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TERRITORIAL AND COURTSHIP DISPLAYS IN BORNEAN CHLOROCYPHIDAE (ZYGOPTERA)

A.G. ORR*
Biology Department, Universiti Brunei Darussalam,
Bandar Seri Begawan 3028, Brunei

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Territorial and courtship displays and their relation to male ornamentation were examined in 11 spp. in N Borneo. Males of all spp. were territorial, guarding a small area of oviposition substrate and attempting to mate with ovipositing females. Most spp. exhibited a ritualized threat display, in which males faced each other and displayed the terminal markings on their wings. In the genus *Libellago* there was a pronounced stationary wing display, in which the outstretched forewings were held completely still for about a second. This behaviour did not occur in *L. hyalina* which lacks markings on its wings. Apart from *L. hyalina*, some form of courtship occurred in all spp. for which information was available, typically involving the male swinging to and fro in a semicircle to the side of the female, while displaying and vibrating his pruinescent legs. Variations included display of various markings on wings and abdomen, probably associated with species recognition, and in *Rhinocypha aurofulgens*, standing on the substrate during courtship, a modification probably associated with loss of pruinescence on the legs in this spp. Interspecific interactions were frequently intense, and probably have been important in the evolution of displays. An outline of possible evolutionary relationships among display elements is suggested.

INTRODUCTION

The Chlorocyphidae are robust strong flying damselflies ranging throughout the old world tropics from southern Africa to New Guinea. Males frequently exhibit elaborate ornamentation, including bright abdominal markings of blue, green, red or yellow, dark terminal patches on one or both pairs of wings which sometimes include brilliant iridescent areas or fenestrae, and pale blue or white pruinose legs (PAULSON, 1981). Females are mostly drab coloured and unspecialized in their

* **Present address**: 26 Currimundi Road, Caloundra, Qld 4551, Australia

structure or markings, and there is a very little difference in outward appearance between species. The spectacular nature of the male ornaments suggests they may function as signals in territorial defense and in courtship, and this is supported by ROBERTSON's (1982) study of the rather atypical African species, *Platycypha caligata*, and by several brief accounts of courtship and the display of pruinescent tibiae among members of the highly diverse fauna of tropical Asia (CORBET, 1962; FRASER, 1934; UEDA, 1992). However apart from these reports, little else is known either of the nature and form of displays or of the functions of the various male ornaments.

Knowledge of communication systems in the Chlorocyphidae is especially interesting given the exceedingly complex behaviour of *P. caligata* described by ROBERTSON (1982) and the close relationship of the family to the Calopterygidae, in which territoriality, courtship and other aspects of reproductive behaviour have been extensively studied (e.g. ALCOCK, 1979; JOHNSON, 1962; PAJUNEN, 1966; WAAGE, 1973, 1979). With 20 species in 6 genera, the Bornean chlorocyphid fauna is the richest of any comparable area in the world (LAIDLAW, 1950; LIEFTINCK, 1954; DAVIES & TOBIN, 1984), and offers unparalleled opportunities for comparative studies. In this paper I present qualitative descriptions of territorial and courtship behaviour of eleven Bornean species, ranging from supposedly primitive, relatively unspecialized *Libellago* sp. to morphologically advanced species of *Rhinocypha* and *Heliocypha*. Species discussed exhibit considerable variation in the degree of male ornamentation even within genera, and thus provide a useful basis for comparisons. Although information on several species is very incomplete, its inclusion may be justified by the fact that at present almost nothing is known about the behaviour of these or any closely related species. It is hoped that this study will shed light on the evolutionary relationships of various behavioural patterns occurring in the family.

METHODS

Observations were made at different periods between 10/1/94 and 26/1/95, at the following localities: Kuala Belalong Field Studies Centre (KBFSC), Brunei, principal features of which are described below (see also CRANBROOK & EDWARDS, 1994); Badas Forest Reserve, Sg Rampayoh and various other localities throughout Brunei (see below); Mt Kinabalu National Park (Sabah) and the Danum Valley Field Centre (Sabah). Where possible, behaviour of males was monitored for at least three full days from the early morning when they arrived at their territories, to late afternoon when they departed, and in several cases more extensive observations were made. The total observation time, including several half days was about 32 days. In most cases observations were confined to a small section of habitat, not more than 30 m in length, which could be scanned using binoculars. All interactions involving the subject species were recorded and described using a pocket dictaphone. Observations of some species were augmented with video recordings and still photography, which provided the basis for illustrations. For most species a small number of males was marked with a unique number written on the wing with a fine-tipped felt pen providing records of territory occupancy and mating success during the observation period.

