THE ROYAL SOCIETY

Received 30 December 2003
Accepted 21 April 2004

Residency effects in animal contests

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The question of why territorial residents usually win asymmetrical owner–intruder contests is critical to our understanding of animal contest evolution. Game theory suggests that, under certain conditions, residency could be used as an arbitrary means of contest settlement in a manner analogous to tossing a coin. Key empirical support for this idea is provided by a study on the speckled wood butterfly (*Pararge aegeria*); however, this result has proven controversial. We show conclusively that residency does not serve as an arbitrary cue for contest settlement in this species. By means of a series of manipulative experiments, conducted on two phenotypically divergent populations of *P. aegeria*, we also rule out the recently presented alternative that contests are settled due to resource-correlated asymmetries in thoracic temperature. Our results instead suggest that more intrinsically aggressive males accumulate as residents and continue to win due to the self-reinforcing effect of prior winning experience. Truly arbitrary contest settlement may be rare or non-existent in the wild.

Keywords: bourgeois; butterfly; sexual selection; territoriality; uncorrelated asymmetry

1. INTRODUCTION

The finding that resource owners usually win pairwise contests over territories, resources or mates is pervasive in behavioural ecology (Alcock 2001). In many territorial systems, residents are thought more likely to win because they possess greater intrinsic fighting ability (Marden & Waage 1990; Alcock & Bailey 1997), or because they place greater value on the contested resource (Krebs 1982; Johnsson & Forser 2002). Another possibility, suggested by evolutionary game theory, is that territorial contestants could use information regarding the roles themselves as an arbitrary cue to determine contest outcome (Maynard Smith & Parker 1976; Maynard Smith 1982). This hypothesis—hereafter referred to as the uncorrelated asymmetry hypothesis—contends that all (or most) individuals in the population obey an arbitrary rule such as 'resident wins', thus largely sidestepping potentially injurious combat. True or escalated contests occur only when roles are confused; otherwise, contests would be settled almost instantly in a similar manner to tossing a coin. Although valid as a theoretical construct, the real-world applicability of this idea has a history of fierce debate (e.g. Austad *et al.* 1979; Grafen 1987; Stutt & Willmer 1998; Hardy 1998).

Shortly after its inception, Davies (1978) carried out a now classic empirical test of the uncorrelated asymmetry hypothesis using a territorial butterfly, the speckled wood (*Pararge aegeria*). Butterflies are thought to represent an excellent candidate system for the evolution of uncorrelated asymmetry effects (Maynard Smith & Parker 1976), perhaps because it is unclear how these apparently 'weaponless' animals may otherwise settle their disputes (Kemp & Wiklund 2001). Moreover, the most obvious difference between territory residents and intruders in this group is the roles themselves, and residents enjoy a significant and general competitive advantage (see Kemp & Wiklund (2001) for a review). Male *P. aegeria* contest the ownership of sunspot-based mating territories, situated on the forest floor, by means of non-contact aerial manoeuvres typical for butterflies (see § 2 for a description of butterfly contests). Davies' (1978) experiment appeared to indicate that either of two butterflies could beat the other depending upon which was in the resident role, therefore providing key support for the uncorrelated asymmetry idea. This study provided an empirical platform for the widespread acceptance of this hypothesis as a valid biological construct, and has served as a textbook case (McFarland 1999; Dugatkin 2004), and a widely cited paradigm to this day (e.g. recently Olsson & Shine 2000; Johnsson & Forser 2002; Renison *et al.* 2002).

