REPRODUCTIVE BEHAVIOUR OF THE TERRITORIAL DAMSELFLY *CALOPTERYX HAEMORRHOIDALIS ASTURICA* OCHARAN (ZYGOPTERA: CALOPTERYGIDAE)

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The reproductive behaviour of *C. h. asturica* is described. Males fought with each other for the possession of territories which contained the oviposition resource required by females. Females arrived at territories and either copulated and left the territory, copulated and oviposited in that territory or oviposited without a preceding copulation with the territorial male. Territorial males seemed to have a higher mating success than nonterritorial males. Males carried out courtship displays before and after copulation until females finished oviposition. Copulation was divided in two stages which were characterised by the nature of the male's abdominal flexions. The number of abdominal flexions during stage I and II was 50.2 ± 7.2 and 54.5 ± 16.7 (mean ± s.d.) respectively. The sexual behaviour of both sexes is discussed under current knowledge of sexual selection studies in Calopterygidae.

INTRODUCTION

Adult odonates are good field models for behavioural studies of reproduction. They are large, easy to mark and observe since their reproductive behaviour is spatially-restricted. Amongst the odonates, the family Calopterygidae is perhaps the most widely studied. Adult calopterygid males defend (from hours to several days) fixed areas which contain oviposition resources and prevent other conspecific males from approaching those resources (e.g. BUCHHOLTZ, 1951, 1955; JOHNSON, 1962; PAJUNEN, 1966; HEYMER, 1973; WAAGE, 1973, 1988; ALCOCK, 1979; SUZUKI & TAMAISHI, 1981; MIYAKAWA, 1982; CONRAD & HERMAN, 1987; SIVA-JOTHY & TSUBAKI, 1989a, 1989b; CÓRDOBA-AGUILAR, 1995; GRETHER, 1996a, 1996b; PLAISTOW & SIVA-JOTHY, 1996). Males able to defend such a resource are termed "territorial" males (e.g. WAAGE, 1973), and such males usually court any female that enters their terri-

tory (BUCHHOLTZ, 1951, 1955; JOHNSON, 1962; PAJUNEN, 1966; HEY-
MER, 1973; WAAGE, 1973, 1988; ALCOCK, 1979; SUZUKI & TAMAISHI,
1981; MIYAKAWA, 1982; CONRAD & HERMAN, 1987; HOOPER, 1994;
PLAISTOW & SIVA-JOTHY, 1996). The resource is defended by agonistic
aerial interactions in which intruding males are chased away from the resource
(e.g. MARDEN & WAAGE, 1990; MARDEN & ROLLINS, 1994; PLAISTOW
& SIVA-JOTHY, 1996). When the density of males exceeds the number of terri-
tories some males adopt "nonterritorial" mating tactics (e.g. PAJUNEN, 1966;
WAAGE, 1973; FORSYTH & MONTGOMERIE, 1987; GRETHER, 1996a,
1996b; PLAISTOW & SIVA-JOTHY, 1996). These nonterritorial males rarely
show agonistic behaviour against conspecific males and, instead, attempt to secu-
re matings with females that arrive at reproductive sites, or with females that are
already present on a male's territory when the territorial male is occupied (copu-
lating or fighting) (e.g. PAJUNEN, 1966; WAAGE, 1973, 1988; SIVA-JOTHY &
TSUBAKI, 1989a, 1989b; PLAISTOW & SIVA-JOTHY, 1996).

Female calopterygid damselflies visit the defended territories to copulate and/or
oviposit. A unique feature of the calopterygid reproductive behavioural repertoi-
re is that copulation is usually preceded, and often followed, by a series of ste-
reotyped male displays (e.g. PAJUNEN, 1966; HEYMER, 1973; WAAGE, 1973,
1988; KUMAR & PRASAD, 1977; CONRAD & HERMAN, 1987; PLAISTOW,
1997). Pre-copulatory male displays directed at visiting females are one of two
types: (a) either the "cross display" (sensu WAAGE, 1973) during which the
flying male "faces" an approaching female with his wings held open, with the
hindwings barely touching the water surface, whilst his 8th and 9th abdominal
segments are bent upwards, or (b) the "hovering" (sensu WAAGE, 1973)/"court-
ship arc" (sensu CONRAD & HERMAN, 1987) display during which the male
flies in a bobbing motion in front of a perched female. He keeps his wings open
by flying with a high-frequency, shallow amplitude wing beat and his 8th and 9th
abdominal segments are often bent upwards. If a female does not reject the male's
advances, copulation may follow. However, females can avoid the male's atten-
tion by leaving the area or by showing a "refusal display" (WAAGE, 1973) to the
courting male. During the refusal display, the female quickly opens and closes
both pairs of her wings when the male approaches her.

