

Egg-Dumping Behavior Is Not Correlated With Wider Host Acceptance in the Seed Beetle *Callosobruchus maculatus* (Coleoptera: Chrysomelidae: Bruchinae)

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ABSTRACT If typical host plants are absent, some herbivorous insects “dump” eggs on unsuitable substrates, even though this can cause complete larval mortality and reduced maternal life span. In the seed beetle *Callosobruchus maculatus* (F.) (Coleoptera: Chrysomelidae: Bruchinae), the tendency to dump eggs varies genetically both within and between populations. A previous study hypothesized that egg-dumping behavior facilitates host-range expansions, and suggested that such expansions have served to maintain “dumper” genotypes in beetle populations. We tested this hypothesis in two experiments. For both African and Asian beetle populations, full-sib females from >60 families were split among three treatments: no seeds, a less-preferred novel host, and a preferred host. Within each population, we found no correlation among families between the tendency to dump eggs and the tendency to accept the novel host. We also compared egg dumping between selection lines that had adapted to a novel host and a line that had remained on the ancestral host. Females from lines that had evolved greater acceptance of the novel host did not dump more eggs if hosts were absent. Thus, neither experiment supported the host-range expansion hypothesis. Egg distributions on the preferred host in the first experiment provided weak support for a more proximate explanation: family-level variation in the tendency to dump eggs is inversely related to the tendency to avoid superparasitism of seeds. Such a relationship is also evident in comparisons between populations. Given the considerable short-term costs of egg dumping, we suggest that the host-range expansion hypothesis requires unrealistically high frequencies of host deprivation and subsequent host shifts in *C. maculatus*.

KEY WORDS *Callosobruchus*, egg dispersion, genetic correlation, host deprivation, oviposition behavior

Ovipositing females of many herbivorous and parasitic insects must distribute their eggs among hosts that are both scattered and unpredictable with respect to availability and quality. Females may respond to variation in host availability by adaptively adjusting egg maturation rates, oosorption rates, clutch sizes, or allocation of resources between survival and reproduction (Ellers and van Alphen 1997, Papaj 2000, Jervis et al. 2005, Asman and Ekbohm 2006). In some species, however, females may respond to prolonged host deprivation by “dumping” eggs on unsuitable substrates, even though this behavior can lead to complete larval mortality (Košťál 1993, Roberts and Schmidt 2004). Because of the frequently observed cost of reproduction, dumping eggs also can reduce maternal life span and hence decrease the likelihood of locating suitable hosts in the future (Šešljija et al. 2009).

Several hypotheses have been proposed to account for the seemingly maladaptive behavior of egg dump-

ing. Some explanations are largely mechanistic and assume females are subject to inescapable physiological constraints. The egg-load hypothesis posits that females may not be able to halt oocyte maturation, and the steady accumulation of mature oocytes may cause the movement of eggs down the oviduct (Tammaru and Javoiš 2000, Roberts and Schmidt 2004). Other hypotheses propose that egg dumping is an adaptive response to a temporary shortage of hosts. One example is the egg-maturation hypothesis, which may apply if there is a significant time lag in restoring the oocyte maturation process after it has been interrupted (Papaj 2000, Hougardy et al. 2005). In this case, egg-dumping females may be better able to exploit hosts quickly when they become available. Among predatory insects, females that cannot resorb mature oocytes may dump and consume infertile eggs when food is scarce, and thereby recoup some of their reproductive investment (Ferrer et al. 2011).

