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Small-male advantage in the territorial tropical butterfly *Heliconius sara* (Nymphalidae): a paradoxical strategy?

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ABSTRACT

Large size is often decisive to victory in territorial disputes. Here we report for the first time a natural territorial advantage associated with small size, possibly exemplifying a 'paradoxical strategy' (Maynard Smith & Parker 1976, *Animal Behaviour*, **24**, 159–175) in which small individuals with inferior resource holding power win war-of-attrition contests against superior adversaries because resource value/rate of cost accrual (V/K) is greater for small contestants. Males of the aposematic nymphalid butterfly *Heliconius sara* that defend scattered mating arenas in subtropical Brazilian forest have wings that are on average 3% shorter than males caught away from territories during any part of the year. Smaller residents tend to return to territories over longer periods, and field experiments show that intruders retreat faster when confronting smaller than average territory owners. *Heliconius sara* has a second, seemingly much more important mating system in which female pupae attract males pheromonally, and in which large males may be more successful in winning mates. Because it is unlikely that small *H. sara* have intrinsically superior resource holding power, and because territories should be about equally valuable to all males, we propose that large males, supposedly favoured in pupal mating, may risk losing more in terms of future reproductive success through chance injury in territorial fights (large K) and thus avoid combats with small opponents which risk little from injury because of their diminished mating prospects (small K).

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Not all individuals of a population are equally matched in disputes (Parker 1978; Thornhill & Alcock 1983), and conventional wisdom dictates that if size differences are important in confrontations, large individuals will normally prevail over smaller ones (e.g. Darwin 1871; Enquist & Leimar 1987; Grafen 1987). Although small individuals are often favoured in nonterritorial situations where agility or other qualities associated with small size are important (Petrie 1983; Fincke 1988; Neems et al. 1990), the logic that large size gives a territorial advantage is well supported empirically in both vertebrates and invertebrates (Archer 1988), including insects. Examples for the latter include odonates (Moore 1990; Fincke 1992), thrips (Crespi 1988); true bugs (McLain 1984), homopterans (Whitham 1979), wasps (Alcock 1979; Polak 1993), bees (Villalobos & Shelly 1991), beetles

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(Eberhard 1982; Bartlett & Ashworth 1988), flies (Sigurjónsdóttir & Parker 1981; Otronen 1984), caddisflies (Hildrew & Townsend 1980; Englund & Otto 1991), as well as Lepidoptera. In the satyrine butterfly *Coenonympha pamphilus* L., males holding territories are larger than those off territories (Wickman 1985), and in the nymphaline *Limenitis weidemeyerii* Edwards, large males have additionally been shown to be more successful in ousting territory owners (Rosenberg & Enquist 1991).

Although large individuals are not universally favoured in territorial settings (Lederhouse 1982; Dodson & Yeates 1990; Gribbin & Thompson 1991), the only field study of which we are aware that reports a small-size advantage in territorial conflicts is Convey's (1989) investigation of the dragonfly *Libellula quadrimaculata* L. Here success apparently stems from the relatively more massive flight muscles of small males, endowing them with superior acceleration and manoeuvrability during territorial engagements (Convey 1989; Marden 1989). In other

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conflict situations, small males may possibly be favoured by increased agility (McLachlan & Allan 1987) or some context-specific advantage of smallness per se, although examples are wanting.

Evolutionary game theory suggests another means by which less-endowed individuals may win territorial contests (Hammerstein 1981; Hammerstein & Parker 1982): if small individuals have more to gain or less to lose than adversaries with greater resource holding power, it may be advantageous even for a much stronger opponent to give way to a weaker one. An evolutionarily stable strategy (ESS) favouring victory by the less-endowed contestant has been variably refered to as a 'paradoxical strategy' (Maynard Smith & Parker 1976; Hammerstein & Parker 1982), a 'paradoxical solution' (Parker 1982, 1984) or a 'paradoxical ESS' (Enquist & Leimar 1987), and is said to result from a 'contradictory interaction' (Parker & Rubenstein 1981) or 'contradictory asymmetry' (Silbaugh & Ewald 1987).

The present study reports and attempts to interpret territoriality by small males of the tropical aposematic butterfly *Heliconius sara* (Fabr.). Like many other species in the genus, *H. sara* is philopatric and unpalatable (Brower et al. 1963; Chai 1986), and possesses conspicuous markings and a slow gliding flight that advertise this to potential predators (Benson 1972; Papageorgis 1975; Turner 1981). Development takes about 35 days and adults may survive several months more (Brown 1981).

