



Multiple host-plant use may arise from gender-specific fitness effects

Authors: Gibbs, Melanie, Lace, Lesley A., Jones, Martin J., and Moore, Allen J.

Source: Journal of Insect Science, 6(4) : 1-8

Published By: Entomological Society of America

URL: [https://doi.org/10.1673/1536-2442\(2006\)6\[1:MHUMAF\]2.0.CO;2](https://doi.org/10.1673/1536-2442(2006)6[1:MHUMAF]2.0.CO;2)

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.



Multiple host-plant use may arise from gender-specific fitness effects

Melanie Gibbs², Lesley A. Lacey¹, Martin J. Jones¹ and Allen J. Moore²

¹Department of Biological Sciences, Manchester Metropolitan University, U.K.

²School of Biological Sciences, University of Manchester, U.K.

Abstract

Ovipositing females are predicted to select host-plants that will maximise offspring survival and fitness. Yet hosts often differ in the component of larval fitness affected so host-selection often involves a trade-off between short development times and large size and high fecundity of offspring. If host-species can directly affect development rates and body size, and if there are gender differences in resource allocation during development, there can be different sex-specific selection pressures associated with different hosts. Using a Madeiran population of the speckled wood butterfly *Pararge aegeria* (L.) as the model species gender differences in larval development and size were examined in response to the hosts *Brachypodium sylvaticum*, *Holcus lanatus* and *Poa annua*. It was observed that male and female *P. aegeria* larvae differed, with their responses dependent on the host species. These results would suggest that oviposition behavior is a complex process, and use of multiple hosts may have evolved to balance the conflicting needs of male and female larvae. Co-evolution of host selection and oviposition behaviors may help to balance the differing performance needs of offspring.

Keywords: Host species, *Pararge aegeria*, larval development.

Correspondence: melanie.gibbs@man.ac.uk

Received: 2.27.2005 | Accepted: 10.21.2005 | Published: 4.21.2006

Copyright: Creative Commons Attribution 2.5 <http://creativecommons.org/licenses/by/2.5>

ISSN: 1536-2442 | Volume 6, Number 4

Cite this paper as:

Gibbs M, Lacey LA, Jones MJ, Moore AJ. 2006. Multiple host-plant use may arise from gender-specific fitness effects. 8pp. *Journal of Insect Science* 6:04, available online: insectscience.org/6.04

Introduction

Oviposition behavior of females is hypothesised to have evolved to ensure that the host-plant species selected will maximise larval growth and survival (Thompson & Pellmyr 1991). Ovipositing females are thought to show a preference for host-plants that support rapid larval development (Janz et al. 1994; Nylin & Gotthard 1998; Wedell et al. 1997), as short development times act to reduce exposure times to predators and parasitoids (Connor 1991; Klok & Chown 1999), and facilitate rapid reproduction in growing populations (Fischer & Fiedler 2000; Gotthard et al. 1994). However, hosts can also affect offspring body size (Janz et al. 1994; Nylin & Gotthard 1998; Roff 1992; Stearns 1992), therefore, host-plant selection at oviposition may involve a trade-off between plants that support rapid offspring development, and plants that enable offspring to achieve a large size/high fecundity.

Further, oviposition site choice is complex because there are many factors that may impact on larval fitness. Factors that may influence the host-plant choice of females are thought to include the density, diversity and distribution of vegetation surrounding host-plants (Papaj & Rausher 1983), the amount of nutrition the host will afford for larval growth (Leather & Burnand 1987; Ostaff & Quring 2000), host damage (Wise et al. 2002), host-plant-size (Kirk 1991), leaf texture (Lance 1983), the plant part selected (Jallow & Zalucki 2003), host-plant age (Hunter & Elkinton 1999; Lamb et al. 2003; Smyth et al. 2003) and host abundance (Janz et al. 1994; Nylin & Janz 1996). Additionally, host-plant selection by individual females can vary geographically (Lance 1983) and temporally (Tabashnik et al. 1981), and thus offspring survival is also spatially and temporally variable (Van Nouhuys et al. 2003).

Studies with phytophagous insects reveal that there is a large variation in the performance of individuals on different hosts (Lance 1983; Singer et al. 1991; Tabashnik et al. 1981; Tikkanen et al. 2000; Wedell et al. 1997). Wedell *et al.* (1997) observed that the larval host-plant of the comma butterfly (*Polygonia c-album*) strongly affected the propensity to enter diapause, and that males tended to enter diapause to a greater extent than females when reared on poor host-plants. Tikkanen *et al.* (2000) found that *Operophtera brumata* females had higher growth rates than males, and

that the host-plant species affected the weight of adult females, but not the weight of adult males.

