

## **Energetic Constraints and Male Mate-Securing Tactics in the Damselfly *Calopteryx splendens xanthostoma* (Charpentier)**

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# Energetic constraints and male mate-securing tactics in the damselfly *Calopteryx splendens xanthostoma* (Charpentier)

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## SUMMARY

Males of the damselfly *Calopteryx splendens xanthostoma* (Charpentier) demonstrate territorial and non-territorial mate securing tactics. Non-territorial males obtain a territory in one of two ways: they either wait for a territory to become vacant, or they fight with and displace a territory holder. The estimated reproductive success of territorial males was a thousand times greater than that of non-territorial males, suggesting that males should fight hard to become, and remain, territorial. Our results show that the ability to win fights, and therefore be territorial, is dependent on energy reserves (fat). Energy reserves were correlated with the age of the individual. Young, pre-territorial, males had excess fat; territorial males that had gained their territory by fighting had intermediate fat reserves; older males that had been displaced from a territory had very low levels of fat. Previous studies of calopterygid territoriality have suggested that resident–intruder or other uncorrelated asymmetries are important in determining the outcome of a conflict. We provide an alternative explanation centring around Grafen's (1987) 'desperado' effect and the energy constraint on a male's ability to obtain a territory.

## 1. INTRODUCTION

A commonly observed feature of fighting in animals is that contests are often quickly settled, without escalation, in favour of the owner (Davies 1978; Krebs 1982; Waage 1988). Maynard-Smith & Parker (1976) explained this with a game theory model: owners always played 'hawk' and escalated, while intruders always played 'dove' and retreated. They termed this strategy set 'Bourgeois' and found that it was an ESS when the value of winning was less than the cost of fighting. Consequently, Maynard-Smith & Parker (1976) argued that owners won fights because ownership was used as an arbitrary asymmetry to avoid contest costs. This has since been demonstrated empirically (for examples, see Davies 1978; Gribbin & Thompson 1991). However, Maynard-Smith & Parker's model has been criticized by Grafen (1987), who suggested that an arbitrary asymmetry based on ownership, irrespective of whether it is correlated with fighting ability, is unstable and cannot explain why residents win fights when: (i) territories last for some time; (ii) reproduction requires a territory; and (iii) vacant territories are rare. In short, Grafen argues that because non-territorial males playing 'Bourgeois' can only reproduce in the unlikely event of finding a vacant territory, their chances of reproduction are minimal. Consequently, the relative cost of fighting for these males decreases. They are 'desperados' and as such, should not respect an arbitrary asymmetry such as the resident–intruder asymmetry. The outcome of Grafen's logic is that territories should be held by 'better' males

and only change hands after real fights. Fights therefore determine territory ownership and represent the point at which most males switch between the alternative mate securing tactics (AMSTs) in the mating system. Understanding the physiological processes that underlie the settling of fights should therefore provide insight into what is meant by 'better' males, what enables some males to be territorial while others are non-territorial, and whether males are constrained by the arbitrary rules of the bourgeois strategy set or are constrained in more direct ways.

One trait commonly correlated with switching between AMSTs is age. For example, old senescent red deer stags often give up defending harems, and instead attempt to steal matings (Gibson & Guinness 1980). Similarly, older male *Calopteryx maculata* are more likely to cease defending a territory and become non-territorial 'sneaks' (Forsythe & Montgomerie 1987). Such age related switching in behaviour may be caused by a number of factors, including correlated changes in size, experience, and/or condition of the individual (see, for example, Andersson 1994). A functional definition of an individual's condition is its capacity to carry out energetically costly behaviour (for examples, see Gibson & Bradbury 1985; Petersson 1989; Passera & Keller 1990; Marden & Waage 1990; Marden & Rollins 1994; Andersson 1994; Yuval 1994 *et al.*; Otronen 1995). Recent insect studies have shown that energy reserves affect a male's reproductive success in species in which energy reserves are negatively associated with age (Sharma *et al.* 1983; Petersson 1989; Marden & Waage 1990; Sartori *et al.* 1992;

Yuval *et al.* 1994; Otronen 1995). Insects are good models for these kinds of studies because it is relatively easy to measure their total energy reserves (Marden 1989; Otronen 1995) and their size is fixed at adult eclosion, so is independent of age and ageing effects (Banks & Thompson 1982).