SPECIES STUDIED, HABITATS AND GENERAL BEHAVIOUR

Five species, *Libellago semiopaca* (Selys), *L. stictica* (Selys), *Rhinocypha aurofulgens* Laidlaw, *R. cucullata* (Selys) and *Heliocypha biseriata* (Selys) occurred syntopically on accumulations of logs which occurred every 100-300 m on the Belalong River near the KBFSC. The river lies in a steep sided valley running through primary mixed dipterocarp forest. Its entire catchment area is protected and undisturbed. It is subject to rapid fluctuations in water level, and even during the drier seasons heavy rainfall is common resulting in the inundation of most oviposition sites for several days. The river bed at this point is about 25 m wide and the stream is 15-20 m wide when the water is low, the time of greatest odonate activity. Females of all these species oviposited in decaying wood just below the surface of the water and males defended suitable oviposition sites, usually on larger logs. Some segregation in the use of microhabitats within the log jams was apparent but interspecific interactions, both homosexual and heterosexual, were frequent and often quite intense. Sexual activity and oviposition in all species was intensified following a rapid drop in the water level.

Of the other species, *Rhinocypha humeralis* (Selys) and *R. stygia* Foerster were found on much smaller streams running into the Belalong River (rarely on the log jams) and the former species was common in other localities in primary dipterocarp forest, always toward the head of very small streams. *R. humeralis* also occurred syntopically with *R. aurofulgens* and *H. biseriata* on the Palum Tambun, a small stream running into the Segama River at the Danum valley field centre, where the rare *Libellago phaeton* (Laidlaw) was also found, whereas in this location *L. semiopaca* was restricted to the larger main river. *L. aurantiaca* (Selys) occurred in a range of medium sized, gently flowing streams in Brunei, the principal study site being the Sg Rampayoh near Labi, Belait District, while *L. hyalina* (Selys) was abundant and very wide-spread in swampy areas with slowly flowing rivulets and on small shaded sluggish streams, and oviposited mainly in root masses and submerged vegetation, rather than in rotting wood. Detailed observations of this species were made in a shaded drain beside swamp forest near Badas, Belait District, Brunei. *Rhinoneura villosipes* Laidlaw was found only along the Silau Silau, a small montane stream near its type locality at Kinabalu Park Headquarters, Sabah.

In all species males defend small territories around oviposition sites, usually arriving in the morning before the females. In most cases the oviposition substrate is decaying wood, typically large logs on larger streams, where males mostly perch low, near the water surface; on larger log jams elevated perches are often quite rare and seem to be more frequently occupied by other odonates. On smaller streams with overhanging vegetation males often perched higher in the foliage, and even when perches near the water were available, higher perches were sometimes occupied by satellite males which only rarely engaged in territorial or courtship activity. In many species territorial contests between males may be protracted. Males of

all species for which information is available attempt to mount the female while she is ovipositing or testing the substrate, within the male's territory, with or without courtship. No recruitment behaviour of females prior to oviposition was ever recorded, in marked contrast with *Platycypha caligata* (ROBERTSON, 1982) and calopterygids such as *Calopteryx maculata* (WAAGE, 1973). Unreceptive females signal rejection by half opening and vibrating their wings, by fully opening and flattening their wings, and by flying away (see WAAGE, 1984; SIVA-JOTHY & HOOPER, 1995). In all species for which information is available copulation is brief, lasting 1-2 minutes, and infrequent, although probably there are interspecific differences in mating frequency. Most species exhibit some form of guarding behaviour immediately after copulation which varies considerably in duration.

