# Butterfly contests and flight physiology: why do older males fight harder?

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The males of many butterfly species compete for territories via conspicuous aerial wars of attrition, in which the determinants of persistence ability are largely unclear. Flight performance features, such as stamina, acceleration, and maneuverability, are often assumed to be important in this context, yet there is no direct evidence by which to evaluate these possibilities. Recent research has indicated that competitive ability increases with age in a notably territorial species, *Hypolimnas bolina,* which could arise from lifetime morphological or physiological changes that directly affect flight performance. I evaluated this hypothesis by investigating how size-independent variance in body composition, energy stores, flight muscle ratio (FMR), and wing condition change with age in this species. Males in five age categories (spanning the functional life span of territorial individuals) were sampled from encounter sites in tropical Australia. Analysis of body composition with respect to an estimate of eclosion mass (forewing length) indicated that total body mass, abdomen mass, and wing area decrease throughout an individual's lifetime, but thorax mass remains unchanged. Wing loading (the ratio of wing area to body mass) is lowest in intermediately aged individuals, but FMR and energetic status remain largely similar regardless of age. On average, therefore, the energetic cost of sustained flight should first decrease, then increase, with age in a male *H. bolina* (of standardized body size), while available energy reserves decline slightly. Acceleration and maneuverability should remain relatively constant. These results, coupled with the fact that body size is unrelated to contest success in this territorial butterfly, fail to support the idea that age-related competitive ability is mediated simply by energetics or flight performance. *Key words:* biophysiology, intrasexual contest competition, Lepidoptera, sexual selection. *[Behav Ecol 13:456–461 (2002)]*

Intrasexual contests among many animals are settled on the basis of morphological or physiological features that directly determine an individual's resource-holding potential (RHP; Parker, 1974). Conventional theories contend that contests will be settled in favor of individuals with higher RHP (Mesterton-Gibbons et al., 1996), although the determinants of RHP may vary significantly between animal groups and depend on the nature of the contest. In physical battles where the cost of injury is high, RHP is routinely correlated with large body size, physical strength, and weaponry (reviewed by Huntingford and Turner, 1987). In contrast, relatively less violent contests involving protracted periods of display demand high endurance capability. RHP in the context of these staying contests, termed "wars of attrition" (Maynard Smith, 1982), is expected to be determined primarily by traits such as energy reserves and energetic efficiency that affect persistence ability (Marden and Waage, 1990; Mesterton-Gibbons et al., 1996).

Many territorial butterfly species compete via intrasexual contests, yet the determinants of RHP in this group have remained largely a mystery (although see Stutt and Willmer, 1998). Butterfly contests typically consist of noncontact, aerial maneuvers termed "spiral flights" (Davies, 1978) or "spinning wheels" (Wickman and Wiklund, 1983), in which the combatants circle each other in mid-air until one male gives up. These attrition-type persistence duels are not settled by physical force; hence, they offer an important opportunity to increase our understanding of the evolution of weaponless contest settlement. However, although acceleration or maneuverability (Baker, 1972; Hernández and Benson, 1998; Karls-

son, 1994; Stjernholm and Karlsson, 2000; Wickman, 1992; Windig and Nylin, 1999) and energetics (Rutowski, 1991) have been suggested or implied as potential physiological determinants of butterfly RHP, general empirical support is lacking. This is surprising because energetics and flight musculature have been implicated as key determinants of RHP in related insects that compete via conceptually similar aerial wars of attrition (see Convey, 1989; Marden, 1989; Marden and Rollins, 1994; Marden and Waage, 1990; Plaistow and Siva-Jothy, 1996; Plaistow and Tsubaki, 2000).

I used the territorial butterfly *Hypolimnas bolina* (L.) (Nymphalidae) as a model for investigating the potential relevance of energy reserves, flight musculature, and wing condition to the outcome of aerial butterfly contests. Males of this species compete for the ownership of perching territories via circling contests that are typical for butterflies (described later). Recent research has shown that contest success in this species is related to age (see Kemp, 2000b), and this result has been validated experimentally via a demonstration that contest persistence increases throughout the lifetime of an individual (Kemp, unpublished data). Due to seasonally predictable size plasticity (Kemp, 2000a; Kemp and Jones, 2001), coupled with overlapping generations and a relatively long life span, male age in *H. bolina* is also positively related to large adult body size in spring populations but small size in autumn populations. This is because individuals eclosing during spring and summer are substantially smaller than those eclosing at other times, and these males constitute the young members of spring populations and the old members of autumn populations (see Kemp, 2000b, for an expanded explanation). Because older males are competitively superior in all seasons, body size (and correlated variation in other biophysical attributes) appears largely irrelevant to the outcome of territorial contests in *H. bolina* (Kemp, 2000b). However, it remains possible that contest outcome is mediated by asymmetries in biophysiological features not correlated with body size, such as

size-independent variance in body composition, energy stores, relative flight muscle mass, and wing condition.