Male *Calopteryx splendens xanthostoma* have two AMSTs: territorial males defend small isolated patches of the freshwater angiosperm *Ranunculus penicillatus* into which females oviposit, while non-territorial males do not defend an oviposition resource but attempt to copulate with females visiting territories. Similar behaviour is common in other odonate species (Waage 1973; Campanella & Wolf 1974; Higashi 1981; Harvey & Hubbard 1987; Tsubaki & Ono 1986, 1987; McVey 1988; Convey 1989; Siva-Jothy & Tsubaki 1989). Non-territorial male *C. s. xanthostoma* acquire a territory in one of two ways. Males either enter, and win, an escalated fight with a territory owner or wait and occupy an abandoned, vacant territory. Empirical work on *C. maculata* (Waage 1988; Marden & Waage 1990) has indicated: (i) that escalated fights were the primary mechanism of turnover in territory ownership; and (ii) escalated fight winners had significantly more post-contest fat reserves compared with escalated fight losers. The main energy reserve in odonates is fat (Kallapur & George 1973): accumulation of these reserves during the pre-reproductive, but adult, 'teneral' period of a male may therefore be very important in determining what a male's AMST options are. In *C. s. xanthostoma* pre-territorial males (males arriving at a reproductive site after their teneral period) commonly fought with, and displaced, territorial males from their territories, whereas post-territorial males (older individuals that had previously defended a territory) rarely fought for territories, but tended to occupy vacated ones instead (Plaistow 1996).

In this study we examine the role of fat in determining male fitness in *C. s. xanthostoma* by combining observational data that examines: (i) the reproductive pay-off associated with different AMSTs; (ii) age related changes in energy reserves; (iii) the energy reserves and age of males adopting different AMSTs; and (iv) the role of energy reserves in determining fight outcomes. Finally, we estimate the energetic cost of obtaining a territory by doing a simple removal experiment.

## 2. METHODS

### (a) Study site

The study was done between June–August 1994 and 1995, on the River Vidourle in southern France (43° 52' N, 04° 03' E). The study sites consisted of isolated sections of shallow, fast flowing stream, containing dispersed clumps of *R. penicillatus* (territories). At each site all territories were manipulated so that they were of an equal size (0.5 m<sup>2</sup>), with an equal rate of water flow ( $\approx 0.4 \text{ m s}^{-1}$ ) passing over them (see Siva-Jothy *et al.* 1995). Territory density was maintained at five to seven territories at sites where observations were made. All males at each site were caught, individually marked on the hind wings with an enamel pen, and their age category determined. The process of marking and ageing did not have any overt effect on individuals; in most cases males

resumed reproductive activity within 10 min of release. Because the individual marks on males were site-specific we could determine how frequently males moved between our three study sites (twice in 400 h of observation). The distances between our three study sites were 400 m and 2000 m. As there were no other populations within a 40 km radius, migration between sites was minimal.

### (b) Observations

Daily observations were made between 10h00 and 18h00 EST. We recorded the position and reproductive tactic employed by males at specific sites; new males arriving, previously marked males failing to arrive, and any males switching between tactics. In cases where escalated fights were involved, fights were watched continuously until they were resolved. Escalated fights differed from the brief (2–10 s) pursuit flights during which territorial males chased intruders out of their territory. By contrast escalated fights proceeded through several stages of hierarchical escalation, during which flight speed increased, and culminated in a high speed, spiralling chase that spanned the whole reproductive site. Contests between males were considered to be over when the successful male had defended the territory for at least 10 min without any further interference from the losing male.

### (c) Estimation of reproductive success

The reproductive success of territorial and non-territorial tactics was estimated from 31 h of continuous observation of males over a period of 6 d. For each hour we recorded: (i) the total number of copulations obtained by territorial and non-territorial males; and (ii) the number of territorial and non-territorial males that were present. For 11 of the 31 h of observation we also recorded female oviposition durations after each copulation. To obtain an estimate of the reproductive success attributable to territorial and non-territorial tactics we multiplied the mean copulation rate per male per hour for each tactic by the mean bout of oviposition following copulation with either a territorial or a non-territorial male, and the mean oviposition rate (0.25 eggs per second) into *R. penicillatus* (Hooper 1994). Given that last male sperm precedence is high in this species (Hooper & Siva-Jothy 1996) this provides an estimate of reproductive success in terms of the mean number of fertilized eggs per male per hour for each tactic.

