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## Larval host plant affects fitness consequences of egg size variation in the seed beetle *Stator limbatus*

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**Abstract** Egg size variation often has large effects on the fitness of progeny in insects. However, many studies have been unable to detect an advantage of developing from large eggs, suggesting that egg size variation has implications for offspring performance only under adverse conditions, such as during larval competition, periods of starvation, desiccation, or when larvae feed on low-quality resources. We test this hypothesis by examining the consequences of egg size variation for survivorship and development of a seed-feeding insect, *Stator limbatus*, on both a low-quality (*Cercidium floridum*) and a high-quality (*Acacia greggii*) host plant. Our results are consistent with the hypothesis. *S. limbatus* larval performance was affected by egg size only when developing on the poor-quality host (*C. floridum*); larvae from large eggs survived better on *C. floridum* than those from small eggs, while there was no evidence of an effect of egg size on progeny development time, body weight, or survivorship when larvae developed on *A. greggii*. These results indicate intense selection for large eggs within *C. floridum*-associated populations, but not in *A. greggii*-associated populations, so that egg size is predicted to vary among populations associated with different hosts. Our results also support this hypothesis; females from a *C. floridum*-associated population (Scottsdale) laid larger eggs than females from an *A. greggii*-associated population (Black Canyon City).

**Key words** *Acacia greggii* · *Cercidium floridum* · Egg size · Survivorship · *Stator limbatus*

### Introduction

Propagule size is a particularly important character in organismal life history evolution because it is simultaneously a maternal and offspring character (Sinervo 1990); eggs are produced by mothers, but also determine initial offspring resources/size. In animals, egg size, and thus offspring starting resources and size, typically varies within and among populations (Fleming and Gross 1990; Mashiko 1992). Some studies have shown that this variation has large effects on the fitness of progeny in both insects (review in Fox 1994a) and vertebrates (Kaplan 1980a,b; Reid and Boersma 1990; Marteinsdottir and Able 1992; reviews in Fleming and Gross 1990; Kaplan 1990; Reznick 1990); progeny developing from large eggs generally survive better, develop faster, and emerge larger than progeny from smaller eggs. However, other studies have been unable to detect an advantage of developing from large eggs (Richards and Myers 1980; Wiklund and Persson 1983; Steinwascher 1984; Karlsson and Wiklund 1984, 1985; Wiklund and Karlsson 1984; Fox 1993). These latter studies have generally examined larval growth and development in benign environments. In contrast, many of the studies that have demonstrated that egg size variation has implications for offspring performance examined larval growth and development under adverse conditions, such as during larval competition, periods of starvation, desiccation, or when larvae feed on low-quality resources (e.g., Solbreck et al. 1989; Carlberg 1991; Tauber et al. 1991; Sota and Mogi 1992; Braby 1994).

Here, we test the hypothesis that variation in egg size has implications for offspring growth and development only under adverse conditions by examining the consequences of egg size variation for survivorship and development of a seed-feeding insect, *Stator limbatus* (Horn) (Coleoptera: Bruchidae), on both a high-quality and a low-quality resource. *S. limbatus* is a generalist seed-beetle that uses more than 50 host plants throughout its large geographic range (northern South America to the southwestern United States; Johnson and Kingsolver

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1976; Johnson et al. 1989). In Arizona, *S. limbatus* uses primarily three host plants: *Acacia greggii* (Fabaceae: Mimosoideae), on which survivorship is high (>90% in all populations examined; Fox et al. 1994, 1995a) and development time short (Fox et al. 1994, 1995a); *Cercidium microphyllum* (Fabaceae: Caesalpinioideae), on which survivorship is also high ( $\approx 75\text{--}89\%$ ; Siemens et al. 1990; Fox et al. 1996a); and *C. floridum*, on which survivorship is very low (generally <50%) and development time is long (Siemens and Johnson 1992; Fox et al. 1994, 1995a). Previous research has indicated that *C. floridum*-associated populations of *S. limbatus* lay larger, and thus fewer, eggs than *A. greggii*-associated populations (Fox et al. 1995a). Although its sources are not yet known (e.g., genetic vs. environmental), this among-population egg-size variation suggests that selection favors large eggs on *C. floridum* (due to high mortality of small eggs) and small eggs on *A. greggii* (due to low mortality of small eggs and a substantial egg size/egg number trade-off; C. W. Fox, unpublished work).