*Hypolimnas bolina* provides an excellent model by which to assess the relevance of biophysical factors to butterfly contests because, if these factors determine RHP, then we should expect to see age-related changes and expect these changes to proceed in specific directions (outlined below). Lifetime changes in size-independent male properties such as body composition, energy stores, relative flight muscle mass, and wing condition have been reported for butterflies (Karlsson, 1994; Stjernholm and Karlsson, 2000) and are implicated as determinants of RHP in other insects (Marden and Waage, 1990; Petersson, 1989). Here I aimed to chart how these parameters change with age in male *H. bolina* and to explicitly evaluate the possibility that they contribute to RHP in this territorial species.

## Specific predictions

The generalized physiological-based RHP hypothesis contends that older male *H. bolina* possess a biomechanical advantage that allows them increased persistence in an aerial war of attrition. The simplest potential application of this idea is that persistence is determined by fuel reserves, such that the male with the largest energy budget is willing or able to ultimately persist the longest (Rutowski, 1991). Male contest persistence is strongly linked with fat stores in several odonates that compete for territories via prolonged aerial wars of attrition (Marden and Rollins, 1994; Marden and Waage, 1990; Plaistow and Siva-Jothy, 1996; Plaistow and Tsubaki, 2000). Butterflies store fat in extensive abdominal fat bodies similarly to odonates (Pullin, 1987) and are known to use lipids as a fuel for extended flight (beyond the first few seconds; Crabtree and Newsholme, 1975). Because aerial contests in *H. bolina* routinely last longer than one min, and may last up to 15 min (Kemp, unpublished data), persistence in escalated or true contests (i.e., the ''reserve strategy'' of Parker and Rubenstein, 1981) will be ultimately determined by lipid reserves. If energetic costs are ecologically relevant, then butterflies would be expected to evolve schedules of contest behavior that minimize energetic expenditure, possibly involving pairwise assessment of energy reserves (Parker, 1974). In the case of *H. bolina,* this energetic constraint hypothesis predicts that older males should possess greater fat reserves (per unit body weight [flight load]) than their younger counterparts.

A related prediction concerns wing loading and the potential energetic advantage to having a lower ratio of body size to wing area (Marden and Chai, 1991; Marden and Rollins, 1994; Wickman, 1992). In general, having a higher wing loading (high body size:wing area ratio) requires higher wing-beat frequencies to maintain a given level of flight performance (Byrne, 1988) and therefore will increase the energetic demands of flight (Wickman, 1992). Wing loading has the potential to vary with age in *H. bolina* due to the cumulative effects of wing tattering (see Rutowski, 1992, for reports of wing damage in males of this species) and changes in body mass. Wing loading could conceivably either increase or decrease with age depending on the relative magnitude of the changes in wing area and body mass. If energy stores are limiting to male contest persistence, then individuals with relatively lower wing loading would be more advantaged because contests would be relatively less energy expensive per unit time for these individuals (i.e., contest costs would accrue at a lower rate). This hypothesis therefore predicts that older male *H. bolina* should possess relatively lower wing loading values.

The final prediction draws upon the possibility that acceleration and maneuverability determine the outcome of male butterfly contests. These parameters have been implicated as determinants of RHP in male odonate contests (see Convey, 1989; Marden, 1989; Plaistow and Tsubaki, 2000) and are often discussed with respect to butterfly contest ability (e.g., Baker, 1972; Hernández and Benson, 1998; Stjernholm and Karlsson, 2000; Wickman, 1992; Windig and Nylin, 1999). Although the precise mechanisms of such competitive advantage are obscure, more agile individuals could gain from an increased ability to avoid potentially damaging collisions or evade predatory attempts during the contest. Because flying animals generate approximately constant force per unit flight muscle during high-intensity bursts of flight (Marden, 1987), the most relevant physiological feature with respect to acceleration and maneuverability is the ratio of flight muscle mass to body mass (Marden, 1989). This feature, termed the flight muscle ratio (FMR), is expected to directly determine acceleration and maneuverability in butterflies (Marden and Chai, 1991; Srygley and Kingsolver, 2000; Wickman, 1992). FMR is also tightly associated with the position of center of body mass in this taxon (Srygley, 1994); the center of body mass is a potential biophysical determinant of flight performance (see Srygley and Chai, 1990; Srygley and Dudley, 1993; Srygley and Kingsolver, 2000). The specific prediction is that, if acceleration and maneuverability are important to the outcome of intrasexual butterfly contests, then we would expect to see FMR generally increase with age in *H. bolina*.