Egg dumping has been especially well studied in seed beetles (Coleoptera: Chrysomelidae: Bruchinae) (Huignard and Biemont 1979, Parsons and Credland 2003), and the cowpea weevil, *Callosobruchus maculatus* (F.) (Coleoptera: Chrysomelidae: Bruchinae),

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has been used to address both adaptive and nonadaptive (constraint-based) explanations. In human stores of grain legumes, this insect is typically a "capital breeder"; fecundity depends mostly on larval-acquired resources. Females emerge from seeds with several mature oocytes and can begin oviposition within several hours after emergence (Credland and Wright 1989). If mated females are deprived of hosts, they sometimes dump large numbers of eggs, though the behavior is highly variable (Wilson and Hill 1989). Larvae hatching from such eggs invariably die, because eggs are glued to the substrate and larvae can only burrow directly beneath the oviposition site. Dumping eggs also entails a considerable cost by reducing female longevity in *C. maculatus* (Messina and Slade 1999, Messina and Fry 2003).

Wilson and Hill (1989) suggested that egg dumping in *C. maculatus* is mainly caused by the physiological constraint of crowding within the oviducts of mated females, particularly because the capacity for oosorption may be limited, and females do not turn off egg maturation until oviducts are full of mature oocytes. Wang and Horng (2004) later suggested that egg dumping is adaptive in *C. maculatus*. Females that do not stop egg maturation and dump more eggs during host deprivation may achieve higher lifetime fecundities when seeds become available (the egg-maturation hypothesis). They proposed that costs associated with resuming the process ultimately exceed the costs of dumping eggs. However, Messina et al. (2007) found that the number of dumped eggs was inversely, not positively, related to the number subsequently laid on seeds. That study also used artificial-selection and common-environment experiments to confirm that egg dumping varies genetically both within and between populations. Females from an African population dumped more than seven times as many eggs than did females from an Asian population, and many Asian females dumped no eggs over their lifetimes. In addition, bidirectional selection within the African population caused divergence in the degree of egg dumping after only a few generations. Messina et al. (2007) thus failed to support the adaptive, egg-maturation hypothesis and also demonstrated that nonadaptive, physiological constraints do not apply equally to all populations or genotypes.

In this study, we address a second adaptive explanation for egg dumping. Cheng et al. (2008) proposed that egg dumping facilitates host-range expansions, because "dumper" genotypes are more likely to accept novel hosts when familiar oviposition hosts are unavailable. Frequent previous encounters with nonpreferred but suitable hosts can thus maintain dumping behavior in populations. It has long been supposed that females with relatively low oviposition specificity may play an important role in initiating host shifts by herbivorous insects (Wiklund 1981, Courtney et al. 1989, Fox and Lalonde 1993, Mercader and Scriber 2007, Singer et al. 2008). Low oviposition specificity or thresholds might be favored in a patchy environment in which nonpreferred but suitable hosts are commonly encountered, and the availability of familiar

hosts is unpredictable. This scenario may apply especially to stored-product insects (such as seed beetles) that use large but ephemeral quantities of a single host and then may encounter a new and possibly less preferred host. Seed beetles that freely deposit eggs in the absence of any suitable substrate may be those with low oviposition specificity and thus prone to accept an unfamiliar legume host.

Here, we used a split-family design to test whether the tendency to dump eggs is positively genetically correlated with the tendency to accept a novel host, lentil (*Lens culinaris* Medikus). Lentil is distantly related to the typical hosts of *C. maculatus* (Choi et al. 2004). It is generally unsuitable for larval growth (Credland 1987, 1990) and one of the least preferred grain legumes for oviposition (Wasserman 1986, Credland 1987). We also addressed the host-range expansion hypothesis by comparing egg dumping in experimental beetle lines that had rapidly evolved increased oviposition on lentil with egg dumping in the ancestral line from which the lentil-adapted lines were derived (Messina et al. 2009a,b). If egg dumping is associated with a generally low degree of oviposition specificity, we expect selection for high acceptance of lentil to simultaneously increase the frequency of "dumper" genotypes.