We examine the consequences of egg size variation for larval survivorship, development time, and subsequent adult body weight in two populations of *S. limbatus* feeding on *A. greggii* and *C. floridum*. We find that egg size has no detectable effect on any life history character when larvae are reared on *A. greggii*, but has a large effect on survivorship of larvae reared on *C. floridum*.

## Methods

### Biology of *S. limbatus*

Like most species in the family Bruchidae, female *S. limbatus* oviposit directly onto seeds of their host plants, generally while fruits are still attached to the maternal plant. 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 host their mother has chosen for them. In the laboratory, mating and egg laying begin approximately 24–48 h post-emergence. Beetles require only a single seed to complete development and reproduce. Thus, neither food nor water supplementation of parents is necessary for the following laboratory experiments.

### Field collections of *S. limbatus*

Beetles for these experiments were collected from two localities in central Arizona. On 5–6 September 1993, beetles were collected from *C. floridum* along Scottsdale Highway, 2.7 km north of Bell Rd (behind the Scottsdale Well), in Scottsdale, Arizona. On 7 September 1993, beetles were collected from *A. greggii* in numerous locations throughout Black Canyon City, Arizona. These two populations are approximately 50 km apart, and differ in the host plants available to them. In Black Canyon City, *A. greggii* and *C. microphyllum* are the primary hosts for *S. limbatus*, although *C. floridum* is also present (though less common). In Scottsdale, *C. floridum* is the primary host for *S. limbatus*, although *C. microphyllum* is present (though uncommon). Further details on the ecology of these beetles and these populations can be found in Fox et al. (1994, 1995a).

Beetles and seed stock were both collected by picking mature seed pods from >25 *C. floridum* (Scottsdale) and >25 *A. greggii*

plants (Black Canyon City). Mature pods were transferred to the laboratory, and seeds containing beetles were separated from unfested 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 500–1000 field-collected individuals.

Before initiating the laboratory experiments, all beetles were reared in the laboratory for one generation at 26°C, 24 h light, on the host from which they were collected in the field. The two experiments were initiated within 1 month of each other.

### Experiment 1

Within each population, 60 virgin females were collected less than 24 h after emergence from the seed (total=120 females) and randomly paired with a virgin male from their own population. Half of these pairs were then confined in 30 mm petri dishes (1 pair per dish) with ten seeds of *A. greggii* (30 pairs from each population), and half with ten seeds of *C. floridum* (30 pairs from each population), and allowed to lay eggs. Dishes were checked at 12-h intervals, and all seeds bearing eggs were replaced with clean seeds. When females had laid >10 eggs on this initial host, they were transferred to the other host (from *A. greggii* to *C. floridum*, or from *C. floridum* to *A. greggii*). Again, dishes were checked at 12-h intervals, and all seeds bearing eggs were replaced until a female had laid >10 eggs on this second host.

All eggs were reared to adult at densities of one beetle per seed (additional eggs were scraped from each seed), 28°C, constant light. Development time (days), adult body weight (mg; within 12 h of emergence from the seed), and survivorship were recorded for all offspring. Development time was estimated as the time between egg-laying and adult emergence, and thus included both embryonic, larval, and pupal development time. To estimate body weight, emerging adults were weighed individually within 12 h of adult emergence on an electronic balance. Body weight is positively correlated with lifetime fecundity in both populations of *S. limbatus* (Fox et al. 1995b) and should thus correlate with fitness of the offspring.

Length and width of all eggs laid by parental females were measured at 50 $\times$  with a dissecting scope. There was some evidence that eggs laid by a female on the first host experienced were larger than eggs laid on the second host experienced (Wilcoxon signed-rank tests, significant for egg width, but not egg length, for Black Canyon City beetles, and significant for egg length, but not width, for Scottsdale beetles;  $P < 0.05$ ). Thus, separate mean egg sizes were calculated for a female's eggs on each host so that performance on *A. greggii* was compared to the mean size of the female's eggs laid on *A. greggii*, and performance on *C. floridum* was compared to the size of eggs laid on *C. floridum*. Because eggs are glued to seeds, removing them for weighing is generally destructive, and very time-consuming. Thus, mass was estimated for only a small sample of eggs ( $n=30$ ) to confirm that it was positively correlated with both egg length ( $r^2=0.88$ ) and egg width ( $r^2=0.61$ ).

