Behavioural thermoregulation in butterflies: the interacting effects of body size and basking posture in *Hypolimnas bolina* (L.) (Lepidoptera : Nymphalidae)

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Abstract

The evolutionary significance of body size variation in male insects is often obscure. One way in which this parameter could affect reproductive success is via its relevance to thermoregulation. In this study we investigated the relevance of body size to heat exchange rates in a tropical nymphalid, the common eggfly (*Hypolimnas bolina*) (L.). Males of this territorial species elevate their body temperature above ambient levels via a series of basking postures coupled with strategic choice of perching microhabitat. In an experiment with dead butterfly models we found, as expected, heightened rates of heat exchange (heating and cooling rates) in smaller individuals. There was also a significant interaction between basking posture and body size, with smaller individuals exhibiting significantly greater variation in heating rate with increasingly open wing postures. This suggests that smaller males would have greater control over their rate of basking heat gain (by having at their disposal a greater potential range of heating rates), but they would also radiate body heat at a higher rate than their larger conspecifics. Using 'grab and stab' techniques, we found no evidence that smaller individuals are closer to their putative thermal optimum under a range of ambient conditions in the field. However, a more substantive field program, incorporating a more precise characterisation of the ambient thermal environment, will be required to fully evaluate the thermal significance of body size variation in males of this territorial butterfly.

Introduction

Body size at maturity is a key life-history trait that is closely tied to fitness in many organisms (Stearns 1992). Among the insects, most research into the reproductive consequences of adult body size has focused on readily quantifiable aspects of female fitness, such as fecundity, egg size and longevity (e.g. Wickman and Karlsson 1989; Honek 1993; Braby and Jones 1995). Although the situation is complex (e.g. Klingenberg and Spence 1997), and there is clearly much more to learn, the general principle emerging from these studies is that, due primarily to effects upon fecundity, adult fitness increases with increasing body size (although this advantage can be opposed, for example, by juvenile viability selection, resulting in stabilising net selection upon body size). This general adult size–fitness relationship, however, does not appear to extend to male insects. Empirical investigations into the reproductive consequences of variation in adult body size in this sex have routinely produced conflicting findings (see Rosenberg and Enquist 1991 *v.* Hernández and Benson 1998 *v.* Kemp 2000), and sometimes, failed to find any effect (Lederhouse 1982; Strohm and Lechner 2000).

Whereas the fitness of female insects is generally prescribed by their ability to produce and lay eggs, the fitness of males depends upon their success in locating and mating with sexually receptive females, and in fertilising female gametes (Thornhill and Alcock 1983). Numbers of receptive females are in most cases greatly outweighed by sexually receptive

males, a situation that fosters both intense competition between males for mates, and the opportunity for mate discrimination by females (Andersson 1994). Body size is sometimes clearly important in these competitive contexts; for example, larger males are advantaged in mating systems involving direct physical combat over females or mating resources (e.g. bees: Alcock and Houston 1996). However, there are many more cases when the relevance of adult body size to male competition is obscure (e.g. butterflies: Kemp 2000). In a few instances, body size apparently varies with male competitive status even when it is not clear how or why this may be the case (Alcock 1979; Rosenberg and Enquist 1991; Hernández and Benson 1998).

One context in which body size may affect the fertilisation success of male insects is thermoregulation. As heliotherms, the ability of male insects to move around the environment – and thus compete for matings – is often heavily constrained by their ability to maintain an optimal body temperature in the face of environmental perturbations. Consequently, the mate-locating activities of many species include, as a key feature, a suite of thermoregulatory adaptations, including basking behaviours (Clench 1966), shivering (Srygley 1994) and thermal-specific strategies of microhabitat selection (Rutowski *et al*. 1994). The requirement for efficient thermoregulation has also directed a host of morphological adaptations, including thermal insulation and colour patterning (Kingsolver 1987). Adult body size is not generally recognised as such an adaptation; however, this trait will have some effect on an individual insect's ability to attain and/or maintain an optimal body temperature because larger objects possess greater thermal inertia (Heinrich 1986; Gilchrist 1990). Depending upon the specifics of the thermal environment, this effect may advantage males of particular size, and thus implicate body size as a determinant of reproductive success in particular species (Kingsolver and Watt 1983).