Given that host-plant species can directly affect development rates or body size, male and female larvae may face different life history trade-offs on different hosts. A sexual dimorphism in size occurs in the speckled wood butterfly, *Pararge aegeria*, due to differences in the allocation of larval derived resources (Sibly et al. 1997). Sibly *et al.* (1997) suggested that males may 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 to the abdomen for reproduction (Karlsson & Wickman 1990). Since *P. aegeria* feed on a more protein-rich food source during their larval stage than during their adult stage (Svärd & Wiklund 1989) and because spermatophores contain only a small percentage of protein, therefore providing unsubstantial nuptial gifts (Boggs 1981), there is little opportunity for adult females to accumulate additional nitrogenous resources for reproduction. Males, however, can gain additional lipid resources through adult feeding. Thus, female fecundity is largely dependent on the resources accumulated during the larval stage (e.g. Wiklund et al. 2001). Differences in host-plant utilisation during larval development, perhaps due to nutritional differences between host species, may therefore 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.

Given the propensity of *P. aegeria* to use more than one host, and the gender differences in larval resource allocation, the hypothesis was tested that male and female larvae differ in their relative performance on different hosts. Larvae were reared on *B. sylvaticum*, *H. lanatus* and *P. annua* and the effects of host plant species on development time, pupal mass and survival in a Madeiran population of *P. aegeria* were examined. *Pararge aegeria* is an important model system for insect life history and ecology and Northern European populations of *P. aegeria* have been extensively studied (e.g. Gotthard et al. 1994; Van Dyck et al. 1997; Gotthard et al. 2000; Van Dyck & Wiklund 2002). Although the natural history of host plant use and larval densities has not been extensively studied in natural populations of *P. aegeria* on Madeira, it is known that although the preferred host plant *B. sylvaticum* is very widespread and abundant, eggs laid are not always uniformly distributed, with large

numbers of eggs sometimes observed on single host plants (Jones et al. 1998). By examining the effects of host plant species on gender specific life-history and fitness in another population of *P. aegeria* from a very different environment, this study aims to add additional information to the extensive knowledge of the life history of this species.

Materials and Methods

Study organism

In 1999 at Portela on Madeira, 50 eggs of *P. aegeria* were collected from *Brachypodium sylvaticum*, and returned to the Manchester Metropolitan University butterfly house for rearing. 36 adults eclosed and were maintained for three generations in a flight cage 1.25 x 3.90 x 1.80m. Adults were fed daily with a 10% honey solution via five artificial flowers (for design see Cory & Goulson 1993), distributed at random in the flight cage. Honey supplies were replenished daily. Ten *Brachypodium sylvaticum* plants were made available for the F3 generation females (n = 24) to lay their eggs. These 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 $21 \pm 2^\circ \text{C}$ and a humidity of $50 \pm 10\%$ 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 eight ceiling lamps.

Host-plants

The larval host-plants *B. sylvaticum*, *H. lanatus* and *P. annua* were grown from commercially produced seed, and sown in 4-inch pots containing soil-based compost. To reduce the affect of environmental variation on host plant growth, all of the plants were reared under identical conditions at a temperature of $23 \pm 2^\circ \text{C}$ and a humidity of $45 \pm 10\%$. Light was provided at an intensity of 7000 Lux over a 16:8h LD cycle. Each of the plant species responded well to these standardised growth conditions. Plants were watered daily, but never fertilised. Host-plant age is known to affect the quality of the plant as a resource for larvae, (Scriber & Slansky 1981), and can act to lengthen larval development (Hunter & Elkinton 1999). Therefore, all of the plants used in this study were of young ages (i.e. were used when they had between 50 and 70 blades).

Experimental design

Eggs were collected daily from F3 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 either *B. sylvaticum*, *H. lanatus* or *P. annua* at densities of 10 larvae per plant. A total of 150 larvae were distributed at this density over 15 plants. Older larvae have been shown to have a significant competitive advantage (Briggs et al. 2000; Krebs & Barker 1995), therefore all of the larvae assigned to an individual plant shared the same hatching date, although not the same parent, thus families were randomly assigned across treatment groups. Plants were similar in size with approximately 50 blades per plant. The individual plants were placed into separate 0.5m³ netted cages in the butterfly house. To avoid food shortages, all plants were changed before they had been completely defoliated.

