# Sexual selection constrained by life history in a butterfly

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Trait evolution via sexual selection has traditionally been viewed as isolated from life-history constraints. Recent theoretical treatments, however, predict that costly sexually selected characters should be mediated by the same allocational trade-offs that apply to more conventional aspects of reproductive investment. Participation in risky competitive behaviours, for example male–male combat, should therefore increase as the opportunity for future reproduction declines. However, the demonstration of such trade-offs has proven to be elusive due to concomitant age-based variation in the physical determinants of fighting 'ability'. Here, I exploit the unique nature of a butterfly contest system to provide compelling evidence for lifetime partitioning of risky and aggressive sexually selected behaviours. I show that male *Hypolimnas bolina* become more willing to persist in contests over mating territories, and more generally accepting of injury risks, as they age. Contest persistence in this species is not mediated simply by physical condition, and I experimentally isolate the effect of ageing *per se* from resource ownership and previous contest experience. These results demonstrate how sexually selected behaviours can be ultimately mediated by a shifting trade-off between contemporary reproductive effort and future opportunities.

**Keywords:** territoriality; contest behaviour; trade-off; intrasexual selection; mating behaviour

## 1. INTRODUCTION

A fundamental tenet of conventional evolutionary theory is that animal life histories are shaped by trade-offs between current and future reproductive opportunities (Stearns 1992). Empirical attempts to identify such trade-offs have focused on the 'costs of reproduction' (Reznick *et al.* 2000) and charted how reproductive investment varies with advancing age (Magnhagen & Vestergaard 1991; Candolin 1998; Poizat *et al.* 1999). This work shows that investment can increase as the opportunity for future survival and reproduction (i.e. residual reproductive value (Williams 1966)) decreases with age. However, most accounts focus primarily upon readily quantifiable elements of female reproductive investment (e.g. Dixon *et al.* 1993; Poizat *et al.* 1999). Empiricists have almost entirely neglected sexually selected aspects of male reproductive investment, such as sexual advertisement and intrasexual contest behaviour (Höglund & Sheldon 1998). It is therefore unclear how life-history factors, for example allocational trade-offs, influence lifetime investment in sexually selected activities.

Intrasexual contest behaviour is a sexually selected aspect of male reproductive investment in which the underlying costs—including injury and death (but also the costs of producing weapons or status signals)—are clearly extracted in a life-history currency (Enquist & Leimar 1990). The costs of fighting are believed to drive the evolution of optimal (i.e. evolutionarily stable) behavioural strategies (Maynard Smith 1982; Enquist & Leimar 1983, 1987, 1990); however, most contest models fail to consider the principles of life-history evolution. The few verbal (Parker 1974) and mathematical (Enquist & Leimar 1990) treatments that do consider these principles indi-

cate that investment in potentially fatal or 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). However, a clear empirical examination of this phenomenon has often been hindered by lifetime changes in physical attributes (Marden & Waage 1990; Olsson & Shine 1996), resource ownership or prior experience (Whitehouse 1997), which may affect apparent reproductive investment and obscure life-history effects. Here, I employ a novel experimental approach to circumvent these problems and isolate the effect of ageing *per se* upon sexually selected territorial behaviour in a butterfly, *Hypolimnas bolina* (L.).

Male *H. bolina* perch at and defend specific areas in the environment (e.g. forest clearings) as a means of locating receptive females (Rutowski 1992). In northern Australia, males defend territories in most months of the year (Kemp 2001*a*) and show little evidence of alternative mating tactics (Kemp 2001*b*). Like other territorial butterflies (Wickman 1985), most matings are believed to take place on territories, and male *H. bolina* are therefore subject to sexual selection for success in defeating conspecific rivals over sole territory ownership. Butterflies are classic 'doves' (*sensu* Maynard Smith 1982) and territorial disputes in *H. bolina* consist of non-contact manoeuvres in which two combatants circle around each other with relatively constant intensity (Rutowski 1992; Kemp 2000*a*). Contests are decided purely by individual persistence and are most closely allied with the 'war of attrition' theoretical model (Maynard Smith 1982; Mesterton-Gibbons *et al.* 1996). Territorial individuals may live for over 30 days in the wild and show strong fidelity to favoured perching locations (Rutowski 1992).

