Journal of Insect Behavior, Vol. 15, No. 3, May 2002 (© 2002)

Parental Body Mass as a Determinant of Egg Size and Egg Output in an Arctiid Moth (*Utetheisa ornatrix*)

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Accepted January 10, 2002; revised January 31, 2002

Females of the moth Utetheisa ornatrix *(family Arctiidae) mate preferentially with larger males. As a consequence, females have larger sons and daughters, which have been shown to be more acceptable in courtship and more fecund, respectively. We demonstrate that mating with larger males results in accelerated oviposition by the female on the day after mating and that females are intrinsically prone to lay larger eggs in the first days after mating. Both these additional size-dependent effects have potential adaptive consequences.*

KEY WORDS: spermatophore; fecundity; parental investment; Arctiidae; pyrrolizidine alkaloid.

INTRODUCTION

In the arctiid moth, *Utetheisa ornatrix* (henceforth referred to as *Utetheisa*), fitness finds expression in large body size: larger males are more successful in courtship (Conner *et al*., 1990), and larger females are more fecund (LaMunyon, 1997). Body size is a heritable trait in *Utetheisa* (Iyengar and Eisner, 1999a), and females mate selectively with larger males (Iyengar *et al*., 2001). By so choosing, females are able to beget sons and daughters that are larger and, therefore, themselves more fit (Iyengar and Eisner, 1999b). Here we report that there are additional correlates to largeness in *Utetheisa*. Body size correlates positively with egg size in the female, and in the male, it correlates positively with his mate's postcoital egg output. Both effects are subject

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to some constraints, but they are of sufficient magnitude to be potentially adaptive. Our purpose here is to report on these additional correlates, which are best viewed in the context of what is known so far about the reproductive strategy of *Utetheisa*.

In *Utetheisa*, reproduction and defense are inextricably linked, and both relate to one central event in the life of the moth—the acquisition of pyrrolizidine alkaloids (henceforth referred to as alkaloids). *Utetheisa* procure these alkaloids as larvae from their foodplants [legumes of the genus *Crotalaria* (family Fabaceae)]. They retain the compounds systemically through metamorphosis, with the result that larvae and adults are protected against predation (Eisner and Meinwald, 1987, 1995). The eggs receive some of the alkaloid as well, and they too are consequently protected (Dussourd *et al*., 1988; Hare and Eisner, 1993). The alkaloid bestowed upon the eggs stems from both parents. Males transmit alkaloid to the females with the spermatophore at mating, and females transfer part of this gift, together with a fraction of their own alkaloid, to the eggs (Dussourd *et al*., 1988).

Males proclaim the magnitude of their alkaloidal gift by means of a pheromone that they emit during courtship (Conner *et al*., 1981). The pheromone (hydroxydanaidal), which the males air by way of two eversible brush-like organs (the coremata), is a chemical derivative of the alkaloid, produced by the male in proportion to his alkaloid content (Dussourd *et al*., 1991). The female assesses the message conveyed by the pheromone. She mates preferentially with males of high pheromone titer (Conner *et al*., 1981; Iyengar *et al*., 2001), thereby assuring that she receives alkaloidal gifts of larger magnitude (Dussourd *et al*., 1991). She also ensures that she receives genes for large size (lyengar and Eisner, 1999a), since male alkaloid content correlates positively with male body mass in *Utetheisa* (Conner *et al*., 1990). By exercising mate choice on the basis of hydroxydanaidal content, females therefore are guaranteed to receive both phenotypic and genetic benefits. The phenotypic benefits extend beyond the receipt of alkaloid. Males also bestow nutrient with the spermatophore, a commodity that the female invests, in part at least, in egg production. Females mate on average with four to five males over their life span of 2 to 3 weeks (Pease, 1968) and are able to increase their fecundity by 15% with each of the first three matings (LaMunyon, 1997). As expected, males invest heavily in spermatophore production: on average, at mating, a male transfers upward of 10% of his body mass to the female (LaMunyon and Eisner, 1994).

