Contest behavior in territorial male butterflies: does size matter?

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Although intrasexual contests generally favor bigger or stronger individuals, the relevance of body size to war of attrition-type disputes between weaponless animals such as butterflies is unclear. In this study I aimed to investigate the significance of size in this context by studying territorial contests in Hypolimnas bolina (L.), a species that exhibits consistent seasonal plasticity in body size. In this species adult age is positively correlated with large size in spring but with small size in autumn. This shift allowed independent evaluation of the relevance of each variable (size and age) to intrasexual contest success. Observation of a population of marked individuals indicated that only age appeared important, with the winners of pair-wise contests significantly older than losers in both seasons, and with contests lasting longer when the age difference between the combatants was small. Age was also linked to residency: residents won 99% of all contests. This study suggests that size does not matter in these aerial disputes, but age and residency do. It is not yet possible to determine whether older butterflies are intrinsically better competitors, or whether they simply have greater opportunity to find a vacant territory. Key words: aggression, war of attrition, nymphalid, Lepidoptera. [Behav Ecol 11:591–596 (2000)]
were both larger and older than losers, two hypotheses were put forward, each with a straightforward key prediction. The “body size” hypothesis predicted that winners in both spring and autumn should be larger than their opponents, while the “adult age” hypothesis predicted that winners in both seasons should be older. Because the size-age relationship in *H. bolina* is seasonally inverted, these are mutually exclusive possibilities. The form and duration of intrasexual disputes were also investigated to shed further light on the dynamics of intrasexual disputes in this species.

**METHODS**

**Study site**

This study was conducted along a 770 m transect established adjacent to Freshwater Creek, near Cairns in Queensland, Australia (16°53’ S, 145°45’ E). The transect was set within a mown track (5–15 m wide) that separated a cultivated sugarcane field from riparian rainforest vegetation. The margin of the track supported several larval foodplants of *H. bolina*, notably *Synedrella nodiflora* (L.) (Asteraceae), and the area is a popular perching spot for territorial males.

**Sampling methodology**

Sampling was conducted on 31 days from 29 March to 22 May, 1998 (the “autumn round”) and on 45 days from 10 October to 29 December, 1998 (the “spring round”), with the same routine followed each round. For the first 3 days, transects were censused hourly from 0900 h to 1400 h, the period of peak territorial defence (Rutowski, 1992), where as many territory residents were caught as possible. Males were marked with a small number on their ventral hindwing using a green ink marker (Superfine Stabilo-OH Pen 841, waterproof), assessed for size and age (see below), and then cooled before release (Kemp and Žalucki, 1999). Transects were then censused on the days following the initial marking period to determine the form, duration, outcome, and male combatants involved in contests at the site. The different levels of interaction (horizontal chase and escalated contest) are easily distinguishable (Rutowski, 1992), and the duration of each was timed to the nearest second using a digital stopwatch. Sampling was limited to sunny, mild conditions (to control for adverse effects on territorial behavior; Rutowski, 1992), between 0900 h and 1400 h each day.

Participants of pair-wise contests were identified using binoculars either following or prior to each contest. This task was aided by the tendency of losers to remain within the vicinity of the transect. Notes were also taken on which male was the resident at the territory before the dispute, and the prior behavior of the intruding male. This allowed contests to be classified as either resident-transient (contests between a resident and a male not seen defending a territory prior to the contest) or resident-neighbor (contests between a resident and a male previously seen defending a territory on that day).

In addition, unmarked males seen along the transect were caught, marked, and handled in the manner as previously described. Contests involving males on their day of capture were excluded from the analysis to prevent possible handling effects.

**Size and age assessments**

Size was assessed by measuring the length from the apex to insertion of the left forewing to the nearest 0.5 mm (Hernandez and Benson, 1998). In order to assess age, the extent of wing wear was subjectively classified on a five-point discrete scale. These wing wear assessments were based on the degree of fading of darker wing regions (due to systematic scale loss) and “feathering” of the wingtips, rather than larger chips or areas of lost wing which may result from one-off incidents. To maintain assessment accuracy, preserved specimens representing each age class were carried for comparison with captured individuals.