Heliconius sara males locate mates in at least two different ways: sex pheromones and mating territories. In the primary mate-locating system, female pupae attract males pheromonally, and males perch, typically several to a pupa, and mate with virgin females as they free themselves from their pupal skins (Gilbert 1975; Brown 1981; W. W. Benson, personal observations). Deinert et al. (1994) report that larger males are superior at jostling for perches on pupae in the related *H. hewitsoni* Staudinger. In a probable secondary mate-locating system, male *H. sara* guard small, dispersed territories, which are typically 100–300 m apart, and presumably function as mating stations (Benson et al. 1989; unpublished data), for a few hours each day, often over a week or more. Males may additionally search for and court females (Crane 1957) as do other butterflies.

The stereotyped territorial interactions of *H. sara* (Benson et al. 1989) have the earmark of 'war of attrition' contests (Maynard Smith 1974) and are sufficiently unusual and relevant to our present study to provide a brief description here. Resident *H. sara* patrol and perch-guard territories 10–15 m in length and rapidly perceive and attack conspecific male intruders. In a typical extended interaction, contact is followed by the butterflies' diving together rapidly to near ground level where they separate and each flies in circles adjacent to its adversary over an area of about 0.5 m² and about 10 cm above the ground. During an expulsion, the dominant (always the resident in our observations) butterfly positions himself about 0.3 m below his adversary and, maintaining this geometry, evicts the intruder by flying in tandem slowly (ca. 0.3–0.5 m/s) obliquely upwards to perhaps 15–25 m from the territory. After 'escorting' the intruder away, the resident breaks off contact and rapidly returns to its territory where it resumes patrolling. The butterfly that persists longer in circling just above the ground has the advantage (i.e. wins the war-of-attrition phase) for it can position itself under its opponent when it begins to gain altitude and oust it from the territory. Overt aggression, seemingly restricted to the expulsion phase of these ritualized combats, is apparently limited to occasional butting by the dominant male.

During preliminary observations on *H. sara* territorial interactions, we noted that victorious males were often markedly smaller than their vanquished opponents. In this study we attempt to answer the following questions. (1) Do size differences exist between *H. sara* found on and off territories and do these differences remain constant over the year? (2) Does the time over which a butterfly returns to a territory depend on its size? (3) Does the intensity of a territorial interaction depend upon the sizes of the participants? (4) Are territories limiting such that vacant territories are rapidly colonized by floating males? (5) Do males intruding on occupied territories and colonizing vacant ones differ in size from residents? We use our results and additional information to evaluate the possibility that the peculiar life-history traits of *H. sara* are consistent with the evolution of a paradoxical ESS in which individuals with low resource holding power win territorial confrontations.

METHODS

We studied *H. sara* along 3.2 km of a dirt road cutting through lowland subtropical moist forest (Holdridge 1967) at the Reserva Florestal de Linhares (19°10′S, 40°03′W) state of Espirito Santo, Brazil. Rainfall averages 1320 mm/year and temperature ranges between 25.3 and 20.0°C (January and July means, respectively, for 1975 to 1993; data from the reserve meteorological station).

To investigate the size variation of territorial male *H. sara*, and that of both sexes active off territories over a year, we marked and measured butterflies we caught while walking through the area twice each day during monthly visits of 4–6 days each between July 1990 and September 1991. We netted unmarked butterflies and determined their sex from external genitalia. Each butterfly received a number on the underside of the forewing with India ink, and territorial males were given a unique colour mark with quick-drying paint or a marking pen to permit their visual identification upon resighting.

We used forewing length as an index of butterfly size. For wing-length measurements, we used flat forceps to hold a butterfly's wings folded over its back and recorded the distance from the forewing insertion on the thorax to the wing tip using a plastic millimetre scale held flush across the forceps for stability. We estimated wing length to the nearest 0.5 mm. To evaluate the measurement error associated with the method, each author remeasured 20 dead *H. sara* under simulated field conditions. These measures gave 60% reproducibility and a maximum deviation of one 0.5-mm size class.

