

Assessment of energy reserves by damselflies engaged in aerial contests for mating territories

JAMES H. MARDEN & ROBERT A. ROLLINS

Department of Biology, 208 Mueller Labs, Pennsylvania State University, University Park, PA 16802, U.S.A.

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Abstract. Male *Calopteryx maculata* (Odonata) damselflies engage in prolonged, highly escalated aerial contests for mating territories. A previous study (Marden & Waage 1990, *Anim. Behav.*, **39**, 954–959) found that winners of contests had a higher fat content than losers in 88% of cases, whereas differences in physical variables related to size and flight ability were not related to the outcome of contests. Here that study is extended in order to determine whether contests proceed until one contestant reaches a lower physical limit in fat reserve, or alternatively, whether contestants are able to assess each other's fat reserves and thereby settle contests before physical limits are reached. The physical limitation hypothesis was not supported, as losers showed no reduction in variability of fat content relative to winners. The assessment hypothesis was supported by an increase in the accuracy of the 'fatter wins' rule with increasing contest duration. Winners were fatter in 17 of 25 (68%) short contests (duration <500 s), versus 20 of 21 (95%) long contests (>500 s), which suggests a gradual accumulation of information during contests. The assessment hypothesis was supported further by a negative relationship between contest duration and energetic asymmetry between contestants in long contests. Duration of long contests was also positively related to the total fat content of the two contestants, which suggests that the ability of contestants to perceive relative energetic status may vary depending on absolute levels of energy reserves. A model that assumes an asymptotic increase in flight performance with increasing fat content (i.e. Michaelis–Menten or 'saturation' kinetics) is proposed to explain the simultaneous effects of relative and absolute fat content on contest duration, and to examine possible mechanisms that damselflies use to assess each other's energy reserves.

Animals often compete directly for limited resources via physical struggles or ritualized display. Behaviour of animals involved in contests has been analysed extensively, both theoretically (e.g. Parker 1974; Maynard Smith 1982) and empirically (recent examples include Dick & Elwood 1990; Beaugrand et al. 1991; Gribben & Thompson 1991). A common theme of this body of work is that there should be strong selective advantage for contestants that make accurate assessments of the capacity of their opponent and the value of the resource at stake. In the absence of accurate assessments, individuals are destined to spend time and energy, and risk injury, fighting superior opponents for resources that may be of low quality. With these considerations in mind, investigators have documented an impressive array of assessment capabilities in various organisms, some of which possess relatively rudimentary sensory and integrative physiology.

Contestants assess their opponents in terms of mass (Reichert 1984), size (Sigurjonsdottir & Parker 1981; Thornhill 1984; Beaugrand & Zayan 1985; Verrell 1986), residency status (Davies 1978; Waage 1988) and vocalization quality (apparently an indirect cue for size; Davies & Halliday 1978; Clutton-Brock & Albon 1979).

One characteristic that has not been widely examined in terms of its role in contests is energy. Energetic costs 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). Although persistence ability may often be constrained by energy reserves, and persistence ability is a key component of certain animal struggles ('wars of attrition'; Bishop & Cannings 1978; Parker & Rubenstein 1981; Maynard Smith 1982),

the degree to which energy reserves constrain competitive behaviour is not well known (but see Parker & Thompson 1980; Marden & Waage 1990). The ability of animals to assess each other's energy reserves has not been rigorously addressed.

Here we present an extension of a previous study that began to examine the role of energy, and assessment of energetic asymmetries, in contests involving *Calopteryx maculata* damselflies (Marden & Waage 1990). Disputes between territorial *C. maculata* males sometimes become highly escalated contests of vigorous and energetic flight manoeuvres. Escalation arises because of confusion over residency, as occurs when an interloper occupies a territory while the resident is temporarily absent, or when intruders persist in contests with residents (Waage 1988). These escalated contests can last for long periods (up to an hour of total flight time) and probably involve considerable energetic expense for the participants.

In an analysis of physical characteristics of winners and losers of escalated contests, the winner had a higher post-contest fat content in 88% of cases (Marden & Waage 1990). Fat content of losers averaged only 2.0% of total fresh mass. These results, together with the duration and apparent expense of contests, led to the conclusion that these encounters are energetic wars of attrition.