Discrete age estimates were used in conjunction with date of capture to estimate an approximate date of eclosion for each marked male. This was done by assuming that on average, each wing wear category represented 20 days of life of a male *Hypolimnas*. This assumption was based on data that suggest males of this species live for a maximum of 3 months in the field (Kemp DJ, unpublished data). Each male was therefore attributed a number of days of adult life on the basis of his wing wear classification, which was subtracted from his date of capture to estimate his eclosion date. This approach gave an approximate age (in days) of each marked combatant in contests observed throughout this study.

**Statistical analysis**

Following screening of variables for normality (Kolmogorov-Smirnov goodness of fit; Sokal and Rohlf, 1995), the relationship between size and estimated eclosion date (age) in each season was investigated using product-moment correlations. This method was adopted because both variables were subject to error, and least squares regression techniques are unsuitable. Derived correlation coefficients were compared by calculating a standard error value for the difference between the coefficients ($t$), then comparing this parameter to the critical value of $t_{0.05,41} = 1.96$ (Sokal and Rohlf, 1995).

Logistic regression was used to model the relationship between contest outcome and explanatory variables (size and age), with model selection based on the stepwise elimination procedure outlined by Hardy and Field (1998). This analysis was conducted with one male from each pair-wise contest randomly allocated as the focal male, and contest OUTCOME (the dependent variable) coded as 0 = focal male lost, 1 = focal male won. The explanatory variables SIZE and AGE were calculated by subtracting the focal male’s size and age from those of his opponent. The question of “when to escalate?” was also examined using logistic regression, with escalated contests defined as those containing a period of spiralling flight (as opposed to those consisting entirely of a horizontal chase). The SIZE and AGE of the losing male were used as continuous explanatory variables in this analysis (because the losing male decides if a contest will escalate), and CONTEXT (0 = resident-transient, 1 = resident-neighbor) was included as a discrete explanatory variable.

The question of “when to give up?” was addressed using survival analysis. The duration of the spiraling stage of escalated contests was analyzed, using a lognormal model, with respect to the SIZE and AGE of the losing male, the magnitude of the size and age difference between winners and losers (SIZEDIFF and AGEDIFF), and the CONTEXT under which the contest took place. Interaction terms between these variables and SEASON were also included, with the most parsimonious model selected using the stepwise elimination process (see Hardy and Field, 1998). Survival analysis and logistic regression analyses were performed using the STATISTICA® computer program.

Although only unique dyads were used in these analyses (only the first of repeat contests between the same two combatants was analyzed), a small proportion (less than 10%) of males were involved in multiple contests. In order to assess the potential bias arising from partially repeated observations, the additional explanatory variable EXPERIENCE was added.
Table 1
Summary of sampling details

<table>
<thead>
<tr>
<th></th>
<th>Autumn</th>
<th>Spring</th>
</tr>
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<tbody>
<tr>
<td>Mean male count per transect</td>
<td>7.4 ± 0.3</td>
<td>4.1 ± 0.3</td>
</tr>
<tr>
<td>Number of marked males</td>
<td>84</td>
<td>60</td>
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<tr>
<td>Total contests seen</td>
<td>91</td>
<td>52</td>
</tr>
<tr>
<td>Contests involving two marked males</td>
<td>70 (76.9%)</td>
<td>35 (67.3%)</td>
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Chases

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<tr>
<td>Number timed</td>
<td>30</td>
</tr>
<tr>
<td>Mean duration (s)</td>
<td>12.9 ± 1.8</td>
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</tbody>
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Escalated contests