We recorded territorial patrolling and transect position for both newly observed and resighted insects. Territorial *H. sara* typically patrol by flying back and forth over their territories several times a minute, whereas nonterritorial individuals normally do not remain in restricted areas unless visiting flowers or concentrating near host plant patches. We observed each butterfly sighted 1–3 min to determine whether or not it was engaged in territorial patrolling. We induced perched butterflies to fly by jarring their plant supports.

In 1993, we conducted experiments along a 1.5-km section of the study area. To investigate the effect of the sizes of residents and intruders on the intensity of territorial confrontations, we observed marked butterflies using resighting methods during normal territorial interactions. We arbitrarily selected 20 marked resident males for observation that had been seen on the same territory on the visit immediately preceeding the day of observation. In this way, the sizes of residents and of marked intruders were known. If an intruder was unmarked, it was classified as being smaller, equal in size or larger than the resident when both could be observed clearly and simultaneously silhouetted against the sky. These measurements were aided by the shallow wing beat, slow speed and visual alignment of butterflies during the expulsion phase of typical territorial encounters (Benson et al. 1989).

We measured the intensity of conflicts using a three-level scale based on the behavioural sequence of the contest phase of *H. sara* territorial interactions (Benson et al. 1989). The weakest level of interaction was characterized by the resident expelling the intruder directly after initial contact, without diminishing its flight altitude. Intermediate intensity interactions were characterized by the intruder and resident diving towards the ground before reversing direction, with the intruder being expelled from the territory. The strongest interaction occurred when the resident and interloper descended to just above the ground and flew in tight circles until the resident regained the territory. Interaction intensity is apparently controlled by the tenacity of the intruder. If intruders assess residents during interactions, and if size is an important correlate in winning fights, inferior challengers should give up more quickly in interactions having large size asymmetries in favour of residents (Rosenberg & Enquist 1991).

We collected data for testing the influence of size (relative and absolute) of residents on contest intensity in three blocks during 1993: February–March (summer), August (winter), and October–December (spring). Because butterflies were markedly smaller in August than at other times, we excluded the August sample to normalize size distributions for tests involving absolute size. We also observed interactions between marked combatants to determine whether intruders, possibly representing floaters in search of territories, differed in size from residents.

We conducted a removal experiment to evaluate the demand for territories by floater males and to compare the sizes of floaters colonizing vacant territories with those of former occupants. The experiment used marked males observed defending a territory for at least 2 days.
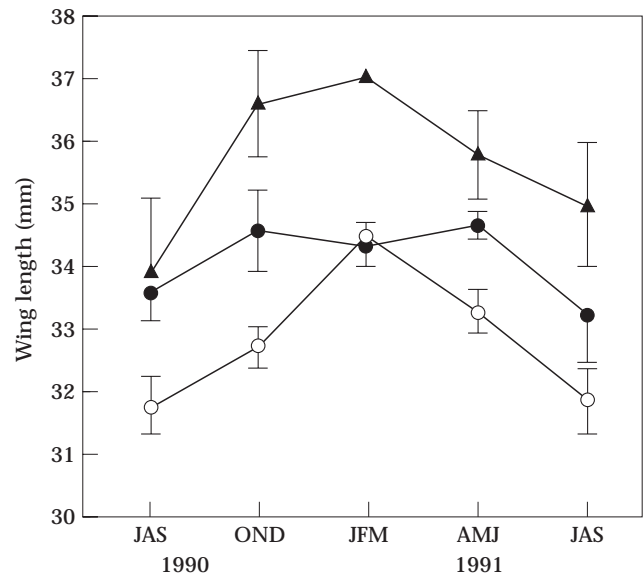

Figure 1. Seasonal variation in the forewing length of *H. sara* as a function of sex and male territorial status at the Reserva Florestal de Linhares, Espírito Santo, Brazil. Males on territories (○) were smaller than those caught off territories (●) (t_{223}=2.34, $P<0.05$), and males overall were smaller than females (▲) (t_{253}=2.04, $P<0.05$). Labels on the abscissa indicate the months comprising each sample period. Error bars show ±1 SE of the mean. The sample sizes for each butterfly type, presented in chronological order from left to right, are as follows: females: 7, 5, 1, 10, 2; males off territories: 9, 10, 3, 42, 6; males on territories: 24, 47, 40, 23, 21.