This system offers a unique opportunity to examine the operation of life-history trade-offs, for two reasons. First, unlike most other animal fights (e.g. Marden & Waage

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1990), contest participation is not simply mediated by variation in intrinsic physiological parameters that may otherwise vary with age, such as body mass, energy reserves and flight musculature (Kemp 2002). Persistence costs in *H. bolina* contests are most likely to accrue from exogenous sources, such as injury risk from indiscriminate collisions or predation (Kemp & Wiklund 2001). Persistence itself is therefore determined by an individual's willingness to allocate fighting effort in the face of such risk, which should ultimately relate to his residual reproductive value (Parker 1974; Enquist & Leimar 1990; Kokko 1997). Second, nectar-feeding adult butterflies, such as *H. bolina*, eclose with largely non-renewable energy stores and pristine wing membranes that are eroded irreversibly with age (Karlsson 1994; Kemp 2002). This 'capital' breeding regime (Jönsson 1997) indicates that mortality rates will accelerate with adult age, and that future mating opportunities—and hence residual reproductive value—will scale inversely with age in these species.

Life-history constraints in the *H. bolina* contest system would therefore be evidenced as age-related increases in risky sexually selected behaviours, including increased allocation to territorial contest persistence. A recent field study (Kemp 2000*a*) identified old age as a covariate of contest success in this species; however, the causal relevance of this parameter is unclear. Here, I investigate how contest persistence changes with male age, using an artificial cage habitat and a novel experimental design that controls for potential age correlates such as prior residency, opponent identity and site value. Due to the fact that males in this longitudinal experiment accumulated experience with losing contests as they aged, I conducted a companion experiment to evaluate the effect of prior experience upon fighting behaviour. Last, as an independent line of inquiry, I used an artificial startle stimulus (Elwood *et al.* 1998) to investigate whether older males are more motivated to persevere with territorial mate-locating behaviour under conditions of heightened risk (Magnhagen & Vestergaard 1991; Candolin 1998). These investigations were collectively designed to address the hypothesis that lifetime investment in male mating behaviour is ultimately mediated by life-history trade-offs (Reznick *et al.* 2000), as predicted by conventional life-history theory (Stearns 1992).

## 2. MATERIAL AND METHODS

### (a)  *Age-specific contest persistence*

Lifetime variation in contest persistence was assessed between April 1999 and June 2000 using a $15 \text{ m} \times 6 \text{ m} \times 4 \text{ m}$ flight enclosure at Cairns (16°53′ S, 145°45′ E). The enclosure was subdivided into three equally sized compartments by removable 'curtains', with each compartment vegetated to mimic field territory sites (Rutowski 1992). Trials were set up by establishing a single 1-day-old reared male within each of the end compartments and a single wild-caught resident within the middle compartment. Reared males were the progeny of different wild-caught females, and were cultured on *Asystasia gangetica* (Acanthaceae) at a constant temperature of $27 \pm 0.5$ °C and photoperiod of 10 L : 14 D (refer to Kemp (2000*b*) for rearing protocols). Wild-caught males were older (more than about two weeks old, as adjudged by wing wear) territorial residents netted from popular territorial locations in Cairns (Kemp 2000*a*).

These individuals were selected with the intention that they would persist for longer in contests against reared males, thus allowing the use of contest duration as a direct assay of reared male persistence at each age.

Each of the two reared males was sequentially pitted against the wild-caught male on day 5 of each trial (i.e. reared-male age = 5 days) and approximately every fifth day thereafter. On each occasion, the appropriate curtain was raised and the wild-caught male coaxed into the respective reared male's compartment. The ensuing contest was timed to the nearest second and judged to be complete when one male broke from the circling formation while exhibiting a submissive flying action (Rutowski 1992). At this point, the curtain was restored and the males returned to their respective enclosures. This experimental design removed any residency asymmetry (Kemp & Wiklund 2001) because all males were liberated into their respective compartments on the same day and allowed sole ownership of these compartments between contest days. Opponent identity and lifetime variation in perceived resource value (Enquist & Leimar 1987) were also controlled because each reared male only ever faced the same opponent, always remained in the same compartment and never encountered a conspecific female (a potential measure of site value).

The relationship between reared-male age and (log-transformed) contest persistence was assessed using linear regression. Due to the fact that temperature drives insect metabolic rates, age was converted to physiological time by calculating the area under a sine curve (joining the daily maximum and minimum temperatures) above the developmental threshold temperature for this species at 13.0 °C (TEMPSUM computer program, written by R. E. Jones, James Cook University). Although persistence was measured sequentially for each male, Durbin–Watson tests on individual regressions were non-significant in all cases ($0.69 < d < 2.09$, evaluated against Bonferroni adjusted $p = 0.0005$), indicating a lack of serial correlation. Only trials lasting at least 20 days (i.e. reared-male age = 20 days) were analysed.