## MATERIALS AND METHODS

### Territoriality in *H. bolina*

Like many nymphalid, papilionid, and hesperiid butterflies, male *H. bolina* occupy and defend perching sites in forest clearings and along flight paths as a means of maximizing their encounters with receptive females (Kemp, 2000b; Kemp and Rutowski, 2001; Rutowski, 1992). Intrasexual contests are generally initiated when one male encroaches upon another's perching territory. The escalated (true) component of the ensuing contests consists of both males flying around each other in circles (100–300 mm diam), close to the ground (< 1–2 m), before one male retreats with a stereotyped submissive flying action (Kemp, 2000b; Rutowski, 1992). In field studies throughout autumn and spring 1998, Kemp (2000b) found that escalated contests lasted, on average, 65.4 ± 19.3 and 11.7 ± 2.6 s, respectively, but they can last up to 15 min (Kemp, unpublished data).

### Butterfly sampling and age assessment

Butterflies were sampled haphazardly throughout February 2000 (late summer) from field encounter sites near Cairns, Australia (16°53′ S, 145°45′ E). Most males were sampled along the transect used recently to document the effect of size and age on contest outcome (Kemp, 2000b), but some were taken from similar sites nearby. I initially observed all individuals for 5–10 min to ensure that they were exhibiting behavior consistent with territorial defense (see Rutowski, 1992). Males were then caught and aged on a five-point scale based on wing wear—the same scale used by Kemp (2000b) to relate age to competitive ability in this species. The wing wear assessments utilized the degree of fading of darker wing regions and feathering of the wingtips, rather than the extent of lost wing area per se, and are hence more sensitive to the cumulative effects of wing scale loss due to aging. This aging technique has been widely used in studies of butterflies (e.g., Karlsson, 1994; Stjernholm and Karlsson, 2000) and other insects (e.g., Plaistow and Siva-Jothy, 1996; Plaistow and Tsubaki, 2000). I also consulted a set of preserved specimens representing each age

class to ensure that butterflies were aged in a manner similar to that of Kemp (2000b). A total of 57 butterflies (at least 11 individuals in each age class) were retained; these were transported to the lab in individual glassine envelopes and immediately frozen.

Data presented by Kemp (2000b) and Kemp and Rutowski (in press) indicate that field populations are composed of males of varying ages encompassing a broad range of competitive abilities. Even after defeat, less competitive younger males remain in the vicinity of an encounter site (such as the major sampling site used here) to occupy less popular perching locations (Kemp, 2000b). Males in this study were captured from many individual perching locations (of presumably varying popularity); hence sampling can be considered random with respect to any relationship between age and intrinsic RHP.

### Physiological and morphological characterizations

After drying at 70°C for 4 days, each whole animal was weighed (to the nearest 0.0001 g) using a Sartorius BP 210 s model digital balance, and the abdomen and thorax were dissected (less wings and legs). I then weighed each body part (again to the nearest 0.0001 g) before lipid extraction. Lipid was extracted from each individual body part using a micro-soxhlet apparatus (refer to Marden, 1989; Marden and Waage, 1990). Samples were placed in a fat-free cellulose thimble (Whatman $19 \times 50$ mm) and exposed to refluxing petroleum ether for 8 h. Repeated 120-min extractions on seven abdomens indicated no further weight change after the sixth hour (paired $t$ test on the abdomen dry weight between 6- and 8-h extractions; $t_6 = 2.12$, $p > .05$). After extraction, remaining tissues were dried for a further day at 70°C before reweighing. I calculated body fat mass by subtracting post-extraction dry weight from pre-extraction dry weight.

The two pairs of wings of each specimen were carefully laid out and laminated between two sheets of transparent contact adhesive. The silhouette of each wing was then projected onto a wall so that it aligned with the outline of a "perfect" wing drawn on graph paper (perfect forewing = 31 squares high [155 mm] $\times$ 34 squares wide [170 mm], perfect hindwing = 35 squares high [175 mm] $\times$ 36 squares wide [180 mm]). I counted the number of squares within the perfect outline that were not covered by the projected wing silhouette to quantify the area of lost wing membrane.

I calculated the total area of each male's wings by first determining the area of a perfect set of wings (WA) corresponding to the size of each specimen using the equation WA/WL = 90,650/245, where WL = the specimen forewing length (measured from the specimen to the nearest 0.5 mm and corrected for wingtip damage where necessary; see Kemp, 2000b), 90,650 = the area of the projected perfect (graph paper) wings in square millimeters, and 245 = the length of the perfect forewing in millimeters. WA was then multiplied by the proportion of all (3626) grid squares covered by the specimen's collective wing silhouettes to give the total area of intact wing.