MALE ORNAMENTATION

When determining which features should be regarded as ornaments, (i.e. markings specifically associated with display), account is taken of the degree of specialization exhibited and the way in which they are presented in display. The most obvious and unambiguous signalling devices are those specialized, often bright, markings which are displayed by means of the insect adopting a distinctive, sometimes unusual posture, or moving in a specialized fashion. Features which most clearly meet these requirements include dorsal, and less commonly, ventral markings on the abdomen; dark, typically slightly iridescent terminal patches on either forewings, hindwings or both pairs of wings; brilliant iridescent areas within the darker wing markings; and white or pale blue pruinescence on the anterior face of

Table I

Taxonomic distribution of various types of ornaments and their probable functions – [+ specialized marking; – - no specialized markings; – A used in threat displays; – C used in courtship displays; – sr, probably concerned with species recognition]

Species	Abdomen dorsal	Abdomen ventral	Fw	Hw	Legs	Head
L. aurantiaca	+C(sr)	-	+A	-	+C	+?
L. stictica	+C(sr)	-	+A	-	+C	+?
L. phaethon	+C(sr)	-	+A?	-	+C	+?
L. semiopaca	+C(sr)	-	+A	-	-C*	-
L. hyalina	-	-	-	-	-	-
R. villosipes	+C?	-	-	+A	+C?	+?
R. aurofulgens	+A	-	+AC	+A?C	-	+sr?
R. cucullata	+A	+C?	+AC	+A?C	+C	-
R. humeralis	-	+C?	+AC	+A?C	+C	+sr?
R. cognata	+?	-	-	+A	-	-
H. biseriata	-	-	+A?	+C	+C	-

* Although *L. semiopaca* displays legs in a specialized way, they are morphologically unspecialized

the tibia and femora of the legs. The distribution of such ornaments among the species studied is summarized in Table I, together with indications of their probable role as sexual and/or agonistic sign stimuli as deduced from the way in which they are displayed during various types of interaction.

Less clear is the role of several other types of markings which may have some signalling function without being closely associated with recognizable displays. For example, markings of the mesepisternum or the lateral part of the synthorax which differ markedly between closely related species may be important in overall species recognition, but since the posture and relative positions of males in combat or males courting females is such that these markings would be seen obliquely, if at all, it is concluded that they are not specifically displayed, and are probably of minor importance in communication during these encounters (but perhaps have a more important signalling function before the commencement of displays). This supposition is supported by the frequent occurrence of similar interspecific variation amongst other Zygoptera which have no corresponding display pattern. It is also difficult to assess the possible communicative role of anterior markings on the head (i.e. frons, genae, labrum), which must be plainly visible during most frontal displays. Interspecific differences do occur and although these are not particularly striking and also find many parallels among other Zygoptera, it is possible that in some cases they may form an integral part of the display, aiding in species recognition (Tab. I). Detailed descriptions of male ornamentation and the form of the displays are provided in the following species accounts.

SPECIES ACCOUNTS

LIBELLAGO AURANTIACA

MALE ORNAMENTATION. – Abdomen dorso-ventrally flattened and red on dorsal surface; yellowish markings on head; large dark slightly iridescent blue spot at tip of forewing; all legs with white pruinescence on femora and tibia which are not expanded.

TERRITORIALITY AND AGONISTIC BEHAVIOUR. – During three days observation 217 contests were recorded on a 25 m section of a stream, occupied by 5-8 territorial males. Males establish territories 1.5-3 m in diameter wherever decaying wood suitable for oviposition is present. Maximal activity is between 0900 h and 1300 h and marked individuals remain in the same territory for up to 10 days. They perch on emergent twigs, on semi-submerged logs, and on floating leaves and sticks in larger pools, usually in full sunlight. Even in the absence of other individuals, they continually leave their perch every minute or so and fly around for a few seconds, rarely venturing more than a metre from the perch, behaviour which may be exploratory, or may serve to advertize their presence to females. Territorial disputes although frequent are not of long duration (usually less than 5 min; mean, 2.7 min,

n=217), except when an ovipositing female is present. Two males face each other at a distance of about 5-15 cm and hover in a mutual frontal threat display (see PAJUNEN, 1966). They often make darts at each other which stop short of physical contact, and may ascend slowly, usually not more than 1 m in 10-30 sec, then disengage briefly and loop back down to resume the contest near the water surface. During the contest the abdomen is held horizontal and the legs are not displayed. The forewings are mostly held well forward and canted so that the underside faces the opponent. Frequently one individual will hold his forewings completely stationary for up to 1 sec, flying with his hindwings. In this case the wings are held straight out from the body, slightly elevated and canted vertically, displaying the dark apical spot. This appears to be a strongly agonistic display and is frequently followed by the other male retiring. A male returning after a successful contest often flies over the entire territory holding his forewings in the stationary display. If both males adopt the stationary wing display, the contest normally terminates, at least temporally, and both perch within 1 or 2 m of each other.

