

**VARIATION IN NON-TERRITORIAL BEHAVIOUR IN MALE
CALOPTERYX SPLENDENS XANTHOSTOMA (CHARPENTIER)
(ZYGOPTERA: CALOPTERYGIDAE)**

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Male calopterygid damselflies commonly demonstrate 2 alternative mate-securing tactics, occurring as either territorial or non-territorial individuals. Previous studies have assumed that non-territorial males constitute one category. This study describes variation in non-territorial behaviour which is dependent upon whether or not the non-territorial male had been displaced from a territory. Consequently, non-territorial males are classified as pre-territorial or post-territorial. Pre-territorial males are agonistic towards conspecific territorial males and fight to obtain territories. Post-territorial males rarely fight; instead they wait for territories to become vacant.

INTRODUCTION

Calopterygid damselflies have been the focus of much research, often concentrating on aspects of their reproductive biology (JOHNSON, 1962; PAJUNEN, 1966; HEYMER, 1973; WAAGE, 1973, 1979a, 1979b, 1987, 1988; FORSYTH & MONTGOMERIE, 1987; MARDEN & WAAGE, 1990; MARDEN & ROLLINS, 1994; SIVA-JOTHY & TSUBAKI, 1989a, 1989b; SIVA-JOTHY et al., 1995). One of the most interesting features of calopterygid mating systems is the variation in reproductive behaviour or alternative mate-securing tactics commonly exhibited by males. These have been reported for a large number of calopterygid species (WAAGE, 1973; FORSYTH & MONTGOMERIE, 1987; PAJUNEN, 1966; HIGASHI, 1981; SIVA-JOTHY & TSUBAKI, 1989a). As in other calopterygid damselflies, male *Calopteryx splendens xanthostoma* demonstrate two alternative mating tactics; males are either territorial or non-territorial.

Previous work on odonates has shown that (i) males may employ both territorial and non-territorial tactics within a lifetime (TSUBAKI & ONO, 1986; FORSYTH

& MONTGOMERIE, 1987; (ii) the proportion of non-territorial males generally increases with increasing population density (WAAGE, 1972; TSUBAKI & ONO, 1986; CONVEY, 1989); (iii) territorial males have a higher copulation rate (CAMPANELLA & WOLF, 1974; FINCKE, 1984; HARVEY & HUBBARD, 1987; FORSYTH & MONTGOMERIE, 1987; CONVEY, 1989); and (iv) non-territorial males will become territorial if provided with vacant territories (WAAGE, 1973; CONVEY, 1989). All these observations suggest that territoriality is the favoured mating tactic and provides increased fitness benefits.

Non-territorial males become territorial in one of two ways: they either occupy a vacated territory or they enter into, and win, an escalated fight with a territory owner. There has previously been no detailed study of calopterygid damselflies that examines variation in the way non-territorial males obtain territories. This is surprising because the costs associated with fighting for a territory, or waiting/searching for vacated territories are likely to be very different. Whilst fighting is energetically costly, with possible risks of injury or death, the costs of waiting for a vacant territory is manifest as lost reproductive opportunity, a cost which will increase the longer a male waits to obtain a vacant territory.

Because individual male *C. splendens xanthostoma* may adopt both territorial and non-territorial mating tactics within a lifetime, non-territorial males must therefore occur as one of two types: males that have recently matured and are reproductively active, but have yet to obtain a territory (pre-territorial males), and those males that have previously occupied and defended territories (post-territorial males) and have since been displaced. Previous studies of calopterygids have assumed that all non-territorial males are the same (e.g. PAJUNEN, 1966; HIGASHI, 1981; WAAGE, 1973; FORSYTH & MONTGOMERIE, 1987; MARDEN & WAAGE, 1990). Post-territorial males will, on average, be older than pre-territorial males. Previous work on calopterygids (FORSYTH & MONTGOMERIE, 1987; MARDEN & WAAGE, 1990) has suggested that the ability of a male to defend/regain a territory declines with age. Similarly, experience and knowledge of the reproductive site will also differ between pre- and post-territorial males. Differences in age, and the changes allied with it, have often been associated with variation in behaviour (see ANDERSSON, 1994). The aims of this study were (i) to describe the alternative mate-securing tactics of male *C. splendens xanthostoma* and (ii) to examine to what extent pre- and post-territorial males are distinguishable physically and behaviourally.

