

## Dung Fly Struggles: A Test of the War of Attrition

G.A. Parker\* and E.A. Thompson  
 King's College, Cambridge, England

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**Summary.** 1. In Maynard Smith's 'war of attrition' model of animal conflict, two identical opponents fight over a unitary resource and the winner is the individual that is prepared to go on longer. The evolutionarily stable strategy (ESS) is for individuals to vary in their selection of 'bids' (fighting durations) so that the probability density of bids follows a negative exponential distribution. In nature, the distribution of selected bids cannot be observed directly, because contests are terminated by the opponent with the lower bid. We therefore derive an expected distribution of contest persistence times.

2. Struggles between male dung flies (*Scatophaga stercoraria*) for possession of a female can be evaluated in terms of Darwinian fitness as expected number of eggs fertilised/time. Fitness calculations must account for the energetic costs of struggling relative to searching for an alternative female; a plausible range of relative energetic costs is deduced. Though there is a superficial concordance of observed struggle persistence times with that predicted from a war of attrition with linear costs, this breaks down when the data are analysed in component categories. Further, dung fly struggles are clearly asymmetric contests. We suggest that struggles are settled by a form of assessment strategy involving acquisition of information during the contest about the relative resource holding powers of the two contestants.

### Introduction

Maynard Smith's development of the 'evolutionary stable strategy' (ESS) concept (e.g. Maynard Smith and Price 1973; Maynard Smith 1974) is probably the most important recent development for sociobiol-

ogy. A strategy is an ESS if, when fixed in a population, it cannot be invaded by any alternative mutant strategy. ESSs can be pure or mixed. Following the terminology of game theory, an ESS for a given set of circumstances is said to be 'pure' if all individuals play the same unique strategy. It is 'mixed' if a set of strategies coexists with probabilities prescribed by the ESS.

The 'war of attrition' type of animal contest (Maynard Smith and Price 1973; Maynard Smith 1974) gives a mixed ESS solution. In this game, two animals engage in combat for a resource that would increment the Darwinian fitness of either opponent by  $V$  fitness units. Combat is by display or struggling, which continues until one animal gives up. The one that is prepared to persevere longest wins the resource. The cost of the contest to both opponents is equal and fixed by the individual that gives up first. Contest costs are linear and described by variable  $x$ , and the ESS is to select, before a contest, a value  $x$  specified by the probability distribution

$$p(x) = \frac{1}{V} \exp(-x/V) \quad (1)$$

(see Maynard Smith 1974). It makes no difference whether a given individual always plays the same strategy [and frequencies of individuals follow  $p(x)$ ], or whether each individual plays strategies with the probability density  $p(x)$ , though the first solution creates major genetic problems with sexually reproducing diploidy (Maynard Smith and Parker 1976).

The war of attrition has been examined analytically in detail in general form by Bishop and Cannings (1978). Norman et al. (1977) noted that with a general cost function in which the costs  $c(x)$  are positive, differentiable, and increasing [ $c'(x) > 0$ ] and satisfy

$$c(0) = 0 \quad \text{and} \quad \lim_{x \rightarrow \infty} c(x) = \infty$$

then the ESS corresponding to (1) is

\* Present address: Department of Zoology, University of Liverpool, Liverpool L69 3BX, England

$$p(x) = \frac{1}{V} c'(x) \exp[-c(x)/V] \quad (2)$$

which reduces to (1) when  $c(x) = x$  (i.e. linear costs).

We know of no attempts to examine whether animal disputes fit the war of attrition model by estimating  $V$ ,  $c(x)$ , and observing persistence durations. In the present paper, we first find the distribution of persistence durations that will be observed if (2) holds. We then examine the distribution of struggle durations shown by male dung flies fighting for possession of females, for which we can estimate  $V$  and  $c(x)$ .

## Results

### *The Model: Distribution of Persistence Times in Wars of Attrition*

In (1) and (2),  $p(x)$  is the distribution of costs that individuals in a population are prepared to play, not that which will actually be played, because disputes are terminated by the opponent selecting the lower persistence time  $x$ . Norman et al. (1977) noted this problem, but did not attempt a solution, when discussing distribution of display times in brown-headed cowbirds, *Molothrus*. To investigate whether persistence durations in nature fit the war of attrition ESS, we must derive the expected distribution of persistence times,  $p_o(x)$ , that will be observed if individuals select strategies in accordance with  $p(x)$ .