For all statistical analyses, siblings were pooled to calculate the mean development time, body weight, and survivorship of progeny produced by each female. Only analyses for egg width are presented below, except when statistical analyses for egg width and length were qualitatively different.

### Experiment 2

This second experiment was identical to experiment 1 except that (1) females were presented with only *C. floridum* (no rotation of hosts was employed and *A. greggii* was not used in this experiment), and (2) beetles were reared in the laboratory for two generations before initiating the experiment. As above, results are presented for analyses of egg width only, except where results for egg length are qualitatively different.

**Table 1** The relationship between egg size (egg width) and progeny development time and adult body weight in two populations of *Stator limbatus* reared on two hosts (linear regression analyses of family mean performance on maternal egg size; SAS Institute

1985, proc GLM). Data are from experiment 1. The one significant analysis (marked with \*) is not significant following a Bonferroni multiple-comparisons correction (Rice 1989), *n*=number of families

	<i>Cercidium floridum</i>			<i>Acacia greggii</i>		
	<i>n</i>	Slope±SE	<i>r</i> <sup>2</sup>	<i>n</i>	Slope±SE	<i>r</i> <sup>2</sup>
<b>Black Canyon City Population</b>						
Body weight						
Males	34	-0.02±0.25	0.00ns	55	0.33±0.17	0.07ns
Females	35	-4.28±3.74	0.04ns	55	0.22±0.14	0.05ns
Development time						
Males	34	-0.14±1.46	0.00ns	55	-0.22±0.45	0.00ns
Females	34	-0.71±1.87	0.00ns	55	-0.71±0.32	0.09*
<b>Scottsdale Population</b>						
Body weight						
Males	36	0.08±0.28	0.00ns	52	0.45±0.25	0.06ns
Females	35	0.17±0.19	0.02ns	51	0.24±0.14	0.05ns
Development time						
Males	36	0.08±1.50	0.00ns	52	-0.46±0.50	0.02ns
Females	35	-1.40±1.14	0.04ns	51	-0.34±0.57	0.00ns

**Results**

There was no evidence in either population of a maternal egg size effect on progeny development time or body weight when larvae were reared on *A. greggii* (Table 1); there were no significant relationships between egg size and either development time or body weight following a Bonferroni multiple comparisons test (Rice 1989) to correct for multiple analyses (linear regression analyses of family mean development time or body weight against maternal egg size, *P*>0.05 for each). Similarly, egg size had at most a small effect on body weight and development time of progeny reared on *C. floridum*; there were no significant relationships between egg size and either progeny development time or body size in experiment 1 (Table 1), and only three of eight analyses were significant in experiment 2 (Table 2) and none were significant following a Bonferroni multiple-comparisons test to correct for multiple analyses.

There was also no evidence that egg size affected survivorship of larvae on *A. greggii* (Table 3). This is likely because most families had 100% survivorship on this host (Black Canyon City population, 45 of 57 families; Scottsdale population, 46 of 53 families), such that there was very little variation in survivorship, and thus no significant relationship between egg size and survivorship (*r*<sup>2</sup><0.06 for each analysis in each population). However, because data for survivorship on *A. greggii* do not satisfy the assumptions of the linear models, we analyzed these data in two additional ways. First, families were divided into two classes: those with survivorship of 100%, and those with survivorship less than 100%. Egg size was compared between the two classes. In this analysis, there was no evidence of an effect of egg size on survivorship (Mann-Whitney *U*-tests with 1 *df*, *P*>0.05). Second, the regression between egg size and survivorship was exam-

**Table 2** The relationship between egg size (egg width) and progeny development time and adult body weight in two populations of *S. limbatus* reared on *Cercidium floridum* (linear regression analyses of family mean performance on maternal egg size; SAS Institute 1985, proc GLM). Data are from experiment 2. None of the analyses are significant following a Bonferroni multiple-comparisons correction (Rice 1989); *n*=number of families

