

Mass and production rate of ejaculates in relation to monandry/polyandry in butterflies

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Summary. The mating system maintained in a species has a strong effect on the degree of sperm competition, and certainty of paternity should accordingly influence the optimal sperm content, nutrient content, and mass of the ejaculate. We investigated how ejaculate mass relates to the degree of polyandry in 20 species of butterflies belonging to the families Pieridae and Satyridae. We found that the degree of polyandry has a substantial effect on the reproductive performance of males. The allometric line between ejaculate mass and male body mass has a higher elevation in the pierids compared to the satyrids. The mean number of matings performed by the pierid species is also higher compared to the mean of the satyrids. Thus, the relative ejaculate mass is larger in the family in which polyandry is more pronounced. A within family effect of degree of polyandry on relative ejaculate mass was also detected in the pierids. Since males of polyandrous species on average mate more often than males of monandrous species, they should be expected to have a higher capacity for producing many ejaculates. We investigated how this capacity was influenced by the degree of polyandry, by allowing males of seven different species (*Danaus plexippus*, *Lasiommata megera*, *Papilio machaon*, *Pararge aegeria*, *Pieris napi*, *Pieris rapae*, and *Polygonia c-album*) to mate twice, with different time intervals between matings. The results showed that not only is the mass of the ejaculate greater in more polyandrous species, but also the rate at which males are able to produce sperm and accessory substances is greater. Hence our data indicate that sperm competition is important for explaining variation in ejaculate mass in butterflies.

Introduction

In many insect species males transfer an ejaculate to the female at mating that contains not only sperm but also substances produced by the accessory glands of the males. In butterflies the ejaculate may serve three functions. Firstly, the sperm fertilize the eggs of the female, and as a rule one mating provides a female with enough sperm to fertilize all of the eggs (Sims 1979; Suzuki 1979; Lederhouse 1981; Rutowski 1984). Secondly, the accessory substances may provide nourishment that can be used by females to increase their fecundity, the quality of their eggs, or their longevity (Boggs and Gilbert 1979; Boggs 1981 a, 1981 b). Thirdly, the ejaculate may determine the length of the period during which females are unwilling to remate, as the refractory period of the female is dependent on stretch receptors in the bursa that are sensitive to the mass of the ejaculate (Sugawara 1979). The refractory period may also be dependent on the amount of sperm transferred to the female spermatheca (Taylor 1967; Benz 1969; Thibout 1975).

Spermatophore counts on wild caught females have shown that the females of some species as a rule mate only once during their lifetime, e.g., *Pararge aegeria* (Wickman and Wiklund 1983), *Aphantopus hyperantus* (Wiklund 1982) and *Coenonympha pamphilus* (Wickman 1986). Other species are polyandrous, like *Pieris napi*, in which females can mate up to five times and *Danaus plexippus*, in which females can mate up to eight times (Pliske 1973).

In those species where females mate more than once, there is thus a possibility for sperm from different males to be in competition, and consequently paternity assurance is important for these males. As Parker (1970, 1984) pointed out, there

seem to be two conflicting selective forces related to paternity assurances. One is selection favoring mechanisms for removing or incapacitation of other males' stored sperm. The other is counter selection favoring anti-removal or anti-incapacitating mechanisms in order to prevent future males from reducing the effectiveness of the first male's sperm. The fact that most butterfly species have a nearly complete sperm displacement (Drummond 1984) suggests that removal or incapacitation of other males' stored sperm is important in this group. There also appear to be many adaptations in butterflies to prevent or delay other males' mating with the female, i.e., prolonged copulations (Svärd and Wiklund 1988a), mating plugs or sphragis' (Scott 1972), and antiaphrodisiacs transferred to the female at mating (Gilbert 1976).

From the perspective of the males, the mating system maintained in a species thus has a strong effect on the degree of sperm competition, and the mass of the ejaculates produced by males belonging to polyandrous species should be positively related to the degree of polyandry because of sperm competition and the female remating delay aspect.

Another aspect of the reproductive capacity of male butterflies concerns the ability of males to produce many ejaculates. Since the number of matings achieved by males should reflect the degree of polyandry, the capability of males to produce many ejaculates should be positively correlated to the degree of polyandry.

