# Maternal Effects in Insect-Plant Interactions: Lessons From a Desert Seed Beetle

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## Abstract

Maternal effects occur when the phenotype or environment of a mother affects the phenotype of her offspring via some mechanism other than the transmission of genes. The primary objective of this review is to use examples from my own research on the interaction between seed beetles and their host plants to illustrate how maternal effects influence ecological interactions in nature. I explain how maternal effects generate many patterns observed in nature. I also discuss how maternal effects may be influenced by the genotypes of females or their progeny and can thus respond to natural selection and evolve. I will emphasize that maternal effects often evolve as mechanisms by which females can manipulate the phenotype of their progeny to prepare them for environmental conditions that they will encounter (adaptive cross-generational phenotypic plasticity).

## Introduction

Early in the 20th century animal and plant breeders developed a simple conceptual framework within which they could quantify sources of phenotypic variation within populations and understand the consequences of this variation for the production of new strains of agricultural plants and animals. In this framework, phenotypic variation among individuals ($V_P$) is partitioned into a component due to genetic differences among individuals ($V_G$), another due to environmental differences among individuals ($V_E$), and the interaction between these components, producing the now standard quantitative genetic relationship $V_P = V_G + V_E +$ interactions (10, 56). Each of these components ($V_G$, $V_E$, and interactions) can be further subdivided into sub-components (such as dominance variation, additive genetic variation, etc.). This simple framework has proven invaluable for understanding responses of agricultural plants and animals to artificial selection – the response to selection is easily predicted if you know the magnitude of natural selection and the proportion of phenotypic variation in a population that is due to genetic differences among individuals. Ecologists working with natural systems also use this simple framework for understanding selection in natural systems, and a large body of literature has blossomed in which techniques of quantitative genetics are applied to non-agricultural organisms (review in 56).

This conceptual framework is invaluable for understanding evolutionary processes in nature because it has focused our attention on analyses of genetic differences among individuals (the $V_G$ in the above equation). Such differences are basis for responses to natural selection. In this manuscript I will attempt to convince readers that some types of environmental variation (the $V_E$ in the above equation) can also be of ecological and evolutionary importance. Specifically, I will discuss mechanisms by which phenotypes of mothers or the environments they experience can affect the phenotypes of their progeny. Until very recently researchers have rarely considered or measured the impact of environmental effects experienced in previous generations on contemporary phenotypic expression (55, 50, 51, 52). I will argue here that maternal effects produce many of the patterns that we observe in nature and that the study of maternal effects is very important for understanding the evolution of many types of ecological interactions. Using examples from my own work, I will explain how maternal effects generate many patterns observed in nature and how they influence population responses to natural selection. I also will discuss how maternal effects may be influenced by the genotypes of females or their progeny and can thus respond to natural selection and evolve. I will emphasize that maternal effects often evolve as mechanisms by which females can manipulate the phenotype of their progeny to prepare them for environmental conditions that they will encounter (adaptive cross-generational phenotypic plasticity).

## What are Maternal Effects?

In the simplest terms, maternal effects occur when the phenotype or environment of a mother affects the phenotype of her offspring via some mechanism other than the transmission of genes (50, 51, 52). By this definition, I exclude the inheritance of genes in cytoplasmic organelles (mitochondria and chloroplasts) from being considered a maternal effect; they are inherited through mothers but are better classified as traits that are inherited via non-Mendelian genetic inheritance rather than as a maternal effect.

Maternal effects are a fundamental consequence of the differences in reproductive biology between males and females – mothers provide much of the environmental context within which progeny develop and progeny genotypes are expressed (78) while in most organisms males provide little more than small gametes. Mothers determine how many resources are allocated to eggs (13, 14, 17), what type of resources are allocated to eggs (1), and when and where eggs are laid (57). In some taxa mothers even determine the sex of their progeny (79). After egg production, mothers generally determine how much parental care their progeny receive, although fathers provide parental care in a few insects (e.g., 74). All of these maternal "decisions" are chances for a mother's phenotype or environment to influence the phenotype of her progeny (e.g., 25).

Maternal effects have been identified across a wide variety of taxa and for a wide variety of traits (50, 51, 52, 61, 62). One of the most commonly observed maternal effects is the influence of maternal age on the phenotype of her progeny (54). In vertebrates and many aquatic and marine arthropods females tend to produce larger progeny as they get older (e.g., 2), but females of most insect species produce smaller progeny as they get older (17). The seed beetle *Callosobruchus maculatus* (Coleoptera Bruchidae) exhibits the typical insect pattern – older females produce smaller eggs than younger females (Fig. 1a) and progeny hatching from these smaller eggs tend to have lower survivorship and take longer to reach maturity (Fig. 1b), although they tend to mature at roughly the same size as their siblings that hatched from eggs laid by their

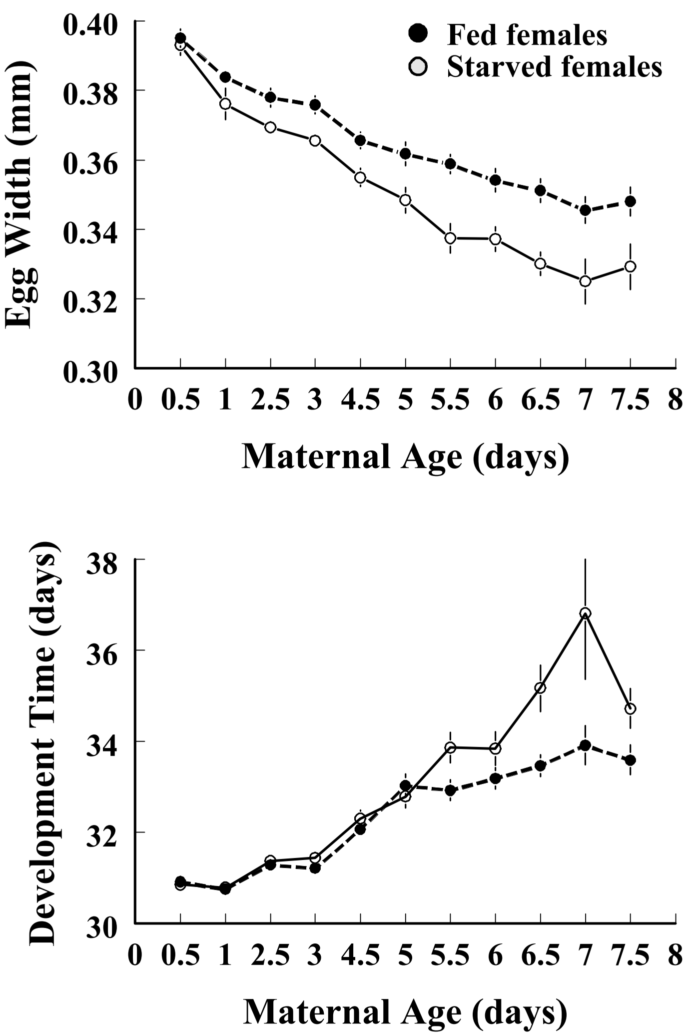


**Figure 1** (a) Female *Callosobruchus maculatus* produce progressively smaller eggs as they get older. (b) This decline in egg influences the egg-to-adult development time of a female's progeny (development time of female progeny is shown). Note that the rate at which egg size decreases with age depends on the female's nutritional status – egg size decreases more slowly for females that have access to food (shown) or that obtain multiple ejaculates from males, and this influence on egg size corresponds to a change in progeny development time. Data from 11 and 20.

mother when she was younger (11, 20). Thus, a maternal effect explains much of the phenotypic variation in survivorship and development time within a single family; progeny from older females hatch from smaller eggs and must compensate for their small size by extending development time to eventually mature at a normal body size.

Maternal effects can also explain much of the phenotypic variation among families. For example, although the size of egg that a female lays decreases with increasing age, the rate of this decrease varies among females depending on their nutritional status (Fig. 1a). Females that have ready access to food and water or access to extra mates (from which they obtain nutritional contributions) exhibit a slower decline in egg size as they get older (11). This influence of maternal nutritional status on egg size translates into effects on progeny growth – progeny hatching from eggs produced by well fed females mature sooner than progeny hatching from eggs laid by food-stressed females (Fig. 1b; 11, 20).