Distribution  $p_o(x)$  can be solved from (2) as follows. The probability that a given combatant has selected a strategy greater than  $x$  is

$$\begin{aligned} \int_x^\infty p(y) dy &= \int_x^\infty \frac{1}{V} c'(y) \exp[-c(y)/V] dy \\ &= [\exp[-c(y)/V]]_x^\infty \\ &= \exp[-c(x)/V] \end{aligned}$$

and the probability that *both* opponents independently select a value  $> x$  (and hence that the combat lasts longer than  $x$ ) is

$$\exp[-c(x)/V]^2 = \exp[-2c(x)/V].$$

The probability that a combat lasts less than  $x$  is therefore

$$1 - \exp[-2c(x)/V].$$

Thus the probability that a combat is observed to last exactly  $x$  is

$$p_o(x) = \frac{d}{dx} [1 - \exp[-2c(x)/V]]$$

$$p_o(x) = \frac{2c'(x)}{V} \exp[-2c(x)/V], \quad (3)$$

which is the distribution of observed persistence times we are seeking. For the linear penalty function  $c(x) = \alpha x$ , (3) is

$$p_o(x) = \frac{2\alpha}{V} \exp(-2\alpha x/V). \quad (4)$$

In the generalised war of attrition described by Bishop and Cannings (1978),  $V$  is not a constant but is itself a function of  $x$ . Calling this function  $b(x)$ , the general ESS is

$$p(x) = \frac{c'(x)}{b(x)} \exp\left[-\int_0^x \frac{c'(y)}{b(y)} dy\right]$$

and we can show that the observed distribution of persistence times will be

$$p_o(x) = \frac{2c'(x)}{b(x)} \exp\left[-2\int_0^x \frac{c'(y)}{b(y)} dy\right].$$

Figure 1 gives some idea of the way that  $p(x)$  and  $p_o(x)$  can be modified by the cost function  $c(x)$ . Some useful rules evident from (2) and (3) and demonstrated by the graphs (see also Norman et al. 1977) are:

a) Since  $p(0) = c'(0)/V$  and  $p_o(0) = 2c'(0)/V$ , the initial value for  $p$  or  $p_o$  is determined by the initial slope of  $c$ , and the starting value of  $p_o$  is always twice that of  $p$ .

b) The derivative  $c'(x)$  can be interpreted as the marginal cost, i.e. the extra cost incurred by an individual that fights for an additional small unit of time after he has already fought for time  $x$ . If the marginal costs are constant (Fig. 1 a),  $p(x)$  and  $p_o(x)$  are negative exponentials. If marginal costs are increasing (Fig. 1 b), the effect is to reduce the probability of selecting higher 'bids'. If  $c'(x)$  approaches zero, then  $p(x)$  and  $p_o(x)$  must also approach zero. Thus in Fig. 1 c,  $c'(1) = 0$ , and so  $p(1) = 0$  and  $p_o(1) = 0$ . It is intuitively obvious that if costs do not increase between  $x$  and  $x + \delta x$ , selection of a bid at the upper limit ( $x + \delta x$ ) must always be better than one within the limit; it has higher winning prospects but equal costs. Thus a bid should never be selected where marginal costs are  $\leq 0$ . Complex cost functions of the type in Fig. 1 c can therefore yield more than one peak for  $p(x)$  and  $p_o(x)$ .

c) As would be expected, the observed distribution of persistence times is strongly skewed to the left of the distribution of bids.