### Statistical analyses

I used the standardized residuals from regressions of (1) post–lipid-extraction thorax mass (dependent variable; log transformed) on dry body weight (independent variable; log transformed), and (2) dry body weight (log transformed) on wing area (log transformed), to give the values of FMR and wing loading, respectively, for each individual. This approach was used to yield size-independent measures of flight muscle and wing area relative to total load (body weight) and follows the

usage by Marden and Chai (1991), Marden and Rollins (1994), and Plaistow and Tsubaki (2000). Because variation in body size per se is unrelated to contest ability in *H. bolina* (Kemp, 2000b), only size-independent variance in these variables is relevant to this analysis (simple ratios between bodily tissue regions would not be appropriate because these values are subject to size dependence). I calculated an index of energetic status (Marden and Rollins, 1994) using the standardized residuals from a regression of fat dry weight (log transformed) on body dry weight (log transformed). This approach controls for differences in absolute fat content in the face of differences in body size and should provide the best estimate of aerial persistence ability for each insect (Marden and Rollins, 1994). All measures (wing loading, FMR, and energetic status) were compared between age classes using univariate ANOVAs.

In addition to these analyses, I regressed overall body dry weight, abdomen dry weight, and thorax dry weight against wing length (all variables log transformed) and used the residuals to estimate how the mass of different body regions change, relative to eclosion mass, with age. Wing length is strongly related to eclosion mass in *H. bolina* (see Kemp, 2000a), and using this parameter to estimate eclosion mass follows the precedent of Stjernholm and Karlsson (2000). I assessed differences in standardized mass values between age classes using univariate ANOVAs.

Dry masses were used throughout this study due to the difficulties in controlling for the extent of dehydration in fresh samples. The results of all body size-controlled analyses are robust to scaling differences between wet and dry mass because these scaling effects act chiefly on the regression slope (which is removed) and not the residual, size-independent variance in each composite biophysical variable.

## RESULTS

As expected from the findings of Kemp (2000b), the older specimens sampled throughout this study were smaller (in terms of wing length and hence eclosion mass) on average than their younger counterparts (Table 1). Older members of late summer populations are expected to have eclosed as relatively smaller adults because they developed under warmer temperatures and longer days during late spring/early summer (see Kemp, 2000a,b; Kemp and Jones, 2001). The presence of this age–size relationship validates the present usage of wing wear as an age estimator.

All studied properties varied with age, except for thorax lipid weight (Table 1), and regressions conducted to yield standardized residuals for age-based analyses were highly significant (Table 2). Analysis of body mass with respect to wing length (the estimate of eclosion mass; see Kemp, 2000a) revealed a marginally significant effect due to age on body mass (ANOVA on standardized residuals; $F_{4,51} = 2.60$, $p = .047$; Figure 1). Standardized body mass was higher in younger age classes, indicating that individuals lose weight with age. Similar analyses, conducted separately for abdomen and thorax mass, revealed significant age-related variation in abdomen mass (ANOVA on standardized residuals; $F_{4,51} = 3.54$, $p < .05$; Figure 1) but not thorax mass (ANOVA on standardized residuals; $F_{4,51} = 0.788$, $p = .538$; Figure 1). This suggests that the age-related decline in body mass largely reflects the loss of abdominal mass. As expected (because butterfly wings become increasingly tattered with age), standardized wing area decreased significantly with age (ANOVA on arcsine-transformed proportion of maximum wing area; $F_{4,48} = 23.1$, $p < .0001$).

Analysis of size-independent variation in energetic status, wing loading, and FMR (Figure 2) failed to find any support

**Table 1**
**Properties of *H. bolina* grouped by age class**

| Wing wear | $n$ | Wing length (mm) | Wing area (%) | Body mass (g) | Thorax mass (g) | Abdomen mass (g) | Thorax lipids (g) | Abdomen lipids (g) |
|---|---|---|---|---|---|---|---|---|
| 1 | 11 | 42.13 ± 0.78 | 0.98 ± 0.01 | 0.1554 ± .0152 | 0.0442 ± .0025 | 0.0541 ± .0076 | 0.0011 ± .0001 | 0.0301 ± .0065 |
| 2 | 11 | 39.07 ± 0.67 | 0.96 ± 0.01 | 0.1038 ± .0069 | 0.0358 ± .0018 | 0.0329 ± .0035 | 0.0013 ± .0002 | 0.0146 ± .0030 |
| 3 | 13 | 37.17 ± 0.72 | 0.94 ± 0.02 | 0.0753 ± .0035 | 0.0301 ± .0011 | 0.0189 ± .0016 | 0.0009 ± .0001 | 0.0042 ± .0007 |
| 4 | 11 | 35.07 ± 0.59 | 0.88 ± 0.02 | 0.0626 ± .0029 | 0.0251 ± .0014 | 0.0155 ± .0009 | 0.0014 ± .0006 | 0.0040 ± .0007 |
| 5 | 11 | 34.89 ± 0.68 | 0.79 ± 0.02 | 0.0625 ± .0031 | 0.0247 ± .0014 | 0.0154 ± .0011 | 0.0007 ± .0001 | 0.0022 ± .0002 |
| $F$ | | 19.21 | 23.16* | 25.58 | 24.42 | 17.73 | 1.75** | 26.97** |
| $p$ | | <.001 | <.001 | <.001 | <.001 | <.001 | .152 | <.001 |

