

# Life History Effects Upon Contest Behaviour: Age as a Predictor of Territorial Contest Dynamics in Two Populations of the Speckled Wood Butterfly, *Pararge aegeria* L.

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## Abstract

Although empirical studies of life history effects upon sexually selected phenomena have largely overlooked contest behaviour, recent research suggests that territorial contest participation in butterflies may be mediated by ageing per se. Verbal and mathematical arguments predict lifetime increases in the expression of risky male reproductive behaviours, such as fighting, under a range of ecological conditions. Here we explored the relevance of ageing per se to contest dynamics in two phenologically distinct populations of the speckled wood butterfly, *Pararge aegeria*. We established 160 experimental like-population contests among naïve south Swedish and Madeiran dyads, 112 of which we varied the age difference between combatants by 3–4 d. Although this age asymmetry did not influence contest outcome in either population, we found weak positive covariance between the loser's age and contest duration amongst Madeiran males. This is consistent with a slight lifetime increase in aggression because the duration of these aerial persistence contests is a sensitive measure of the losing male's level of aggressive intent. However, the size of this effect (semi-partial correlation = 0.281) suggests age is not as strongly relevant to contest behaviour in *P. aegeria* as in other territorial butterflies. We discuss the ways in which ecological differences between butterfly species, particularly with respect to predation risk, may have influenced the evolution of lifetime aggressive strategies in this group.

## Introduction

Evolutionary theory contends that animal life histories are shaped by trade-offs between current and future reproductive opportunities (Stearns 1992). This is based upon the premise that individuals live finite lifespans and possess finite expendable resources, and that investments channelled into various activities at various life stages cannot be considered strictly independent of one another (Williams 1966; Stearns 1992). Empirical investigations into the presence of allocational trade-offs have focused upon age-based changes in reproduc-

tive investment (Candolin 1998; Poizat et al. 1999). These studies have demonstrated that investment can increase when the opportunity for future survival and reproduction (i.e. residual reproductive value, RRV; Williams 1966) decreases; however, the focus has mostly concerned female reproductive investment (e.g. Dixon et al. 1993; Poizat et al. 1999). Life history principles are equally relevant to sexually selected male investments into advertisement signals and armaments, and behavioural traits like mate searching, fighting and sexual display. We presently know very little about whether and how such sexually selected traits are shaped by life

history principles (although see Kemp 2002a; Hunt et al. 2004).

Male–male contest behaviour is one sexually selected aspect of male reproductive investment in which the underlying costs are clearly extracted in a life history currency. The few verbal (Parker 1974) and mathematical (Enquist & Leimar 1990) treatments that consider life history principles suggest that investment in potentially injurious fighting should generally increase with age. This is because younger individuals would generally pay a greater cost, in terms of lifetime fitness, if killed or injured while fighting (Parker 1974). If it is possible to accrue at least some reproductive opportunities using lower risk tactics, then investment into these behaviours may be favoured over more risky behaviours (such as fighting) relatively early in adult life. However, clear empirical examination of this phenomenon has been hindered by lifetime changes in physical attributes (i.e. resource-holding potential; Marden & Waage 1990), resource ownership (Alcock & Bailey 1997) and/or prior fighting experience (Whitehouse 1997), which may all affect apparent fighting investment and obscure life history effects. An experimental approach will therefore be ultimately necessary to isolate the effect of ageing per se upon male fighting behaviour.

Butterfly territoriality offers an excellent model system for specific investigation into how life history optimization affects lifetime investment in aggressive behaviour. The males of many species contest the ownership of specific perching territories via non-contact aerial interactions that are settled purely by persistence (Kemp & Wiklund 2001). Butterflies are classic 'doves' in the sense that they are clearly unable to impose physical costs upon each other, and exogenous factors – such as predation risk or injury from indeterminate collisions – appear as the potentially most relevant cost to contest persistence in this group (Kemp & Wiklund 2001). Whereas energy reserves have been implicated as a decisive factor in some territorial insect contests (e.g. Marden & Waage 1990), this is not clearly the case in butterflies, in which older males of low energetic status have been reported as most successful (see, e.g. Kemp 2002b). Persistence in butterfly contests may therefore be primarily determined by an individual's willingness to accept exogenous costs, which should relate, in turn, to RRV (Hernández & Benson 1998; Kemp 2002a). In preliminary support of this notion, males of the model territorial butterfly *Hypolimnas bolina* (Nymphalidae) persist longer in contests as they age, and this lifetime increase is not a function