We netted residents near the beginning of the normal territorial period (0900–1100 hours) and stored each temporarily in an opaque cannister in the shade. After approximately 1 h ($\bar{X} \pm SD=72 \pm 9$ min), we observed these vacant territories for recolonization. Marked colonists were visually identified and unmarked ones were marked and measured using standard protocol. At the end of the observation period, we released and observed the original owner for further territorial behaviour (none was observed immediately following release). We observed territories on subsequent days for delayed recolonization or return of the original owner.

We conducted parametric analyses using SYSTAT (Wilkinson 1990). Sokal & Rohlf (1995) and Rohlf & Sokal (1995) were used for chi-square tests. Two-tailed probabilities are given. Measures are given as means ± SE.

RESULTS

The wing lengths of male *H. sara* sampled over 15 months in 1990–1991 (33.39 ± 0.141 mm, $N=230$) were significantly shorter than those of females (35.40 ± 0.498 mm, $N=25$; *t* test: $t_{253}=2.04$, $P<0.05$). Moreover, males captured while patrolling territories had significantly shorter wings overall (33.00 ± 0.176 mm, $N=155$) than those captured off territories (34.37 ± 0.189 mm, $N=70$; *t* test: $t_{223}=2.34$, $P<0.05$).
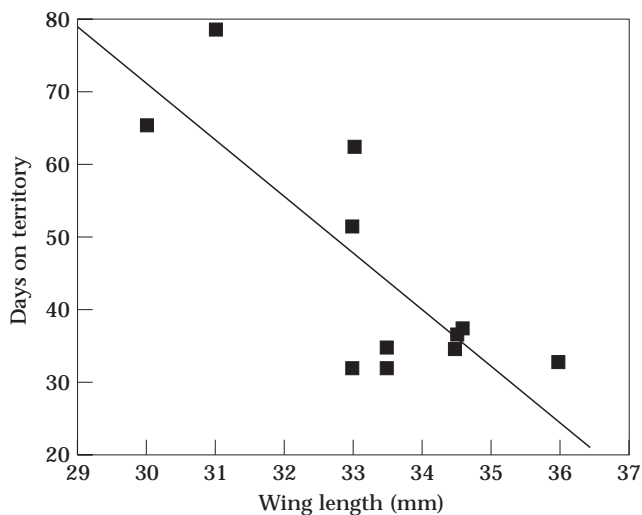
To test whether size varied with respect to territorial status and time of year, we averaged wing lengths for day

Table 1. Two-way ANOVA for *H. sara* wing length for territorial males and males off territories over five consecutive seasons at the Reserva Florestal de Linhares, Espírito Santo, Brazil

Source of variation	Sum of squares	Degrees of freedom	Mean square	*F*	*P*
Territoriality category	41.75	1	41.75	12.2	0.001
Season	58.23	4	14.56	4.3	0.002
Interaction	9.41	4	2.35	0.7	0.601
Error	735.30	215	3.42		

of first capture by season for males on and off territories (Fig. 1). Analysis of variance revealed (Table 1) highly significant differences for butterfly size both among the five seasons and for territorial status, with territorial males being smaller than males caught away from territories. The seasonal comparison showed a regular pattern of increasing size during January–March (summer) and decreasing size during July–September (winter) (Fig. 1), perhaps related to temperature or food quality during larval development. The nonsignificant interaction term indicates that the seasonal size response was similar for each male category. Thus, the similarity in size of males marked on and off territories during the summer of 1991 (see Fig. 1) was not considered to be meaningful within the context of the overall analysis. Additional measurements made on experimental insects in 1993 (see below) further support the idea that butterflies were on average larger in summer and spring (February–March: 33.96 ± 0.215 mm, $N=57$ and October–December: 34.42 ± 0.375 mm, $N=18$, respectively) than in winter (August: 32.43 ± 0.468 mm, $N=7$).

Size may also influence the time a butterfly persists in territorial behaviour or survives. We examined the relationship between wing length and territorial time span (days) for the 11 butterflies observed in territorial activity with at least 30 days between first and last sighting. Regression analysis (Fig. 2) showed that persistent males increased their territorial tenures in the study area by about a week for each reduction of 1 mm in wing length ($Y=305(\pm 68.4) - 7.80(\pm 2.05)X$; *t* test: $t_{b,9}=3.80$, $P(b=0)<0.005$).