Oviposition decisions made by a female, such as where to lay her eggs or how many eggs to lay in a locality, will influence the environment within which her offspring will develop (47, 57). In most seed beetles (Coleoptera: Bruchidae) larvae develop inside a single host seed and are incapable of moving among seeds. Females of many species will either lay clutches (23) or will readily superparasitize seeds (22; but see 47, 48). Each additional egg that a female lays on a seed reduces the amount of resources available for the larvae (including her progeny) inside the seed. Fortunately for the larvae, many species have evolved developmental plasticity in which larvae can mature at a smaller than normal body size when reared under intense larval competition (Fig. 2a; but see 46). Thus, when females lay multiple eggs per seed their progeny mature at a smaller size than progeny reared at lower densities (e.g., 15, 19, 27). These smaller progeny produce smaller eggs (and have lower fecundity), which influences the phenotype of the next generation. In *C. maculatus*, progeny hatching from these smaller eggs eventually mature at a smaller size (Fig. 2b; 13, 14). In both *Stator limbatus* and *S. pruininus* progeny hatching from these smaller eggs extend development time to eventually mature at a normal body size (the size at which

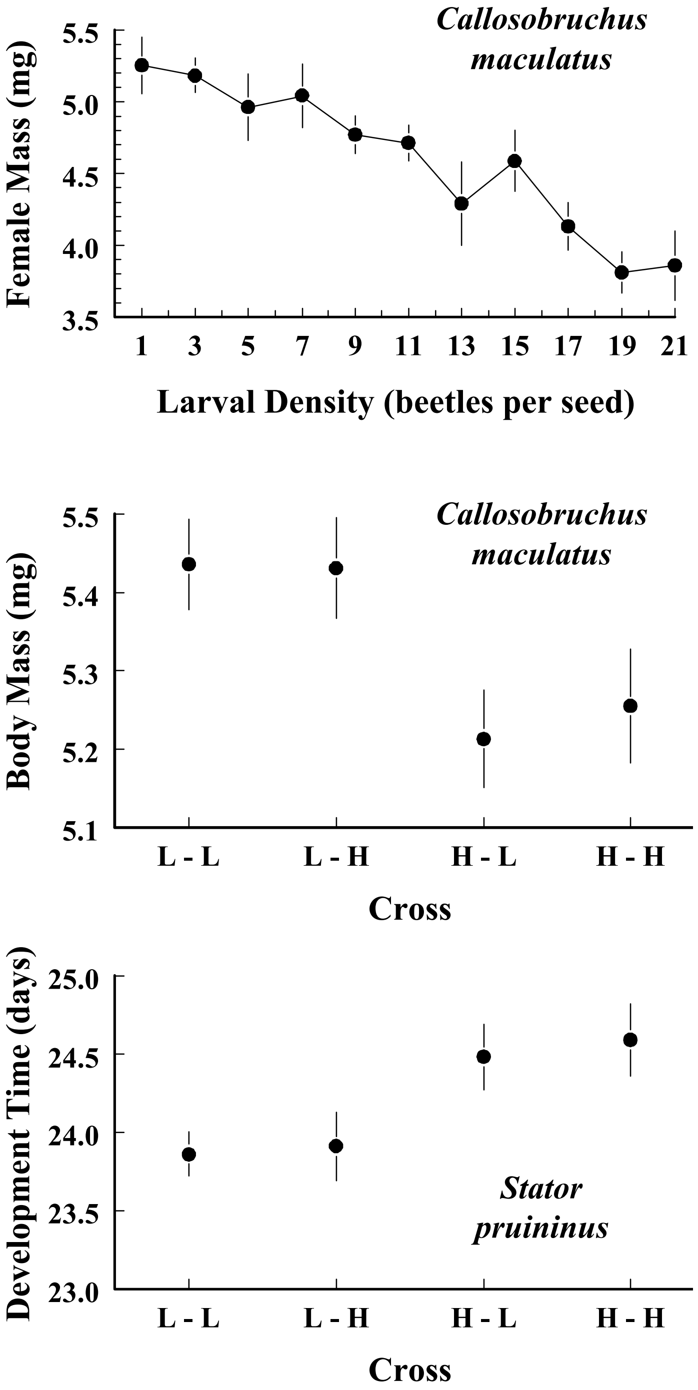


**Figure 2** (a) The influence of larval density on body mass at adult emergence for the seed beetle, *Callosobruchus maculatus*. Similar patterns are observed in *Stator limbatus* and *S. pruininus* (data from 27). (b) The size of progeny produced by a pair of adult *C. maculatus* is influenced by the density at which the female parent was raised, but not the density at which the male parent was raised. L - L is a female reared at low density crossed to a male reared at low density, L - H is a female reared at low density crossed to a male reared at high density, and so forth (data from 27). (c) For *Stator pruininus* and *S. limbatus*, the density at which a female is raised affects the development time of her progeny, but not the size at which those progeny mature (data for *S. pruininus* from 19).

they would have matured if reared at low density; Fig. 2c; 15, 19).

In each case we can demonstrate that these differences in body size (*C. maculatus*) or development time (both species of *Stator*) are environmental effects inherited through mothers by crossing progeny from lines reared at high density with lines reared at low density. In these crosses we observe that the size of *C. maculatus* progeny (at maturation; Fig. 2b) and the development time of *Stator* progeny (Fig. 2c) are each influenced entirely by the density at which their mother was reared. Paternal density has no effect of the phenotype of progeny in either species (Fig. 2b and 2c). These experiments demonstrate two points. First, maternal oviposition decisions can affect the phenotypes of both their progeny and their grand-progeny; females that lay multiple eggs per seed produce smaller progeny, that in turn produce smaller eggs, which in turn affects the development time or body size of the grand-progeny. This is a maternal effect. Second, even though both *Callosobruchus* and *Stator* have very similar life cycles, the two beetles exhibit very different types of maternal effects in response to similar ecological stresses (in this case, high larval density). Thus, the form in which maternal effects are exhibited can vary substantially among organisms (e.g., influences on development time vs. body size), even when those organisms are ecologically quite similar.

## Paternal Effects

Although I will focus on maternal effects in this manuscript, I want to acknowledge that paternal effects (the influence of a father's genotype or environment on the phenotype of his progeny) are probably more common in nature than previously suspected. In most insects, males contribute large ejaculates, spermatophores or other accessory gland secretions to a female during mating (4, 75) and nutrients in these contributions can be incorporated into eggs or used by females for somatic maintenance (e.g., 3). For example, in both *Callosobruchus* and *Stator*, males contribute ≈ 5% of their body mass to females during mating, and these contributions can have large effects on female fecundity (12, 63-66) and egg size (11). It is likely that the size and composition of these contributions affect progeny growth and development in many species but we have not yet explored this issue in seed beetles. In some insects, defensive chemicals sequestered by males may be transferred to progeny via male ejaculates or spermatophores (9), potentially protecting progeny from predators or parasites. To acknowledge the potential importance of paternal effects in nature, some authors have argued that we should replace the phrase "maternal effect" with the more general "parental effect" (e.g., 42). However, for consistency with my previous work and because I will not discuss "paternal effects" I will use the more widely accepted phrase "maternal effects" throughout this manuscript.

## Genetics and the Evolution of Maternal Effects

Although I have defined maternal effects as influences of a female's phenotype or environment on the phenotype of her progeny that are due to some mechanism other than the transmission of genes, maternal effects are not necessarily independent of maternal or progeny genotypes. In some cases, the maternal traits that influence the progeny phenotype may be influenced by the maternal genotype (a genetically-based maternal effect) and can thus evolve in response to natural selection. In other cases, the maternal traits that influence the progeny phenotype may be influenced by the maternal environment (an environmentally-based maternal effect; 42). However, the response of females to their environmental conditions and the degree to which mothers influence progeny phenotypes in response to these environmental conditions may be influenced by the maternal genotype. Environmentally-based maternal effects can thus have a genetic component and, if genetically variable, they can evolve within a population.

