

TO STAY OR NOT TO STAY: DECISION-MAKING DURING TERRITORIAL BEHAVIOUR OF *CALOPTERYX HAEMORRHODALIS* AND *CALOPTERYX SPLENDENS SPLENDENS* (ZYGOPTERA: CALOPTERYGIDAE)

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Abstract

The effect of copulation and presence of predators on territorial behaviour of male *Calopteryx haemorrhoidalis* (in southern France) and of male *C. splendens splendens* (in northern Germany) was studied in nature. A male obtaining a copulation early in the day often secured more copulations later that day than did males not obtaining an early copulation. Predators such as Green frogs, *Rana esculenta*, and water spiders, *Dolomedes* sp., affected subsequent behaviour of male *Calopteryx* that they attacked but failed to catch. A male *C. haemorrhoidalis* that had only recently occupied a territory when attacked by a spider, vacated the territory immediately, whereas a male first attacked after having occupied a territory for more than three hours and that had already courted females there remained, while avoiding the predator's immediate location. Results are discussed in the context of the value of the territory as a resource.

Introduction

The mating system widespread among calopterygids is based on resource-defence promiscuity (Emlen & Oring, 1977; Meek & Herman, 1991): males occupy and defend territories where copulation and oviposition take place (Pajunen, 1966; Heymer, 1973; Waage, 1987; Plaistow & Siva-Jothy, 1996).

Territoriality is a high cost-high yield tactic: territories are energetically costly to defend but usually provide the owner with a greater number of copulations than is obtained by (non-territorial) sneakers or satellites (Waltz & Wolf, 1984). In calopterygids relevant findings vary considerably: Plaistow & Siva-Jothy (1996) estimated the reproductive success of a territorial male *Calopteryx splendens xanthostoma* (Charpentier) to be about a thousand times greater than that of a non-territorial male; and Forsyth & Montgomerie (1987) found that male *C. maculata* (Beauvois) averaged 3.9 copulations per day whereas sneakers achieved only 0.14 although, because of their greater reproductive lifespan, the lifetime reproductive success of males that did some sneaking was almost twice as high as that of territorial males.

A territorial male has to choose a territory and often fight to defend it, and in the course of a day has to decide whether to vacate a territory or to stay there. Such decision-making depends on extrinsic factors such as weather, harassment by rivals or predators, and the attractiveness of a territory for females, and the outcome can be expected to balance costs and benefits in a way that optimizes lifetime reproductive success (Andersson, 1994; Hilfert-Rüppell & Rüppell, in prep.). Risk of predation for odonates is especially high during copulation and oviposition, but there is no evidence that intersexual signals increase such risk (Rehfeldt, 1995).

The aim of this study was to find out how fighting, copulation and predation affect the resource value of a territory, and the decision whether to defend or vacate a territory, in *C. haemorrhoidalis* (Vander Linden) and *C. splendens splendens* (Harris).

Methods

Observations were conducted in 1996 from 28 May to 18 June in southern France on *C. haemorrhoidalis*, and from 14 July to 20 August in northern Germany on *C. splendens splendens*. Times are expressed as MESZ (Middle European Standard Time); during the study period solar noon at the study sites fell at about 1300 MESZ in southern France and at about 1303 MESZ in northern Germany.

In southern France the study site was an irrigation canal running from northeast to southwest through a stony steppe — the Crau (43°33'N, 40°51'E). The canal, about 2 m wide and up to 50 cm deep, was only sparsely vegetated, having been cleared during winter 1995-1996. It supported plants such as *Berula erecta* (Coville), *Juncus articulatus* (L.) and *Mentha aquatica* (L.).