A second hypothesis addressed by this study is that genetic and phenotypic variation in egg dumping is correlated with variation in host discrimination, i.e., a female's tendency to avoid adding eggs to occupied seeds (superparasitism). In addition to dumping very few eggs when no seeds are available, females from our Asian strain of *C. maculatus* distribute their eggs highly uniformly among seeds. Because larvae from this population engage in an especially strong, contest-type competition (Messina 1991), the benefit to avoiding superparasitism is especially high in the Asian strain. If all seeds already bear two or three eggs, Asian females also typically cease ovipositing, and die without laying a significant proportion of their eggs (Thanthianga and Mitchell 1987, Messina 1991). In contrast, females from our African strain readily superparasitize occupied seeds and larvae engage in a scramble-type competition (Messina and Karren, 2003, Messina 2004). The same seeds that yield only one or two Asian adults (because of contest competition) can routinely yield several African adults. We hypothesized that, because Asian females cease egg-laying when all available seeds bear a few eggs, they may also possess a more effective mechanism for egg retention when hosts are absent. To investigate the potential relationship between egg dumping and host discrimination, we included egg dispersion as a third treatment in the split-family experiment.

Materials and Methods

Source Populations. The African population was collected from infested cowpea, *Vigna unguiculata* (L.) Walpers, in Ouagadougou, Burkina Faso (Messina 1993); it is sometimes referred to as the BF population (Fox et al. 2004a,b). The Asian population

(also called the SI population) was established from infested mung bean, *Vigna radiata* (L.) Wilczek, and black gram, *Vigna mungo* (L.) Hepper, in Tirunelveli, India (Mitchell 1991). In addition to differing in egg-dumping behavior, the populations are divergent in several fitness-related traits, such as larval competitive ability, body size, and life span (Fox et al. 2004a,b). Each population has been maintained in the laboratory on its respective host for >200 generations and yet has maintained heritable variation for most measured traits (Messina and Karren 2003, Messina 2004, Messina et al. 2007). The Asian population used here was divided into distinct Kentucky and Utah laboratory strains that had been evolving in separate laboratories for ≈ 80 generations at the time of the experiments.

Full-Sib Correlation Experiment. We used a full-sib, split-family design to test for genetic correlations among the tendencies to dump eggs, to accept a novel host, and to distribute eggs evenly among seeds, i.e., avoid superparasitism. For both the African and Asian (Kentucky strain) populations, we created full-sib families by placing newly emerged pairs (one virgin male and one virgin female from the same population) in 60-mm petri dishes containing 100 seeds of mung bean. Dishes were kept in an environmentally controlled chamber at 26°C and a photoperiod of 15:9 (L:D) h. We created a total of 65 African families and 74 Asian families. Parental females were allowed to lay eggs for 1 wk, after which seeds bearing a single egg were isolated in individual 35-mm dishes. Dishes were randomly arranged with respect to family and population.

Dishes containing individual seeds were checked daily and emerging females were randomly assigned to one of the three treatments described below. In total, 62 African families and 69 Asian families produced enough female progeny to be represented in all treatments. Each emerging female was mated to a nonsibling male from the same population. Females that failed to mate were provided a second male; if the pair again failed to mate, the female was discarded. We respectively assigned 954, 950, and 949 females to the egg-dumping, novel-host, and egg-dispersion treatments, with an average of 6.8 females per treatment per family. All test females developed in mung bean, which is a high-quality rearing host for both the African and Asian populations (Fox et al. 2004b, Messina 2004).

The egg-dumping treatment consisted of confining a mated female to an empty 35-mm petri dish for 6 d, after which we recorded the number of eggs laid on the dish (glued to the plastic surface). For the novel-host treatment, females were placed in 60-mm dishes containing 60 lentil seeds for 6 d, and we counted the total number of eggs laid. In the egg-dispersion treatment, females were confined with 40 mung beans for 48 h, after which we recorded the number of eggs per seed. Egg dispersion was quantified as the uniformity index, U (Messina and Mitchell 1989). It is based on a female's number of "mistakes," which is defined as the number of eggs that would need to be transferred

among seeds to transform the observed distribution into the most uniform one possible. This observed number of mistakes is then compared with the expected number that would be committed by a female depositing the same number of eggs randomly, i.e., according to a Poisson distribution. Once the observed and expected number of mistakes is known, U is calculated as (expected - observed)/expected. U scores usually range between 0 (a random dispersion) and 1 (a completely uniform dispersion). U scores are largely independent of the number of eggs per seed, but, because random and uniform distributions become indistinguishable if mean egg number is very low, we included in the analysis only females that laid ≥ 10 eggs.