The mean of distribution  $p(x)$  is

$$m = \int_0^\infty x \exp[-c(x)/V] dx,$$

while that of  $p_o(x)$  is

$$m_o = \int_0^\infty x \exp[-2c(x)/V] dx.$$

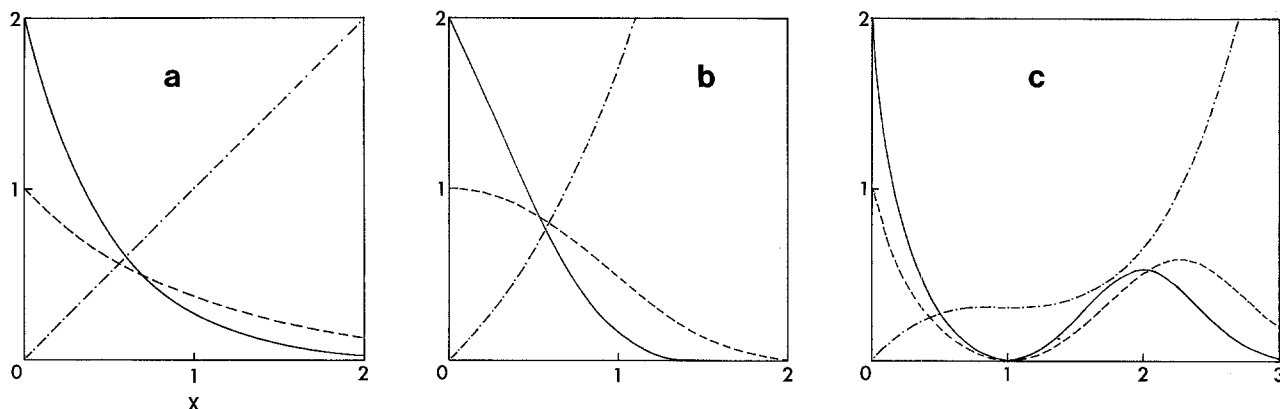


Fig. 1a-c. ESS distribution of  $p(x)$  the selected 'bids' for persistence times, and  $p_o(x)$  the observed persistence times, for various cost functions  $c(x)$ , with  $V$  standardised to 1. See also Norman et al. (1977). Dash-dot line =  $c(x)$ ; broken line =  $p(x)$ ; unbroken line =  $p_o(x)$ . In a,  $c(x) = x$ ;  $p(x) = \exp(-x)$ ;  $p_o(x) = 2\exp(-2x)$ . In b,  $c(x) = [\exp(x) - 1]$ ;  $p(x) = \exp[x - \exp(x) + 1]$ ;  $p_o(x) = 2\exp[x - 2\exp(x) + 2]$ . In c,  $c(x) = [(x - 1)^3 + 1]/3$ ;  $p(x) = (x - 1)^2 \exp\{-[(x - 1)^3 + 1]/3\}$ ;  $p_o(x) = 2(x - 1)^2 \exp\{-2[(x - 1)^3 + 1]/3\}$

d) The mean of  $c(x)$  under distribution  $p_o(x)$  is always exactly  $\frac{V}{2}$ , so that the expected payoff to each opponent is zero (see also Maynard Smith 1974; Bishop and Cannings 1978).

#### An Empirical Test:

##### Are Dung Fly Struggles Wars of Attrition?

**Settlement of Disputes.** Male dung flies (*Scatophaga stercoraria*) meet and mate with females around fresh cattle droppings, in which the females oviposit (Hammer 1941; see Parker 1978a, for a recent review of work on the dung fly mating system). After copulating, the male does not dismount, but guards his female until she has laid all her mature eggs; this part of the male behaviour has evolved to prevent other males from mating with the female and displacing the sperm of the first male. The last male to mate fertilises 80% of the eggs remaining to be laid. Details of sperm competition have been established by irradiation experiments (Parker 1970a). Females mate before each oviposition and may mature several successive batches of eggs.

There are two main mating strategies open to a male. He can either search on or around the dropping for females that are arriving to the oviposition site. Alternatively, he may attempt 'take-over' of a female already paired to a male either during copulation or oviposition. Because of the relative ease of finding paired females on the dung surface, take-overs are virtually restricted to this area. Pairs in copula often emigrate to the safety of the downwind surrounding grass if they meet on the dropping (Parker 1971). Ovipositing pairs, however, have no such alternative,

and take-overs are relatively much commoner during egg-laying.

Disputes over females are settled in two rather distinct ways. Normally an attack is settled conventionally with minimal costs, the convention being that the owner wins. As the attacker contacts a pair, it is deflected away from the female by the paired male by a series of elaborate defensive responses (Parker 1970b), and the attacker leaves virtually immediately. Conventionally settled disputes have the following very low time costs (Parker 1970b):

|  |               |
|--|---------------|
| Attack duration (struggles excluded) with: |               |
| Pairs in copula                            | = 1.0 ± 0.1 s |
| Ovipositing pairs                          | = 1.1 ± 0.1 s |

However, on some occasions, if the attacker manages to touch the female, a struggle takes place between males for possession of the female. Struggles are very obvious, can be prolonged, and are (at a fly's level) fairly dramatic and possibly energetically expensive. The attacker attempts to dislodge the holder by stretching and pushing backwards with the middle and hind legs in a sort of 'pushing and prizing' contest. In a struggle during oviposition, the holder attempts to regain genital contact. This presumably reduces the chance that the attacker can gain genital contact and begin sperm transfer. If an attacker is successful, he mates with the female and guards her during oviposition.