For example, consider that the size of eggs laid by a mother generally influences the hatchling phenotype of her progeny. All progeny within a family may hatch from similar sized eggs and thus will exhibit similar phenotypes (such as size at hatching and development time) even though they may be genetically quite different from each other. However, egg size, and thus the maternal effect, may vary substantially among maternal genotypes such that the maternal effect can evolve in a population. Consider also the various environmental influences on the size of eggs that a female lays. For example, if a female is food-stressed or very old she may lay smaller eggs that produce smaller progeny. In this case the maternal environment (food level or age), rather than the maternal genotype, influences the size of eggs that she lays and thus the phenotype of her progeny. However, the extent to which a female responds to environmental variation may depend on her genotype, and thus natural selection can result in the evolution of this environmentally-based maternal effect. Also, the degree to which mothers can influence the phenotype of their progeny may depend of the genotype of their progeny, resulting in yet another opportunity for the evolution of maternal effect.

For a similar example, consider parental care in animals. Progeny phenotypes may depend on the amount of parental care received, but the amount of parental care exhibited by mothers may vary substantially among maternal genotypes. Thus, changes in maternal genotypes may influence the phenotype of progeny via changes in the maternal effect, even if those genes are not expressed by progeny. Parental care may also vary with maternal nutritional status or age (an environmentally-based maternal effect), although the degree to which females change their parental care in response to environmental stress or maternal age may vary among female genotypes and also evolve in response to natural selection.

Maternal effects and traits influenced by maternal effects have different evolutionary dynamics than "normal" traits (41, 43, 78). For example, theoretical models (41, 43) have demonstrated that maternal effects can result in time lags in response to natural selection and can even result in short-term maladaptive responses to natural selection (i.e., a response in the opposite to expected direction). This is because progeny phenotypes are influenced by genes influenced in the maternal generation. We thus cannot partition evolution into the simple components of selection within generations and the response to selection across generations (78). The progeny environment is in part genetically based (through the mother's genotype) and can evolve through selection on progeny.

Maternal traits that influence offspring phenotypes also experience selection at the level of the family rather than just at the level of the individual, changing the dynamics of the selection response and changing the equilibrium allele frequencies and heterozygosities expected to evolve at maternal effects loci (78). When a genotype affects both the fitness of a mother and the fitness of her progeny in the same way (both positively or negatively) the response to selection will be accelerated because the among-family component of selection enhances the effect of selection at the individual level. Thus, adaptation may be significantly influenced by selection occurring at levels other than the level of the individual, contrary to the widely accepted understanding of adaptation.

When the genes affecting the maternal effect are different from the genes affecting the phenotype of progeny, we can observe epistasis between the genes influencing the maternal effect and the genes influencing the progeny traits (78). We can think of the genes that influence maternal effects as the genes that influence the progeny environment, such that interactions between maternal and offspring genotypes result in the simultaneous evolution of the progeny environment (maternal effect) and progeny adaptations to that environment. This accelerates the rate of coevolution between maternal traits and traits that affect progeny fitness.

Maternal effects can also create a conflict of interest between progeny and their parents. For example, the size of egg that maximizes maternal fitness is generally different from the egg size that will maximize progeny fitness (because of fecundity selection on mothers), resulting in selection on progeny for the ability to manipulate the amount of resources allocated to each egg and selection on mothers for the ability to prevent this manipulation. Parent-offspring conflict has been extensively explored with regards to parental care (e.g., 35) and thus will not be discussed here.

## The Ecological Significance of Maternal Effects

So far I have focused on the influence of maternal effects on evolutionary dynamics. Why should ecologists care about maternal effects? There are numerous reasons. Many of the phenotypes that influence ecological properties and population dynamics of organisms are maternally controlled traits. For example, recent theoretical research demonstrates that population cycles of rodents and forest moths can be driven by maternal effects (34, 60). Dispersal (and thus dispersion) in plants is generally influenced by fruit and seed-coat traits, both of which are maternally produced (7, 8). Niche-breadth is often determined by maternal oviposition decisions rather than progeny feeding decisions (especially in herbivorous insects; 26, 57). Dormancy of progeny (e.g., diapause), which affects generation time and voltinism, is often maternally controlled (5, 8; see below).

Maternal effects also provide a tool by which females can adaptively manipulate the phenotype of their progeny. In many organisms the maternal environment provides a reliable indicator of the environmental conditions that their progeny will encounter (either biotic or abiotic). In such cases, maternal effects may evolve as mechanisms for cross-generational phenotypic plasticity (also called "trans-generation phenotypic plasticity"; 25, 50) whereby, in response to a predictive environmental cue (e.g. high or low host density, short or long photoperiod) a mother can program a developmental switch in her offspring, or change her pattern of resource allocation to those progeny in a manner appropriate for the environmental conditions predicted by the cue. In other words, females can respond to predictive cues by changing the type of progeny that they produce to maximize progeny fitness (25).

Examples of cross-generational phenotypic plasticity abound in insects (review in 25) and other organisms (e.g., plants; 8). For example, in many multivoltine species, females that encounter rapidly cooling temperatures or decreasing day lengths produce offspring that immediately enter diapause (a quiescent state) whereas females that encounter increasing day lengths or warming temperatures produce progeny that immediately start growth and development (5, 50). For insects using seasonal/ephemeral resources, environmental cues such as crowding, temperature, or photoperiod may be predictable indicators of future deterioration of habitat quality and impending food shortage. In many species, the environment that females experience prior to (or during) egg laying influences the flight phenotype of their progeny (review in 25). Also, females that must oviposit on low quality larval substrates may produce larger progeny than if they had encountered higher quality oviposition substrates (e.g., 29). The ability of females to manipulate the phenotype of their progeny in response to environmental conditions provides an important mechanism by which insect populations can adapt to living in a variable environment.

## Host Plant-Mediated Maternal Effects in *Stator limbatus*

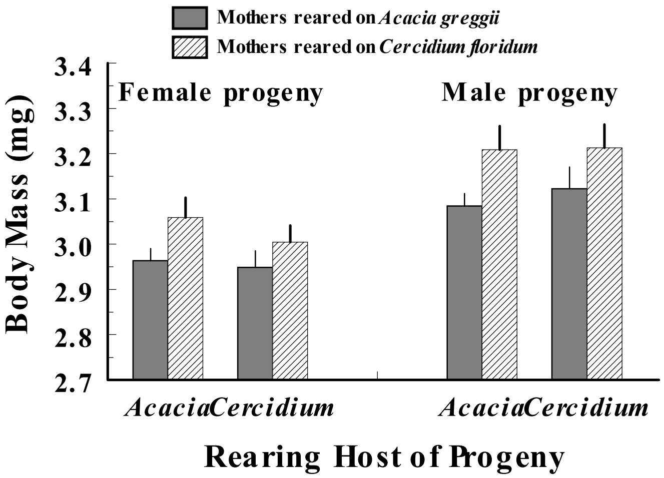
Recent theoretical and empirical research thus indicates that maternal effects are common in nature and that they can be evolutionarily and ecologically very important (reviews in 51). One objective of this manuscript is to encourage ecologists to examine maternal effects in their own study system. This is contrary to the perspective of many biologists up until recent times, which can be illustrated by a quote from Doug Falconer's (10) classic text in quantitative genetics. Falconer notes that maternal effects are a "troublesome source of environmental resemblance" that need to be controlled for when doing genetic and evolutionary experiments. Until recently, most biologists shared this opinion. Maternal effects are considered in experiments because they can be confounded with genetic effects, leading to overestimation of genetic variances, and may even obscure the detection of genetic variances (67). Few researchers have examined maternal effects to understand their evolutionary and ecological significance. I will argue here that simply controlling for maternal effects or, even worse, ignoring maternal effects in our studies will ensure that we misunderstand the mechanisms producing many of the patterns that we observe in nature. I will attempt to convince readers that maternal effects need to be considered in ecological studies because they (a) influence responses to natural selection, and (b) can respond to natural selection, providing an important mechanism for adaptation to variable environment (via cross-generational phenotypic plasticity).

To illustrate the importance of maternal effects I am going to review recent work done by myself and my colleagues on the biology of the seed beetle, *Stator limbatus* (Coleoptera: Bruchidae). Like other seed beetles, the biology of *S. limbatus* revolves around seeds. Females lay eggs directly onto the surface of their host seeds. When these eggs hatch, larvae burrow into the seed where they complete development and pupate. Larvae cannot move among seeds; they are restricted to the seed that their mother has chosen for them. They eventually emerge from the seed as adults. Females take ≈ 1 to 2 d to mature and then begin mating and laying eggs on seeds. *S. limbatus* is great for laboratory studies of insect life histories and maternal effects because egg-to-adult development time is short (about 3 weeks at 30° C), adult females can lay almost all of their eggs within about 5 d post-emergence, and females do not need access to food or water as an adult (they are facultatively aphagous; providing access to food and water has very little affect on the their life history).

