



# Individual Variation in Trophic Egg Production: Evidence for Maternal Manipulation in Response to Resource and Competition Levels

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## Abstract

Females of the subsocial shield bug *Parastrachia japonensis* (Heteroptera: Parastrachiidae) incorporate trophic eggs (nutritive eggs) into their egg mass. Considerable variation occurs among females in trophic egg number and the proportion of an egg mass that is composed of trophic eggs. Because trophic eggs are essential to the development and survival of young, this variation could significantly impact female fitness. We tested the hypothesis that trophic egg abundance is induced by maternal phenotype (weight, body size) and resource exposure. We predicted that resource limitations would cause females to produce fewer fertile eggs and more trophic eggs and that larger and heavier females would produce more of each egg type. Females ovipositing early in the season are exposed to different resource conditions than those that oviposit late. Thus, we compared egg production patterns between these two groups and several other factors related to nesting. No correlation was seen between body size and trophic egg abundance, or, indeed, egg production, overall; however, heavier females produced heavier egg masses. Counter to our prediction, late females, which had greater access to food, produced significantly more total eggs, fewer fertile eggs, and more trophic eggs than early females. A binomial generalized linear model analysis indicated that the factors most correlated with the percentage of an egg mass destined to become trophic eggs were resource abundance, resulting from early or late oviposition, and distance of the nest from the host tree, with closer females producing more trophic eggs. The findings support our hypothesis that resource availability and, to a lesser extent, maternal phenotype affect trophic egg abundance.

## Introduction

Phenotypic plasticity describes the phenomenon whereby a single genotype exhibits a range of phenotypes in response to variation in the environment (Bradshaw 1965; Fordyce 2006; Whitman & Agrawal 2009). Virtually any trait can be phenotypically plastic. Phenotypic plasticity allows organisms to respond to environmental fluctuations experienced

over evolutionary time, and they may be responsive or anticipatory (see Whitman & Agrawal 2009; for a comprehensive review). Adaptive individual variation, whether solely genetic or phenotypically plastic, may be maintained within a population and so have important evolutionary implications (Clutton-Brock 1991; Budaev et al. 1999).

Maternal effects represent a specific type of adaptive phenotypic plasticity that is induced by genetic

and environmental factors and can manifest when the maternal generation experiences environmental (external or internal) conditions that affect the phenotype of the offspring (Mousseau & Dingle 1991a,b; Mousseau & Fox 1998; Wolff & Wade 2009). Females can use information about ecological conditions that they experience, including resource abundance and competition level, to manipulate allocation of resources to eggs in such a way that would allow offspring to best respond to the conditions in which they will develop.

Resource type and abundance are of prime importance in predicting offspring success, but a more subtle factor that contributes to offspring success manifests when reproduction within a population does not occur synchronously; individuals hatching later will have to compete with older, earlier-hatching nymphs for the food resource, because older nymphs will be more experienced and efficient feeders. Thus, the level of competition with siblings and with other individuals that offspring will experience is a considerable constraint on the development of young and one that a mother could assess and utilize in determining brood size, and egg size (Mock & Parker 1997; Creighton 2005).

In the semelparous subsocial shield bug, *Parastrachia japonensis* Scott (Heteroptera: Parastrachiidae), there is yet another variable that might be manipulated by mothers in response to these constraints. Females engage in a variety of parental care behaviors, including guarding of eggs and nymphs and progressively provisioning offspring with drupes of the host tree. These behaviors enhance offspring success considerably (Tsukamoto & Tojo 1992; Filippi-Tsukamoto et al. 1995; Filippi et al. 2000a). In addition, females incorporate trophic eggs into their single egg mass (Hironaka et al. 2005). Trophic eggs are non-viable eggs that serve as food for developing nymphs. Production of trophic eggs allows parents to provision young using an extreme version of the 'food cache' strategy (Alexander 1974; Polis 1981, 1984; Mock & Parker 1997). It is seen across an array of animal taxa, including anurans, arthropods, and gastropods (Wilson 1975; Polis 1981; Baur 1992; Kim & Horel 1998; Heying 2001; Perry & Roitberg 2005; Ento et al. 2008). Several species in the Heteroptera have recently been shown to produce trophic eggs, which enhance offspring survival considerably (Nakahira 1994; Hironaka et al. 2005; Filippi et al. 2008; Baba et al. 2010; Mukai et al. 2010). In systems where trophic eggs are produced, fertile and trophic egg numbers and their ratios within a given egg mass are potential sources for manipulation by females, as

well. In particular, when environments experience temporal or spatial heterogeneity in resource abundance, natural selection would be expected to favor adaptive plasticity in egg phenotype and ratio of egg types as a maternal effect that would allow offspring to optimize the resource conditions they are born into (Filippi & Seger 1989; Kaplan 1991; Kudo & Nakahira 2004, 2005).