of changes in physical fighting ability (including flight performance and energy reserves), resource ownership, or prior contest experience (Kemp 2002a,b). Older males are also more accepting of non-contest-related risks (Kemp 2002a), thus suggesting that many aspects of this species' reproductive behaviour may be shaped by life history factors. However, while these reports support the notion of lifetime trade-offs, research into other species, particularly territorial butterflies, is required to assess the generality of this phenomenon.

In this study, we set out to investigate the effect of ageing upon territorial contest investment in two populations of the speckled wood butterfly (*Pararge aegeria*). Males of this species perch at and defend specific areas, such as forest sunspots, as a means of locating receptive females (Davies 1978; Wickman & Wiklund 1983; Jones et al. 1998; Stutt & Willmer 1998). The territorial contests are superficially very similar to those of *H. bolina*, and consist of non-contact aerial manoeuvres in which two combatants circle around each other with relatively constant intensity, until one individual (the loser) gives up and departs the contested area. There is some experimental evidence that success in these contests may increase with age (Kemp et al. in press). Here we assessed the generality of potential age-based contest strategies in *P. aegeria* by selecting butterflies from two populations: (1) south Sweden and (2) the Atlantic island of Madeira. Males of both populations are strongly territorial (see Jones et al. 1998 regarding the Madeiran population), and have been used in previous studies of butterfly contests (Wickman & Wiklund 1983; Kemp & Wiklund 2004; Kemp et al. in press). The two populations differ markedly in a range of life history factors, including body size at maturity and lifespan (Gotthard et al. 2000), and they also exhibit contrasting reproductive phenologies, which may affect a population difference in age structure (see Discussion for an expansion of this point). We therefore undertook the between-population comparison of age-based contest behaviour as a preliminary assessment of the relevance of these ecological factors to lifetime schedules of aggression in this group.

## Methods

### Butterfly Husbandry

We reared butterflies from both populations (south Sweden and Madeira) under 17°C and 20:4 L:D photoperiod, using *Poa annua* as a larval host. Upon

emergence, adults were placed individually in small plastic cups with gauze lids, allowed ad libitum access to a cotton wool bud moistened with 15% sugar solution, and stored under constant  $18 \pm 2^\circ\text{C}$ . All butterflies were handled identically.

### Experimental Procedures

We staged pair-wise contests between in an outdoor experimental enclosure situated at the Tovetorp field station ( $58^\circ56'\text{N}$ ,  $17^\circ08'\text{E}$ ), on 13 d between 14 Jun. and 3 Sep. 2003, and on 22 d between 20 May and 11 Aug. 2004. The semi-cylindrical enclosure (dimensions:  $6 \times 8$  m base, 4 m radius) was covered with 32% UV-absorbing shade-cloth cover overlaid with an opaque green plastic tarpaulin. We removed a  $2 \times 2$ -m section of the tarpaulin to create a sunspot that tracked across the cage floor from 09.00 to 15.00 h (the daily time range over which we conducted contests), and cut a series of 0.1–0.4 m diameter holes to create a mosaic of smaller sun flecks. We further mimicked the forest habitat of this species using artificial 2-m high Christmas trees, dried leaves, twigs and rocks.

