



## Intraspecific competition in the speckled wood butterfly *Pararge aegeria*: Effect of rearing density and gender on larval life history

Melanie Gibbs<sup>1</sup>, Lesley A. Lacey<sup>1</sup>, Martin J. Jones<sup>1</sup> and Allen J. Moore<sup>2</sup>

<sup>1</sup>Department of Biological Sciences, Manchester Metropolitan University, U.K.

<sup>2</sup>School of Biological Sciences, University of Manchester, U.K.

[melanie.gibbs@man.ac.uk](mailto:melanie.gibbs@man.ac.uk)

Received 10 November 2003, Accepted 10 April 2004, Published 19 May 2004

### Abstract

In insects, the outcome of intraspecific competition for food during development depends primarily upon larval density and larval sex, but effects will also depend on the particular trait under consideration and the species under study. Experimental manipulations of larval densities of a Madeiran population of the speckled wood butterfly *Pararge aegeria* confirmed that intraspecific competition affected growth. As densities increased *P. aegeria* adults were smaller and larval development periods were longer. Sexes responded differently to rearing density. Females were more adversely affected by high density than males, resulting in females having smaller masses at pupation. Survivorship was significantly higher for larvae reared at low densities. No density effect on adult sex ratios was observed. Intraspecific competition during the larval stage would appear to carry a higher cost for females than males. This may confer double disadvantage since females are dependent on their larval derived resources for reproduction as they have little opportunity to accumulate additional resources as adults. This suggests that shortages of larval food could affect fecundity directly. Males, however, may be able to compensate for a small size by feeding as adults and/or by altering their mate location tactics.

**Keywords:** Larval density, larval development, sex differences, fecundity

### Introduction

Intraspecific competition has been shown to affect development of insects (Applebaum and Heifetz 1999), usually because variation in density affects the amount of food available to larvae (Dethier 1959; Putman 1977). For example, in *Aedes polynesiensis* (Diptera: Culcidae) and *Epirrita autumnata* (Lepidoptera: Geometridae), intraspecific competition resulted in a longer larval development period (Mercer, 1999; Tammaru *et al.* 2000). Long larval development periods are generally considered to be disadvantageous since they may limit opportunities for reproduction (Fischer and Fiedler 2000; Gottard *et al.* 1994), and they lengthen the larva's exposure time to predators and parasitoids (Klok and Chown 1999). Under some conditions, however, there may be advantages of longer development. Longer development can result in an increase in body mass (Wiklund and Forsberg 1991) because the ability to consume more food over a longer period is thought to result in larger adults (Rahman 1969). For the species *A. polynesiensis* and *E. autumnata* however, larval competition resulted in the production of small adults over long development periods (Mercer 1999; Tammaru *et al.* 2000). Generally, small adult size is considered disadvantageous because large size is often positively correlated with fecundity and/or competitive capacity (Gotthard *et al.* 1994; Nylin and Gotthard 1998; Putman 1977;

Ullyett 1950). These findings suggest that intraspecific competition during the larval period has the potential to reduce overall fitness. However, fitness effects will depend on adult, as well as larval ecology.

Larval density depends on the size, number and distribution of larval food resources, as well as the number and distribution of eggs (Dethier 1959). Female oviposition behavior will therefore determine the conditions under which newly hatched larvae will begin their growth period. The speckled wood butterfly *Pararge aegeria aegeria* (L.), prefers to lay on *Brachypodium sylvaticum* (Owen *et al.* 1986), and is extremely selective about host-plants and their location (Baez *et al.* 1992). Such selectivity can lead to some plants, and locations, being used by more than one female (Shreeve and Smith 1992). When multiple eggs are laid on a single plant there will be a decrease in the amount of food available for each larva, leading to competition for resources. Over-crowding of eggs therefore has the potential to decrease larval survival (Masumoto *et al.* 1993).