Mating in the provisioning subsocial shield bug, *P. japonensis* occurs over a 10–14-d period from late April to mid-May at our field site in Saga, Japan (33°20'N, 130°22'E). *Parastrachia japonensis* is a strictly specialized feeder and is further constrained by obligate semelparity (Nomakuchi et al. 2001). The reproductive period of the insect is precisely coordinated with the host tree's (*Schoepfia jasminodora*; Olacaceae: Rosidae: Santales) phenology (Tsukamoto & Tojo 1992). Specifically, in mid-May, inseminated females move to a nearby host tree, where they sequentially feed on the small amount of endosperm formed in as yet tiny and immature green drupes (Filippi et al. 2000b). Eggs develop in the ovarioles as females feed over an approximately 10-d period. Females oviposit a round, cohesive egg mass comprising 60–220 eggs in shallow burrows under the leaf litter from late May through mid-June. After hatching, the females make repeated foraging trips to the host tree, dragging high-quality drupes back to the nest to feed the aggregated nymphs (Tsukamoto & Tojo 1992; Nomakuchi et al. 1998). This progressive provisioning is essential to the development and survival of young nymphs (Filippi-Tsukamoto et al. 1995; Filippi et al. 2000a). However, good drupes are ephemeral and scarce, and females often do not find a suitable drupe for one or 2 d after hatch (Filippi-Tsukamoto et al. 1995; Filippi et al. 2002). Apparently to counter the very real risk of starvation and cannibalism, females incorporate trophic eggs into the egg mass (Hironaka et al. 2005). Offspring feed on these eggs during the first instar (Hironaka et al. 2005). In an earlier study, we found that nymphs deprived of trophic eggs were significantly less successful in terms of body weight, survival, and developmental rates than those allowed to feed on them, thus access to trophic eggs is essential (Hironaka et al. 2005).

An interesting finding of the earlier study was the considerable variation among females in the number and percentage of trophic eggs produced. Among 51 egg masses containing 60–220 total eggs (average  $\pm$  SD,  $130.5 \pm 36.2$ ), between 10 and 80% (average  $33.5 \pm 11.9$ ) were trophic eggs (Hironaka et al. 2005). This variation could impact the success of off-

spring and female fitness. An earlier study (Filippi et al. 2002) demonstrated that females showed plasticity in nesting behavior, apparently assessing environmental conditions before deciding how close to the host tree they will nest. The authors concluded that risk-sensitive decision-making allows females to optimize provisioning behavior. In the present study, we investigated how plasticity with regard to female allocation of resources to fertile and trophic eggs during egg production might be regulated. We tested the hypothesis that the abundance of trophic eggs in an egg mass is a maternal effect induced by maternal phenotype (body size) and environmental experience (resource abundance). Because drupes gradually mature over the course of the reproductive season, resource abundance increases as the season progresses. We predicted that fertile eggs would decrease and trophic eggs would increase with lower actual levels of resource availability and that both fertile and trophic egg production would increase with large body size and mass. As additional potential factors affecting trophic egg production via their impact on resource availability, we also measured the following conditions of nesting females: temporal conditions, specifically early or late oviposition because the respective females would be exposed to different resource levels. We predicted that earlier females would produce more trophic eggs to compensate for the lower resource level. Spatial conditions with regard to distance from the host tree were assessed because resource is less abundant further from the crown, but competition with, and interference in the nest from, other provisioning females is also less. We predicted that closer females would produce fewer trophic eggs because they and their offspring would be located in high resource abundance areas. Finally, physiological state as indicated by weight just prior to hatch was measured, because weight reflects the physiological resources that can be allocated to egg production and provisioning behavior. We predicted that heavier females should produce more of both types of eggs.