We transferred adults from the laboratory to the field site in an icebox (approx. temp. =  $13 \pm 4^\circ\text{C}$ ), and stored them in this icebox when not being used. Pre-cooled subjects were introduced into the enclosure using moistened cotton wool buds (15% sugar solution), upon which they perched, warmed up and initiated flight several minutes thereafter (Kemp & Wiklund 2004 provide heating rates of live and freshly killed *P. aegeria* treated identically in this flight cage, under similar ambient temperatures). Individuals settled in the primary sunspot and behaved indistinguishably from sunspot-defending males in the field. We only used males that perched in the primary sunspot, after an initial and unchallenged flight around the enclosure, and responded with an investigative flight to thrown objects (small bark chips). We have found in previous experiments of this nature (Kemp & Wiklund 2004; Kemp et al. in press) that responses of perching males to nearby moving objects, such as small bark chips, indicates territorial intention and willingness to enter into an escalated circling contest. We have also found that giving each male the opportunity for a short 'maiden' flight in the cage prior to confronting another male is vitally important to its subsequent territorial behaviour and aggression. A freshly liberated male that is 'discovered' (by another male) either prior to or during this maiden flight generally attempts to flee the cage without engaging in an escalated flight,

and this experience apparently has long-lasting negative effects on its aggression. We therefore limited ourselves to using contests in which each male had a chance to settle into the cage environment and was apparently 'ready' for territorial defence, as indicated by his response to thrown bark chips.

We established role symmetrical contests by placing two contest-naïve subjects simultaneously at opposite corners of the sunspot and allowing them to discover each other naturally, or encouraging mutual detection using thrown bark chips to coax one individual to within the visual range of the other. We timed the duration of the 'escalated' (circling) contest phase (as above) to the nearest second, and determined the winner as the male that clearly pursued the other before returning to perch in the sunspot. This escalated phase appears highly ritualized and differs markedly from the flight behaviour of butterflies at all other times; hence, we could determine the duration of this phase with accuracy (see also Kemp & Wiklund 2004). Winners and losers also clearly distinguished themselves because losers often tried to escape the confines of the cage and were not willing to fight again if detected by the winner. We measured ambient temperature (nearest  $0.5^\circ\text{C}$ ) inside the enclosure at the start and end of each contest using a shaded mercury thermometer, and averaged these two values to give an estimate of temperature at contest time.

### Experimental Design and Statistical Analysis

We established like-population contest pairings in which one member of each pair was 3–4 d older than its opponent. This design allowed analyses of the factors affecting (1) contest outcome and (2) contest duration (i.e. the loser's contest persistence). In the analysis of contest outcome we modelled the probability of one (randomly chosen) 'focal' member of each dyad winning on the basis of the independent variables age and body size, each of which we calculated by subtracting that male's parameter value from that of its opponent. We also included a discrete variable coding for population, and the age  $\times$  population and size  $\times$  population interaction terms. Males of this species are thought to live about six days in the field (at least on average in Sweden; Wickman & Wiklund 1983); therefore, the 3–4 d asymmetry (which equated to 10–15% of the maximum lifespan of males in this study), coupled with our large sample size, should allow detection of a medium to large effect of age on contest outcome (if such an effect is present).

In our analysis of losing male contest persistence, we analysed contest duration (the duration of the circling contest phase) using a generalized non-linear model approach. We chose a log-normal distribution in this analysis because aerial insect contests are typically distributed in this manner (e.g. Kemp 2003), and because our natural log-transformed data did not deviate from normality (Kolmogorov–Smirnov test; Swedish males  $d = 0.10$ ,  $p > 0.20$ ; Madeiran males  $d = 0.11$ ,  $p > 0.15$ ). In all of our analyses we used an information theoretic approach to select the most parsimonious of all candidate (best subsets) models as the one that minimized Akaike's information criterion (AIC; with the caveat that main effects must be present along with interaction terms). The AIC is a derivative of the log-likelihood function that better facilitates comparison between candidate models containing varying numbers of parameters, and is thus statistically superior to the stepwise approach to model selection (Burnham & Anderson 2002). Our maximum likelihood-based approach to parameter estimation is free of many of the necessary statistical assumptions of least squares methods, such as homoscedasticity. We included the loser's age, body size and ambient temperature in our models because these variables have been related to contest dynamics in *P. aegeria* (Stutt & Willmer 1998; Kemp et al. in press). Finally, we calculated Wald statistics and semi-partial correlation coefficients to investigate the strength and direction of covariances for individual variables included in the most informative models, where such models proved significantly predictive.

