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Protandry and female size-fecundity variation in the tropical butterfly *Brassolis sophorae*

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Abstract Protandry (the emergence of males before females) is currently explained either as a mating strategy to maximize number of matings in the males, or a way to minimize pre-reproductive mortality in females. Models of protandry have generally ignored variation in female quality (reproductive potential). We recorded the sex ratio, female body mass, wing length and potential fecundity (number and mass of eggs) of the tropical butterfly *Brassolis sophorae* through the emergence period. Temporal variation in female size and fecundity correlated with male potential for acquiring mates. Females from the end of the emergence period showed lower fecundity and size. Males emerging before and close to the median date of the female emergence period had greater mating opportunities. Males emerging either very early or late were penalized by few mating opportunities, or by encounters with small, low-quality females, respectively.

Key words Protandry · Size-fecundity variation · Mate opportunity · Tropical Lepidoptera · *Brassolis sophorae*

Introduction

Protandry, the earlier emergence or maturation of males within a population (or brood), is prevalent among insects with discrete generations (Wiklund and Fagerström 1977; Thornhill and Alcock 1983) as well as in other arthropods such as spiders (Foelix 1982). Darwin (1871) was the first to perceive the theoretical importance of protandry explaining it as a result of sexual selection.

Several theoretical models have been proposed to explain the origin and maintenance of protandry (Fagerström and Wiklund 1982; Bulmer 1983; Iwasa et al. 1983; Zonneveld and Metz 1991). All these models share the assumptions of discrete generations and female monogamy, while males could potentially serve several mates. Experimental evidence supports the view that differences in emergence timing between the sexes are adaptive per se (Wiklund et al. 1992; Nylin et al. 1993). Adjusting the timing of emergence may be advantageous to both sexes, but for different reasons: later-emerging females benefit by minimizing pre-reproductive death (Fagerström and Wiklund 1982; Zonneveld and Metz 1991), and early-emerging males could maximize number of matings (Wiklund and Fagerström 1977; Bulmer 1983). Thus, optimal timing of emergence may result from the balance of different demands of the sexes. Few papers relate emergence time to possible variation in female quality (reproductive potential).

Baughman et al. (1988) pointed out the implicit assumption of protandry models that all mates have reproductive equality may be unrealistic. In the mosquito *Aedes sierrensis*, female fecundity is size-specific; predictions derived from current protandry models are improved when a temporal variation in female quality is incorporated (Kleckner et al. 1995).

As far as we know, studies on the origin and maintenance of protandry have been restricted to species from temperate regions. This paper analyzes protandry in the common tropical butterfly *Brassolis sophorae* (Nymphalidae), with empirical evidence for temporal variation in female size-fecundity and discussion of whether this could influence protandry.

Brassolis sophorae, the palm or coconut caterpillar, is well known as a pest in the neotropics (Cleare 1915; Costa Lima 1936; Rai 1973). It has two discrete gener-

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ations per year, with an opportunistic strategy of colonization and dispersal, and frequently reaches outbreak levels like other brassolines (Young and Muyshondt 1975).

Many palm trees (Arecaceae) species are used as larval host plants, both native (*Syagrus* spp., *Euterpe* spp., *Copernicia* spp.) and exotic (*Cocos* spp., *Washingtonia* spp.). Pupating larvae leave the palm tree and spread out in search of pupation sites, such as crevices or other protected places. In urban areas, these are usually overhangs on buildings, such as windows sills and girders, retracted skirting-boards or instrument boxes, which act as partial refuges against parasitoids (Ruszczyk 1996). Pupal mortality due to parasitoid load is not sex-biased (Ruszczyk 1996).

The adult emergence period of *B. sophorae* lasts nearly 5 weeks. Both sexes are able to mate soon after emergence. The flight period of adults is restricted to dusk when males usually patrol free aerial spaces. Males have a fast, erratic flight, while females show slower planar flight. When perched males and females are disturbed by an approaching observer, males take flight first, being harder to collect than females. Mating may occur within one day after emergence. Females are larger than males, both in adult body mass and wing length (Ruszczyk and Carvalho 1993). This affects their abdomen, characteristically distended by the egg complement, and their dispersal capacity. Adult predation by the guira cuckoo, *Guira guira* (Cuculidae), and deaths related to human disturbance have been shown to be female-biased (Ruszczyk and Carvalho 1993).

Since adults of *B. sophorae* have a degenerate proboscis and do not feed or drink, almost all their activities relate to reproduction. Freedom from foraging demands may give more weight to selection on mating behavior, especially in males. They thus represent good material for investigation of selective forces related to protandry.