Marked $F$ values indicate that the data were either arcsine (\*) or log (\*\*) transformed in order to obey normality. All reported masses are dry masses.

for the originally posed predictions (see Introduction). First, the effect of age on energetic status was only marginally significant (ANOVA on standardized residuals; $F_{4,52} = 2.41$, $p = .06$), and contrary to prediction, this parameter appeared slightly decreased in the older age classes (Figure 2). Second, no difference in FMR was detected across the age classes (ANOVA on standardized residuals; $F_{4,51} = 0.567$, $p = .687$). Finally, although wing loading varied significantly according to age (ANOVA on standardized residuals; $F_{4,48} = 4.60$, $p < .005$), this variation did not support the prediction. Rather than decreasing with age, wing loading was high in relatively younger and older individuals (Figure 2).

## DISCUSSION

This investigation has shown that over the lifetime of a male *H. bolina,* absolute body mass, abdomen mass, and wing area decrease with age, while absolute thoracic mass remains constant. This study has also shown that, within a population of variously aged males (of standardized body size), wing loading is lowest in intermediately aged individuals, FMR (and probably also center of body mass) is similar regardless of age, and energetic status decreases slightly in older individuals. Therefore, on the basis of size-independent factors, the energetic cost of sustained flight (such as seen during an escalated contest) should first decrease, then increase, with age in a male *H. bolina,* while available energy reserves should remain unchanged or even decline slightly. Performance attributes of flight, such as acceleration and maneuverability, should remain relatively constant regardless of male age. These results find no support for the notion that older male *H. bolina* possess a simple biomechanical advantage allowing greater intrasexual contest persistence. Because older males are generally competitively superior regardless of body size differences (Kemp, 2000b), doubt must be cast on the relevance of the studied physiological determinants of energetics and flight

performance to the outcome of naturally occurring aerial contests.

Territorial butterfly contests, including those of *H. bolina,* essentially represent disputes over indivisible resources between individuals incapable of inflicting serious injury (i.e., "doves" in the sense of Maynard Smith, 1982). In the classic situation where two doves compete via a process of attrition, persistence must be costly; otherwise, contests would never be settled (Maynard Smith, 1982). The interpretive problem with butterfly contests is that it is not at all clear what form these costs take (Rosenberg and Enquist, 1991). The findings of this investigation, coupled with the results of Kemp (2000b), suggest that competitive ability in *H. bolina* is not mediated by the simple biophysiological constraints apparently important to other taxa (e.g., size: Alcock, 1993; musculature: Convey, 1989; energy reserves: Marden and Waage, 1990; Plaistow and Siva-Jothy, 1996). These findings therefore indicate that the proximate costs associated with maintaining a given level of flight performance may not be significant enough (in the face of other potential persistence costs) to have directed the evolution of conflict resolution in this species. This finding is important because energetic and flight-related parameters are frequently invoked as potential determinants of RHP in territorial butterflies (Baker, 1972; Karlsson, 1994; Hernández and Benson, 1998; Rutowski, 1991; Stjernholm and Karlsson, 2000; Wickman, 1992; Windig and Nylin, 1999).

This result also contrasts markedly with findings across several insect groups that age-based variation in reproductive performance relates to lifetime changes in male energy reserves (refer to Marden and Waage, 1990; Otronen, 1995; Petersson, 1989; Plaistow and Siva-Jothy, 1996; Sartori et al., 1992; Yuval et al., 1984). Perhaps the best such comparison is provided by several odonate species whose males compete for territory ownership via noncontact aerial maneuvers (see Convey, 1989; Finke, 1992, and references therein; Waage, 1988). Accumulated evidence strongly suggests that these odo-