COURTSHIP AND MATING. – Courtship was observed on over 70 occasions which resulted in 13 matings. Upon discovering an ovipositing female, the male almost always courted her. He arched his abdomen upwards at an angle of about 45° displaying the brilliant red dorsal surface, extended and vibrated his pruinescent legs, and flew back and forth to one side of the female, describing a semicircle of 10-15 cm radius about her. Each completed movement (back and forth) took 0.7 ± 0.1 sec, and there was frequently a distinct pause of 0.2-0.5 sec as he hovered directly in front of her. After 7-15 cycles the male pounced on the female's thorax, even when she was signalling rejection, and commonly after two or three such attacks the female flew away pursued briefly by the male. Unreceptive females were often spared further attacks by the arrival of another male who engaged the first in a contest. In successful courtships there was considerable variation in the number of attempts a male made before the female allowed tandem formation. In most cases the female copulated about 1-2 sec after tandem was achieved, the two exceptions being females who were taken in tandem while perched insecurely on a very small floating twig; in both cases the pair flew to nearby foliage before the female made genital contact. Mating lasted from 95-130 sec (mean 112 sec, n=13). Following separation the female oviposited for 6-47 min (mean 18 min, n=13) in the male's territory, during which time he remained within about 50 cm guarding her. Males from neighbouring territories frequently approached and attempted to court the female but were prevented from doing so by the guarding male who at once engaged them in a contest which was usually protracted.

LIBELLAGO STICTICA

MALE ORNAMENTATION. – Very similar to *aurantiaca* but abdomen yellowish basally, toning to orange distally, with median black line; mesepisternum with broad

pale green dorsal bands; head with orange marking; wings and legs as in *aurantiaca*.

TERRITORIALITY AND AGONISTIC BEHAVIOUR. – Males maintain territories towards the centre of the stream on partially submerged logs on the Belalong river. They seldom arrive before 1200 h, and remain active until 1600 h. They are fairly mobile, and rarely stay for more than 1-2 hr in a locality, during which time they may change their position several times. It is a restless species, and, as with *L. aurantiaca* males regularly fly up from their perch every minute or so, making reconnaissance and/or display flights of up to 2 m. Contests between neighbouring males were observed infrequently (13 occasions), because it was unusual for two males to be in close proximity. The general form of the contest was similar to that of *L. aurantiaca* but more vigorous, the opposing pair ascending vertically to about 2 m in about 5-10 sec, frequently incorporating a series of rapid feints at one another. Contests were of short duration, rarely lasting more than 3 min (mean 1.2 min, n=13), and conclusive, the winner retaining the territory without further challenges. The winning male usually exhibited a brief stationary wing display.

COURTSHIP AND MATING. – Courtship was observed on 10 occasions but did not result in mating, and probably involved in some cases a *L. semiopaca* female. The form of courtship was similar to that of *L. aurantiaca* but considerably more vigorous, the male, with abdomen raised and white legs thrust forward and vibrating, swooped back and forth in a semicircle approximately 0.3-0.5 m in diameter about the female, diving towards her at each end of the arc. Each cycle took about 0.8-1.0 sec with the usual pause directly in front of the female. The male pounced on the female and attempted copulation after 5 to 10 cycles, and in all cases the female flew away and did not return.

LIBELLAGO PHAETHON

MALE ORNAMENTATION. – Abdomen segments 2-4 with dorsal, lateral blue markings and brick red markings at edge of segments 5-8; mesepisternum with broad blue vertical bands; head with orange markings; wings and legs as in *aurantiaca* but with tibia of foreleg slightly flattened.

MALE AGONISTIC BEHAVIOUR. – Not observed, owing to the low density of males.