One curious aspect of these contests is their tremendous variability in duration. Some last less than 1 min, whereas others proceed for up to 1 h. Assuming that the energy and time costs are very high, males should persist in contests only long enough to determine who will eventually win if both contestants continue to persist. However, because fat content is an internal physiological characteristic that may not be assessable by others, or perhaps even by self, there may be no way of settling contests without proceeding until one male has reached the limit of his mobilizable fat reserve. Thus, there are two competing hypotheses for how these contests might be settled: 'assessment' versus 'physical limitation'. Marden & Waage (1990) began to explore these hypotheses by examining the relationship between fat asymmetry and contest duration; they found no evidence for the inverse relationship predicted by the assessment hypothesis (i.e. shorter contests when fat asymmetry is greater). Thus, they concluded that losers quit contests when their energy

reserves fall to some threshold level, however this conclusion was arrived at by default, since no test of the physical limitation hypothesis was performed. The present study extends the data set for physical characteristics of winners and losers of escalated contests, and makes a detailed examination of the competing 'physical limit' versus 'assessment' hypotheses.

METHODS

Territorial contests between *C. maculata* males were observed over a period of 2 months during the summer of 1991 on the Chenango, Sangerfield, and Unadilla Rivers in Madison Co., New York.

Contests between neighbouring *C. maculata* males were staged by gradually merging the clumps of floating vegetation that constituted their territories (see Waage 1974 for a detailed description of territorial and mating behaviour of *C. maculata*; Waage (1988) and Marden & Waage (1990) give detailed descriptions of the method for merging territories). Merging of neighbouring territories causes both males to act as residents of the same territory, thereby removing the normal resident-intruder asymmetry and permitting direct analysis of the physical and energetic factors affecting the outcome of escalated contests. The escalated contests that ensued consisted of sequences of bouts of intense spiralling flight, interspersed with brief periods when both males perched on or near the territory (Marden & Waage 1990). Time spent flying was recorded separately from time spent perching, and we used total flight time (summed across bouts) as a characterization of contest duration. Contests 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 27 contests were collected, dissected and compared for the following physical characteristics: two indices of size (lean dry mass and wing area), wing loading (traditionally measured as body mass/wing area; here we used residuals from a regression of wing area on fresh mass in order to achieve a size-independent measure of wing area relative to total load), wing aspect ratio (wing length/wing area) and flight muscle ratio (traditionally measured as flight muscle mass/body mass; here we used residuals from a regression of lean dry thorax mass on fresh

body mass as a fat- and size-independent measure of flight muscle content relative to total load). Characteristics such as these have previously been shown to affect the outcome of aerial contests in other flying animals (Kodric-Brown & Brown 1978; Tsubaki & Ono 1987; Marden 1989; Marden & Chai 1991).

Bilateral symmetry of the wings of each individual was estimated from the absolute difference in wing chord (i.e. maximum width) of the right versus left hind wing. Wing chord was used instead of wing length or area because small differences in how close to the body the wings were cut during dissection would have a large impact on estimates of bilateral symmetry. Thornhill (1992) found that bilateral symmetry in wing size affected the outcome of terrestrial contests in scorpionflies.

Post-contest fat content (fat is the primary energy source for flight in odonates: Kallapur & George 1973) was measured 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. Standardized residuals from a regression of fat content on lean dry body mass were used as an index of energetic status. This index corrects for differences in absolute fat content between males that varied widely in body mass (range=58–95 mg), and should be the best estimator of persistence ability, that is, the amount of fuel available versus the energetic cost of flight (which is determined primarily by mass). All analyses of fat content presented below use these standardized residuals.

Age of contestants was broadly categorized as young, middle, or old, based on marking records and/or wing wear. We further categorized contestants as younger, older, or of no discernible age difference from their opponent.

Note that our method for measuring fat content is destructive and can be performed only after contests are completed. Thus, we are restricted in the types of hypotheses we can test and the inferences we can draw. The relationship between pre-contest fat reserves and contest duration would be of particular interest; however, there is presently no method for non-destructive measurement of fat in animals as small as damselflies.

