



FORUM

Butterfly contests: neither paradoxical nor contradictory

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Intrasexual contests in many animal groups are clearly settled on the basis of straightforward physical asymmetries, or on threats or displays based upon those asymmetries (Huntingford & Turner 1987). Contest competition in butterflies, however, has proven difficult to interpret because it is unclear how males are capable of inflicting costs upon one another (Baker 1972; Rosenberg & Enquist 1991). Male butterflies engage in two broad types of contest: (1) territorial contests, where males compete for ownership of specific mating sites (see Davies 1978; Wickman & Wiklund 1983; Rosenberg & Enquist 1991; Kemp, *in press*), and (2) pupal mating contests, where males compete directly over freshly emerging females (see Gilbert 1975; Elgar & Pierce 1988; Deinert *et al.* 1994). Territorial contests involve conspicuous pairwise aerial manoeuvres known as 'spinning wheels' (Wickman & Wiklund 1983) or 'spiral flights' (Davies 1978; Rosenberg & Enquist 1991; Stutt & Willmer 1998), and these contests are settled on the basis of persistence alone (hence they have been described as wars of attrition: Hernández & Benson 1998; Kemp, *in press*). By contrast, males of pupal mating species jostle for positions on about-to-emerge pupae, and then compete to mate with emerging females. Contest success is believed to translate into increased male reproductive success; in the first case by enabling a male to retain sole residency of a site where receptive females will visit (see Wickman 1985, 1988), and in the second case by leading directly to a mating.

Although several studies have specifically investigated how territorial butterfly contests are settled, this question remains essentially unsolved. In cases where biophysical variables, such as size (Rosenberg & Enquist 1991), body temperature (Stutt & Willmer 1998) and age (Kemp, *in press*) have been related to contest outcome, it is unclear how these variables actually function to settle the

dispute. In a recent study, Hernández & Benson (1998) found that war-of-attrition-like territorial contests amongst male *Heliconius sara* (Nymphalidae) are settled in favour of smaller individuals. These authors concluded that, since smaller male *H. sara* may have reduced reproductive value (see below), contests between individuals of varying sizes are settled on the basis of a cost asymmetry (based on the reasoning that it may be relatively more costly for a larger male to persist in a territorial contest). Hernández & Benson (1998) then concluded that this territorial system represents a case of a paradoxical strategy: a situation where contest winners have lower resource holding potential (RHP), resource value (RV), or a lower ratio of resource value to cost accrual than losers (Maynard Smith & Parker 1976). If this interpretation is correct, then Hernández & Benson's (1998) study represents an important step in the process of relating the mathematics of theoretical models to nature. It also provides a breakthrough in the study of butterfly contests by indicating that motivation to persist may be more important than actual physical differences between the combatants.

In response to Hernández & Benson's (1998) paper, Field & Hardy (2000) pointed out that if the biological assumptions presented by Hernández & Benson (1998) are correct (see below), then settlement of these contests is commonsense rather than paradoxical. However, due to an apparent inverse correlation between RV and RHP, a contradictory interaction (*sensu* Parker & Rubenstein 1981) is operating during contest settlement (contradictory because the male with the greater RHP has less to gain from winning: Parker & Rubenstein 1981). The interpretive distinction between 'contradictory' and 'paradoxical' is theoretically important (see Field & Hardy 2000 for a comprehensive discussion), but the underlying mechanism of contest settlement proposed by Hernández & Benson (1998) remains unchanged through this correction. Here I point out some problems with the original assumption that smaller male *H. sara* actually have low reproductive value, and hence, I suggest that

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territorial contests in this species may not correctly fit the definition of a contradictory system.

Male *H. sara* compete for mates using one of two alternative tactics. In the primary tactic, males locate about-to-eclose female pupae using olfactory cues, and then compete with each other to mate with the emerging female (Gilbert 1975; Brown 1981). In the secondary tactic, males defend landmark territories in rainforest clearings, where the encounter rate of receptive females is supposedly higher than throughout the surrounding environment (Benson et al. 1989). Although there are no data available to contrast the reproductive success of males engaged in either tactic, it seems reasonable to suspect that territorial males should encounter relatively few receptive females, and those females may be already mated and hence of lower reproductive value than virgins (Rutowski 1991). On this basis, Hernández & Benson (1998) suggest that territoriality in *H. sara* represents a low-return alternative tactic, and that the individuals that are most successful in pupal mating should have the highest reproductive value (and also the highest intrinsic RHP). These authors suggest that since 'larger *H. sara* may be better at competing for mates at emergence sites', the smaller males have 'diminished mating prospects' (hence low reproductive value) and are forced into territoriality to make the best of a bad job (see Dawkins 1980). Larger males, since they 'have more to lose than small ones in terms of expected future reproductive success', are said to 'avoid combats with smaller opponents' over the ownership of these territorial sites. Thus, larger males with higher RHP have less to gain from holding a territory (i.e. lower RV), and it is in this sense that the outcome of aerial contests over territory ownership can be classified as contradictory (Field & Hardy 2000).

The assumption that small male *H. sara* have low reproductive value, on which Hernández & Benson's (1998) interpretation depends, is based entirely on the work of Deinert et al. (1994) on pupal mating in the congener *H. hewitsoni*. The males of this closely related species possess a very similar primary mating tactic to *H. sara*, in which they locate and compete for access to about-to-emerge female pupae. In order to study the correlates of success in this context, Deinert et al. (1994) identified two selective events: (1) competition between males for a perching position on a pupa, and (2) competition between males to mate with the emerging female. These authors then captured individuals and measured their size using the same character, forewing length, as used by Hernández & Benson (1998) to assess size in *H. sara*. Although the size of male *H. hewitsoni* was found to be important in both selective events, the nature of this effect varied between events. Large males were more successful in jostling for positions on pupae, but once perched, smaller males were more successful in actually mating with the female. As a result of these opposing selective forces, Deinert et al. (1994) found no net difference in forewing length between the males that mated and those that did not. Hence, although larger males were more successful in jostling for perching positions, this did not translate to greater reproductive success for those individuals.

Hernández & Benson (1998) used comparative evidence from the study of Deinert et al. (1994) to infer the dynamics of pupal mating in *H. sara*. However, in supposing that small male *H. sara* have low reproductive value, these authors only accounted for the first selective event in the pupal mating process, competition for a perching spot on a female pupa. The net effect of all selective events in the pupal mating process needs to be considered when determining the likely reproductive value of individuals. When both events are considered, it becomes unlikely that a large male *H. sara* would enjoy a competitive advantage in this context, and hence, have intrinsically greater reproductive value (based on the data presented by Deinert et al. 1994). On current evidence, therefore, Hernández & Benson's (1998) cost asymmetry explanation for contest settlement in *H. sara* appears unjustified.

Hernández & Benson's (1998) explanation can only work if size truly does influence competition in the context of pupal mating in *H. sara* (meaning that larger males do indeed possess relatively higher reproductive value). This would appear unlikely based on the comparative evidence gained using *H. hewitsoni*, however it is still possible. Relative size of combatants has been found to influence the outcome of pupal competition in the lycaenid *Jalmenus evagoras* (Elgar & Pierce 1988), although pupal mating in this species may proceed differently than in *Heliconius*. As Hernández & Benson (1998) correctly point out, further information is required in the case of *H. sara*, particularly regarding the effect of size on competition for pupal matings. This type of information would be immensely valuable, not only in adding to our currently limited understanding of what determines the outcome of territorial butterfly contests, but in helping us evaluate the biological relevance of mathematically derived game-theoretical models of animal aggression.

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