Despite its popularity, Davies' (1978) research has been challenged (Austad *et al.* 1979; Wickman & Wiklund 1983), most recently by the suggestion that residents of this sunspot-defending ectotherm could be mechanistically advantaged by higher body temperatures (Stutt & Willmer 1998). Under this hypothesis, contests would be asymmetric for body temperature, with high temperature—thus putative fighting 'ability'—intimately linked with sunspot residency (non-residents are forced to patrol shaded under-canopy regions, and therefore are vulnerable to convective cooling). However, although thoracic temperature does influence some insect flight performance parameters (such as acceleration), it is not clear whether or how this parameter would contribute to endurance ability in a war-of-attrition-type contest. Aside from other more theoretical concerns (outlined in Kemp & Wiklund 2001), there are also some doubts regarding the biological realism of the experimental set-up used by Stutt & Willmer (1998) to evaluate their hypothesis. Both the experiments of Davies (1978) and Stutt & Willmer (1998) involved considerable handling of subjects and resulted in contests markedly shorter than those observed in the wild (e.g. Wickman & Wiklund 1983). A more thorough and biologically realistic approach is warranted to examine the significance of territorial residency in this model contest system (Kemp & Wiklund 2001).

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DOI 10.1098/rspb.2004.2775

We report upon experiments designed to isolate the effects of residency and body temperature upon contest outcome in territorial *P. aegeria*. We used a large outdoor flight enclosure, furbished to mimic a woodland habitat, which enabled a greater degree of control over experimental subjects in a more biologically realistic situation than realized previously (e.g. Davies 1978; Stutt & Willmer 1998). We also assessed the generality of contest resolution mechanisms in this species by using laboratory-reared males from phenotypically divergent (Gotthard *et al.* 2000) *P. aegeria* populations in Sweden and the Portuguese island of Madeira. The experiments were designed to specifically test (i) whether residency is used in the manner of an uncorrelated asymmetry, or (ii) whether contests are settled instead due to residency-related asymmetries in body temperature. We draw upon additional features of our results, such as variation in contest duration, to further illuminate the mechanisms of contest resolution in this conventionally 'weaponless' taxon.

2. MATERIAL AND METHODS

(a) *Territoriality and contest competition in butterflies*

The males of many butterfly species establish and defend territories, such as forest clearings, sunspots and hilltops, as a means of maximizing their encounters with receptive female conspecifics (Davies 1978; Wickman & Wiklund 1983; Kemp 2000). Territorial contests consist of non-contact aerial wars of attrition in which the two combatants generally circle, or hover near each other, for a period of time before one male gives up (Kemp & Wiklund 2001). This true or 'escalated' decisive contest phase, which in *P. aegeria* may last several minutes (Wickman & Wiklund 1983), is followed by a chase in which the loser is pursued for some time before the winner returns to the contested area. The two contest phases are clearly demarcated and always clearly recognizable. Only the duration of the first phase is relevant to the question of how these contests are settled (i.e. this is the 'true' war of attrition phase), and only interactions that include this phase can be truly considered contests. Meetings between two males that constitute a chase only, which are reasonably common in *P. aegeria* and other territorial species (e.g. *Hypolimnas bolina*; Kemp 2000), indicate that one male (the 'chasee') is not interested in truly contesting site ownership, due, for instance, to lack of territorial motivation. This is also the type of 'quick' interaction that we would expect, based upon the uncorrelated asymmetry hypothesis, in contest situations where roles are clearly perceived by both contestants (Davies 1978; Maynard Smith 1982).

(b) *Experimental enclosure*

The experimental enclosure was semi-cylindrical in shape (dimensions: 6 m × 8 m base, 4 m radius) and covered with 32% UV-absorbing shade-cloth cover overlaid with an opaque green plastic tarpaulin. We removed a 2 m × 2 m section of the tarpaulin to create a primary sunspot, which tracked across the cage floor from 09.00 to 15.00, and cut a series of smaller (0.1–0.4 m diameter) holes to create a mosaic of smaller sun flecks. All experiments were conducted using this cage floor sunspot as the primary territory, and experimental subjects quickly recognized the sunspot as a suitable territory. We further mimicked a forest habitat in the cage using artificial 2 m high Christmas trees, dried leaves, twigs and rocks. The enclosure was situated less than 100 m from suitable field woodland habitat (at Tovetorp, central Sweden) in which free-flying males were actively defending territories at the times in which our experiments were being conducted.