## Results

### Contest Outcome

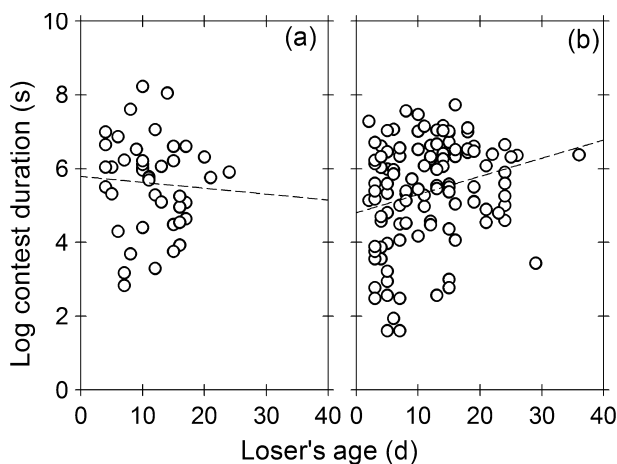
We conducted a total of 112 contests with a 3- or 4-d age difference between the combatants (i.e., age-asymmetrical contests suitable for the analysis of contest outcome), and these were all conducted in 2004. We first ran analyses separately for each population, including as predictor variables age and size (both calculated as differences between the focal male and its opponent). For Swedish males, in which older males won 12 (52.2%) of 23 contests (Yates-corrected  $\chi^2_1 = 0$ ,  $p = 1.0$ ), the most informative model (AIC = 34.6) included the variable age; however, this model proved non-significant ( $G_1 = 0.162$ ,  $N = 23$ ,  $p = 0.687$ ). For Madeiran males, in which older males won 45 (52.9%) of 85 contests (Yates-corrected  $\chi^2_1 = 0.188$ ,  $p = 0.664$ ), the most informative model (AIC = 121.3) included size,

however, this again proved non-significant ( $G_1 = 0.503$ ,  $N = 86$ ,  $p = 0.478$ ). Finally, we combined males from both populations in a model including population, size, age and the population  $\times$  size and population  $\times$  age interaction terms. The most informative but non-significant ( $G_1 = 0.774$ ,  $N = 108$ ,  $p = 0.379$ ) logistic regression model in this case (AIC = 152.6) included the variable coding for population as a sole predictor.

### GLM (Log-Normal Model) of Loser Male's Persistence

We conducted 39 (2003) and 121 (2004) contests suitable for the analysis of loser persistence time. The age range of losing males in these analyses was 4–24 d (Swedish males,  $N = 43$ ) and 2–36 d (Madeiran males,  $N = 117$ ), and losing male persistence (i.e. contest duration) ranged from 5 to 3761 s ( $\bar{x} \pm 95\%$  CI =  $463 \pm 86$ ). We initially analysed loser persistence separately for each population, including the variables loser's age, loser's size, ambient temperature, year and the year  $\times$  age, year  $\times$  size and year  $\times$  ambient temperature interaction terms. For Swedish males, the most informative model (AIC = 138.0;  $G_2 = 8.3$ ,  $p < 0.05$ ) included the variables year (Wald = 9.09,  $p < 0.005$ ; semi-partial  $r = 0.377$ ) and size (Wald = 2.52,  $p = 0.112$ ;  $r = -0.200$ ). Year was the strongest and only significant predictor, with losers persisting for longer in 2004 trials. For Madeiran males, the most informative model (AIC = 403.1,  $G_2 = 15.4$ ,  $p < 0.001$ ) included ambient temperature (Wald = 8.62,  $p < 0.005$ ; semi-partial  $r = 0.260$ ) and loser's age (Wald = 10.4,  $p < 0.005$ ;  $r = 0.281$ ).