*P. aegeria* is a major model system for insect life history and ecology. This study aims to add additional information to the extensive knowledge of the life history of this species by addressing how larval density and larval sex affects life history. In addition, we examined a population of *P. aegeria* from Madeira, whereas other studies have focused on mainland Europe populations. Karlsson

*et al.* (1997) showed that male and female *P. aegeria* larvae differed in their relative sensitivity to poor host-plant conditions, with male larvae maturing at smaller sizes and reacting more strongly to low quality host-plants than females. This finding supported the predictions made by Leimar *et al.* (1994) who suggested that for monandrous species such as *P. aegeria* (Gotthard *et al.* 2000), where males do not provide nuptial gifts, the selective pressure on males to mature at a large size will be negligible. Given that adult *P. aegeria* feed on nectar, which is nutritionally poor and does not significantly contribute to female reproductive reserves (Karlsson 1994), and because males produce small spermatophores with unsubstantial nuptial gifts (Svård and Wiklund 1989), female *P. aegeria* are completely dependent on their larval-derived resources for reproduction. A decrease in the quantity of food available during larval development, perhaps due to intraspecific competition, is therefore expected to carry a higher cost for female *P. aegeria* than for male *P. aegeria*, as large body size is expected to be more important for adult females than adult males. Studying these effects in the Madeiran population will provide an interesting contrast with studies examining *P. aegeria* populations from Northern Europe.

In this experiment the effect of density on larval development and survival, as well as sex differences in response, were investigated with *P. aegeria*. Since life history traits during development are frequently plastic, and given that life history traits are strongly correlated to fitness, life history and fitness, they are expected to be strongly affected by food availability and quality. More specifically, the sex-difference in effects of food shortage found by Karlsson *et al.* (1997) will be examined further by studying the effects of larval competition on sex-specific life history traits and fitness.

## Methods

### Rearing conditions

#### *Pararge aegeria*

In 1999 50 eggs of *P. aegeria* were collected from their host-plant, *Brachypodium sylvaticum* on Madeira and brought to the Manchester Metropolitan University butterfly house for rearing. After eclosion adults (n = 36) were maintained for three generations in a flight cage 1.25 x 3.90 x 1.80 m. Adults were fed daily with a 10% honey solution via 5 artificial flowers (for design see Cory and Goulson 1993) distributed at random in the flight cage. Honey supplies were replenished daily. Ten *B. sylvaticum* plants were made available to the F<sub>3</sub> generation ovipositing

females (n = 24) for egg laying, and these eggs were used in the subsequent experiments. Host-plants were distributed randomly throughout the flight cage. Photoperiod (Nylin *et al.* 1995) and temperature (Sibly *et al.* 1997) are known to affect the development of *P. aegeria* larvae. A 12:12h LD cycle, a temperature of 21 (± 2)°C and relative humidity of 50 (± 10) % were therefore strictly maintained for the whole of the growth period (i.e. from egg stage to adult stage). Lighting in the butterfly house was provided at an intensity of 1500 lux by 8 ceiling lamps.

#### *Brachypodium sylvaticum*

The larval host-plants, *B. sylvaticum*, were grown from commercially produced seed and sown in 4-inch pots containing soil-based compost. All of the plants were grown under identical conditions at a temperature of 23 (± 2) °C and a humidity of 45 (± 10) %. Light was provided at an intensity of 7000 lux over a 16:8h LD cycle. Plants were watered daily, and fertilizers were not used.

### Experimental procedure

Eggs were collected daily from F<sub>3</sub> generation females maintained in the laboratory population. These eggs were removed from the host-plants and single eggs were placed into individual 8 ml transparent containers until hatching. Upon hatching, the larvae were randomly assigned to potted plants of *Brachypodium sylvaticum* at densities of either 1, 5 or 10+ (between 10 and 20) larvae per plant. Older larvae have been shown to have a significant competitive advantage (Krebs and Barker 1995; Briggs *et al.* 2000), therefore all of the larvae assigned to an individual plant shared the same hatching date. A total of 308 larvae were distributed over 63 plants. Plants were similar in size with approximately 40 blades per plant. The individual plants were placed into separate 0.5m<sup>3</sup> netted cages in the butterfly house. The number of larvae on the plant was checked daily and larval deaths were recorded. In addition, to maintain the density at the appropriate level throughout growth, any larvae found crawling from the plant were returned to their host-plant. Any plants that had been completely consumed by the larvae were changed 12 hours after defoliation, so that there was food limitation but not food deprivation. At high densities, larvae had more frequent periods of food shortage, and food was therefore limiting (Table 1).