Assuming an isometric relationship between males of different sizes, the 1-mm difference in wing length between males on and off territories suggests that the mass of an average territorial male *H. sara* should be about 10–15% less than a male not occupying a territory. Thus, blows from the body and wings by small butterflies may have considerably less impact than those from large ones, suggesting that aerial shocks should be proportionately more severe and potentially damaging to smaller contestants in territorial disputes. However, territorial success in *H. sara* does not seem to mirror this consideration.

In the 31 territorial interactions involving marked resident males observed during 1993, owners always won. We used these observations to assess the association between interaction intensity and (1) relative sizes of the resident and intruder and (2) absolute size of the resident male.

In the analysis of relative size, we excluded four observations in which the contestants did not differ notably in size. In addition, we combined 16 interactions in which both resident and intruder had been previously marked with 11 additional observations in which the relative sizes of unmarked intruders had been evaluated visually. In these combats, interaction intensities tended to be weaker, almost significantly so, when residents were small relative to intruders (chi-square test: $\chi^2_2=5.76$, $P=0.055$; Table 2).

Figure 2. Elapsed time between first and last observation of territoriality in male *H. sara* as a function of butterfly size for 11 individuals resighted over a period in excess of 30 days over 12 months during 1990–1991. The regression has a highly significant negative slope ($b=-7.80$, $P<0.005$).

Table 2. Interaction intensity of territorial disputes in *H. sara* as a function of the relative ($P=0.055$) and absolute ($P<0.025$) size of the resident (see text for details)

Interaction intensity	Relative and | absolute | size of resident				Total number of interactions	
	Small		Large			
Strong	3	| 4 |	7	| 7 |	10	| 11 |
Intermediate	5	| 3 |	2	| 5 |	7	| 8 |
Weak	8	| 10 |	2	| 2 |	10	| 12 |
Sums	16	| 17 |	11	| 14 |	27	| 31 |

To evaluate the association between the absolute size of residents and interaction strength, we classified territory owners as large or small based on their size relative to the population mean. The 75 territorial *H. sara* marked for behavioural studies during the summer and spring of 1993 had a mean wing length of 34.07 ± 0.16 mm, and males with wings of 34.0 mm or less were classified as 'small' and those with longer wings were classified as 'large'. Territorial interactions involving smaller than average residents tended to be of low intensity and those involving large males were mostly of medium and high intensity (chi-square test: $\chi_2^2=8.91$, $P<0.025$; Table 2). The less intense interactions with smaller than average residents suggest that intruders quickly recognized small residents as unfavourable adversaries and desisted sooner from take-over attempts against these residents.

Results from the removal experiment indicate that the demand for territories was not high. In 45 cases in which a resident male was temporarily removed from a territory which it had occupied on the 2 preceding days, only 17 (38%) were colonized by a new resident, all within the hour following removal of the original owner. About half of these new occupants ($N=9$) were replaced by the original resident by the following day. In 13 (46%) of the 28 cases in which territories were not immediately occupied, the original resident also returned by the next day. (A total of 25 experimental males returned to their original territories within 5 days, six (24%) on the day they were removed, 16 (64%) on the following day and three (12%) on subsequent days.)

On the 16 occasions for which it was possible to determine the size of the butterfly colonizing a vacant territory, colonizers (34.16 ± 0.40 mm) were similar in size to the original owners (34.00 ± 0.42 mm; paired *t* test: $t_{15}=0.265$, NS). Also, the average size of 16 different marked intruders involved in 17 territorial confrontations (33.63 ± 0.47 mm, $N=16$) did not differ from that of the 13 resident males (34.08 ± 0.32 mm, $N=13$) with which they interacted (paired *t* test: $t_{16}=0.321$, NS). Thus, butterflies colonizing vacant territories and those intruding on occupied territories were similar in size to territory owners.

DISCUSSION

The territorial advantage demonstrated for small *H. sara* males was unexpected both in the light of simple contest theory (Parker 1978; Thornhill & Alcock 1983) and existing data: where size differences have been detected between winners and losers in natural animal confrontations, the winners have always been larger (Archer 1988) or more muscular (Convey 1989) than their adversaries. Within the realm of evolutionary game theory, there seem to exist two hypotheses that might explain this pattern of territorial success. First, small male *H. sara* may possess some unrecognized context-specific characteristic giving them superior prowess when defending territories. Second, the success of small males may represent a paradoxical strategy (sensu Maynard Smith & Parker 1976) which promotes victory despite lower resource holding power.