In this paper we investigate how ejaculate mass relates to the degree of polyandry in 20 species of butterflies belonging to the families Pieridae and Satyridae. Since the mass of the ejaculate is dependent on male body mass (Rutowski et al. 1983), we examined the relation between these two parameters as well. We also investigate how remating capacity is influenced by degree of polyandry, by allowing males in 7 species to remate after 1, 2, 3, 4, and 5 days and analyzing the weight of the ejaculate relative to number of days passed since the last mating.

Methods

Measures on body mass, ejaculate mass, and degree of polyandry were obtained as follows:

Male mass and ejaculate mass

The males used in the study were either caught in the field (Table 1, species 6, 8–18, 21 and 22) or were laboratory-reared offspring of wild-caught ones (Table 1, species 1–5, 7, 19, 20, 23–25). The wild males were caught while in copula with wild females (species 8, 9, 12–18, 21, and 22) or with laboratory-

reared females released in the field (species 6, 10, and 11). The males reared in the laboratory were given a 25% sucrose solution daily and were mated when released in the field (species 1, 7) or in indoor cages (species 2–5, 19, 20, 23–25). After mating (or after eclosion in the laboratory-reared species), to obtain an estimate of the mean male weight in each species, males were weighed on a Sauter AR electrobalance. In order to assess the mean weight of the ejaculate passed, the female was decapitated and dissected under a stereo microscope. The bursa copulatrix with its content, the ejaculate, was extracted and weighed on a Cahn 28 Automatic electrobalance.

Degree of polyandry

An estimate of the degree of polyandry in each species was obtained by calculating the mean number of spermatophores found in the bursa copulatrix in wild-caught females (Table 1). The females were all caught in Sweden except *Papilio machaon* females, which were caught in Italy. Information on the mean number of spermatophores for the monarch was calculated from Pliske (1973).

It is important to emphasize that the measurement of some of the parameters assessed in this study are difficult, and, therefore, the data presented must be regarded as tentative. The weight of adult butterflies varies with age and, moreover, their weight is strongly sensitive to whether they have recently fed or not. Secondly, in the case when ejaculates were obtained from wild males, it is conceivable that some males may have mated before, in which case the ejaculate mass obtained for that individual may represent an underestimate. Thirdly, one of the most difficult parameters to estimate is the average number of times females of a given species usually mate. Although the number of spermatophores found in the bursa copulatrix of wild-caught dissected females is easy to assess, the number of times that females of a given species mate in nature may vary not only with female age but also with population density both within and between seasons. However, the most important conclusion drawn, with the realization that many of the parameters studied in this paper are difficult to assess, is that the coefficient of determination cannot be expected to be high.

A possible phylogenetic difference in the allometric relation between male mass and ejaculate mass was searched for by calculating separate regression lines for the two butterfly families in study: the pierids and the satyrids. A difference in slope or elevation between the groups would then reflect a difference in the allometric relation. We used data from 11 Swedish pierids (Table 1, species 1–11) and 11 Swedish satyrids (Table 1, species 12–22).

A multiple regression was performed within each family to examine the influence of the degree of polyandry on ejaculate mass when the allometric effect of male mass had been removed. We gathered data on the degree of polyandry in the same 11 pierid species and in 9 of the satyrid ones (Table 1).

The ejaculate production capacity was studied in seven species (Table 1, species 3, 4, 19, 20, 23, 24 and 25). The species were of Swedish origin, except the monarch that was flown in from Florida in the pupal stage. The same procedures as already described were carried out to obtain data on male mass, ejaculate mass, and degree of polyandry. The measures of ejaculate weights in Table 1 are from the males' first matings. The males were remated on the same day or 1–5 days after the first mating, and their ejaculates were weighed. Ejaculate weights in rematings were regressed for the days following the first mating in each species. The regression lines were calculated for the 4 or 5 days following the first mating (Fig. 3). The rate

Table 1. Male weight, ejaculate weight, ejaculate weight as % of male weight, mean number of spermatophores per female, egg weight as % of female weight, rate at which males were able to produce sperm and accessory substances (sas), and sas as % of male weight in different butterfly species