(c) *Residency asymmetry experiment*

We conducted a two-stage experiment in which the winner of an initial symmetrical contest over the cage sunspot was made to assume the role of 'intruder' in a successive contest against the same opponent. The two contests were separated by a variable (mean of 16.6 ± 2.3 min, range of 3–38 min) 'grace' period during which initial losers were granted sole ownership of the sunspot territory, and winners were stored in a cooler. This created a clear residency asymmetry and allowed the prediction that, if residency serves as an arbitrary cue for contest settlement, then initial losers should quickly win their subsequent contest (i.e. when in the resident role). This regime of repeat contests over a single territory is a relatively general natural phenomenon in butterflies (e.g. Kemp 2000), including *P. aegeria* (Wickman & Wiklund 1983).

All males were introduced into the enclosure on moistened cotton wool buds (15% sugar solution), upon which they perched and fed, and were never handled directly. Naive subjects were first allowed 5 min to acquaint themselves with the environment, and we used only males that perched in the primary sunspot and chased thrown objects (more than 95% of individuals). We established the initial symmetrical contest by placing two contest-naive, age-matched subjects simultaneously at opposite corners of the sunspot and allowed them to discover each other naturally. Immediate contests always ensued at this point. Subsequent winners were stored during the loser's 'grace' period in small plastic cups within a cooler (16–17 °C). These butterflies were re-released and allowed to bask in the sun (for at least 300 s) and initiate flight at their leisure, thus triggering the second role-asymmetric contest. Males from both populations were used in this experiment, and in all following experiments, always in like-population dyads.

(d) *Thermal asymmetry experiment*

We carried out a second set of (otherwise procedurally identical) trials in which we deliberately created a body temperature asymmetry in the resident–intruder contest by releasing 'chilled' intruders in a shaded position and coaxing them to fly to the sunspot prematurely. We chilled males by placing them in a cooler containing ice blocks (internal temperature: 12–13 °C) for 300 s prior to releasing them in a shaded location. Chilled releasees were encouraged to fly to the sunspot promptly (mean of 88 ± 5 s after release, range of 30–132 s), and thus trigger a contest, by tossing small bark chips overhead. We predicted that, if body temperature is an important determinant of fighting ability, then chilled intruders should lose the second contest. Contrary to the residency asymmetry experiment, here we made no prediction as to how quickly such contests should be settled.

Although we could not directly measure the temperatures of residents and intruders during the experiment, we re-enacted a series of trials and measured the thoracic temperatures of live butterflies and freshly killed models over the time-frame and under the conditions in which contests generally occurred. All measurements were made using a hypodermic-mounted 40-guage Type T (Cu-Cu/Ni) thermocouple connected to a Microtherma-2 model digital reader (Pentronic, Sweden). Freshly killed butterflies were cooled as per trial subjects and impaled on the probe in the dorsal basking position typically

Table 1. The outcome of resident–intruder contests in two stage trials.
(Proportional intruder success rates are given in parentheses. χ^2-values calculated for each experiment are Yates-corrected for continuity.)

experiment	population	*n*	intruders won	χ_1^2	*p*
residency asymmetry	Swedish	14	14 (1.00)		
	Madeiran	12	11 (0.92)		
	total	26	25 (0.96)	20.34	< 0.0001
residency and thermal asymmetry	Swedish	7	7 (1.00)		
	Madeiran	19	18 (0.95)		
	total	26	25 (0.96)	20.34	< 0.0001
both	Swedish	21	21 (1.00)		
	Madeiran	31	29 (0.93)		
	total	52	50 (0.96)		

assumed by released subjects. We logged the rate of heat gain in these models over the time range of 0–210 s. Live butterflies were chilled and released in either the shade or the sunspot as in the experiments. We measured the temperature of sunspot- and shade-released males, respectively, at 555 ± 113 s (range of 322–1045 s) and 105 ± 12 s (range of 30–152 s). Individuals were immediately immobilized between two sheets of fibreglass gauze, a method facilitating rapid (2–3 s) T_{th} measurement. Several shade-released males flew immediately prior to capture and measurement, indicating that, as with true trials, free flight was possible in chilled individuals. Experimental and re-enacted trials were conducted under an ambient (cage) temperature range of 17.3–28.7 °C and 23.1–25.1 °C, respectively.