### (b)  *Effect of experience*

Experience effects were assessed between September 2000 and June 2001 using the compartmentalized flight enclosure. Trials were set up as described earlier (see § 2(*a*)), with a 1-day-old reared male in each end compartment and an older wild-caught male in the centre compartment. Reared males in each trial were the progeny of the same wild-caught female (i.e. they were full siblings). One sibling—the randomly designated 'experienced' sibling—was pitted against the wild-caught male every 2 days until day 10, when both siblings were sequentially pitted against the wild-caught male (in random order). Contests were staged and timed as per the earlier protocols, and day-10 contest persistence was compared between siblings using a paired *t*-test.

### (c)  *Simulation of risk*

Motivation to remain perching in the face of simulated risk was assessed at a field site near Cairns (Kemp 2000*a*) in October and November 1999 (the 'pilot' study) and in two discrete rounds on 17 December 1999 and 8 January 2000. In the latter two rounds, territorial incumbents were removed from the site a week earlier to allow 're-colonization' of the territories by a fresh set of males. This ensured that variation in prior male site fidelity on sampling days was reduced to less than a week, whereas it may normally range up to one month (Rutowski

1992). A standard methodology was used to assess motivation. Males were first observed for 10 min (including at least one encounter with another male) to confirm their residency status, to note perching site boundaries and to assess age on a five-point wing-wear scale (Kemp 2000*a*). Territorial boundaries are normally designated by obvious changes in vegetative structure or shading (as in the case of a forest clearing), or otherwise by the outer range of patrolling flights occasionally made by males around their site (Kemp 2001*b*). A butterfly net (handle length 1.3 m, hoop diameter 450 mm, white nylon bag) was used to provide the following sequence of startle stimuli:

(i) net sweep—the net was swept swiftly within 20–30 mm of (but never contacting) the flying male, causing him to deviate visibly;

(ii) net crash—the net was swept into foliage where the male was perching so that he was contacted lightly; and

(iii) capture and detention for 180 s.

Butterflies were judged to have abandoned site defence after each level of stimulus if they (i) flew out of their designated perching area and did not return within 5 min; or (ii) remained but did not exhibit territorial behaviour (Rutowski 1992; Kemp 2001*b*) for at least 5 min (the ultimate assay of territorial behaviour was whether a perched male responded to a thrown pebble by flying out to investigate). Otherwise, after 5 min the next level of stimulus was applied. Whether a male abandoned territoriality as a result of each stimulus level was used to score each individual's motivation as:

(i) net sweep leave;

(ii) net crash leave;

(iii) capture leave; or

(iv) not leave (most motivated).

## 3. RESULTS

### (a) *Age-specific contest persistence*

In total, nine reared individuals participated in 51 contests against six wild-caught opponents (each reared male only ever faced the same opponent). Reared males were always first to 'give up', hence contest duration served as an estimate of their motivation for persistence at each age. As predicted, persistence increased significantly with physiological age in all reared individuals (figure 1).

### (b) *Effect of experience*

Eight paired trials were successfully completed in this experiment and, as previously, reared males gave up first in all contests. Designated 'experienced' siblings participated in four contests and accumulated an average of $117 \pm 38$ s of contest time prior to age 10. However, comparison of age 10 contest duration (figure 2) indicated that experienced males persisted for shorter durations than their contest-naive siblings (paired *t*-test on log-transformed contest duration; $t_7 = 3.55$, $p < 0.01$).

### (c) *Simulation of risk*

As predicted, older individuals were less inclined to abandon territoriality in the face of risk in the pilot sampling round (Spearman correlation between age classes and motivation scores; $r_s = 0.69$, $n = 36$, $p < 0.001$). This
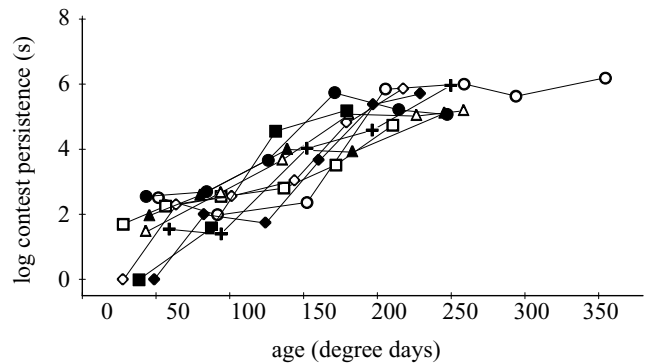