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<tbody>
<tr>
<td>Number timed</td>
<td>32</td>
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<tr>
<td>Mean duration (s)</td>
<td>82.2 ± 19.7</td>
</tr>
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To the logistic models. In the analysis of contest outcome, this ordinal variable was coded plus 1 for every previously observed win, and minus 1 for every previous loss recorded for each individual. Similarly, in the analysis of when to escalate, the variable was coded plus 1 for each previous contest that a male was seen to escalate, and minus 1 for every non-escalated contest (horizontal chase). In each analysis, the variable EXPERIENCE tested whether any of the variance in the dependent variable could be explained by the previous experience of males. To account for partially repeated observations in the analysis of contest duration, the giving up times of individual males were averaged across all of the escalated contests in which they were seen to lose. Similarly, in separate comparisons of winner and loser attributes (size and age) in each season, the attributes of winners (of multiple contests) were compared to the mean attributes of the group of males they were observed to defeat.

RESULTS
Seasonal size–age relationships
Totals of 84 autumn and 60 spring males were marked during this study (see Table 1). The size and wing wear of each marked male, as a function of capture date, is indicated by Figure 1. Once both wing wear and date of capture were accounted for (by estimating an eclosion date for each individual), size was related to age as predicted in each season. Forewing size was positively related to estimated eclosion date in autumn ($r = .465, n = 84, p < .001$), but negatively related to this parameter in spring ($r = -.408, n = 58, p < .001$), and these correlations differed significantly ($t = 5.36, p < .0001$). Older butterflies were therefore larger on average than their younger counterparts in autumn, but this situation was reversed in spring.

Male-male contests
One hundred thirty-six contests were seen in their entirety (see Table 1). Of these, 70 were non-escalated (consisting only of a horizontal chase), while 66 were escalated and included an initial period of spiraling flight followed by a horizontal chase in which the loser was pursued from the territory. In line with the spring 1997 observations (see introduction), winners in spring were on average larger (paired $t_{9} = 2.79, p < .05$) and older (paired $t_{9} = 4.43, p < .001$) than their corresponding losers. However, winners in autumn were relatively smaller (paired $t_{84} = -2.34, p < .05$) and older (paired $t_{58} = 2.56, p < .05$), and therefore age was the only seasonally consistent predictor of contest outcome. Winning butterflies were up to 9.5 mm (28%) larger than their corresponding losers in spring, but up to 14.0 mm (30%) smaller than losers in autumn. This result supports only the prediction drawn from the “age-based” hypothesis.

In addition to age, territory residency was a near perfect predictor of contest outcome, with residents winning 86 (99%) of 87 contests in autumn, and all 49 contests in spring. The one clear case of resident loss occurred in autumn, and involved a male (male #16) that had been seen defending the most popular territory (site A) for 6 days. At 0930 h on the morning of his seventh day of residency (26 April, 1998), male #16 was defeated by an apparent newcomer to the transect (male #27) in an escalated contest lasting 137 s. The winner, male #27, was smaller (33.5 compared to 40.5 mm forewing length), and of equal age to male #16 (both estimated 60 days old). After being defeated, the male #16 set up at a nearby territory (20–30 m along the transect), and defended this area over a period of 13 days. During this time he was defeated again by male #27 on one other occasion (interaction lasting...
male. The variable CONTEXT accounted for significant de-
to either the age, size, or previous experience of the losing
escalation was therefore seasonally consistent, and unrelated
SIZE*SEASON (G1 = 28.72, p < .001; see Figure 2).

When to escalate?
The probability of escalation was examined with respect to the
variables CONTEXT, SIZE, and AGE (of the losing male),
SEASON, EXPERIENCE, and the interaction variables
SIZE*SEASON, AGE*SEASON, and CONTEXT*SEASON.
The initial model was significant (G1 = 18.8, n = 85, p < .05),
however all variables except CONTEXT were sequentially re-

When to give up?
The most parsimonious lognormal regression model to de-
scribe the duration of spiralling contests included only the
variable AGEDIFF, with all others sequentially eliminated (χ2 =
2.9, p > .05). This model described a significant amount
of deviance from that of a null model (a model including no
predictors; χ2 = 5.60, n = 38, p < .05). Since AGEDIFF was
negatively correlated to spiralling duration (β = −0.22), lon-
ger contests were observed when the combatants were more
equally matched for age.

