

Unpredictable environments, nuptial gifts and the evolution of sexual size dimorphism in insects: an experiment

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SUMMARY

Many insects have a mating system where males transfer nutrients to females at mating, which are often referred to as 'nuptial gifts'. Among butterflies, some of the characteristic features of these species are polyandry (females mate multiple times), and relatively large male ejaculates. When males produce part of the resources used for offspring, the value of body size might then increase for males and decrease for females. The male/female size ratio is also observed to increase when the degree of polyandry and gift size increase. Butterfly species where gift-giving occurs are generally more variable in body size, suggesting that food quality/quantity fluctuates during juvenile stages. This will cause some males to have much to provide and some females to be in great need, and could be conducive to the evolution of a gift-giving mating system. In such a system, growing male and female juveniles should react differently to food shortage. Females should react by maturing at a smaller size since their own lack of reproductive resources can partly be compensated for by male contributions. Males have to pay the full cost of decreased reproduction if they mature at a small size, making it more important for males to keep on growing, even when growth is costly. An earlier experiment with the polyandrous and gift-giving butterfly, *Pieris napi*, supported this prediction. The pattern is expected to be absent or reversed for species with small nuptial gifts, where females do not benefit from mating repeatedly, and will thus be dependent on acquiring resources for reproduction on their own. To test this prediction, we report here on an experiment with the speckled wood butterfly, *Pararge aegeria*. We find that growth response correlates with mating system in the two above species, and we conclude that differences in environmental conditions between species may act as an important factor in the evolution of the mating system and sexual size dimorphism.

1. INTRODUCTION

Many insects have a mating system where males transfer nutrients to females at mating, which are often referred to as 'nuptial gifts' (Thornhill 1976; Thornhill & Alcock 1983). Nutrients can be supplied as items eaten by the female, or as ejaculate material produced by male accessory organs which is later absorbed within the female's reproductive tract. Several studies on orthopterans (Gwynne 1984, 1988; Simmons 1990) and lepidopterans (Boggs & Gilbert 1979; Boggs 1981; Boggs & Watt 1981; Pivnick & McNeil 1987; Rutowski *et al.* 1987; Watanabe 1988; Oberhauser 1989; Wiklund *et al.* 1993; Svård & McNeil 1994) demonstrate that material from ejaculates is incorporated into female soma and eggs and that females make use of male-derived nutrients to boost reproductive performance and longevity.

Recent studies on butterflies by Kaitala & Wiklund (1994), Bissoondath & Wiklund (1995) and Karlsson (1995, 1996) further support the idea that some butterflies have a mating system entailing a transfer of resources from males to females. Females of these species mate multiple times during their life (poly-

andry), and several male adaptations have been discovered in conjunction with polyandrous mating systems. Some of the characteristic features of males in these species are (i) a higher investment of total resources in reproduction (Karlsson 1995); (ii) ejaculate mass constitutes a large part of body mass (Svård & Wiklund 1989; Karlsson 1995); and (iii) increased nutrient content in reproductive reserves (Karlsson 1996) and in ejaculates (Bissoondath & Wiklund 1995). Higher ejaculate production capacity is also observed among males of polyandrous species compared to males of monandrous species (Svård & Wiklund 1989). Sperm competition is probably a major factor for the evolution of large ejaculates, although male parental effort might also have an influence.

In a comparative study, Wiklund & Forsberg (1991) showed that sexual size dimorphism can be affected by the mating system. Males are as a rule smaller than females in most animals, and insects are no exception (Darwin 1871). However, the male/female size ratio tends to shift when the degree of polyandry and the relative ejaculate size increase (Wiklund & Forsberg 1991; Wedell 1993; Nylin & Wedell 1994). It therefore