RESULTS

As in Marden & Waage's (1990) analysis of contests in Rhode Island, contest winners in New

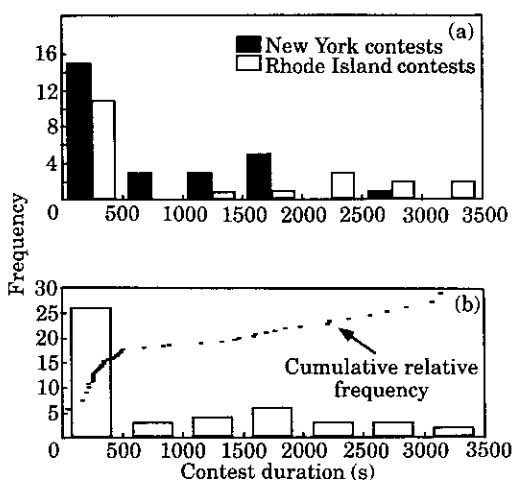


Figure 1. (a) Distribution of contest duration in our New York study and a previous study in Rhode Island (Marden & Waage 1990). (b) The distribution for data pooled from both studies, together with a superimposed plot of cumulative relative frequencies for these data. Note the inflection in the normal probability plot at about 500 s that we used to categorize contests as either long (>500 s) or short (<500 s).

York were significantly fatter than losers (mean difference (\pm SD)=0.760 \pm 0.14, $P=0.001$; two-tailed t -test for mean difference of fat content between winners and losers), with the fatter male winning 22 of the 27 contests. Differences in size, characters associated with aerodynamics and/or flight performance, and bilateral symmetry were not significantly different between winners and losers. These comparisons used two-tailed tests for mean difference of each variable between winners and losers, using the sequential Bonferroni technique (Rice 1989) to maintain type I error at the 0.05 level for multiple comparisons. The comparison of fat content described above is significant at this error level. Thus, contests were decided similarly in New York and Rhode Island; the fatter male usually won (41 of 51 contests for the two studies combined), and differences in other physical attributes were apparently not important.

Contest duration was non-normally distributed ($P<0.002$ for both sites), with similar range and central tendency for the New York and Rhode Island studies. In New York, the median contest duration was 480 s of flight time (range=2530 s), compared with a median of 461 s (range=2953 s) in Rhode Island (Fig. 1; Mann-Whitney U -test, $P>0.05$). When data for contest duration were

pooled for the two sites (Fig. 1), the resulting distribution showed a bimodal shape with a distinct inflection point in cumulative relative frequencies at approximately 500 s. We used this inflection point to categorize contests as either short or long, in order to determine whether characteristics of contests varied with contest duration.

The assessment hypothesis predicts an increasing probability of accurate assessment as contest duration increases (assuming that accumulation of information is gradual rather than immediate). To examine this hypothesis, we pooled data from New York and Rhode Island, and tested the 'fatter wins' rule as a function of contest duration. In short contests, the fatter male won 17 out of 25 times, compared with 20 out of 21 times in long contests ($G=6.09$, $P<0.02$; total $N<51$ here because duration was not measured for five contests). Thus, the certainty of the 'fatter wins' rule increased significantly with contest duration. The fatter male won 68% of the time in short contests versus 95% of the time in long contests. The single case in which a male with lower relative fat content won a long contest was unusual in that this winner had one of the five lowest fat contents of all the 102 contestants we measured (equivalent to 0.7% body fat), which may indicate a measurement error.

There was no apparent effect of size difference on contest duration. Size difference (difference in lean dry mass) had no significant effect on contest duration in either long or short contests ($P=0.24$ and $P=0.54$, respectively, for regression of duration on size difference), and the mean absolute value of size difference between males that engaged in long contests was not different from that of males that engaged in short contests ($P=0.64$). Thus, there is no evidence that males that were closer in size were more likely to have longer contests.