### (d) Collection of samples

Males were collected and assigned to one of the following categories (see below). Fat analysis of these males was used to evaluate the role of energy reserves, age class, flight muscle ratio (FMR), and size on the outcome of escalated fights.

#### (i) Pre-territorial males

Newly arrived, non-territorial males that attempted to copulate with females on occupied territories without prior courtship. These males always arrived at the site unmarked, indicating they had only recently matured to reproductive condition.

#### (ii) Territorial males

Males that had defended a territory for at least a day.

#### (iii) Post-territorial males

Marked males, previously observed defending a territory, but who were not defending a territory, or did not attempt to court a female before copulation at the time of capture.

*(iv) Fighting males*

A total of 19 pairs of males (a 'fight winner' (post-fight territory holder) and a 'fight loser') were collected after escalated fights. All individuals were aged before being decapitated and gutted. They were stored in thin paper envelopes within a sealed box containing silica gel. This storage process rapidly dried out the soft body tissues and was ideal for preparing and storing samples for subsequent fat extraction.

*(e) Age categories*

Because we didn't commence our observations at the start of the season it was not possible to determine absolute age by the date of marking. Consequently we placed individuals into age categories (see also Marden & Waage 1990; Siva-Jothy & Tsubaki 1994) based on the following scheme. A total of four age classes of adult male *C. s. xanthostoma* were defined mainly by the stiffness of the leading edge of the wings (in turn determined largely by the stiffness of the costal and subcostal veins, S. Plaistow, personal observation). All of these age categories were clearly distinguishable from teneral, which did not have fully developed wing pigmentation. The youngest individuals, age class 1, had soft undamaged wings that were dorso-ventrally flexible along their whole length. Age class 2 males had harder wings which were only flexible from the nodus to the tip. Age class 3 males had hard wings that were flexible only at the distal tip and showed slight wearing. Age class 4, the oldest males, had inflexible, well worn wings that were 'papery' to the touch and had a calcium carbonate film on the wings and body (caused by contact with the hard water in this region of France).

*(f) Fat extractions*

Fat extractions were done on the thorax and abdomen. The wings and legs contained almost no measurable fat, while the head contains no metabolically usable fat. Unpublished data show that freeze-drying field-dried samples increases the efficiency of Marden's (1989) fat extraction procedure. Consequently all field-dried samples were freeze dried (LYOLAB B- freeze drier) before the dry mass of the thorax and abdomen was weighed to the nearest 10 µg (Mettler AE160 balance). Fat extractions were based on the method of Marden (1989), but used fat-free paper thimbles (Whatman, single thickness, 10 mm × 50 mm). Body parts were re-weighed after fat extraction to obtain the dry fatless mass. Fat content was calculated from the difference between the dry mass and the dry fatless mass, and was expressed as the standardized residual from a regression of total fat content over dry fatless body mass (see Marden & Rollins 1994).

*(g) Body size and flight muscle ratio*

We used dry fatless mass as the measure of an individual's body size (see 'Fat extractions'). An individual's flight muscle mass was determined by placing the dry, fatless thorax in 0.2 M potassium hydroxide at room temperature for 48 h: this resulted in the total digestion of the flight muscle. The remaining cuticle was then washed in distilled water, dried, and re-weighed. FMR was defined as dry flight muscle mass/total dry abdomen and thorax mass.