*Stator limbatus* is a generalist seed-feeder that is distributed throughout the southwestern United States and south into northern South America (38, 39) where it uses > 70 host plant species in at least 9 genera. In central Arizona, *S. limbatus* commonly uses seeds of two host plants, blue paloverde (*Cercidium floridum*) and catclaw acacia (*Acacia greggii*). These species differ substantially in their suitability for larval development – beetles reared on seeds of acacia have higher survivorship (>97% vs. < 50%) and develop faster (mature sooner) than beetles reared on seeds of paloverde (21, 31, 32).

My interest in *Stator* was initially stimulated by research published by David Siemens and his collaborators (68-72). They demonstrated that *S. limbatus* collected from seeds of blue paloverde (*C. floridum*) in the field produce progeny that performed better when reared on this host in the lab than did progeny of populations of *S. limbatus* collected from seeds of other species. This same result was obtained when they compared beetles reared from these same hosts within a single population; beetles reared from blue paloverde produced progeny that performed better on blue paloverde. David proposed two explanations for this result. *S. limbatus* populations may be genetically differentiated (among populations) or genetically sub-structured (within populations), such that some beetles are adapted to blue paloverde and other beetles are adapted to a different host. Alternatively, these results may be produced by a host-plant mediated maternal effect in which beetles reared from blue paloverde produce progeny that are better able to use this host, possibly because females turn on genes in their progeny. The diet upon which mothers are reared has been shown to influence the phenotype of their progeny in a few other herbivorous insects (e.g., 36, 37, 45, 49, 58-60; but see 76 for an exception) so we decided to test this maternal effects hypothesis.

To test the maternal effects hypothesis, we (32) performed a simple experiment in which beetles were reared in the lab for a couple generations on a common host (*A. greggii*) to remove environmental effects brought in from the field, and then split beetles onto seeds of two host plants, blue paloverde and catclaw acacia. After one generation of rearing, we randomly mated all individuals in the experiment (acacia-reared females mated to acacia-reared males, acacia-reared females mated to paloverde-reared males, etc.), and split all progeny between acacia and paloverde seeds. As observed in previous studies, we found that paloverde seeds were a poor host for *S. limbatus* larvae, compared to catclaw acacia; egg-to-adult mortality was much higher (> 50% vs. < 5%), and development time is much longer (≈ 28 vs. ≈ 23 days) for larvae reared on



seeds of paloverde than for larvae reared on seeds of acacia (21, 31). Most interestingly, we observed a striking host-plant mediated maternal effect; mothers reared on paloverde produced progeny that survived better, were larger at maturation and matured sooner than progeny produced by mothers reared from acacia, regardless of the host on which the progeny were reared (e.g., Fig. 3). The effect of maternal host species on progeny survivorship is probably due to natural selection occurring during the experiment; remember that mortality is very high on paloverde seeds so that there is intense natural selection for larvae that can survive better on this species. However, we cannot explain the effect of maternal diet on progeny development time and body size at maturation as a response to selection during the experiment – the host that fathers were reared upon did not affect these traits in their progeny. Only the host that mothers were reared on mattered, indicating an environmentally-based maternal effect.

The take-home messages from this first experiment: (1) females reared on paloverde (*C. floridum*) produce progeny that have higher survivorship, develop faster, and mature at a larger body size than do progeny of mothers that were reared on acacia (*A. greggii*), and (2) this effect in due to an environmentally-based maternal effect – the father's diet does not affect the phenotype of his progeny.

## Maternal Effects Mediate Diet Expansion in *Stator limbatus*

One of my primary research interests is in how insects shift among host plants or expand their diet to include new host plants. Understanding the evolution of insect diet breadths is of central importance to understanding the evolution and diversification of insect-plant relationships, a key component in our broader attempt to understand species interactions and diversity. Unfortunately, most studies of insect diet evolution suffer from having limited information on the history of host use patterns; historical patterns can only be inferred from modern patterns. However, recent introductions of non-native plants and the subsequent expansion of herbivores onto these plants provide a powerful tool for analyses of diet breadth evolution.

*S. limbatus* has a very broad diet relative to the diet of other species of *Stator* (38, 39, 53) or even other genera of bruchids. Despite its extensive diet breadth, *S. limbatus* has never been found to use seeds of Texas ebony (*Chloroleucon ebano*; Fabaceae; Mimosoideae) within the natural distribution of this plant (southern Texas and northern Mexico; 53). This is a particularly interesting observation because Texas ebony is used as a host plant by *S. beali*, the sister species to *S. limbatus* (53). Recently, Texas ebony has been introduced as an ornamental tree in the Phoenix metropolitan area of Arizona (introduced post-1972; Phoenix Botanical Garden records). *S. limbatus* has since colonized this plant; adults readily oviposit on Texas ebony seeds in both nature and the lab, and seeds of Texas ebony successfully produce reproductively mature *S. limbatus* adults in nature. In the field, egg-to-adult survivorship averages > 10% in the sites that I have examined (26).

In a series of experiments (26, 28) my colleagues and I examined two features of the ecology and evolution of this expansion by *S. limbatus* onto Texas ebony. First, is there pre-existing variation in the ability to survive on Texas ebony within populations of *S. limbatus* that are not associated with this host? Such variation, if genetic, provides the raw material for adaptation to this host once it has been colonized by adults. Second, have populations of *S. limbatus* that are using Texas ebony in central Arizona begun to adapt to this host in the short time since its introduction? As you'll see shortly, this study evolved into an examination of how maternal effects, stimulated by the parental host plant, influence the ability of progeny to survive on Texas ebony.

To address the two questions asked above, we performed a simple experiment in which we (a) collected beetles from four populations in nature (one in northern Texas where there is no Texas ebony, two in central Arizona where ornamental Texas ebony is uncommon or not present, and one population in Papago Park in Phoenix where beetles use ornamental Texas ebony), (b) raised these beetles in the lab for at least one generation on seeds of *A. greggii* (to remove maternal effects associated with the hosts that beetles were collected from in nature), and then reared all populations for one generation on seeds of Texas ebony. We found that although egg-to-adult survivorship on seeds of Texas ebony varied among families (a prerequisite for adaptation to be possible), there was no evidence that a population using this host in nature (Papago Park population) had begun to adapt to it (Fig 4a). However, the most interesting observation from this experiment was that larval survivorship on Texas ebony was less than 4% in all populations, including the population that uses Texas ebony. You'll remember that in previous field work we had found that survivorship on Texas ebony seeds is generally >10% in the field (26). Why this discrepancy? We expected survivorship to be higher in a controlled, parasite-free lab environment.

To answer this question we must consider the conditions under which *S. limbatus* populations were maintained in the lab. To control for host-associated maternal effects we had raised each of our populations on *A. greggii* for one generation prior to the experiment. However, in nature beetles in Papago Park are colonizing Texas ebony from blue paloverde, *C. floridum* (there is no *A. greggii* in the vicinity). We know from previous experiments that larvae produced by mothers that had been reared on *C. floridum* are different from those produced by mothers reared on *A. greggii*. Maybe rearing *S. limbatus* on *A. greggii* (instead of *C. floridum*) for a single generation in the lab can account for the difference in survivorship on Texas ebony between lab and field populations. To test this hypothesis, we performed an experiment in which we reared beetles for one generation on seeds of either *A. greggii*, *C. floridum*, or Texas ebony, and then reared progeny of these beetles on seeds of Texas ebony. As expected the host that parents were reared upon influenced the survivorship of their progeny. When parents were reared on *A. greggii*, survivorship of progeny on Texas ebony was about 3% (Fig. 4b), exactly as seen in the previous experiment (Fig. 4a). When parents were reared on Texas ebony, survivorship of progeny on this host increased a bit, to between 4 and 8 %, as would be expected if high mortality during the parental generation resulted in some adaptation to this host in the lab. Most interestingly, however, was the result that when parents were reared on seeds of paloverde (*C. floridum*) the survivorship of their progeny on Texas ebony