Pupation date, pupal mass and eclosion date 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 adult was recorded.

Statistical analyses

A two-way analysis of variance, with replicate plants nested under species, was used to investigate the effects of host-species, gender and the host species x gender interaction on larval development time, pupal time, pupal mass and larval growth rate. Nesting replicate plants under a given species controlled for measures from more than one individual derived for a given plant (a plant effect). Larval growth rate (mg/day) was calculated by dividing pupal mass (mg) by larval development time (days). A Pearson chi-square test was used to compare the proportion of surviving adults on each host-plant, and to determine whether there were host-plant dependent differences in adult sex-ratio. A logistic regression was performed to determine how the size of the individual at pupation affected survivorship to adulthood. All tests were two-tailed. The statistical procedures were performed using Systat 9.0.

Results

Development time

There was an overall significant effect of host-plant species on the length of the larval growth period, but no effect of gender and no gender x host-plant interaction. Larval development time was shortest when offspring were reared on *H. lanatus* and longest when reared on *P. annua* (Table 1).

There was no effect of host-plant on the amount of time spent as pupae, and no effect of gender (Table 1).

Total development time (larval time + pupal time) was significantly affected by host-plant species, but there was no effect of gender and no gender x host-plant interaction. Total development time was observed to be shortest when larvae were reared on *H. lanatus*, and longest when larvae were reared on *P. annua* (Table 1).

Pupal mass

Pupal mass was significantly affected by host-plant species, gender, and there was also a significant gender x host-plant interaction (Table 1). Both sexes showed a general trend of small pupal mass on *B. sylvaticum* and large pupal mass on *P. annua*, but the response to *H. lanatus* was different between the sexes (Table 2). Females attained larger pupal mass than males when reared on *H. lanatus*.

Growth rate

Growth rate was significantly affected by host plant species, and there was a significant gender x

host-plant interaction, but no affect of gender alone (Table 1). Males had faster growth rates than females on *B. sylvaticum* and *P. annua*, but on *H. lanatus* females had faster growth rates than males (Figure 1).

Survivorship of adults

There was no effect of host-plant on survival to pupation (Table 3; $\chi^2 = 3.470$, d.f. = 2, $P = 0.176$) or eclosion (Table 3; $\chi^2 = 4.376$, d.f. = 2, $P = 0.112$). There was however, a significant relationship between size at pupation and likelihood of surviving to adulthood (logistic regression; $\chi^2 = 12.674$, d.f. = 1, $P = < 0.001$).

Discussion

Life-history theory predicts that an optimal host-plant will facilitate short growth times and large size, and also maximise survival rates. Life history studies also show a trade-off between size and rate of development (Janz et al. 1994; Nylin & Gotthard 1998; Roff 1992; Stearns 1992). In this study, a gender difference was found in response to different host plant species. Males had the highest growth rates when reared on *P. annua*, whereas females had the highest growth rates when reared on *H. lanatus*. Given the unequal fitness effects of host-plants on male and female larvae, ovipositing *P. aegeria* could use a mixture of host-plants, as a 'bet-hedging' strategy.