Species	Male weight (mg)	(n)	Ejaculate weight (mg)	(n)	% of male weight	Mean number of spermatophores/female	(n)	Egg* weight as % of female weight	Rate of sas-prod.	% of male weight
1. <i>Aporia crataegi</i>	166.2±5.8	2	25.09±1.12	3	15.1	1.69±0.14	23	0.06		
2. <i>Pieris brassicae</i>	112.2±6.6	6	11.34±0.74	6	10.1	1.22±0.04	90	0.08		
3. <i>Pieris rapae</i>	49.2±2.0	23	6.72±0.21	23	13.4	2.13±0.09	129	0.17	1.12	2.3
4. <i>Pieris napi</i>	44.5±1.0	66	6.66±0.22	66	15.0	2.03±0.11	87	0.18	0.46	1.0
5. <i>Pontia daphidice</i>	50.2	1	4.21	1	8.4	1.84±0.15	31	0.21		
6. <i>Anthocharis cardamines</i>	44.5±1.9	3	1.88±0.13	3	4.2	1.11±0.07	19	0.28		
7. <i>Colias hyale</i>	110.5	3	6.29	1	5.7	1.53±0.21	17	0.21		
8. <i>Colias nastes</i>	52.7±2.3	3	8.18±0.82	4	15.5	1.86±0.26	7	0.19		
9. <i>Colias palaeno</i>	92.1	1	6.63	1	7.2	1.17±0.17	6	0.12		
10. <i>Gonopteryx rhamni</i>	97.2±8.2	5	5.71±1.00	5	5.9	1.20±0.07	35	0.08		
11. <i>Leptidea sinapis</i>	23.0±0.4	2	2.71±0.64	2	11.8	1.14±0.07	29	0.52		
12. <i>Hipparchia semele</i>	87.5±2.2	5	4.48±0.78	5	5.1	1.20±0.06	44	0.22		
13. <i>Erebia ligea</i>	48.2±2.5	2	0.94±0.90	2	2.0	1.00±0.00	54	0.63		
14. <i>Maniola jurtina</i>	47.9±3.8	2	1.57±0.16	2	3.3	1.00±0.00	13	0.18		
15. <i>Aphantopus hyperantus</i>	37.6	1	0.67	1	1.8	1.05±0.02	107	0.49		
16. <i>Coenonympha pamphilus</i>	21.2±0.8	4	0.31±0.03	4	1.5	0.97±0.05	63****	0.75		
17. <i>Coenonympha tullia</i>	23.6±1.4	8	0.62	1	2.6			1.11		
18. <i>Coenonympha arcania</i>	20.3±0.9	5	0.60±0.09	2	3.0			1.03		
19. <i>Pararge aegeria</i>	57.6±1.3	14	0.81±0.03	14	1.4	1.00±0.04	53	0.66	0.04	0.1
20. <i>Lasiommata megera</i>	68.2±3.2	20	1.98±0.05	21	2.9	1.12±0.05	57	0.56	0.18	0.3
21. <i>Lasiommata maera</i>	52.9±1.3	4	2.56±0.42	4	4.8	1.04±0.04	26	0.57		
22. <i>Lasiommata petropolitana</i>	47.5±1.7	2	2.03±0.10	2	4.3	1.22±0.15	9	0.63		
23. <i>Danaus plexippus</i>	697.3±20.9	16	36.64±1.91	16	5.3	2.13±0.17	91**		6.42	0.9
24. <i>Papilio machaon</i>	312.0±0.10	15	10.86±0.29	15	3.5	1.16±0.11	12***		0.70	0.2
25. <i>Polygonia c-album</i>	169.0±7.94	11	11.46±0.57	22	6.8	2.42±0.31	12		1.81	1.1

* data from Wiklund et al. (1987); ** data from Pliske (1973); *** data collected in Italy; **** data from Wickman (1986)

at which males are able to produce sperm and accessory substances in each species is reflected by the slope of its regression line (Table 1).

The influence of degree of polyandry on the rate at which males were able to produce sperm and accessory substances was investigated in a multiple regression analysis, which allowed us to remove the effect of male size on the variable under study. The relation between the mass of the ejaculate delivered in the first mating and the males' capacity to produce additional sperm and accessory substances were analyzed in a regression analysis. Since both variables are dependent on male body mass, the analysis was done on residuals from regressions of the variables on male body size. In all regressions on male mass, natural logarithmic values were used.

