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, Lasionmata 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 1981a, 1981b). 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-incapacitation 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 Wlkund 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...