During copulation, some damselfly species (e.g. WAAGE, 1979a, 1988; MIL-
LER & MILLER, 1981; MIYAKAWA, 1982; MILLER, 1987a, 1987b; CORDE-
RO, 1989; SIVA-JOTHY & TSUBAKI, 1989a; CORDERO & MILLER, 1992;
CORDERO et al., 1995; SAWADA, 1995; SIVA-JOTHY & HOOPER, 1995) go
through a stereotyped series of behavioural phases characterised by different rates
and amplitudes of abdominal flexions. Based on the stereotyped aspects of this
behaviour, different copulatory stages have been defined (MILLER & MILLER,
1981). During stage I, the male genitalia displace sperm from the female's sperm
storage organs, while sperm transfer occurs in stage II and/or III (e.g. WAAGE,

1979a, 1988; MILLER, 1987a; SIVA-JOTHY & TSUBAKI, 1989a; CORDERO & MILLER, 1992; CORDERO et al., 1995; SAWADA, 1995; SIVA-JOTHY & HOOPER, 1995; CÓRDOBA-AGUILAR, 1999).

Some calopterygids show a post-copulatory display that precedes oviposition. During this post-copulatory display, the male "lands" on the water surface and allows himself to be taken by the stream in front of the female for a variable distance (see e.g. ROBERT, 1958). The male opens his wings and bends up his 8th and 9th abdominal segments during the display.

In this paper several aspects of the sexual behaviour of *Calopteryx h. asturica* are described and discussed in the context of current knowledge of sexual selection studies in Calopterygidae.

MATERIAL AND METHODS

A population was studied at a narrow (0.5-1 m) stream, approximately 2.5 km W of Pontevedra, Spain, during the summer (June-early September) of 1996, 1997 and 1998. A concrete tunnel (of approximately 50 m of length) divided the stream into two sections, each having an approximate length of 200 m. Both stream sections were surrounded by corn fields and eucalyptus trees. The stream contained several species of freshwater plants, roots, pieces of wood, and other submerged substrata. Other calopterygid species occurring there were *C. splendens* and *C. virgo*. Interspecific encounters among the three species were not common as *C. h. asturica* occurred at the highest density.

During 1996 and 1997, all unmarked adult males and females were captured and marked every day. Marking of males consisted of combinations of dots of four colours (yellow, red, white and blue; using enamel paint) painted on the right side of the thorax and abdomen. A distinctive individual number was written on the posterior right wing of females. Along with the marking process an identification of male status (territorial and nonterritorial; for a description and definition of both see results section) was carried out.

Focal individuals were observed for two hours during which I recorded the duration (in seconds) and type of behaviour of adult males and females directed towards a conspecific during reproductive activity. To record the identity and number of females and males present in the stream, a census was carried out everyday, from 1300 to 1500 hr.

Duration of behaviours is presented in seconds. Data on male-male interactions were log-transformed so that they fulfilled the assumptions of the parametric statistical tests used. Statistical analyses were performed using Minitab ®, version 11.2. Means ± standard deviations are provided unless stated otherwise.

MALE REPRODUCTIVE BEHAVIOUR

Observations revealed that some males were faithful to an oviposition site for several days (10.2 ± 8.5 days, range 2-32, N = 64). These males showed strong agonistic behaviour towards conspecific males and always approached them whenever they came within approximately 0.5-2 m of the defended oviposition site. A territorial male was consequently defined as any male showing (a) diurnal site-faithful behaviour on an oviposition resource for more than one day, and (b) exhibiting strong agonistic responses to conspecific males approaching that site. Males that did not meet these criteria were defined as nonterritorial.

Territorial males defended areas centred on isolated, emergent patches of aquatic vegetation. The size of the defended area (hereafter territory), varied between 0.5 and 1.5 m².