Figure 1. Relationship between reared-male age (measured in physiological time) and log-transformed contest persistence. Data for each reared male are connected and denoted by a unique symbol and are described by the following regressions: male 1 (open circles), $y = 1.20 + 0.016x$, $F_{1,5} = 17.3$, $p < 0.01$; male 2 (open diamonds), $y = -0.31 + 0.028x$, $F_{1,4} = 57.8$, $p < 0.005$; male 3 (open squares), $y = 1.21 + 0.015x$, $F_{1,4} = 46.4$, $p < 0.005$; male 4 (open triangles), $y = 1.03 + 0.018x$, $F_{1,4} = 40.9$, $p < 0.01$; male 5 (closed circles), $y = 1.87 + 0.015x$, $F_{1,4} = 13.8$, $p < 0.05$; male 6 (closed squares), $y = -1.15 + 0.85x$, $F_{1,2} = 32.3$, $p < 0.05$; male 7 (closed diamonds), $y = -1.36 + 0.63x$, $F_{1,4} = 59.9$, $p < 0.005$, male 8 (closed triangles), $y = 1.40 + 0.32x$, $F_{1,3} = 53.7$, $p < 0.01$; male 9 (pluses), $y = -0.29 + 0.025x$, $F_{1,3} = 54.7$, $p < 0.01$.

result was replicated in the two subsequent sampling rounds (round 1: $r_s = 0.90$, $n = 14$, $p < 0.001$; round 2: $r_s = 0.85$, $n = 22$, $p < 0.001$), in which incumbents were removed a week beforehand to restrict intra-individual variation in site fidelity (see § 2). Fourteen territorial locations were occupied in each of the two latter sampling rounds. However, the motivation scores of these two sets of incumbents were not related ($r_s = 0.09$, $n = 14$, $p > 0.70$). Perching motivation was therefore more closely linked to male age than territory location.

## 4. DISCUSSION

Traditionally, studies of sexually selected phenomena have ignored the consequences of life-history evolution, and vice versa (Höglund & Sheldon 1998). The data presented here indicate two independent lines of evidence that sexually selected behaviour in a territorial butterfly is mediated by the cost of reproduction. First, male contest persistence—the key measure of fighting investment in a war of attrition (Mesterton-Gibbons *et al.* 1996)—increased with advancing male age. Second, older males were more motivated to persist with mate location itself in the face of simulated predation risk. These findings are consistent with a life-history explanation (Stearns 1992) because residual reproductive value is expected to decrease progressively with advancing age in this capital breeding organism (Kemp 2002).

The first experiment demonstrated that males persist for increasing durations in pairwise territorial contests as they age (figure 1). This simple, yet powerful, experimental design controlled for opponent identity (reared males only ever faced one opponent), prior residency (males were 'residents' of their own compartment between contests) and variation in perceived resource value over time (males
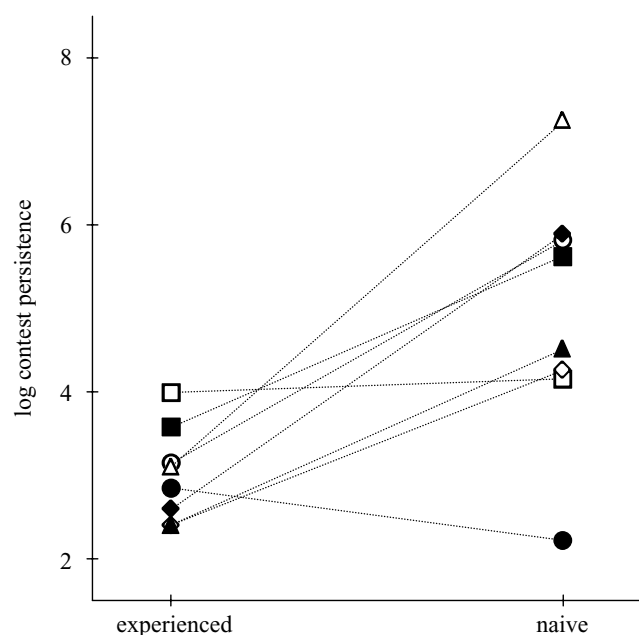
Figure 2. Log-transformed contest persistence of 10-day-old contest-'experienced' and 'naive' siblings measured against the same older wild-caught opponent. Siblings constituting each experimental pair are connected and denoted by a unique symbol.