A box (dimensions 30 x 30 cm) containing *Berula erecta* was placed in the stream where *C. haemorrhoidalis* was abundant, as a focus for a potential territory (the “experimental territory”). Mature males ($n=184$) were marked as individuals by applying a fast-drying silvery paint (Edding 780) to the hindwings. Many were marked to ensure that most males flying in the observation area were marked ones. A Sartorius balance (± 0.1 mg) was used to measure live weight ($n=176$). Head width, hind-wing length and abdomen length ($n=182$) were measured with a dial calliper (Mitutoyo) $\gg \ll 0.01$ mm).

The experimental territory and nearby territories were observed continuously from about 0900 to 1800 h, and time budgets for territorial males were constructed for fighting, courting, territorial flights, flights following females, changes of perch site and copulation. If a male was territorial in the experimental territory, his behaviour was manipulated, either by hand-pairing (using the method of Oppenheimer & Waage, 1987) or by capturing and confining him for variable periods, allowing another male to become dominant in this territory. The confined male was kept in a gauze container in the shade and was released after a rival had become resident in his territory or the experiment was stopped when no new male arrived in the territory within 30 min.

In northern Germany the study site was north-northwest of Braunschweig (52°26'N, 10°23'E), on the Oker river where it is about 14-18 m wide and up to 0.7-1.50 m deep in the main channel. Observations were conducted continuously on 23 days at a

highly frequented territory about 2.5 m long situated beside the riverbank. This territory was demarcated on either side by patches of *Phalaris arundinacea* (L.) and featured about 1 m² of floating *Ceratophyllum demersum* (L.) used as oviposition substrates by *C. splendens splendens* at this site.

Results (Fig. 1)

Influence of copulation on behaviour

On 16 June the behaviour of three male *C. haemorrhoidalis* (nos. 102, 112 and 215), occupying adjacent territories, was monitored simultaneously. From 1145 to 1345 h, 102 courted significantly less frequently and more briefly than the other two did (Table 1). Nevertheless 102 was the first to copulate on that day. During the subsequent hour 102 copulated three times, and there were up to 5 females ovipositing in his territory simultaneously. The male tried several times to grasp a female but only twice succeeded — when a female was surfacing after underwater oviposition. During the two hours' observation 102 copulated eight times, and both 112 and 215 twice each, whereas another male (154), occupying a territory nearby, obtained no copulations.

Table 1. Total duration of courting time (seconds) and the number of courting flights and matings for three males of *C. haemorrhoidalis* in neighbouring territories during two hours' observation on 16 June and three hours' observation on 17 June 1996.

Time	Male number		
	102	112	215
16 June			
Courting flights	36 s (<i>n</i> =10)	134 s (<i>n</i> =36)	97 s (<i>n</i> =27)
Matings	8	2	2
17 June			
Courting flights	89 s (<i>n</i> =20)	17 s (4)	29 s (<i>n</i> =8)
Matings	0	0	0

On 17 June male 102 was foraging at its roosting site, making 52 foraging flights between 0910 and 1008 h, before becoming territorial — 42 min and 39 min respectively after 112 and 215 did so. Between 1010 and 1310 h on that day, during which interval no copulations occurred, 102 made significantly fewer territorial flights (sum of duration 48 sec, *n*=17) than either 112 (77 sec, *n*=24; *U*=254.5, *P*<0.05) or 215 (83 sec, *n*=28; *U*=219, *P*<0.01), but significantly more courting flights (*U*=69.5, *P*<0.05) (Table 1).

In the evening of 17 June at 1755 h and 29 °C, after all males at the study site had ceased to exhibit reproductive behaviour since 1737 h, 102 was captured and hand-paired. Promptly within one minute after copulation this male recommenced reproductive behaviour and was the only one which courted and chased foraging females

for the next 20 min, during which period reproductive behaviour progressively decreased and the frequency of foraging flights progressively increased.

This experiment was repeatable: after hand-pairing the onset of territoriality in the morning occurred up to 30 min earlier than in controls ($n=8$) and in the evening, after territoriality had ceased spontaneously, it was resumed for 15-50 min after hand-pairing.