Population	<i>n</i>	Slope±SE	<i>r</i> <sup>2</sup>
<b>Black Canyon City Population</b>			
Body weight			
Males	138	0.40±0.17	0.04*
Females	136	0.26±0.15	0.02ns
Development time			
Males	138	-2.35±1.06	0.04*
Females	135	-0.85±1.05	0.01ns
<b>Scottsdale Population</b>			
Body weight			
Males	122	-0.01±0.13	0.00ns
Females	130	0.02±0.12	0.00ns
Development time			
Males	122	1.73±0.70	0.05*
Females	131	0.47±0.76	0.00ns

ined after all families with 100% survivorship were deleted from the data set. As before, there was no evidence for an effect of egg size on offspring survivorship (*y*=survivorship, *x*=egg size; *P*>0.05).

Although egg size had no detectable effect on survivorship when larvae were reared on *A. greggii*, it had a large effect on survivorship when larvae were reared on *C. floridum*; larvae developing from large eggs had higher overall survivorship, resulting from greater success entering a seed and higher survivorship after entering a seed (Tables 3 and 4; Fig. 1). Interestingly, the magnitude of this relationship differed between the two experiments; values of *r*<sup>2</sup> were >0.64 for both egg-to-adult sur-

**Table 3** The relationship between egg size (width) and progeny survivorship on *C. floridum* and *Acacia greggii* for two populations of *S. limbatus* (model: survivorship=constant + egg width; SAS Institute 1985, proc GLM). Analyses for egg length are similar (for all analyses:  $P < 0.001$  on *C. floridum* and  $P > 0.05$  on *A. greggii*). Males and females are lumped because early instars could not be sexed. Survivorship "entering seed" is the proportion

of offspring that survived until no body parts were protruding from the seed. Survivorship "within seed" is the survivorship of all larvae that successfully entered the seed (i.e., larvae that died entering the seed are not included in this estimate). All significant analyses are still significant following a Bonferroni multiple-comparisons correction (Rice 1989);  $n$ =number of families

	<i>Cercidium floridum</i>			<i>Acacia greggii</i>		
	<i>n</i>	Slope±SE	$r^2$	<i>n</i>	Slope±SE	$r^2$
<b>Black Canyon City Population</b>						
Egg-to-adult	57	0.97±0.09	0.67***	57	-0.03±0.07	0.00ns
Entering seed	57	1.02±0.10	0.64***	57	0.02±0.01	0.06ns
Within seed	46	0.73±0.17	0.30***	57	-0.05±0.07	0.01ns
<b>Scottsdale Population</b>						
Egg-to-adult	55	1.14±0.10	0.70***	53	-0.01±0.03	0.00ns
Entering seed	55	1.20±0.10	0.72***	53	-0.03±0.03	0.02ns
Within seed	46	0.59±0.16	0.23***	53	0.01±0.02	0.01ns

