Unpredictable food and sexual size dimorphism in insects

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SUMMARY

The evolution of sexual size dimorphism is likely to be affected by the amount of resources each sex invests in offspring. Male nuptial gifts, occurring in many insect species, might reduce the value of large size in females and increase the value for males. We suggest that food variability, causing some males to have much to provide and some females to be in great need, would be conducive to the evolution of such a mating system, and we present comparative data on butterflies supporting the suggestion. In a gift-giving mating system, growing male and female juveniles should react differently to food shortage. A female maturing at small size can to some extent buffer her disadvantage through nuptial gifts, whereas a male maturing at small size will suffer from his inability to provide substantial gifts. Thus, males benefit more than females from continued growth in the face of food shortage, leading to a shift in size dimorphism. Here we confirm this prediction in a butterfly, Pieris napi, with large nuptial gifts.

1. INTRODUCTION

When juveniles of both sexes lead similar lives, one would expect the evolution of sexual size dimorphism mainly to depend on differences between males and females in the value of being large as an adult. In insects, as in many other groups of animals, females tend to be the larger sex (Darwin 1871). The explanation commonly given is that larger females are more fecund and that this effect is stronger than the possible advantage of a larger male in competition with other males over matings (Darwin 1871).

In some groups of insects, males donate nutritious nuptial gifts to females around the time of mating (Thorhill 1976; Thorhill & Alcock 1983). These gifts can be of considerable value to females and expensive for males to provide (Parker & Simmons 1989; Gwynne 1990, 1993; Markow et al. 1990; Simmons 1990; Wiklund et al. 1993; Wiklund & Kaitala 1994), potentially affecting the relative reproductive advantages of large adult size in the two sexes.

When males produce part of the resources going into offspring, the value of size might thus increase for males and decrease for females, leading to a shift in dimorphism. Comparative data are available for two groups of insects, butterflies (Sväräd & Wiklund 1989; Wiklund & Forsberg 1991) and bush crickets (Wedell 1993), and show such a shift, with males reaching the size of females in species with large gifts. For butterflies, there is further comparative evidence showing that the shift is associated with greater allocation of resources to the abdomen in males and less in females (Karlsson 1994).

Several of the selective forces that could maintain a gift-giving mating system and, potentially, affect adult size have been investigated. A male might benefit from a larger gift either through the increased fecundity of his mate or by fertilizing a greater proportion of her eggs (Simmons & Parker 1989; Simmons 1990; Wedell 1991; Wiklund et al. 1993; Wiklund & Kaitala 1994). Remating females foraging for gifts in response to nutritional needs (Boggs 1990; Gwynne 1990; Simmons & Gwynne 1991) could produce such selection on gift size. Females typically do not mate indiscriminately, accepting all gifts, probably because mating can be risky and takes time that could be used for egg laying (Thorhill & Alcock 1983). If mating is costly, a female should remate only if she cannot acquire similar resources at a lower cost, for instance during her larval stage.

2. THE HYPOTHESES

A general principle for trade in a market is that variation in needs to obtain and abilities to provide results in more intense transactions. One might expect the same principle to hold when nuptial gifts are traded for offspring. If some males are in a better position to produce gifts, and some females are in greater need of gifts, these females have an incentive to remate. Also, a female receiving a small gift has an incentive to remate more quickly, because better options are available on the market. Unpredictable food, either for juveniles or adults, would lead to this kind of variation, and we suggest that food variability could be an important factor explaining differences between species in nuptial gift giving, and thus in sexual size dimorphism. More generally, any random environmental variation causing males and females to
vary in adult size could have the same effect. Thus, we suggest that nuptial gifts should be larger in species with greater within-population size variation.

Unpredictable food and gift giving also have implications for individual plasticity in adult size. If females receive substantial amounts of resources through matings, a female larva should react strongly to food shortage by maturing at a smaller size, since her own lack of reproductive resources is partly compensated by male contributions. However, a male larva experiencing food shortage has to pay the full cost of decreased reproduction if he matures at a very small size, making it more important for him to keep on growing. Thus, size dimorphism should vary with larval growing conditions, with the male to female size ratio being greatest for larvae experiencing poor conditions.