We then constructed a model with data from both populations pooled, including as predictor variables population, ambient temperature, loser's age, loser's size and the population  $\times$  age, population  $\times$  size and population  $\times$  ambient temperature interactions. Given that year was a significant effect upon Swedish male contest persistence, we also included a discrete variable coding for this factor, as well as the year  $\times$  population, year  $\times$  ambient temperature, year  $\times$  size and year  $\times$  age interaction terms. The most informative model (AIC = 546.3,  $G_4 = 18.7$ ,  $p < 0.001$ ) contained population (Wald = 4.34,  $p < 0.05$ , semi-partial  $r = -0.147$ ), ambient temperature (Wald = 10.5,  $p < 0.005$ ,  $r = 0.245$ ), loser's age (Wald = 0.274,  $p = 0.601$ ,  $r = -0.0557$ ) and the population  $\times$  age interaction (Wald = 4.29,  $p < 0.05$ ,  $r = 0.147$ ). The nature of the age  $\times$  population interaction indicates that age affected contest persistence more strongly in the



**Fig. 1:** The effect of loser's age upon natural log-transformed contest duration in (a) south Swedish and (b) Madeiran populations of *Pararge aegeria*

Madeiran population, although this interaction does appear marginal (Fig. 1).

Given that there was a difference in sample size between the Swedish ( $N = 43$ ) and Madeiran ( $N = 117$ ) populations, it is possible that the relative lack of an age effect in the former population stemmed merely from a reduction in statistical power. We therefore calculated effect size (Pearson's  $r$ ) for this parameter in each population. In a model containing loser's age as the sole predictor variable, the Madeiran population loser age effect was larger and opposite in sign to that of the Swedish population ( $r = 0.243$  vs.  $r = -0.063$ , respectively; Fig. 1). As reported above, the effect size (semi-partial  $r$ ) for loser's age in the most informative Madeiran model was  $r = 0.260$ , which is even more divergent from the comparable estimate for loser's age ( $r = -0.111$ ) in the 'best' Swedish model (i.e. the model including loser's age along with year and body size).

## Discussion

Recent research into territorial insects (Kemp & Alcock 2003), including butterflies (Kemp 2002a, 2003) suggests that an appreciation of life history factors may be key to understanding the mechanisms of aerial contest resolution. Age is a key life history factor that is likely to covary with a range of potentially relevant contest parameters, such as condition (i.e. wear and injuries to body structures), muscle function (Marden 2000), energy reserves (Marden & Waage 1990) and prior contest experience. Given the presence of senescence, age will also

relate to the amount of time remaining to undertake reproductive activities (i.e. future reproductive opportunities), which may affect contemporary investments into certain reproductive behaviours (e.g. Poizat et al. 1999). Our present study was designed to experimentally test for an effect of age on contest behaviour in two ecologically distinct populations of *P. aegeria*. We failed to find an effect of age asymmetries upon contest outcome, but we did find a positive relationship between age and contest duration (i.e. loser male persistence) amongst Madeiran males. We believe that this apparently contradictory result (i.e. an effect upon contest duration but not outcome) can be explained by the differential sensitivity of the two analyses, and that the results are consistent with a slight effect of age upon contest behaviour in the Madeiran population. Analyses dealing with loser male persistence (i.e. contest duration) should be more sensitive than those of contest outcome because the former is a continuous – rather than discrete – variable, and because we limited the pairwise age asymmetry to 3–4 d (thus limiting the statistical power of this contrast). Thus, we feel that the effect on contest duration in Madeiran males reflects the presence of a very small age-based effect, one that may have ultimately expressed itself in contest outcome given a large enough sample with a large enough age asymmetry.

Our use of male *P. aegeria* from two distinct populations (Madeira and southern Sweden) was motivated partly by the possibility that these populations may have diverged in life history traits. The populations are known to differ in their reproductive phenology: whereas the south Sweden population is strongly seasonal and exists in three largely discrete cohorts (the adults of each fly for 3–4 wk; C. Wiklund, unpubl. data), individuals on Madeira breed continuously throughout the year (refer to Gotthard et al. 2000). One consequence of this is that the populations would differ in standing age structure, with Swedish populations perhaps more homogeneous for age. Inter-population differences of this nature could impinge upon evolutionarily stable strategies of contest settlement; however, our data do not suggest particularly large differences in contest behaviour between these two populations (at least with respect to age and body size).