MATERIAL AND METHODS

STUDY SITE. – The study was conducted between June and August 1994 and 1995, on the river Vidourle in southern France (43°52'N, 04°03'E). The study sites comprised of isolated sections of shallow fast flowing stream, containing dispersed clumps of *Ranunculus penicillatus* (territories). At each site all territories were manipulated so that they were of equal size (0.5 m²), with an equal rate of water flow (> 0.4 ms⁻¹) passing over them, and a similar perch (15-20 cm upright stick) within them

(see SIVA-JOTHY et al., 1995). Territory density was maintained at 5-7 territories per site. All males at each site were caught, individually marked on a hindwing with an enamel pen, and their age category determined (see below). Male forewings were measured (± 0.01 mm) using a pair of digital callipers (Mitutoyo) and the date of initial capture recorded. The process of marking and ageing did not have any overt effect on individuals; in most cases males resumed reproductive activity within a few minutes of release. Males marked at a particular site were rarely found at neighbouring sites (twice in 400 hrs of observation), and no other populations were found within a 40 km radius: migration between sites was therefore minimal.

AGE CATEGORIES. – Because we did not commence our observations at the start of the season it was not possible to determine absolute age (days) 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.

Four age classes of adult males 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). All of these age categories were clearly distinguishable from juveniles, 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).

DISTINGUISHING PRE- AND POST-TERRITORIAL MALES. – Pre- and post-territorial males were distinguished on the basis of marking records and continuous field observations. As the study sites were effectively isolated and all males at a site were individually marked, pre-territorial males could clearly be identified as newly arriving un-marked individuals, suggesting they had only recently matured to reproductive condition. This assumption was supported by the observation that most pre-territorial males were young individuals, recorded as either age category 1 or age category 2. Post-territorial males were defined as marked individuals that had previously been observed defending a territory at the site. Data from individuals which could not be clearly assigned to either pre- or post-territorial categories were not used in the analyses.

OBSERVATIONS. – Daily observations were carried out between 10.00-18.00 h EST. 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 were recorded. Territory take-overs were recorded as either (i) TOV (take-over of a vacant territory), or (ii) DIS (active displacement of a territory holder involving an escalated fight).

Detailed records were made of all 'non-territorial patrol flights' seen. These are rapid, low flights, approximately 10-20 cm above the water surface. Non-territorial patrols always occurred through territories, and ranged from a patrol over a single territory, to patrolling over all territories present at a site. Data collected included the time non-territorial patrols occurred, the individual that made the non-territorial patrol, the propensity of the patrolling male to fight and whether or not the patrol resulted in the acquisition of a territory. The number of territories males patrolled over was noted, and a dispersion index (see SOUTHWOOD, 1978) used to assess the aggregation of non-territorial patrol flights. In cases where males either vacated, or were displaced from, their territories, the territory they had previously held was recorded. Data were collected from 543 non-territorial patrols, made by 89 males.

RESULTS

TERRITORIAL BEHAVIOUR

Territorial males of *Calopteryx splendens xanthostoma* defended isolated, emergent patches of *Ranunculus pennicillatus*, used by females as oviposition sites. These males were site and territory faithful, and perched on the territory itself or on nearby vegetation. They intercepted and chased any conspecific male that entered their territory. As with *C. maculata* (WAAGE, 1988), in the majority of cases the intruder was repelled after a brief (< 10 s) pursuit flight. However, on occasion, an intruding male persisted in his intrusion into the territory and a fight developed. Fights were classified as two types: 'territory disputes' and 'escalated fights'. Territory disputes occurred when the intruding male did not retreat after encountering the resident male. The two males hovered approximately 50-100 cm above the territory surface (often facing each other) and carried out short chases, backwards and forwards, over the territory. Occasionally one of the males would attempt to perch on the territory, following which, the opponent would repeatedly attempt to physically dislodge the perching male. Territory disputes generally lasted for about 30-120 s, after which, one of the males retreated or the fight became escalated. Escalated fights were clearly identifiable as they proceeded through several distinctive, hierarchical stages progressing from slow, stereotyped 'see-saw' flights (see PAJUNEN, 1966; WAAGE, 1988) which gradually speeded up and ranged over increasing distances (often overlapping with neighbouring territories and involving other males), and culminated in high-speed, spiralling chases, spanning the whole reproductive site. The duration of escalated fights (including the time males were perched between bouts of fighting) ranged from 360 to 8220 s ($\bar{x} \pm se = 2550 \pm 821.4$ s).

