The consequences of sexual dimorphism in body size for butterfly flight and thermoregulation

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Abstract. The body size differences between male and female insects of a species can result in different flight and thermoregulatory abilities, potentially causing marked behavioural differences between the sexes. In the butterfly *Euphydryas phaeton* Drury (Lepidoptera: Nymphalidae), females are twice the size of males, with greater wing loadings throughout most of their lives. Males are able to fly at lower body temperatures than females, but multiple-regression analysis of body temperature as a function of weather variables reveals that females are better able to maintain elevated body temperatures against short-term thermal fluctuations. Males perch in exposed sites where they are more vulnerable to convective cooling; heat loss is counteracted by basking for the majority of the daylight hours. Females inhabit a warmer, more sheltered microenvironment and spend less time basking. I argue that the flight of females is sluggish and more constrained by environmental conditions than that of males due to their greater wing loading, yet in spite of the difference in the degree of environmental constraint, males and females spend an equal amount of time in flight. These results show that small behavioural differences can place ectotherms in different thermal environments, dramatically offsetting the physical constraints imposed by a given body size.

Key-words: Behaviour, butterflies, *Euphydryas phaeton*, flight, habitat selection, physiologial ecology, thermoregulation

Introduction

Sexual dimorphism in body size is common among butterflies (e.g. Singer, 1982); males are smaller than females in most dimorphic species.

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Large body size in females may be favoured by natural selection for increased fecundity (Wiklund & Karlsson, 1988), while small size in males may evolve indirectly through sexual selection for rapid development, a correlated trait, leading to early eclosion (Wiklund & Fagerstrom, 1977; Singer, 1982; but see Wiklund & Karlsson, 1988). Sex differences in body size can also differentially affect the ability of male and female butterflies to fly and thermoregulate. This may force males and females to adopt different diurnal activity patterns or to inhabit different microenvironments. In this paper, I will show how intraspecific variation in body size can affect thermoregulation and flight behaviour.

Butterflies require a relatively high thoracic temperature in order to fly (e.g. *Colias* spp.: 28–30°C [Watt, 1968]; *Papilio polyxenes* (Fab.): 24°C [Rawlins, 1980]; *Thymelicus lineola* (Ochs.): 20–22°C [Pivnick & McNeil, 1986]). They rely on basking in bright sunlight to raise their body temperatures (T_{body}) above the ambient levels in cool environments (Clench, 1966). Because these factors limit activity to periods of warm, sunny weather within the short (3–10 day) life-span of adults in many temperate zone species, the time available for flight may be a limiting resource (Dempster, 1983; Kingsolver, 1983a,b).

Blau (1981) suggested that selection on thermoregulatory ability to maximize the amount of time available for flight might affect the body size of butterflies. He argued that small body size would be advantageous under cool, variable conditions because the rapid warming of small individuals would allow them to fly during short periods of favourable weather (but see Kingsolver & Watt, 1983; and discussion). Pivnick & McNeil (1986) used Blau's (1981) reasoning to argue that sexual selection to maximize the time available for flight to locate mates was in part responsible for the reduced body size of male *T. lineola*, relative to that of females. Other studies, however, have argued that natural selection on females to increase their time available for flight should be strong since realized fecundity is frequently limited by poor weather conditions which prevent the location of host plants (Gossard & Jones, 1977; Hayes, 1981; Stamp, 1982a; Courtney & Duggan,

1983; Dempster, 1983; Kingsolver, 1983b; reviews in Courtney, 1986; Kingsolver, 1985).

Perching butterflies raise their body temperatures by the absorption of solar radiation through the dorsal surface of the body and at the base of the wings (Wasserthal, 1975). Heat is primarily lost from the body through forced convection and, to a lesser extent, thermal radiation to the environment (Church, 1960; Kingsolver & Moffat, 1982). The rate of convective heat loss per unit surface area is inversely proportional to the boundary layer thickness about the body, which is, in turn, directly proportional to the square root of the body's diameter. Thus, at steady state, a large body will have a relatively lower rate of convective heat loss, and hence a higher equilibrium body temperature, than a small body. The transient time constant (τ) reflects the effects of convective and thermal radiative heat flux on body temperature in a fluctuating environment; τ is the time it would take a body not at equilibrium temperature to move $1/e$ (37%) of the way towards thermal equilibrium (Campbell, 1977). The time constant is inversely proportional to the surface-area-to-body-mass ratio, so large insects have large time constants and relatively slow rates of temperature change. These arguments imply that:

1 Females will attain higher equilibrium T_{body} than males under similar environmental conditions.

2 Male T_{body} will track environmental temperature fluctuations more closely than females.

Body size differences may also affect the relative flight capabilities of males and females. If body size increases more rapidly than wing area as one scales up from males to females, the wing loading (body mass/wing area) of females will be greater than that of males. As wing loading increases, wing-beat frequency should also increase to develop adequate lift for flight (Casey & Joos, 1983; Unwin & Corbet, 1984; Marden, 1987). The temperature dependence of wing-beat frequencies means that an insect with greater wing loading must attain a higher minimum body temperature for flight (T_{min}) than a conspecific with a lower wing loading (Heinrich, 1974).

Here I explore the consequences of sexual dimorphism in body size for thermoregulation and flight in the butterfly *Euphydryas phaeton* Drury (Lepidoptera: Nymphalidae). Do sex differences in body size result in detectable differences in thermoregulatory performance under field conditions? How do these differences affect flight ability? Can behavioural differences between the sexes circumvent, to some degree, the thermodynamic constraints imposed by body size? I will close with a discussion of how flight and thermoregulatory ability may constrain the evolution of sexual size dimorphism.

Methods and materials

The study organism and field site

E. phaeton butterflies form localized populations throughout north-eastern North America. They are univoltine, with a flight season from mid-June through mid-July in coastal Massachusetts. Females lay clusters of about 275 eggs (Stamp, 1982b) on leaf surfaces. The primary host in this population was *Plantago lanceolata* L. (Plantaginaceae), with some late instar caterpillars feeding on *Viburnum acerifolium* L. (Caprifoliaceae). The larvae enter diapause and overwinter in the fourth instar, emerging in May to complete development and pupation in early June (Bowers, 1978).

The study site was an old field measuring 0·67 ha in Swansea, Bristol County, Massachusetts. About 100 last instar caterpillars were collected from plantain in a nearby field during early June and were reared on cuttings in the Brown University greenhouse. They were held in 8 × 16 × 30 cm plastic boxes with screened tops for 24 h after eclosion to ensure that the wings were fully hardened. The butterflies were stored in vials at 5 °C for up to 5 days before being used in the laboratory portion of this study.