Materials and methods

Study sites

Observations were made of *B. sophorae* on the external walls, and in the gardens and surrounding lawns of eight buildings on the campus of the Campinas State University (UNICAMP), Campinas, São Paulo State, Brazil in October–November 1987 and 1989 (see Ruszczyk and Carvalho 1993). Several palm species grow in the gardens, mainly *Syagrus romanzoffiana* (Cham.) Glassman. The climate in the Campinas region is tropical and markedly seasonal in rainfall: wet and hot from October to March and dry and colder from April to September (70–120 mm, 200 mm in some years vs. 40–70 mm; year total: 1400 mm), with a mean temperature of 20.5°C.

Data collection and analysis

Individual adults, collected in 1987 (on alternate days), were marked on the hind wings with waterproof pilot pens, recording sex, collecting site, dates of emergence and recaptures. In 1989, all individuals newly emerged from pupae (on four buildings) were measured (forewing length) and weighed, and the crepuscular adults were collected in flight.

In 1989, longevity was estimated in the laboratory, at ambient temperature. Measured butterflies were numbered and placed in two cages (60 × 90 × 150 cm) separated by sex, with dead individuals being recorded each day.

Reproductive potential of females was estimated as two fecundity correlates: total number of mature oocytes (eggs) inside female ovaries and mean egg mass. The 36-day emergence period was divided into three equal sections. In the first two sections 15 individual females were sampled at random, while in the third section only 8 females were collected and these 38 newly emerged females were dissected for potential fecundity estimate. Eggs, disconnected from the other tissues, were counted in a Petri dish under the stereo-microscope, and separated into two categories: fully developed (larger, regular shaped, with a hard surface) and undeveloped (smaller, fragile, irregularly shaped). The set of developed eggs from each butterfly was dried in an oven at 60°C for 24 h before weighing.

Male mating success was evaluated following Hastings (1989) through a mating opportunity index (MOI) for each of the 20 recorded cohort of newly emerged butterflies along the emergence period. The MOI was calculated as [(number of newly emerged females recorded on day x) + 1/(total number of males available on day x) + 1] summed over 9 days, the mean lifetime of male adults as observed in cages. We added 1 to each factor to avoid zeroes in the denominator. Newly emerged individuals were identified by their characteristic behavior, staying close to, or perching on the pupal skin before the first flight (to expand their wings), along with distinctive meconium droppings.

The means of mass, wing length, and egg weight of *B. sophorae* from the three sections of the emergence period were compared by analysis of variance.

Results

Protandry was a prevailing pattern of adult emergence in both years and most sites, with a varying degree (Table 1). In 1987 only 35 marked adults (25 males and 10 females) were recaptured from a total of 611 (5.7%), with a clear male bias. Since females are easier to capture than males, this bias may have been even greater, suggesting a higher dispersal of females.

Females from the earlier two sections of the emergence period had equivalent body mass (Fig. 1; ANOVA, $F_{(1,\ 93)} = 0.18$, $P = 0.673$), greater than that of females from the latest section (Fig. 1; ANOVA, $F_{(1,\ 93)} = 6.26$, $P < 0.02$). This same pattern was especially evident for fecundity correlates affecting egg numbers with an even greater decrease in later-emerged females (Fig. 2; ANOVA, $F_{(1,37)} = 1.547$, $P = 0.224$ and $F_{(1,37)} = 14.035$, $P < 0.001$; respectively, for total egg number; $F_{(1,37)} = 7.33$, $P < 0.02$, and $F_{(1,37)} = 17.58$, $P < 0.002$; for developed eggs), but not the average mass of each egg.

Egg size, measured as the mean mass of developed eggs (Fig. 2C), and percent of undeveloped eggs per individual female remained nearly constant along the emergence period (ANOVA, $F_{(2,\ 37)} = 0.213$, $P = 0.809$, and $F_{(2,\ 37)} = 2.617$, $P = 0.087$, respectively). Total number of developed eggs and female body mass at emergence were not correlated with the mean mass of developed eggs ($r = -0.104$, $n = 38$ and $r = 0.051$, $n = 33$, respec-

Table 1 Protandry in emerging adults of *Brassolis sophorae* in the UNICAMP university campus, São Paulo state, Brazil. A zero indicates absence of protandry and negative values indicate protogyny (n = newly emerged adults, N = total number of butterflies)

Season	Site	$n(N)$	Difference between first female and male emergences (days)	Difference between medians of female-male emergence curves (days)
1987	1	83 (210)	6	3
	2	40 (154)	2	8
	3	3 (66)	4	–
	4	2 (58)	1	–
	5	2 (47)	8	–
	6	8 (41)	−6	–
	7	4 (35)	0	–
1989	8	48 (104)	8	13
	1	29 (115)	5	−1
	2	19 (83)	5	5
	3	10 (36)	8	13