Territorial males attempted to court all females that landed on, or flew past, their territory, although they rarely pursued females for any great distance outside the bounds of their territory. During courtship, males carried out a characteristic hovering flight around the perched female. Flight was predominately sustained using just the forewings, which noticeably increased in wing beat frequency. In comparison, hindwings were held relatively stationary, and away from the body in a distinctive 'cross-like' manner. Following this display, males threw themselves onto the water surface and floated with the current, continuing to hold their hindwings out. HEYMER (1973) and SIVA-JOTHY et al. (1995) provide more detailed descriptions of the courtship display. Copulation either occurred on the territory itself, or in nearby vegetation. After returning to the territory, territorial males showed close, non-contact, post-copulatory guarding of their recent mate.

NON-TERRITORIAL BEHAVIOUR

Non-territorial males did not defend a resource, but perched in the bank-side bushes close to other male's territories. Non-territorial males were not always site-specific; they were often seen occupying different perch sites within the same observation period and in some cases were mobile over the entire reproductive site. As non-territorial males defended no resource, copulation attempts involved flying down from a perch site and attempting to grab females that were ovipositing on defended territories. As in *C. maculata* (WAAGE, 1973; FORSYTH & MONTGOMERIE, 1987), non-territorial male *C. s. xanthostoma* showed no courtship display towards females. This tactic was, on the whole, relatively unsuccessful and most commonly resulted in the territorial male chasing off the intruding male. Sometimes, females would attempt to flee these copulation attempts with the non-territorial male pursuing her for considerable distances. On the few occasions ($n=5$ in 400 h of observation) when non-territorial males were successful in getting a female in tandem, copulation took place in bank-side vegetation, after which females usually returned to the territory from which they had been abducted. Non-territorial males rarely showed guarding behaviour towards these females ($n=1$ in 400 h of observation), and typically retreated if challenged by territory holders; furthermore, they tolerated the presence of conspecific non-territorial males.

NON-TERRITORIAL PATROL FLIGHTS

Non-territorial patrol flights were characteristic of intruding, non-territorial males, although territorial males occasionally made these flights over neighbouring territories. Non-territorial patrols generally resulted in one of four outcomes. (i) The intruding male attempted an abduction of a female; (ii) the intruding male obtained a vacant territory; (iii) the intruding male was repelled after a brief pursuit flight; (iv) a fight occurred.

Of the 543 non-territorial patrol flights observed, 21 (3.9%) were associated with an attempted abduction of a female of which only 5 (0.9%) were successful, 49 (9.0%) resulted in the male obtaining a vacant territory, 361 (66.5%) resulted in brief pursuit flights by resident males, and 112 (20.6%) resulted in a fight.

In total, 345 of the 543 flights observed (63.5%) were unequivocally assignable to either a pre- or a post territorial male. Of these, post-territorial males were responsible for 242 flights (70.1%), compared to 103 (29.9%) for pre-territorial males. The remaining 198 flights (36.5%) were made by territorial males defending neighbouring territories, or by non-territorial males whose previous alternative mate-securing tactic was not known.

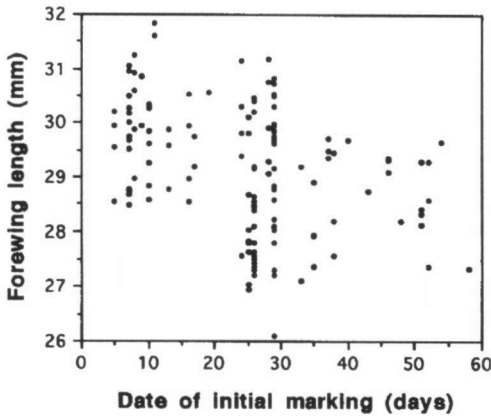


Fig. 1. The relationship between male size (forewing length) and time of season. Date of initial marking provides a good indicator of seasonality because unmarked males were new arrivals (see Methods). All unmarked individuals were marked the first time they were observed at the study site. Day 1 of the season was 25th June 1995 whilst day 58, was 21st August 1995.