Male-male interactions were common over territories. Intruding males could either be territorial (usually males occupying neighbouring territories; N = 568 interactions of this type) or nonterritorial (N = 752). The events occurring during territorial-nonterritorial male interactions are shown in Figure 1 and are described here. Most timed interactions (174 out of 201 that could be timed) of this type were of short duration (4.3 ± 3.5 s). During these, the nonterritorial intruding male was chased out of the territory by the territorial male. Only rarely did these short interactions result in a change in territory ownership (2 out of 174). Some interactions lasted significantly longer (1728 ± 1431 s, N = 27; t-test [log transformed data] = -32.16, d.f. = 41, P < 0.0001) and took place when the intruding male
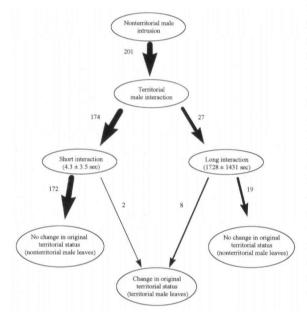

Fig. 1. Flow diagram for 201 male-male interactions when a nonterritorial male flew into a territorial male's territory. [Arrows indicate direction of events; width of arrows indicates the relative proportion of events].

did not leave when approached by the territorial male. These interactions consisted of a spiralling, ascending and descending flight during which both males chased each other over several territories. These encounters finished when one male left the territory. Such encounters were more likely to result in a change in territory ownership (8 out of 27) than those of the short interactions (chi squared test χ^2 = 115.6, d.f. = 1, P < 0.0001).

PRE-, SYN- AND POST-COPULATORY BEHAVIOUR

Both territorial and nonterritorial males courted females. Copulations carried out by the territorial male (29/30) were more common than those carried out by nonterritorial males (1/30). On those occasions (N = 39) when nonterritorial

males displayed to females, the males were approached and chased out of the territory by the territorial male. Consequently, I only report the sexual interactions between territorial males and females (for a graphical description see also Fig. 2).

A territorial male initiated an interaction with a female when she flew over his territory. Two types of pre-copulatory male behaviour were then observed: the cross display and the courtship arc. The cross display continued for 3.1 ± 1.4 s (range 0.7-5.3, N = 24) and occurred whenever a female was flying over an area of submerged plants. The male either landed on the water surface, sometimes letting himself be taken by the stream current for 5-10 cm with his wings open and his last four abdominal segments bent upwards (at approximately 45°), or on a substrate nearby. If the female stayed in the territory or landed on a nearby perch, the courtship arc then followed (N = 112). This display lasted 4.9 ± 2.5 s (range 1-23, N = 112) and took the form of a stereotyped flight in front of the perched female, during which the males used their forewings to sustain flight whilst keeping their hindwings motionless and bending up their last four abdominal segments (at approximately 45°).
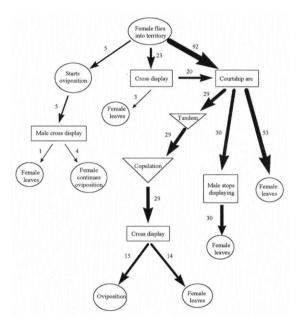

Fig. 2. Flow diagram for 120 territorial male-female interactions that started when a female flew into the male's territory. [Squares and ovals indicate male and female actions respectively. "Female flies" means the female leaves the territory. Direction of events is indicated by the arrows; width of arrows indicates the relative proportion of events].

The courtship arc always preceded copulation. All females (N = 112) initially gave a number of refusal displays (7.3 ± 3.8, range 1-14) to displaying males (both pairs of wings of the female were opened and closed very quickly during this). "Receptive" females stopped showing the refusal display as the male continued the courtship arc. Those events that did not lead to copulation were characterised by the male stopping the display (N = 30) or the female simply flying away from the territory (N = 53). In those events that led to copulation, the male was able to land on the female and walk down her folded wings to reach and grab the dorsal part

of her thorax and enter tandem. Once in tandem, the male translocated sperm from his primary sperm reservoir (located at the 9th abdominal segment) to his seminal vesicle (2nd abdominal segment). After this, both animals showed a short (1-2 s) bout of genital contact and copulation ensued.

