

Escalated damselfly territorial contests are energetic wars of attrition

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Abstract. Thirteen pairs of neighbouring *Calopteryx maculata* (Odonata: Calopterygidae) males were manipulated such that members of each pair became residents in the same territory, thereby removing the normal resident–intruder asymmetry and permitting direct analysis of the physical and energetic factors affecting the outcomes of the prolonged, escalated contests that resulted. Energy reserves (fat remaining at the end of contests) were more often correlated with winning these contests than size or physical attributes related to flight ability. This pattern was also true for 11 natural contests in which persistent intruders displaced residents. Fat content varied with age, being lowest in immature (teneral) and older males, and highest in young males first appearing at the water. Our results indicate that escalated territorial contests in *C. maculata* favour males with the greatest energy reserves. High fat content in some males, especially young ones, may allow them to overcome the normal resident–intruder asymmetry and displace established territory residents. Since males rarely feed while at their territories and since territories are important for obtaining and protecting mates, energy reserves may be crucial to reproductive success and escalated fights may be especially costly.

Animals often compete directly for limited resources via physical struggles or ritualized display. Theoretically, these disputes should be settled by asymmetries between the contestants that reflect physical advantages or residency (Hammerstein & Parker 1982; Maynard Smith 1982; Leimar & Enquist 1984). Contestants in territorial disputes usually differ in both residency and physical attributes, making it difficult to determine which asymmetries are actually used to settle contests (Hammerstein & Parker 1982; Leimar & Enquist 1984; Waage 1988) or whether the residency asymmetry is ultimately based on underlying physical attributes like size, strength or energy. Energetic costs are known to influence the way animals defend territories and compete for mates (Davies & Houston 1984), and energy expended in territoriality and mating is often high compared to other activities (Stevens & Josephson 1977; Bucher et al. 1982; Taigen & Wells 1985). In addition, depletion of energy reserves over the mating season may constrain behaviour and reproductive success (MacNally 1981; Clutton-Brock et al. 1982). Thus, energy reserves may often be an important

asymmetry in animal contests. Although game theoretic ‘war of attrition’ models (Bishop & Cannings 1978; Parker & Rubenstein 1981; Maynard Smith 1982), wherein the winner is determined by relative persistence, recognize this possibility, wars of attrition based on energy constraints have not been reported (but see Parker & Thompson 1980). Here, we present evidence for a direct connection between energy reserves and ability to win prolonged territorial disputes that resulted when we removed the normal residency asymmetry or when intruders persisted in contests with residents.

Territorial male *Calopteryx maculata* damselflies normally expel intruders and neighbours with brief (<15 s) pursuit flights (Waage 1988). However, about 20% of encounters last much longer (up to an hour or more), and increase in intensity to involve rapid back-and-forth chasing and spiralling flight by both males. These escalated contests arise most commonly from confusion over residency, as for example when an interloper occupies a territory while a resident is temporarily absent. Occasionally, intruders persist in contests with residents, and may eventually expel them after an escalated contest (Waage 1988). Aside from mortality, the outcome of these escalated contests appears to be the primary mechanism for turnover in territory ownership.

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METHODS

In the summer of 1988, pairs of oviposition sites of uniform quality were established along a section of a small river (Palmer River, Bristol County, Massachusetts) using clumps of bur reed (*Sparganium* spp.), a plant commonly used for oviposition (Waage 1974, 1987). Initially, the sites for each pair were attached to stakes with fishing line and separated by about 3 m until each was occupied and defended by an individually marked male. Then, they were gradually drawn together so that two males' territories were fused, and each male behaved as if the newly merged oviposition site was his territory. Escalated contests always ensued (Waage 1988). We repeated this procedure for 13 pairs of males.

We also observed 11 contests during which intruders persisted and replaced residents in escalated contests over natural oviposition sites. Seven of these took place in 1988 on the Palmer River and four occurred in July 1989 on Brown's River (Chittenden County, Vermont). Contests were timed and were considered complete when one male left the area and began feeding away from the water. This male was declared the loser.

Winners and losers of each manipulated and natural contest were collected, dissected and compared for the following physical characteristics: two indices of size (lean dry thorax mass and wing area), wing loading (body mass/wing area), wing aspect ratio (wing length/wing area), and flight muscle ratio (flight muscle mass/body mass). These characters have previously been shown to affect the outcome of aerial contests in other species (Kodric-Brown & Brown 1978; Tsubaki & Ono 1987; Marden 1989). We also determined fat content by subtracting lean dry body mass (following fat extraction for 4 h with refluxing chloroform in a Soxhlet apparatus; Marden 1989) from dry body mass. Fatty acids are known energy sources for odonates (Kallapur & George 1973). We also measured fat content for 92 males from various age categories. Age categories were based on a combination of marking records, wing wear and appearance. Immature males were newly emerged or up to 10 days old and not yet at the water, young males had just begun to be territorial or had been resident for less than 5 days; middle-aged males had been territorial for approximately 5–10 days; and old males had been territorial for more than 10 days.