remained in one compartment and never encountered a female). As reared males never won a contest, this design also controlled neatly for the potential effects of previous victories (Whitehouse 1997). However, contest participation itself could influence an individual's subsequent behaviour as a result of him learning how to fight or make accurate assessments of relative fighting ability (Parker 1974; Enquist & Leimar 1983). This possibility was ruled out by the results of the second experiment, in which previous losses to the same opponent actually reduced future contest persistence. Hence, the experimentally observed lifetime increases in persistence (experiment 1) occurred *in spite* of a significant 'loser effect' (Whitehouse 1997) and in spite of the potential for individual recognition between opponents. This experiment therefore provides compelling evidence for lifetime partitioning of aggressive behaviour that is independent of the effects of resource ownership and fighting experience. Importantly, this is a system where contest performance is not chiefly constrained by physical (Kemp 2000*a*) or physiological (Kemp 2002) parameters that may themselves vary with age (Marden & Waage 1990; Olsson & Shine 1996).

Animals engaging in pairwise contests may be selected to assess their relative chances of success and modify their fighting tactics accordingly (Parker 1974; Enquist & Leimar 1983). In conjunction with field contest data (Kemp 2000*a*), this study indicates that age has a primary causal bearing on fighting ability in *H. bolina* due to its effects on motivation, a situation that is evolutionarily stable (Grafen 1987). The presence of assessment in this species would therefore be indicated by negative covariance between contest duration and age asymmetry (Parker 1974; Enquist & Leimar 1983), as reported in Kemp (2000*a*). However, the first experiment demonstrated that male contest persistence varies greatly even when ages remain constant relative to those of the opponents. This mediates against

pairwise age assessment as a major determinant of contest duration and indicates that butterfly contests could truly represent non-assessment wars of attrition (Mesterton-Gibbons *et al.* 1996). However, it is possible that the sensory cues used to assess age (e.g. wing wear) were modified with age differently under the experimental conditions, perhaps leading to the wild-caught male being perceived as increasingly younger than he actually was (note that this possibility is itself contingent upon an underlying effect of ageing on contest persistence).

Intrasexual contest persistence is only one sexually selected aspect of male reproductive biology that could be mediated by lifetime allocational trade-offs. This concept extends logically to encompass all behavioural and morphological traits that carry the risk of mortality or similar viability costs (Höglund & Sheldon 1998), for example intersexual advertisement (Kokko 1997) and status signalling (Gosling *et al.* 2000). The field-based startle investigation on *H. bolina* provided valuable evidence for the generality of life-history influences in this species. This investigation showed that motivation for mate-searching behaviour *per se* is best related to age, rather than to territory location and variation in previous site fidelity (which was largely controlled in the latter two rounds). Startle stimuli have been used previously to probe motivational state in animals (Elwood *et al.* 1998) and variation in reproductive effort under predation risk has previously been related to residual reproductive value (Magnhagen & Vestergaard 1991; Candolin 1998). This report of age-based motivation in *H. bolina* represents the use of a startle stimulus to assess the interaction between sexual selection and life-history evolution.

Data presented here are consistent with the interpretation that risky male reproductive behaviours are subject to life-history trade-offs. Both verbal (Parker 1974) and mathematical (Enquist & Leimar 1990) models indicate that lifetime increases in costly male reproductive activities will be evolutionarily stable under a range of conditions. Nevertheless, lifetime risk taking on the basis of residual reproductive value should be balanced against lifetime variation in other viability parameters. For instance, if physical fighting ability (i.e. the ability to avoid contest costs) decreases sharply with age, as in some territorial invertebrates (Marden & Waage 1990), then this will mitigate against postponed lifetime aggression. *H. bolina* is a relatively long-lived territorial butterfly (Rutowski 1992) with continuously overlapping generations (Kemp 2001*a*) in which contest participation is not constrained by morphological or physiological factors that could otherwise vary with age (Kemp 2002). Populations of this species will therefore contain individuals of similar physical ability but varying residual reproductive value (as a result of varying age), which may be most conducive to the evolution of age-specific territorial risk-taking outlined here.

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