3. MATERIALS AND METHODS

(a) Comparative study

To look for a relation between adult size variation and nuptial gift size, we collected data on wing length variation in 16 Swedish species of butterflies (given in table 1). Size variation was measured as the coefficient of variation (cv) of wing lengths of females sampled in one locality in one year, thus controlling for average size differences between species and avoiding effects of size variation between different populations and years. Female size was used because we have few data on male size; ideally, the average of the male and female cv should have been used.

Nuptial gifts in butterflies consist of ejaculates, and data on male ejaculate and body mass for the 16 species are available in the literature (Svard & Wiklund 1989). Since ejaculate mass tends to increase allometrically with body mass in butterflies, we tested for a cv–gift size relation by performing regressions of log ejaculate mass on log male mass and the cv, thus controlling for male mass.

The butterflies in the study (table 1) are from two families: species 1–8 are from the Pieridae, and species 9–16 are from the Satyridae. For phylogenetic analysis, we used a phylogeny suggested for European pierids (Geiger 1980), and for the satyrids the genera were assumed monophyletic, and P. aegeria was also grouped with Lasiommata, since these species belong to the generally recognized subfamily Pararginae. The independent contrasts method (Purvis 1991) was then used to test for a relation between ejaculate mass and adult size variation.

(b) Food quality experiment

The reactions of male and female larvae to growing conditions were investigated in an experiment with the green-veined white, P. napi. Several observations show that, among butterflies, this species has a strongly developed gift-giving mating system: males are slightly bigger than females (Wiklund & Forsberg 1991), males produce large ejaculates (Svard & Wiklund 1989), females remate extensively (Svard & Wiklund 1989), and male ejaculates influence female fecundity (Wiklund et al. 1993).

Larvae were reared on high- and low-quality plants of, respectively, Alliaria petiolata and Berteroa incana, resulting in four growth-condition treatments. High-quality plants were fresh and in ample supply; low-quality plants were older and smaller. The two host plants were chosen with the intent of having one suitable and one less suitable species. The leaves of B. incana are tougher than those of A. petiolata and are covered with small, star-shaped hairs, probably making B. incana a suboptimal host for P. napi.

The animals were kept in the same environmental room on a 22 L:2 D, 23°C cycle. Newly hatched larvae (60 per treatment) were reared individually on food plants in 380 ml transparent plastic jars, with treatments randomized with respect to jar position in the environmental room. Pupae were weighed 2 d after pupation, and adults frozen after eclosion and then dried to constant mass in 50°C. Dry mass was measured separately for the abdomen and for the remainder of an individual. Sex differences in reaction to growth conditions was tested for by examining sex × treatment interactions in two-way analyses of variance.

Individuals entering pupal diapause were not used in the analysis of pupal mass, and those emerging with deformed

<table>
<thead>
<tr>
<th>species</th>
<th>cv (%)</th>
<th>n</th>
<th>ejaculate</th>
<th>body</th>
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<tr>
<td>Aporia crataegi</td>
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<td>23</td>
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<td>6.72</td>
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<tr>
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<td>23</td>
<td>6.66</td>
<td>44.5</td>
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<tr>
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<td>15</td>
<td>4.21</td>
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</tr>
<tr>
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<td>12</td>
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<td>9</td>
<td>2.03</td>
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4. RESULTS

(a) Comparative study

Adult size variation and ejaculate mass for the 16 species are given in table 1. If, at first, we treat each species as an independent data point, the regression of log ejaculate mass \( y \) on log body mass \( x_1 \) and \( cv \) \( x_2 \) is

\[
y = 1.485x_1 + 0.602x_2 - 7.644, \quad R^2 = 0.886. \]

In this species regression, the effect of \( x_2 \) on \( y \) is highly significant \( (t_{13} = 5.68, p = 0.00008) \). Log ejaculate mass controlled for body size can be expressed as the partial residual

\[
y_{res} = 1.485 + 0.602x_2 - 2.760. \]

However, both the partial residual and the \( cv \) are significantly greater for the pierids than for the satyrids \( (t-tests, p = 0.0002 \text{ and } p = 0.0007, \text{ respectively}) \), showing the need to control for shared ancestry. Assuming phylogenies for the two families as specified above, 12 independent contrasts for each of log ejaculate mass \( y \), log body mass \( x_1 \) and \( cv \) \( x_2 \) were extracted (Purvis 1991). The regression through the origin for these contrasts is

\[
y = 1.833x_1 + 0.690x_2, \quad \text{with a significant effect of } \ x_2 \text{ on } \ y \ (t_{10} = 2.52, p = 0.030). \]

Thus, it appears that males provide larger gifts in species with greater size variation.