**Table 2**
**Summary of regression equations used to generate standardized residuals for age-related physiological analyses**

| Parameter | Regression | ANOVA | $R^2$ |
|---|---|---|---|
| Energetic status | Lipid mass = −0.085 + 1.96(body mass) | $F_{1,55} = 125$ | .69 |
| Wing loading | Body mass = −22.2 + 2.09(wing area) | $F_{1,51} = 113$ | .69 |
| FMR | Thorax mass = −1.76 + 0.68(body mass) | $F_{1,54} = 464$ | .89 |
| Body mass | Body mass = −16.6 + 3.89(wing length) | $F_{1,54} = 278$ | .83 |
| Abdomen mass | Abdomen mass = −23.1 + 5.37(wing length) | $F_{1,55} = 84$ | .60 |
| Thorax mass | Thorax mass = −14.1 + 2.92(wing length) | $F_{1,55} = 534$ | .91 |

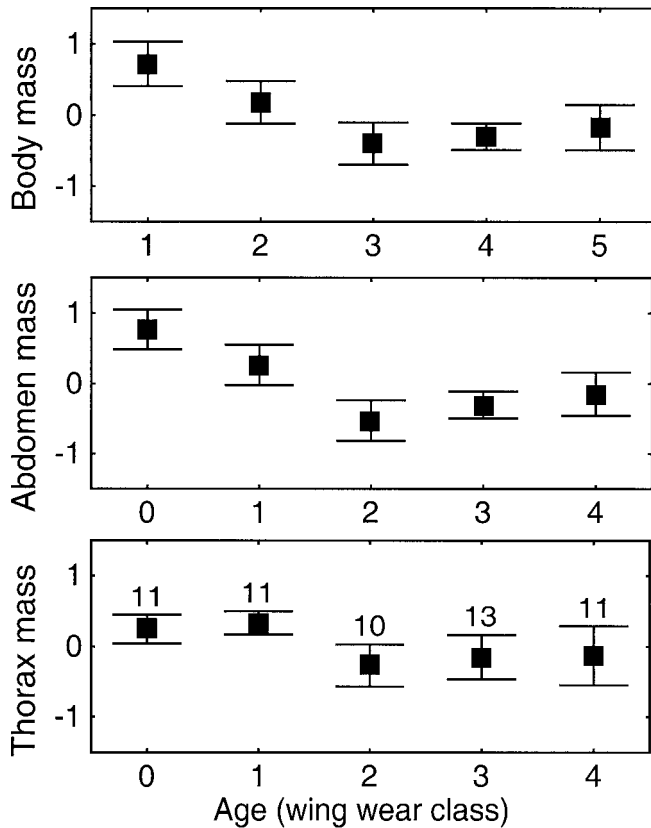All variables were log-transformed prior, and reported ANOVAs are significant at $p < .0001$.

**Figure 1**
Mean body mass, abdomen mass, and thorax mass, grouped by age class. All measures are standardized by eclosion mass (see Table 2), and the sample size for all plots is given in the thorax mass plot.



**Figure 2**
Age-related variation in energetic status, flight muscle ratio (FMR), and wing loading among sampled male *H. bolina*. These parameters were calculated as the standardized residuals of the regressions outlined in Table 2.

nate contests are settled on the basis of age-related variation in FMR and energy reserves (Convey, 1989; Marden and Rollins, 1994; Marden and Waage, 1990; Plaistow and Siva-Jothy, 1996; Plaistow and Tsubaki, 2000). The apparent irrelevance of these factors to butterfly contests may relate to differences in contest intensity and duration between these two taxa. Escalated damselfly contests can last for several hours and lead to exhaustion (Forsyth and Montgomerie, 1987), which could place comparatively greater emphasis on proximate factors such as flight efficiency and energetics as determinants of RHP in this group.