**The Cost of Struggles.** Costs  $c(x)$  can be estimated in terms of missed opportunities to find, mate, and oviposit with an alternative female. The mean value of time spent around a dropping to a male is about 0.23 eggs/min (Parker 1970c). However, a struggle lasting  $x$  seconds may be more expensive energetically than  $x$  seconds spent searching and mating, etc. Sup-

**Table 1.** Estimation of  $V$  (resource value) in dung fly struggles. For further explanation, see text. Egg gains marked \* are taken directly from Parker (1970a); egg gains marked + are derived by the 'approximate' method described in that paper

| State              | Average egg gain if: |                  | Difference in egg gain<br>(a) | Average additional time costs incurred by winner (min)<br>(b) | Direct value $E$<br>(a) - 0.23x(b) | Average extra struggles expected by winner $\beta$ | Value of $V$ |
|--------------------|----------------------|------------------|-------------------------------|---|------------------------------------|--|--------------|
|                    | Wins                 | Loses            |                               |   |                                    |  |              |
| <i>Copulation</i>  |                      |                  |                               |   |                                    |  |              |
| Attacker           | 33.9*                | 0                | 34                            | 46.5  | 23                                 | 1.0  | 12-22.5      |
| Holder             | 34.9*                | 4.8 <sup>+</sup> | 30                            | 31.5  | 23                                 | 1.0  | 12-22.5      |
| <i>Oviposition</i> |                      |                  |                               |   |                                    |  |              |
| Attacker           | 18.5*                | 0                | 19                            | 38.25   | 9.5                                | 0.6  | 3-9          |
| Holder             |                      |                  |                               |   |                                    |  |              |
| This batch         | 15.0 <sup>+</sup>    | 2.0 <sup>+</sup> | 17                            | 8.25  | 15                                 | 0.4  | 12-15        |
| Future batches     | 5.0                  | 0.9              |                               |   |                                    |  |              |

pose that a male has a fixed energy budget available for a bout of reproductive activity so that when reserves drop to a critical level, it must leave the mating site for a feeding stage of constant mean duration. If a struggling male spends energy at  $k$  times the searching rate, one second spent struggling costs  $k$  seconds searching. We therefore assume that

$$c(x) = \frac{0.23}{60} kx$$

where  $x$  is the struggle time in seconds, giving an energetic cost rate of struggling =  $0.23 k/60$  eggs/s.

The easiest way to monitor energy expenditure is by measuring oxygen consumption. Dung fly struggles are relatively short (on average 28.2 s) and so it is not feasible to compare oxygen consumption during struggles and during searching experimentally. However, there is considerable data for insects on the difference in oxygen consumption between flight activity and resting. Prosser and Brown (1961) quote a 50-200-fold increase in consumption rate (flight/resting metabolism). A literature search revealed values of 7-1,000 times; the extremely high values (>500) noted by some early workers are probably erroneous. Discounting these, a plausible range seemed to be 7-170 times.

However, dung fly struggles involve the legs (which have become disproportionately large in males) and the abdomen, not the flight muscles. Thus in estimating  $k$ , it must be noted that the muscle mass in the legs and abdomen is less than that of the flight muscles. Secondly, various activities occur sporadically during searching (Parker 1974b) that will raise energy consumption for searching above that of resting. Thirdly, struggles may involve oxygen debt. A final consideration is that records of proportionate increases in metabolic rate during flight activity tend to be lower for Diptera than for some other insects

(notably Lepidoptera). An estimate of 7 times given by Hocking (1953) for *Drosophila melanogaster* is probably low, but Chadwick and Gilmour (1940) and Chadwick (1947) found a value of 13 times in *Drosophila repleta*. Perhaps closest to *Scatophaga*, McCann and Boettiger (1952) give a value of 25 times for *Sarcophaga bullata*.

Bearing all these considerations in mind, we decided that a plausible range for  $k$  (the relative energetic cost of struggling) is 5-100, the true value probably lying towards the lower end of this range. Until further data are available, it is impossible to be more precise.