PHYSICAL DIFFERENCES BETWEEN PRE- AND POST-TERRITORIAL MALES

Post-territorial males were older and had significantly longer wings than pre-territorial males (Tab. I). Male size (measured as forewing length) progressively declined throughout the season (Spearman's r , $r = -0.332$, $N = 135$, $p < 0.0001$) (Fig. 1).

BEHAVIOURAL DIFFERENCES BETWEEN PRE- AND POST-TERRITORIAL MALES

Pre-territorial males had a significantly greater propensity to fight during non-territorial patrol flights, and obtained significantly more territories through escalated fights with territory holders. In comparison, post-territorial males avoided fights during non-territorial patrols, and obtained significantly more territories by occupying vacated territories without a fight (Tab. I). There was a significant difference in the time taken for pre- and post-territorial males to obtain territories, with post-territorial males taking 7.1 times as long to obtain a territory. However, pre-territorial and post-territorial males showed no significant difference in the number of territories patrolled over per hour, or the number of non-territorial patrol flights they made per hour (Tab. I). A comparison of the dispersion and distribution of non-territorial patrols over territories revealed that (i) pre-territorial males showed a random distribution of non-territorial patrols over territories; and (ii) post-territorial males showed a non-random allocation of non-territorial patrols, preferentially patrolling on the last territory they had defended (Tab. I).

DISCUSSION

Differences in age and size have frequently been correlated with variation in adult male odonate mating behaviour (TSUBAKI & ONO, 1987; FORSYTH &

Table I
A comparison of pre- and post-territorial male *Calopteryx splendens xanthostoma*

Features considered	Male type		Test statistic	<i>p</i>
	pre-territorial	post-territorial		
Number of males observed	36	30		
Wing length (mm)	29.09±0.25	30.07±0.18	un-paired t-test, <i>t</i> = 3.16, <i>n</i> ₁ = 19 <i>n</i> ₂ = 24	<i>0.003</i>
Age	2.043±0.12	2.733±0.14	MWU-test ^a , <i>n</i> ₁ = 23, <i>n</i> ₂ = 30	<i>0.0007</i>
Type of takeover	TOV ^b : 5 DIS ^c : 16	TOV ^b : 14 DIS ^c : 5	χ ² test, χ ² = 9.950	<i>0.005</i>
Fight or no fight?	fight: 22 no fight: 5	fight: 8 no fight: 18	χ ² test, χ ² = 13.867	<i>0.001</i>
Time to obtain a new territory (mins)	54.2±15	387.0±81	MWU-test ^a , <i>n</i> ₁ = 19, <i>n</i> ₂ = 17	<i>0.0008</i>
Number of territories patrolled over (male ⁻¹ hr ⁻¹)	5.96±1.3	2.59±0.38	MWU-test ^a , <i>n</i> ₁ = 26, <i>n</i> ₂ = 29	0.12
Mean number of non-territorial patrol flights (male ⁻¹ hr ⁻¹)	2.32±0.45	1.48±0.21	MWU-test ^a , <i>n</i> ₁ = 26, <i>n</i> ₂ = 29	0.23
The mean 'dispersion' ^d of non-territorial patrol flights (1 = random, <1 = dispersed, >1 = aggregated)	0.99±0.16	2.78±0.76	MWU-test ^a , <i>n</i> ₁ = 25 <i>n</i> ₂ = 26	<i>0.028</i>
The difference in dispersion compared to a random distribution	0.99±0.16		Wilcoxon 1-sample test, stat = 70.5, N for test = 17	0.795
The difference in dispersion compared to a random distribution		2.78±0.76	Wilcoxon 1-sample test, stat = 184, N for test = 21	<i>0.018</i>
Proportion of non-territorial patrol flights on the last territory defended, compared to that expected by chance		0.38±0.05	Wilcoxon 1-sample test, stat = 292, N for test = 25	<i>0.001</i>

Results are significant at *p*<0.05, and indicated in italics.

^aMWU-test, Mann Whitney U-test.

^bTOV, takeover of a vacant territory.

^cDIS, active displacement of a territory holder after an escalated fight.

^dThe dispersion index is defined as variance/mean (SOUTHWOOD, 1978).