Pupation dates and pupal masses were recorded for each individual. At pupation, individuals were removed from their host-plant, and suspended (by a cotton thread) in separate 38ml transparent plastic containers until eclosion. Upon emergence, the sex of the

**Table 1.** Experimental design. Mean number of host-plants used per treatment and the number of replicates in each treatment

Larval density	Number of replicates	Number of times plants replaced (mean)
1	28	0.4
5	22	1.0
10+	13	2.8

**Table 2.** Two-way ANOV for effects of larval density on life history traits in *Pararge aegeria*.

Trait	Source	d.f.	MS	F-Ratio	P
Larval time (days)	Density	2	139.08	3.35	0.04
	Sex	1	5.06	0.122	0.72
	Interaction	2	23.23	0.56	0.57
	Error	105	41.49		
Pupal mass (mg)	Density	2	0.003	15,755	<0.001
	Sex	1	0.004	21,729	<0.001
	Interaction	2	0.001	4,053	0.020

**Table 3.** Life history data for male and female *Pararge aegeria* reared at different densities.

Larval density	Trait	male	female
1	Larval time (days)	(n=7) 28.86 ± 2.43	(n=9) 26.33 ± 2.15
	Pupal mass (mg)	(n=7) 110 ± 5	(n=8) 130 ± 5
5	Larval time (days)	(n=18) 30.94 ± 1.52	(n=11) 30.73 ± 1.94
	Pupal mass (mg)	(n=19) 98 ± 3	(n=12) 118 ± 4
10+	Larval time (days)	(n=39) 31.64 ± 1.03	(n=27) 32.85 ± 1.24
	Pupal mass (mg)	(n=37) 97 ± 2	(n=27) 101 ± 3

**Table 4.** Density-dependent differences in the survival of *Pararge aegeria* larvae

Density	Survival to pupation		Survival to adulthood		m : f sex ratio
	n larvae	% survival	n larvae	% survival	
1	28	82	28	61	0.44 : 0.56
5	110	36	110	29	0.59 : 0.41
10+	170	57	170	42	0.57 : 0.43

adult was recorded.

### Statistical Analyses

Two-way analysis of variance was used to investigate the effects of density and sex on larval development. To investigate specific hypotheses regarding the nature of the effects, a-priori focused contrasts (Rosenthal and Rosnow 1985) were used. Specifically, a linear comparison among density treatments was tested by contrast analysis. The effect of a social influence (i.e. a comparison of the effects of solitary versus group reared larvae) was also made using contrasts. A Pearson Chi-square test was used to compare the proportion of surviving adults at each density, and to determine whether there was a density-dependent difference in adult sex ratio. All tests were two-tailed. The statistical procedures were performed using Systat 9.0.

## Results

### Larval development

There was an overall significant effect of larval density on the length of larval development, but no effect of sex and no interaction of sex and density (Table 2). Focused contrasts showed significant specific effects of density. Development increased linearly with increasing density (Table 3; linear contrast  $F = 6.587$ ,