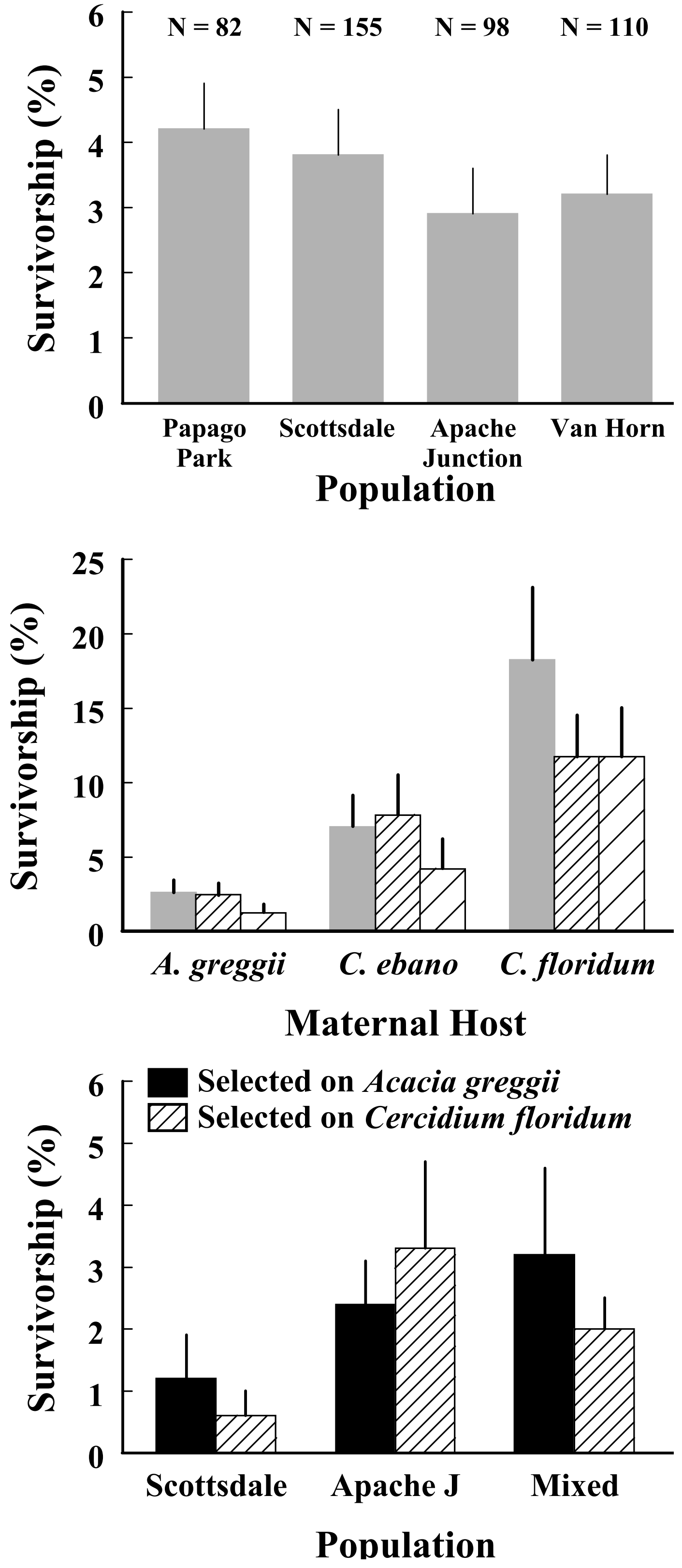


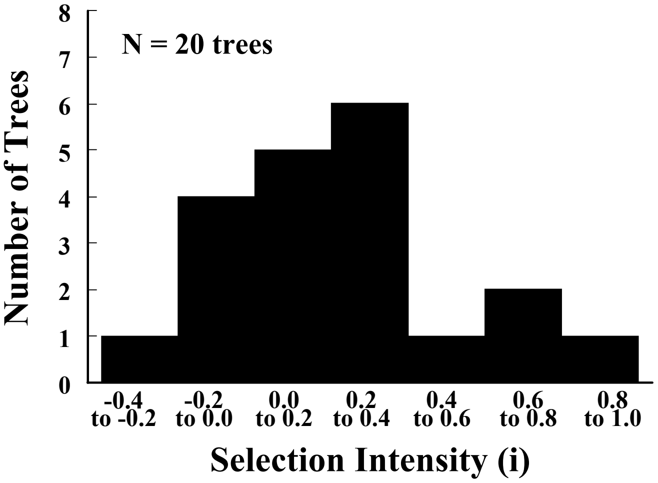
**Figure 4** Survivorship of *Stator limbatus* larvae on seeds of Texas ebony (*Chloroleucon ebano*). (a) Comparison among populations of *S. limbatus*; the Papago Park population was collected from Texas ebony in nature; (b) Parents reared on *C. floridum* or Texas ebony produce progeny that have higher survivorship on Texas ebony (the three color bars represent three replicates of the experiment); (c) One generation of rearing on seeds of *A. greggii* nullifies treatment differences, indicating that the parental host effect in non-genetic (the two color bars are replicates). Data from 26.

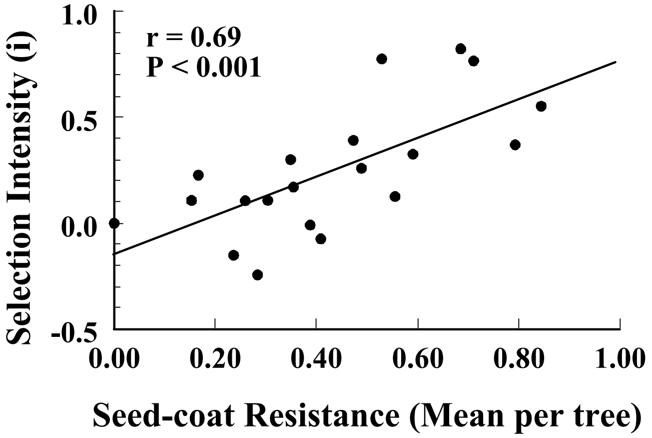
increased to >11%, matching the survivorship observed in the field on this host.

Rearing parents on paloverde most likely affects the survivorship of their progeny on Texas ebony due to a environmentally-based maternal effect, as seen in our first set of experiments (previous section of this manuscript). However, it is also possible that, because beetles experience high mortality when reared on paloverde (generally >50%; discussed earlier), evolution (genetically-based change) may occur in the lines reared on paloverde, and adaptation to paloverde may result in simultaneous adaptation to Texas ebony (due to genetic correlations across environments; 77). We thus need to experimentally demonstrate that this parental host effect is an environmentally-based maternal effect rather than a genetically-based response to natural selection during the experiment. To do this we reared beetles on seeds of either paloverde or acacia for multiple generations and then asked whether the two types of lines had begun to differentiate in their ability to survive on Texas ebony. Our first group of lines was reared on seeds of paloverde for four generations; if evolution in response to paloverde could occur in a single generation in our earlier experiment, then a fair bit of evolution should occur over four generations. For comparison, we reared another set of lines continuously on seeds of acacia, with no access to seeds of paloverde. At the end of our short natural selection experiment, we reared all beetles on seeds of acacia for a single generation, and then scored survivorship of larvae on seeds of Texas ebony. The logical basis for this experiment is as follows; if observed effects of parental rearing on paloverde represent genetic responses to selection, then genetic differences should develop between the paloverde and acacia lines during the experiment, and these differences should persist in the population when the beetles are reared for a single generation on seeds of acacia. However, if observed effects of parental rearing on paloverde represent non-genetic effects of parental environment, then a single generation of rearing on a common host species should reduce or even eliminate these differences. This latter possibility is what we in fact observed (Fig. 4c); the two types of lines did not differ in larval survivorship on seeds of Texas ebony, and survivorship of all lines was <4%, as was observed when parents were reared on acacia in each previous experiment (Figs. 4a and 4b).