DISCUSSION
The clear outcome of this “natural” experiment is that wing
size is inconsistently related to the outcome of territorial con-
tests in male H. bolina. This indicates that, unless there is an
underlying size-related advantage that undergoes a seasonal
inversion, contests in this aggressive species are settled irres-
spective of asymmetries in body size. This result is biologically
significant, because relative combatant size is perhaps the
strongest and most consistent proximate determinant of in-
trasexual contest outcome in animals (reviewed by Andersson,

Size has previously been correlated with the outcome of
territorial disputes in butterflies, but the direction of this re-
lation has varied between species. Rosenberg and Enquist
(1991) found that larger males of the nymphalid Limenitis
weidemeyeri were more successful in defending and taking
over perching territories. Although they also demonstrated
that contest duration was negatively correlated with the magni-
tude of the size asymmetry, their results do not discount the
hypothesis that successful males may have also been older.
This study on H. bolina has reiterated that covariance between
size and contest outcome does not necessarily indicate that
these variables are causally linked. Intrinsic correlates of fight-
ing success may themselves covary, and hence, care must be
taken in reaching conclusions regarding the causal merit of
individual attributes.
In a result contrasting with that of Rosenberg and Enquist (1991), Hernandez and Benson (1998) reported that territorial contests among male Heliconius sara (the minor component of the mating system) were settled in a manner related to small wing size. In this species, they speculate that large males are less inclined to engage in territorial disputes due to the risk of injury and potential sacrifice of residual (future) reproductive value. Size is believed to be important in this system due to its influence on motivational fighting strategy rather than as a proximate influence on territorial fighting ability. Hernandez and Benson (1998) speculate that larger male H. sara have intrinsically high reproductive value because they may be competitively superior in gaining perches on about-to-emerge female pupae (although this may not relate to increased reproductive success; refer to Deinert et al., 1994). A similar type of large male advantage has been noted for Jalmenus evagoras (Elgar and Pierce, 1988), a lycaenid species that also competes for the possession of eclosing females. However, this rarer form of male-male competition in butterflies differs markedly from the conspicuous aerial disputes of territorial species (the stereotyped war of attrition-type contests). The evidence from the present investigation, taken in concert with other studies that report either no size-associated territorial advantage (Knapton, 1985; Lederhouse, 1982), or contradictory size-related advantages (Hernandez and Benson, 1998; Rosenberg and Enquist, 1991), suggests that body size has limited proximate bearing on the outcome of spiraling aerial contests in territorial male butterflies.