Morphological measurements

Body mass, wing loading (body mass/wing area), thickness of insulation, wing reflectivity, and thorax diameter were measured on 39 females and 40 males collected from the field. I also collected 16 pairs *in copula* to determine wing loading of females carrying a full complement of eggs. Female *E. phaeton* mate only once shortly after eclosion and begin ovipositing within a day after mating (unpublished observation). The butterflies were held overnight under refrigeration and weighed the following morning. Wing wear was noted as fresh (little or no scale loss or tattering) or worn (substantial scale loss and tattering) to control for age-related changes in body mass. Thirteen males and 18 females were selected haphazardly; they were killed by freezing and the wings were removed and photographed. The width of the pronotum at its widest point was measured with vernier calipers to ± 0·1 mm. Wing area was

measured from the photographs with a polar planimeter to $\pm 10\,\mathrm{mm}^2$. Fur (setal) thickness on the distal end of the left second coxa was measured to $\pm 0.01\,\mathrm{mm}$ under a dissecting microscope equipped with an ocular micrometer on 10 males and 10 females selected haphazardly. The reflectivity of the dorsal wing surface at the base of the discal cell on the right forewing of five males and five females was measured with a portable spectro-radiometer (LI-1800; Li-Cor, Inc., Lincoln, Nebraska, USA). The Li-Cor unit was programmed to average five scans between 400 and 1100 nm for each wing. The value reported is the proportion of light within the visible and near-infrared solar spectrum reflected from the wing surface.

Measurement of thermal requirements

The minimum temperature required for flight ($T_{\min}$) was determined by timing the flight of butterflies at various body temperatures when released from a uniform height (Pivnick & McNeil, 1986). For each sex, 20 individuals were selected from the laboratory stock. They were placed in 40-ml brown plastic vials in an open box partially submerged in a water-bath at 1 °C, which was gradually warmed over the next 4 h on an electric hotplate. Temperature was recorded continuously with a pair of 0.05 mm copper-constantan thermo-couples placed within two vials. I assume that the body temperature of the butterflies is approximately the same as the air temperature within the vials. The vials containing the butterflies were shuffled every minute or so. At each 2 °C interval from 10 to 46 °C, three males and three females were selected haphazardly. Each of the selected individuals was held at a height of 2 m and released. The time between release and landing was recorded to the nearest second with a stop-watch. If uninjured, the butterfly was returned to the vial in the water-bath. No individual was used for successive trials or for more than six trials throughout the experiment. The flight threshold was defined as the lowest temperature at which the duration of time between release and landing exceeded 4 s, the shortest time interval over which flapping flight was observed.

Body temperature measurements

Freshly killed butterflies were used to determine the effect of air temperature and solar irradiance on T_{body} in dorsally basking (wings held open at 180° angle and oriented normal to the solar rays) and closed (wings folded over the dorsal surface

parallel to the solar rays) individuals of each sex. A pair of size-matched individuals of the same sex were selected from the laboratory stock. They were secured to a small spreading board, one in the basking posture and the other with the wings folded. The board was placed in a killing jar with ethyl acetate for 30 min which effectively fixed the wings in position. The butterflies were then removed and a 0.05 mm copper-constantan thermo-couple was inserted ventrally into the thorax. They were glued to wooden toothpicks to facilitate handling and placed 35 cm above ground level in the north-east corner of the field. The butterflies were realigned in relation to the sun each hour. A windscreen was used to prevent the butterflies from blowing away in gusty winds. Air temperature was measured to $\pm 1.0\,°\mathrm{C}$ with a shaded 0.1-mm copper-constantan thermocouple at 35 cm. The horizontal flux of solar irradiance was measured to $\pm 10\,\mathrm{W\ m^{-2}}$ with a pyranometer (LI-200S, Li-Cor, Inc., Lincoln, Nebraska, USA) at a height of 35 cm. These instruments were connected to a multiplexer and chart recorder. Basking body temperature, closed body temperature, air temperature and solar irradiance were recorded every 30 s. A total of six pairs of males and six pairs of females were monitored on 12 separate days. The body temperature of one butterfly in each of two male pairs and two female pairs became erratic early in the day, indicating that the body had become dehydrated (J.G. Kingsolver, personal communication). Observations for those days were discarded. Readings at 5-min intervals for 1 h between 11.00 and 14.00 h each day were used in the analysis.

Behavioural studies

Three types of behavioural observations were made: continuous observations of individual behaviour, forced flight ability and microhabitat usage. A total of 139 individual butterflies were followed for a short period of time (mean $\pm$ SD; males: $358 \pm 156.7\,\mathrm{s}$, range 115–910 s, $n = 70$; females: $480 \pm 604.1\,\mathrm{s}$, range 110–3610 s, $n = 69$) to assess patterns of behaviour. Activities were classified as basking (perched with wings held open such that the sun's rays fell on the dorsal surface of the thorax), closed (wings folded over the dorsal surface of the body), flight, and host search (walking over the plant surface with bouts of tarsal pawing). Feeding and oviposition were rarely observed and will not be discussed in this paper. Behavioural changes were recorded continuously on a tape recorder and subsequently

transcribed. Simultaneous recordings of air temperature and irradiance were made every 30 s and averaged over the observation period. The mean duration, rate of initiation and percentage of observation time were calculated for each behaviour on each individual. Observations were made on both sunny and cloudy days.

Forced flight was used to assess the relative importance of weather conditions, body size and basking on flight ability. At the end of their individual observations, each of the 69 females and 70 males was prodded into flight. Of these, 39 females and 40 males were recovered. Most of the 'lost' individuals were not actually lost, but had become confused with other conspecifics nearby, so individual identification could not be certain. The flight duration was timed to the nearest second. Air temperature and irradiance level at the time of flight were recorded. The proportion of time basking in the 2 min prior to flight was calculated. The 79 individuals recovered were collected for measurement of mass as described above.

Perching butterflies could exploit temperature differences within the boundary layer of still air trapped by standing vegetation. Throughout the study period, casual observations were made on the perch height (to the nearest 5 cm) of dorsal basking and closed perching individuals. Air temperatures on a warm, sunny day (18 July 1986) were measured from 11.15 to 17.00 h with two thermocouples at 1 and 35 cm above the ground to estimate the temperature gradient within the vegetational boundary layer. Readings at 5-min intervals were used in the analysis.