## Materials and Methods

On May 27, 2005, at our field site at Hinokuma Mt. in Kanzaki Town, Saga Prefecture, Japan, we began looking for pregnant females with distended abdomens, indicating imminent oviposition, that were walking on the ground searching for a nest site. Females were mass marked using one or two marks on the dorsum (pronotum and elytra) made with automobile paint markers (Mitsubishi; Tokyo,

Japan). We used three different colors to mass mark females according to the timing of their nest-searching behavior. We found no females on May 27, one on May 28, and seven on May 29. The numbers increased dramatically until May 31. On May 30 and May 31, 26, and 30 females were found, respectively. The 63 females found from May 29, 30, and 31 were mass marked as 'early' females. From June 1 through 3, the numbers of females searching for nests dropped dramatically to just five. Although we considered the females from June 1 to 3 were 'middle' females, and marked them as such, because we were not confident that these females were not in fact 'early' females that had been roaming around for a few days unable to find a nest, females that we had failed to mark earlier, we did not use them for any further study. The mark was to exclude them from the early and late groups. Numbers picked up again on June 4, so we were confident that these were new, late females; numbers remained fairly steady, although lower than for the early group, at 12, 15, and 17 on June 4, 5, and 6, respectively. No females were found on June 7, and only two were found and marked on June 8 as two additional late females. Thus, a total of 46 females were mass marked as 'late' females. All 63 females marked as 'early' females were thus considered to have finished feeding during the 3 d of May 29, 30, and 31, and 44 of 46 of the females marked as 'late' were considered to have finished feeding during the 3 d of June 4, 5, and 6; two finished feeding on or about the June 8. All marked females were left in the field to establish a nest and oviposit under natural conditions.

On June 10, after most females had been nesting for at least a week, we searched over a  $15 \times 15$  m area of the nesting ground and collected marked and unmarked early and late females guarding an egg mass in a nest. We excluded 'middle' marked females, because of the uncertainty expressed earlier. To minimize the number of confounding variables, we took care to search for females in an area where we anticipated they were all using the same host tree. This factor, along with natural mortality and failure to find many of the marked females' nests, resulted in a far smaller number of females actually being recovered: 13 early and 12 late nesting females were collected. The distance from the host tree to each nest was recorded. Females, together with their egg masses, were carefully placed into individual clear plastic containers with clear perforated (for air exchange) lids (8-cm diameter, 4-cm height) containing 2 cm of dirt collected from the nesting area

and a few dry leaves. The containers were transferred to an incubator in the laboratory where they were maintained at 25°C under a photoregime of 16L/8D and sprayed every other day with distilled water to maintain moisture. The condition of each egg mass was inspected daily. In addition, we left a portion of the egg-guarding females marked according to each nesting group (early, middle, and late) in their nests in the field. The nests were enclosed in sturdy 2-mm-thick opaque plastic cylinders (height, 15 cm; diameter, 10 cm) to protect them from predation, so that we could compare hatch dates in the field with observations in the laboratory. The condition of these egg masses was also inspected daily. The hatch dates of the eggs left in the field coincided with the predicted hatch dates of the respective groups of eggs brought into the laboratory (data not shown).

Eggs have been recorded to hatch  $13.31 \pm 1.25$  d after oviposition in the field (Filippi et al. 2005), but the duration of this period is very temperature sensitive. The day prior to hatch, fertile eggs turn a deep pink, and the eyespots are clearly visible. This day occurred after a somewhat longer period in 2005 than in the earlier documented years, perhaps because of cooler temperatures that year and also because females may not have oviposited on the dates that we saw them as pregnant females searching for nests. It is possible that they found a nest and remained in it for a day or two before actually ovipositing. At any rate, based on the color of the eggs and the clarity of the eyespots on the eggs of the collected, incubating females (not the date they were first seen in the field), the estimated dates of hatch of early females (as determined by the color of their marking) were from 14 to 16 June, which would have been about 16–18 d after the pregnant mothers were first seen in the field; marked and unmarked females that fit into this expectation were assigned to the early female group. Similarly, marked and unmarked females with estimated dates of hatch from 19 to 22 June were assigned to the late group.

One day prior to the date of estimated hatch, the weight (g) and pronotum width (mm) of the female, weight of the egg mass, and numbers of fertilized and trophic eggs in each mass were determined. Means were calculated for early and late group data.

### Statistical Analyses

An unpaired two-tailed Student's *t*-test was used to determine the significance of the differences between the means of the two groups. To determine

the impact of the different factors on the percentage of trophic eggs produced, data were analyzed by performing a binomial generalized linear model (GLM) analysis using the free software R 2.10.1 (R Development Core Team). The ratio of trophic eggs/total eggs was used as the response variable, and timing of oviposition, distance of the nest from the host tree, and female weight were used as the explanatory variables. To determine whether the data for the percentage of trophic eggs followed a normal distribution, data were arcsine transformed and applied to a Kolmogorov–Smirnov test for normality. An *F* test was used to test for the difference in variance among the percentage of trophic eggs produced in an egg mass between early and late females.