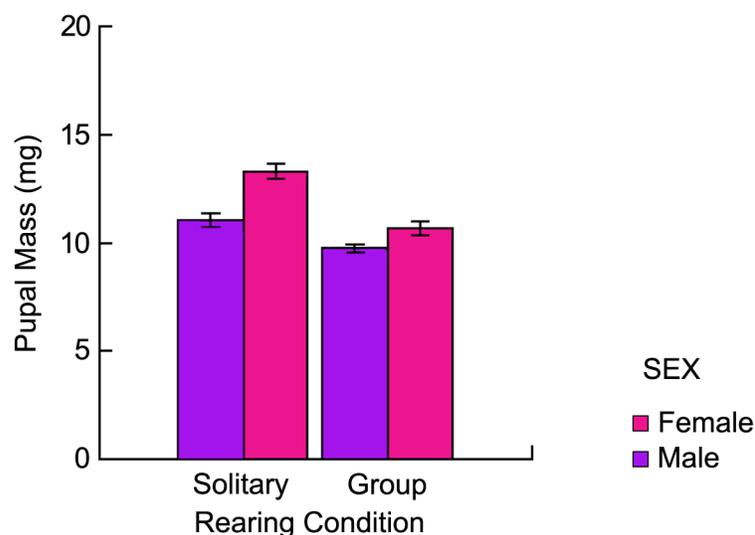
d.f. = 1, 105,  $P = 0.012$ ). In addition there was a significant effect of social exposure, with larvae reared solitarily taking significantly less time to develop than larvae reared in groups (contrast of 1 versus more than 1 larva,  $F = 4.902$ , d.f. = 1, 105,  $P = 0.029$ ).

### Pupal masses

Pupal mass was significantly affected by larval density, and sex, and there was a sex x density interaction (Table 2). Pupal mass decreased with increasing larval density (Table 3; linear contrast  $F = 28.71$ , d.f. = 1, 105,  $P < 0.001$ ). There was also a significant effect of social exposure, with larvae reared alone being significantly heavier than larvae reared in groups (contrast of 1 versus more than 1 larva,  $F = 18.24$ , d.f. = 1, 105,  $P < 0.001$ ). The sexes also differed significantly in mass (Table 2), with females being significantly heavier than males (Female:  $N = 48$ , mean =  $111 \pm 2.82$  mg; Male:  $N = 63$ , mean =  $99 \pm 1.68$  mg). Males and females both showed a significant decline in size with increasing larval density (Table 2), but the response of females to high densities was stronger than that for males (Figure 1).

### Survivorship

Density had a significant effect on survivorship to pupation (Table 4;  $\chi^2 = 22.06$ , d.f. = 2,  $P < 0.001$ ). Survival to adulthood was also affected by rearing density (Table 4;  $\chi^2 = 10.06$ , d.f. = 2,



**Figure 1.** Sex-specific effect of social condition on pupal mass. Group reared larvae of both sexes were smaller than solitary larvae, but females responded significantly more strongly than males.

$P = 0.007$ ). In both cases, survivorship was highest when individuals were reared alone. There was no significant difference in adult sex ratio across treatments (Table 4;  $\chi^2 = 1.368$ , d.f. = 2,  $P = 0.505$ ).

## Discussion

In this experiment density affected size, development and survivorship in *P. aegeria*. Additionally, there was a strong sex-dependant effect of density on size. These responses may, at least in part, reflect adult ecology. On Madeira, virgin females emerge throughout the year and there is a considerable overlap between the generations (Gotthard *et al.* 2000), therefore protandry appears to offer no competitive advantage to males (Gotthard *et al.* 1994). Ready availability of mates reduces the selection pressure on males to develop more rapidly than females, and sexual dimorphism by size is therefore not a result of selection for protandry in this species (Nylin *et al.* 1993). To attain a larger size in a similar amount of time, females have higher growth rates than males (Gotthard *et al.* 1994). Since sexual differences in food utilization efficiencies are usually small (Scriber and Slansky 1981), females probably maintain higher growth rates by either having faster relative consumption rates (Scriber and Slansky 1981), or by spending a greater proportion of their time feeding. The results of this study are contrary to those of Leimar *et al.* (1994) and Karlsson *et al.* (1997) and suggest that it is the growth rate of the sexes that is of highest importance for adult weight loss under food shortage, rather than the relative fitness premium of large size in the sexes. Madeiran and Swedish populations of *P. aegeria* differ more from each other in sex-specific growth rates and protandry, than in the effects of adult size on fitness.