COURTSHIP AND MATING. – Courtship was observed on five occasions, always following the almost same pattern as described for *L. stictica*. Unguarded females oviposited on partly submerged logs or rafts of driftwood and males flew rapidly back and forth in a semicircle at about 0.5-0.7 m distance, swooping as close as 5 cm at the ends of the arc. The abdomen was strongly arched and the white legs were particularly conspicuous. In every case the female signalled rejection by quivering her wings and after 5-7 cycles the male desisted.

LIBELLAGO SEMIOPACA

MALE ORNAMENTATION. – Abdomen segments 2-5 with light green dorsal marking; head black; forewing wider than hindwing (in other *Libellago* it is narrower) and with outer one quarter to one third dark and faintly iridescent; legs black and unmodified.

TERRITORIALITY AND AGONISTIC BEHAVIOUR. – In 5 days observation of a 22 m section of habitat 4-10 males per day engaged in 282 contests. Territories are maintained on partially submerged logs in the vicinity of water flowing at moderate speeds (0.05-0.3 m/s). If population density is not high, males tend to space themselves 2-3 m apart along the logs which lie parallel with the stream, but at higher densities it is common for pairs of males to perch facing one another 20-40 cm apart, within a territory. In the absence of other individuals males remain perched for long periods, not engaging in exploratory/display flights as do *L. aurantiaca* and *L. stictica*. Contests are extremely frequent and often prolonged, sometimes lasting up to 30 or 40 min with almost no break. This is especially so if an ovipositing female is present. The mean duration of all encounters recorded was 4.7 min (n=282). The general form of the contest is similar to that described for *L. aurantiaca*, with the two individuals facing one another, but the pair usually approach closer (5-10 cm) and there is little vertical movement (Fig. 1A). As the pair hover they gradually rotate through about 90° and then back again. The stationary wing display (Fig. 1B) is given frequently, but it is not uncommon for the apparent loser of a contest to return to perch in the territory, upon which the other male normally flies at him giving a strong stationary wing display (which in this species is considerably more dramatic than in other *Libellago* owing to the extensive dark terminal patch on the relatively broad forewing), which normally induces him to resume the contest or to fly away. Quite frequently both males adopt the stationary wing display, which normally culminates in them both sharing a territory.

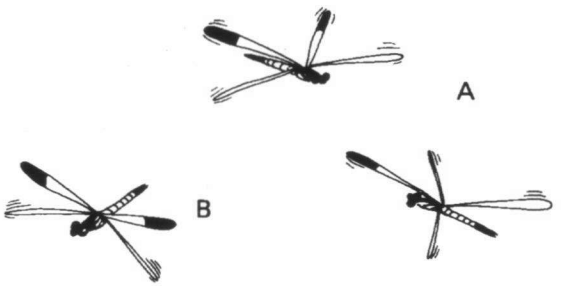

Fig. 1. Agonistic behaviour in *Libellago semiopaca*: (A) male contest; – (B) stationary wing display.

COURTSHIP AND MATING. – 327 courtships and 52 matings were observed in 10 days observation. Females normally begin arriving in the territories between 1000 and 1100 h and at this time of day almost all are courted. The general form of the courtship resembles that of *L. aurantiaca*, with the male, his abdomen arched upward at 45° (displaying the green dorsal colour), describing semicircular movements to and fro beside the female at a distance of about 10 cm (Fig. 2). In *L.*