So far these results indicate that maternal rearing host affects the ability of progeny to survive on Texas ebony. But is it really maternal diet that influences performance of her progeny? In 1997 we (28) performed a simple experiment in which we exposed females to seeds of either the native blue paloverde or the non-native Texas ebony while these females were maturing their eggs (within 12 h after emerging as an adult). We then forced these females to lay eggs on Texas ebony. Females had all been reared on seeds of *A. greggii*, so the two treatments differed only in the seed species that they encountered during egg maturation. Also, females cannot feed externally on dried seeds, so the two treatments are nutritionally identical. When females matured eggs in contact with seeds of blue paloverde, nearly 50% of their progeny survived from egg-to-adult, compared to only about 5% survivorship for progeny of mothers that had never encountered seeds of paloverde! This is a substantially larger treatment effect than we observed in any previous experiments. Why? I interpret this result as indicating that it is not female diet that affects the survivorship of their progeny, but instead it is female experience after they emerge from a seed. In our previous experiments females encountered their rearing host immediately after emerging from a seed, but were quickly transferred to their test host. Thus, the post-emergence experiences of females differed among treatments, but only for a short period of time. We should thus only expect a small difference in survivorship among treatments in the previous experiments, relative to the effects observed in this last experiment.

These results have interesting implications for the ecology of *S. limbatus*. Remember that *S. limbatus* does not use Texas ebony as a host anywhere that the beetle and tree are *naturally* sympatric. Our results suggest that they may not use Texas ebony in these areas because there is no paloverde present to facilitate the diet expansion (Texas ebony is also grown as an ornamental tree in parts of southern Texas but these trees are not used by *S. limbatus* indicating that colonization of Texas ebony in Arizona is not the result of differences between naturally occurring and ornamental trees). More generally, our results indicate that whether insects incorporate non-native plants into their diet will depend in part on the species composition of the local plant community and that changes in the plant community may facilitate shifts between host species by herbivorous or parasitic insects. For example, introducing paloverde into southern Texas may facilitate the expansion of *S. limbatus* onto Texas ebony. Our results also indicate that patterns of host use by insects in one locality may not adequately predict whether plants will be colonized by insects if they are introduced to another locality, nor the hosts that insects will colonize when the insects are introduced to a new locality (e.g., as a biocontrol agent). For *S. limbatus*, host use in southern Texas does not predict host use in central Arizona because interactions between the insect and its hosts are influenced by community composition. Interactions such as these may explain why many introduced biological control agents





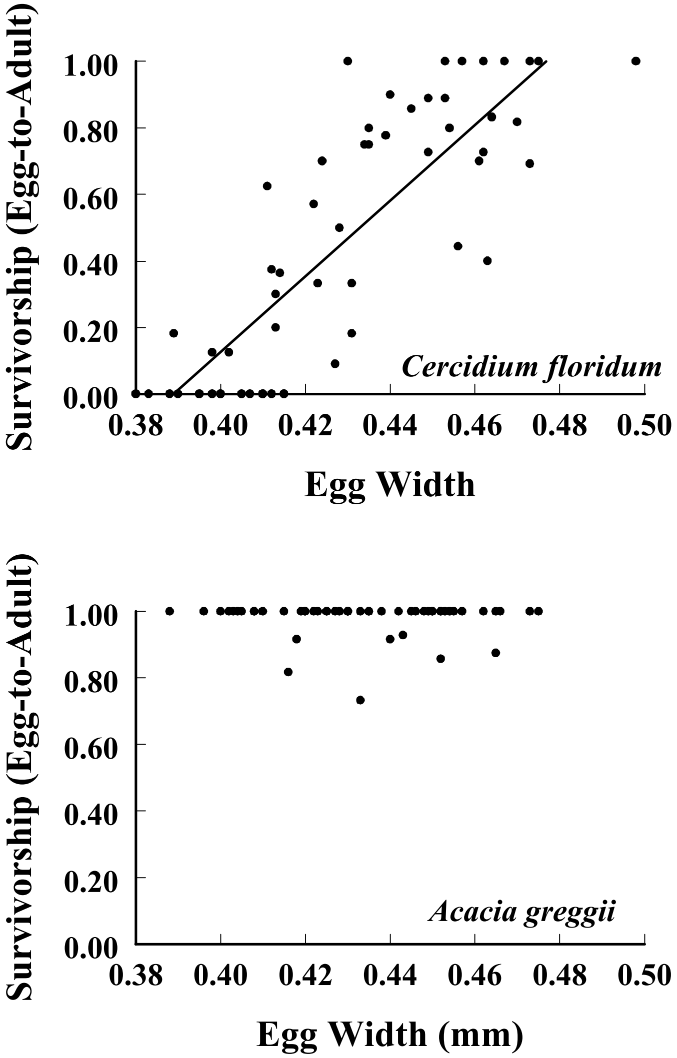
unexpectedly attack non-target species (44) and why plants may be attacked by insects in one locality but not another. Thus maternal effects can have a previously unrecognized role in influencing species interactions within communities and we should consider these maternal effects when predicting the ecological and evolutionary consequences of changing species distributions.

### Egg Size Plasticity: An Adaptive Maternal Effect

What are females doing to their progeny that influences the survivorship of larvae on seeds of Texas ebony? The answer involves changes in egg size and composition. However, before we can understand the mechanism by which female encounters with host seeds influences the survivorship of their progeny, we must spend a moment discussing some basic concepts concerning the evolution of egg size.

Mathematical analyses of optimal egg size are largely based on the simple but illuminating framework initially established by Smith and Fretwell (73). They noted that the number of grand-progeny a female will produce depends on both the number of progeny that she produces and the fitness of those progeny. They started with two basic assumptions; progeny fitness increases with increasing parental investment per offspring (e.g., egg size) and for any fixed amount of parental investment into reproduction there is a trade-off between the size of progeny that a female can make and the number of progeny that she can make. Thus, selection favors larger progeny because larger progeny have higher fitness and thus produce more grand-progeny, but selection also favors making smaller progeny because then females can make more progeny and thus produce more grand-progeny. Egg size is thus under balancing selection, with some intermediate value of egg size maximizing maternal fitness (note, however, that the size of egg that maximizes offspring fitness is necessarily larger than the size that maximizes maternal fitness, creating a conflict between mothers and their offspring). This simple model also demonstrates that any environmental variable that affects the relationship between egg size and progeny fitness can result in a change in the optimal egg size. For example, as the difference in survivorship between larvae hatching from small vs. large eggs increases, the optimal egg size will shift toward a larger value and we would expect larger eggs to evolve in our population.

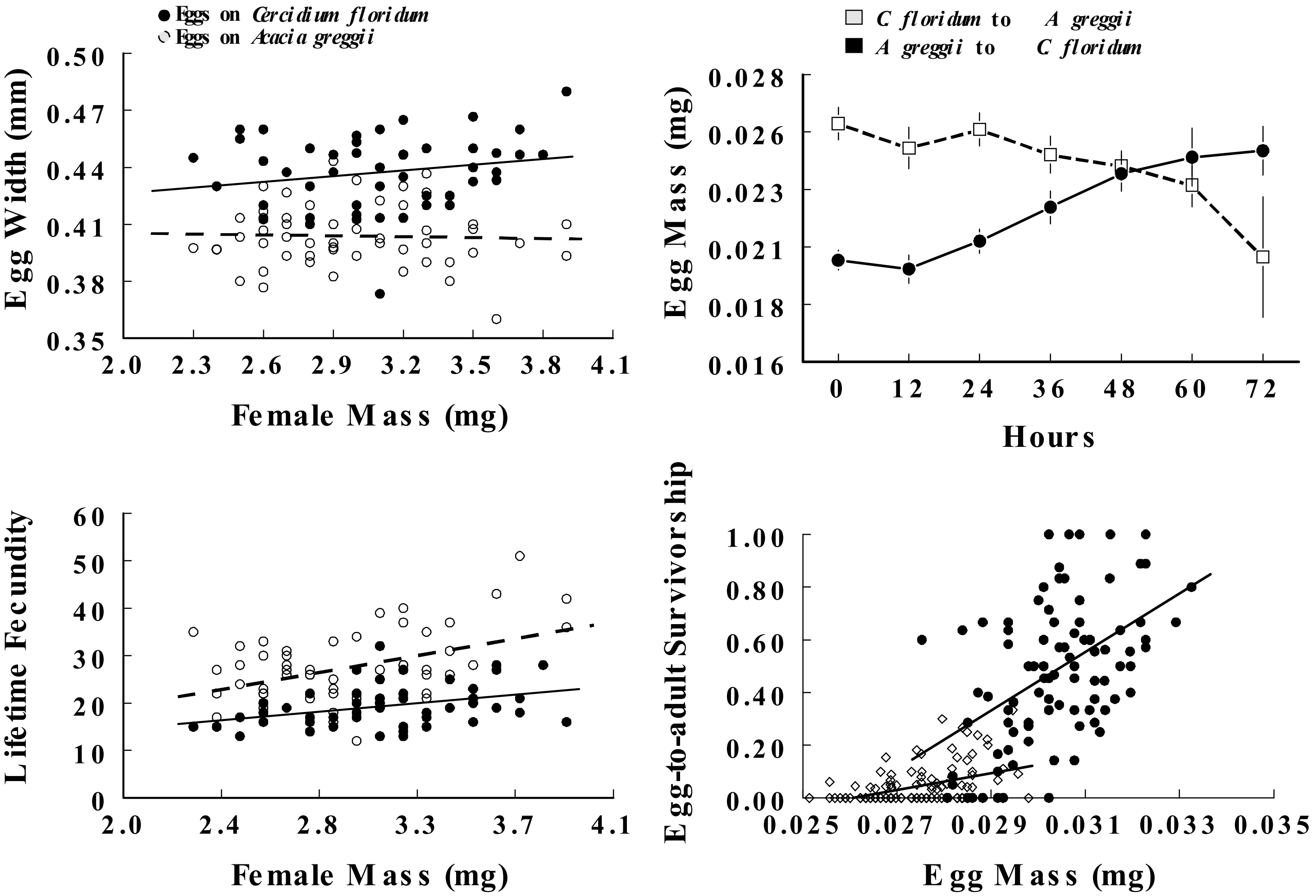
For *S. limbatus*, the fitness consequences of variation in egg size differ substantially among tree species and among individual trees within