*The Resource Value.* The value  $V$  of the resource to be gained from a struggle is the difference in an individual's reproductive success between winning and losing the contest, all costs included other than those of the contest itself. Table 1 shows steps in computing approximate  $V$  values, derived as follows. There is an expected egg gain (number of eggs fertilised) if an individual wins a struggle. This can be estimated from a model based on the results of sperm competition experiments (Parker 1970a). Even if it loses a struggle, a displaced holder can experience some gain from the lost female since it has already transferred some sperm. The difference in egg gain between winning and losing must be devalued by the average time cost (spent finishing the cycle of copulation and oviposition) incurred by the winner. This approximates to the average time to complete the cycle (one full cycle = 30 min copulation +  $16\frac{1}{2}$  min oviposition) multiplied by 0.23 eggs; i.e. it is the gain a loser could expect from *other* females, over the same time period.

We made rough estimates of time costs by assuming that struggles occur at random throughout a stage (copulation or oviposition) to calculate the direct dif-

ference in egg gain,  $E$  (see Table 1). A further devaluation of  $E$  is necessary because the winner may sustain more struggles during the time it takes to complete the cycle. The average probability density of struggles per male during reproductive activity is estimated as approximately 0.023/min; the probability density during copulation is about 0.029/min, and during oviposition 0.0385 (calculated from data in Parker 1970b, c, 1971). Hence we can calculate  $\beta$ , the difference in expected number of struggles sustained during the completion of the cycle. Finally, we can then calculate a range for  $V$  as

$$V = E - \frac{0.23 k \beta \bar{x}}{60}; \quad 5 \leq k \leq 100$$

in which  $\bar{x} = 28.2$  s, the mean struggle duration.

The above method to estimate  $V$  is necessarily very imprecise, but an exact model would be spurious in view of the wide range in  $k$ . The assumption that a struggle occurs at a single random time during copulation or oviposition is clearly an approximation. Take-overs, though relatively infrequent, would tend to decrease time costs slightly (their effect is included in the model used to estimate egg gains; Parker 1970a). In general, asymmetry in  $V$  between holder and attacker will increase throughout the cycle mainly because of the increasing disparity in time costs between a winning holder and a winning attacker.

For fights occurring at random times during copulation,  $V$  is approximately equal for holder and attacker (Table 1) so that a symmetric war of attrition may be applicable. However, we must note that this is an *average* symmetry. Because of tendencies to copulate off the dropping (Parker 1971), attack probability is highest towards the end of copulation as pairs arrive for oviposition. A rough calculation showed that this could increase the average  $V$  for the holder

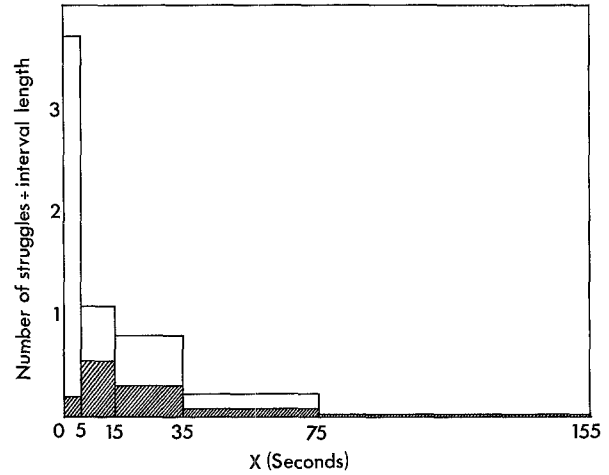


Fig. 2. Observed distribution of struggle persistence times in the dung fly, *Scatophaga stercoraria*. Open histograms, combined data, all categories; cross-hatched histograms, distribution of persistence times for struggles in which the attacking male won

by up to two eggs. For ovipositing pairs, it seems less likely that the contest could approximate to a symmetric war of attrition since  $V$  is markedly higher for the holder than the attacker.

*The Fit with the War of Attrition.* Dung fly struggles were timed in the field, and it was noted whether the struggle occurred during copulation or oviposition and whether the holder won or the attacker won. Figure 2 shows the observed distribution of struggle durations.