The assessment hypothesis predicts a negative relationship between contest duration and the degree of energetic asymmetry between contestants, such that more evenly matched contestants should take longer to determine their relative status and thereby conclude their dispute. To examine this hypothesis, we compared differences in fat with contest duration. For all contests considered together, the predicted negative trend did not occur ($r^2=0.01$, $P=0.45$). However, the result was very different when short and long

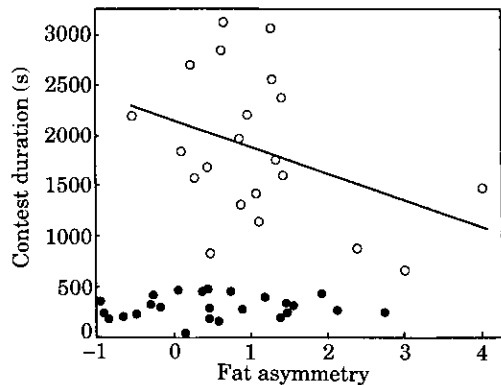


Figure 2. Contest duration as a function of the difference in fat between contestants (winner - loser; units are standard deviations). ●: Short contests (<500 s); ○: long contests (>500 s). Only in long contests was there a significant relationship between duration and fat asymmetry.

contests were considered separately. For short contests, there was no relationship between fat asymmetry and contest duration ($r^2=0.005$, $P=0.73$; Fig. 2), whereas in long contests, there was a significant negative trend ($r^2=0.14$, one-tailed $P=0.045$; Fig. 2). A multivariate model that included total fat content (estimated as the sum of fat content for both contestants) as a second independent variable doubled the explanatory power ($r^2=0.31$, $P=0.035$). In this two-factor model, total fat had a significant positive effect (two-tailed $P=0.05$), and fat asymmetry had a significant negative effect (one-tailed $P=0.008$).

We tested the effect of age on contest duration to determine whether perhaps young, less experienced males are more likely to engage in longer contests. Losers determine contest duration, so it is the association between loser age and duration that is of interest. There was no significant association between loser age and duration category ($G=4.32$, $P=0.12$), however the trend was for younger males to engage more frequently in long contests, whereas old males tended to have predominantly short contests.

It is possible that the relative age of the two contestants is a more important factor than absolute age. Although there was no effect of relative age on probability of engaging in a short or long contest ($G=3.14$, $P=0.21$), there was an interesting effect of age difference on the 'fatter wins' rule. In eight contests where the winner was older, the

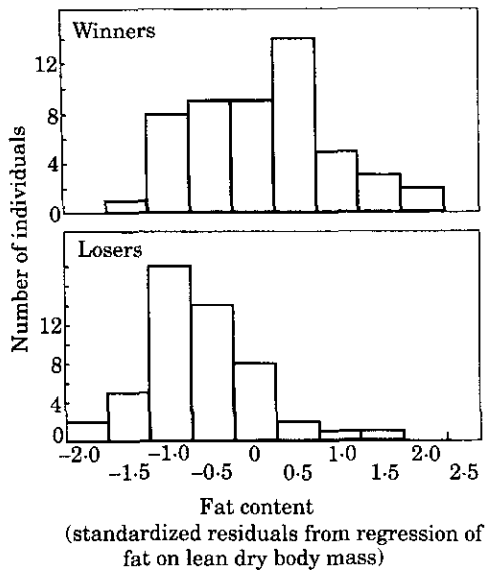


Figure 3. Pooled data set (New York and Rhode Island studies) for the distribution of fat content in winners and losers of escalated territorial contests. Variability is similar within the two distributions, which indicates that losers did not proceed until they reached a common lower limit of fat.

winner was fatter only four times. In the remaining 30 contests where the winner was younger or of no discernible age difference, the fatter male won 28 times ($G=7.4$, $P=0.01$; total $N<51$ because age estimates were not made for some contests). This result indicates that males with more experience are much more likely to overcome the usual convention of 'fatter wins' and to prevail in a contest against a male with greater energy reserves.

