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MATERNAL EFFECTS MEDIATE HOST EXPANSION IN A SEED-FEEDING BEETLE

CHARLES W. FOX¹ AND UDO M. SAVALLI

Louis Calder Center, Biological Field Station and Department of Biological Sciences, Fordham University, 53 Whipoorwill Road, Box K, Armonk, New York 10504 USA

Abstract. Texas ebony (*Chloroleucon ebanum*) has recently been introduced as an ornamental tree in the Phoenix metropolitan area of Arizona (USA). It has since been colonized by the seed beetle *Stator limbatus* (Coleoptera: Bruchidae), and seeds of Texas ebony support the development of beetles to reproductive maturity in nature and in the laboratory. Egg size affects the larval survivorship of beetles on seeds of Texas ebony. Females of *S. limbatus* exhibit egg-size plasticity in response to native host plants; they lay small eggs if they encounter seeds of catclaw acacia (*Acacia greggii*) and lay large eggs if they encounter seeds of the blue paloverde (*Cercidium floridum*). We tested the hypothesis that oviposition experiences of female *S. limbatus* on native plants affects the ability of their larvae to develop on seeds of the nonnative Texas ebony. We demonstrate that females that encounter the native *C. floridum* while they are maturing their eggs produce progeny that have survivorship 10 times higher on seeds of the introduced Texas ebony than that of progeny produced by females that do not encounter *C. floridum* during egg maturation. However, this result cannot be explained entirely by egg-size plasticity; survivorship of larvae differed among treatments even in the range of egg sizes that overlapped between treatments. These results thus indicate that females exhibit plasticity in egg size and egg composition, and that this plasticity facilitates the expansion of *S. limbatus* onto seeds of a nonnative plant. Our study thus demonstrates that maternal effects can influence species interactions within communities, and that we should consider these maternal effects when predicting the ecological and evolutionary consequences of changing species distributions.

Key words: *Bruchidae*; *Cercidium floridum*; *Chloroleucon ebanum*; *diet breadth*; *diet expansion*; *egg size*; *exotic plants*; *insect–plant interactions*; *maternal effects*; *phenotypic plasticity*; *Stator limbatus*; *Survivorship*.

INTRODUCTION

Human activities are rapidly changing the environmental conditions that organisms experience (Vitousek et al. 1997). Many species are undergoing range expansions due to profound human modifications of the environment (Pitelka et al. 1997) or due to transport to new areas (Vitousek et al. 1996). Changes in organism distributions and resulting changes in patterns of predation, food availability, or competition provide the opportunity to study ecological responses to changing environmental conditions (e.g., Strong 1974) and allow for direct empirical study of evolutionary responses that could otherwise only be inferred indirectly (Carroll and Boyd 1992). For instance, changes in plant distributions, and the expansion of herbivores onto

these plants, provide the opportunity to study the evolution of insect diet breadth (Tabashnik 1983, Thomas et al. 1987, Bowers et al. 1992, Carroll and Boyd 1992, Fraser and Lawton 1994, Fox et al. 1997a), which is central to understanding the evolution and diversification of insect–plant interactions.

Phenotypic plasticity—the existence of genotypes that exhibit different phenotypes in different environments—is generally interpreted as an adaptation for dealing with a variable environment (Gotthard and Nylin 1995). This plasticity evolves because selection occurring simultaneously in multiple environments favors environment-specific growth and life-history adaptations (Via 1993). In some insects, this phenotypic plasticity is maternally induced—mothers that experience a predictive environmental cue can change the type of progeny that they make so that their progeny are best suited to the conditions predicted by that cue (reviews in Mousseau and Fox [1998]). For example, in the seed beetle *Stator limbatus* (Coleoptera: Bruchidae), fe-

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¹ Present address: Department of Entomology, University of Kentucky, Lexington, Kentucky 40546.

males change the size of eggs that they make in response to host stimuli, so that their progeny are prepared for the host plant upon which they will develop (Fox et al. 1997b). Here we demonstrate that maternally mediated life-history plasticity in response to seeds of a native host allows larvae of *S. limbatus* to develop successfully on seeds of a novel, nonnative plant that has recently been introduced into the southwestern United States.