RESULTS

Contests comprised 2–43 bouts of intense spiraling flight, interspersed with brief periods when both males perched on or near the territory. Individual bouts ranged in duration from 1 to 1480 s ($\bar{X} \pm \text{SE} = 130 \pm 16.3$ s, $N = 151$); total contest duration ranged from 180 to 3133 s ($\bar{X} \pm \text{SE} = 1313 \pm 266$ s, $N = 19$). Since contestants flew very close to each other (frequently touching wings) and appeared to mirror precisely each other's flight pattern, their rates of energy expenditure were probably similar.

Winners and losers of the 13 experimental and 11 unmanipulated contests did not differ significantly in physical characteristics related to size or flying ability: lean dry thorax mass (mean difference, $\bar{X} \pm \text{SE} = -0.029 \pm 0.19$ mg, $P > 0.88$), wing area (0.040 ± 0.14 cm², $P > 0.78$), wing loading (0.006 ± 0.01 newtons/m², $P > 0.51$), aspect ratio (0.0046 ± 0.04 , $P > 0.91$), or flight muscle ratio (0.0001 ± 0.002 , $P > 0.97$). Each comparison is for 24 contests, and is a two-tailed *t*-test of the mean difference between winners and losers versus an expected mean difference of 0 and corrected for repeated comparisons of the same individuals (Rice 1989).

Winners and losers did, however, clearly differ in energy reserves remaining at the end of contests ($\bar{X} \pm \text{SE} = 0.71 \pm 0.17$ mg, $P < 0.01$, as above). Winners had greater fat content in 21 of 24 contests, with one tie (Fig. 1). The difference pattern for thorax mass, also shown in Fig. 1, was typical for the other variables that we compared. Fat content was relatively low among all contestants (0.4–5.0% of body mass), compared to mature males of other odonate species, which typically have at least 5% body fat (Marden 1989, unpublished data). Together, these observations suggest that *C. maculata* males are severely constrained by energy reserves and that losers may quit contests when their fat reserves fall to some threshold level.

The 11 natural contests between residents and persistent intruders (Fig. 1, contests 14–24) are of particular interest because the intruders overcame the residency asymmetry and displaced the territory owner after an escalated fight. In four of the contests, the intruder had an unusually high fat content (more than 3 mg).

Fat content of males varied significantly with age class ($F = 11.6$, $P < 0.001$), although there was considerable overlap among age classes (Fig. 2). Immature males had significantly lower levels of