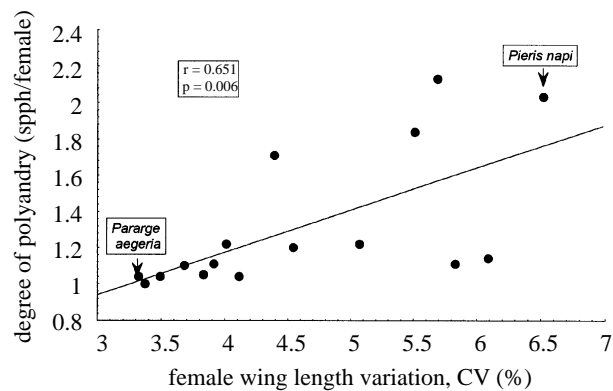


Figure 1. Degree of polyandry, measured as the number of spermatophores per female (data from Wiklund & Forsberg (1991) and unpublished results) increases with variation in female wing length (data from Leimar *et al.* (1994)) in a sample of 16 butterfly species. Values for *Pieris napi* and *Pararge aegeria* are indicated by arrows.

appears that sexual size dimorphism in insects is affected by the amount of resources each sex invests in offspring. When males produce part of the resources used for offspring, the value of body size and reproductive reserves might increase for males and decrease for females.

Taking this into account together with the observation that species with large nuptial gifts tend to be more variable in body size, Leimar *et al.* (1994) proposed a hypothesis about when a gift-giving system, where resources from males are traded for offspring, might evolve. If food quality and/or quantity fluctuates during juvenile stages, some males will have much to provide and some females will be in great need, which could be conducive to the evolution of a gift-giving system. When some males can offer resources that females are in need of, females with little resources or those which have received a small gift, have an incentive to mate again. Consequently, the degree of polyandry should covary with body size variation, and figure 1 shows that this occurs in the 16 species investigated by Leimar *et al.* (1994). According to the hypothesis, any random environmental variation causing adult size to vary could facilitate the evolution of a polyandrous gift-giving system, with a concomitant shift in sexual size dimorphism. Nevertheless, it might also be possible that the observed correlation across species between mating system and size variability could be the result of host plant shifts among polyandrous species to more variable food sources.

To test their hypothesis, Leimar *et al.* (1994) conducted an experiment on the green-veined white butterfly, *Pieris napi*. This species is strongly polyandrous, with males delivering ejaculates that on average correspond to 15% of male body weight (Svård & Wiklund 1989); individual males can transfer ejaculates up to a quarter of their body mass (Forsberg & Wiklund 1989). Moreover, *P. napi* exhibits considerable variation in adult size, as indicated by wing length variation in wild-caught butterflies belonging to 16 species, where it is the most variable of all species (figure 1 and Leimar *et al.* (1994)). Since variation in adult size is to a large extent mediated by larval food,

it appears that larvae of *P. napi* experience conditions in the wild where the quality and quantity of their food plants are rather variable, and thus unpredictable.

If females receive substantial amounts of resources through matings, a female larva should react to food shortage by maturing at a smaller size, since her own lack of reproductive resources is partly compensated for 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 even when growth is costly.

In support of their theory, Leimar *et al.* (1994) presented evidence that there is a shift in sexual size dimorphism with growing conditions in *P. napi*. As predicted, poor growing conditions produced a relatively greater decrease in the size of females than in the size of males.

Males of monandrous species deliver small ejaculates relative to their body mass (Svård & Wiklund 1989; Karlsson 1995), suggesting that proteinous nuptial gifts to females are small under this mating system (cf. Bissoondath & Wiklund 1995). Under these conditions, a female is not likely to benefit from mating repeatedly, and will therefore be dependent on acquiring resources for reproduction on her own through larval feeding. Hence, under monandry, female larvae should continue to grow in poor conditions because they cannot compensate for small reproductive reserves once they have matured. Although male size may be an important factor in male reproductive success (e.g. Phelan & Baker 1986; Wickman 1985; Wiklund & Kaitala 1995, but see Suzuki & Matsumoto (1992)), it might be less associated with size when no nuptial gifts are transferred. Thus, under a monandrous system, male larvae might react to food shortage more strongly than females. We predict that the shift in size dimorphism with differences in larval food conditions found in the polyandrous gift-giving butterfly, *Pieris napi*, will be absent or possibly take the opposite direction in a monandrous non-gift-giving butterfly when larvae are grown under different food conditions.