We look here into whether the body mass or diet of the parents affects egg mass or fecundity and whether egg mass correlates with either egg fitness or larval fitness. Specifically, we examined for the effects of (i) parental diet (alkaloid-free vs alkaloid-laden) on egg mass and egg output, (ii) parental body mass and spermatophore mass on egg mass, (iii) parental diet and egg

mass on egg fitness (viability, egg stage duration, larval mass at hatching), (iv) egg mass on larval fitness (survivorship, duration of larval development, pupal mass), and (v) spermatophore mass on egg output and egg viability.

MATERIALS AND METHODS

Utetheisa. All *Utetheisa* were reared in the laboratory (16L:8D photoperiod), from stock originally collected in Lake Placid, Highlands County, FL.

Larval Diets. These were of two types (Conner *et al.*, 1981): one based on pinto beans and lacking alkaloid [(−) diet]; the other [(+) diet] also based on pinto beans but containing a supplement of seeds of *Crotalaria spectabilis*, a major foodplant of *Utetheisa*. *Utetheisa* reared on (+) diet [(+) *Utetheisa*] contain the principal alkaloid in *C. spectabilis*, monocrotaline, at a level [628 ± 48 μg (SE) per adult] (Bogner and Eisner, 1992) commensurate with that of alkaloid in *Utetheisa* reared on *C. spectabilis* plants [701 ± 59 μg (SE) per adult] (Conner *et al.*, 1990). *Utetheisa* reared on (−) diet [(−) *Utetheisa*] contain no detectable alkaloid (Conner *et al.*, 1981).

Body Size Criteria. Adults were judged to be "size matched" if they differed by less than 5 mg in body mass. They were judged to be "different sized" if they differed by at least 20 mg (about 10%) in body mass. In males, a difference of 20 mg ensured that the individuals transferred spermatophores of different sizes to females.

Matings. Virgin males and females, both 3 days old and of known body mass, were confined in pairs for 24 h in small, humidified, cylindrical plastic containers (0.35 L). Pairs were monitored at 6-h intervals to check on mating success [copulation lasts 10–12 h in *Utetheisa* (LaMunyon and Eisner, 1994)]. After 24 h, mated males were weighed and euthanized, while mated females were weighed and placed in separate containers lined with wax paper, upon which they readily oviposited.

Spermatophore Mass. This parameter was assessed indirectly, by taking the average of the male's weight loss and the female's weight gain during the mating period [both weights were corrected for spontaneous (daily) mass loss (LaMunyon and Eisner, 1994)]. Spermatophore mass was measured for all matings.

Egg counts and Egg Mass. Numbers of eggs laid were determined by direct counts of the eggs visible on the wax paper linings of the oviposition containers. Egg mass is defined herein as the average egg mass, which was calculated by weighing groups of eggs on their paper backing, subtracting the weight of the paper, and dividing by the total number of eggs. Weighed eggs were not themselves used for determination of other parameters since we knew from experience that removal from the wax paper affects egg viability.

Experiment 1: Effect of Parental Diet on Egg Mass and Egg Output. Twenty randomly selected (+) males were each mated to a randomly selected (+) female. During the first 4 days after mating, the female was placed in a new wax paper-lined container daily and the eggs laid in each container were counted and weighed. Mean egg mass was calculated as the average of the four daily weighings, whereas lifetime fecundity was expressed as the sum total of eggs laid over the female's life span.

A parallel series of 20 matings was carried out with (−) individuals, which were paired in accord with the size matching used with the (+) individuals. The two series of matings were therefore comparable, in that for each (+) pairing there was an identically sized (−) pairing.

Experiment 2: Effect of Parental Body Mass and Spermatophore Mass on Egg Mass. For this experiment we considered only eggs laid during a 5-h period, extending from 2 h before onset of the dark phase of the L/D cycle to 3 h into the dark phase, because we know from experience that over 85% of a female's daily egg output is laid during that period in the laboratory. Also, weighings were taken only of eggs laid on the first 4 days after mating, because approximately half of the total egg output (of once-mated females) is laid during this time period (unpublished data).

Fifteen randomly selected (+) males were each mated to a randomly selected (+) female, and 15 randomly selected (−) males were each mated to a randomly selected (−) female. For the next 4 days, over the designated period of 5 h, mated females were placed into a new wax paper-lined container at the end of each hour, and the eggs laid within each container were counted. For each female, on each of the 4 days, a weighing was also taken of a sample of 20 eggs (from the first hourly batch to a number in excess of 20 eggs), to establish a value for the egg mass, per day, per female.