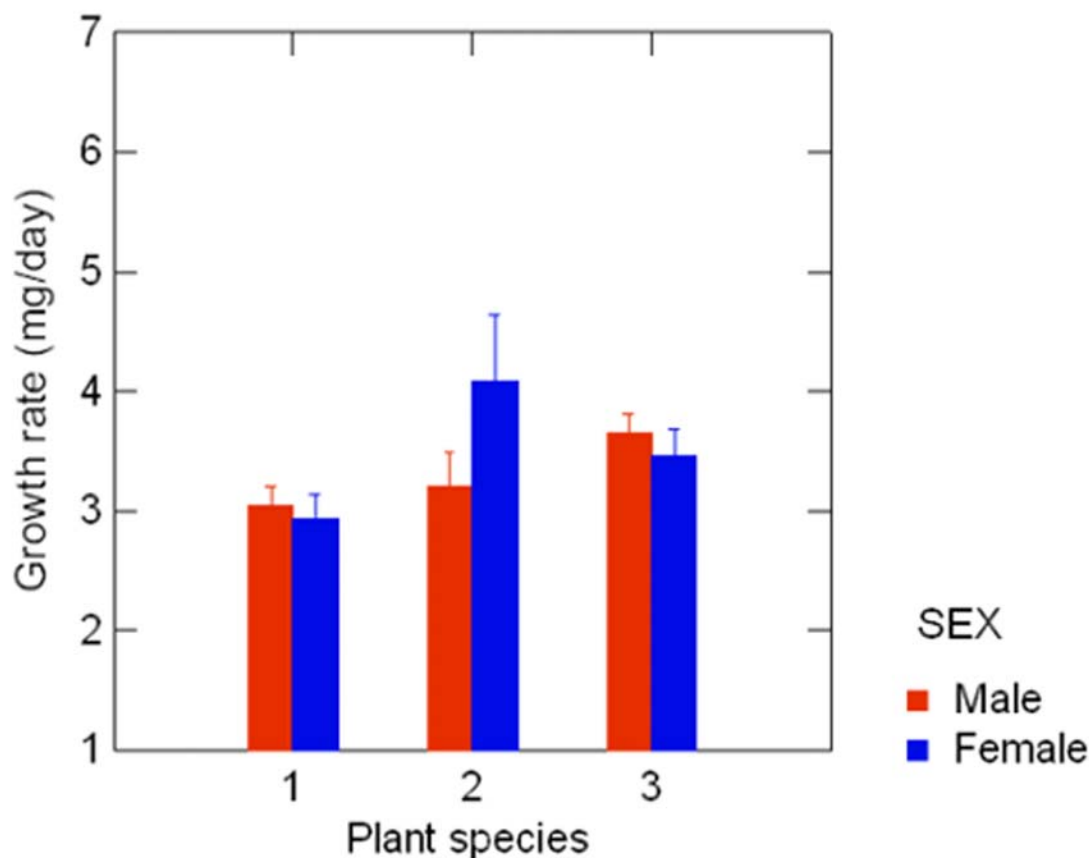
On Madeira, the preferred host plant *B. sylvaticum* is widespread and abundant (Owen et al. 1986, Jones et al. 1998). In the laboratory, under crowded

Table 1. Nested Two-way ANOVA for effects of host-plant and gender on life history traits in *Pararge aegeria*

Trait	Source	d.f	MS	F-Ratio	P
Larval time (days) Mean R2 = 0.55	Host plant	2	77.032	3.38	0.040
	Gender	1	0.022	0.001	0.975
	Interaction	2	30.35	1.33	0.271
	Plant (species)	12	116.24	5.1	0.000
	Error	65	22.81		
Pupal time (days) Mean R2 = 0.49	Host plant	2	10.84	1.96	0.151
	Gender	1	5.88	1.07	0.307
	Interaction	2	3.79	0.69	0.508
	Plant (species)	11	13.42	2.43	0.017
	Error	48	5.52		
Total development time (days) Mean R2 = 0.59	Host plant	2	137.69	5.03	0.010
	Gender	1	9.57	0.35	0.557
	Interaction	2	24.99	0.91	0.408
	Plant (species)	11	110.93	4.05	0.000
	Error	48	27.39		
Pupal mass (mg) Mean R2 = 0.78	Host plant	2	0.003	23.59	0.000
	Gender	1	0.001	4.15	0.046
	Interaction	2	0.001	7.09	0.002
	Plant (species)	12	0.001	6.92	0.000
	Error	61	0.000		
Growth rate (mg/day)	Host plant	2	4.28	10.75	0.000
	Gender	1	0.50	1.26	0.266
	Interaction	2	1.69	4.24	0.019
	Plant (species)	12	2.16	5.42	0.000
	Error	61	0.40		

Table 2. Life history data for male and female *P. aegeria* larvae reared on different host plants.