Results

Ejaculate weight was dependent on male weight in both pierids ($r^2=0.57$, $F=11.89$, $P=0.007$, $n=11$) and satyrids ($r^2=0.71$, $F=22.54$, $P=0.001$, $n=11$; Fig. 1). When the regression lines for the two families were compared, their slopes did not

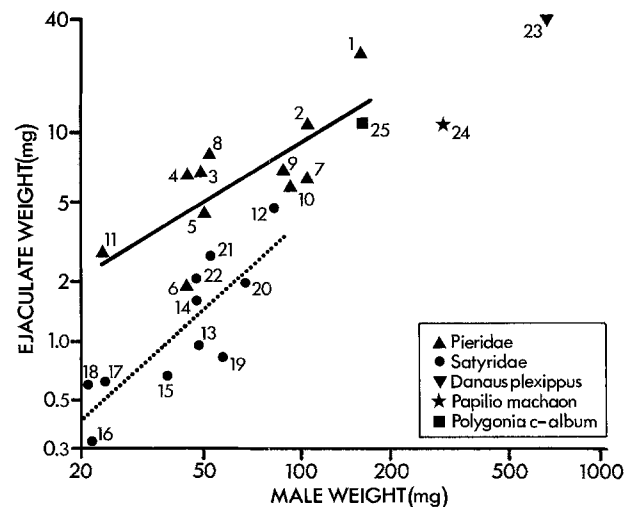


Fig. 1. ln ejaculate weight (mg) regressed on ln male weight (mg) in 11 pierids, ($\ln y = -\ln 1.95 + 0.90 \ln x$) and 11 satyrids, ($\ln y = -\ln 5.04 + 1.38 \ln x$) and three additional species. Numbers refer to butterfly species in Table 1

Table 2a, b. Multiple regression of ln male weight (mg) and ln polyandry on ln ejaculate weight (mg) for: **a** Pierids; **b** Satyrids. Significance was tested by analysis of variance

Variable	Coefficient	SE	Significance level
a			
Constant	-2.507	0.938	0.0283
ln male weight	0.924	0.215	0.0026
ln polyandry	1.126	0.487	0.0497
<i>n</i> = 11			
Overall <i>F</i> = 11.48	<i>P</i> = 0.0045		
<i>r</i> ² (adj. for <i>df</i>) = 0.68			
b			
Constant	-5.244	1.646	0.0189
ln male weight	1.366	0.440	0.0209
ln polyandry	3.223	2.070	0.1706
<i>n</i> = 9			
Overall <i>F</i> = 13.04	<i>P</i> = 0.0065		
<i>r</i> ² (adj. for <i>df</i>) = 0.75			

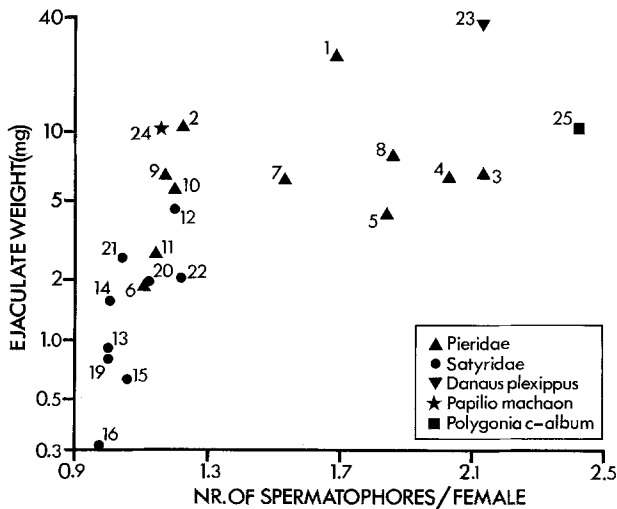


Fig. 2. ln ejaculate weight (mg) in relation to mean number of spermatophores per female in the 25 species included in this study. Numbers refer to butterfly species in Table 1

Table 3. Multiple regression of ln male weight (mg) and ln polyandry on ln daily ejaculate production (mg). Significance was tested by analysis of variance

Variable	Coefficient	SE	Significance level
Constant	-6.155	1.028	0.0039
ln male weight	0.874	0.212	0.0147
ln polyandry	3.072	0.601	0.0069
<i>n</i> = 7			
Overall <i>F</i> = 25.76	<i>P</i> = 0.0052		
<i>r</i> ² (adj. for <i>df</i>) = 0.89			

differ ($t = 1.23$, $P > 0.2$, $n = 22$); however, their elevations did ($t = 12.09$, $P < 0.001$, $n = 22$). The regression line for pierids has a higher elevation than for satyrids (Fig. 1).