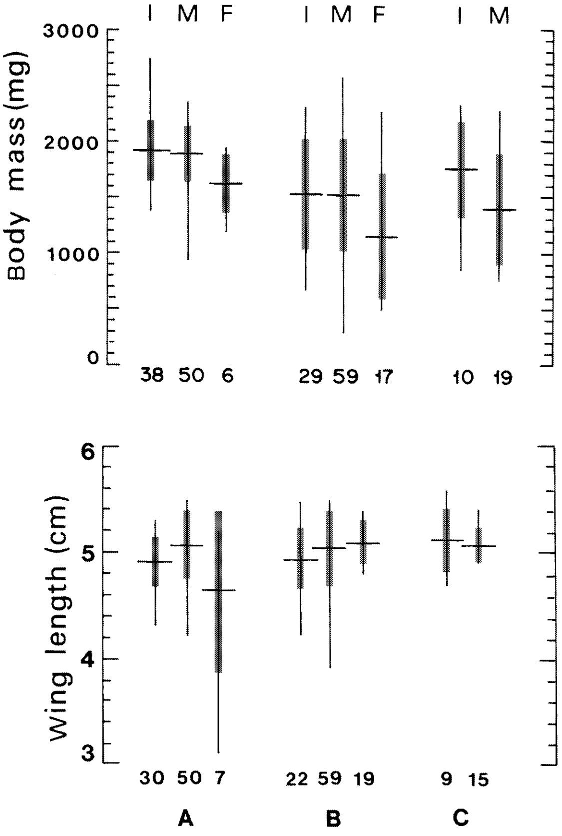

Fig. 1A–C Body size (fresh body mass and wing length) of *Brassolis sophorae* females from the initial (*I*), middle (*M*), and final (*F*) sections of the emergence period. **A** Newly emerged individuals, **B** perched (mainly on building walls), and **C** flying at dusk. *Lines* indicate means (*horizontal*) and ranges (*vertical*), *bars* are ±SD. *Sample sizes* are shown at the bottom of each vertical line

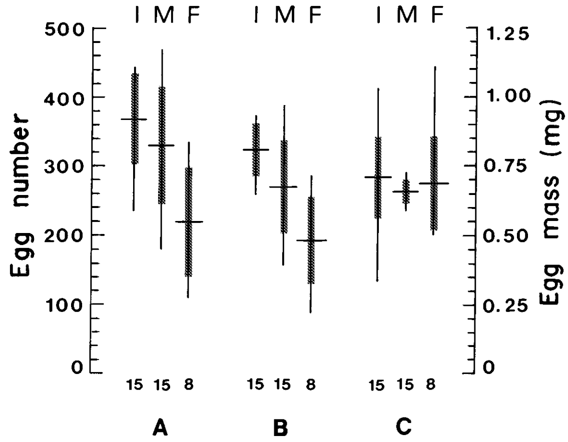

Fig. 2A–C Fecundity correlates of newly emerged females of *B. sophorae* from the initial (*I*), middle (*M*), and final (*F*) sections of the emergence period. **A** Total number of eggs (potential fecundity) present in female ovaries, **B** number of developed eggs only, and **C** mean mass of individual eggs. *Lines* indicate means (*horizontal*) and ranges (*vertical*), *bars* are ±SD. *Sample sizes* are shown at the bottom

tively). Number of developed eggs per female averaged 274.7 ± 12.1 (mean ±SD), with a range of 105–392.

There was a weak, positive correlation between total egg number and female body mass at emergence ($r = 0.390$, $P < 0.05$, $n = 32$). Total egg number per female averaged 326.5 ± 94.3 (mean ±SD), with a range of 105–468.

Females in the middle of the emergence period had longer wings than females from extreme periods (Fig. 1; ANOVA, $F_{(1,\ 79)} = 7.91$, $P < 0.01$).

Adult longevity was very similar for both sexes: 9 ± 2.89 (mean ± SD) days for males and 9 ± 2.80 days for females. There was a non-significant positive correlation between longevity and size (measured either as body mass or as wing length) for both sexes.

Male mating opportunity indexes were different between the three sections of the emergence period (ANOVA, $F_{(2,\ 20)} = 5.14$, $P < 0.02$). Higher MOI values were found around the median of male emergence and within the interval eight days before to one day after the median of female emergence dates (Fig. 3). Variation in MOI along the emergence period was parallel to the patterns of variation in female body mass and potential fecundity (Figs. 1 and 2) but with great variability in the first section (Fig. 3).