Host plant	Trait	Mean male (\pm SE)	Mean female (\pm SE)
<i>B. sylvaticum</i>	Larval time (days)	(n = 21) 32.27 \pm 1.14	(n = 18) 34.84 \pm 1.38
	Pupal time (days)	(n = 17) 10.41 \pm 0.72	(n = 7) 10.12 \pm 0.94
	Total development time (days)	(n = 17) 43.02 \pm 1.60	(n = 7) 45.06 \pm 2.10
	Pupal mass (mg)	(n = 19) 96.00 \pm 3.00	(n = 17) 98.00 \pm 4.00
<i>H. lanatus</i>	Growth rate (mg/day)	(n = 19) 3.07 \pm 0.16	(n = 17) 2.88 \pm 0.19
	Larval time (days)	(n = 17) 31.49 \pm 1.47	(n = 6) 28.95 \pm 2.23
	Pupal time (days)	(n = 14) 9.51 \pm 0.73	(n = 6) 9.47 \pm 1.10
	Total development time (days)	(n = 14) 41.34 \pm 1.63	(n = 6) 38.27 \pm 2.44
<i>P. annua</i>	Pupal mass (mg)	(n = 16) 101.00 \pm 4.00	(n = 6) 126.00 \pm 6.00
	Growth rate (mg/day)	(n = 16) 3.47 \pm 0.19	(n = 6) 4.41 \pm 0.29
	Larval time (days)	(n = 11) 35.39 \pm 1.67	(n = 10) 35.48 \pm 2.08
	Pupal time (days)	(n = 11) 12.41 \pm 0.82	(n = 10) 10.59 \pm 1.02
	Total development time (days)	(n = 11) 47.81 \pm 1.82	(n = 10) 46.08 \pm 2.28
	Pupal mass (mg)	(n = 11) 127.00 \pm 4.00	(n = 10) 121.00 \pm 5.00
	Growth rate (mg/day)	(n = 11) 3.62 \pm 0.22	(n = 10) 3.46 \pm 0.27

**Figure 1.** The effects of host-plant and gender on growth rates (mg/day) in male and female *P. aegeria* larvae where plant species 1 = *B. sylvaticum*, 2 = *H. lanatus* and 3 = *P. annua*

conditions, development on *B. sylvaticum* potentially carries a fitness cost for female larvae because females do not achieve high growth rates on this species compared to *H. lanatus* and *P. annua*. It is known that under optimal conditions female *P. aegeria* have higher growth rates than males (Gibbs et al. 2004) and selection for large

female size (and hence high fecundity) would appear to be more important for fitness than selection for large male size (Gotthard et al. 1994; Leimar et al. 1994). Given the strong selection for large size in females, this might suggest a possible parent-offspring conflict between oviposition preference and female offspring performance.

However, further studies designed to examine this specific idea are required, especially given that, in nature, an oviposition preference for *B. sylvaticum* may enhance larval fitness through other factors (e.g. density of vegetation surrounding host plants, Papaj & Rausher 1983) that are controlled for during laboratory studies. Also, during this laboratory experiment offspring performance was examined under sub-optimal conditions (larval crowding) where larvae experienced periods of food shortage. High growth rates have been predicted to be costly in terms of fitness (e.g. increased mortality) during periods of food shortage (Gotthard et al. 1994). Offspring performance, particularly female performance, is therefore likely to be enhanced under more optimal conditions, where the costs associated with a high growth rate would be reduced. For example, it is known that when reared under solitary conditions on *B. sylvaticum*, female offspring have higher growth rates than when reared in groups, and they also have higher growth rates than males (Gibbs et al. 2004). Studies examining the costs associated with high growth rates deserve further attention, particularly in relation to how oviposition behavior could act to minimise the effect. For example, if ovipositing females avoided crowded egg-laying sites, and laid single eggs on host plants, they may act to; 1) buffer the size disadvantage incurred by their female offspring starting life on a poor host-plant 2) increase larval survival to adulthood 3) decrease the magnitude of the female preference-performance conflict and 4) reduce male-female larval competition. To achieve this, ovipositing females would need to devote time to searching for optimal host plants and locations.

Plant phenology may have a strong affect on offspring performance, and it would be interesting to examine plastic responses to host species of *P. aegeria* within natural populations. More specifically, further studies are recommended to explore host plant niches with respect to environmental conditions, host plant use during oviposition, and larval densities typically observed on different host species on Madeira. Such studies may provide a valuable insight into the evolution of life history trade-offs in *P. aegeria*.

This study has shown that there are gender-related differences in larval performance on different hosts, and that host-plant selection may carry fitness consequences to offspring. However, the host-plant species selected for oviposition is not the only

factor that may influence larval fitness, and adult females may be able to buffer any disadvantages through other behaviors during oviposition (e.g. by avoiding egg clumping). The co-evolution of host-specificity and oviposition behaviors may have helped to balance the conflicting needs of female offspring, male offspring and their mother.