Experiment 3: Effect of Parental Diet and Egg Mass on Egg Fitness. To ascertain this relationship, eggs from experiment 2 were used. Groups of 30 eggs, from samples of over 50 that had been laid by females during any hourly interval (and of which 20 had been weighed for determination of egg mass for the sample), were set aside and monitored on a regular basis for determination of the following fitness parameters: viability (% hatching), egg stage duration, and larval mass at hatching. Given the constraints on sampling, only 39 egg clusters could be included for analysis, of which 26 were produced by females on the first day after mating, and 13 were produced on the second day.

Experiment 4: Effect of Egg Mass on Larval Fitness. The larvae used here were derived from the egg batches allowed to proceed to hatching in experiment 3 (that is, the unweighed eggs for which egg mass was determined by inference). For each batch where a group of 10 larvae could be obtained

that hatched within an hour (that is, more or less synchronously), these 10 larvae were allowed to develop. Twenty-nine batches yielded such larvae ($n = 20$ laid on the first day after mating; $n = 9$ laid on the second day). Each group of 10 larvae was placed in a dish with (+) diet (renovated every 4 days) and monitored for the following parameters: larval survivorship, duration of larval development (days from hatching to pupation), and pupal mass at pupal age of 7 days [the value is a good correlate of the 3-day-old adult body mass (Iyengar and Eisner, 1999a)]. The values obtained for each larva per sample provided the basis for calculating the means that were used in the statistical analyses.

Experiment 5: Effect of Spermatophore Mass on Egg Output and Egg Viability. For a given trial, two size-matched (+) sisters were mated to two different-sized (+) brothers. Each trial, consequently, consisted of two pairings that differed only in the mass of the spermatophore transferred. Fourteen such paired matings were carried out. Eggs from each mating were counted daily until death of the female, and all eggs were monitored to ascertain the percentage that hatched.

Statistical Analyses. We compared egg masses, egg quantities, and spermatophore masses using paired or unpaired t tests, while we compared egg survivorship using nonparametric equivalents [Wilcoxon signed-rank tests or Mann–Whitney U tests (Snedecor and Cochran, 1989)]. When comparing multiple parameters, we performed an analysis of variance (ANOVA), followed by post hoc comparisons with Bonferroni corrections (Snedecor and Cochran, 1989).

For all correlation analyses, we used partial correlation coefficients, which measure the relationship of two quantities while controlling for the effect of other variables (Snedecor and Cochran, 1989).

RESULTS

Experiment 1: Effect of Parental Diet on Egg Mass and Egg Output. There was no difference in the mass of eggs from parents raised on (+) versus (−) diet [mean ± SE; (+) eggs, 140.97 ± 0.51 μg; (−) eggs, 140.95 ± 0.53 μg; paired t test, $t = 0.25$, $P = 0.81$]. Furthermore, there was no difference in lifetime egg output based on diet [(+) females, 417.05 ± 27.46 eggs; (−) females, 412.75 ± 30.43 eggs; $t = 0.82$, $P = 0.42$]. The females, on average, laid 29% of their lifetime total of eggs in the first 2 days and 49% in the first 4 days after mating.

Experiment 2: Effect of Parental Body Mass and Spermatophore Mass on Egg Mass. Partial correlation analyses revealed that only female body mass had a significant effect on egg mass (Table I). Egg mass, however, was

Table I. Partial Correlation Coefficients (r) for the Effect of Female Body Mass, Male Body Mass, and Spermatophore Mass on Egg Mass ($n = 30$)

	Egg mass (μg) on specified night after mating			
	First day	Second day	Third day	Fourth day
Female body mass (mg)	0.891**	0.557**	0.618**	0.258
Male body mass (mg)	−0.256	0.194	0.196	−0.106
Spermatophore mass (mg)	0.248	−0.196	−0.204	0.132

**Statistically significant difference, $P < 0.005$.

positively correlated with female body mass for the first 3 days after mating only, not for the fourth day (Table I). Mean egg mass was not correlated with male body mass or spermatophore mass for any of the 4 days tested (Table I).