Is this distribution, a negative exponential following  $p_o(x)$ , the distribution of persistence times suggested by the war of attrition with a linear cost function? For our model, this is

$$p_o(x) = \frac{2(0.23 k)}{60 V} \exp \left( -2 \left( \frac{0.23 k x}{60 V} \right) \right).$$

Table 2. Examination of dung fly struggle durations in relation to the war of attrition model with linear costs (see text)

| Category  | $n$ | Fit of observed distribution with negative exponential | Mean observed struggle duration in seconds | Predicted range for $V$ from war of attrition model |
|---|-----|--|--|---|
| <i>All data combined</i>  | 69  | $\chi^2_8 = 11.48$ (good fit)                          | 28.2                                       | 1.1–21.6  |
| <i>Copulation</i>   |     |  |  |   |
| Holder wins   | 29  | $\chi^2_4 = 1.00$ (good fit)                           | 17.0                                       | 0.7–13.1  |
| Attacker wins   | 3   | Insufficient data                                      | —  | —   |
| <i>Oviposition</i>  |     |  |  |   |
| Holder wins (all data)  | 23  | $\chi^2_3 = 8.09$ (not exponential)                    | 24.5                                       | (Not exponential)                                   |
| Holder wins (excluding single outlying point)                   | 22  | $\chi^2_3 = 2.59$ (good fit)                           | 13.0                                       | 0.5–10.0  |
| Attacker wins   | 14  | $\chi^2_3 = 9.43$ (not exponential)                    | 37.9                                       | (Not exponential)                                   |
| <i>Combined data for holder wins (excluding outlying point)</i> | 51  | $\chi^2_8 = 4.88$ (good fit)                           | 15.3                                       | 0.6–11.7  |

We tested whether the observed distributions of persistence times were good fits to a negative exponential distribution, and whether the mean persistence duration was consistent with a range of 5–100 for  $k$ . The mean  $\mu$  of the distribution  $p_o(x)$  is  $\frac{60 V}{0.46 k}$ .

Thus  $V$  lies between  $0.0077$  ( $\min k$ ) $\mu$  and  $0.0077$  ( $\max k$ ) $\mu$ . Support for the war of attrition model is obtained if the range of  $V$  thus obtained (see Table 2) overlaps with that derived in the last section (see Table 1), and if the distribution appears to be a negative exponential (Table 2).

The combined data concur rather seductively with the war of attrition solution; there is a good fit to a negative exponential and the range for  $V$  spans all those obtained in Table 1. However, analysis of the component categories (see Table 2) indicates that this is an oversimplification of the situation. In most cases, either the distribution is significantly different from a negative exponential, or the  $V$  ranges barely overlap (suggesting that resource value is higher than is consistent with the war of attrition).

Of course neither of these features can be claimed with certainty to rule out the war of attrition solution. The plausible range of  $k$  (5–100) is debatable and there is always the possibility that the cost function  $c(x)$  is non-linear, which would alter distribution  $p_o(x)$ .

However, certain features militate strongly against using the symmetric war of attrition as an explanation. Firstly, there is a much higher probability that the holder will win than the attacker (Table 2, see also Parker 1970b) in the ratio 52 (holder wins):17 (attacker wins) and this difference is highly significant ( $\chi^2_1 = 17.75$ ). Secondly, the data in which the attacker wins are *not* exponentially distributed, whereas the data (excluding a single outlying point) for wins by holders are consistent with an exponential distribution (see Table 2 and Fig. 2). Mean persistence times are also different (Table 2; see also Parker 1970b); bouts in which the attacker wins are usually longer than those in which the holder wins.

## Discussion

This suggests that struggles are a form of asymmetric contest. When contests are asymmetric and animals can perceive the asymmetry, distribution  $p_o(x)$  generated by the assumption of symmetry collapses to give a pure ESS solution (Maynard Smith and Parker 1976; Selten 1978). If one opponent in a contest occupies role A and the other role B, the ESS is: 'when in A, be prepared to play  $x > V$  if the opponent does not withdraw; if in B, withdraw without incurring

any cost' (or equivalently vice versa). Roles A and B could be owner/attacker, bigger/smaller, or could reflect asymmetric values of the resource. The most likely 'conventions' of this sort to evolve are those in which the individual with the higher 'resource holding power' (RHP) is allowed to win, or the one (say A) with the most to gain is allowed to win, i.e.  $V_A > V_B$  (see Maynard Smith and Parker 1976). The mean expectation of this sort of strategy in a population adopting such a convention would be  $\frac{V_A}{2}$ , whereas the mean expectation of any individual in a population playing the mixed ESS for the war of attrition will be zero (Maynard Smith 1974).