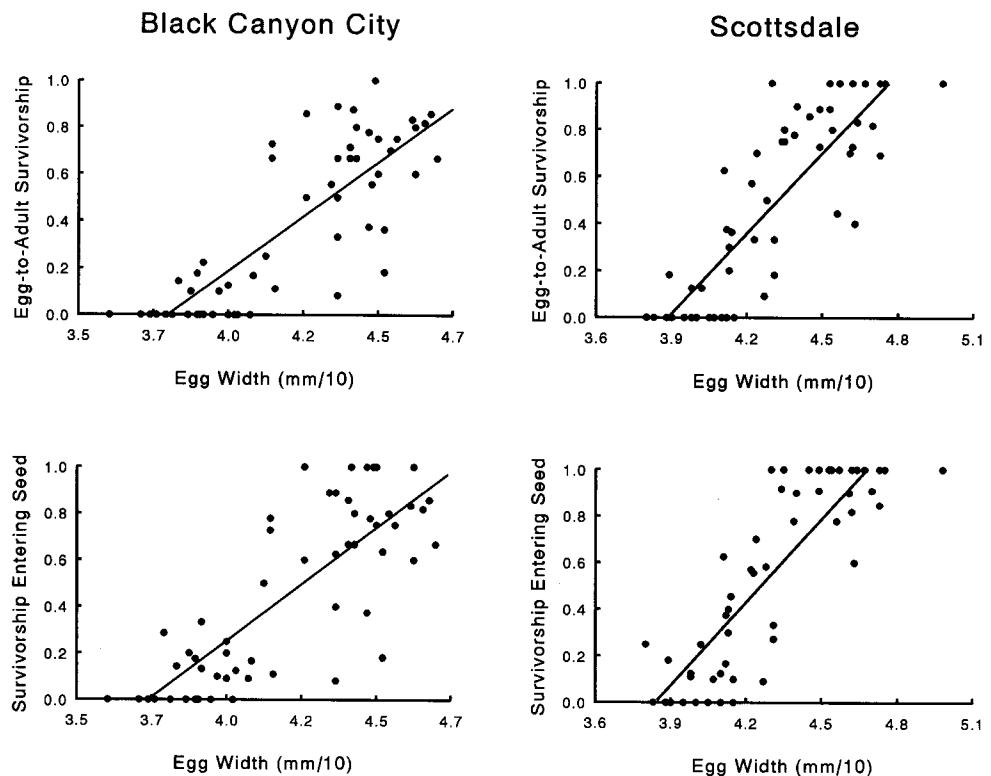
**Table 4** The relationship between egg size (egg width) and progeny survivorship for two populations of *S. limbatus* reared on *C. floridum*. Data are for experiment 2. Details as in Table 3. All significant analyses are still significant following a Bonferroni multiple comparisons correction;  $n$ =number of families

	<i>n</i>	Slope±SE	$r^2$
<b>Black Canyon City Population</b>			
Egg-to-adult	169	0.69±0.10	0.23***
Entering seed	169	0.78±0.09	0.29***
Within seed	159	0.17±0.10	0.02ns
<b>Scottsdale Population</b>			
Egg-to-adult	154	0.41±0.08	0.14***
Entering seed	154	0.43±0.08	0.16***
Within seed	146	0.08±0.08	0.00ns

and survivorship entering seeds (see Table 1 for definitions) in experiment 1, but were  $< 0.29$  for these same characters in experiment 2. Also, egg size had a detectable effect on survivorship within seeds in experiment 1 (Table 3) but not in experiment 2 (Table 4), despite the larger sample sizes in experiment 2.

Due to intense selection on egg size on *C. floridum*, but not on *A. greggii*, we expect *C. floridum*-associated populations to lay larger eggs than *A. greggii*-associated populations. Our data support this hypothesis; in both experiments females from the *C. floridum*-associated population laid larger eggs than females from the *A. greggii*-associated population (Fig. 2; Mann-Whitney  $U$ -tests,  $P < 0.05$  for each except egg length in experiment 2).

**Fig. 1** The relationship between egg size (egg width) and survivorship in two populations of *Stator limbatus* reared on *Cercidium floridum*. Data are for experiment 1. Statistics and details as in Table 3. Each data point represents a single family. Results for egg length versus survivorship are qualitatively identical





Whether the observed mortality patterns of *S. limbatus* on *C. floridum* are due to egg size variation, or due instead to mortality selection on some character correlated with egg size, selection for large eggs on this host is clearly intense, while selection for large eggs on *A. greggii* is undetectable in our experiment. However, if selection on egg size is intense in *C. floridum*-associated populations, why is there so much variation in egg size within populations? Instead, intense selection should reduce the amount of variation present. We propose three potential (and non-exclusive) explanations. First, the phenotypic variation in egg size within populations may not be heritable. We think this unlikely because egg size (Larsson and Forslund 1992; Mashiko 1992; Potti 1993) and quality (Rossiter et al. 1993) are heritable in other animals. Also, preliminary analyses from laboratory experiments demonstrate that egg size of *S. limbatus* is heritable in the laboratory (C. W. Fox, unpublished work). However, the heritability of egg size may be very low for *S. limbatus* in a natural environment due to large environmental effects on body size; egg size is positively correlated with both female and male body sizes (i.e., large females lay large eggs, and females mating with large males lay larger eggs than females mating with small males; Fox et al. 1995b). Larval density in seeds has a tremendous effect on body size of females (Siemens and Johnson 1992; Fox et al. 1996c). This variation in larval density among seeds can generate substantial phenotypic variation in body size, and subsequent variation in egg size, reducing egg size heritability and thus dampening a response to selection on egg size.