Attempts to hand-pair *C. haemorrhoidalis* ($n=75$) and *C. splendens splendens* ($n=70$) respectively resulted in copulation in 81% and 79% of cases.

In another experiment inferior and dominant males of *C. haemorrhoidalis* at territories were distinguished. An inferior male perched beside and not in the centre of the territory, did not initiate fights, and was the first to perch again after a threatening fight, whereas a dominant male behaved in the opposite way and also patrolled the territory. After hand-pairing, inferior males won fights significantly more often (contingency table: $n=28$; $\chi^2=26.5$, $P<0.001$) and became dominant in the territory they had previously occupied. When no hand-pairing preceded territorial fights, the resident won 19 of 23 such fights. After having lost a fight (against either a hand-paired or an unmanipulated male) some males became territorial the same day in another territory from a few metres up to 200 m away ($n=7$).

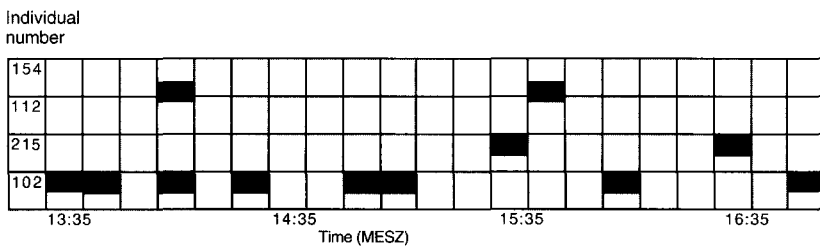


Figure 1. Matings (black cells) of four *C. haemorrhoidalis* males (nos. 154, 112, 215, 102, listed in the order in which they occupied territories in the river) on 16 June 1996 from 1335–1655 h MESZ.

Influence of predation on behaviour

Green frogs and C. splendens splendens. Green frogs (*Rana esculenta* L.) lurking in *Calopteryx* territories were usually motionless but sometimes crept closer to a perched male or an ovipositing female. Of the 26 predation attempts by Green frogs, 12 were successful (Fig. 2): 10 males and 3 females were captured, two of these being captured while in copula.

Male *Calopteryx* were captured during various activities (Fig. 2). *C. splendens splendens* males were courting in flight as well as sitting on the water surface presenting the abdominal lantern. While courting on the water surface two of three males were caught by a frog, whereas in flight, only one of three was killed. *Calopteryx* males were never captured by Green frogs while fighting or patrolling. Only one of the males that evaded capture failed to react to the frog's attack and continued fighting; 7 of 13 (54%) left the territory immediately after the attack, whereas 5 of 13 (38%) flew into vegetation 50-100 cm above the water surface. In two such instances ovipositing

females were no longer guarded by the territorial male and were grasped and mated by incoming sneakers.

One male copulated and showed the oviposition substrate to the female whereupon a frog unsuccessfully tried to capture her. The male continued to defend the territory and obtained a second copulation with a different female, whereupon the frog tried unsuccessfully to capture the male. Despite these events, the male remained the dominant resident in the territory and became dominant at that site the next day.

While ovipositing, two females were captured by frogs and one that evaded capture promptly submerged.

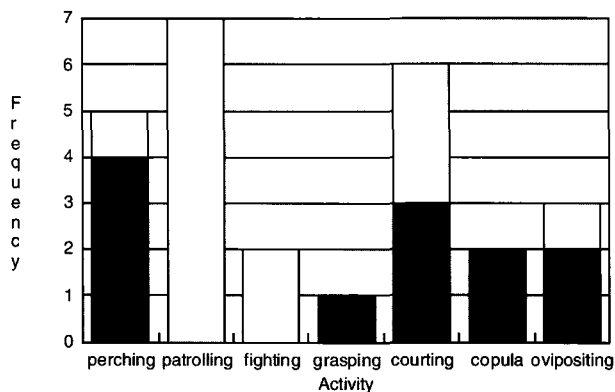


Figure 2. Predation attempts (white bars) and predation success (black bars) by Green frogs (*Rana esculenta*) on male and female *C. splendens* during different activities in a territory. Females were involved only when in copula and ovipositing.