Discussion

Higher mating opportunities for *B. sophorae* males in the two earlier sections of the emergence period agreed with current explanations of protandry, in which earlier-

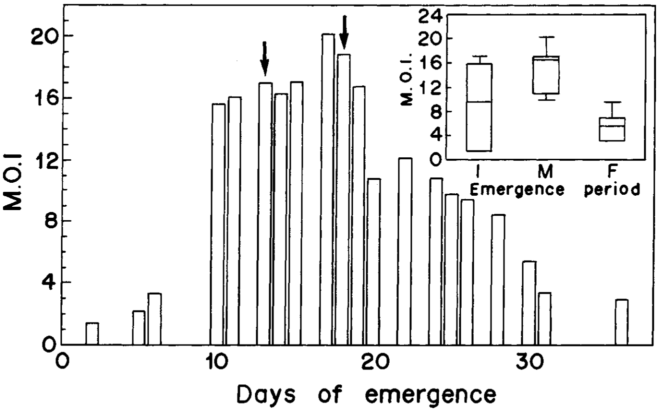

Fig. 3 Mating opportunity index (MOI) of male newly emerged *B. sophorae* from 20 cohorts along the emergence period of 1989 at UNICAMP university campus (*left arrow* median of male emergence, *right arrow* median of female emergence). *Upper right corner*: grouped MOI values from each section of the emergence period (*I* initial, *M* middle, *F* final), median (*horizontal line*), *boxes* give upper and lower quartiles (75% and 25%) and *whiskers* are maximum and minimum values

emerging males maximize their reproductive success (Wiklund and Fagerström 1977). According to these proposals, the fitness payoff works through higher probability of mating success for earlier males and a disadvantage for later ones with low mating expectation. The distribution pattern of male mating opportunities, together with decreasing female quality in the final section of emergence, suggests that, by emerging earlier, males *B. sophorae* increased the probability of meeting larger and more fecund females as well as to maximizing the number of matings. These results do not support the hypothesis that protandry is an evolutionarily stable strategy of males achieved through equality in number of matings (Bulmer 1983; Iwasa et al. 1983), though such a pattern of mating success unaffected by date of emergence is found for the butterfly *Euphydryas editha* (Baughman 1991). Instead, concentration of peak MOI values close to the median male cohorts agreed with the results of Kleckner et al. (1995) for *Aedes sierrensis*. These authors developed simulations accounting for temporal variation in female size-fecundity which increased the robustness of current protandry models. They found that the male fitness landscape is higher near the median of male emergence which, as they suggest, tends to stabilize protandry rather than favor extreme values.

Size-fecundity correlations are weaker in *B. sophorae* than most insects studied, such as other butterflies where this correlation is pronounced (but see Leather 1988).

Absence of a trade-off between short development time and large adult body mass is well demonstrated by Nylin et al. (1993) for several populations of the butterfly *Pararge aegeria*. In *B. sophorae* the smaller size of later-emerging females pointed to relationship in the opposite direction, giving the worst of both worlds (long development time and small adult body mass), perhaps due to differential larval growth rates resulting from intraspecific competition for larval food as is demonstrated by Kleckner et al. (1995) for *Aedes sierrensis*. Whatever the nature of the causal agent, this agrees with the elegant experimental evidence demonstrating independence between body size and protandry (Nylin et al. 1993).

After mating, females appear to disperse from their eclosion area, perhaps seeking new individual host plants for oviposition, due to patch depletion that may result from larval development. As *Guira guira* and *B. sophorae* are sympatric and common over a wide range (from disturbed suburban and rural areas to the savanna-like vegetation of central Brazil), the predation pressure exerted by *G. guira* on female *B. sophorae* (Ruszczyk and Carvalho 1993) could support models that explain protandry through reduction of female predation risk with minimization of female pre-reproductive period and maximization of encounter rates (Fagerström and Wiklund 1982; Zonneveld and Metz 1991).

As food availability for *B. sophorae* seems to be independent of the tropical climatic fluctuations, this study showed that protandry may not be a function of the degree of environmental seasonality as Singer (1982) predicted. However, protandry seems to be more pronounced in temperate butterflies, which must synchronize emergence with flowering of nectar source plants such as *Gonepteryx rhamni* (Wiklund et al. 1996). The absence of adult feeding in *B. sophorae* may be a factor related to this difference in intensity of protandry. The variability in degree of protandry we found, sometimes larger than that observed in temperate regions (Nylin et al. 1993), may be explained by variability in larval density between sites as showed for *Aedes sierrensis* (Kleckner et al. 1995).

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