Results

Morphological measurements

Females from the field-collected sample weighed nearly twice as much as males and had significantly greater wing loadings in the younger age class (Table 1). Males and females in mated pairs showed an even more striking difference, suggesting that as females aged and deposited their eggs, their mass and wing loadings decreased substantially. The sexes did not differ in fur thickness (mean ± SD; males: 0.088 ± 0.0079 mm, $n = 10$; females: 0.093 ± 0.0106 mm, $n = 10$; $t = 0.116$, $P > 0.9$). The pronotum of females is slightly wider than that of males (males: 1.8 ± 0.27 mm, $n = 13$; females: 2.0 ± 0.24 mm, $n = 18$; Mann–Whitney U: $t_s = 2.198$, $P < 0.05$). There was no difference in the reflectivity of the dorsal wing surface between

the sexes (males: 0.088 ± 0.0100, $n = 5$; females: 0.085 ± 0.0097, $n = 5$).

Sex differences in thermal requirements and body temperature

Under laboratory conditions, T_{min} was estimated at 22–24 °C for males and at 26–30 °C for females. The method used provides a conservative estimate of the minimum body temperature at which flapping flight is physiologically possible. The 'preferred' temperature for flight is probably somewhat higher, but it may vary with the motivational state of the animals. Thus, T_{min} provides a more accurate reflection of how body size may physiologically constrain flight ability at low air temperatures.

Body temperatures of basking males and females increased with air temperature and irradiance level; the relative contribution of each factor, analysed by a stepwise partial linear regression, differed between the sexes. Air temperature was the first variable entered in the regression for basking males; the addition of irradiance level increased the explained variance (r^2) by only 0.044 (standardized regression coefficients; step 1 = T_{air}: $\beta = 0.8004$, $P < 0.001$, total $r^2 = 0.6831$; step 2 = S_{irr}: $\beta = 0.2106$, $P < 0.05$, total $r^2 = 0.7268$). Irradiance level was the first variable entered in the regression for females; adding air temperature increased the r^2 by 0.171 (step 1 = S_{irr}: $\beta = 0.5990$, $P < 0.001$, total $r^2 = 0.7629$; step 2 = T_{air}: $\beta = 0.4964$, $P < 0.001$, total $r^2 = 0.9340$). These results suggest that the T_{body} of males tends to track the frequent small fluctuations in T_{air}

Table 1. Body mass and wing loading (mean ± SD) of *Euphydryas phaeton* butterflies. The mating class consists of females and males collected *in copula*. The fresh and worn classes refer to differences in wing wear of field samples and reflect different age classes. Means of each class were compared using Mann–Whitney U-tests and significant differences between the sexes are indicated next to Class.

Class	Females	Males
Mass (mg)		
Mating***	250.3 ± 49.54 (16)	88.1 ± 14.78 (16)
Fresh***	191.5 ± 47.28 (23)	95.0 ± 13.13 (19)
Worn***	142.7 ± 29.38 (16)	90.3 ± 15.02 (21)
Wing loading (mg mm^{-2})		
Mating***	0.21 ± 0.021 (16)	0.10 ± 0.012 (16)
Fresh*	0.16 ± 0.046 (11)	0.11 ± 0.009 (7)
Worn	0.13 ± 0.014 (7)	0.11 ± 0.009 (6)

$*P < 0.05$; $**P < 0.01$, $***P < 0.001$.

while the T_{body} of females remains more constant, as predicted by thermodynamic theory. Air temperature was the best predictor of T_{body} in closed, non-basking males and females (males: $r^2 = 0.782$; females: $r^2 = 0.875$), as would be expected. The closed body temperatures remain above ambient levels because of the absorption of diffuse solar radiation and reflected and radiant energy from the unshaded ground beneath the body (Watt, 1968). Air temperature and solar irradiance were moderately correlated ($r = 0.47$, $P < 0.001$).

The sex differences in body temperature excess ($T_{xs} = T_{body} - T_{air}$) were compared with an analysis of covariance to remove the effects of weather variation between days. Males and females did not differ significantly in T_{xs} while basking (adjusted mean ± SE; males: 14·8 ± 2·48 °C; females: 15·3 ± 3·73 °C; $F_{1, 92} = 1.208$, $P > 0.25$). Female T_{xs} was significantly higher in the closed posture (males: 3·5 ± 1·81 °C; females: 4·7 ± 1·98 °C; $F_{1, 92} = 8.767$, $P < 0.005$).

Sex differences in behaviour

The continuous observations of individuals allowed a contrast of the behaviour of males and females. This method is preferable to recording the instantaneous behaviour of individuals along a transect because the less conspicuous individuals in closed postures are less likely to be overlooked and because variation within an individual's behaviour can be detected. Males spent much of the day basking, while female basking was concentrated in the early morning and late afternoon (Fig. 1a). Males basked more of the time at nearly all observed air temperatures than did females (Fig. 1b; mean ± SE; males: 53 ± 4·5%, $n = 70$; females: 26 ± 4·0%, $n = 69$; Mann–Whitney U: $t_s = 4.049$, $P < 0.001$). The mean flight duration of males was longer than that of females at most air temperatures (Fig. 2a; mean ± SE: males: 9 ± 1·1 s, $n = 54$; females: 5 ± 0·7 s, $n = 46$; Mann–Whitney U: $t_s = 1.979$, $P < 0.005$), but the percentage of time spent in flight did not differ significantly between the sexes (Fig. 2b; mean ± SE; males: 13 ±2·9%, $n = 70$; females: 8 ± 1·6%, $n = 69$; Mann–Whitney U: $t_s = 1.367$, $P = 0.1715$). Males increased the amount of time spent in the closed posture at air temperatures above 34 °C (Fig. 3), perhaps to prevent overheating (Watt, 1968). These males orientated parallel to the incoming solar rays to minimize the absorptive surface of the body. Females increased the amount of time spent searching for host plants over the same range of air temperatures (Fig. 4); this behaviour involves

walking about on a potential host, usually with the wings folded in the closed posture.

Behavioural patterns correlate with variation in abiotic conditions (Table 2) because *E. phaeton* butterflies, like most ectotherms, are unable to maintain their body temperatures within the preferred range at all times. I found that male and female behaviour are correlated with the means of air temperature and solar irradiance in similar ways, but differed somewhat in response to fluctuation in irradiance level, as measured by the coefficient of variation (Table 2). Males tended to fly less and bask more during times of variable cloudiness, whereas female behaviour patterns were not disrupted. Weather factors which affect individual flight behaviour also affect the interactions between individuals. Male chases of flying insects usually involved conspecifics and were probably investigatory in nature; the proportion of time spent chasing and the rate of chase initiation followed the same trends as free flight (Table 3). Female host searching behaviour was also positively correlated with air temperature (Table 3).