Although it may be premature to conclude that butterfly contests are free of proximate physiological constraints, this study at least shows that more elaborate potential solutions must be sought. Recent research has suggested a link between body temperature and contest ability in a sunspot-defending temperate species, *Pararge aegeria* (Stutt and Willmer, 1998). However, thermal issues are of doubtful relevance to *H. bolina* and other tropical species (e.g., *Heliconius sara*; Hernández and Benson, 1998), in which territorial residency is less likely to create consistent residency-linked asymmetries in body temperature (sensu Stutt and Willmer, 1998). Competitive ability in *H. bolina* also increases with age, and there is no evidence of concomitant increases in the ability to attain a more favorable thermal state in older members of this species (Kemp, unpublished data). Other potential mechanisms, such as the ability to maintain nutrient and/or oxygen supply to the site of oxidization, remain to be investigated, although these have not been convincingly shown to determine insect RHP independently of overall energy reserves (see Marden and Rollins, 1994).
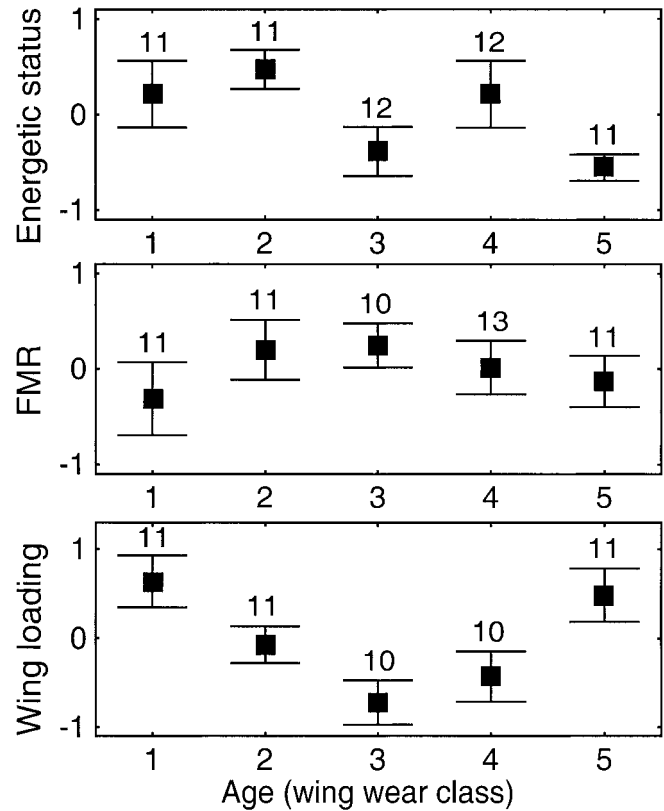
As an alternative to seeking increasingly elaborate physiological solutions, it may pay future students of butterfly contests to be more sensitive to the possibility of extrinsic costs, such as the probability of indeterminate predation or of sustaining physical injury. The presence of such costs could affect an RHP asymmetry even if combatants are equally vulnerable because individuals of varying reproductive value will vary in their willingness to accept costs (see Hernández and Benson, 1998; Kemp, 2000b). Several authors have recently stressed the importance of taking life-history constraints into account when interpreting sexually selected processes (see Kokko, 1997, and references therein), and butterfly contests should be considered no exception. In this vein, research is underway to examine the hypothesis that older male *H. bolina* are more persistent in contests—and hence competitively superior in the short term—due to their relatively reduced opportunity for future survival and reproduction.

## REFERENCES

Alcock J, 1993. The effects of male body size on territorial and mating success in the landmark-defending fly *Hermetia comstocki* (Stratiomyidae). Ecol Entomol 18:1–6.

Baker RR, 1972. Territorial behaviour of the nymphalid butterflies, *Aglais urticae* (L.) and *Inachis io* (L.). J Anim Ecol 41:453–469.

Byrne DN, 1988. Relationship between wing loading, wing beat frequency and body mass in homopterous insects. J Exp Biol 135:9–23.

Convey P, 1989. Influences on the choice between territorial and satellite behaviour in male *Libellula quadrimaculata* Linn. (Odonata: Libellulidae). Behaviour 109:125–141.

Crabtree B, Newsholme EA, 1975. Comparative aspects of fuel utilisation and metabolism by muscle. In: Insect muscle (Usherwood PNR, ed). London: Academic Press; 405–485.

Davies NB, 1978. Territorial defence in the speckled wood butterfly (*Pararge aegeria*): the resident always wins. Anim Behav 26:138–147.

Finke OM, 1992. Consequences of larval ecology for territoriality and reproductive success of a neotropical damselfly. Ecology 73:449–462.

Forsyth A, Montgomerie RD, 1987. Alternative reproductive tactics in the territorial damselfly *Calopteryx maculata*: sneaking by older males. Behav Ecol Sociobiol 21:73–81.

Hernández MIM, Benson WW, 1998. Small-male advantage in the territorial butterfly *Heliconius sara* (Nymphalidae): a paradoxical strategy? Anim Behav 56:533–540.

Huntingford FA, Turner AK, 1987. Animal conflict. New York: Chapman & Hall.

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

Kemp DJ, 2000a. The basis of life history plasticity in the tropical butterfly *Hypolimnas bolina* (L.) (Lepidoptera: Nymphalidae). Aust J Zool 48:67–78.

Kemp DJ, 2000b. Contest behavior in male butterflies: does size matter? Behav Ecol 11:591–596.

Kemp DJ, Jones RE, 2001. Phenotypic plasticity in field populations of the tropical butterfly *Hypolimnas bolina* (L.) (Nymphalidae). Biol J Linn Soc 72:33–45.

Kemp DJ, Rutowski RL, 2001. Spatial and temporal patterns of territorial mate locating behaviour in *Hypolimnas bolina* (L.) (Lepidoptera: Nymphalidae). J Nat Hist 35:1399–1411.

Kokko H, 1997. Evolutionarily stable strategies of age-dependent advertisement. Behav Ecol Sociobiol 41:99–107.