Copulation lasted 167.2 ± 66.5 s (N = 27) and was characterised by rocking abdominal flexions. Two copulatory stages could be distinguished on the basis of the frequency and amplitude of these flexions. Stage I occurred as a constant series of 50 (50.2 ± 7.2, N = 28) relatively rapid (approximately 1 Hz), shallow abdominal flexions of approximately 100 s duration (104.2 ± 10.2). Stage II was more variable in the number of flexions (54.5 ± 16.7, N = 28 of the same data set as stage I) and duration (110 ± 30.2 s), and was characterised by slower (approximately 0.5 Hz) and deeper flexions. Copulation terminated with the separation of both sexes' genitalia and the "release" of the female's prothoracic mesostigma by the male's abdominal claspers.

After copulation (but within the territory), females did not usually initiate oviposition the first time they landed on an oviposition substrate. Instead, they made a series (3.2 ± 2.7, range 1-6, N = 15) of short (approximately 5-10 s) visits to different oviposition substrates and went back to their perching sites. Males invariably preceded them during these occasions and showed a cross display. This display was similar to that that took place before copulation (the male landing either on the water surface (N = 7) or on a substrate (N = 8) with his wings open and last four abdominal segments bent up). Once she started oviposition, the male remained close to her for 251.1 ± 135.2 s (range 64-501, N = 15) and then returned to a higher perching site. Females oviposited either at the water surface or while submerged. Eggs were inserted into several substrates (e.g. roots, leaves, pieces of wood). Oviposition duration was highly variable (3312 ± 2538 s, range 30-8040, N = 20).

In some cases (N = 5) females initiated oviposition without a preceding copulation. Males displayed to these females using the cross display. However, most of these females (4 out of 5) continued oviposition for a variable duration (5941 ± 1854 s, range 3564-8052) whilst evading the male's advances.

DISCUSSION

MALE SEXUAL BEHAVIOUR

As with other calopterygid species (see references in the introduction), adult male *C. h. asturica* defend a space of submerged vegetation that females use for oviposition. These territorial males chased any male that entered their territory. The male-male interactions were directed at nonterritorial as well as territorial males and took the form of aerial contests of variable duration. The outcome of the long interactions was a change in the occupying male; this is, the intruding male becoming the territorial male. Similar territorial interactions are common in

other calopterygids and are wars of attrition based on fat reserves (MARDEN & WAAGE, 1990; MARDEN & ROLLINS, 1994; PLAISTOW & SIVA-JOTHY, 1996).

Securing a territory is a major determinant of copulatory success for calopterygid males (WAAGE, 1973; FORSYTH & MONTGOMERIE, 1987; SIVA--JOTHY & TSUBAKI, 1989a, 1989b; GRETHER, 1996a, 1996b; PLAISTOW & SIVA-JOTHY, 1996). In *C. h. asturica*, some males did not defend a territory. It has been shown that, usually, these nonterritorial males are relatively old, fat--depleted individuals who avoid fighting (PLAISTOW & SIVA-JOTHY, 1996) but try to secure copulations (e.g. PAJUNEN, 1966; WAAGE, 1973, 1988; SIVA--JOTHY & TSUBAKI, 1989a, 1989b; PLAISTOW & SIVA-JOTHY, 1996). *C. h. asturica* nonterritorial males avoided fighting but courted females before copulation. Observations suggested that nonterritorial males obtained a lower number of matings compared to territorial males because, although they courted females, they were chased away, and the courtship was interrupted by the territorial male. Another reason why they may have received a lower number of matings is that females preferentially mate with territorial males in order to secure a place for oviposition as occurs in other species (WAAGE, 1973, 1979b; FORSYTH & MONTGOMERIE, 1987; SIVA-JOTHY & TSUBAKI, 1989a).

In other species, nonterritorial males have been documented not to exhibit any pre-copulatory courtship display (e.g. WAAGE, 1973; HOOPER, 1994; but see PAJUNEN, 1966). *C. h. asturica* nonterritorial males, however, performed a courtship display to females. These behavioural differences might not be species specific but rather environmentally dependent, as recent evidence suggests that when male density increases, both territorial and nonterritorial males stop courting females prior to copulation and, simply, take them in tandem (CORDERO, 1999).

PRE-, SYN- AND POST-COPULATORY INTERACTIONS

Males displayed to females prior to copulation using two distinct behaviours: the cross display and the courtship arc. These behaviours were performed, to some extent, sequentially, until copulation.