The above correlations suggest that flight performance and, therefore, the fitness-related activities associated with flight, may be physiologically limited by cloudy or cool weather, but this effect may be confounded by differences in the motivation to fly. To overcome this problem, I used the duration of forced flight as an index of maximum physiological performance under a given set of environmental conditions. When prodded, butterflies flew away rapidly in a straight line, as in escape from a potential predator. Male flights were longer than those of females (mean ± SE; males: 10 ± 2·2 s, $n = 40$; females: 5 ± 0·6 s, $n = 39$; Mann–Whitney U: $t_s = 3.222$, $P < 0.002$), paralleling the results obtained by following individuals and recording their behaviour. The effects of body mass, irradiance level, air temperature, and basking on flight performance were analysed using partial linear regressions on log-transformed data for each sex. Within-sex body mass did not correlate with performance in either sex and so was omitted from the final analysis. Female flight duration increased with the proportion of time spent basking and the level of solar irradiance, but was independent of variation in air temperature, whereas none of the regressors was significant for males (males: $\beta[T_{air}] = -0.0719$, $P > 0.1$; $\beta[S_{irr}] = 0.1569$, $P > 0.05$; $\beta[\text{bask time}] = 0.3006$, $P < 0.05$; females $\beta[T_{air}] = -0.0100$, $P > 0.1$; $\beta[S_{irr}] = 0.5810$, $P < 0.05$; $\beta[\text{bask time}] = 0.4073$, $P < 0.05$). The air temperature was above the male flight threshold in all but one of the trials, so this result is

Table 2. Spearman's rho correlation coefficients between behaviours and weather conditions observed during animal observations. Mean = mean of individual means of the duration of each behaviour; rate = mean individual rate of behaviour initiation; per cent = mean percentage of time an individual spent in that behaviour. Environmental variability during each observation is measured by the coefficient of variation (CV).

|	Females (n = 69)				Males (n = 70)			
	Mean temperature	Temperature CV	Mean irradiance	Irradiance CV	Mean temperature	Temperature CV	Mean irradiance	Irradiance CV
Flight:								
Mean	0·228	-0·014	-0·159	0·026	0·342*	-0·076	-0·042	-0·001
Rate	0·257	-0·081	0·273*	0·044	0·481***	0·103	0·323**	-0·312**
Per cent	0·294*	-0·113	0·242*	0·053	0·478***	0·068	0·269*	-0·237*
Dorsal bask:								
Mean	-0·463***	0·080	-0·529***	0·197	-0·365**	0·050	-0·362**	0·322*
Rate	-0·283*	-0·067	0·049	-0·040	-0·148	0·290**	0·058	-0·072
Per cent	-0·421***	0·002	-0·259*	0·053	-0·528***	0·109	-0·381***	0·307**
Closed perch:								
Mean	-0·173	0·015	-0·142	-0·096	0·006	-0·228	0·070	-0·052
Rate	-0·385***	-0·097	0·399***	0·083	0·250*	0·269*	0·319**	-0·287*
Per cent	-0·172	-0·018	0·198	-0·076	0·220	0·143	0·319**	-0·223

*$P < 0.05$; **$P < 0.01$, ***$P < 0.001$.
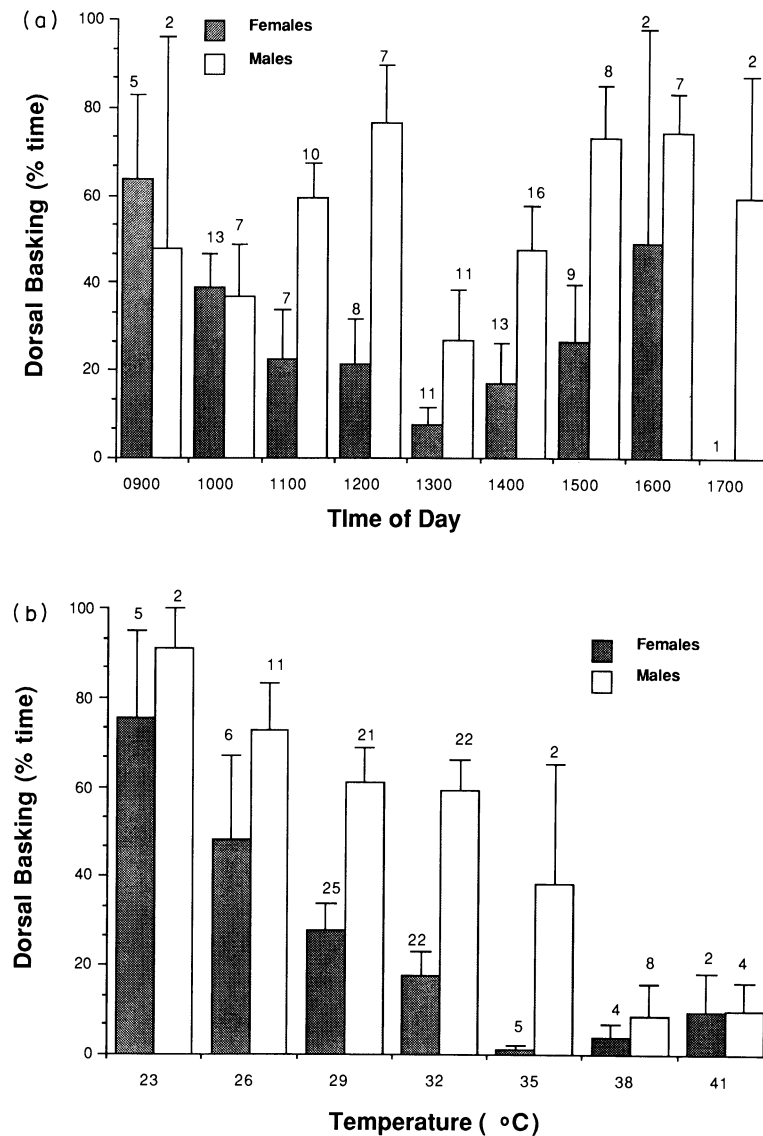
Fig. 1. The mean proportion of time spent dorsal basking by individual male and female *Euphydryas phaeton* butterflies (the error bars indicate 1 SE and the numbers indicate sample size). (a) The distribution of basking with regard to time of day. (b) The distribution of basking with regard to air temperature.

not totally surprising. In that one trial, the male would not fly.