The second major outcome of this study is that contest success was related to both age and prior residency, with residents almost always winning, and older males winning significantly more contests in both seasons. Prior residency is often related to contest outcome in butterfly species that compete for perching territories (see Davies, 1978; Rosenberg and Enquist, 1991; Wickman and Wiklund, 1983). Residency may be used by male H. bolina as a means to settle the dispute quickly and in most cases without escalation (an uncorrelated asymmetry; Maynard-Smith, 1982). Under this scenario, older males may accumulate as residents (and therefore appear to have a competitive advantage; see Figure 2) simply because of their increased opportunity to gain these territories over time. This possibility is supported by the finding that, as with the territorial butterfly Papilio polyxenes (Lederhouse, 1982), contests between male H. bolina were escalated more often in the resident-neighbor context, a situation where residency may be confused (Alcock and Bailey, 1997; Waage, 1988). However, there are several potential problems with this interpretation. First, because the prior intentions of the losers of horizontal chases are not always apparent, it is possible that many losers in resident-transient chases were not actually motivated to perch in a territory in the first place (see Davies, 1978; Grafen, 1987). Resident-neighbor contests would be expected to escalate more often than resident-transient contests simply because a proportion of the latter interactions may involve males “accidentally” encroaching on an occupied territory. The second problem is that residency is often correlated with other asymmetries that may impinge on combatant resource holding potential (RHP) or motivation to fight (Austad et al., 1979; Maynard-Smith, 1982). Body temperature is one such attribute that may be particularly relevant to butterfly disputes (Stutt and Willmer, 1998). Residents may win more contests simply because they are able to maintain their body temperature closer to the optimum, which may allow greater perseverance in a spiraling maneuver. If body temperature determines RHP in H. bolina, then escalation should occur most often between males of similarly high body temperature, which would explain why resident-neighbor contests were often escalated. However, we would also expect these contests to last longer than resident-transient contests, which was not observed. Last, in the few cases where repeat contests were observed (involving males #16, #23 and #27), the outcome appeared to be consistent regardless of changes in immediate residency. This result, which has also been observed by Wickman and Wiklund (1983) for the nymphalid Pararge aegeria, and Alcock (1988) for several territorial hesperids, weighs heavily against the uncorrelated asymmetry hypothesis.

Even though age was a less perfect predictor of contest outcome, this variable may influence the fighting ability of a male butterfly. One possible explanation is that because the conspicuous spiraling displays are potentially risky, age may influence motivation. This might apply because age is negatively related to future reproductive value, and therefore opponents of different ages would vary in what they have to lose. A younger male, if injured or killed in a contest, would pay a relatively higher cost than an older male in terms of lifetime fitness (Parker, 1974). On this basis, because they are risking relatively less, older males may be prepared to spiral for consistently longer, and hence, win more contests against younger opponents. This strategy is evolutionarily stable (Grafen, 1987), and theoretically similar to that advanced by Hernandez and Benson (1998) for H. sara with respect to body size (see earlier discussion).

A second possibility is that the ability to survive to old age is determined by the same intrinsic attributes that determine RHP, such as flight ability or agility. Under this scenario, poorer competitors of each successive generation are selected against by “natural” agents such as predation, and hence do not survive to old age. Contests between males should therefore be settled, on average, in favor of the older individual since there is greater probability that he will possess higher RHP. This hypothesis predicts that younger males may win some contests, which was observed in this study, but also that fights will be always won by the faster or more agile male (regardless of age).

If age does determine fighting ability, or motivation to fight, then there should be a positive relationship between contest duration and the age of the losing male. This simplistic prediction was not supported: spiraling duration was negatively related to the magnitude of the age asymmetry (as also found by Rosenberg and Enquist, 1991 with respect to body size) rather than to age per se. This result raises the possibility that male H. bolina may assess the age of their opponent and vary their fighting tactics accordingly (Enquist and Leimar, 1983). However, although this strengthens the possibility that age is indeed causally relevant, the field-based nature of this investigation makes it difficult to evaluate alternative explanations.

Also, precise information on the age of individual butterflies was not available here, which reduces the sensitivity of these analyses.

Although the main hypotheses based on age and residency each have a reasonable degree of accordance with the facts, currently exposed evidence does not permit a clear test of all possibilities. As noted in relation to body size, causality cannot be ascribed to individual variables solely on the basis of significant correlation. The value of this “natural” experiment is, therefore, limited to evaluating the relevance of size to war of attrition-type butterfly disputes, and to suggesting primary hypotheses for experimental tests, which are currently underway. Nevertheless, the significance of this outcome should not be understated, because it provides strong, new evidence that size does not substantially influence the outcome of weaponless butterfly disputes.

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REFERENCES

Kemp DJ, Jones RE, in press. Phenotypic plasticity in field populations of the tropical butterfly Hypolimnas bolina (L.) (Nymphalidae). Biol J Linn Soc.