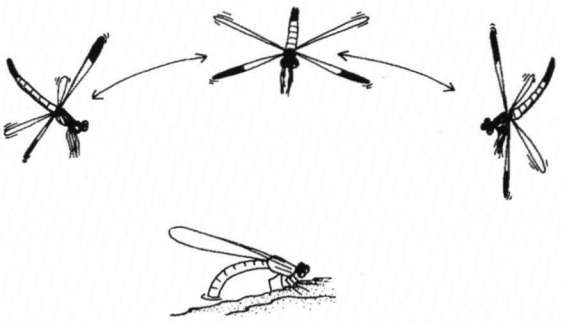

Fig. 2. Courtship display of *L. semiopaca.*

semiopaca the period of each cycle is 1.2 ± 0.2 sec, slower than *aurantiaca*, and the legs, which have no white coloration are dangled rather than thrust at the female. The legs are however vibrated as in other species. In the usual pattern males make from 10-20 cycles, then pounce on the female's thorax, which may result in mating, or may cause the female to fly a short distance (usually less than a metre), whereupon the male courts her again. Towards the end of a prolonged and unsuccessful courtship males become disrupted in their rhythm and sometimes describe complete circles about the female. After 3-5 attempts males usually desist but when they are especially persistent the female may fly out into the stream, followed by the male, and then return to her oviposition site. If her way is blocked by the male the female lowers her legs as she hovers, facing the male, upon which he always gives way and does not court her further. There was no evidence of organized courtship while the female remained airborn, although a male will sometimes describe a few poorly coordinated circles around a hovering female. These interactions were never seen to result in mating. Very frequently a persistent male attracts a rival from a neighbouring territory and during the protracted contest which ensues, the female is allowed relatively undisturbed oviposition.

All matings observed took place on the log near the male's perch, although two couples flew some distance away when another male persistently attacked them. matings lasted from 61-128 sec (mean 83 sec, n=52), and the male guarded the female closely for about 30 min following mating, although females often remained ovipositing in a male's territory for over 1 hr. Marked females, which frequently returned to oviposit at the original site of capture, were never observed to remate in under 3 days. Between 1200 and 1300 h many females arrived to oviposit, and usually formed loose aggregations of 2-8 individuals in favourable sites. Males sometimes courted new arrivals but were almost never successful if other females were present, partly because attentions were accidently shifted from one female to another mid courtship.

LIBELLAGO HYALINA

MALE ORNAMENTATION. – Abdomen dull iridescent purplish on dorsal surface; wings unmarked; legs black with faint pruinescent dusting; apparently lacking in

any specialized ornamentation.

MALE AGONISTIC BEHAVIOUR. – Males maintain territories of several square metres around pools and runnels in their swampy habitat. They arrive between 0800 and 0900 h and remain until about 1500 h. Marked males usually occupy the same territories every day for periods of up to 10 days. Males perch, usually on twigs and grass stems 20-40 cm above the water surface. Contests tend to be initiated by the resident male and occur either when a newly arriving male attempts to perch in an occupied territory, or when the male from an adjacent territory encroaches on that of his neighbour, typically when following an ovipositing female which has passed through his territory without mating. The resident male leaves his perch and flies at the intruder and the contest soon assumes a fairly regular pattern. The two males face each other, hovering at a distance ranging from between 10 and 50 cm, sometimes darting in at one another but never making physical contact. There is no evidence for any ritualized display during this phase. After about 10-30 seconds they begin to rapidly switch sides every few seconds. This may happen 20 or 30 times and is followed by a brief period of a few seconds where one hovers directly below the other facing in the opposite direction and then reverses his position so the two are facing in the same direction. The lower male is noticably more active, waggling his abdomen up and down, perhaps displaying the dorsal coloration. Sometimes the upper and lower males exchange positions several times. This stage rarely lasts more than 30 sec and is followed by a high speed chase with usually the lower male pursuing the upper male. Contests between neighbours are usually brief (mean 47 sec, n=195) and conclusive, with the resident returning to his original perch and the intruder retiring. Contests involving a new arrival can be quite protracted, sometimes involving a series of bouts taking place continually for up to 30 min. In these cases it was more common for the resident to retire, or for the two to perch in the same original territory with little interaction except when an ovipositing female appeared.

COURTSHIP AND MATING. – In 7 days observation over 70 attempted matings and 22 successful matings were witnessed along a 40 m section of habitat. Females were captured and mated without courtship as they oviposited within a male's territory, mostly between 1000 and 1130 h. The oviposition substrate of submerged leaves and root masses was apparently fairly uniformly distributed within the habitat and females were not always detected immediately among the emergent vegetation. Mating lasted from 115-149 sec (mean 132 sec, n=22), following which females usually remained for 15-60 min ovipositing in the male's territory and were closely guarded by him. At times the male hovered in front of the female, seemingly trying to keep her within his territory boundary as she strayed. Guarding usually ceased when another female entered the territory, and was pursued. On entering a new territory females were pursued by the occupant and were often driven away if they refused to mate, although some covert oviposition among the vegetation bordering the territory occurred undetected. A female who had escaped

from a male typically perched low on the vegetation within the territory for a few minutes before resuming oviposition. If a female strayed onto the boundary of two territories the males often engaged in a protracted contest which enabled her to oviposit unhindered but it was more usual for one male to drive the other away in under 5 min and return to harass the female. In 3 cases females which abandoned their original mate's territory less than 10 minutes after mating submitted to a second mating with a new male. In 5 cases a female was seized in tandem by a male and carried to a nearby perch but refused to copulate, even though held for 78-130 sec and lifted into the appropriate position several times.