We first used nonparametric Kruskal-Wallis tests to compare each oviposition variable (number of dumped eggs, number of eggs on lentil, number of eggs on mung bean, and egg dispersion on mung bean) between the African and Asian populations. Nonparametric tests were conducted in each case because the distribution of family means was highly non-normal for the egg-dumping and egg-dispersion treatments. We then used family means to examine full-sib correlations involving egg dumping, novel-host acceptance, and egg dispersion within the African and Asian populations. For each population, we calculated three Spearman-rank correlations (r_s): egg dumping versus novel-host acceptance, egg dumping versus egg dispersion, and novel-host acceptance versus egg dispersion. We chose nonparametric correlations because the distribution of family means within each strain again deviated substantially from normality in the egg-dumping and egg-dispersion treatments. Spearman-rank correlations do not strictly estimate parametric genetic correlations (we cannot assume $r_s = r_c$) but should differ from zero in the same direction as the corresponding genetic correlation.

Selection-Line Comparisons. A second experiment compared egg dumping in four selection lines derived from the Asian population (Utah strain): three lines (L1-3) that had independently adapted to a novel host (lentil) by increasing oviposition on that host and a line (M) maintained on the ancestral host, mung bean. Formation of the L lines via quasi-natural selection (Fry 2003) is described in detail by Messina et al. (2009a, b). In brief, they were established by adding 2,000-2,500 adults (L1) or 4,000-5,000 adults (L2 and L3) from the M line to ≈ 750 or 1,500 g of lentil seeds ($\approx 12,000$ or 24,000 seeds). After all lines underwent a severe bottleneck, larval survival to adult emergence rose consistently from 1 to >80% in <20 generations, and acceptance of lentil by egg-laying females rose two- to three-fold. Thereafter, new generations of all lines were formed by adding 1,500-2,500 adults to ≈ 750 g of lentil (L1-3) or mung bean (M). To eliminate potential effects of rearing host on female behavior, all L lines were reverted to mung bean for a generation before the experiment, which was conducted in an environmentally controlled chamber at 24°C and constant light. At that time of the experi-

Table 1. Egg-laying behavior (means \pm SE) of *C. maculatus* females from African and Asian populations

Trait	Beetle pop			P
	African	Asian	Kruskal-Wallis χ^2	
No. dumped eggs (6 d)	20.5 \pm 1.1	6.3 \pm 0.4	77.3	<0.001
No. eggs on lentil (6 d)	24.2 \pm 1.6	24.8 \pm 1.9	0.1	0.81
No. eggs on mung bean (48 h)	41.5 \pm 0.6	40.3 \pm 0.4	4.4	0.04
Egg dispersion on mung bean (<i>U</i> score)	0.85 \pm 0.01	0.97 \pm 0.01	70.4	<0.001

Means are derived from 62 African and 69 Asian families, with an average of 6.8 full-sib females tested per family per treatment; df = 1 in each test.

ment, the L1, L2, and L3 lines had spent 48, 34, and 30 generations on lentil, respectively.

We collected 60 beetle pairs from each line on three successive days. Cultures were first sieved to remove already emerged adults, and newly emerged pairs were collected within 1 h. On the first day, pairs were placed in empty 60-mm dishes to estimate egg dumping. We recorded the number of eggs laid per female after 6 d. Because any differences in egg dumping between lines could simply reflect differences in fecundity, pairs collected on the second day were placed in dishes containing \approx 100 seeds of mung bean, a highly preferred host, for 6 d. Pairs collected on the third day were placed in dishes containing \approx 100 lentil seeds, again for 6 d. This treatment was meant to confirm that the L and M lines differed in their acceptance of the novel host (Messina et al. 2009b). None of the 720 test females (four lines \times 3 host treatments \times 60 replicate females per treatment) had prior egg-laying experience, because they were collected within an hour of adult emergence. Because egg number was not distributed normally in the egg-dumping treatment (most females laid no eggs), we used nonparametric Kruskal-Wallis tests to compare lines for all three treatments.