Stator limbatus is a generalist seed parasite distributed throughout the southwestern United States and south into northern South America (Johnson and Kingsolver 1976, Johnson et al. 1989) where it uses >70 host-plant species in at least nine genera. Females lay eggs directly onto host seeds; upon hatching, the larvae burrow into the seed, where they complete development, pupate, and emerge as adults. In central Arizona *S. limbatus* commonly uses seeds of two host plants, blue paloverde (*Cercidium floridum*) and catclaw acacia (*Acacia greggii*) that differ substantially in their suitability for larval development—beetles reared on acacia have higher survivorship and faster development than beetles reared on paloverde (Fox et al. 1994, Fox et al. 1995). This difference in seed suitability translates into a difference in the magnitude of selection on egg size on these hosts. When reared on paloverde, larvae hatching from large eggs have higher egg-to-adult survivorship than larvae hatching from small eggs (larvae hatching from small eggs are incapable of penetrating the seed coat; Fox and Mousseau 1996, 1998). However, when larvae are reared on acacia, egg size does not affect larval survivorship; almost all larvae survive to adult (Fox and Mousseau 1996, 1998). Presumably in response to this variation among host species in selection on egg size, females have evolved egg-size plasticity in which they lay larger eggs on paloverde than on catclaw acacia (Fox et al. 1997b, Fox and Mousseau 1998). Females are capable of modifying egg size in response to early host experience because they delay oviposition for >24 h after emergence from their host seed. During this 24 h they mature eggs, often while in contact with their oviposition substrate. When experimentally conditioned to lay large eggs by exposure to paloverde during the maturation of their eggs, females produce progeny that have survivorship on paloverde that is 80 times greater than that of progeny produced by females conditioned to lay small eggs (by exposure to acacia during egg maturation) (Fox et al. 1997b).

Despite its extensive diet breadth, *S. limbatus* does not use every potential host. For example, it has never been observed to use seeds of Texas ebony (*Chloroleucon ebano*; Fabaceae; Mimosoideae) within the natural distribution of this plant (Nilsson and Johnson 1993), although the beetle and tree occur sympatrically in parts of their distributions. However, Texas ebony has recently been introduced as an ornamental tree in the Phoenix metropolitan area of Arizona, USA (intro-

duced post-1972; Phoenix Botanical Garden records). It has since been colonized by *S. limbatus*, and seeds of Texas ebony support the development of *S. limbatus* to reproductive maturity in nature and in the laboratory (Nilsson and Johnson 1993, Fox et al. 1997a). Egg-to-adult survivorship of *S. limbatus* on seeds of Texas ebony in central Arizona is ~10–15% (Fox et al. 1997a).

Because (1) egg size affects *S. limbatus* larval survivorship on seeds of some of its host plants, and (2) the size of eggs that female *S. limbatus* lay is affected by the host that they encounter during egg maturation, we expect that oviposition experiences of female *S. limbatus* will affect the ability of their larvae to develop on seeds of Texas ebony. Previous results indicate that females often encounter paloverde seeds prior to colonizing Texas ebony in central Arizona (Fox et al. 1997a). We thus tested the hypothesis that maternal encounters with seeds of the native plant, blue paloverde (*Cercidium floridum*), during egg maturation allow *S. limbatus* larvae to survive on seeds of the nonnative plant, Texas ebony (*Chloroleucon ebano*). Our results demonstrate that the egg-size plasticity exhibited by female *S. limbatus* in response to their native host plant facilitates the ability of this insect to expand its diet and survive on seeds of the nonnative plant, Texas ebony.

MATERIALS AND METHODS

Natural history of Stator limbatus

Female beetles oviposit directly onto host seeds inside fruits that have either dehisced or been damaged by other organisms. Upon hatching, the larvae burrow into the seed, where they complete development, pupate, and emerge as adults. Adults are the only dispersing stage; larvae are restricted to the seed that their mother has chosen for them. In the laboratory, mating and egg laying begin ~24–48 h post-emergence. Beetles require only the resources inside a single seed to complete development and reproduce. Thus, neither food nor water supplementation is necessary for the following laboratory experiments.

Study populations

Beetles for this experiment were collected from an *S. limbatus* population in central Arizona and another in southern California (USA). On 8 August 1997 beetles were collected from mature pods of catclaw acacia (*Acacia greggii*) along the Colorado River near Earp, San Bernardino County, California (California population). On 9–10 August 1997 beetles were collected from two species of paloverdes (*Cercidium floridum* and *C. microphyllum*) at various locations in northern Phoenix, Scottsdale (both Maricopa County), and Apache Junction, (Pinal County), Arizona (Arizona population).