The asymmetries that are probably most important in dung fly disputes are:

*a) RHP Asymmetries.* There can be a 5–6-fold size difference between large and small males; this is likely to exert effects on the outcome of struggles. Also there is likely to be a strong RHP asymmetry in favour of the holder because of his positional advantage.

*b) Resource Value Asymmetries.* Because of the approximations used to obtain values for  $V$  (Table 1), differences in resource value for a copulating holder ( $V_{HC}$ ) and a copulating attacker ( $V_{AC}$ ) are as yet undefined, although probably  $V_{HC} > V_{AC}$ . For oviposition, it is quite clear that the holder stands to gain more than the attacker ( $V_{OH} > V_{OA}$ ).

Thus disputes between male dung flies over females are generally asymmetric in favour of the holder, and would consequently be most likely to lead to evolution of an 'owner wins' convention in which there is no escalation and the interloper withdraws immediately. Escalation would be expected only when both contestants 'believe' that they are owners. This can often be achieved experimentally (examples reviewed in Parker 1978b) but the work of Baker (1972) on peacock butterflies suggests that occasionally such 'mistakes' can occur in nature. Escalation may result if an intruder settles in a territory without being noticed by the owner (who may leave the territory temporarily to follow females, etc.). At one level, dung fly disputes are compatible with this sort of interpretation; generally there is a conventional settlement following 'owner wins', but when both can touch the female (i.e. the information used to define ownership?), there is escalation. This still begs the question of what should happen in the struggles (escalated contests). If an 'owner wins' convention applies, escalations must be a less advantageous strategy, but struggles are not infrequent events in dung fly life. We find it hard to imagine that selection could not

favour means of obtaining better information about the reality of ownership. Further, the fact that males continue to attack pairs suggests that there is no fixed 'owner wins' convention.

Why then, do male dung flies attack pairs and (often) engage in costly struggles? We feel that the most likely explanation relates to 'assessment strategy' (Parker 1974a), and in particular, to a special form of assessment concerning information acquired during a contest (Maynard Smith and Parker 1976).

Firstly, selection probably maintains the attack behaviour because take-overs are possible. However, 92%–93% of attacks are characterised by the attacker's immediate withdrawal. Struggles tend to occur only in special circumstances (holder fails to reject; pair topples sideways; two males attack simultaneously) characterised by the fact that the attacker is able to touch the female with his front tarsi – a struggle is then inevitable (Parker 1970b). We interpret this in terms of a correlation between being able to touch the female and a dramatic reduction in RHP asymmetry; put simply, it now pays to hang on to the female to obtain further information about *own* size relative to *holder's* size. What follows may depend on how good a grasp the attacker gains initially and on the relative sizes. The holder is likely still to have a positional RHP advantage, and because  $V_A > V_H$ , a relatively larger attacker size is likely to be necessary for the attacker to continue escalation.

From the model for 'information acquired during a contest' (Maynard Smith and Parker 1976), it is evident that when the outcome of a particular stage in a contest is a good predictor of the outcome of the next stage (i.e. high RHP asymmetry), solutions are pure ESSs and bouts should terminate relatively quickly. When success at one stage conveys little information about subsequent success (low RHP asymmetry), there can be a mixed ESS distribution of persistence times. It is not yet possible to evaluate whether this type of model could generate the observed distribution of struggle durations in dung flies. Much would depend on the rate at which information can be perfected relative to the rate at which costs are expended, but in general payoffs from the attack behaviour would be positive (though they will be strongly dependent on male size).

In conclusion, the total distribution of contest lengths of dung fly struggles is consistent with the war of attrition ESS. However, there are many indications that this is not the true model. Holders win more often than attackers and there are also significant differences in means and distributions of persistence times for 'holder wins' and 'attacker wins' outcomes. In nature, most contests will involve various asymmetries, but there is no guarantee that animals

will always be able to perceive them. Mixed strategies of the 'war of attrition' type may therefore be observed in animal conflicts. Some forms of resource value asymmetry may be very difficult to detect. RHP asymmetries may be most easily detected during physical combat where opponents appear visually to be reasonably matched. Further, some fraction of contests within a population must occur between opponents that are so closely matched that the result must be a mixed ESS (some form of war of attrition) unless an asymmetry uncorrelated with RHP or  $V$  can be used to settle the dispute.

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