*P. aegeria* responded to intraspecific competition by producing small adults over elongated development periods. Due

to their higher relative growth rate, the response of females to food shortages was significantly greater than that of males. A significant sex times density interaction was observed because females gained less weight than males as densities increased. These results support the prediction of Gotthard *et al.* (1994) that a high growth rate is costly in terms of fitness during periods of food shortage. The effect of solitary versus group rearing (Fig. 1) also suggests that social influences have an effect, although this effect may be confounded by food limitation in our study. The nature of these social influences is unclear but may include social stimulation of feeding (Nahrung *et al.* 2001; Stamp 1980), an increase in induced host-plant responses (Bernays and Chapman 1994; Hanson 1983) or direct interference (personal observation). During this experiment, at high larval densities four separate instances of direct interference were observed, where larvae were involved in prolonged (up to 20 minutes in duration) aggressive encounters. During these encounters, when two larvae came into contact with each other while feeding on the same leaf, head and tail biting and head butting were observed. During one of these encounters one larva became partially dislodged. The effect that such interference may have on feeding requires further study.

Although higher densities during the growth period resulted in a decline in pupal size for both sexes, it is expected that small size will be more costly for females than males. Size dimorphism occurs in *P. aegeria* because males and females allocate their larval derived resources differently (Sibly *et al.* 1997). Males invest in lipid reserves to enable longer mating flights or territorial disputes (Sibly *et al.* 1997), whereas females invest in nitrogen reserves, which are allocated for reproduction (Karlsson and Wickman 1990). Since *P. aegeria* feed on a more protein-rich food source in their larval stage than in their adult stage (Svärd and Wiklund 1989) and because spermatophores contain small percentages of protein (Boggs 1981), there is little opportunity for adult females to accumulate additional resources for reproduction through nuptial feeding. Thus, female fecundity is largely dependent on the resources accumulated during the larval stage (e.g. Bergström *et al.* 2002; Wiklund *et al.* 2001). Food shortages during larval development may therefore result in a reduction in fecundity. For *P. aegeria* males, however, small size may not affect their competitive ability or hinder their mate locating success. To secure as many matings as possible male *P. aegeria* adopt one of two mate location strategies; patrolling or territory defense (Davies 1978; Wickman and Wiklund 1983; Shreeve 1984; Shreeve 1987). Gotthard *et al.* (1999) argued that, in the Madeiran population of *P. aegeria*, there may actually be a preference for territorial males, over non-territorial perchers, due to the greater cost of searching in a male biased mating system. Van Dyck *et al.* (1997) showed that larger and darker *P. aegeria* males are more likely to be patrollers whereas small, pale males are mainly territorial perchers. These findings suggest that males may be able to compensate for a small size as adults by adjusting their behaviors to maximize their female encounter rate. Additionally, since nectar consists of a dilute aqueous solution of sugar, amino acids and lipids (Murphy *et al.* 1983), extra resources for flight can be obtained from feeding as adults. Small male size may therefore not be as costly, in terms of fitness, as small female size.

Females of many butterfly species, including *P. aegeria*, are known to lay large eggs at the start of oviposition and lay

gradually smaller eggs over time (Harvey 1977; Karlsson 1987; Karlsson and Wiklund 1985; Wellington 1965; Wickman and Karlsson 1987; Wiklund and Karlsson 1984). Wiklund & Persson (1983) suggested that *P. aegeria* females could maximally increase their fecundity by 25% if they laid small eggs only, and questioned why *P. aegeria* females had not been selected for high fecundity. Since the time available to search for suitable habitats and host-plants for larval growth and survival is limiting, the number of surviving offspring may be higher for females that lay relatively fewer eggs but spend more time searching for oviposition sites (Wiklund and Persson 1983). This experiment has shown that females are more susceptible than males to competition during larval development. It is possible, therefore, that female *P. aegeria* are not selected for a high fecundity because such a strategy would be detrimental to their female offspring. If more time is available for the adult female to search for optimal host-plant locations, and to avoid plants that have already been oviposited on by other adult females, females could ensure solitary locations for maximal growth of their female offspring