(e) *Controlled experience experiment*

We conducted one further experiment using pairs of winners and pairs of losers from the thermal asymmetry experiment. Contestants in these pairings shared an identical contest history since they each either won or lost two prior contests. Trials consisted of a single role-asymmetrical contest in which a cool intruder faced a warm resident, with roles assigned randomly. Individuals were handled as per the thermal asymmetry experiment, with the exception that (since these trials consisted of a single contest) sunspot residents were introduced at least 500 s prior to releasing the chilled intruders. We timed the duration of the circling (escalated) contest phase, as in the two previous experiments, to the nearest second using a digital stopwatch.

3. RESULTS

(a) *Residency asymmetry experiment*

We conducted 26 residency asymmetry trials. In clear contradiction of the uncorrelated asymmetry prediction, the winners of the initial contest won again (when in the intruder role) in all but one case (table 1). The asymmetric contests were also relatively prolonged, with a circling (escalated) phase lasting an average of 166 ± 59 s (range of 4–1279 s).

(b) *Thermal asymmetry experiment*

We also conducted 26 thermal asymmetry trials. In re-enacted trials (see § 2) mean intruder temperature (22.11 ± 0.58 °C, $n = 8$) was more than 9 °C lower than that of residents (31.24 ± 0.60 °C, $n = 6$) a difference that is highly statistically ($t_{12} = 10.71$, $p < 0.0001$) and biologically significant (Stutt & Willmer 1998; Berwaerts *et al.* 2001). These values are also largely consonant with the thermal equilibria achieved by freshly killed and chilled males placed either in the sunspot or the shade (figure 1), which suggests the presence of a large thermal asymmetry in contest trials. Despite this probable asymmetry, and the reduction in intruder flight performance, intruders were again successful in 25 out of 26 contests (table 1).

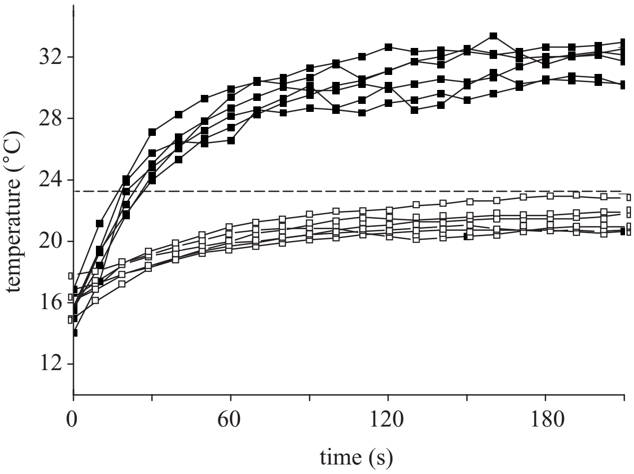

Figure 1. Warming rates of freshly killed butterfly models situated in the shade (open squares) and sun (filled squares). Models were chilled for 300 s prior to placement (see § 2). The dashed line indicates the mean ambient temperature ($T_{\mathrm{a}} = 23.2$ °C) inside the enclosure at measurement times.

Logistic regression (Hardy & Field 1998), conducted on data from both experiments pooled, indicated that the probability of resident loss did not vary due to experiment ($G_1 = 0$, $p = 1.0$), population ($G_1 = 2.23$, $p = 0.13$) or their interaction ($G_1 = 0$, $p = 1.0$). Non-significance of the experiment term, which encapsulates the effect of thermal asymmetry (since no such asymmetry was present in the first experiment), shows conclusively that thoracic temperature is unlikely to present a mechanistic constraint to competitive ability. In further support of this conclusion, the duration of the circling phase in resident–intruder contests did not differ between experiments or according to ambient temperature, instead covarying positively with the duration of the 'grace' period and the first contest (table 2). Non-significance of the population term indicates that the conclusion regarding contest outcome is relatively robust (i.e. it holds equally for both Swedish and Madeiran males). However, contest duration did vary significantly between populations, with Madeiran males persisting for longer in their contests (table 2).