Acknowledgements

Michael Dockery, Richard Preziosi, W. Ed Harris, Per. T. Smiseth, Philip Astles, Nina Wedell, Derek Yalden and Casper Breuker provided helpful comments on earlier versions of the manuscript. Also, thanks to Maggi Gapper and Janet Bunter for their technical support and plant maintenance.

References

- Boggs CL. Selection pressures affecting male nutrient investment at mating in heliicine butterflies. *Evolution* 1981; 35:931–940.
- Briggs CJ, Sait SM, Begon M, Thompson DJ, Godfray CJ. What causes generation cycles in populations of stored-product moths?. *Journal of Animal Ecology* 2000; 69:352–366.
- Connor EF. Colonization, survival, and causes of mortality of *Cameraria hamadryadella* (Lepidoptera: Gracillariidae) on four species of host plants. *Ecological Entomology* 1991; 16:315–322.
- Cory JS, Goulson D. Flower constancy and learning in foraging preferences of the green veined butterfly *Pieris napi*. *Ecological Entomology* 1993; 18:315–320.
- Fischer K, Fiedler K. Sex-related differences in reaction norms in the butterfly *Lycaena tityus* (Lepidoptera: Lycaenidae). *Oikos* 2000; 90:372–380.
- Gibbs M, Lacey LA, Jones MJ, Moore AJ. Intraspecific competition in the speckled wood butterfly *Pararge segeria*: effect of rearing density and gender on larval life history. *Journal of Insect Science* 2004; 4:1–6.
- Gotthard K, Nylin N, Wiklund C. Adaptive variation in growth rate: life history costs and consequences in the speckled wood butterfly, *Pararge aegeria*. *Oecologia* 1994; 99:281–289.
- Gotthard K, Nylin N, Wiklund C. Mating opportunity and the evolution of sex-specific mortality rates in a butterfly. *Oecologia* 2000; 122:36–43.
- Hunter AF, Elkinton JS. Interaction between phenology and density effects on mortality from natural enemies. *Journal of Animal Ecology* 1999; 68:1093–1100.