In addition to the effect of male weight, the degree of polyandry also had a positive influence on ejaculate weight in pierids (Table 2). The fact that a wide variation in both relative ejaculate weight and degree of polyandry was found in two subfamilies, the pierinae (species 1–6) and coliadinae (species 7–10) furnished more support to this relation. This effect was not significant in satyrids (Table 2). However, the satyrids showed little variation in the degree of polyandry, most of the species being essentially monandrous (Fig. 2).

The rate at which males were able to produce sperm and accessory substances was likewise influenced by male weight and degree of polyandry in the seven species examined (Table 3). There was also a positive correlation between the residuals from the regressions of ejaculate weight in the first mating on body weight, and the rate at which males were able to produce sperm plus accessory substances on body weight ($r^2 = 0.77$, $P = 0.009$, $n = 7$). A greater tendency to reach values of the same magnitude as in the first mating was observed in more polyandrous species when ejaculate weights in rematings was examined (Fig. 3).

To test if relative ejaculate mass was related to female fecundity (since a larger number of spermatozoa may be needed to fertilize a larger number of eggs), we regressed relative ejaculate weight against relative egg weight in the pierid and the satyrid species (data on relative egg weight, see Table 1, were obtained from Wiklund et al. 1987). The assumption is that egg weight is negatively correlated with fecundity. However, no significant regression was found in either of the two families (pierids: $r^2 = 0.00$, $F = 0.03$, $P = 0.87$, $n = 11$; satyrids: $r^2 = 0.01$, $F = 1.39$, $P = 0.26$, $n = 11$), yielding no support to the conception that high fecundity selects for large relative ejaculate mass.

Discussion

How strong is the evidence that different species differ with respect to degree of polyandry, and what determines female remating frequency? Within species the number of matings performed increases with female age (Pliske 1973; Drummond 1984 and references therein; Rutowski and Gilchrist 1986), and the same holds true for males (Drummond 1984; Elgar and Pierce 1988), creating the possibility that male mating capacity may also be