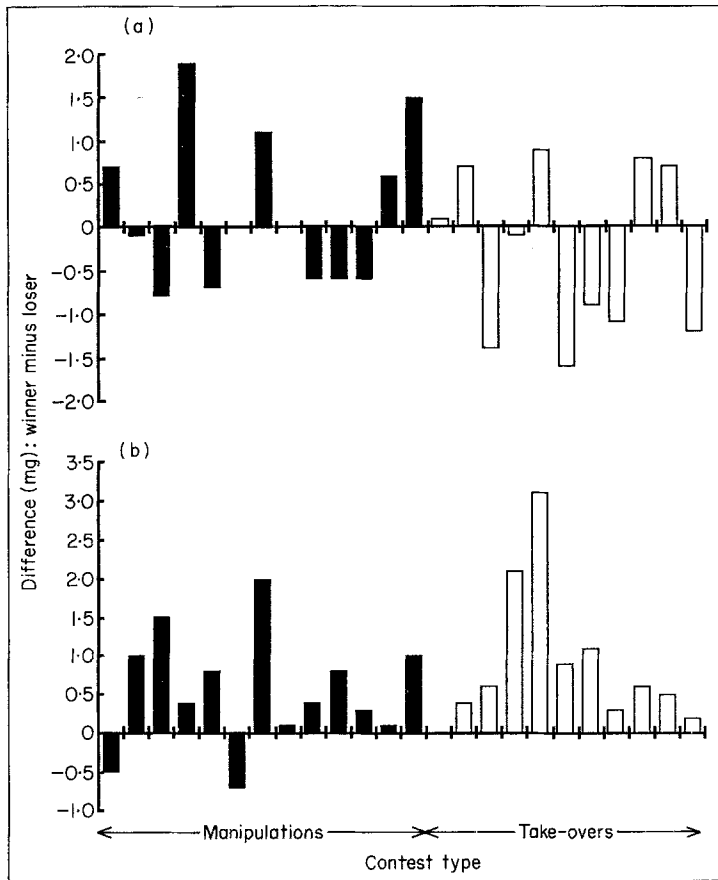


Figure 1. Differences (mg) in lean dry thorax mass (a) and fat content (b) between winners and losers of 24 escalated territorial contests. The pattern of differences for lean dry thorax mass was typical for all of the other variables measured except fat content. Contests 1–13 (■) were manipulations that placed two males in the same territory, and 14–24 (□) were natural contests in which intruders persisted and displaced residents. The fat contents (mg) of the 24 winners, from left to right, were: 0.5, 1.3, 2.4, 1.3, 2.4, 1.2, 3.0, 1.7, 2.2, 2.0, 1.9, 1.2, 1.4, 1.3, 2.1, 2.0, 3.6, 3.8, 3.1, 1.4, 2.2, 3.9, 2.4 and 2.9. Fat content of losers can be calculated by subtracting the fat differential (height of bars) from the winner's fat content.

fat than young (Scheffe $F=10.23$, $P<0.05$) and middle-aged territorial males (Scheffe $F=5.13$, $P<0.05$). Young territorial males had significantly higher fat levels than did old territorial males (Scheffe $F=5.01$, $P<0.05$).

DISCUSSION

Because the outcomes of escalated contests described in this paper appear to be determined by persistence dependent on energy reserves, we have classified them as energetic wars of attrition. To our

knowledge, this is the first direct demonstration that differences in energy reserves are an important asymmetry between animals engaging in wars of attrition. Parker & Thompson (1980) made a detailed examination of a possible energetic war of attrition for dungflies, but their study did not directly involve estimating energetics.

A number of game theory models have examined evolutionarily stable strategies for animals involved in wars of attrition; however, these models were based on assumptions that do not apply to *C. maculata*. For example, when *C. maculata* males enter contests their persistence time is constrained

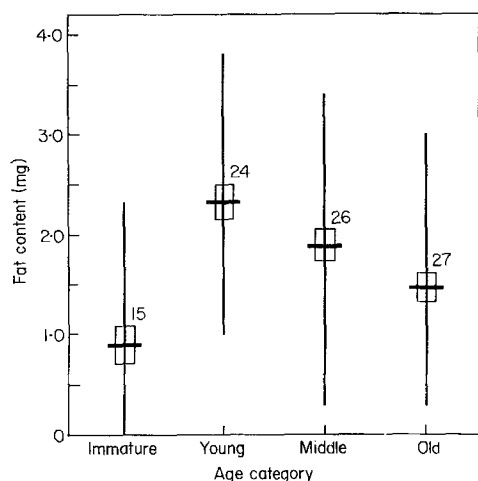


Figure 2. Fat content (mg) of males versus age category. Data are presented as range, \pm SE (box), mean (horizontal line), and sample size. See text for definitions of age categories.

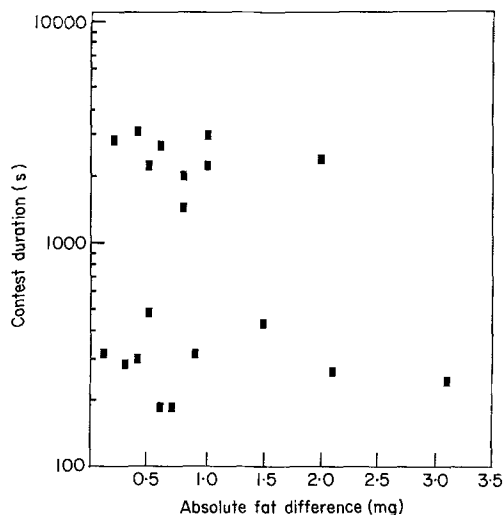


Figure 3. Total contest duration (s on log scale) versus the absolute difference in fat content (mg) between contestants. Time perching between bouts has been omitted. Data are from 19 of the contests in Fig. 1; five other contests were not timed.

by current energy reserves rather than being freely variable. Bishop & Cannings' (1978) model incorporated an upper limit to persistence time, but this was assumed to be the same for both contestants. Because of these differences, and our lack of specific knowledge regarding fitness costs and gains for winners and losers, we cannot quantitatively test our results against predictions of existing game theory models.

One question of general interest in game theory war of attrition models is the ability of contestants to assess each other's persistence potential before or during contests (Parker & Rubenstein 1981; Enquist & Leimar 1983; Leimar & Enquist 1984). In the case of contests between *C. maculata* males, assessment ability might be indicated by a negative relationship between the difference in fat content between contestants and the duration of contests, since males facing opponents with much greater fat reserves should quit as soon as they perceive their disadvantage. Our data show no such trend, as there was no significant correlation between final fat differential and contest duration ($r = -0.108$, $P > 0.65$; Fig. 3). The apparent absence of assessment ability for this species is intriguing given (1) the considerable energetic costs to both winners and losers of prolonged contests (see below), (2) the fact that males rarely feed while on their territories, and (3) the fact that displaced residents are unlikely

to obtain new territories (Waage, unpublished data). Perhaps some degree of assessment does occur, but the costs of losing are high enough to push contests to physical limits (Grafen 1987).