Results

Full-Sib Correlation Experiment. When placed in empty dishes, African-origin females dumped more than three times as many eggs as did Asian females (Kentucky strain) (Table 1). They did not differ, however, in their acceptance of lentil as an oviposition host. Lentil was clearly a less preferred host in both populations; females laid almost twice as many eggs on mung bean in 48 h as they did on lentil in 6 d (Table 1). On mung bean, African females laid slightly more eggs than did Asian females (Table 1). As expected, females from both populations distributed their eggs among available mung beans in a highly uniform manner (*U* scores were much closer to 1 than to 0), but egg dispersion was significantly more uniform in the Asian population (Table 1). Interestingly, African females provided no seeds laid nearly as many eggs as those provided lentil, whereas Asian females laid many fewer eggs in the no-seeds treatment (Table 1).

Family-mean correlations within each population also did not support the hypothesis that greater egg dumping is associated with greater acceptance of a novel host. Among families, the number of eggs

dumped in empty dishes was not correlated with the number of eggs laid on lentil in either the African ($r_s = 0.10$, $P = 0.43$) or Asian ($r_s = 0.08$, $P = 0.53$) populations. There was a marginal, negative relationship between the tendency to dump eggs and the degree of uniformity of the egg distribution in the African population (Fig. 1; $r_s = -0.24$, $P = 0.07$). Egg dumping and egg dispersion were not correlated in the Asian population ($r_s = -0.04$, $P = 0.72$), which exhibited little among-family variation in either trait (Fig. 1). In neither population was there a significant relationship between the uniformity of egg distributions and the number of eggs laid on lentil ($r_s = 0.11$, $P = 0.40$ and $r_s = -0.11$, $P = 0.38$, for the African and Asian populations, respectively).

Selection-Line Comparisons. Predictably, Asian females (Utah strain) exhibited an extremely low tendency to dump eggs in the absence of seeds (Table 2). Across the four selection lines (L1–3 and M), 61–78% of females failed to lay any eggs over 6 d in empty dishes. More importantly, there was no evidence of higher egg dumping in the three L lines that had independently evolved higher acceptance of a novel host (Table 2). Thus, it is unlikely that the evolution of greater oviposition on lentil was mediated by an increased frequency of “dumper” genotypes relative to nondumper genotypes. The L and M lines also did not seem to differ in potential fecundity, because they laid similar numbers of eggs on the preferred, ancestral host, mung bean (Table 2). In contrast, the number of eggs laid on lentil was, as expected, \approx 2.5 times greater

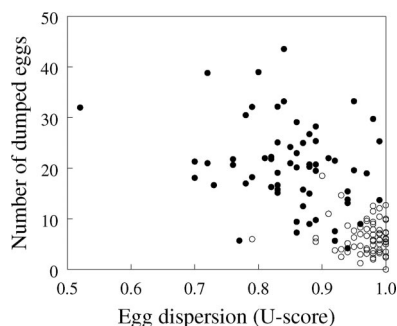


Fig. 1. Relationship between the number of eggs “dumped” in the absence of seeds and the dispersion of eggs (*U* score) on mung beans for African (closed circles) or Asian (open circles) females of *C. maculatus*. Each point represents a family, with an average of 6.8 full-sib females tested per family.