- Jallow MF, Zalucki MP. Relationship between oviposition preference and offspring performance in Australian butterfly *Helicoverpa armigera* (Hubner) (Lepidoptera: Noctuidae). *Journal of Animal Ecology* 2003; 42:343–348.
- Janz N, Nylin S, Wedell N. Host plant utilisation in the comma butterfly: Sources of variation and evolutionary implications. *Oecologia* 1994; 99:132–140.
- Jones MJ, Lace LA, Harrison EC, Stevens-Wood B. Territorial behaviour in the speckled wood butterflies *Pararge xiphia* and *Pararge aegeria* of Madeira: a mechanism for interspecific competition?. *Ecography* 1998; 21:297–305.
- Karlsson B, Leimar O, Harrison EC, Wiklund C. Unpredictable environments, nuptial gifts and the evolution of sexual size dimorphism in insects: an experiment. *Proceedings of the Royal Society of London, Series B* 1997; 264:475–479.
- Karlsson B, Wickman P-O. Increase in reproductive effort as explained by body size and resource allocation in the speckled wood butterfly, *Pararge aegeria* (L.). *Functional Ecology* 1990; 4:205–211.
- Kirk WDJ. The size relationship between insects and their hosts. *Ecological Entomology* 1991; 16:351–359.
- Klok CJ, Chown SL. Assessing the benefits of aggregation: thermal biology and water relations of anomalous Emperor Moth caterpillars. *Functional Ecology* 1999; 13:417–427.
- Krebs RA, Barker SF. Larval age differences and competition between *Drosophila aldrichi* and *D. Buzzatii*. *Ecological Entomology* 1995; 20:60–64.
- Lamb RJ, Sridhar P, Smith MAH, Wise IL. Oviposition preference and offspring performance of a wheat midge *Sitodiplosis mosellana* (Gehin) (Diptera: Cecidomyiidae) on defended and less defended wheat plants. *Environmental Entomology* 2003; 32:414–420.
- Lance DR. Host-seeking behaviour of the gypsy moth: The influence of polyphagy and highly apparent host plants. In: Ahmad S, editor. *Herbivorous insects: Host seeking behaviour and mechanisms*. New York: Academic Press; 1983. p. 201–219.
- Leather SR, Burnand AC. Factors affecting life-history parameters of the pine beauty moth, *Panolis flammea* (D&S): the hidden costs of reproduction. *Functional Ecology* 1987; 1:331–331.
- Leimar O, Karlsson B, Wiklund C. Unpredictable food and sexual size dimorphism in insects. *Proceedings of the Royal Society of London, Series B. Functional Ecology* 1994; 258:121–125.
- Nylin S, Gotthard K. Plasticity in life-history traits. *Annual Review of Entomology* 1998; 43:63–83.
- Nylin S, Janz N. Host-plant preferences in the comma butterfly (*Polygona c-album*): Do parents and offspring agree?. *Ecoscience* 1996; 3:285–289.
- Nylin S, Wickman P-O, Wiklund C. Life-cycle regulation and life history plasticity in the speckled wood butterfly: are reaction norms predictable?. *Biological Journal of the Linnean Society* 1995; 55:143–157.
- Ostaf DP, Quiring DT. Role of host plant in the decline of populations of a specialist herbivore, the spruce bud moth. *Journal of Animal Ecology* 2000; 69:263–273.
- Owen DF, Shreeve TG, Smith AG. Colonisation of Madeira by the speckled wood butterfly, *Pararge aegeria* and its impact on the endemic *Pararge xiphia*. *Ecological Entomology* 1986; 11:349–352.
- Papaj DR, Rausher MD. Individual variation in host location by phytophagous insects. In: Ahmad S, editor. *Herbivorous insects: Host seeking behaviour and mechanisms*. New York: Academic Press; 1983. p. 77–117.
- Roff DA. *The evolution of life histories: Theory and analysis*. New York: Chapman & Hall; 1992.
- Scriber JM, Slansky F. Nutritional ecology of immature insects. *Annual Review of Entomology* 1981; 26:183–211.
- Sibly RM, Winokur L, Smith RH. Interpopulation variation in phenotypic plasticity in the speckled wood butterfly, *Pararge aegeria*. *Oikos* 1997; 78:323–330.
- Singer MC, Ng D, Moore RA. Genetic variation in oviposition preference between butterfly populations. *Journal of Insect behaviour* 1991; 4:531–535.
- Smyth RR, Hoffman MP, Shelton AM. Larval performance in relation to labile oviposition preference of *Crociodolomia pavonana* (F.) (Lepidoptera: Pyralidae) among phenological stages of cabbage. *Environmental Entomology* 2003; 32:765–770.
- Stearns SC. *The evolution of life histories*. Oxford: Oxford University Press; 1992.
- Svärd L, Wiklund C. Mass and production rates of ejaculates in relation to monandry/polyandry. *Behavioural Ecology & Sociobiology* 1989; 24:395–402.
- Tabashnik BE, Wheelock H, Rainbolt JD, Watt WB. Individual variation in oviposition preference in the butterfly, *Colias eurythem*. *Oecologia* 1981; 50:225–230.
- Tikkanen O-P, Niemelä P, Keränen J. Growth and development of a generalist herbivore, *Operophtera brumata*, on original and alternative host plants. *Oecologia* 2000; 122:529–536.
- Thompson JN, Pellymyr O. Evolution of oviposition behavior and host preference in lepidoptera. *Annual Review of Entomology* 1991; 36:65–89.
- Van Dyck H, Matthysen E, Dhondt AA. The effect of wing colour on male behavioural strategies in the speckled wood butterfly. *Animal Behaviour* 1997; 53:39–51.

- Van Dyck H, Wiklund C. Seasonal butterfly design: morphological plasticity among three developmental pathways relative to sex, flight and thermoregulation. *Journal of Evolutionary Biology* 2002; 15:216–225.
- Van Nouhuys S, Singer MC, Nieminen M. Spatial and temporal patterns of caterpillar performance and the suitability of two host plant species. *Ecological Entomology* 2003; 28:193–202.
- Wedell N, Nylin S, Janz N. Effects of larval host plant and sex on the propensity to enter diapause in the comma butterfly. *Oikos* 1997; 78:569–575.
- Wiklund C, Karlsson B, Leimar O. Sexual conflict and cooperation in butterfly reproduction: a comparative study of polyandry and female fitness. *Proceedings of the Royal Society of London, Series B* 2001; 268:1661–1667.
- Wise MJ, Weinberg AM. Prior flea beetle herbivory affects oviposition preference and larval performance of a potato beetle on their shared host plant. *Ecological Entomology* 2002; 27:115–122.