Various functions have been attributed to pre-copulatory displays. It has been suggested that they accomplish a species, or sexual, recognition function (BUCHHOLTZ, 1951; DUMONT, 1972; HEYMER, 1973; DUMONT et al., 1987, 1993; WAAGE, 1975, 1979b; FINCKE, 1984; DE MARCHI, 1990). More recent observational (HOOPER, 1994) and experimental evidence (SIVA--JOTHY, 1999) suggests that these pre-copulatory behaviours might also function to advertise male resource holding potential and thereby influence a female's mate choice.

Males also displayed to females after copulation by using the cross display. Unlike pre-copulatory displays, very little is known about the functional basis of

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post-copulatory displays in calopterygids. I suggest two hypotheses to explain its function: (a) similar to calopterygid pre-copulatory courtship (GIBBONS & PAIN, 1992; SIVA-JOTHY et al., 1995), it may help the female locate suitable oviposition patches; and/or, (b) it may function as an extension of the male pre-copulatory courtship to induce females to use the male's sperm (EBERHARD, 1985, 1996).

The first hypothesis for the possible function of the post-copulatory display may be that proposed for pre-copulatory courtship: that females use the speed at which males are towed by the water flow during their display to assess the quality of an oviposition site (the faster the water flow, the better; GIBBONS & PAIN, 1992; SIVA-JOTHY et al., 1995). The second hypothesis was proposed by EBERHARD (1985, 1996) as a general explanation for post-copulatory displays in a variety of animal taxa. Interpreting the calopterygid post-copulatory behaviour in the context of Eberhard's ideas, males are inducing females to oviposit immediately after copulation: if males did not do this, females could remate again and the sperm of these males would be removed by subsequent copulating males (WAAGE, 1979a, 1988; SIVA-JOTHY & TSUBAKI, 1989a; SIVA-JOTHY & HOOPER, 1995; LINDEBOOM, 1998; CÓRDOBA-AGUILAR, 1999).

Two copulatory stages were distinguished in C. h. asturica. In this species, displacement of rival sperm by the male genitalia is followed by transfer of sperm in stage I and II respectively (CÓRDOBA-AGUILAR, 1999). In other species (see e.g. MILLER & MILLER, 1981; SAWADA, 1995; SIVA-JOTHY & HOOPER, 1995), three stages have been described with the difference that sperm transfer occurs during stage II and III. In C. h. asturica, males displace spermathecal sperm by stimulating the female's sensory physiology that controls fertilisation and egg laying (CÓRDOBA-AGUILAR, 1999). During copulation, the spermathecal muscles may be induced to contract and thereby release spermathecal sperm. Interestingly, the number of abdominal flexions in stage I were relatively more constant compared to those during stage II. Possibly, 50 flexions is the number of abdominal flexions males might need to induce, via stimulation, the release of the maximum amount of spermathecal sperm. This possibility is currently being investigated.

As with other calopterygids (SIVA-JOTHY & TSUBAKI, 1989a; SIVA-JOTHY & HOOPER, 1995, 1996), C. h. asturica females show a form of oviposition that is not preceded by copulation on that female visit ("SAG oviposition" of SIVA-JOTHY & HOOPER, 1995, 1996). SIVA-JOTHY & HOOPER (1996) provided evidence that this behaviour enabled females to use sperm stored in one of their sperm storage organs, and effectively provided a "cache" of sperm from previous mates. They suggested that females may gain fitness benefits from doing this. The cache was stored in the spermathecae (SIVA-JOTHY & HOOPER, 1995): by storing sperm in this discrete sperm storage organ females may be able to exercise a degree of control over paternity. My estimate of this type of oviposition suggests

at least 21% of events. However, these data are likely to be an under-estimate since SAG oviposition is very cryptic (SIVA-JOTHY & HOOPER, 1995). In *C. h. asturica*, males remove most bursal sperm but show a great variation in spermathecal sperm displacement (CÓRDOBA-AGUILAR, 1999). If females of this species can utilise spermathecal sperm during SAG oviposition events, males may gain a fertilisation advantage if they remove most, or all of the female's spermathecal sperm cache. If *C. h. asturica* females benefit from using the sperm in this cache [and SIVA-JOTHY & HOOPER (1995) showed one benefit may be the high genetic diversity of sperm in this site] then having it all removed and replaced by a single male's sperm may represent a loss of that potential benefit.

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