Here we set out to assess the relevance of body size to thermoregulatory ability in mate-locating males of the nymphalid butterfly, the common eggfly (*Hypolimnas bolina*) (L.). Like many butterflies, male *H. bolina* perch at and defend geographically prominent locations, such as forest clearings and edges (Rutowski 1992; Kemp and Rutowski 2001), as a way of maximising their encounters with receptive females (i.e. virgins, since females of this species generally mate only once: Kemp 2001). Males engaged in this behaviour perch for long periods on the outermost leaves of trees and shrubs, or similar vantage points, and launch themselves at objects passing within their visual range. If a conspecific female is located she is then courted (Rutowski 1992); if a male is encountered then a contest over territory ownership generally ensues (see Kemp 2000). Regulation of thoracic muscle temperature is crucially important to males engaging in this behaviour because it determines thoracic power output, and thus the ability to respond quickly to a passing female (Rutowski *et al*. 1994). There is also some evidence that the ability of butterflies to win territorial contests, and thus to monopolise key mate-locating sites, is influenced by thoracic temperature (Stutt and Willmer 1998). As expected, therefore, territorial male butterflies exhibit behaviours geared towards regulating their thoracic temperature to within specific limits, usually in the range of 35–40°C (Rutowski *et al*. 1994; Srygley 1994; Dreisig 1995).

Our aims in this study were two-fold. First, we aimed to experimentally investigate how the processes of heat exchange in adult male *H. bolina* are modified by variation in body size. Males of this species elevate their body temperature above suboptimal ambient levels using a series of basking postures (outlined in detail below); hence, we focused on the thermal relevance of body size in this behavioural context. Previous investigations have studied the effects of behavioural posture and body size to thermoregulation in butterflies

(e.g. Heinrich 1986; Kingsolver 1987; Berwaerts *et al*. 2001), but little is known about whether and how these effects interact. Second, since the net effect of body size on heating and cooling rates will be ultimately determined by aspects of the thermal environment, particularly the temporal scaling of environmental temperature fluctuations (Kingsolver and Watt 1983; Gilchrist 1990), we also aimed to investigate whether there are consistent thermal differences between males of different sizes under field conditions.

Methods

Behavioural thermoregulation in H. bolina

In north Queensland male *H. bolina* perch at mate-encounter sites for an extended diel period (0900–1700 hours) throughout most of the year, and are thus subject to widely ranging environmental conditions (Rutowski 1992; Kemp and Rutowski 2001). Under relatively cool conditions (in the early morning, late afternoon, or immediately after extended overcast spells), individuals perch in the sun with their wings fully spread and angled downwards so that the distal edges are appressed to the substrate (hereafter, the 'appression' posture). As ambient temperature increases, males continue to select perches in the sun, but adopt wing postures ranging from horizontally spread (the 'classic' dorsal basking posture: Clench 1966) to completely closed. Under still hotter conditions, males perch with closed wings in the shade. The most common perching substrate is tree/shrub foliage (Rutowski 1992).

Experimental determination of heat-exchange rates

Our experimental procedure has been documented previously (refer to Kemp and Krockenberger 2002). Briefly, we set out to measure the rate at which butterflies (of different sizes and basking postures) warmed with exposure to sunlight, and how quickly they lost heat once shaded. As with previous investigations into butterfly thermoregulation (e.g. Gilchrist 1990; Rutowski *et al*. 1994), we used immaculate specimens that were reared and immediately frozen 4–12 weeks earlier. Our experimental apparatus consisted of a platform (200 × 200 mm) of 10-mm polystyrene through which we inserted four hypodermic-mounted thermocouple probes in a 100-mm square pattern. The probes each consisted of a 40-gauge copper–constantan thermocouple seated within a 29-gauge hypodermic needle. We placed this platform in an open polystyrene box situated on a laboratory bench where it could be exposed to direct sunlight through an opened westward-facing window. We conducted experiments only under cloudless conditions between 1100 and 1400 hours in mid-May, hence solar radiation intensity should have been relatively consistent across trials. Temperature in the laboratory was controlled to within 21–24°C.