species. In general, the harsher the environment for progeny (and thus the higher the larval mortality) the greater the difference in survivorship between progeny hatching from large vs. small eggs, and thus the greater the magnitude of selection favoring larger eggs. For example, selection intensities vary between *i* ≈ -0.4 to *i* ≈ 1.0 among individual trees within a single population of blue paloverde (*C. floridum*; Fig. 5a). This variation appears to result from variation in chemical defenses among trees; beetles experience high mortality on seeds of well-defended trees, resulting in substantial selection favoring large eggs, but experience relatively low mortality on seeds of poorly defended seeds, resulting in weak or even no selection favoring large eggs (Fig. 5b).

For our purposes here, though, variation in selection on *S. limbatus* egg size among species of trees is of more interest. Mortality of larva is generally > 50% on seeds of *C. floridum*. Most of this mortality occurs as larvae attempt to penetrate the seed coat (due to chemical defenses on the seed coats; M. E. Czesak & C. W. Fox, unpublished data). Because larvae hatching from larger eggs are better able to penetrate *C. floridum* seed coats, we observe strong directional selection for large eggs when eggs are laid on this host (averaged across all trees in a population; Fig. 6a). On seeds of *A. greggii* and a different paloverde species, *C. microphyllum* (small-leaf paloverde, a host species that we have not yet discussed in this paper), larval mortality is quite low (generally < 3% on *A. greggii* and < 25 % on *C. microphyllum*) and there is little or no selection favoring large eggs on these hosts (Fig. 6b); progeny hatching from small eggs survive about as well as progeny hatching from large eggs. Thus, selection strongly favors progeny hatching from large eggs when females oviposit on seeds of *C. floridum*, but, because progeny hatching from small eggs perform well on *A. greggii* or *C. microphyllum*, selection favors females that lay smaller eggs on these hosts because they will have higher fecundity (due to the previously discussed trade-off between egg size and fecundity).

Based on this difference in selection among hosts we would expect populations of *S. limbatus* collected from *C. floridum* (upon which selection favors larger eggs) to evolve larger eggs than populations collected from *A. greggii* or *C. microphyllum*. This is exactly what we have observed (24; C. W. Fox unpublished data). However, many populations of *S. limbatus* have access to both *C. floridum* and one of the two host species upon which selection favors small eggs (either *A. greggii* or *C. microphyllum*). This results in disruptive



selection within the beetle population, with selection variably favoring large eggs (when a female encounters *C. floridum*) or small eggs (when they encounter *A. greggii* or *C. microphyllum*). This type of disruptive selection can have interesting evolutionary implications; it can maintain genetic variation in a population (by simultaneously favoring multiple extreme phenotypes; 33), can result in population sub-structuring (a prerequisite to sympatric speciation; 6), and can lead to the evolution of phenotypic plasticity (77). Interestingly, if we collect *S. limbatus* eggs from seeds of these three host species in regions where *C. floridum* is sympatric with at least one of the other two hosts, we find larger eggs on *C. floridum* than on either of the other two hosts, suggesting that either some degree of population substructure has evolved in these populations, or that females are capable of producing different size eggs in response to the different host plants (i.e., plasticity in egg size).

To test the hypothesis that females exhibit egg size plasticity in response to their host species, we collected beetles from the field, reared them in the lab on a common host (*A. greggii*) for at least one generation, and then exposed females to seeds of either *C. floridum* or *A. greggii*. When females were forced to oviposit on seeds of *C. floridum* they laid substantially larger eggs than did females exposed to *A. greggii* (Fig. 7a; note that the Y-axis in the figure is egg width; egg mass differs by >25% between the treatments; 29) (see 25 and 30 for comparable data for the comparison between *C. floridum* and *C. microphyllum*). Females are capable of adjusting egg size in response to the host upon which they lay eggs because they delay oviposition for at least 24 h after emergence, during which time they finish maturing eggs. If they are in contact with their oviposition substrate (seed) during egg maturation they know upon which host their progeny will develop, and have the opportunity for facultative responses to the host species. Females take advantage of this to manipulate the phenotype of their offspring (i.e., they exhibit a maternal effect) by laying large eggs on *C. floridum* (where progeny hatching from large eggs have a substantial fitness advantage) and laying small eggs on *A. greggii* or *C. microphyllum*. However, laying large eggs on *C. floridum* comes at a fecundity cost to females – they lay substantially fewer eggs on *C. floridum* than on either *A. greggii* or *C. microphyllum* (Fig. 7b) due to a trade-off between egg size and egg number. A trade-off between egg size and egg number is also evident within treatments (hosts); there is a negative correlation between egg size and egg number, after controlling for body size, on each host (29).

Egg size plasticity in *S. limbatus* is not the result of female reluctance to lay eggs on *C. floridum*. Because larval survivorship is very low on *C. floridum* we might expect females to evolve avoidance of this host in preference for *A. greggii* or *C. microphyllum* (on which larval survivorship is high). Such reluctance to oviposit would result in prolonged egg retention when encountering *C. floridum*, and thus possibly increased resource allocation to these eggs. Females do in fact delay egg-laying approximately 6-12 h on *C. floridum* relative to laying on *A. greggii*. However, paired oviposition preference tests indicate that, despite high larval mortality, females either prefer to oviposit on *C. floridum* (when compared with *A. greggii*), or show no preference for either host (31). Also, when deprived of hosts during egg maturation, and thus forced to retain eggs longer, first-laid eggs are small (i.e. the size they normally lay on *A. greggii*) regardless of the host upon which eggs are laid. When females are forced to lay on other non-preferred hosts (or non-hosts), on which egg-laying is also delayed, they also lay small, *Acacia*-size eggs (C. W. Fox, unpublished data). Thus, it appears that the delay in oviposition on seeds of *C. floridum* is a consequence of laying larger eggs on this host and not the cause of the difference in egg size between hosts.

When female *S. limbatus* are forced to switch among host species in the laboratory (from *A. greggii* to *C. floridum* or from *C. floridum* to *A. greggii*) they shift the size of eggs that they lay (Fig. 7c), but the switch doesn't begin until approximately 24 h after exposure to the new host. We took advantage of this observation to test whether egg size plasticity in *S. limbatus* is adaptive; we conditioned females to lay large eggs (conditioned on *C. floridum*) or small eggs (conditioned on *A. greggii*), and then forced all females to oviposit for 24 h on seeds of *C. floridum*. Eggs from the *A. greggii*-conditioned females subsequently had very low egg-to-adult survivorship on *C. floridum* (< 1%), while eggs laid by females that were conditioned on *C. floridum* had substantially higher egg-to-adult survivorship on this host (24%). This demonstrates that females that fail to exhibit egg size plasticity in response to *C. floridum* will have very low fitness (because all of their progeny will die) compared to females that switch to laying larger eggs on this host.