RHINONEURA VILLOSIPES

MALE ORNAMENTATION. – Abdomen long, golden yellow basally; apices of hindwings with small dark mark; femora of meso- and metathoracic legs with creamy pruinescence.

MALE TERRITORIAL AND AGONISTIC BEHAVIOUR. – Males maintain small territories about 1.5-3 m in diameter on logs and twigs near the stream, and on surrounding vegetation. Generally sunlit positions are preferred, although these may be slightly removed from the site of oviposition. Contests were frequent and often protracted (mean 5.1 min, n=32). Males faced each other about 5-10 cm apart and hovered with their long abdomens held horizontal or slightly depressed. Sometimes they slowly ascended for up to 3 m (the ascent lasting 5-10 sec) but frequently they remained in the one position with relatively little vertical movement for 5-15 min. The hindwings were generally held forward and canted in a vertical plane and were sometimes held stationary for short periods (less than 1 sec), presumably displaying the dark apical mark (Fig. 3). The legs were not displayed.

Fig. 3. Agonistic display of *Rhinoneura villosipes.*

COURTSHIP AND MATING. – Not observed; females were seen ovipositing within male territories.

RHINOCYPHA AUROFULGENS

MALE ORNAMENTATION. – Dorsal surface of abdomen entirely bright blue, except for a fine dark median line; head bears characteristic blue markings; wings with terminal dark brown patches, shot with a coppery iridescence; distinct, wholly iridescent patch on the underside; legs black and unmodified.

MALE AGONISTIC BEHAVIOUR. – Territorial males perch on logs near the water's edge where females oviposit. Sunny patches appear to be preferred but they are

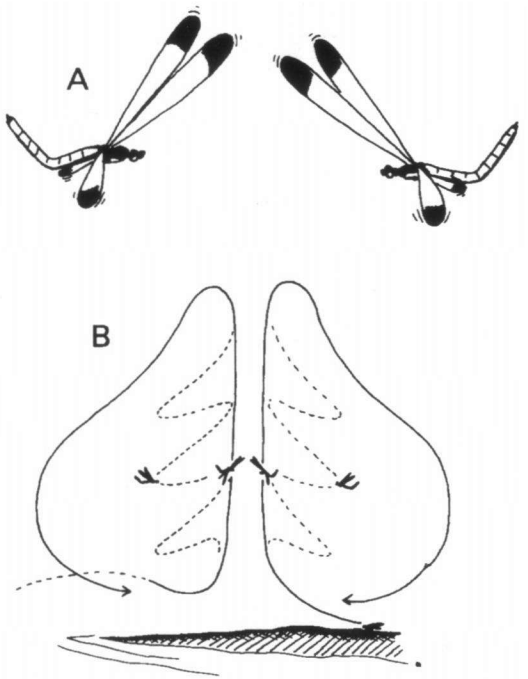

Fig. 4. Agonistic behaviour of *Rhinocypha aurofulgens*: (A) males at point of closest approach showing cocked abdomen; – (B) general form of ascending flights.