We assessed the effect of body size and wing posture simultaneously by impaling specimens of varying body sizes in each of four postures on the four thermocouple probes and logging their thoracic temperatures after exposure to midday sunlight. The four postures were (1) 'closed' = wings held closed over the thorax in the resting position; (2) 'partially open' = wings opened 45° from normal; (3) 'flat' = wings fully opened (i.e. each wing 90° from normal); and (4) 'appressed' = wings fully opened but angled downwards such that the tips contacted the substrate (each wing ~100° from normal). We mounted individuals so that the thermocouple probe protruded 2–3 mm into their thorax, and their wings were arranged using nylon-tipped entomological pins (only the nylon tips contacted the specimen's medial wing tissue). We oriented the platform such that the butterflies were perpendicular to the plane of the incident solar radiation. Upon exposure to the sun, we logged the thoracic temperature of all specimens each second, using a 10-channel Data Electronics DT-500 data-logger. When all specimens exceeded 40°C the entire apparatus was cast in shade and thoracic temperatures again logged until thoracic temperatures returned to below 30°C.

We employed a balanced randomised experimental design in which four males were randomly assigned among the four thermocouples, and the four wing postures were randomly assigned among individuals in each of four successive trials. Each individual butterfly was therefore trialed sequentially on the same probe, adopting each of the four wing postures in a randomised order. Specimens were placed in a humidifier between trials to reduce desiccation, and weighed (nearest 0.001 g) immediately before each trial. Six sets of males were used, totalling 96 separate trials. Thoracic heat gain and loss in the range of 25–40°C was slightly curvilinear, hence we calculated the rate of heat exchange as the slope of a regression of thoracic temperature against the square root of time. Since the optimum operational temperature of this tropical species is ~37°C (see below), the range of 25–40°C should be relevant to the likely (suboptimal) thermal stresses faced by individuals under field conditions.

We conducted two slightly different analyses to assess the effect of body size, wing posture and their interaction upon heating/cooling rates. First, we analysed the effects of posture (main effect) and body size (covariate) upon heat exchange using ANCOVA. For simplicity we excluded individual ID, trial order or probe as potential predictors in this model. The non-inclusion of these factors renders our test of body size effects conservative, although the variance attributable to these factors is relatively minor (refer to Kemp and Krockenberger 2002). Second, we calculated the mean and variance in between-trial (thus between-posture) heating/cooling rate for each individual, and compared these values to body size. Significant covariance between body size and mean heating rate in this analysis would indicate an effect of body size *per se*, whereas covariance between between-specimen variance in size and heating rate would indicate that the effects of posture and body size interact. This analysis is less powerful than the ANCOVA but controls for any effects due to non-body-size-related morphological variation between the specimens. We conducted both analyses in order to affirm the robustness of our results.

In all analyses we corrected for slight, uncontrollable, variations (in the order of 1–3°C) in the temperature at the time of trial commencement by expressing heating/cooling rates as a residual from a linear regression against starting temperature; hence, the values of these variables given throughout (e.g. Figure 1) are arbitrary and not directly cross-comparable.