*(h) The cost of fighting*

We determined the energetic cost of displacing a territorial male by removing the resident male soon after an escalated

fight began. This effectively provided the pre-territorial male with a vacant territory. A pre-territorial male was considered to have taken the territory if he subsequently began defending, or courting, on it in which case he was immediately collected for fat analysis and the original territory holder released. We allowed other pre-territorial males to engage in, and complete, fights with territory holders and displace them, after which we collected both males for fat analysis. If fights are energetically costly then we would predict that pre-territorial males obtaining vacant territories should have significantly greater fat reserves than males that had to fight for a territory. Moreover, the differential in fat reserves provides a good indication of the energetic cost of fighting. We estimated the rate of energy usage ( $W g^{-1}$ ) during an escalated fight in the following way. The difference in the expected absolute fat (calculated from the absolute fat per gramme dry fatless mass from pre-territorial males that didn't have to fight for a territory) and actual absolute fat for each male that fought for a territory was estimated. The calorific value of fat is  $9.4 kcal g^{-1}$  (and  $1 kcal h^{-1} = 1.16 W$ ) (Schmidt-Nielsen 1990). For each 'fighting' male we had a measure of: (i) dry fatless mass, which was converted to wet weight (dry fatless mass (mg) =  $0.159 \times$  wet mass (mg) + 1.806,  $r^2 = 0.629$ ,  $p = 0.0001$ ,  $n = 59$ ); and (ii) the duration of the escalated fight leading to the take-over. We used these data to calculate the rate of energy usage during an escalated fight. The error in our result will come mainly from individual deviation from the mean pre-fight fat content.

**3. RESULTS***(a) Reproductive success of territorial and non-territorial males*

The estimated mean hourly reproductive success of a territorial male was more than a thousand times greater than a non-territorial male (see table 1).

*(b) Size dependent differences in fat content*

Regression analysis revealed a positive linear relation ( $n = 153$ ,  $r^2 = 0.07$ ,  $F = 12.48$ ,  $p = 0.0005$ ) between the total fat content of males and their dry fatless mass (i.e. size). We therefore use the standardized residual from this regression as our size-corrected assessment of the fat content of each male.

*(c) Age related changes in fat content*

Fat content declined significantly with age (one-way ANOVA,  $F = 7.458$ , 3 d.f.,  $p < 0.001$ , figure 1). In a pairwise comparison between the fat content of adjacent age categories only age categories 1 versus 2 and 3 versus 4 were not different ( $p > 0.05$ ). Males in age category 2 had significantly more fat than age category 3 males (Scheffe  $F = 2.98$ ,  $p < 0.05$ ).

*(d) Male tactic and age*

There was a significant difference between the age of males employing different mate securing tactics (Kruskal-Wallis test, 2 d.f.,  $H = 11.49_{adj}$ ,  $p = 0.0003$ ): pre-territorial males ( $2.043 \pm 0.117$ ) were significantly younger than post-territorial males ( $2.73 \pm 0.152$ ) (non-parametric multiple comparisons test,  $Q = 3.11$ ,  $p < 0.05$ ), although there was no difference in age

Table 1. *Estimated hourly reproductive success of territorial and non-territorial males*(The oviposition rate of female *C. s. xanthostoma* is 0.25 eggs per second, Hooper (1994).)

	territorial males ( $\pm$ s.e.)	non-territorial males ( $\pm$ s.e.)	statistical tests
copulation rate males per hour	0.287 $\pm$ 0.03	0.034 $\pm$ 0.01	unpaired <i>t</i> -test, $t = 6.71$ , d.f. = 60, $p < 0.0001$
mean oviposition duration per copulation/min	16.05 $\pm$ 4.28	0.07 $\pm$ 0.07	MWU-test, $n_1 = 19$ , $n_2 = 5$ , $U = 175$ , $p < 0.001$
estimated hourly reproductive success (eggs fertilized per male per hour)	65.27	0.06	