Beetles were collected by picking mature seed pods

from more than 25 plants at each site. Mature pods were transferred to the laboratory and seeds bearing beetle eggs were separated from uninfested seeds. Seeds containing entrance or emergence holes of other bruchids (such as *Mimosestes* sp.) were discarded. We estimate that both laboratory populations were initiated with >200 field-collected individuals. The populations were reared on seeds of *A. greggii*, at 30°C, L:D 15:9 h, for two generations before the start of the experiment. Because larval mortality is very low on *A. greggii* (egg-to-adult mortality generally <5%), rearing beetles for two generations on this host allows beetles to acclimate to laboratory conditions while minimizing the risk of natural selection occurring during these two generations.

Experimental design

To examine the effects of female exposure to host seeds on the subsequent survivorship of their larvae on Texas ebony, females were exposed to seeds of either the native paloverde (which stimulates the production of large eggs) or the nonnative Texas ebony (which, like *A. greggii*, stimulates the production of small eggs) during egg maturation, and were then forced to lay eggs on Texas ebony. To establish the treatments, virgin males and females were collected from isolated acacia seeds from the main colony within 12 h of their emergence from the seed. Each beetle was paired with a single virgin beetle of the opposite sex. Pairs were confined in 60-mm-diameter petri dishes containing either (a) eight Texas ebony seeds ($N = 145$ California and 105 Arizona pairs) or (b) eight paloverde seeds ($N = 103$ California and 91 Arizona pairs). Dishes were checked every 12 h until females began laying eggs (which generally occurred 24–48 h later), after which they were transferred to a new petri dish containing 20 Texas ebony seeds. Females were allowed to oviposit on these new Texas ebony seeds for 24 h; after this time they begin to respond to their new oviposition substrate by changing the size of eggs that they lay.

All larvae were reared to adult at low density (1–2 larvae/seed); excess eggs were scraped from the seed. Egg-to-adult survivorship was recorded for all families. Using a 55× dissecting microscope, egg size (length and width) was recorded for each female by measuring two eggs haphazardly chosen from those laid on Texas ebony during the 24-h oviposition period. Because eggs are glued to seeds, removing them for weighing is destructive and very time consuming. Egg mass is positively correlated with both egg length and egg width (Fox and Mousseau 1996), and was estimated from the equation: egg mass = $-0.035 + 0.086$ (egg length) + 0.022 (egg width), where egg mass is estimated in milligrams and egg dimensions are measured in millimeters. This equation was derived empirically in the laboratory ($R^2 = 0.89$), and estimates egg mass better than either egg mass = constant × egg length × (egg

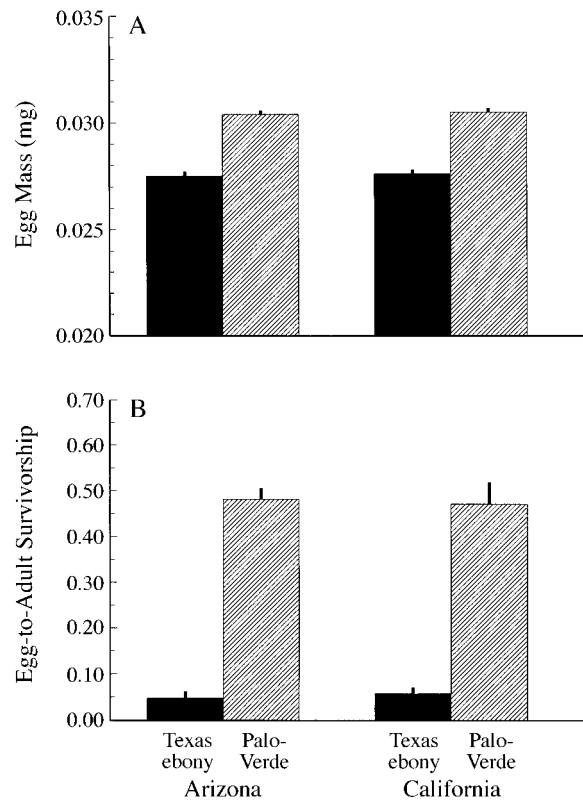


FIG. 1. (A) The size of eggs laid (mean + 2 SE) by *Stator limbatus* females on seeds of Texas ebony when females were first exposed to seeds of either Texas ebony (*Chloroleucon ebano*) or blue paloverde (*Cercidium floridum*). (B) The egg-to-adult survivorship of progeny hatching from these eggs (mean + 2 SE).

width)² ($R^2 = 0.75$) or egg mass = constant × egg width × (egg length)² ($R^2 = 0.83$).