To test this prediction, we report here on a growth experiment with the speckled wood butterfly, *Pararge aegeria*. This species is monandrous and delivers ejaculates which are only about 1.4% of male body weight (Svård & Wiklund 1989). *P. aegeria* shows considerably less adult size variation than *P. napi*. In fact, of the 16 species investigated by Leimar *et al.* (1994), *P. aegeria* is the least variable (figure 1).

2. MATERIALS AND METHODS

Larvae of *Pararge aegeria* are graminivorous and can be found on several species of grass in the wild (Wiklund 1984). In order to create variation, male and female larvae were reared on high and low quality specimens of the grass, *Poa annua*. High quality plants were fresh and in ample supply, low quality plants were older and smaller. Newly hatched larvae of *P. aegeria* were placed individually on tufts of the host plant, growing in 380 ml transparent plastic jars. The larvae were reared individually until eclosion in a 23 °C, 22 h:2 h light:dark cycle. All animals were kept in the same room. At emergence, the adults were sexed and, as soon as

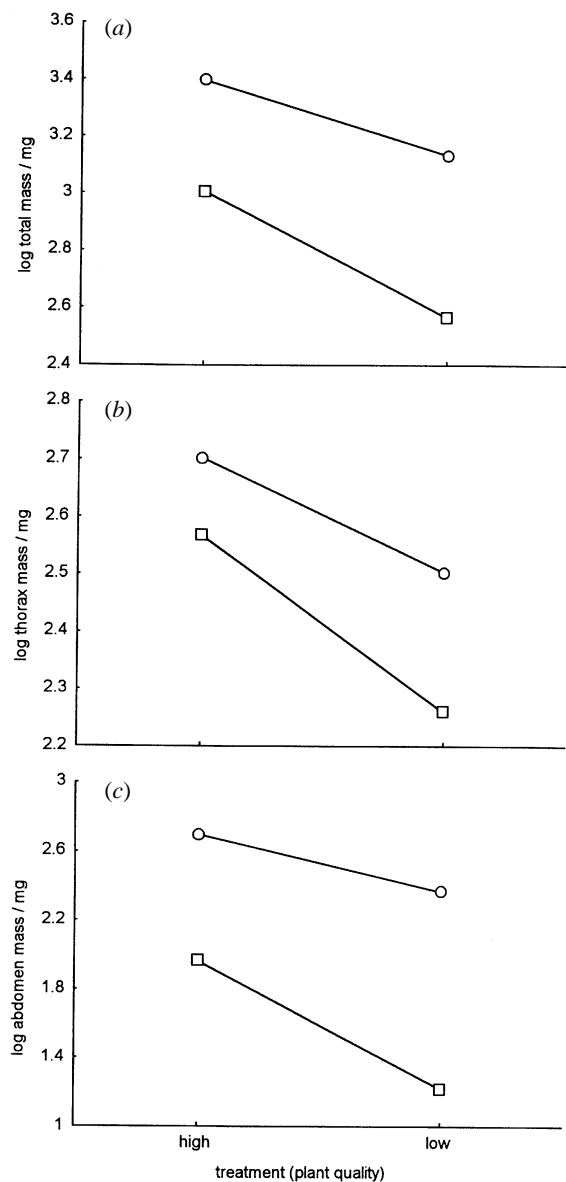


Figure 2. Female (circles) and male (squares) total (a), thorax (b) and abdomen (c) dry masses of newly eclosed adults of the monandrous butterfly, *Pararge aegeria*, under two different larval growth conditions (treatments). Comparing responses to high and low quality, low quality food reduced male mass more than it did female abdomen mass.

they had released their pupal waste products, they were frozen and then dried to constant mass at 50 °C. Dry mass was recorded separately for the abdomen and for the remainder of an individual (henceforth named the 'thorax'). Individuals emerging with deformed wings were not included in the analysis, since such individuals may fail to eject pupal