The lack of strong age effects in either population of *P. aegeria* contrasts interestingly with recent research conducted on the tropical Nymphalids *H. bolina* (old male advantage; Kemp 2002a) and *Melanitis leda* (young male advantage; Kemp 2003). *Hypolimnas* males, in particular, compete for forest

clearing or forest edge territories via circling aerial duels that are superficially almost identical to those of *P. aegeria*. From the viewpoint of reproductive phenology, *H. bolina* are most similar to Madeiran *P. aegeria*, as both populations breed almost continuously throughout the year and generations are thus highly overlapping and heterogeneous for age. The two species do, however, differ markedly in other aspects of their biology and ecology, such as functional adult lifespan (see Kemp 2001). In *M. leda*, young males tend to be more successful in competition for favoured perching territories (Kemp 2003). This crepuscular species is again likely to differ on a host of ecological and behavioural counts, including the nature of the territorial contests themselves (see Kemp 2003 for a description of these low 'rhythmical looping' interactions). The crepuscular activity regime would probably also mean that adult *M. leda* experience different predatory risk than either *P. aegeria* or *H. bolina*. The risk of predation, either during a contest or while engaged in non-reproductive activities such as feeding or diurnal/nocturnal roosting, may have important consequences to optimum lifetime schedules of reproductive risk taking (particularly if predation risk poses a major cost to contest participation). Future comparative studies may be the best way to examine the extent to which these apparent ecological differences are responsible for variation in the occurrence and nature of age effects across territorial butterflies.

Whereas *P. aegeria* has proved an excellent model for studies of territoriality (e.g. Davies 1978; Wickman & Wiklund 1983; Shreeve 1987; Stutt & Willmer 1998; Kemp & Wiklund 2004), the explanation for how individuals of this species settle their contests has remained elusive. Research that appeared to demonstrate contest settlement due to asymmetries in residency (Davies 1978) and body temperature (Stutt & Willmer 1998) has recently been cast in doubt by an experimental demonstration that cooler non-residents (of both populations used in this study) can indeed routinely succeed in contests (Kemp & Wiklund 2004). Furthermore, as previously reported under field conditions (Wickman & Wiklund 1983), Kemp & Wiklund (2004) found that repeat contests between the same two individuals ended with the same result, thereby suggesting variation among males in their intrinsic capacity or motivation for contest persistence. In follow-up experiments, Kemp et al. (in press) found no evidence for a link between contest 'ability' and individual flight morphology (as a potential determinant of flight performance ability). Similarly, here we

appear to have ruled out the possibility that contests are settled on the basis of age, or some close correlate of this life history variable. This conclusion is subject to the caveat that ageing (i.e. the passage of physiological time) in this experiment proceeded under relatively unnatural conditions, and was independent of field activity. Nevertheless, there is some evidence in British *P. aegeria* that wing-wear (an estimator of field activity and age) is independent of the outcome of territorial interactions (Shreeve 1987), which strengthens our present conclusion that age is not of strong importance to competitive success in this species.

In line with prior field (Shreeve 1987) and laboratory-based (Kemp et al. in press) investigations upon *P. aegeria*, we failed to relate body size to contest behaviour. Interestingly, however, we did detect a small effect of ambient temperature upon contest duration. Given that asymmetries in thoracic temperature have been convincingly ruled out as determinants of contest outcome (Kemp & Wiklund 2004), we do not feel that ambient temperature influenced male contest persistence due to any effect upon individual thoracic temperature and subsequent flight ability. Ambient temperature in this experiment, as we measured it, is likely to have covaried with time of day, and the strength/amount of direct sunlight striking the flight cage during the contest period, which often varied due to the presence of cloud cover. There are therefore several ways by which our measure of contest ambient temperature could have covaried with putative mechanisms of site valuation (as per the suggestions of Wickman & Wiklund 1983 and Stutt & Willmer 1998). In any event, because both contestants experienced identical cage conditions, ambient temperature (or weather conditions) could not have mediated actual contest settlement unless the individuals varied in their use of this parameter to value the cage territory. Although this possibility appears unlikely, perceptual differences in the valuation of different perching sites per se (and irrespective of changes in weather conditions) could mediate differences in apparent competitive 'ability' (Kemp & Wiklund 2001), and this appears as an interesting area for future work in this system.

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