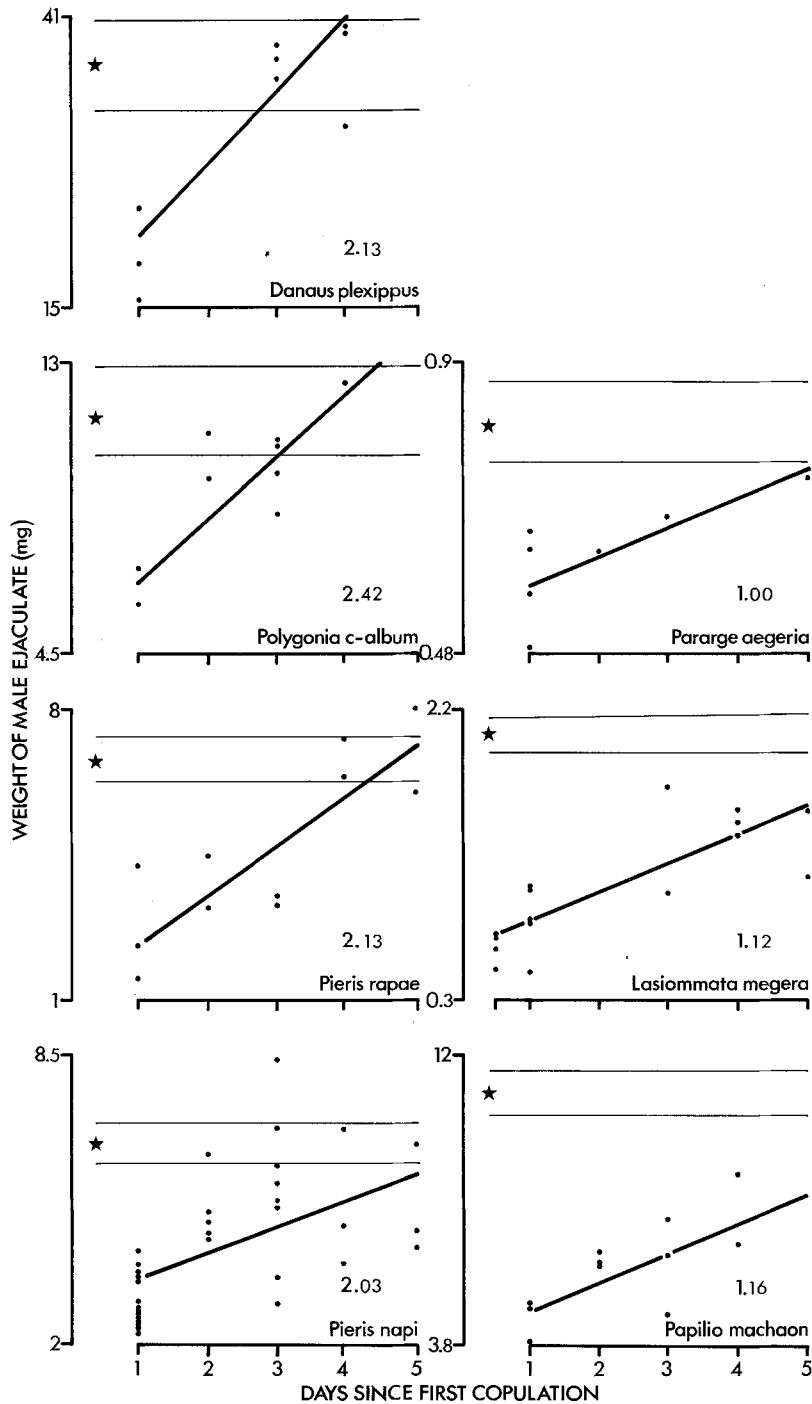


Fig. 3. Ejaculate weight (mg) of second matings by males of seven butterfly species in relation to time elapsed since the first mating. All regressions are significant at the 0.05 level. Mean ejaculate weight of first mating is indicated by *; the horizontal lines show the 95% confidence interval around the mean. The mean number of matings per female in each species is indicated above the species names

associated with male and/or female life expectancy. However, although the number of matings performed by both males and females should increase with age under polygamy, this does not mean that the number of matings performed increase with age in species where females as a rule mate only once in their lifetime. For example, when males and females of the satyrids *Pararge aegeria* and

Lasiommata megera are kept in breeding voliaries for several weeks, the majority of females still mate only once in their lifetime (Wiklund and Persson 1983; Wiklund and Karlsson 1984). Moreover, individuals were also collected throughout the flight season, among them satyrids that had an average number of spermatophores per female around 1.0 (*Erebia ligea*, this study; *Aphantopus hyperanthus*,

Wiklund 1982; *Coenonympha pamphilus*, Wickman 1986; *Pararge aegeria*, Wickman and Wiklund 1983; see Table 1), strongly indicating that these satyrids approach a monandrous mating system.

Since most butterfly species live for about a week in the field (Scott 1986), there is little evidence to suggest that there is a between species association between longevity and the degree of polygamy. Indeed, available data show the life expectancy of pierids, e.g., *Pieris napi*, *P. rapae* (Chew 1981), *P. brassicae* (Feltwell 1982), and *Lepidea sinapis* (Warren et al. 1986) varies between 5 and 12 days as does the life expectancy of monandrous satyrids, like *P. aegeria* (Wickman and Wiklund 1983), *C. pamphilus* (Wickman 1985), and *Maniola jurtina* (Brakefield 1984). This yields little support to the idea that the degree of polyandry is associated with the life expectancy of butterflies.

Even though the assessment of male mass, ejaculate mass, and degree of polyandry may be subject to critical examination and discussion, the coefficients of determination were rather high in the significant regressions. Therefore, our contention is that the pattern found in this study is likely to reflect "real" patterns in nature. Although it has been suggested that male butterflies of all species deliver roughly the same proportion of their body weight as ejaculates at mating (Rutowski et al. 1983), this study clearly supports the expectation by Boggs (1981a) that a wide range of variation in the ejaculate mass relative to male body mass is found in the Lepidoptera.