The strongest test of the physical limit hypothesis involves variation in fat content. If contests proceed until one male reaches a lower limit of energy reserves, then losers should have less variable fat content (relative to their lower mean) than winners. We compared the relative variation (Lewontin 1966) of fat in winners versus losers in all contests (Fig. 3), and also in long contests only. In neither case was there a significant difference in variability among winners and losers (data pooled for Rhode Island and New York; $F=1.11$, 1.41 , $P>0.15$). We also found no significant difference in variability of fat in losers of short versus long contests ($F=1.62$, $P>0.15$). In each of these cases, the non-significant trends in variability run

counter to the hypothesis. That is, relative variability was greater for losers than for winners (and for losers of long contests versus losers of short contests), whereas the physical limitation hypothesis predicts the opposite trend. Using absolute fat content (mg) instead of standardized residuals in these comparisons yields the same result ($P>0.15$ in all cases). Thus, there was no indication that contests were decided by one contestant reaching a lower limit in energy reserves.

DISCUSSION

Our results refute the hypothesis that *C. maculata* males persist in escalated territorial contests until one male reaches a lower limit of energy reserves. The critical result that falsifies the physical limitation hypothesis is the absence of a decrease in variability of post-contest fat content among losers, as there must be if losers persist until they reach a common lower limit of fat reserve.

The alternate hypothesis, that contestants assess each other's energy status, is supported by the observation that the likelihood of 'fatter wins' increases with contest duration, as would be expected if information accumulates gradually over the course of a contest. Furthermore, there was a significant negative relationship between fat asymmetry and contest duration in long contests, which was strengthened by inclusion of total fat content as a second independent variable. A mechanistic model presented below provides an explanation for how total fat content and the asymmetry in fat between contestants combine to determine the ability of contestants to make an assessment of each other's energetic status.

Accurate resolution of contests based on an assessment mechanism requires that contesting *C. maculata* males perceive their relative energy status. The most likely way for relative fat content to be perceived by damselflies is via changes in flight performance over the course of a contest. That is, some characteristic of performance must depend on the rate of delivery of fuel, and the rate of delivery must decrease as fuel reserve decreases (i.e. unlike an automobile that will run at full speed up to the point of complete fuel depletion).

Escalated contests involve a series of bouts that consist of two basic elements, an initial 'face-off', wherein opponents hover briefly (typically about 3–5 s) in front of each other using rapid wing

beats, followed by a prolonged chase (typically 30–300 s, ranging up to 1480 s) that covers hundreds of cubic metres of airspace and involves a complex series of ascents, descents, spiral turns, and rapid changes in direction. For the sake of illustration, assume that some aspect of maximum flight performance or wingbeat frequency depends on fuel reserve, and that subtle differences can be perceived by self and opponent during aerial contests. Because contestants closely mirror each other's behaviour throughout a contest, their rates of energy expenditure should be nearly equal, and they could potentially monitor and compare their own rate of decline of performance versus that of their opponent. In that case, any non-linear relationship between maximum performance and fat reserve could convey information about fat reserve based upon the rate of decay of performance.

The relationship between concentration of a substrate like fat, and whole animal performance that arises from a series of enzyme–substrate interactions, is likely to approximate Michaelis–Menten kinetics (Atkinson 1977), where high levels of substrate (i.e. fat) 'saturate' performance, with a curvilinear decline in performance at lower levels of fat (Fig. 4). Note that an instantaneous assessment based on an opponent's absolute level of performance would probably not be an accurate indicator of fat content, since performance is likely to vary from day to day with fluctuations in temperature and sunlight (*C. maculata* is an ectotherm), or, in the case of wingbeat frequency, there is likely to be size-related variation among individuals that is unrelated to fat content. Only by persisting in a contest and comparing their rate of degradation of performance could two males accurately assess their relative status. The fact that *C. maculata* males achieve 95% accuracy in their assessments when they persist for at least 500 s is a stunning result, and testimony to the precision of their perceptual capacities.

An interesting feature of this mechanistic model (Fig. 4) is that the ease of perceiving an asymmetry in fat content is not the same at all levels of absolute fat content. For a Michaelis–Menten type of relationship between fat content and performance, two individuals with high fat would need to expend more energy (i.e. a longer contest) to generate a given change in performance than would two low-fat individuals that started with a similar, or even lower level of asymmetry (Fig. 4).