Water spiders and C. haemorrhoidalis. A water spider, *Dolomedes* sp. (body length excluding legs ca 2 cm), was resting cryptically on the water surface among stems of *Berula erecta* on which territorial males of *Calopteryx* were perching and females were ovipositing. The spider jumped 13 times at *Calopteryx* males that were patrolling, fighting or courting but failed each time (Fig. 3). Once a spider was seen to capture a female climbing downwards on a stem of *Berula erecta* to submerge and oviposit in it. In the late morning of another day, the detached wings of a female were found floating beneath the same plant; so presumably a spider had captured her.

Males missed by a spider reacted to the attempted capture in several ways. Three males that had been territorial for 5, 7 and 8 min all left the territory immediately after the attack. A fourth male that had been territorial for more than three hours was patrolling when a spider first tried to capture him. At that time he had been courting four females 48 times during 273 sec. The spider jumped for him twice more while he was patrolling and once while he was courting on the water surface, but without success. Despite these attacks this male remained territorial the whole day but, when courting or patrolling, he avoided the area by the plant where the spider was sitting. This male obtained two copulations during the day and became a dominant resident in the same territory on the two following days.

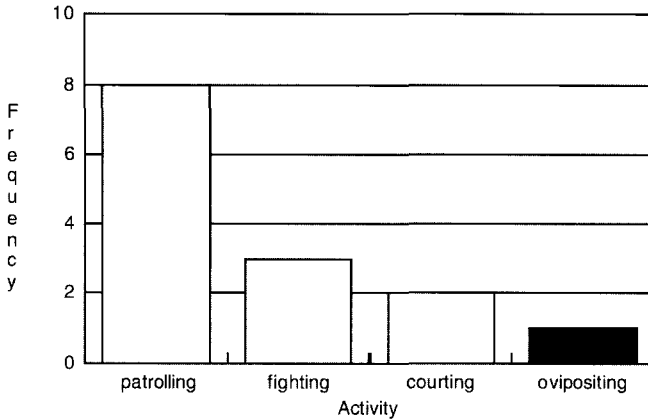


Figure 3. Predation attempts (white bars) and predation successes (black bar) by a spider (*Dolomedes* sp.) on male and female *C. haemorrhoidalis* during different activities in a territory. Females were involved only in ovipositing.

Discussion

Mating success

Factors that correlate with site quality (e.g. encounter rate with rival males and females; safety from predation) can influence mating success and movement between sites in odonates. Tsubaki & Ono (1986) found that male *Nannophya pygmaea* Rambur were more site-faithful in high-quality sites. Because prime territories attract more intruders, defence costs will increase with territory quality (Ewald & Charpenter, 1978). The costs of occupying such prime territories may be further increased because, as in this study, predators chose them for hunting grounds. Failed predation attempts often made *Calopteryx* males abandon territories. But when a male had courted several females or had obtained copulations he sometimes decided to stay in a territory despite having to share it with a predator. The quality of a male's territory correlates with the number of females attracted to it, and his fitness gain can be predicted to covary with this measure (Waltz, 1982). Individuals use their own reproductive success to assess the quality of a site, as Switzer (1997) found in *Perithemis tenera* (Say), males of which were more likely to change sites when prevented from mating than when allowed to do so. Switzer assumed that cues such as habitat structure and the presence of conspecifics may enable habitats to be recognized but that reproductive success may be the best criterion of habitat quality. This assumption matches the findings of the present study: copulations (whether or not they were accomplished by hand-pairing) caused males to win fights and to achieve dominance in a territory, thus increasing the likelihood of their mating again. After copulations the behaviour of territorial male *C. splendens splendens* changed significantly as they engaged in more patrol and threatening flights (Hilfert-Rüppell & Rüppell, in prep.), indicating that the resource value of the territory had increased. Not only the number of copulations achieved in a day, but also the time of day when they occur can influence future mating success:

after a male had the first copulation of all males in the observed part of the canal, his female oviposited in his territory. Other females were attracted, seven further females oviposited and the male succeeded in copulating with three of them.