Survivorship, both to pupation, and to adulthood, was significantly higher for larvae that were reared alone. Oviposition in solitary locations would therefore also act to increase the survival chances of larvae. Although no significant differences in adult sex ratios were observed across treatments, there was a higher female:male sex ratio when larvae were reared alone, and a lower female:male sex ratio when larvae were reared in groups. Larger sample sizes would be necessary to investigate whether this represents a real trend or an effect of social exposure on sex-specific survivorship.

These results suggest that *P. aegeria* females could enhance the fitness of their larvae by avoiding laying eggs on host-plants where females have already oviposited. Egg clumping would affect the performance of female offspring, decreasing their body size and potentially reduce fecundity. Selective oviposition may not be possible, however, if there is competition for oviposition sites from other species (Owen *et al.* 1986; Jones *et al.* 1998). Further investigations would be valuable to determine whether the oviposition behavior of female *P. aegeria* acts as a factor in sexual size dimorphism.

## Acknowledgements

Michael Dockery, Patricia Moore, Richard Preziosi, Rory Putman, Christer Wiklund and an anonymous referees provided helpful comments on earlier versions of the manuscript. Also, thank you to Maggi Gapper and Janet Bunter for their technical support and plant maintenance. Thanks to Casper Breuker for his help with the figures.

## References

Applebaum SW, Heifetz Y. 1999. Density-dependent physiological phase in insects. *Annual Review of Entomology* 44: 317-341.

Bergström J, Wiklund C, Kaitala A. 2002. Natural variation in female mating frequency in a polyandrous butterfly: effects of size and age. *Animal Behaviour* 64: 49-54.

Bernays EA, Chapman RF. 1994. *Host plant selection by phytophagous insects*. Chapman and Hall, New York.

Boggs CL. 1981. Selection pressures affecting male nutrient investment at mating in heliconiine butterflies. *Evolution* 35: 931-940.

Briggs CJ, Sait SM, Begon M, Thompson DJ, Godfray CJ. 2000. What causes generation cycles in populations of stored-product moths? *Journal of Animal Ecology* 69: 352-366.

Cory JS, Goulson D. 1993. Flower constancy and learning in foraging preferences of the green veined butterfly *Pieris napi*. *Ecological Entomology* 18: 315-320.

Davies NB. 1978. Territorial defence in the speckled wood butterfly (*Pararge aegeria*): the resident always wins. *Animal Behaviour* 26: 138-147.

Dethier VG. 1959. Food-plant distribution and larval dispersal as factors affecting insect populations. *Canadian Entomologist* 88: 581-596.

Fischer K, Fiedler K. 2000. Sex-related differences in reaction norms in the butterfly *Lycaena tityus* (Lepidoptera: Lycaenidae). *Oikos* 90: 372-380.

Gotthard K, Nylin S, Wiklund C. 1994. Adaptive variation in growth rate: life history costs and consequences in the speckled wood butterfly, *Pararge aegeria*. *Oecologia* 99: 281-289.

Gotthard K, Nylin S, Wiklund C. 1999. Mating system evolution in response to search costs in the speckled wood butterfly, *Pararge aegeria*. *Behavioral Ecology and Sociobiology* 45: 424-429.

Gottard K, Nylin S, Wiklund C. 2000. Mating opportunity and the evolution of sex-specific mortality rates in a butterfly. *Oecologia* 122: 36-43.

Hanson FE. 1983. The behavioral and neurophysiological basis of food plant selection by lepidopterous larvae. In: Ahmad S, editor. *Herbivorous insects: Host seeking behavior and mechanisms*. New York: Academic Press.