Table 2. Number of eggs (means \pm SE) laid by Asian *C. maculatus* females from lines switched to a novel host (lentil, L1–3) for \geq 30 generations or kept on the ancestral host (mung bean, M)

Treatment	Selection line				Kruskal-Wallis χ^2	P
	L1	L2	L3	M		
No seeds	1.4 \pm 0.4	1.7 \pm 0.5	1.4 \pm 0.3	1.7 \pm 0.4	2.4	0.49
Mung bean	41.6 \pm 1.2	39.5 \pm 0.9	39.6 \pm 0.9	40.9 \pm 1.1	3.7	0.30
Lentil	20.6 \pm 1.7	18.0 \pm 1.4	19.7 \pm 1.4	7.6 \pm 1.5	44.8	<0.001

The L lines were reverted to mung bean for a generation to eliminate effects of rearing host on egg-laying behavior. $n = 58$ – 60 females per treatment; $df = 3$ in each test.

in all three of the L lines than it was in the M line (Table 2).

Discussion

Three components of this study addressed the hypothesis that egg dumping persists in *C. maculatus* populations because it facilitates colonization of new hosts (Cheng et al. 2008). At the population level, host-deprived females from the African population were much more prone to dump eggs than Asian females. Contrary to the hypothesis, however, African females did not show greater acceptance of lentil (Table 1), which represented both a novel and less preferred host. Before we conducted the selection experiments that eventually yielded the L lines in this study, a similar comparison was performed using the Utah strains of the African and Asian populations (Messina et al. 2009b; unpublished data). Although these strains were even more divergent in the tendency to dump eggs (Messina et al. 2007), they too did not differ in the number of eggs laid on lentil (respective means [\pm SE] were 10.8 ± 1.4 and 10.2 ± 1.1 ; $t = 0.32$, $df = 175$, $P = 0.75$).

Correlations of family means within populations also showed no association between egg dumping and the degree of acceptance of the novel host. This result may not be surprising for the Asian population, which dumps few eggs and hence displayed a relatively narrow range of family means. However, the African population exhibited considerable among-family variation (Fig. 1) and is known to harbor substantial genetic variation for egg-dumping behavior. Even a single generation of bidirectional selection was sufficient to cause a divergence between “dumper” and “non-dumper” lines, and a half-sib/full-sib breeding design yielded a narrow-sense heritability of 0.4 for the number of eggs laid by host-deprived African females (Messina and Fry 2003, Messina et al. 2007). Any pleiotropic relationship between acceptance of lentil and egg dumping therefore seems unlikely.

The third line of evidence addressed the host-range expansion hypothesis in the reverse direction: is the evolution of increased acceptance of lentil (Messina et al. 2009b) accompanied by an increase in the tendency to dump eggs? Comparisons of egg dumping between the L and M lines suggest it is not. It could be argued that adaptation to lentil is unlikely to increase egg dumping in the Asian population, because this population possesses so little phenotypic variation for the

trait (Table 2; Messina et al. 2007). Nevertheless, each L line possessed ample genetic variation for increased oviposition on lentil, so that variation in the tendency to accept this host again must be decoupled from variation in the tendency to dump eggs. Previous work also suggested that greater acceptance of lentil is not mediated by a generally lower threshold for ovipositing on any substrate (Messina and Jones 2009). Despite their very different responses to lentil, females from the L1 and M lines did not differ in their acceptance of five of six novel legume hosts, including some that were more closely related to lentil than to the ancestral host, mung bean. The two lines also did not differ in their acceptance of an inert artificial host, glass balls (Messina and Jones 2009). More studies are needed to determine whether host shifts by plant-feeding insects are often instigated by individuals with below-average feeding or oviposition specificities. If so, adaptation to one novel host might then promote an even further host-range expansion (Courtney et al. 1989, Agrawal 2000).