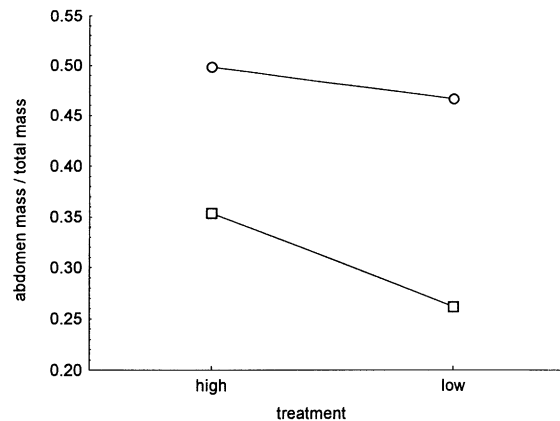


Figure 3. The proportion of total dry mass invested in the abdomen at eclosion in *Pararge aegeria*. Compared to females (circles), males (squares) invest a smaller proportion in their abdomens when growing conditions are poor.

waste products. Individuals entering pupal diapause were also excluded from the analysis. In total, 29 females and 30 males were reared under high quality conditions, and 25 females and 30 males under low quality conditions.

3. RESULTS

Males were smaller than females in both high and low plant quality treatments (figure 2, table 1). Both males and females reacted to low quality food by maturing at smaller sizes (figure 2, table 1). However, males reacted more strongly to low quality food compared to females, since their body mass decreased more under the low quality condition (figure 2). That males and females reacted differently to larval food conditions is shown by significant sex \times treatment interactions in table 1.

The sex difference in the effect of the treatment was particularly apparent for resources invested in the abdomen. For males, the proportion of dry mass allocated to the abdomen dropped from 36% to 25%, whereas females only decreased their proportion from 50% down to 47% (figure 3), and this difference between the sexes is statistically significant ($F_{1,110} = 57.81$, $p < 0.00001$, sex \times treatment interaction, log-transformed proportions).

4. DISCUSSION

Our study demonstrates that the relative sensitivity to poor conditions of male and female *Pararge aegeria* larvae is opposite to that observed in *Pieris napi*, which supports the predictions made by Leimar *et al.* (1994),

Table 1. ANOVA of log total, log thorax, and log abdomen dry mass of newly eclosed adults of *Pararge aegeria*.

(Larvae were reared on high and low quality specimens of *Poa annua*.)

	log total mass	log thorax mass	log abdomen mass
sex	$F_{1,110} = 341.23$ $p < 0.00001$	$F_{1,110} = 101.73$ $p < 0.00001$	$F_{1,110} = 560.16$ $p < 0.00001$
treatment	$F_{1,110} = 183.96$ $p < 0.00001$	$F_{1,110} = 182.45$ $p < 0.00001$	$F_{1,110} = 182.72$ $p < 0.00001$
sex \times treatment	$F_{1,110} = 11.70$ $p < 0.001$	$F_{1,110} = 8.38$ $p < 0.005$	$F_{1,110} = 27.77$ $p < 0.00001$

that females in monandrous species with small nuptial gifts should react less strongly to food shortage than males. The results from this study and from Leimar *et al.* (1994) indicate that the underlying mating systems have a strong influence on the species pattern of variation in sexual size dimorphism.

Although male weight should be less important for males in monandrous species compared to males in polyandrous species, another factor that could influence male size, and therefore the degree of sexual size dimorphism is pre-mating male–male competition (Darwin 1871). Since males of *Pararge aegeria* are territorial and have intense flight interactions (Wickman & Wiklund 1983), male weight might be of importance just as it is for males in another satyrid species, *Coenonympha pamphilus* (Wickman 1985). However, the possible negative effects of reduced size among males growing under poor conditions may be somewhat reduced by the fact that these males shift their allocation pattern and invest less in their abdomens (figure 3), and thus more in the thorax region, which contains the flight muscles. Since several studies indicate that relative thorax mass correlates with flight performance (e.g. Srygley & Chai 1990; Wickman 1992), flight performance and flight manoeuvrability might actually increase with reduced body size.

Thus, we argue that the observed difference in size variation and growth response correlate with polyandry and nuptial gift size according to our hypothesis in these two species. Differences in environmental conditions between these species may act as an important factor in the evolution of the mating system and in sexual size dimorphism. Our results also demonstrate that sexual size dimorphism should not be viewed as a fixed trait. Further experiments are needed to reveal if our proposed hypothesis can be applied to other insect groups.

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