The heretofore singular report of small-male territorial advantage in the dragonfly *L. quadrimaculata* seems adequately accounted for by the proportionately larger flight muscles in smaller individuals (Convey 1989). Territorial dragonflies feed and can undergo considerable muscular development after metamorphosis, before attaining sexual maturity (Marden 1989; Anholt et al. 1991), suggesting that if individuals with long wings have trouble capturing prey, they may not grow strong enough to hold territories. Imaginal butterflies apparently do not grow in muscle mass (see Gilbert & Singer 1975; Vane-Wright & Ackery 1984), and it seems unlikely that larger *H. sara* do badly in territorial contests because they are relatively underfed.

Smallness may be favoured when larger individuals are poorly adapted to local conditions, as may be the case in *L. quadrimaculata*, and when large size is pathological. In *Drosophila*, small males may win territorial disputes when size differences are induced by manipulating developmental temperature (Zamudio et al. 1995). We suspect that large size often becomes fleetingly suboptimal when environments are variable (e.g. Gibbs & Grant 1987) and that gene flow may similarly have unpredictible effects on size-related performance. The *H. sara* studied by us belonged to several overlapping demes inserted in a regional population spread over a rather homogeneous landscape. Although butterfly size varied seasonally, small individuals predominated on territories over essentially the entire year, suggesting that small-male advantage in *H. sara* is not a fluke effect of fluctuating environment or gene flow.

In isometrically scaled organisms, smaller size may diminish acceleration and force of impact, although aerobatic agility may be increased (McLachlan & Allen 1987; Convey 1989), particularly with regard to a smaller turning radius (McLachlan & Cant 1995). While a number of studies have associated agility and other qualities imparted by small size with increased mating success (references in Introduction), greater fighting ability and capacity to hold territories are not among them. Thus, increased manoeuvrability may be important to small *H. sara*, although it does not explain why small-male territoriality has evolved in *H. sara* but not in other species.

It is, of course, possible that other unmeasured qualities bestow a context-specific advantage to small territorial *H. sara*. However, more detailed studies would be required to detect them, and if none were found, it could always be argued that the relevant factors were not studied. An alternative approach is to ask whether special conditions conducive to a paradoxical small-size strategy pertain in *H. sara* but not in species where big individuals win.

We believe that the use of pheromones by female pupae to attract males for mating may be the key to understanding the small-male territorial advantage in *H. sara*. In butterflies, apart from *H. sara* and some of its close relatives (Gilbert 1975), the release of sex pheromones by pupae seems uncommon (Borch & Schmid 1973; Elgar & Pierce 1988). In *H. sara*, males congregate at pupation sites and typically several hang clustered on each female pupa, one of which mates with the female as

she emerges. Wing fluttering by perched males may interfere with competitor landings, and Dienert et al. (1994) showed for the closely related *H. hewitsoni* that medium to large males are generally more successful at gaining perches than small ones.

In the dual mating system of *H. sara*, female pupae may contribute much more to male reproductive success than those females that have already emerged and are no longer localizable by pheromones. If this is so, territorial defence may represent a low-return alternative mating tactic. However, if small males are generally unsuccessful in competing for matings at pupae, territorial matings may be a major means by which these males leave descendants.

Territorial males presumably mate with rare females whose pupae go unfound (e.g. pupae concealed, few males available locally, etc.) and with previously mated older females. Matings with older female *Heliconius* may not contribute greatly to male reproductive success because these females already have diminished egg production (Dunlap-Pianka et al. 1977) and females of the pupal-mating group seem rarely to remate (Pliske 1973; Ehrlich & Ehrlich 1978; Brown 1981).

Although we have not observed matings at territories, and the above considerations lead us to expect these events to be infrequent, Benson et al. (1989) reported finding a teneral female mating with a male adjacent to a frequently used *H. sara* territory. In other arena butterflies, unmated females may seek out territory sites (Lederhouse 1982; Wickman & Wiklund 1983; Wickman 1985, 1988) and seem to mate preferentially with associated males (Wickman 1985, 1986; Wickman et al. 1995). Unmated female *H. sara* may lose much of their sexual attractiveness by the time they are a few days old (Crane 1957), and thus finding a mate rapidly may be important to assure fertilization.