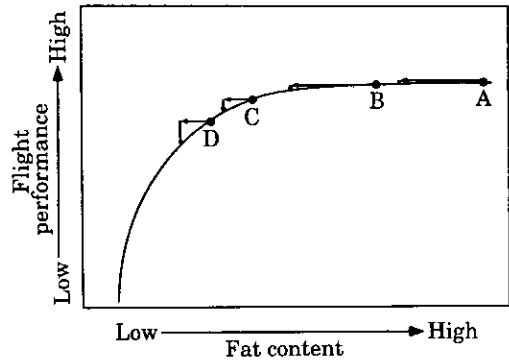


Figure 4. Hypothetical relationship between flight performance and fat content. The convex curve is based on the assumption of Michaelis–Menten type rate kinetics, where high substrate concentration (i.e. fat) saturates processes of fat transport and consumption, with lower levels of fat becoming increasingly limiting. Given this relationship, consider two individuals that have a fairly large difference in fat content, yet each with sufficient fat to place them on the flat portion of the curve (individuals A and B). Flight performance of A and B will degrade slowly over the course of a contest (vertical arrows), and a long contest and large consumption of fat reserves (horizontal arrows) will be required before these individuals can perceive a difference in the rate of degradation of their performances. In contrast, contestants C and D have a lower fat content, and a smaller asymmetry in fat than A and B. However, because D is starting on the steep portion of the curve, his performance will decline more quickly than C's, and therefore these two individuals could perceive their asymmetry more quickly than could A and B, despite the larger asymmetry between A and B. Thus, both the energetic asymmetry between contestants, and their absolute levels of energy reserve should affect the ability of contesting males to assess their relative status and thereby conclude their dispute.

This is because the slope of the fat content–performance relationship is not equal across the distribution of fat content; where the slope is greater, differences between contestants would be perceived more quickly. Long contests may often arise between two males that have a large asymmetry in fat content, but because they both have a high enough fat content to place their performance on the flat portion of the curve, they require a long contest before they can perceive their asymmetry. Our observation that duration of long contests was positively affected by total fat content, and negatively affected of fat asymmetry, supports this model.

Short contests (<500 s) were decided in a strikingly different fashion than were long contests. Winners of short contests were usually fatter, but the certainty of the 'fatter wins' rule was much lower in short than in long contests (68 versus 95%). In addition, the duration of short contests was not influenced by either total fat content or fat asymmetry. Thus it appears that *C. maculata* damselflies have two different behavioural regimes during escalated territorial contests, and it would be interesting to determine what factors influence these two modes of behaviour. A prediction that arises from game theory is that contestants should base their level of effort on the perceived value of the resource at stake. Value of a territory for a *C. maculata* male should primarily be a function of how attractive the territory is to females, which leads to the prediction that willingness to engage in a prolonged contest should increase for males whose territories have been visited by females. J. K. Waage (unpublished data) tested this hypothesis and found that the degree of escalation of contests (including their duration) increased when males had prior contact with females at their territory. This observation supports the game theory prediction of resource value as an important factor affecting contest behaviour, and supplies a likely explanation for the differences we observed in behaviour during short versus long contests.

Older males often overcome the usual 'fatter wins' rule. Thus, it appears that older males may be capable of communicating false information about their fat content, somehow interfering with their opponent's ability to make an accurate assessment, or have such a low probability of obtaining another territory that they communicate a willingness to persist to absolute physical limits and thereby discourage younger males (i.e. the 'desperado effect'; Grafen 1987). One set of behaviour patterns that might constitute interference with assessment is the tendency of resident males to fly along the shoreline, away from the centre of their territory whenever they are challenged by other males. Flying away from the territory causes neighbouring territorial males to become involved intermittently in the dispute, such that the challenger encounters a variety of opponents during each bout of a contest. Encountering a series of different opponents may prevent an accurate assessment from being formed, and older males may be

more adept at engaging a challenger with neighbours, or they may be more familiar with their neighbours and less likely to be confused by the involvement of neighbours in contests.

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