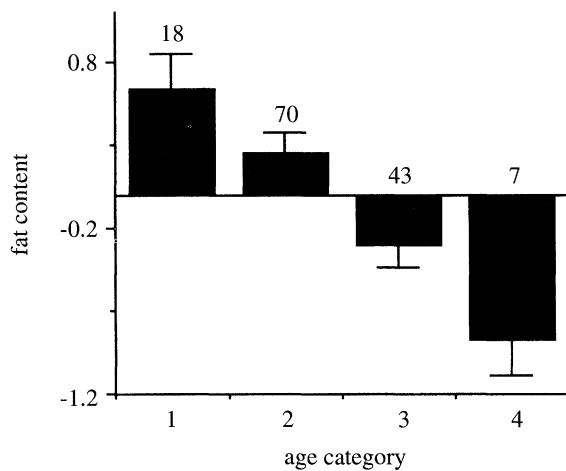


Figure 1. Mean fat content ( $\pm$ s.e.) of males in different age categories. Numbers in parentheses refer to sample sizes. To remove size bias, fat content is expressed as the standardized residuals of a regression of fat content (mg) over dry fatless body mass (mg) ( $r^2 = 0.07$ ,  $n = 153$ ,  $F = 12.48$ ,  $p = 0.0005$ ). See text for age category definitions.

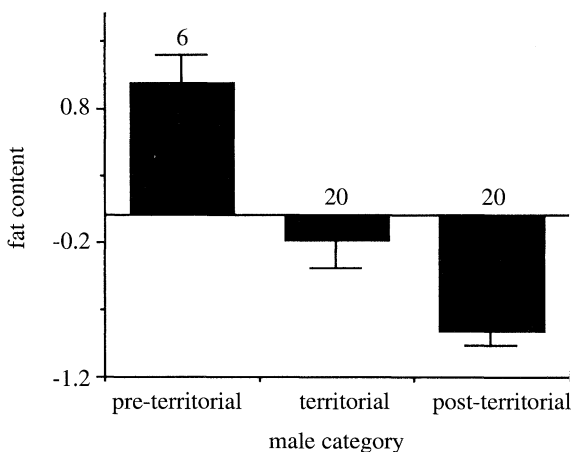


Figure 2. Mean fat content ( $\pm$ se) for males with different mate securing tactics (see text for definitions of male categories). Numbers in parentheses refer to sample sizes. Fat content is expressed as in figure 1.

between pre-territorial and territorial males ( $2.37 \pm 0.143$ ) (non-parametric multiple comparisons test,  $Q = 1.72$ ,  $p > 0.05$ ), or between territorial and post-territorial males (non-parametric multiple comparisons test,  $Q = 1.42$ ,  $p > 0.05$ ).

### (e) Fat differences between tactics

There was a highly significant difference between the fat content of males employing different mate securing tactics (one-way ANOVA,  $F = 16.237$ , 2 d.f.,  $p < 0.001$ , figure 2). Pre-territorial males ( $0.98 \pm 0.202$ ) had significantly more fat than territorial males ( $-0.195 \pm 0.205$ ) (Scheffe  $F = 6.33$ ,  $p < 0.05$ ) and territorial males had significantly more fat than post-territorial males ( $-0.862 \pm 0.109$ ) (Scheffe  $F = 4.44$ ,  $p < 0.05$ ). Age was not included as a factor in this analysis because each tactic did not include all age categories preventing the determination of an interaction term for male age and male tactic.

### (f) Escalated fights

Fight winners had significantly more fat at the end of the contest ( $0.133 \pm 0.195$ ) compared with fight losers ( $-0.81 \pm 0.13$ ) (paired *t*-test, d.f. = 18,  $t = 4.509$ ,  $p = 0.0003$ ). There was, however, no significant difference between the age of winning ( $2.2 \pm 0.223$ ) and losing ( $2.6 \pm 0.163$ ) males (Wilcoxon signed ranks,  $z = -1.072$ ,  $p = 0.2836$ ), the size of winning ( $17.82 \pm 0.517$  mg) and losing ( $18.15 \pm 0.66$  mg) males (paired *t*-test, d.f. = 18,  $t = -0.714$ ,  $p = 0.485$ ), or the FMR of winning ( $0.462 \pm 0.01$ ) and losing males ( $0.486 \pm 0.01$ ) (paired *t*-test,  $t = -1.84$ , d.f. = 16,  $p = 0.084$ ).