In enclosures *C. splendens splendens* that obtained copulations at the beginning of the experiments enjoyed the highest mating success thereafter (Hilfert-Rüppell & Rüppell, in prep.). Alcock (1979, 1987) and Waage (1987) have shown that greater numbers of *Calopteryx* females are attracted to oviposition sites of higher quality, where quality can be objectively measured according to other criteria. Furthermore, the presence of a female at an oviposition site attracts other females (Waage, 1987; Rüppell, pers. comm.), there being several selective advantages to group oviposition (Martens & Rehfeldt, 1989).

Predation by Green frogs

In this study male *C. splendens splendens* were never seen to be caught by Green frogs while fighting or patrolling in their territories. More than 50% of the males left the territory after an attack, indicating that the costs (in terms of predation risk) of remaining exceeded the reproductive benefit of doing so. All other males except one reacted by perching higher above the water, thus placing them farther from oviposition sites where they were less able to prevent ovipositing females from being grasped by intruders, an event witnessed twice during this study. Because during copulation a male *C. splendens splendens* removes up to 98% of rivals' sperm in the storage organs of his partner (Lindeboom, 1996, 1998), the costs for such high-perching males were very great in terms of lost reproductive success. As the average number of copulations per day achieved by a male in a 'good' territory was 2-3, one lost mating represented a high proportion of his daily reproductive success.

One male, after having copulated, witnessed a predation attempt on his former partner; he then copulated again and escaped himself from a predation attempt. Despite these experiences, he remained in the territory and became dominant there again the next day. The indication in this instance is that enhancement of potential mating success was valued more highly than avoidance of predation risk.

Green frogs were successful as predators when territorial males were perching, courting or copulating. The courting flight of calopterygids is slower and features a higher wingbeat frequency than normal flight (Rüppell, 1985, 1989), thus making possible an even and cautious approach to the female; at the same time courting is energetically costly and entails reduced manoeuvrability. Such aerodynamic consequences and the fact that a courting male probably focuses more on the female than his surroundings can be expected to make it easier for a frog to capture a *Calopteryx* male that is courting than one that is fighting or patrolling.

Predation by water spiders

In a searching study, Rehfeldt (1995) found major predators of *C. haemorrhoidalis* to be reptiles (Squamata), dragonflies (Aeshnidae, Gomphidae and Libellulidae) and spiders (Araneidae, Pisauridae, Salticidae and Thomisidae). Because of their increased activity while fighting, territorial males were more likely to be caught in spider webs than were females or immature adults of both sexes.

In my study males that had been territorial for only some minutes before first being attacked by a spider all left the territory immediately. In contrast, the male that had been territorial for more than three hours and that had been courting four females in sequence when first attacked, remained at the territory. Probably this male showed stronger site attachment because he had witnessed females being attracted to the territory and because he was sufficiently familiar with its topography that, while courting or patrolling, he could avoid the dangerous parts where the predator was sitting. The trade-off for him was evidently positive, despite the costs resulting from the predator's presence: after the attacks he obtained two copulations, a success that presumably enabled him to occupy the territory for the next two days. The trade-off for the two males that were attacked by the spider soon after having entered the territory, and before any female had arrived at the territory, was evidently negative, resulting in their prompt departure.

The present study shows that male calopterygids can assess the quality of a territory. Prior mating success can influence the outcome of fights and seems to be a key factor influencing resource value and accordingly a male's decision to stay in a territory or to leave it.

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