*Mechanistic biology of seed-coat resistance and egg size plasticity* — So females respond to the host upon which they will lay eggs by shifting egg size in a manner consistent with our understanding of natural selection on egg size. Why do progeny hatching from large eggs have a fitness advantage over progeny hatching from small eggs when reared on seeds of *C. floridum*? What cues are females responding to? How does this influence survivorship of larvae on the exotic host, Texas ebony? At this time, we cannot answer these questions, but we can begin to make some educated guesses.

The primary cause of mortality of *S. limbatus* larvae on seeds of *C. floridum* appears to be chemical defenses upon the seeds; extractions from *C. floridum* seeds cause mortality of larvae when precipitated onto seeds of *C. microphyllum* or *A. greggii* (70; M. E. Czesak & C. W. Fox, unpublished data). It is not yet known what chemicals result in larval mortality, but it is clear that these chemicals are different from the cues that females respond to when deciding what size egg to lay. We have two kinds of evidence demonstrating this. First, females do not respond behaviorally to seed coat extractions that kill larvae when precipitated onto seeds of other hosts. Second, we have examined *S. limbatus* egg size and larval mortality in a paloverde hybrid swarm in eastern California (USA) where *C. floridum* and *C. microphyllum* hybridize and backcross (40, 72). Hybrid trees vary substantially in how well defended their seeds are against larvae of *S. limbatus*, ranging from well defended (< 25 % of larvae successfully penetrate the seed coat) to almost completely undefended (nearly 100% of larvae successfully penetrate the seed coat; Fox et al. 1997c). Hybrid trees also vary in whether females recognize them as a *C. floridum* (and lay large eggs on their seeds) or recognize them as a *C. microphyllum* (and lay smaller eggs on their seeds). However, the degree to which seeds are resistant to beetles and the size of eggs that females lay on these seeds are uncorrelated among trees, indicating that they must be influenced by different traits of the seeds (30).

Does egg size plasticity have anything to do with the ability of *S. limbatus* larvae to use seeds of Texas ebony? In our earlier experiment when we exposed females to seeds of either the native blue paloverde or the non-native Texas ebony while these females were maturing their eggs, and then forced these females to lay eggs on Texas ebony, we found that progeny of paloverde-exposed females had substantially higher survivorship on seeds of Texas ebony than did progeny of mothers that had never experienced paloverde seeds. When we measure eggs in these treatments we find that paloverde-exposed females laid larger eggs than females that had never encountered paloverde, and that egg size correlated positively with larval survivorship within each treatment (Fig. 7d), suggesting that the difference in larval survivorship between treatments is due at least in part to plasticity in egg size. However, plasticity in egg size is only part of the explanation. In the range of egg sizes that overlap between the two treatments, survivorship of progeny of paloverde-exposed mothers is still substantially higher than the survivorship of progeny of Texas ebony-exposed mothers, indicating that eggs also differ between treatments in their composition or gene expression. Unfortunately, we do not yet understand how eggs differ in composition.

## The Evolutionary Genetics of Egg Size Plasticity

The most recent focus of my laboratory has been on the evolutionary genetics of this egg size plasticity. For a trait to continue to evolve in nature, there must be genetic variation present within populations. For two traits to differentiate from each other, the genetic correlation between them must be < 1.0. In this case, we can treat the size of eggs that females lay on *C. floridum* and the size of eggs that they lay on *A. greggii* as two different traits. For egg size to evolve it must be heritable (i.e., the variation among individuals must in part be caused by genetic differences among individuals). For egg sizes to evolve separately on these two hosts (smaller eggs on *A. greggii* and larger eggs on *C. floridum*) then the genetic correlation between them must be < 1.0; a genetic correlation of 1.0 indicates that selection for a change in egg size on one host will result in exactly the same change on the other host, preventing egg sizes from further diverging on the two hosts.

We can quantify these genetic variances and genetic correlations using a standard quantitative genetic technique called a half-sib breeding design. In this design, we mate each of a random selection of males in our study to multiple females (in this study, each male was mated to four females) creating a population of progeny that is composed of full-sibs (share the same mother and father), half-sibs (share fathers but not mothers) and unrelated individuals. We then raise these progeny and collect data on egg size and other traits of interest from every individual. The strength of this half-sib design is that it allows us to tease apart additive genetic variances and covariances (the kind that influence responses to natural selection) from other sources of variance and covariance that result in similarity among individuals within a family (including some types of genetic and non-genetic variances). We found that genetic variation is present within populations for the size of eggs laid on seeds of both *A. greggii* and *C. floridum* (the heritability, $h^2$, ranged between 0.217 and 0.908), and that the heritability of egg size differed between populations and was higher on *A. greggii* than on *C. floridum* (18). We also found that the evolution of egg size plasticity is in part constrained by a high genetic correlation across host plants ($r_G > 0.6$). However, the cross-environment genetic correlation is less than 1.0, indicating that the size of eggs laid on these two hosts can diverge and that egg size plasticity is thus capable of evolving in response to natural selection.

We have since been expanding our genetic analyses to include examination of the genetic correlation between egg size and fecundity, the influence of male parental investment (a paternal effect) on egg size and female fecundity, and covariation between egg size and other phenotypic traits. Also, as I write this chapter, we are in the midst of an artificial selection experiment in which we are creating populations of beetles that lay either larger or smaller eggs on *C. floridum* and *A. greggii* to test hypotheses concerning the evolution of genetic correlations between traits and to examine the genetic basis of the selection responses.

## The Take-home Message

*Stator limbatus* is a widely distributed seed beetle that uses many host species throughout it’s broad distribution. These host species vary substantial in their suitability for larval development. However, females have information on what hosts their progeny will develop upon before they lay eggs, allowing them the opportunity to manipulate the phenotype of their progeny in a manner likely to increase progeny fitness in each environment. In part females manipulate progeny phenotype (and fitness) by changing the size of eggs that they lay (laying larger eggs on the better defended host species) and in part they manipulate progeny phenotype by manipulating egg composition (28).

Thus, maternal effects are an essential component of the biology of *S. limbatus*. They appear to have evolved as an adaptation for dealing with a variable environment (variation among hosts in suitability). Also, females are genetically variable in their expression of the maternal effect so that the maternal effect may still be evolving within populations. Yet, despite the fact that we know more about the significance of maternal effects for the biology of *S. limbatus* than for most other organisms (but see 51 for other examples of well studied systems) we really know very little about this system. Do females respond to other host species (we have only examined three species)? How does variation in the relative abundance of host species influence the evolutionary and ecological dynamics of egg size and egg size plasticity? How does egg size plasticity influence other ecological interactions, such as larval competition between beetle species, and how do these interactions influence the evolution of egg size and egg size plasticity? What constraints are there on the evolution of egg size plasticity? The list of questions yet to be asked and answered is long.

Most ecologists and entomologists give little thought to maternal effects. Some design their experiments in a manner that allows them to remove maternal effects from their genetic analyses, allowing them to better estimate genetic variances and covariances for the traits of interest (discussion in 67). Others simply ignore maternal effects. The primary objective of this review was to use examples from my own research on seed beetles to illustrate how understanding maternal effects can be essential to understanding ecological interactions in nature. Of one thing we can be sure; future research on maternal effects promises to hold great explanatory power for understanding the evolution of life cycles and adaptation to spatially and temporally variable environments.

## Acknowledgements

I thank M.E. Czesak, K. Donohue, B. Pass, and C. Rauter for helpful comments on this manuscript. I also thank all of my collaborators over the last few years, without whom much of this work would not have been possible. Research discussed in this manuscript has been funded by NSF DEB grant nos. 98-07315 and 99-96371 (to Charles Fox), USDA/CSRS grant no. 93-01887 (to Timothy Mousseau at the University of South Carolina) and a NSF postdoctoral fellowship (DEB 94-03244) to Charles Fox.

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