### (g) The cost of fighting

Males that were allowed to occupy territories from which the resident had been removed had significantly more fat ( $0.978 \pm 0.247$ ) than males that fought and displaced a territorial male ( $-0.023 \pm 0.274$ ) (Mann-Whitney U test,  $z = -2.096$ ,  $p = 0.0361$ , see figure 3). Furthermore, the cost of one contest was enough to deplete the fat content of pre-territorial males to the level associated with territorial males. There was no significant difference in the fat content of new territorial males ( $-0.138 \pm 0.265$ ) (i.e. fight winning males that successfully displaced a resident male to obtain a territory) and established territorial males ( $-0.519 \pm 0.177$ ) (unpaired *t*-test, d.f. = 29,  $t = 1.235$ ,  $p = 0.227$ ).

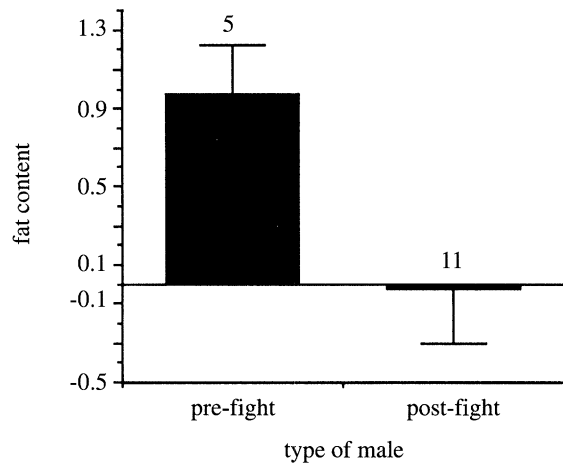


Figure 3. Mean fat content ( $\pm$  s.e.) of males from the cost of fighting experiment. Post-fight males fought and displaced a male to obtain a territory. Pre-fight males initiated a fight, after which the resident was removed from the territory. Numbers in parentheses refer to sample sizes and fat content is expressed as in figure 1.

Our estimated rate of energy usage during escalated fights was  $0.726 \pm 0.32 \text{ W g}^{-1}$  ( $n = 8$ ). This corresponds well with previously published data on the energetic cost of flight in other odonates (May 1984).

#### 4. DISCUSSION

Theory suggests that the willingness of, and level to which an animal is prepared to fight will be dependent upon: (i) the value of the contested resource; (ii) the value of potential future reproduction; (iii) the cost of fighting (which may affect future reproduction); and (iv) the probability of winning a fight (Maynard-Smith & Parker 1976; Grafen 1987; Enquist & Leimar 1990). In general, males will fight hard, sometimes even to the death, when the contested resource has high potential reproductive value. The extent to which the cost of fighting, or the probability of winning has an effect, is largely dependent on the disparity between current and future reproduction. So, for example, when the contested resource enables future reproduction and there is little or no potential for reproduction without the resource, males should pay any cost to obtain the resource (but see Shutler & Weatherhead 1992).

*C. s. xanthostoma* male AMSTs do not have equal fitness payoffs. Territorial males not only obtained more copulations per male per hour, but also secured more oviposition following copulation than did non-territorial males. Resource-holding males achieve, on average, a thousand times more reproductive success than non-territorial males. The females of this species can gain access to oviposition sites without remating on later visits (Siva-Jothy & Hooper 1995), but there is no evidence to suggest that this female behaviour will benefit one AMST more than the other. Our results suggest that males obtain most of their reproductive success during periods of territoriality. As with other territorial odonates (Tsubaki & Ono 1987; Finke 1992), the ability to obtain a territory, and the

duration for which it can be defended, are likely to be the main determinants of a male's lifetime reproductive success.