Marden JH, 1987. Maximum lift production during takeoff in flying animals. J Exp Biol 130:235–258.

Marden JH, 1989. Bodybuilding dragonflies: costs and benefits of maximising flight muscle. Physiol Zool 62:505–521.

Marden JH, Chai P, 1991. Aerial predation and butterfly design: how palatability, mimicry, and the need for evasive flight constrain mass allocation. Am Nat 138:15–36.

Marden JH, Rollins RA, 1994. Assessment of energy reserves by damselflies engaged in aerial contests for mating territories. Anim Behav 48:1023–1030.

Marden JH, Waage JK, 1990. Escalated damselfly territorial contests are energetic wars of attrition. Anim Behav 39:954–959.

Maynard Smith J, 1982. Evolution and the theory of games. Cambridge: Cambridge University Press.

Mesterton-Gibbons M, Marden JH, Dugatkin LA, 1996. On wars of attrition without assessment. J Theor Biol 181:65–83.

Otronen M, 1995. Energy reserves and mating success in males of the yellow dung fly, *Scatophaga stercoraria*. Funct Ecol 9:683–688.

Parker GA, 1974. Assessment strategy and the evolution of fighting behaviour. J Theor Biol 47:223–243.

Parker GA, Rubenstein DI, 1981. Role assessment, reserve strategy, and acquisition of information in asymmetric animal conflicts. Anim Behav 29:221–240.

Petersson E, 1989. Age-associated mating success in three swarming caddis fly species (Trichoptera: Leptoceridae). Ecol Entomol 14:335–340.

Plaistow SJ, Siva-Jothy MT, 1996. Energetic constraints and male mate-securing tactics in the damselfly *Calopteryx splendens xanthostoma* (Charpentier). Proc R Soc Lond B 263:1233–1238.

Plaistow SJ, Tsubaki Y, 2000. A selective trade-off for territoriality and non-territoriality in the polymorphic damselfly *Mnais costalis*. Proc R Soc Lond B 267:969–975.

Pullin AS, 1987. Adult feeding time, lipid accumulation, and overwintering in *Aglais urticae* and *Inachis io* (Lepidoptera: Nymphalidae). J Zool 211:631–641.

Rosenberg RH, Enquist M, 1991. Contest behaviour in Weidemeyer's admiral butterfly *Limenitis weidemeyerii* (Nymphalidae): the effect of size and residency. Anim Behav 42:805–811.

Rutowski RL, 1991. The evolution of male mate-locating behavior in butterflies. Am Nat 138:1121–1139.

Rutowski RL, 1992. Male mate-locating behavior in the common eggfly, *Hypolimnas bolina* (Nymphalidae). J Lepid Soc 46:24–38.

Sartori M, Keller L, Thomas AGB, Passera L, 1992. Flight energetics in relation to sexual differences in the mating behaviour of a mayfly, *Siphlonurus aestivalis*. Oecologia 92:172–176.

Srygley RB, 1994. Locomotor mimicry in butterflies? The associations of positions of centres of mass among groups of mimetic, unprofitable prey. Phil Trans R Soc Lond B 343:145–155.

Srygley RB, Chai P, 1990. Flight morphology of Neotropical butterflies: palatability and distribution of mass to the thorax and abdomen. Oecologia 84:491–499.

Srygley RB, Dudley R, 1993. Correlations of the position of centre of body mass with butterfly escape tactics. J Exp Biol 174:155–166.

Srygley RB, Kingsolver JG, 2000. Effects of weight loading on flight performance and survival of palatable Neotropical *Anartia fatima* butterflies. Biol J Linn Soc 70:707–725.

Stjernholm F, Karlsson B, 2000. Nuptial gifts and the use of body resources for reproduction in the green-veined white butterfly *Pieris napi*. Proc R Soc Lond B 267:807–811.

Stutt AD, Willmer P, 1998. Territorial defence in speckled wood butterflies: do the hottest males always win? Anim Behav 55:1341–1347.

Waage JK, 1988. Confusion over residency and the escalation of damselfly territorial disputes. Anim Behav 36:586–595.

Wickman P-O, 1992. Sexual selection and butterfly design—a comparative study. Evolution 46:1525–1536.

Wickman P-O, Wiklund C, 1983. Territorial defence and its seasonal decline in the speckled wood butterfly (*Pararge aegeria*). Anim Behav 31:1206–1216.

Windig JJ, Nylin S, 1999. Adaptive wing asymmetry in males of the speckled wood butterfly (*Pararge aegeria*)? Proc R Soc Lond B 266:1413–1418.

Yuval B, Holliday-Hanson ML, Washino RK, 1994. Energy budget of swarming male mosquitoes. Ecol Entomol 19:74–78.