Microhabitat variation

Habitat selection can be an especially important mechanism of behavioural thermoregulation. Considerable microhabitat variation in the thermal environment was observed at this site. Over the course of one sunny day, the temperature at 1 cm averaged 4·7 ± 1·2 °C (mean ± SD, $n = 70$) warmer than at 35 cm. Males perched higher in the

vegetation both while basking and while in the closed posture (Fig. 5). Perch height is also correlated with weather conditions. Both sexes moved up while basking in hot, sunny weather (Spearman's rho; males: $r_s[T_{air}] = 0·3884$, $P < 0·001$; $r_s[S_{irr}] = 0·2598$, $P < 0·05$; females: $r_s[T_{air}] = 0·3649$, $P < 0·05$; $r_s[S_{irr}] = 0·3526$, $P < 0·05$). The perch height of males, but not females, increased with air temperature in the closed, heat-avoidance posture (Spearman's rho; males: $r_s[T_{air}] = 0·4794$, $P < 0·001$; $r_s[S_{irr}] = 0·0620$, $P > 0·1$; females: $r_s[T_{air}] = -0·0791$, $P > 0·1$; $r_s[S_{irr}] = 0·0576$, $P > 0·1$).
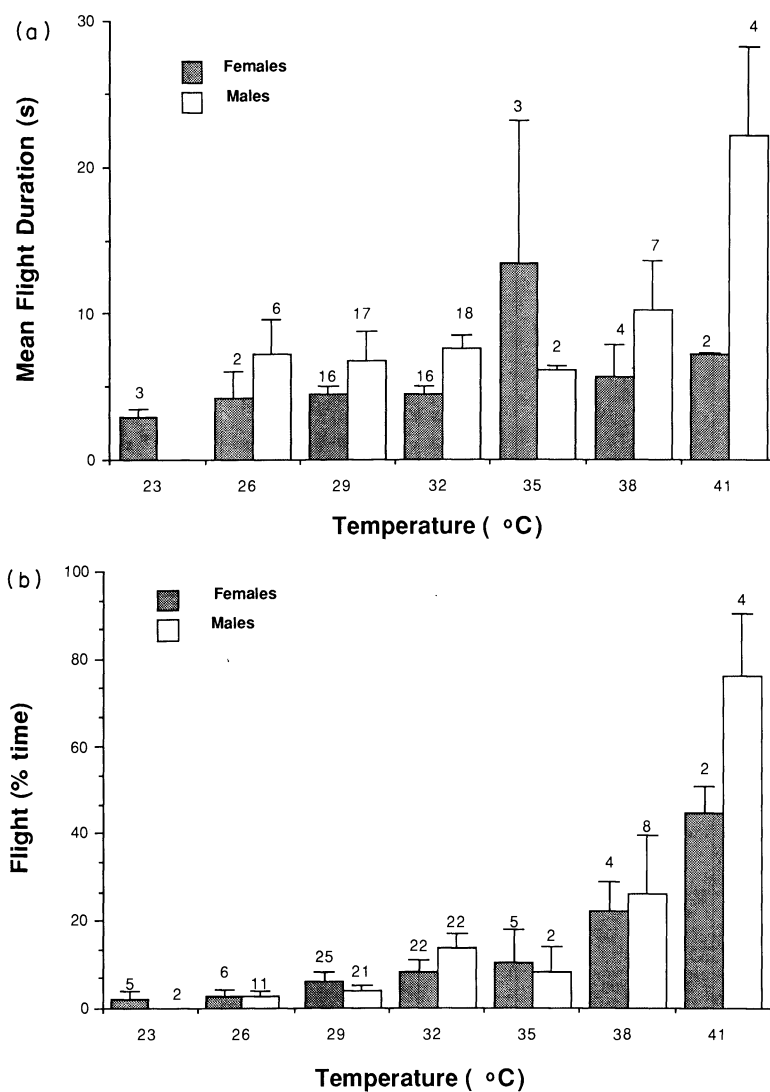
Fig. 2. Flight behaviour of individual male and female *Euphydryas phaeton* butterflies (the error bars indicate 1 SE and the numbers indicate sample size). (a) Mean flight duration with regard to air temperature. (b) Mean proportion of time in flight at different air temperatures.

Table 3. Spearman's rho correlation coefficients between reproductive behaviours and weather conditions. For males, both chases and spiral flights are combined as interactions.

	Mean air temperature	Temperature CV	Mean irradiance	Irradiance CV
Males (n = 70)				
Proportion of time spent in interactions	0·3735**	0·0259	0·2961*	−0·2284
Rate of interaction initiation	0·4872**	−0·0451	0·3326**	−0·2949*
Females (n = 69)				
Proportion of time spent in interactions	0·3262**	−0·0820	0·1781	−0·0476
Rate of interaction initiation	0·3509	−0·0862	0·2072	0·0541

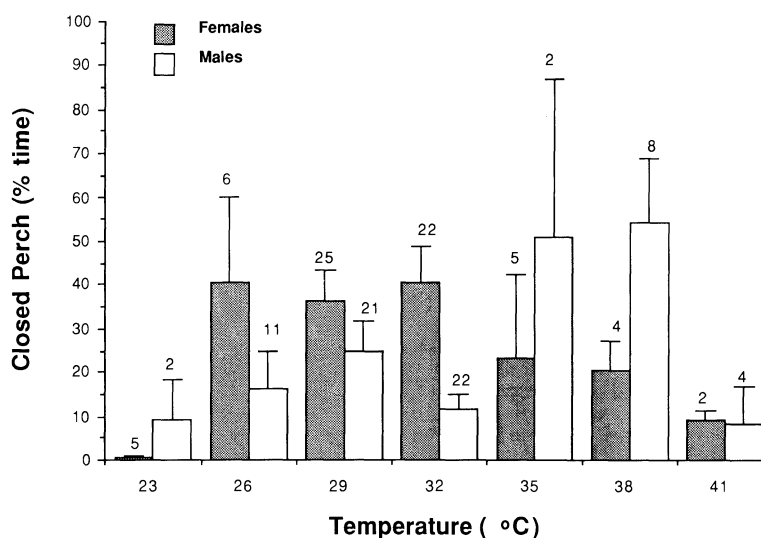*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

Fig. 3. Mean proportion of time spent by individual butterflies in the closed perching posture with regard to air temperature (the error bars indicate 1 SE and the numbers indicate sample size).