Harvey GT. 1977. Mean weight and rearing performance of successive egg clusters of eastern spruce budworm (Lepidoptera: Tortricidae). *Canadian Entomologist* 109: 487-496.

Jones MJ, Lace LA, Harrison EC, Stevens-Wood B. 1998. Territorial behavior in the speckled wood butterflies *Pararge xiphia* and *Pararge aegeria* of Madeira: a mechanism for interspecific competition. *Ecography* 21: 297-305.

Karlsson B. 1987. Variation in egg weight, oviposition rate and reproductive reserves with female age in a natural population of the speckled wood butterfly, *Pararge aegeria*. *Ecological Entomology* 12: 473-476.

Karlsson B. 1994. Feeding habits and change of body composition with age in three nymphalid butterfly species. *Oikos* 69: 224-230.

Karlsson B, Leimar O, Wiklund C. 1997. Unpredictable environments, nuptial gifts and the evolution of sexual size dimorphism in insects: an experiment. *Proceedings of the Royal Society of London, Series B* 264: 475-479.

Karlsson B, Wickman P-O. 1990. Increase in reproductive effort as explained by body size and resource allocation in the speckled wood butterfly, *Pararge aegeria* (L.). *Functional Ecology* 4: 609-617.

- Karlsson B, Wiklund C. 1985. Egg weight variation in relation to egg mortality and starvation endurance of newly hatched larvae in some satyrid butterflies. *Ecological Entomology* 10: 205-211.
- Klok CJ, Chown SL. 1999. Assessing the benefits of aggregation: thermal biology and water relations of anomalous Emperor Moth caterpillars. *Functional Ecology* 13: 417-427.
- Krebs RA, Barker SF. 1995. Larval age differences and competition between *Drosophila aldrichi* and *D. Buzzatii*. *Ecological Entomology* 20: 60-64.
- Leimar O, Karlsson B, Wiklund C. 1994. Unpredictable food and sexual size dimorphism in insects. *Proceedings of the Royal Society of London, Series B* 258: 121-125.
- Masumoto T, Nomakuchi S, Sawada K. 1993. Host plant conspicuousness and the distribution of eggs and larvae in the butterfly, *Anthochais scolymus* (Lepidoptera: Pieridae). *Researches on Population Ecology* 35: 241-250.
- Mercer DR. 1999. Effects of larval density on the size of *Aedes polynesiensis* adults (Diptera: Culicidae). *Journal of Medical Entomology* 36: 702-708.
- Murphy DD, Launer, AE, Ehrlich PR. 1983. The role of adult feeding in egg production and population dynamics of the checkerspot butterfly *Euphydryas editha*. *Oecologia (Berlin)* 56: 257-263.
- Nahrung HF, Dunstan PK, Allen GR. 2001. Larval gregariousness and neonate establishment of the eucalypt-feeding beetle *Chrysophtharta agricola* (Coleoptera: Chrysomelidae: Paropsini). *Oikos* 94: 358-364.
- Nylin S, Gotthard K. 1998. Plasticity in life-history traits. *Annual Review of Entomology* 43: 63-83.
- Nylin S, Wickman P-O, Wiklund C. 1995. Life-cycle regulation and life history plasticity in the speckled wood butterfly: are reaction norms predictable? *Biological Journal of the Linnean Society* 55: 143-157.
- Nylin S, Wiklund C, Wickman P-O, Garcia-Barros E. 1993. Absence of trade-offs between sexual size dimorphism and early male emergence in a butterfly. *Ecology* 74: 1414-1427.
- Owen DF, Shreeve TG, Smith AG. 1986. Colonisation of Madeira by the speckled wood butterfly, *Pararge aegeria* and its impact on the endemic *Pararge xiphia*. *Ecological Entomology* 11: 349-352.
- Putman RJ. 1977. The dynamics of the blowfly *Calliphora erythrocephala* within carrion. *Journal of Animal Ecology* 46: 853-866.