Determination of field thoracic temperatures

We determined the thoracic temperatures of actively mate-locating male *H. bolina* at a field encounter site near Cairns, Australia (16°53′S, 145°45′E), on 14 days between 25 January and 23 February 2000. This popular male perching site consists of a 5–15-m open corridor separating riparian rainforest vegetation from sugarcane (Kemp and Rutowski 2001). We selected males haphazardly and watched them for 5–10 min to ensure that they exhibited behaviours consistent with mate location (as per Rutowski 1992). Once a focal male perched and consistently adopted one of four wing postures (as earlier described) for ~10 s, we netted him and measured his thoracic temperature using a thermocouple probe similar to those used in the experiments (above). This probe was inserted ventrally ~3 mm into the male's thorax while he was restrained (via the net) against a polystyrene sheet. Peak thoracic temperature was read (to the nearest 0.1°C) using a Sable Systems TC-1000 digital thermocouple thermometer. At no stage was the butterfly directly handled, and we used only those measurements obtained within approximately 6 s of capture. We also immediately measured ambient temperature at the point of each capture using an additional shielded thermocouple probe (specifications as above). All probes were calibrated previously (see Kemp and Krockenberger 2002).

In our analyses of male thermal status in the field, we expressed the body temperatures of males in terms of their absolute departure from a proposed mean thermal optimum of 37°C (hereafter we refer to this as 'thermal departure'). This temperature corresponds roughly to the average thoracic temperature at which males of this species switch from basking to heat-avoidance behaviours (DJK, unpublished data; refer also to fig. 2 of Kemp and Krockenberger 2002). We also calculated the thermal excess for each male by subtracting the ambient air temperature at the time and site of measurement from his thoracic temperature.

Results

Experimental determination of heat exchange rates

As previously reported in detail (Kemp and Krockenberger 2002), heating rate was affected by wing posture (ANCOVA, $F_{3,88} = 159.5$, $P < 0.00001$). The rate of heat gain was also significantly affected by (the covariate) body mass ($F_{1,88} = 37.88$, $P < 0.0001$), and the interaction between these effects was significant ($F_{3,88} = 10.32$, $P < 0.0001$). The difference in heating rate between postures increased with decreasing body size (Fig. 1*a*, Table 1), which suggests that smaller individuals have greater potential to vary their rate of heat gain (via choice of behavioural posture) than larger butterflies. The rate at which specimens lost heat was also affected by body size (ANCOVA, $F_{1,88} = 13.25$, $P < 0.0005$), with smaller individuals losing heat more rapidly than larger butterflies (Fig. 1*b*, Table 1). However, neither wing posture ($F_{3,88} = 0.009$, $P = 0.99$) nor size × posture interaction ($F_{3,88} = 0.027$, $P = 0.95$) significantly affected cooling rates.

These findings were replicated by our analysis of heating/cooling rates averaged for each specimen; thus, our results appear robust. Body mass varied negatively with both
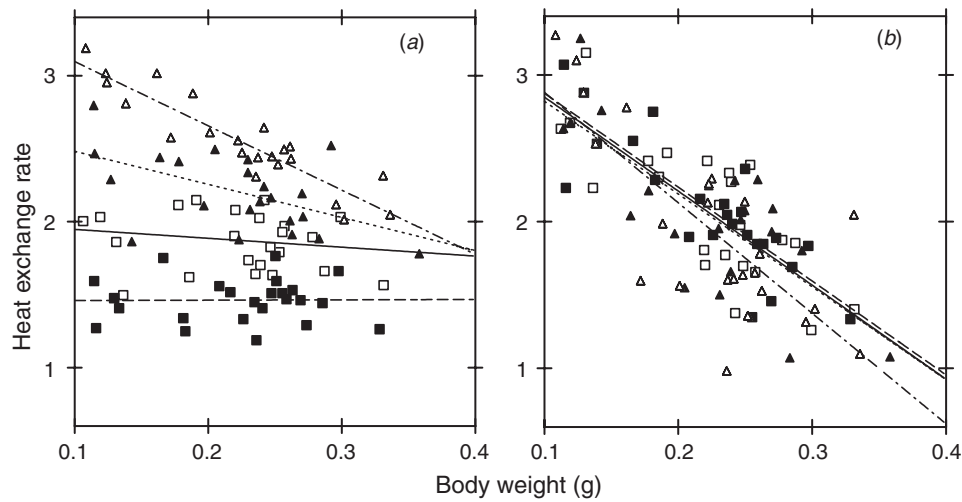
Fig. 1. Relationships between bodyweight and (*a*) heating rate and (*b*) cooling rate (both expressed in arbitrary units). Data are grouped by posture (solid squares, dashed line = 'closed'; open squares, solid line = 'partially closed'; solid triangles, dotted line = 'flat'; open triangles, dashed and dotted line = 'appressed'). The equations corresponding to the fitted regression lines are given in Table 1.