The energy reserves of male *C. s. xanthostoma* declined with age. Fried & May (1984) calculated energy budgets for reproductively active males of the territorial libellulid *Plathemis lydia* and found that males were often in negative energy balance, suggesting a reason why energy reserves decline, and become limiting, with age. We found significant differences in the level of stored energy reserves between AMSTs: pre-territorial males had the most fat, territorial males had intermediate fat levels, while post-territorial males had minimal fat. This correlation suggests fat may play a role in determining the AMST a male can adopt. It does not however enable us to conclude that energy reserves alone constrain a male's choice of AMST as age also differed between mating tactics. Learning or experience may also play a role. Marden & Waage (1990), showed that fight winning *C. maculata* males had greater post-contest fat reserves compared to losing individuals. They concluded that escalated contests were a 'war of attrition' and that age alone was unlikely to determine the outcome. The analysis of fat content after escalated fights in *C. s. xanthostoma* support the 'war of attrition' hypothesis: winning males had greater energy reserves at the end of the fight despite the similarity in the age, size, and FMR of winning and losing males. Energy reserves therefore appear to be a factor, if not the principal factor, determining a male's ability to become territorial. We suggest age covaries with energy reserves because older males will have been reproductively active for longer and so will have used more of their fat reserves. Of all the costs associated with territoriality, Marden & Waage (1990), suggested that fighting may be the highest: our results support this idea. Entering into an escalated fight and displacing a male from his territory reduces the energy reserves of a pre-territorial male by 40–50%. Territorial males defending their territory must pay an equivalent cost as, during a fight, both males engage in similar flight behaviours for similar durations.

Because the cost of obtaining and maintaining a territory is so high, males may only be able to fight for, and defend, a territory once in their lifetime: once a male is displaced from his territory he is unlikely to obtain another (unless he finds a vacant one) because his fat reserves are so low. This, and the disparity in reproductive payoffs between AMSTs, are key conditions favouring the evolution of 'desperados' (Grafen 1987). Because the reproductive payoffs of being non-territorial are so low, males that have fat reserves but don't have a territory should not respect resident-intruder asymmetries, but should always fight. Likewise, territory owners should also be prepared to fight. Once displaced from his territory a male is faced with a dilemma. He probably cannot accumulate more fat because it takes too long, and he doesn't have the resources to displace a male from another territory. He is a reproductive 'has-been' and must either wait to occupy a vacated territory (which he may be unable to defend) and mate with the females it attracts, or he

must secure copulations with females trying to oviposit on defended oviposition resources. These post-territorial has-beens will generally receive low reproductive rewards.

In his exposition of the desperado effect Grafen (1987) suggested that confrontations may occur as the result of non-territorial individuals acquiring information about whether the territory is occupied, or even the fighting ability of the resident: they are not looking for a fight. Most of the territorial interactions in calopterygid mating systems take the form of short pursuit flights (Waage 1988; Plaistow 1996). Waage (1988) suggested that such flights in *C. maculata* were indicative of males respecting a resident–intruder asymmetry (i.e. playing ‘bourgeois’). Our data suggest that intruding post-territorial males respect a resident–intruder asymmetry because they do not have the resources to fight. Residents do not know whether the intruder is a desperado or a has-been and so must escalate. The common, brief conflicts that occur between residents and intruders are territorial interactions with post-territorial has-beens who do not have enough fat to fight. Escalated fights, on the other hand, occur when a territorial male meets a pre-territorial male, or there is a ‘confusion of residency’, both of which are comparatively rare events (Plaistow 1996).

For non-territorial male *C. s. xanthostoma* the potential for future reproduction is contingent on the probability of: (i) obtaining a territory either through fighting, or waiting for one; plus (ii) the negligible gain associated with obtaining copulations with females while not holding a territory (Waage 1973; Forsythe & Montgomerie 1987; this study). A previous model has considered a range of life-history parameters that might influence whether males should fight or wait for a territory (Dunham *et al.* 1995); however it was based on the assumption that ‘fighting’ and ‘waiting’ were fixed options. We have shown (as have others: Marden & Waage 1990) that the ability to win fights is dependent on fat reserves. Therefore pre-territorial males with excess fat reserves have a relatively high probability of winning a fight, while post-territorial males with depleted fat reserves have a relatively low probability of winning. Plaistow (1996) has shown that pre-territorial males that fight obtain territories seven times quicker than post-territorial males that wait: on average, post-territorial males take almost a day to obtain a (vacated) territory. The reason fat depleted, post-territorial males do not escalate is probably because their chance of winning a fight and displacing a territorial male is less than that of finding a vacant territory.

In conclusion the stored energy reserves of male *C. s. xanthostoma* are important in enabling a male to become, and remain, territorial: depleted energy reserves constrain a male’s chances of further reproductive success. Stored energy reserves, and the processes that affect energy assimilation and the rate of energy usage, are likely to be main determinants of male lifetime reproductive success.

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