

Some workers seem anxious to conclude that not only do there exist general solutions to the propagule size problem, but that both theoretical and empirical study have progressed sufficiently so as to expose these generalities (*e.g.*, Stearns, 1992; Roff, 1992). Yet current models fail to explain the great diversity of propagule size variation that exists at virtually any taxonomic, temporal, or spatial scale of consideration. Two observations suggest that these conclusions are premature.

One reason is that these conclusions are based upon optimality models that ignore important features of organismal biology, including physiological and functional constraints, and genetic capacity to evolve different phenotypes. Another reason is that optimality models generally treat the phenotype of interest in a relative vacuum from other phenotypes with which they are genetically or phenotypically correlated, so as to efficiently model them. Such simplifications might lead to conclusions that are invalid when phenotypes of interest actually coevolve with other, unmodeled parts of the phenotype (Rausher, 1992). Evolutionary theory of life history correctly pertains to variation within populations that contain interbreeding individuals; patterns arise from natural selection operating on fitness differences among individuals within populations. Every empirical study of a natural population that I examined documented substantial variation in propagule size at this level, a result that is inconsistent with current models of propagule size variation.

An important issue in trying to discern patterns and explain them with evolutionary models is to seek them at an appropriate level of generality. In ecology and evolutionary research, too often patterns are sought that are overly general—trying to unify all data under a single schema—and this is true of life history generalizations. It is plausible that the diversity of life history strategies that exist in nature will escape explanation via a single general model because peculiarities of physiology, anatomy, and ecological contexts, among other features, probably create diversity via multiple mechanisms (Strathmann, 1995). Although it is clear that propagule size, like other life history attributes, is closely tied to fitness, the life history phenotypes of an organism reflect compromises and constraints imposed by many agencies and these realities need to be reflected in the assumptions of life history models if the models are to have any other than heuristic utility. Recent theoretical advances concerning the evolution of traits that are subject to maternal influence, coupled with the enormous and diverse empirical literature on variation in propagule size within natural populations,

provide the grist for novel, more realistic models of propagule size maternal effects.

By novel models, I mean models that do not rely on the optimal propagule size construct, and its implicit assumptions, as a starting point. Rather, future theory should attempt to account for the multitude of selective factors that influence both maternal and propagule phenotypes. Incorporation of such complexity is likely to make models simultaneously more realistic and less general. Nevertheless, such models that take account of specific aspects of organismal physiology will make explicit, quantitative predictions that can be unequivocally tested by empiricists. Cautious description of the assumptions, and hence, limitations of future models will facilitate such evaluation, providing purchase on the propagule size problem.

Empirical researchers should continue to describe variation in propagule size in natural populations. In such studies, great care should be exercised to sample populations sufficiently so that adequate descriptive statistics can be computed and reported. Sample sizes must be reasonable as well: as is true of any small sample, confidence intervals about data from one or a few clutches are likely to be large, and therefore, of limited value for making inferences. Sampling designs should be planned carefully to allow for adequate replication at the level at which inferences are to be made: among females within-populations, among females through time, or among populations. Clutch phenotypes of laboratory-reared animals should be interpreted cautiously. Special attention should be given to associating clutch phenotypes with individual females, whose phenotypes should also be scored; such data are badly needed, and because maternal phenotypes covary with clutch phenotypes, interpretation of the latter requires information about maternal characters (Parker and Begon, 1986; Ford and Seigel, 1989a).

Information concerning the shape of PSPF functions in natural populations is sparse yet the shape of these curves is a pivotal assumption of optimality models. Relaxing this assumption has seldom been done, but yields quite different predictions

about propagule size variation (Kaplan and Cooper, 1984). Most information concerning this assumption is based on point estimates, comparisons of small *versus* large eggs. Estimation of the form of any function requires as a bare minimum, three points to estimate curvature. Of particular importance are estimates of fitness at the high per-propagule investment extreme to assess whether fitness may actually decline with very large propagules, at least under some environmental conditions. If this is true, the assumption that the PSPF function is monotonic and asymptotic is violated, and this will dramatically affect the predictions of the optimality approach. Extreme phenotypes are rare, and possibly nonexistent in nature due to selection, especially if they are maladaptive. Experimental approaches (review: Bernardo, 1991) to generate such phenotypes via hormonal (Sinervo and Licht, 1991, surgical (Sinervo, 1990; Sinervo and Huey, 1990) or resource-based manipulations of mothers may be necessary to produce propagule phenotypes at this end of the distribution. Such manipulations must be interpreted cautiously, however, because they could produce changes in propagule composition as well as size, thus confounding the size phenotypes with other propagule characters. Resource manipulation experiments may also alter total reproductive investment, and the functional relationship between propagule size and number (Winkler and Wallin, 1987).

Estimation of PSPF functions should be made under different natural conditions for two reasons. First, as several workers have noted (Crump, 1984; Berven and Chadra, 1988; Ebert 1993), the relatively benign conditions often used in the laboratory probably mask the ecological role of variable egg size in nature. Second, the contingent nature of maternal effects (Berven and Chadra, 1988; Semlitsch and Gibbons, 1990; Bernardo, 1996) means that the shape and position of PSPF functions are dynamic; although theoreticians have claimed that this is unlikely, empirical work has suggested the opposite, and it is a key assumption of optimality models that, surprisingly, remains largely unverified. Variation in

PSPF functions will also affect the predictions of optimality models. Estimation of these relationships is best done under natural conditions so that the inferences made are extendible to natural populations in which fitness is operationally defined. When estimates are made in the laboratory, great attention should be given to linking laboratory conditions to natural conditions using field data on temperature, prey abundance, and so on, estimated from the field.

One aim of this paper was to illustrate that propagule size phenotypes are subject to evolutionary interactions with other phenotypes, namely attributes of the mother such as body size, that experience selection that may have little to do directly with propagule phenotypes. As a phenotype itself, propagule size is under the scrutiny of both maternal selection and extrinsic selection, and its relative fitness is highly susceptible to local conditions. Genetic models alone indicate that maternal inheritance and grandparental genetic effects on propagule size will obstruct direct evolution of propagule size, even when the environmental context for progeny is constant. Propagule size may be one of nature's most complicated phenotypes, and it deserves more careful study by both theoretical and empirical researchers.

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