There are several direct and indirect costs of escalated contests in this species. First, the speed, acceleration and complexity of manoeuvres used during escalated contests far exceed what is apparent during feeding, mating, or other activities. These characteristics of flight must make rates of energy expenditure during escalated contests very high. Second, prolonged contests result in lost mating opportunities and the probability of a third male becoming resident on the territory (and thereby requiring another escalated contest to evict him; Waage 1988). Finally, prolonged escalations leave the winner with lowered fat reserves and thus vulnerable to future contests.

This raises the question of whether there are fighting tactics that would minimize contest duration or energetic cost for one of the opponents. One such tactic would be for one contestant to slow its display (i.e. reduce speed and complexity of flight) so as to reduce its rate of energy expenditure. We frequently noticed instances when one contestant would momentarily fly in a slower or straighter path, while the other flew in tight spirals around him. Such instances were brief, as the faster male would quickly slow his flight, and the pace would

then increase as the usual 'follow-the-leader' or precise 'mirroring' flight pattern was resumed.

In *C. maculata*, a resident-intruder asymmetry results in most contests being settled in a few seconds (Waage 1988). Our results suggest that the asymmetry exists because residents have highly variable energy reserves (Figs 1 and 2), and because each contestant may not be able to gauge quickly the other's energetic status. These conditions would generally discourage intruders from persisting, since they face potentially high costs and no certainty of success. Occasional persistent intruders may be recently matured males or others with maximal fat reserves and therefore a good chance of winning.

Previous studies indicate that the ability of *C. maculata* males to win contests, hold territories and acquire mates does decline with age (Forsyth & Montgomerie 1987; Waage, unpublished data), and that old males often adopt an alternative mating strategy where they do not defend territories but attempt to mate with females on other male's territories. Forsyth & Montgomerie (1987) hypothesized that this change in territorial success and behaviour may be due to the high cost of territorial defence and declining energy reserves of older males. Our results support their hypothesis, but raise the question of why displaced males cannot rebuild energy (fat) reserves.

The correlation between fat content and age (Fig. 2) raises an important question concerning our conclusion that energy reserves affect the outcome of territorial contests. Is it possible that the winners of our staged contests were simply younger males, and that the greater energy reserves of winners were a spurious correlation due to age-related differences in fat content? We cannot completely eliminate this possibility, since our age estimates are not precise enough to allow an exact determination of the age of most contestants. However, we note that there is considerable variation in fat reserves within age classes which, despite the significant trend toward decreasing fat reserves with age (Fig. 2), should make relative age an inconsistent predictor of energy reserves.

This can be illustrated by using the data in Fig. 2 to see how well age class predicts an advantage in energy reserves. We randomly paired all of the males between each age class and compared their fat contents. This procedure was repeated 10 times and the results are presented as the mean proportion of times (\pm SE) that the younger male in

each pairing had a greater fat content. For young versus middle-age pairings, young males had more fat $59 \pm 1.2\%$ of the time (range = 54–67%). For middle versus old age pairings, the proportion was $67 \pm 1.6\%$ (range = 58–73%) and, for young versus old age pairings, it was $74 \pm 2.4\%$ (range = 63–87.5%). Therefore the ability of relative age to predict relative energy reserve (average 59–74% correct) was less than the observed ability (Fig. 1) of relative energy reserve to predict the winners of 21 of the 24 contests (87.5%).

Finally we note that take-overs are rare relative to escalated contests due to confusion over residency, which our staged contests mimicked (Waage 1988). Thus, most escalations in nature may not be between the youngest and oldest males in the population. For example, our staged contests were between established territorial males who were predominantly middle-aged or old males and only four of the natural take-overs involved displacement of middle-aged and old males by young males. We conclude that it is unlikely that age differences alone determined the outcome of the escalated contests we reported. We suggest that any correlation between age and the likelihood of winning would most likely reflect a decrease in fat reserves with age among territorial males because of decreased feeding time and the energetic costs of territory defence.

Detailed studies of damselfly and dragonfly lifetime mating and reproductive success (Fincke 1982, 1988; Banks & Thompson 1985; Koenig & Albano 1987; McVey 1988) suggest that length of reproductive life is a major determinant of success. Since possession of a territory enhances reproductive success in *C. maculata* (Waage 1974, 1979), involvement in escalated contests that decrease energy reserves and thus territory tenure may prove to be an important source of variance in male reproductive success in this species.

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