### Results

Table 1 presents the data for the different variables measured for early and late nesting females. In 2005, there were significant differences between early and late females for all variables except pronotum width (body size). The nests of earlier females were, on average, significantly farther away from the host tree than those of later females, but distances in both groups had similarly wide ranges (2.5–12.1 m for early females; 3.1–12.7 m for late females). Despite the finding that there was no difference in body size between the two groups of females, late females were significantly heavier just prior to hatch than early females. In addition, the egg masses of late females were significantly heavier than those of early females, although early females had significantly more fertile eggs than late females. The additional weight is consistent with the fact that late females had significantly more trophic eggs, both in terms of absolute numbers and percentage of the egg mass that consisted of trophic eggs. There was no difference in the weight per egg between early and late females.

There was no significant correlation between body size as measured by pronotum width and number of eggs of any type for either group (not shown), although for late females there was a tendency for larger females to produce more fertile eggs ( $r = 0.54$ ;  $t = 2.03$ ;  $p = 0.07$ ). For both early and late females, there was a positive correlation between female weight just prior to hatch and egg mass weight (Fig. 1a), but interestingly, only the late females showed a positive correlation between female weight just prior to hatch and fertile egg number (Fig. 1b). The significance of the findings for late females is clearly driven in part by the

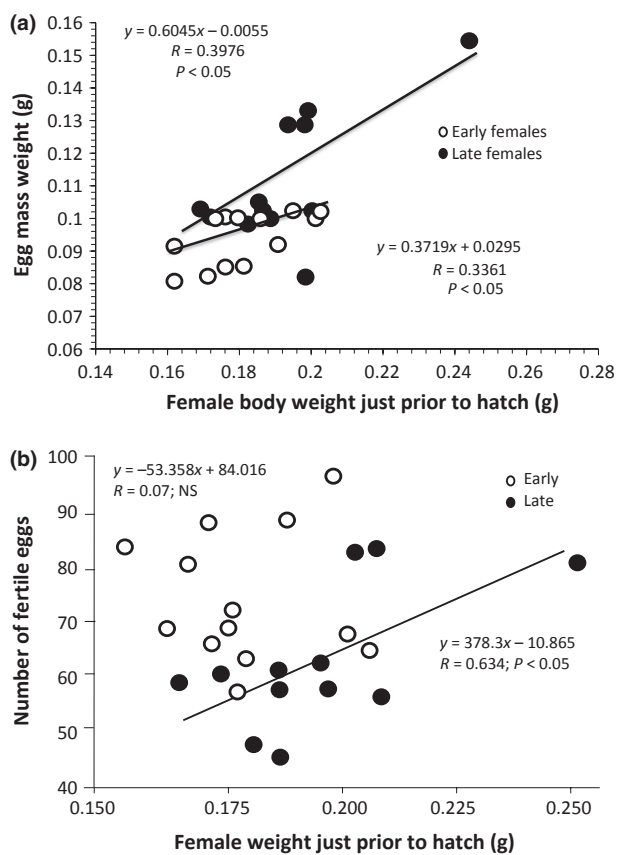
**Table 1:** Nest, female and egg conditions for early and late females

Timing of oviposition	Distance from host tree (m)	Female PNW (mm)	<sup>a</sup> Female BWT. (g)	Egg mass weight (g)	Individual egg weight (g)	No. total eggs	No. fertilized eggs	No. trophic eggs	% Trophic eggs
Early (n = 13)	8.70 ± 2.87	7.43 ± 0.19	0.18 ± 0.02	0.09 ± 0.01	8.4 × 10 <sup>-4</sup> ± 5.59 × 10 <sup>-5</sup>	113.62 ± 12.37	74.54 ± 12.14	39.08 ± 13.38	34.08 ± 10.43
Late (n = 12)	6.35 ± 2.73	7.36 ± 0.29	0.19 ± 0.02	0.11 ± 0.02	8.8 × 10 <sup>-4</sup> ± 9.75 × 10 <sup>-5</sup>	126.92 ± 16.51	62.75 ± 13.09	64.17 ± 8.75	50.79 ± 5.89
t =	2.16	0.77	2.32	2.56	1.26	2.29	2.23	5.5	4.87
p =	0.04	0.45	0.04	0.02	0.22	0.03	0.03	0.0001	0.0001

Data are presented as means ± SD.