Table 2. Survival analysis of the duration of resident–intruder contests in two-stage trials.
(Parameters were sequentially removed from an initial log-normal model ($\chi^2_5 = 19.54$, $p < 0.005$) and their contribution evaluated using the log likelihood ratio (χ^2) statistic. Temperature ($\chi^2_1 = 0.44$, $p = 0.51$) and experiment ($\chi^2_1 = 1.59$, $p = 0.21$) were discarded. First contest was retained in the final model due to its marginal significance level. Population was coded 0 = Swedish and 1 = Madeiran, hence, males from the latter population persisted longer. $n = 50$.)

parameter	d.f.	χ^2	p	$\beta \pm$ s.e.
first contest duration (log)	1	3.75	0.053	0.22 ± 0.11
population	1	6.39	0.011	0.87 ± 0.33
grace period	1	8.76	0.003	0.055 ± 0.018
final model	3	17.52	0.0005	

(c) *Controlled experience experiment*

We conducted four trials between pairs of prior losers and 11 between pairs of prior winners. Chilled intruders were successful in seven cases (2 out of 4 loser trials and 5 out of 11 winner trials), a result close to random expectation (Yates-corrected $\chi^2_1 = 0$, $p = 1.0$) and again suggesting no role for either residency or thermal asymmetries. Circling contests between winners were extremely protracted (mean of 1554 ± 516 s, maximum of 5610 s) and significantly longer than those between losers (loser mean of 150 ± 123 s, maximum of 518 s; t-test on log-transformed data: $t_{13} = 2.94$, $p = 0.011$).

4. DISCUSSION

Game-theoretic models of animal conflict (Maynard Smith & Parker 1976; Maynard Smith 1982; Leimar & Enquist 1984) have contributed much to our understanding of contest evolution in the wild (Riechert 1998). One such contribution, the notion of arbitrary contest resolution, has gained popularity in large measure due to corroborative empirical evidence in *P. aegeria* (Davies 1978). However, in keeping with the general controversy surrounding arbitrary contest settlement (Grafen 1987), this empirical example has been the subject of considerable debate (Austad *et al.* 1979; Hardy 1998; Stutt & Willmer 1998; Kemp & Wiklund 2001). In this study, we aspired to a definitive test of the uncorrelated asymmetry hypothesis in *P. aegeria* by using a similar experimental design to that of Davies (1978), but treating the subjects in a manner less likely to disturb their motivational states (see below for an expansion of this point). Our results show conclusively that residency is not used as an arbitrary or uncorrelated means of contest settlement in this species. Since we set up contests with clear resident–intruder asymmetries, the fact that relatively protracted contests ensued is in direct contradiction of the uncorrelated asymmetry hypothesis (Grafen 1987), let alone the fact that intruders almost always won. We also rule out the recently presented alternative that contests are settled due to resource-correlated asymmetries in thoracic temperature (Stutt & Willmer 1998). These results cast doubt on the uncorrelated asymmetry as a biological construct, and have important implications for our understanding of how 'weaponless' organisms such as butterflies resolve their disputes.

The theoretical notion that contests may be resolved arbitrarily is based upon the evolutionary stability of a so-called 'bourgeois' (resident wins) tactic in the context of Maynard Smith's (1982) classic hawk–dove model of animal conflict. However, mathematical models are only correct to the extent that their assumptions reflect real world facts. Key assumptions of the uncorrelated asymmetry hypothesis—that territories are short lived and that individuals are equally likely to find themselves in either resident or non-resident roles—are probably untenable in most biological situations (Grafen 1987). In many territorial insects, including *P. aegeria*, residents display considerable day-to-day fidelity to individual territories (see Wickman & Wiklund 1983; also Alcock (1993) for a review of insect site fidelity). There are also many cases in which residents consistently differ in some morphological or biophysical parameter, such as body size, energy reserves or age, which is then taken to represent fighting 'ability' (Marden & Waage 1990; Alcock & Bailey 1997; Kemp 2000). These factors mediate against the use of residency as an uncorrelated asymmetry. However, the frequent observation that contests are more likely to escalate when residency is confused (Waage 1988; Alcock & Bailey 1997; Kemp 2000) suggests that certain residency-related conventional effects do apply in insects (Kemp & Wiklund 2001). Based on the notion that better fighters will accumulate as residents (Maynard Smith 1982; Leimar & Enquist 1984), Alcock & Bailey (1997) suggested that roles may be used as a source of information regarding the likely fighting ability of contestants, thus leading to reduced persistence in non-resident individuals.