Second, the observed egg size variation within populations may be maintained by gene flow among host-associated populations. While intense selection favors large eggs when beetles oviposit on *C. floridum*, it likely favors small eggs on *A. greggii* (and likely on *C. microphyllum*, on which survivorship is also very high; Siemens and Johnson 1992) due to selection for high fecundity and a substantial egg size/egg number trade-off (Fox et al. 1996b). However, gene flow among host-associated populations may prevent the fixation of large-egg alleles in Scottsdale and small-egg alleles in Black Canyon City. As observed here, and also in Fox et al. (1995b), Black Canyon City females lay smaller eggs than Scottsdale females, consistent with the hypothesis of variation in selection intensity (and possibly direction) among populations. However, the extent of gene flow among host-associated populations, and thus the amount of genetic variation entering each population each generation, is unknown.

Third, temporal and spatial variation in host quality may contribute to maintaining variability in egg size. For example, while advantages to developing from large eggs were undetectable on *A. greggii* in our laboratory experiment, our experiment may underestimate the actual advantage to developing from a large egg when larval competition is uncontrolled; larvae were reared at densities of one beetle per seed in the laboratory, but often occur at much higher densities in nature (Mitchell 1977; Sie-

mens and Johnson 1992). If larvae developing from large eggs have an advantage at high densities (e.g., they can more rapidly assimilate the limited resources available inside a seed), then size selection may vary spatially, with larger eggs favored when multiple larvae compete inside a seed, and smaller eggs favored when few larvae compete inside a seed (due to an egg-size/egg-number trade-off). Also, while the two populations examined in these experiments overlap little in the host plants available to them, many populations of *S. limbatus* have multiple hosts available simultaneously, including both *A. greggii* and *C. floridum*. In these populations, selection would alternately favor large eggs on *C. floridum* and small eggs on *A. greggii*. Thus, we may expect these populations to demonstrate more variability in egg size than single-host populations.

Although egg size had a large effect on survivorship of larvae when they were reared on *C. floridum*, the magnitude of this relationship differed between the two experiments; values of  $r^2$  were  $>0.64$  for both egg-to-adult survivorship and survivorship entering the seed in experiment 1, but were  $<0.29$  for these same characters in experiment 2 (see Table 3 for definitions of the categories of survivorship), and egg size had a detectable effect on survivorship within seeds in experiment 1 but not in experiment 2, despite the larger sample sizes in experiment 2. Also, eggs laid in experiment 2 were generally larger than eggs laid in experiment 1, indicating that some factor affecting egg size, whether genetic or environmental, varied among experiments. Although the explanation for this difference in  $r^2$  between experiments and the general increase in egg size between experiments are unknown, they may represent rapid adaptation to laboratory conditions. Alternatively, they may represent a shift in environmental effects in experiment 2, due to an additional generation of rearing in a controlled environment. However, there was no evidence that the variance in egg size was lower in experiment 2, suggesting that environmental effects on egg size, if different in source, were similar in magnitude.

In summary, the results of this study indicate that egg size can influence offspring performance on a low-quality resource (an adverse environment), but has no effect on offspring performance on a high-quality resource (a benign environment). In a simple environment where only high- or low-quality hosts are available, local adaptation to the predominant host species is predicted. Our data presented here and elsewhere (Fox et al. 1994, 1995b) suggest that local adaptation to different hosts has occurred in *S. limbatus* where one or a few hosts are predominant. However, in a heterogeneous environment in which both high- and low-quality hosts occur at high frequency, and poor hosts cannot be excluded from the diet (possibly due to phenological variation among hosts), the evolution of phenotypic plasticity, in which females lay large eggs on poor hosts and small eggs on good hosts, is expected. Such maternally mediated plasticity has been reported for many traits in insects (Mousseau and Dingle 1991a,b) and may be very common in species subject to

selection in heterogeneous environments. Presently, we are conducting experiments examining adaptive phenotypic plasticity in egg size to determine the extent to which *S. limbatus* females actively mediate egg size in response to host quality (Fox et al. 1996a).

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