PNW, pronotum width.

<sup>a</sup>Female weight just prior to hatch.



**Fig. 1:** Correlations between female weight just prior to hatch and egg abundance for early and late females. (a) Total egg mass; (b) fertile eggs.

outlier heaviest female to the right of Figs 1a and b, and when we performed the Pearson correlation analyses without this female, the results were not significant. Determining whether these correlations are real or not will require a larger sample size. There was a tendency for early females to show a negative correlation between weight just prior to hatch and percent trophic eggs, and late females to

show a positive correlation for this relationship, but neither of these correlations was statistically significant (not shown).

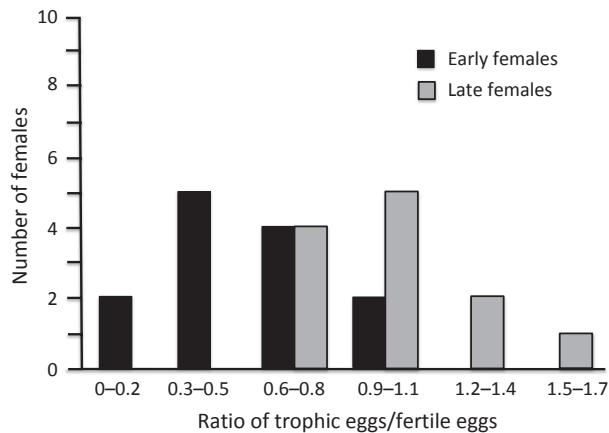
To determine whether the data for the percentage of trophic eggs followed a normal distribution, data were arcsine transformed and applied to a Kolmogorov–Smirnov test for normality. Normality was not rejected ( $p > 0.1$ ). There tended to be a larger variation in the number of trophic eggs produced by early females compared to late females, but an  $F$  test for variance indicated no significant difference ( $F = 3.14$ ;  $p = 0.068$ ). Figure 2 shows a frequency distribution for the rate of trophic eggs produced per fertile egg for early and late females. It is clear that most late females produced about one trophic egg per fertile egg (average ± SD,  $1.06 \pm 0.27$ ) and nearly half produced more than one trophic egg per fertile egg. Among the early females, however, only one produced close to one trophic egg per fertile egg, and nearly 50% of females produced less than half a trophic egg per fertile egg (average ± SD,  $0.55 \pm 0.24$ ).

Table 2 shows the results of the binomial GLM analysis. The factors that had the greatest impact on the percentage of an egg mass destined to be trophic eggs were the timing of oviposition (early females produced a higher percentage of trophic eggs than late females) and the distance of the nest from the foraging area: closer nests had a greater percentage of trophic eggs.

## Discussion

The abundance of trophic eggs in an egg mass was clearly correlated with the timing of oviposition. Late ovipositing females produced significantly greater numbers and a greater percentage of trophic eggs relative to the total egg mass. Moreover, Table 1 shows that there were significantly different values between





**Fig. 2:** Frequency distribution showing rate of trophic eggs produced per fertile egg for early and late females.

**Table 2:** Coefficient table of binomial GLM for analysis of percentage trophic eggs

Coefficients	Estimate	SE	Z value	p-value
Intercept	-0.37288	0.38439	-0.970	0.332
Early/late oviposition	0.57169	0.08702	6.570	0.0000
<sup>a</sup> Distance	-0.05775	0.01403	-4.116	0.0000
<sup>b</sup> Female wt.	-1.95321	1.95897	-0.997	0.319

<sup>a</sup>Distance (m) of nest from host tree.

<sup>b</sup>Weight (g) of females just prior to egg hatch.

GLM, generalized linear model.

early and late females for each of the parameters examined except pronotum width, for example, body size, and individual egg weight. Early ovipositing females nested farther from the foraging area than late ovipositing females. Nesting closer to the host tree, that is, within the foraging area under the crown of the host tree, where the drupes fall, represents a risk-sensitive behavior that occurs more frequently when drupes are particularly scarce, and with late females (Filippi-Tsukamoto et al. 1995; Filippi et al. 2002). The risk derives from the lack of leaf litter under the crown of the host tree, which leaves nests vulnerable to inclement weather conditions, predation, and thievery by other foraging females, which are in particularly high density there (Filippi et al. 2005). In the present study, late females nested significantly closer to the foraging area, despite these constraints. It is likely that the best nesting sites were saturated with early females by the time late females began searching for their nest sites. The correlation between distance of the nest from the host tree and the percentage of trophic eggs revealed in the binomial GLM analysis suggests that mothers closer to the foraging area produced a greater propor-

tion of trophic eggs in response to the intense competition their offspring would be exposed to with other foraging females and earlier hatched, older nymphs.