Discussion

The effect of body size on body temperature and flight

Body size affects many aspects of the ecology and physiology of organisms (Peters, 1983; Calder, 1984), including thermoregulatory ability. Thus, sexual dimorphism in body size might be correlated with sex differences in flight and thermoregulatory behaviour (Kingsolver & Watt, 1983; Pivnick & McNeil, 1986). Butterflies, like most ectothermic insects, must attain a relatively high T_{body} to fly. The time available for flight-related activities is determined by the proportion of daylight hours when individuals can maintain body temperatures between the minimum and maximum levels required for flight. For *E. phaeton*, T_{min} is approximately 23 °C for males and 28 °C for females; as expected, T_{min} is positively correlated with the sex difference in wing loading. The reduced wing loading of males, relative to that of females, allows flight at a lower wing-beat frequency, and hence, at a lower T_{body} (Heinrich, 1974; Unwin & Corbet, 1984; Pivnick & McNeil, 1986). Given the 5 °C difference in T_{min}, I expected males to spend less time basking, to fly more and to fly over a broader range of conditions than females. Males, however, basked more of the time than females at most air temperatures (Fig. 1b), even during midday (Fig. 1a), and the two sexes flew about the same proportion of the time at all but the highest air temperatures (Fig. 2b). This pattern

contrasts with previous comparisons of the flight behaviour of male and female Lepidoptera. A greater proportion of male than female *T. lineola* fly at all observed temperatures (Pivnick & McNeil, 1986). In the butterflies *Heodes virgaureae* (Douwes, 1976), *Pararge aegeria* (Shreeve, 1984) and *Colias* spp. (Kingsolver, 1983b), females were also found to fly less than males.

These results suggest that either some aspect of female morphology acts to counterbalance the 5 °C disadvantage in T_{min}, or else females can physiologically or behaviourally compensate for the difference. As outlined in the Introduction, a large body is expected to have a higher equilibrium temperature than a small body, all else being
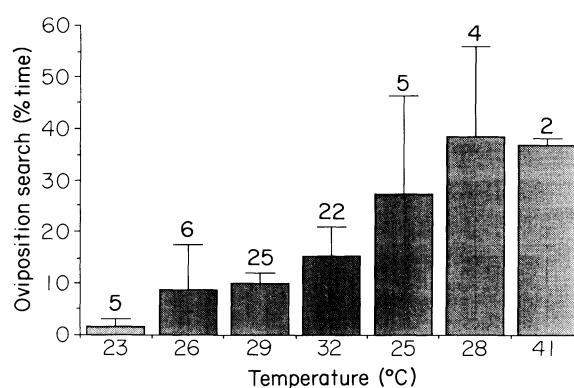

Fig. 4. Mean proportion of time spent by females searching host plants at different air temperatures (the error bars indicate 1 SE and the numbers indicate sample size).
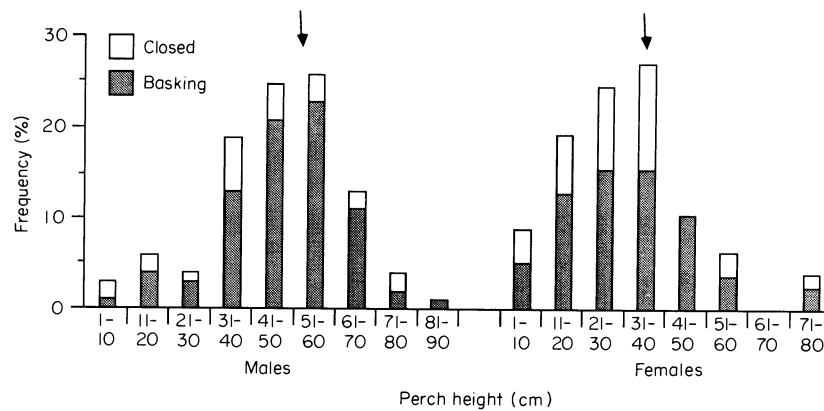
Fig. 5. The proportion of female and male *Euphydryas phaeton* observed at various perch heights during the study. Arrows indicate the mean perch height of each sex.

equal. Female body temperature excess, with the effects of day-to-day variation in weather conditions removed by analysis of covariance, was significantly higher than that of males in the closed posture, but there was no difference in T_{xs} between the sexes in the basking posture. Since there was no significant difference in male and female dorsal wing pigmentation or thoracic fur thickness, sexual dimorphism in body size seems the most likely morphological factor differentially affecting male and female T_{body}. The magnitude of the difference, however, is far less than the 5 °C disadvantage in T_{min} suffered by females. In the only other study I know that compares equilibrium T_{body} in male and female insects, Pivnick & McNeil (1986) found that males of the skipper *T. lineola*, in spite of their smaller size, had higher equilibrium T_{xs} than females. *T. lineola* males may have evolved thicker body fur (K.A. Pivnick, personal communication) to offset the intrinsic thermal disadvantage of small size, thereby allowing them to maintain a higher T_{xs} than females. Thus, the effect of sexually dimorphic body size on T_{xs} is probably small (1–2 °C) and, in some species, may be offset by sex differences in other characters such as insulation.

A second consequence of sexual size dimorphism is the differential response of T_{body} to environmental fluctuation. All else being equal, a small body will have a more rapid rate of convective heat loss than a large body because of its thinner boundary layer. In addition, the smaller distance between the body core and the surface will result in a faster rate of temperature change, resulting in close tracking of environmental temperature fluctuations and a lower equilibrium temperature (Church, 1960; Willmer & Unwin, 1981). The tight correlation between the T_{body} of

basking males with air temperature, revealed in the partial regression analysis of T_{body} on the environmental variables, contrasts with the dependence of female body temperature on solar irradiance, demonstrating that large size does confer a measurable advantage in buffering against temperature fluctuations. This advantage, however, is probably a small one, since male flight behaviour is not negatively correlated with the coefficient of variation in T_{air} (Tables 2 and 3) as would be expected.

Female *E. phaeton* do not appear to be physiologically more efficient than males. In fact, the mean duration of individual flights by females is about half that of males (Fig. 2a), suggesting that high wing loading greatly constrains flight ability. To be certain that this pattern reflected a physiological constraint rather than a difference in motivational state, a forced flight experiment was performed. If the sex difference in flight duration is simply behavioural, it should disappear when males and females respond to a similar stimulus, such as threat by a potential predator. If males and females differ in their physiological capacity, then the difference should remain unchanged. The duration of forced flight by females was about half that of males, supporting the hypothesis that the short duration of female flight reflects physiological constraint. Female flight duration in the forced flight experiment was positively correlated with basking prior to flight and solar irradiance level, as expected from the strong dependence of female body temperature on irradiance level, while male flight was uncorrelated with any measured variable. Thus large body size and high wing loading in females correlates with reduced flight capacity and greater environmental constraint on behaviour.