With respect to residency effects in *P. aegeria*, the stark difference between our findings and those presented previously (Davies 1978; Stutt & Willmer 1998) demands some explanation. We believe that previous experiments were conducted in a manner that disrupted the motivational states of the subjects. Davies (1978) captured residents and held them in a net during a new resident's 'grace' period before release. However, capture and detention in a net is traumatic, and territorial butterflies handled in this manner are unlikely to immediately return to defend their territory (Kemp & Zalucki 1999). Davies' intruders simply may not have been motivated to fight. Stutt & Willmer's (1998) key experiment involved placing butterflies in separate boxes and expecting contests to ensue when the lids were removed. Only 10 out of 72 such trials were deemed successful, thus the strike rate of this method was very low. Moreover, since male behaviour could not be observed immediately prior to the contest, it is not clear whether each male was motivated to perch and defend a territory. Our experiment differed in that both combatants had demonstrated their willingness to defend the sunspot (via the first contest) and contests were initiated by intruders flying to the territory, as they would in the wild. Both prior studies also report much shorter contests than usually occur in the wild and that we observed in all our experiments, which provides further evidence that the experimental subjects possessed reduced territorial motivation.

Although we cannot ultimately conclude how contests are settled in *P. aegeria*, our experiments suggest that two things may be important: (i) intrinsic aggression or fighting ability; and/or (ii) prior contest experience. The fact that the same male almost always won in two-stage trials, regardless of residency, is consistent with field observations (see Wickman & Wiklund 1983; Kemp 2000) and could indicate that some males are more aggressive, more motivated or simply better fighters. Further, since the duration of a war of attrition is a measure of loser persistence (Maynard Smith 1982), the difference between Madeirian and Swedish populations (table 2) suggests that intrinsic persistence levels exist and may have a heritable component (although the reasons for this difference are beyond the scope of this discussion). Both the extremely protracted contests between pairs of winners and the relationship between first and second contest duration in two-stage trials are consistent with intrinsically variable persistence levels, although they could equally reflect an effect of prior experience (e.g. Whitehouse 1997). The clearest evidence for an experience effect is provided by the relationship between grace period and contest duration in two-stage trials. This indicates the presence of a 'loser' effect that decays with time, which has been shown in other territorial insects and has an adaptive interpretation based upon avoidance of entering into contests with superior fighters (Alcock & Bailey 1997). Resource value effects on resident motivation (Krebs 1982; Johnsson & Forser 2002), which could give rise to a similar relationship between grace period and loser persistence, are conceptually unlikely in this taxon (see Kemp & Wiklund 2001).

The question of how territorial butterflies settle their disputes is theoretically interesting since it is not clear whether or how combatants may impose costs upon each other. The intimate relationship between residency and contest success in this taxon suggests that understanding the residency effect may be key to understanding the contests (Kemp & Wiklund 2001). In this study, we realize a step forward by ruling out two popular hypotheses for resident advantage in the model species, *P. aegeria* (Davies 1978; Hardy 1998; Stutt & Willmer 1998). Our results suggest instead that future experimentation should target the working hypothesis that intrinsically aggressive males accumulate as residents (Leimar & Enquist 1984) and win more often due to the self-reinforcing effects of prior experience (Whitehouse 1997).

The authors thank J. Alcock, N. B. Davies, K. Gotthard, O. Leimar, J. Merry and R. L. Rutowski for comments on the manuscript, P. Hammerstein for discussion, and D. Berger for assistance with the experiments.

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