Egg mass did vary as a function of the day laid (ANOVA, $P < 0.0001$). The eggs laid on the first day after mating were significantly heavier than those laid on the second day (mean ± SE; 139.22 ± 1.64 μg vs 132.28 ± 1.27 μg; $P < 0.0005$: significant after Bonferroni correction), and these, in turn, did not differ in mass from those laid on the third and fourth days ($P > 0.50$ for all comparisons).

Experiment 3: Effect of Parental Diet and Egg Mass on Egg Fitness. For eggs laid on the first 2 days after mating, diet did not significantly affect egg viability [Mann–Whitney U test, $U = 182.50, n = 39, P = 0.47$), egg stage duration [$t$ test, $t = 1.12, n = 39, P = 0.27$), or larval mass at hatching ($t = 1.25, n = 39, P = 0.22$). This justified pooling the data from both diets for purposes of statistical analyses.

Egg mass correlated positively with larval mass at hatching for eggs laid on the first 2 days after mating and negatively with egg stage duration for eggs laid on the first day (Table II). Egg mass did not correlate with egg viability for eggs laid on either the first or the second day after mating ($P = 0.49$ and 0.18, respectively).

Table II. Partial Correlation Coefficients (r) for the Effect of Egg Mass on Egg Viability (% Hatching), Egg Stage Duration, and Larval Mass at Hatching

	Egg mass (μg) on specified night after mating	
	First day ($n = 26$)	Second day ($n = 13$)
Egg viability (% hatching)	0.140	−0.406
Egg stage duration (h)	−0.526*	−0.381
Larval mass at hatching (μg)	0.857**	0.794**

*Statistically significant difference, $P < 0.05$.
**Statistically significant difference, $P < 0.005$.

Table III. Comparisons of Egg Viability, Lifetime Fecundity, and Daily Egg Output of Size-Matched Sisters Mated to Different-Sized Brothers ($n = 14$)

Comparison	Statistical test	Stat. value	Large male[a]	Small male[a]	P value
Egg viability (% hatching)	Wilcoxon signed rank	0.85	88.0 ± 1.1	89.1 ± 1.5	0.38
Lifetime fecundity (No. eggs)	Paired t	0.88	411.6 ± 19.2	406.3 ± 17.8	0.39
Egg output					
First 3 days after mating	Paired t	1.91	173.1 ± 9.3	160.8 ± 8.6	0.08
First day after mating	Paired t	2.39	81.2 ± 5.0	64.1 ± 6.2	0.03*

[a]Mean ± SE.
*Statistically significant difference.

Experiment 4: Effect of Egg Mass on Larval Fitness. For eggs laid on the first 2 days after mating, egg mass did not correlate with larval survivorship (first day $r = 0.071$, $P = 0.77$; second day $r = 0.264$, $P = 0.51$), duration of larval development (first day $r = -0.120$, $P = 0.62$; second day $r = -0.295$, $P = 0.45$), mean daughter pupal mass (first day $r = 0.065$, $P = 0.79$; second day $r = 0.054$, $P = 0.90$), or mean son pupal mass (first day $r = 0.073$, $P = 0.76$; second day $r = 0.320$, $P = 0.42$).

Experiment 5: Effect of Spermatophore Mass on Egg Output and Egg Viability. Male spermatophore mass had no effect on egg viability or lifetime female fecundity (Table III). We also compared the egg output of females during the first 3 days following mating and found that females mated to larger males did not lay more eggs than those mated to smaller males (Table III). Closer inspection, however, revealed that although there were no differences in the number of eggs laid on the second and third days, females mated to the larger brother laid significantly more eggs on the first day than those mated to the smaller brother (Table III).

DISCUSSION

The present results shed additional light on the adaptive advantages of being physically large in *Utetheisa*, as either a male or a female. In earlier studies, it was shown that larger females have a higher lifetime fecundity (LaMunyon, 1997) and larger males have a greater chance of being accepted in courtship (Conner *et al.*, 1990; Iyengar *et al.*, 2001). The female, moreover, benefits from her preference for larger males. By so choosing she is able to obtain larger alkaloidal gifts and—since body size is heritable (Iyengar and Eisner, 1999a)—sons and daughters that are themselves larger and therefore increasingly fit (Iyengar and Eisner, 1999b).