Any adaptive explanation for egg-dumping behavior should account for its extensive variation in *C. maculatus*. For example, if the behavior is maintained because it has facilitated frequent host-range expansions (Cheng et al. 2008) or rapid exploitation of newly found resources after host deprivation (Wang and Horng 2004), why do females from some populations dump few or no eggs? Possibly there is a large cost to egg dumping in the absence of heterogeneity in host availability, but then why is egg dumping maintained in some long-term laboratory colonies? A similar problem applies to nonadaptive explanations, including the hypothesis that egg dumping is a simple constraint emerging from the insect's particular ovarian dynamics (Wilson and Hill 1989, Roberts and Schmidt 2004). Physiological constraints (e.g., oviduct capacities, oosorption rates) probably play some role in egg-dumping behavior, but they are obviously not strong enough to cause the trait to be invariant within or between populations of *C. maculatus*.

Across different studies, some variation in egg-dumping behavior could arise simply from different experimental protocols. We note that Utah and Kentucky strains of the African population dumped similar numbers of eggs (cf. Table 1 and Messina et al. 2007), but Asian females from the Kentucky strain dumped more eggs than did females from the Utah strain (cf. Tables 1 and 2 and Messina et al. 2007). Such variation could have been caused by differences in abiotic con-

ditions between laboratories (such as photoperiod and temperature, see Materials and Methods) or differences in the duration of female exposure to mates. However, even if the degree of egg dumping is sensitive to different experimental conditions, such differences did not obscure the fact that African females dump many more eggs than do Asian females or that females from the two populations are similar in their acceptance of lentil. Alternatively, greater egg dumping in the Kentucky strain of the Asian population may have evolved in the 80 generations since the two strains shared common ancestry. Populations of *C. maculatus* (including the Asian one used here) have been divided among multiple laboratories, and Fricke and Arnqvist (2004) found examples of fairly rapid divergence in certain traits (e.g., the effect of mating on female reproductive behavior) under differing laboratory conditions.

Variation in egg dumping could also arise as a correlated response to selection on a trait other than oviposition specificity (Šešlija et al. 2009). Messina et al. (2007) found that artificial selection for a low egg dumping led to longer larval development times and longer adult life spans for both males and females. That study also suggested that the tendency to dump eggs may covary with the tendency to avoid superparasitism. Such a relationship is evident at the population level; African females both distribute eggs less uniformly among seeds and dump more eggs (Fig. 1; Messina et al. 2007). Within the African population, however, there was at best a weak negative relationship ($P = 0.07$), among families, between the number of dumped eggs and egg dispersion (Fig. 1). No relationship was observed in the Asian population, which displayed little family-level variation in either U scores or dumping. Both observational data and selection experiments suggest that the degree of host discrimination itself depends on larval competitiveness and host size (Messina 2004). It remains possible that females from populations with aggressive, contest-competing larvae will be more discriminating overall by expending more effort to search for unoccupied hosts, ceasing oviposition once all seeds have multiple eggs, and refraining from dumping eggs during host deprivation.

Because single-generation breeding designs, such as the family-mean correlations, may not accurately predict evolutionary responses and constraints (Gromko 1995, Fry 2003), a better approach might be to perform bidirectional selection for high and low egg dumping for many generations instead of just a few (Messina et al. 2007, Šešlija et al. 2009). One could then examine potential correlated responses in a suite of behaviors, including acceptance of novel hosts and egg dispersion among seeds. In addition, crosses between “dumper” and “nondumper” lines could be used to estimate the genetic architecture underlying the tendency to dump eggs (Tucić and Šešlija 2007, Fox et al. 2009). Even if egg dumping is pleiotropically related to acceptance of novel hosts in *C. maculatus*, it need not be viewed as a “long-term” strategy for host-range expansions, as it was described by Cheng et al. (2008).

Given the short-term costs of dumping eggs, maintenance of “dumper” genotypes under the scenario of Cheng et al. (2008) would probably require chronically high frequencies of host deprivation followed by common encounters with novel hosts in field or storage populations (Tuda et al. 2006). A more realistic explanation would be that egg dumping (and its variation) persists for other reasons, but may occasionally and fortuitously foster colonization of a new host.

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