Behavioural compensation for the thermal disadvantage of females

The hypotheses of morphological or physiological compensation for the 5 °C difference in T_{min} fail to explain the similarity in the flight pattern of males and females (Fig. 2), suggesting that behavioural differences between the sexes must be considered. Stevenson's (1985) theoretical treatment of behavioural and physiological mechanisms of temperature regulation by terrestrial ectotherms argued that prudent habitat selection was by far the most effective means of maintaining a large T_{xs}. Casey (1981) pointed out that the often different microenvironments inhabited by male and female insects may differ considerably in temperature due to boundary layer effects. Wind velocity is reduced by friction with the ground or vegetational surface, resulting in lower rates of forced convective cooling at lower perch heights (Campbell, 1977). Cells of warm air produced by radiant heat reflected from the earth's surface accumulate near the ground, producing a gradient of air temperatures that decrease with height above the surface. Male *E. phaeton* perch near the top of the vegetation, maximizing their exposure to winds that increase the rate of forced convective cooling, thereby necessitating nearly continuous basking throughout the day (Fig. 1) to maintain the optimal flight temperature. In contrast, the oviposition activity of females takes place largely within the vegetational boundary layer because the host plant, *P. lanceolata*, rarely exceeds 30 cm in height. Convective cooling is minimized and ambient temperatures are 4–5 °C warmer than at the top of the vegetation, thereby reducing the need for basking. Females occasionally leave the vegetational boundary layer to feed on nectar, but most flights are between neighbouring host plants and so occur entirely within the boundary layer. Thus females inhabit a warmer, more thermally stable microenvironment as well as being buffered by large body size against short-term temperature change.

The relative difference in thermal constraint on the flight of male and female *E. phaeton* reflects sex differences in reproductive strategy (Kingsolver, 1983b), especially in habitat utilization. Males have a mixed perching/patrolling strategy (Scott, 1974); they may locate freshly eclosed females via patrolling flights or by perching and giving chase to passing conspecifics. The switch between these reproductive tactics may be temperature mediated, as suggested by Wickman (1984) for *Coenonympha pamphilus* and Shreeve (1984) for *Pararge aegeria*. The duration and

frequency of flight initiation increase with mean air temperature and irradiance level, resulting in a greater proportion of time spent in flight (Table 2) and chases (Table 3) under warm, sunny conditions. Females fly primarily to locate host plants and nectar sources; flight behaviour correlates weakly with mean temperature and irradiance level (Table 2). The proportion of time spent searching host plants increases with temperature but not irradiance level (Table 3). Because this search takes place within the warmer boundary layer, basking under high irradiance is more important for occasional flight between patches of host plants than for the more common movement within a plantain patch. Variable cloudiness, measured by the coefficient of variation in irradiance level during a continuous observation of an individual, tends to disrupt male flight and chase behaviour (Tables 2 and 3). Female behaviour, on the other hand, is unaffected by variable cloudiness (Tables 2 and 3). These observations are consistent with the hypothesis that the small size of males, coupled with their exposed perch sites, renders them more vulnerable than the larger, more sheltered females to high rates of convective heat loss during short periods of unfavourable conditions. Whether or not this sex difference in microhabitat choice is adaptive, in the sense that females actively choose to occupy the warmer microenvironment, thereby relaxing the thermal constraints on flight imposed by high wing loading, or simply a by-product of the fact that the host plant is shorter in stature than the surrounding vegetation is unclear. The preferred host plant of *E. phaeton, Chelone glabra* L. (Scrophulariaceae), is much taller in stature and occurs in damp areas rather than grasslands. A study of the flight space and perch sites of males and females in a population using this host would be most interesting.

Thermoregulatory constraints and sexual size dimorphism

Sex differences in body size have important consequences for thermoregulation and flight in *E. phaeton*, which directly affect the time available for reproductive activities. 'Reversed' dimorphism, where males are smaller than females, is common among invertebrates, but lacks a generally accepted explanation (Wiklund & Karlsson, 1988). Small body size in males may evolve as a correlated response with reduced development time, termed protandry by Wiklund & Fagerstrom (1977); sexual selection should favour males who

can eclose before females in species where females mate only once shortly after eclosion. This hypothesis predicts that the degree of protandry should be correlated with the degree of sexual dimorphism (Singer, 1982); the absence of published data on the body masses of male and female Lepidoptera, however, has prevented an adequate comparative test of this hypothesis (but see Wiklund & Karlsson, 1988). Alternatively, small body size in male insects may directly increase flight performance in some way that yields a mating advantage over larger sized competitors (Marshall, 1988; Steele & Partridge, 1988).

Pivnick & McNeil (1986) argue that sexual selection for thermoregulatory ability in male *T. lineola* has favoured reduced male body size to a greater degree than that predicted by protandry alone. They propose that small size benefits males in two ways. First, reduced wing loading reduces the minimum temperature for flight as described above, potentially expanding the range of temperatures over which males can be active. However sexual variation in microhabitat use, as shown in this study, may compensate for all or part of the thermal disadvantage high wing loading bestows on females. Secondly, Pivnick & McNeil (1986) argue, after Blau (1981), that small body size results in more rapid warming, thereby allowing males to exploit short periods of favourable conditions. In this study, male, but not female, flight behaviour was disrupted by intermittent cloudiness (Tables 2 and 3). Small size is unlikely to be advantageous in this context because small individuals cool down more rapidly as well. The rate of occurrence of environmental fluctuation must be greater than the heating (or cooling) rate of males, but less than the heating (or cooling) rate of females for males to have any advantage (Kingsolver & Watt, 1983; G. W. Gilchrist, unpublished observation). The time rate of change in T_{body} can be described by the transient time constant, τ (Kingsolver & Watt, 1983). For *E. phaeton*, τ_{male} and τ_{female} are approximately 45 and 75 s respectively. It seems unlikely that the time rate of environmental change would regularly fall within these restrictive boundaries.

Rather than selection for thermoregulatory and flight ability favouring small males, I suggest that these factors may often limit the evolution of large body size in female ectotherms. Natural selection for increased fecundity may favour large body size in females, but body size might be constrained by the need to fly. The realized fecundity of female butterflies seems to be constrained by poor weather which prevents oviposition (Gossard &

Jones, 1977; Hayes, 1981; Stamp, 1982a; Kingsolver, 1983b; reviews in Courtney, 1986; Kingsolver, 1985). As greater egg loads cause wing loading to increase, flight becomes more energetically expensive and, eventually, aerodynamically impossible. As long as the advantage of flying to locate dispersed host plants or escape potential predators (Bowers, Brown & Wheye, 1985) outweighs the benefits of increased potential fecundity, the evolution of sexual size dimorphism will be constrained.

Acknowledgments

References

Blau, W.S. (1981) Latitudinal variation in the life histories of insects occupying disturbed habitats: a case study. In *Insect Life History Patterns* (eds. R. Denno & H. Dingle), pp. 75–96. Springer-Verlag, New York.