We now show that, quite aside from the effect on fecundity, being large also enables females to lay larger eggs. The correlation appears to be time-limited. We found it to apply only to eggs laid on the first 3 days after a female's initial mating. It could of course also prevail after later matings, but even if it does not, and the eggs are larger as a sequel to the first mating only, this could be of considerable consequence, given that the *Utetheisa* female lays up to half her eggs in the 4 days immediately following the first mating. It should be noted that the eggs laid on the first day of this 4-day period are actually the largest and that they comprise nearly one-quarter of the female's entire egg complement.

Male body mass had no effect on egg mass, and neither did spermatophore mass [the latter relationship was to be expected, since spermatophore mass varies as a function of male body mass (LaMunyon and Eisner, 1994)]. However, the male body mass did have an effect on the number of eggs laid by the female on the first day after mating. Mating with a larger male did not result in a net increase in egg output over the next 3 days, only in a skewing of the output in favor of the first day. For the male this can be of substantial importance, given that the female *Utetheisa* can remate at intervals of a day or two (unpublished data). It would be interesting to know what regulatory factors are responsible for hastening of egg deposition on the first day after mating. Since both partners can potentially benefit from accelerated oviposition—the male by siring more offspring and the female by increasing the proportion of larger offspring—one can envision either parent being the physiological manipulator of the event.

The ability on the part of larger females to lay larger eggs has adaptive connotations. Larvae hatching from larger eggs are larger, and larger eggs—at least if produced on the day following the first mating—develop faster. Being able to emerge earlier at a potentially more vigorous stage could enable the larvae to compete more effectively with their clustermates for access to the seedpods of the plants, a resource that could be limited at times and upon which the larvae depend to obtain the bulk of their alkaloid (Conner *et al*., 1990).

We found egg mass to have no effect on egg viability, larval survivorship, duration of larval development, or eventual pupal mass (and therefore adult mass). Nor did we find egg viability to be affected by spermatophore mass (and, therefore, by inference, male mass). It should be noted, however, that being larger can convey benefits upon insect eggs. In other species, largeness has been shown to protect eggs against low humidity (McLain and Mallard, 1991), cold (Gwynne, 1988), and nutrient deficiency (Braby, 1994). Perhaps under more natural conditions, *Utetheisa* eggs would similarly benefit from being large.

We also found spermatophore mass to have no effect on lifetime female fecundity, but our finding applies to singly mated females only. Multiple mating, no doubt because of the periodic infusion of nutrient that the female receives as a consequence, does result in increased egg production (LaMunyon, 1997). *Utetheisa* females may in fact mate more often than suspected. Previous estimates had indicated four to five matings, on average, over the female's life span (Pease, 1968). Recent study of a long-established Florida population in which colla within the bursa of females were counted revealed that females may take on average 11 and as many as 22 partners (unpublished data).

We do not know that the events described here are invariable concomitants of mating, but one can envision this being the case. Thus, it seems likely that mating always triggers egg deposition and possible that male body mass is a determinant of the magnitude of the effect. Mating is certainly known to have an immediate stimulatory effect on oviposition in many species of insects (Benz, 1969; Loher *et al.*, 1981; Chen, 1996).

We also found all parameters that we assessed to be unaffected by whether or not alkaloid was present in the larval diet. This means that alkaloid per se, as a component either of the larval diet or of the seminal material transferred with the spermatophore to the female, has no influence on either the number of eggs produced or the size of these eggs. This should not obscure the fact that the alkaloid plays what is unquestionably a primary role in the sexual strategy of *Utetheisa*. As a defensive substance that both sexes allocate to the eggs (Dussourd *et al.*, 1988) and that the female receives as a supplement at mating (González *et al.*, 1999), the alkaloid is very much at the core of what the precopulatory sexual "dialogue" in *Utetheisa* is all about. The data presented here, pertinent to egg size, egg output, and their determinants, are to be viewed as of significance mainly in that they help clarify some of the fine-tuning of the strategy.

ACKNOWLEDGMENTS

We thank P. Buston, P. Feeny, and H. K. Reeve for their helpful comments on early versions of the paper. We also thank the late K. Amerman for technical assistance. Research support was provided by National Institutes of Health Grant AI02908 (to T.E.) and a predoctoral fellowship from the National Science Foundation (to V.I.). This is paper number 179 in the series "Defense Mechanisms of Arthropods."

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