Table 1. Regression equations describing the relationships between heat-exchange rates (dependent variable, *y*) and body size (independent variable, *x*), grouped by posture

These equations correspond directly to the fitted lines in Fig. 1, and n = 24 for all equations. Refer to the Methods section for description of how the rates of heat exchange were calculated

Posture	Heating rate	Cooling rate
Closed	$y = 1.46 + 0.03x$	$y = 3.03 - 12.80x$
Partially closed	$y = 2.01 - 0.61x$	$y = 2.98 - 12.82x$
Flat	$y = 2.70 - 2.25x$	$y = 2.89 - 12.61x$
Appressed	$y = 3.54 - 4.40x$	$y = 3.27 - 15.06x$

mean heating rate (Regression: $F_{1,22} = 16.1$, $P < 0.001$, $R^2 = 0.42$, HEAT GAIN = 2.44 – 1.89MASS) and cooling rate ($F_{1,22} = 112.2$, $P < 0.00001$, $R^2 = 0.84$, COOLING RATE = 3.12 – 13.7MASS). Second, within-specimen variance in heating rate ($F_{1,22} = 93.5$, $P < 0.00001$, $R^2 = 0.81$, HEAT GAIN = 1.86 – 4.00MASS) – but not cooling rate ($F_{1,22} = 0.00047$, $P = 0.98$, $R^2 = 0.000021$) – varied significantly and negatively with body mass. This again indicates that smaller individuals should be capable of modifying their heating rates (via choice of wing posture) more dramatically than large specimens.

Field body temperatures

We found little evidence that different-sized males exhibit field thoracic temperatures consistently closer to their (putative) thermal optimum of 37.0°C. First, forewing length, which ranged from 31.5 to 45.0 mm (mean = 37.0 ± 0.5 mm), was not related to 'thermal departure' in the null sense (i.e. across all individuals, ambient temperatures and postures;

Pearson's $R = 0.11$, $n = 86$, $P = 0.32$; power for detecting medium effect [i.e. $R = 0.30$], $1 - \beta = 0.82$). Second, in the sample of individuals displaying open wing postures (i.e. postures indicative of suboptimal thoracic temperature), thoracic temperature excess was not related to body size (Pearson's $R = -0.0337$, $n = 54$, $P = 0.81$; power for detecting medium effect [i.e. $R = 0.30$], $1 - \beta = 0.62$). Last, we entered ambient temperature and body size in a multiple regression against thermal departure. The overall regression was significant ($F_{2,83} = 15.92$, $P < 0.0001$, $R^2 = 0.27$); however, ambient temperature ($t_{83} = -5.52$, $P < 0.0001$) was the only significant term in this linear model (body size: $t_{83} = 1.25$, $P = 0.215$). This analysis indicates that, even with variation due to ambient temperature controlled (i.e. with ambient temperature as a term in the model), smaller males were not routinely closer to their proposed thermal optimum than their larger counterparts.

Discussion

Whereas basking posture and body size have been previously identified as key determinants of insect thermoregulatory ability (e.g. Heinrich 1986; Pivnick and McNiell 1986; Berwaerts *et al*. 2001), few investigations have stressed the potential for interaction between them. In this study we set out to investigate the relevance of body size to heating and cooling rates in a dorsal basking butterfly species for which the thermal relevance of basking posture has been previously demonstrated (Kemp and Krockenberger 2002). As expected, and in line with prior investigations (e.g. Gilchrist 1990; although see Berwaerts *et al*. 2001), larger individuals exhibited significantly lowered experimental rates of heat exchange (heat gain and loss). At least in the case of heating rates, this result was accompanied, somewhat surprisingly, by a significant interaction between the effects of wing posture and body size (illustrated by Fig. 1). Hence, not only do larger male *H. bolina* gain heat via basking more slowly, but they apparently also have a lowered capacity to modulate their rate of heat gain via the use of wing posture. This is, to our knowledge, the first empirical demonstration of such an effect in butterflies.