Data on male and female pupal mass are available for 13 of the 16 species in table 1 (Wickman et al. 1990; Wiklund & Forsberg 1991). For these 13 species, there is a significant positive correlation between \( cv \) and the male:female mass ratio \( r = 0.67, p = 0.013 \), indicating that size dimorphism covaries with size variability.

(b) Food quality experiment

As predicted, \( P. napi \) females reacted more strongly to low-quality food by maturing at smaller sizes (figure 2). That males and females reacted differently to growth conditions is shown by significant sex \( \times \) treatment interactions in two-way analyses of variance (pupal mass, \( F_{3,149} = 4.71, p = 0.004 \); abdomen dry mass, \( F_{3,139} = 7.37, p = 0.0001 \); non-abdomen dry mass, \( F_{3,139} = 3.95, p = 0.01 \)). Food quality differences are indicated by the fact that development time to pupation for the treatments increased from left to right in figure 2 (one-way ANOVA, \( F_{3,145} = 41.6, p < 0.000001 \)). Also, larvae on \( B. incana \) had higher mortality than those on \( A. petiolata \) \( (37.5\% \text{ against } 17.5\% , \chi^2 = 12.04, p = 0.0005) \), but larvae on low-quality plants did not have significantly higher...
mortality than those on high-quality plants (32.2% against 22.7% \(\chi^2 = 2.74, p = 0.1\)).

The sex difference in the effect of food quality was particularly pronounced for larval resources invested in reproduction, measured as the amount of materials in the abdomen (figure 2). For females, the proportion of dry mass allocated to the abdomen ranged between 45.7% on high-quality *A. petiolaris* to 42.3% on low-quality *B. incana*, and the between-treatment variation was significant (one-way ANOVA on log-transformed proportions, \(F_{55} = 4.9, p = 0.004\)). Males, however, allocated on average 37.7% of the dry mass to the abdomen, and there was no significant variation between treatments (\(F_{53} = 1.6, p = 0.18\)).

5. DISCUSSION

Our experiment showed that *P. napii* females reacted more strongly than males to low-quality food. A possible consequence could be that females experiencing poorer growing conditions rely more heavily on male contributions than the average female. In species with small nuptial gifts, females chiefly depend on their own resources, and we might expect an opposite shift in dimorphism with growing conditions. A complication could be that very small males have little chance to gain access to females. Growth plasticity in males and females has been modelled (Stearns & Koella 1986) and investigated empirically (Gebhardt & Stearns 1993), but only rarely in connection with nuptial gifts (Markow et al. 1990).

Among the many factors that may cause variation in sexual size dimorphism (Darwin 1871; Shine 1989), competition among males for access to mates is the most commonly suggested (Darwin 1871; Clutton-Brock et al. 1977). More recently, sperm competition has been added to the list (Parker 1992; Simmons & Parker 1992). Competition between members of one sex for access to the other is likely to be influenced by the relative parental investments of males and females (Trivers 1972; Thornhill 1986; Clutton-Brock & Parker 1992). If male–male competition is most intense when males invest little, one would perhaps expect the male to female size ratio to decrease with male investment, contrary to observation in species with nuptial gifts. Thus, struggle among males for access to females appears to be less important for the evolution of size dimorphism in these groups of animals. Sperm competition, however, could be a major factor (Wedell 1991). The division of male investment into mating effort and parental effort might well vary among species (Simmons & Parker 1989) but, as long as females remate to obtain reproductive resources, the consequence will be that males as a group invest in offspring.

For orthopterans, several studies have shown that reduced food availability can cause females to compete for access to males (Gwynne 1991, 1993), and this has been interpreted as a response to the average conditions experienced by members of a population (Gwynne 1984, 1991; Thornhill 1986; Boggs 1990). The actions shown by males and females in our experiment (figure 2) are consistent with this, in the sense that in poor average conditions a greater proportion of the reproductive resources would be provided by males (Thornton 1986; Simmons 1992), although we have interpreted these reactions as an adaptation to random variability in conditions rather than to the average. In our view, there are two separate, but related, phenomena. Changes in the average resource levels in the environment might well affect the value females place on male gifts, and thus influence the sex roles (Thornton 1986; Gwynne 1991). The degree of random variability, however, might contribute to differences between species in gift giving, and thus to the evolution of sexual size dimorphism.

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