RESULTS AND DISCUSSION

Females that encountered paloverde seeds during egg maturation laid eggs that were >10% larger than those laid by females exposed only to Texas ebony (Fig. 1A; Mann-Whitney U tests: Arizona, $U = 13\,470$, $df = 1$, $P < 0.001$; California, $U = 14\,439$, $df = 1$, $P < 0.001$). Egg-to-adult survivorship of larvae hatching from these large eggs laid by females exposed to paloverde was 10 times greater than the survivorship of larvae produced by females exposed only to Texas ebony (Fig. 1B; Arizona, $U = 8862$, $df = 1$, $P < 0.001$; California, $U = 14\,092$, $df = 1$, $P < 0.001$). The positive relationship between egg size and larval survivorship within each treatment indicates that this improved survivorship is due at least in part to the difference in egg size (Fig. 2; Spearman rank-sum correlation, $r_s = 0.397$ and 0.451 for progeny of Arizona females exposed to Texas ebony and paloverde, respectively, and $r_s = 0.303$ and 0.405 for progeny of California females; $P < 0.001$ for each). However, plasticity in egg size is only part of the explanation. In the range of egg sizes

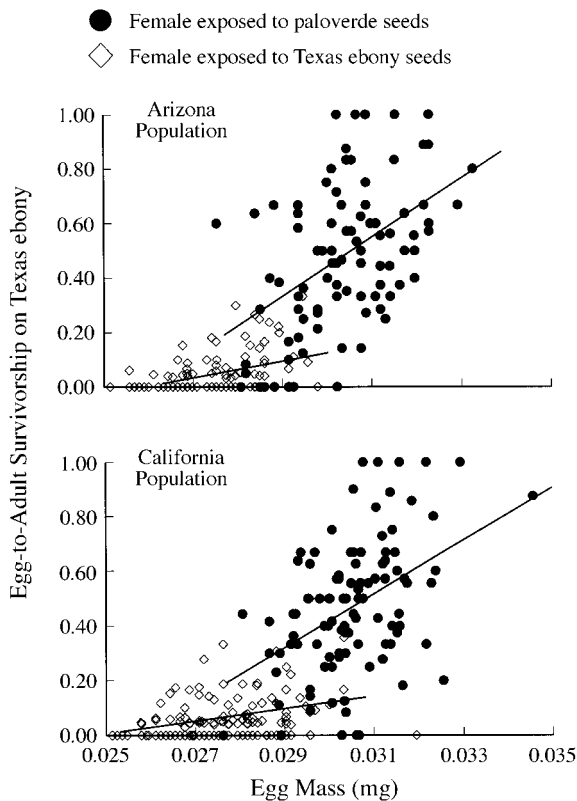


FIG. 2. The relationship between *Stator limbatus* egg size and larval egg-to-adult survivorship on Texas ebony seeds.

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 (Fig. 2; Arizona, $U = 2328$, $df = 1$, $P < 0.001$; California, $U = 3537$, $df = 1$, $P < 0.001$). This result suggests that eggs also differ between treatments in their composition or gene expression.

These results demonstrate that the ability of *S. limbatus* larvae to use the seeds of a novel plant (Texas ebony) is facilitated by maternally mediated plasticity in egg size and composition. Females exposed to seeds of paloverde during egg maturation change the type of eggs that they produce so that their progeny are also capable of developing on seeds of Texas ebony. Females not exposed to paloverde seeds during egg maturation produce progeny that are very much less capable of developing on seeds of Texas ebony. Thus, plasticity of egg size and composition, which has apparently evolved as a maternal adaptation for dealing with variation among larval environments, enables this insect to switch to a recently introduced host plant.

Stator limbatus currently does not use Texas ebony as a host anywhere that the beetle and tree are naturally sympatric (southern Texas and northern Mexico) (Nilsson and Johnson 1993). Our results suggest that they do 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* [C. W. Fox, *personal observations*], indicating that colonization of Texas ebony in Arizona is not the result of differences between naturally occurring and ornamental trees). We thus predict that the spread or introduction of paloverde into southern Texas would allow *S. limbatus* to expand its diet to include Texas ebony (beetles from Texas readily oviposit on paloverde in the laboratory). More generally, our results indicate that whether insects incorporate nonnative plants into their diet will depend in part on the species composition of the local plant community. Conversely, introduced plants may facilitate shifts between native host species by herbivorous or parasitic insects. These results also indicate that patterns of host use by insects in one locality may not adequately predict (a) whether plants will be colonized by insects if they are introduced to another locality, and (b) 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 nontarget species (Louda et al. 1997) and why plants may be attacked by insects in one locality but not another (e.g., Fox et al. 1997a).

Our study thus demonstrates that maternal effects can have a previously unrecognized role in influencing species interactions within communities, and that we should consider these maternal effects when predicting the ecological and evolutionary consequences of changing species distributions.

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