Late females were significantly heavier just prior to hatch than early females. Later in the season, drupe availability for provisioning females and independent young should decrease because of prior provisioning activity by early provisioning females and feeding by their independent offspring. The time required for a provisioning female to find an acceptable drupe (>75% endosperm; Nomakuchi et al. 2001) should increase as resource abundance decreases. The additional weight found in late females would support a greater investment in provisioning activity after hatch.

Late females had significantly higher total egg clutch mass, fewer fertile eggs, and greater absolute numbers and percentage of trophic eggs than early females. Our results suggest that trophic eggs are more important to the success of late nesting females' offspring. When resource conditions over a reproductive season vary in a predictable way, natural selection should favor the evolution of adaptively plastic traits in the mother that would allow her to produce offspring best suited to the environment into which they will hatch (Mousseau & Dingle 1991a,b; Whitman & Agrawal 2009). Early females, at least under the field conditions experienced in 2005, allocated more resources to fertile eggs, while late females allocated much more resources to trophic eggs. It is likely that, even with the lower fecundity, the later females optimize reproductive success with increased trophic eggs. We suspect that early females make more fertile eggs than late females because their offspring will experience less competition for drupes upon hatch, and female provisioning capacity will be greater, so greater numbers of offspring will likely survive. Late females probably produce fewer viable eggs and invest more resources into trophic eggs to compensate for the anticipated poorer provisioning capacity because of lower resource availability.

An interesting finding was the much larger degree of variation in the percentage of trophic eggs produced by early females compared to late females (Table 1; ~33% of the average vs. 10% of the average, respectively), although the difference in variation was not significant at this sample size. As shown in Fig. 2, most late females produced nearly enough trophic eggs for each hatchling to have one entire egg to feed on, and some produced quite a bit more. On the other hand, early females produced on average only half a trophic egg per fertile egg. In

contrast, the degree of variation among fertile egg production did not show this great disparity between groups (~16% of the average vs. ~21% of the average, respectively). One of the constraints limiting offspring number in animals that progressively provision nests is the physiological limitation to provisioning capacity (Lack 1947; Monaghan & Nager 1997). This species is obligatively semelparous, and so lifetime reproductive success is equivalent to the success of the one brood. It seems likely that the number of fertile eggs produced by early females reflects the maximum amount that a female can successfully provision in her lifetime, and any additional resources the female was able to acquire during feeding to produce eggs were allocated to trophic eggs. Moreover, while early and late females alike showed a tendency toward a positive correlation between body weight and total egg number, only late females tended to show a positive correlation between body weight and the number of fertile eggs produced (Fig. 1b). It seems the late females obligatively produced sufficient numbers of trophic eggs to sustain their young in the intensely competitive environment, but apparently also facultatively produced more fertile eggs when their nutrition status allowed it. A similar phenomenon of obligate trophic egg provisioning was reported for the poison frog, *Dendrobates ventrimaculatus* (Poelman & Dicke 2007).

The evidence supports our hypothesis that the resource experience of the mother during feeding to produce eggs determines the proportion of the egg mass that will be allocated to trophic eggs. Much of the provisioning season coincides with consistent weather of the rainy season. The major ecological differences that females experience during this brief time are the quality of the drupes on the host tree and the level of competition, supporting the hypothesis that resource experience induces the maternal effect of trophic egg abundance. Adaptive plasticity would allow females to produce more or fewer trophic eggs as needed. The fact that early females showed no correlation between body size and fertile egg production suggests that their limitation in fertile egg number is based on provisioning capacity, which is likely to be constrained by fat body stores, not body size. When late females had sufficient resources (fat body stores indicated by mass) to produce additional fertile eggs, they apparently did. Future studies will examine the cues that females might be using to anticipate the resource availability their young will be exposed to. We also plan to: (1) induce variation in trophic egg production by manipulating

resource abundance in feeding females; and (2) assess offspring success as a function of trophic egg abundance.

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