- Rahman M. 1969. Effects of different foods on the development of *Pieris rapae* L. larvae (Lep: Pieridae). *Pakistan Journal of Zoology* 1: 35-40.
- Rosenthal R, Rosnow RL. 1985. *Contrast Analysis: Focused comparisons in the Analysis of Variance*, Cambridge University Press. New York.
- Scriber JM, Slansky F. 1981. Nutritional ecology of immature insects. *Annual Review of Entomology* 26: 183-211.
- Shreeve TG. 1984. Habitat selection, mate location, and microclimate constraints on activity of the speckled wood butterfly *Pararge aegeria*. *Oikos* 42: 371-377.
- Shreeve TG. 1987. The mate location behavior of the male speckled wood butterfly, *Pararge aegeria*, and the effect of phenotypic differences in hind wing spotting. *Animal Behaviour* 35: 682-690.
- Shreeve TG, Smith AG. 1992. The role of weather-related habitat use on the impact of the European speckled wood *Pararge aegeria* on the endemic *Pararge xiphia* on the island of Madeira. *Biological Journal of the Linnean Society* 45: 59-75.
- Shreeve TG, Smith AG, Baez M. 1992. Egg-laying sites, distributions and host-plants of members of the Genus *Pararge* (Lepidoptera: Satyrinae). *Entomologist's Record and Journal of Variation* 104: 239-242.
- Sibly RM, Winokur L, Smith RH. 1997. Interpopulation variation in phenotypic plasticity in the speckled wood butterfly, *Pararge aegeria*. *Oikos* 78: 323-330.
- Stamp NE. 1980. Egg deposition patterns in butterflies: why do some species cluster their eggs rather than deposit them singly? *The American Naturalist* 115: 367-380.
- Svärd L, Wiklund C. 1989. Mass and production rates of ejaculates in relation to monandry/ polyandry in butterflies. *Behavioral Ecology and Sociobiology* 24: 395-402.
- Tammaru T, Ruohomaki K, Montola M. 2000. Crowding induced plasticity in *Epirrita autumnata* (Lepidoptera: Geometridae): weak evidence of specific modifications in reaction. *Oikos* 90: 171-181.
- Ulliyet GC. 1950. Competition for food and allied phenomena in sheep blowfly populations. *Philosophical Transactions* 234: 77-175.
- Van Dyck H, Matthysen E, Dhondt AA. 1997. The effect of wing colour on male behavioral strategies in the speckled wood butterfly. *Animal Behaviour* 53: 39-51.
- Wellington WG. 1965. Some maternal influences on progeny quality in the Western Tent caterpillar *Malacosoma plumale* (Dyar). *Canadian Entomologist* 97: 1-14.
- Wickman P-O, Karlsson B. 1987. Changes in egg colour, egg weight, and oviposition rate with the number of eggs laid by wild females of the small heath butterfly *Coenonympha pamphilus*. *Ecological Entomology* 12: 109-114.
- Wickman P-O, Wiklund C. 1983. Territorial defence and its seasonal decline in the speckled wood butterfly (*Pararge aegeria*). *Animal Behaviour* 31: 1206-1216.
- Wiklund C, Forsberg J. 1991. Sexual size dimorphism in relation to female polygamy and protandry in butterflies: a comparative study of Swedish Pieridae and Satyridae. *Oikos* 60: 373-381.
- Wiklund C, Karlsson B. 1984. Egg size variation in satyrid butterflies: adaptive vs. historical, "Bauplan", and mechanistic explanations. *Oikos* 43: 391-400.
- Wiklund C, Karlsson B, Leimar O. 2001. Sexual Cupertino in butterfly reproduction: a comparative study of polyandry and female fitness, *Proceedings of the Royal Society of London, Series B* 268: 1661-1667.
- Wiklund C, Persson B. 1983. Fecundity, and the relation of egg weight variation to offspring fitness in the speckled wood butterfly *Pararge aegeria*, or why don't females lay more eggs? *Oikos* 40: 53-63.