The data indicate that the degree of polyandry has a substantial effect on the reproductive performance of males. Firstly, the allometric line between male body mass and ejaculate mass has a higher elevation in the pierids compared to satyrids (Fig. 1). The mean number of matings performed by the pierid species, $1.54 \pm 0.12 SE$, is also higher compared to the mean of $1.07 \pm 0.03 SE$ in the satyrids. Thus, the relative ejaculate mass is greater in the family in which polyandry is more pronounced. Accordingly, a within family effect of degree of polyandry on relative ejaculate mass is also detected in the pierids (Table 2). Secondly, not only is the mass of the ejaculate greater in more polyandrous species, but also the rate at which males are able to produce sperm and accessory substances, as measured by the increase in the mass of the ejaculate delivered by males after various number of days since the last mating (Fig. 3). Accordingly, since available evidence strongly indicates that male butterflies cannot enforce copulations on females (Wiklund 1982; Wiklund and Forsberg 1985) this study indicates that, as in pri-

mates (Harcourt et al. 1981; Harvey and Harcourt 1984), sperm competition between males selects for greater ejaculate production capacity also among butterflies.

Assuming that different species vary in the tendency of females to remate, what determines this variation? As Parker (1984) has pointed out, female "unreceptivity may be favourable when time and risk involved in additional copulations exceeds that in rejecting males", whereas "polyandry might be beneficial to females for reasons of indirect paternal investment that might be quite important in some species". Parker concludes that in cases where male and female evolutionary interests differ, the game between the sexes may resemble an arms race in which environmental effects will lead to a distribution of arm levels in each sex, and the outcome of contests will vary (Parker 1983).

Among species where females tend to mate more than once, a number of factors could conceivably explain in what way females may benefit from mating repeatedly. Firstly, females may need to replenish their sperm supply to fertilize their eggs. In *Papilio polyxenes* the average fertility of eggs decreased after 10 days, suggesting that the tendency of aging females to remate may be explained by the need to replenish their sperm supply (Lederhouse 1981). Additionally, among satyrids where the majority of females of most species tend to mate only once, females that are found to have mated twice, often have one spermatophore that is much smaller than the other. This suggests that the small spermatophore was received first and may have a sperm content that is inadequate to fertilize all of the eggs (Wiklund 1982). However, as a rule, one spermatophore contains enough sperm to fertilize all of a butterfly female's eggs (Suzuki 1978; Rutowski 1984; Svård and Wiklund 1988b), which excludes this factor as a general explanation for at least high degrees of polyandry. Secondly, females may mate repeatedly to increase the genetic diversity of their offspring. However, Parker (1984) has argued that "the female's mating pattern is much less likely to arise for reasons of 'good genes' or 'genetic diversity' than from the everyday environmental pressures on females due to copulation time waste on the one hand, and energy or time waste in harassment by courting males on the other". Thirdly, behavioral evidence indicates that male butterflies transfer antiaphrodisiacs to females at mating that can be used by females to curtail male courtship (Gilbert 1976; Wiklund and Forsberg 1985). Evidence from *Pieris napi*, in which females mate up to five times in

their lifetime, indicates that the antiaphrodisiac wears off with time, suggesting that females may remate to replenish their reserves of antiaphrodisiacs. Fourthly, females may mate repeatedly to receive nutrients transferred to them at mating. Studies using radioactive amino acids show that male-transferred amino acids are rapidly incorporated into the female eggs and soma (Boggs and Gilbert 1979; Boggs and Watt 1981; Greenfield 1982), and it has been shown that a variety of nutrients are transferred to the female at mating, e.g., pyrrolizidine alkaloids (Goss 1977), sodium (Pivnick and McNeil 1988), zinc (Engebretson and Mason 1980), and lipids and proteins (Marshall 1985). Hence the idea has been put forward that the females can use these male-derived nutrients to increase their reproductive output. At present the extent to which female butterflies use male-derived nutrients to do so appears somewhat undecided, with some studies supporting the idea (Rutowski et al. 1987; Watanabe 1988), and others showing no sign of increased reproductive output as a result of male-derived nutrients received (Greenfield 1982; Jones et al. 1986; Svård and Wiklund 1988b). However, although the possible role of male-derived nutrients in increasing reproductive output in female butterflies is uncertain at present, it is relevant to point out that this factor can potentially provide a rationale for remating among polyandrous butterflies, but it cannot explain the variance in the degree of polyandry per se, unless it is coupled to some theory that explains under what circumstances male-derived nutrients are likely to be important, or relatively unimportant, to females.

In conclusion we have shown that there is substantial variation in the degree of polyandry within the Pieridae and between the Pieridae and Satyridae, and that the capacity of the males to produce large and many ejaculates seems to be associated with the degree of polyandry, suggesting that sperm competition is an important factor for shaping the pattern of male reproductive investment.

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