According to evolutionary game theory, in asymmetric wars of attrition, where adversaries are fully informed about the nature of the asymmetries (respective resource values and confrontation costs), the optimal behaviour for the individual with the lower resource value/rate of cost accrual (V/K) would be to retreat at the beginning of the conflict, leaving his or her opponent as victor (Hammerstein & Parker 1982; Parker 1982). If less capable individuals have larger V or smaller K (despite their low resource holding power), the contest can have a paradoxical solution in which these less endowed individuals win (Maynard Smith & Parker 1976; Parker 1982).

While larger male *H. sara* may be better at competing for mates at emergence sites, size should not greatly influence the fitness rewards of territorial defence. Moreover, large butterflies probably have as great or greater resource holding power than small ones (e.g. Wickman 1985; Rosenberg & Enquist 1991), suggesting that holding territories may be physiologically less costly for large individuals. If debilitating injuries are a real danger in take-over attempts, however, large *H. sara* males may have much more to lose than small ones in terms of expected future reproductive success (Grafen 1987). In real fights (the 'reserve strategy' of Parker & Rubenstein

1981), small *H. sara* males, with supposedly reduced chances of mating at emergence sites, may not be risking much in terms of lost reproductive opportunities, and therefore may have smaller K (and larger V/K) than large adversaries in which injury may mean losing future high-yield mating opportunites at pupation sites. This may be true even if smaller adversaries run a greater risk of serious injury in escalated combats.

We have only one record of an injury in an *H. sara* in the several hundred territorial interactions observed by us and our associates: a small resident male returned from an unusually vigorous chase missing a large part of one forewing. Although injury risks seem minimal in conventional contests, injury rates could increase substantially if and when adversaries fight openly. The costs of fighting needed to estimate K refer to the reserve strategy, and these are not generally available.

Resident *H. sara* have a pronounced advantage both in expelling interlopers (independent of the adversary's size) and in retaking territories occupied by other males during brief absences (Benson et al. 1989; this study). Resident advantage, widespread among territorial species, has been associated with bourgeois ESSs based on arbitrary ownership asymmetries (Davies 1978; Maynard Smith 1982) or information, available only to the owner, making a territory more valuable or less costly to defend (Sigurjónsdóttir & Parker 1981; Archer 1988, page 165). In the case of *H. sara*, an intruder-initiated circling flight may prevent an owner from implementing its reserve strategy because of the ensuing danger of damaging collisions with vegetation or the ground. This may allow intruders to acquire more information concerning territories and the ability of residents to defend them. Similarly, a weak resident may be able to retain its territory longer if diving to the ground increases the chances of invader desistence. The seemingly low demand for territories in *H. sara* suggests that suitable territory sites may not be sufficiently limiting or valuable to risk injury to eject an established resident (Hammerstein 1981; Grafen 1987). Rosenberg & Enquist (1991) further suggest that territorial interactions should take longer in evenly matched contests when sequential assessment is required for adversaries to evaluate one another. In *H. sara*, however, prolonged evaluation does not seem to be necessary to decide victors; residents always won in the interactions observed by us.

Keeley & Grant (1993; see also Enquist & Leimar 1987) review the few experimental investigations on paradoxical ESSs. In two of three studies on value-expectation asymmetries (Dugatkin & Ohlsen 1990; Keeley & Grant 1993) in which subjects with low resource holding power were trained to expect greater payoffs, the subjects did well in some respect when pitted against larger (Dugatkin & Biederman 1991; but see Keeley & Grant 1993) or more experienced opponents (Ewald 1985). State asymmetries, where the same nominal payoffs and costs produce different fitness effects because of individual differences in physiological condition or reproductive value, apparently have not been previously investigated, and to our knowledge, our study provides the first indication that contradictory asymmetries based on cost disparities in

expected future reproductive success can give rise to paradoxical strategies.

Although the territorial advantage shown by small *H. sara* is consistent with a paradoxical ESS, the conclusions presented here must be considered provisional. Critical information is lacking for the costs and benefits associated with the proposed strategies; in particular, the effects of male size on mating success at emergence sites, reproductive success of territorial males and the probability of sustaining injury in nonritualized fights, and alternative explanations (e.g. more muscular, small males) have not been fully explored. Information on *H. sara*'s close territorial relatives, *H. leucadia* Bates (Benson et al. 1989) and *H. antiochus* (L.) (G. V. Andrade & W. W. Benson, unpublished data), and on more distantly related territorial heliconiines, may provide additional insights into the significance of size in insect territoriality.

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