Our experiments suggest that smaller male *H. bolina* may achieve higher (and more variable) rates of basking heat gain, but the data also indicate that this potential thermal advantage will be opposed by higher rates of heat loss. The net thermal significance of body size variation in this species should therefore ultimately depend upon the temporal scale of environmental fluctuations (refer to the expanded reasoning of Kingsolver and Watt 1983; Gilchrist 1990). Field rates of heat exchange will also be significantly influenced by variation in convective cooling due to wind speed. This variable was deliberately excluded in our experiment, although some air flow would have been present: Kingsolver (1985) reported air-flow rates in the order of 0.1–0.2 ms⁻¹ around specimens housed under laboratory conditions similar to ours. Convection currents are also likely to establish around a heated butterfly as rising warmer air is replaced laterally by cooler air (Wasserthal 1975). Kemp and Krockenberger (2002) suggested that a reduction of cooling air flow near thoracic regions may constitute the key thermal advantage of the 'appression' basking posture exhibited by this species.

Whereas we found no effect of posture upon cooling rates, Berwaerts *et al*. (2001) reported differential convective cooling of male *Pararge aegeria* L. (Nymphalidae) in different basking postures, with males in open-wing postures losing heat at a faster rate. Their experiment differed from ours in that cooling rates of models were measured both in the field and the laboratory, with wind (speed = 0.5 ms⁻¹) simulated in laboratory trials. This would again seem to implicate wind as a major determinant of likely heat-exchange rates in the field. However, *P. aegeria* is also considerably smaller than *H. bolina* (the

former generally less than half the mass of the latter: DJK, unpublished data), and so the two species may differ in their general susceptibility to convective cooling. Berwaerts *et al.* (2001) also reported an interaction between the effects of ambient temperature and body size upon rates of experimental heat gain, with the effect of body size diminishing as ambient temperature increased. In this experiment we measured heat-exchange rates at only one, loosely controlled, temperature range (21–24°C); however, this is expected to represent the lower end of field ambient temperatures experienced by *H. bolina*, at least across most of their tropical and subtropical range. The ability to gain heat at this temperature will be an important determinant of overall thermoregulatory ability, which suggests a potential advantage to smaller individuals regardless of whether this effect persists at higher ambient temperatures (that is, irrespective of whether a size × temperature interaction exists).

Nevertheless, we failed to detect any evidence of consistent, size-related thermal differences in mate-locating individuals under field conditions. This could be because body-size variation is relatively unimportant, in the face of other influences upon body temperature in the wild, but there are other explanations. Behavioural thermoregulation encapsulates a complex and dynamic three-way interaction between morphology, behaviour and the ambient thermal environment (Kingsolver 1987). As we mention above, ambient temperature is only one determinant of a butterfly's ambient thermal environment (the others including solar irradiation and wind speed). Moreover, if specimens of a certain body size truly do enjoy a 'baseline' thermal advantage, then there would seem to exist ample opportunity for suboptimally sized individuals to compensate through strategic microhabitat selection and/or behavioural regimes. Variation in behaviour and habitat selection is well known for butterflies that vary in thermally relevant morphological characters such as wing colouration (e.g. Van Dyck *et al.* 1997). The key question would then become whether the different, thermally imposed, behavioural strategies have significant reproductive consequences for the incumbents. Clearly, an expanded behavioural study, coupled with a more detailed characterisation of the thermal microhabitat of individual males, will be required to properly evaluate these hypotheses. Investigations of this broad nature have been performed with other butterfly species (e.g. Pivnick and McNiell 1986), and therefore appear as a key direction for future investigation of the thermal, and thus evolutionary, significance of body-size variation in male *H. bolina*.

Acknowledgments

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