Bowers, M.D. (1978) Over-wintering behavior in *Euphydryas phaeton* (Nymphalidae). *Journal of the Lepidopterist's Society*, **32**, 282–288.

Bowers, M.D., Brown, I.L. & Wheye, D. (1985) Bird predation as a selective agent in a butterfly population. *Evolution*, **39**, 93–103.

Calder, W.A. (1984) *Size, Function, and Life History.* Harvard University Press, Cambridge, Massachusetts.

Campbell, G.S. (1977) *An Introduction to Environmental Biophysics.* Springer-Verlag, New York.

Casey, T.M. (1981) Behavioral mechanisms of thermoregulation. In *Insect Thermoregulation* (ed. B. Heinrich), pp. 79–114. Wiley, New York.

Casey, T.M. & Joos, B.A. (1983) Morphometrics, conductance, thoracic temperature, and flight energetics of noctuid and geometrid moths. *Physiological Zoology*, **56**, 160–173.

Church, N.S. (1960) Heat loss and body temperature of flying insects. II. Heat conduction within the body and its loss by radiation and convection. *Journal of Experimental Biology*, **37**, 187–212.

Clench, H.K. (1966) Behavioral thermoregulation in butterflies. *Ecology*, **47**, 1021–1034.

Courtney, S.P. (1986) The ecology of pierid butterflies: dynamics and interactions. *Advances in Ecological Research,* **15,** 51–131.

Courtney, S.P. & Duggan, A.E. (1983) The population biology of the Orange Tip butterfly *Anthocharis cardamines* in Britain. *Ecological Entomology,* **8,** 271–281.

Dempster, J.P. (1983) The natural control of populations of butterflies and moths. *Biological Reviews,* **58,** 461–481.

Douwes, P. (1976) Activity in *Heodes virgaureae* (Lepidoptera: Lycaenidae) in relation to air temperature, solar radiation, and time of day. *Oecologia,* **22,** 287–298.

Gossard, T. & Jones, R. (1977) The effects of age and weather on egg-laying in *Pieris rapae* L. *Journal of Applied Ecology,* **14,** 65–71.

Hayes, J.L. (1981) The population ecology of a natural population of the pierid butterfly *Colias alexandra. Oecologia,* **49,** 188–200.

Heinrich, B. (1974) Thermoregulation in endothermic insects. *Science,* **185,** 747–756.

Kingsolver, J.G. (1983a) Thermoregulation and flight in *Colias* butterflies: elevational patterns and mechanistic limitations. *Ecology,* **64,** 534–545.

Kingsolver, J.G. (1983b) Ecological significance of flight activity in *Colias* butterflies: implications of reproductive strategy and population structure. *Ecology,* **64,** 546–551.

Kingsolver, J.G. (1985) Butterfly thermoregulation: organismic mechanism and population consequences. *Journal of Research on the Lepidoptera,* **24,** 1–20.

Kingsolver, J.G. & Moffat, R.J. (1982) Thermoregulation and the determinants of heat transfer in *Colias* butterflies. *Oecologia,* **53,** 27–33.

Kingsolver, J.G. & Watt, W.B. (1983) Thermoregulatory strategies in *Colias* butterflies: thermal stress and the limits to adaptation in temporally varying environments. *American Naturalist,* **121,** 32–55.

Marden, J.H. (1987) Maximum lift production during takeoff in flying animals. *Journal of Experimental Biology,* **130,** 235–258.

Marshall, L.D. (1988) Small male mating advantage in mating *Parapediasia teterralla* and *Agriphila plumbifimbriella* (Lepidoptera: Pyralidae). *American Midland Naturalist,* **119,** 412–419.

Peters, R.H. (1983) *The Ecological Implications of Body Size.* Cambridge University Press, Cambridge.

Pivnick, K.A. & McNeil, J.N. (1986) Sexual differences in the thermoregulation of *Thymelicus lineola* adults (Lepidoptera: Hesperidae). *Ecology,* **67,** 1024–1035.

Rawlins, J.E. (1980) Thermoregulation by the black swallowtail-butterfly, *Papilio polyxenes* (Lepidoptera: Papilionidae). *Ecology,* **61,** 345–357.

Scott, J.A. (1974) Mate-locating behavior of butterflies. *American Midland Naturalist,* **91,** 103–117.

Shreeve, T.G. (1984) Habitat selection, mate location, and microclimatic constraints on the activity of the speckled wood butterfly, *Pararge aegeria. Oikos,* **42,** 371–377.

Singer, M.C. (1982) Sexual selection for small size in male butterflies. *American Naturalist,* **119,** 440–443.

Stamp, N. E. (1982a) Selection of oviposition sites by the Baltimore checkerspot, *Euphydryas phaeton* (Nymphalidae). *Journal of the Lepidopterist's Society,* **36,** 290–302.

Stamp, N. E. (1982b) Aggregation behavior in Baltimore checkerspot *Euphydryas phaeton* (Nymphalidae). *Journal of the Lepidopterist's Society,* **36,** 31–41.

Steele, R.H. & Partridge, L. (1988) A courtship advantage for small males in *Drosophila subobscura. Animal Behaviour,* **36,** 1190–1197.

Stevenson, R.D. (1985) The relative importance of behavioural and physiological adjustments controlling body temperature in terrestrial ectotherms. *American Naturalist,* **126,** 362–386.

Unwin, D.M. & Corbet, S.A. (1984) Wingbeat frequency, temperature and body size in bees and flies. *Physiological Entomology,* **9,** 115–121.

Wasserthal, L.T. (1975) The role of butterfly wings in regulation of body temperature. *Journal of Insect Physiology,* **21,** 1921–1930.

Watt, W.B. (1968) Adaptive significance of pigment polymorphisms in Colias butterflies. I. Variation of melanin pigment in relation to thermoregulation. *Evolution,* **22,** 437–458.

Wickman, P. (1984) The influence of temperature on the territorial and mate locating behaviour of the small heath butterfly, *Coenonympha pamphilus* (L.) (Lepidoptera: Satyridae). *Behavioral Ecology and Sociobiology,* **16,** 233–238.

Wiklund, C. & Fagerstrom, T. (1977) Why do males emerge before females? A hypothesis to explain the incidence of protandry in butterflies. *Oecologia,* **31,** 153–158.

Wiklund, C. & Karlsson, B. (1988) Sexual size dimorphism in relation to fecundity in some Swedish satyrid butterflies. *American Naturalist,* **131,** 132–138.

Willmer, P.G. & Unwin, D.M. (1981) Field analysis of insect heat budgets: reflectance, size and heating rates. *Oecologia,* **50,** 250–255.