MONTGOMERIE, 1987; GRIBBIN & THOMPSON, 1991). Whereas age differences may truly be correlated with pre- and post-territorial behaviour, the difference in size may simply be due to a seasonal effect. In many odonates, size of individuals commonly decreases throughout the season (PENN, 1951; BANKS & THOMPSON, 1985; MICHIELS & DHONDT, 1989); this is also true of *C. s. xanthostoma* (Fig. 1). Therefore, the oldest males in a population also tend to be the largest individuals, having emerged earlier in the season. Thus, the difference in size between pre- and post-territorial males may simply be a result of a difference in time of emergence. A second possibility is that smaller males are unable to obtain territories, as is the case in some other odonate species (MILLER, 1983; FINCKE, 1992). If this were true, smaller individuals may have been observed as pre-territorial males, but would never have been recorded as post-territorial males.

Age-related changes in male behaviour are often thought to be the result of either declining resource holding potential (RHP), or changes in the experience or learning of the individual (see ANDERSSON, 1994). Previous studies on calopterygids (FORSYTH & MONTGOMERIE, 1987; MARDEN & WAAGE, 1990) have suggested that a male's ability to defend and/or re-gain territories declines with age, older males having a lower RHP. If this is true, one possible interpretation of the behavioural differences between pre- and post-territorial males in *C. s. xanthostoma* is that young pre-territorial males have a high RHP, enabling them to fight and displace territory holders. Several studies (TSUBAKI & ONO, 1987; FORSYTH & MONTGOMERIE, 1987; WAAGE, 1988; MARDEN & WAAGE, 1990) have reported that territorial males are often displaced by younger individuals. In comparison, post-territorial males of *C. s. xanthostoma* are older, have a lower RHP, and so may be unable to fight and displace territory holders. Consequently, they may be forced to wait for territories to become vacant. Furthermore, the results of this study show that the time taken to obtain a territory was about seven times greater for post-territorial males compared to pre-territorial males. Pre-territorial males were more likely to fight during non-territorial patrols, perhaps suggesting that they are superior competitors compared to post-territorial males.

An alternative, non-exclusive, explanation is that pre- and post-territorial males differ in experience and/or learning. Post-territorial males know the reproductive site, and may have 'information' about conspecific rivals on neighbouring territories, the position of territory boundaries, and the reproductive value of specific territories. Pre-territorial males will tend to be inexperienced individuals with no information about the reproductive site or its occupants. As a result, pre-territorial males may be more likely to enter escalated fights because they do not know who to avoid. WAAGE (1988) has pointed out that, in situations where there is a 'confusion of residency' between two males, escalated fights will be the outcome. However, in *C. s. xanthostoma*, pre-territorial males were commonly the aggressors in fights, suggesting that 'confusion of residency' may not be the explanation. Similarly, a lack of experience does not explain why pre-territorial males normally win

fighters and displace resident males. Although changes in experience and learning may be important, these changes alone are unlikely to explain the differences in behaviour of pre- and post-territorial males.

The results show that the majority of non-territorial patrol flights were not attempts to capture females. In most cases, non-territorial patrol flights elicited only a brief defensive flight from territory holders. A possible function of these patrol flights may be to gather information about poorly defended, or even undefended, territories. Pre-territorial males executed non-territorial patrol flights at random with respect to individual territories, sometimes visiting all territories present at a site. Pre-territorial males may therefore be assessing territories at a reproductive site as well as the fighting ability of the males defending those territories. Post-territorial males, on the other hand, showed non-territorial patrol flights that were aggregated, with a significant preference for the territory they had been displaced from. One reason may be that post-territorial males have information about the male that displaced them that would enable a rapid assessment of any decline in performance. Alternatively, it may represent a refusal of the male to vacate the territory, especially if the male considers the territory to be of high reproductive value. In the libellulid dragonfly *Nannophya pygmaea* males that had been displaced from their territory repeatedly attempted to re-gain it (TSUBAKI & ONO, 1987). Finally, it could be that males are more successful at sneaking on their own territories, particularly if they are still 'recognised' as the holder and are therefore able to avoid conflict with neighbours.

In conclusion, the results of this study demonstrate physical and behavioural differences between pre- and post-territorial males; notably that pre- and post-territorial males adopt very different territory acquisition strategies. The relationship between RHP and male territory acquisition strategies is discussed elsewhere (PLAISTOW & SIVA-JOTHY, 1996).

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