frequently active in open shade. Males arrive as early as 0800 h and remain until 1700 h. Territorial disputes are common between residents and new arrivals or males occupying adjacent territories. Six males were observed to engage in over two hundred contests in the course of one day. Contests begin when a male flies into another's territory, usually within 1.5 m of his perch on the substrate. The resident rises 0.3-1.0 m to meet the intruder head on, approaching to between 1-5 cm, but never actually making physical contact. At the point of closest approach the forewings are thrust forward and may be briefly held almost stationary. The wings are canted almost vertical with the costa uppermost revealing the iridescent flashes on the underside of the terminal patch. In this position the pair ascend rapidly, apparently flying mainly with the hindwings, which are also canted upward and thus also reveal the flashes on their undersides. The broad, flattened abdomen is cocked upwards from segment 4 at an angle of 115° revealing the brilliant blue dorsal coloration (Fig. 4A). The vertical ascent lasts 1.5-3 sec and reaches a height of 1-2 m above the substrate, whereupon they disengage, fly rapidly back to the starting point, and begin the cycle again (Fig. 4B). This stylized "dance", typically lasts for 10-15 cycles, or 0.5-1.5 min (mean 1.2 min, n=207), but depending on the circumstances, it may last much longer especially if a female is present. The engagement is terminated when one male breaks off and is expelled following a brief high speed chase, or when the two return to their original perches, or when both perch within the same territory facing one another at a distance ranging from 0.3-0.8 m. Frequently (in 32% of cases) the ascending flight does not proceed smoothly upward, but involves a series of back and forth rhythmical movements as they alternatively approach and retreat from one another, the distance separating them never exceeding 0.5-0.7 m.

COURTSHIP AND MATING. – Courtship was observed on approximately 40 occa-

sions, 12 of which resulted in mating. Most sexual activity occurred between 0900 and 1100 h, but mating was seen as late as 1520 h. In a majority of cases the male stood on the substrate directly in front of an ovipositing female which had landed in his territory and vibrated his wings which were folded slightly backward with the hindwing raised above the forewing, and canted in a vertical plane with undersides directed forward. The iridescent reddish copper terminal patches on the undersides were thus exposed. The abdomen was held straight and not displayed (Fig. 5). After 10 to 20 sec, during which time the male sometimes turned on the spot so as to always face the female as she moved her position, the male either desisted, if the male was giving strong rejection signals, or flew up and pounced on her, achieving tandem very quickly. Two males courted ovipositing females in an otherwise similar fashion while flying just above the substrate, then successfully mated. In three cases following tandem formation the female did not bring her genitalia into contact with the male's until nearly a minute later, despite being lifted into a copulatory position by the male several times. In one case the tandem pair was chased by another male and copulation occurred after they had reached some high foliage (6 m above the water). Mostly however the pair mated on the log in the male's territory and copulation, lasted from 52-126 sec (mean 86 sec, n=12). After separation the male guarded the female quite closely, usually facing her and always remaining within 30 cm, for about half an hour. Females typically oviposit for 30-180 min in the male's territory and when they leave the males sometimes follow them. A marked female was observed to mate twice within 20 min, when she departed early from one territory and entered another. On two occasions a male mated with two females within 30 min which were guarded together as they oviposited within 10 cm of each other.

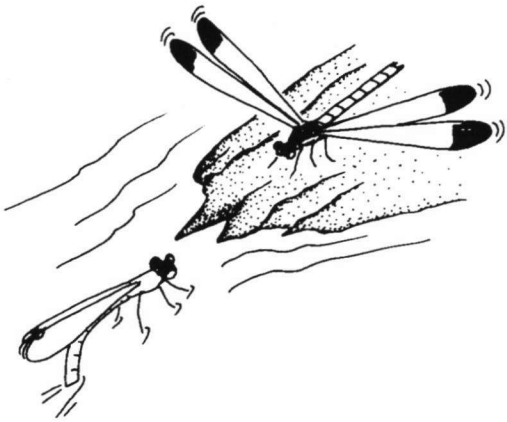

Fig. 5. Courtship display of *R. aurofulgens*.

On five occasions the male appeared to court the female while the pair hovered facing each other, the male somewhat below the female and flashing the terminal iridescent patches on his wings. Females were sometimes also observed apparently following males back to their perches, having either been intercepted in midstream or having been chased out into midstream and returning. However this is probably not recruitment behaviour. None of these interactions resulted in mating, even when the female returned and commenced oviposition, and the male habit of perching as low and close to the water as possible does not lend itself to detecting females

flying over the stream.

RHINOCYPHA CUCULLATA

MALE ORNAMENTATION. – Abdomen dorsally with conspicuous terminal mauve patch on segments 7 and 8, ventrally with lines of bright blue lateral markings on either side on segments 1-7; head unmarked; wings broad, with large dark patch terminally and subterminal iridescent patch on the underside of greenish copper colour; meso- and metathoracic legs with slightly flattened tibia and pale blue tibia and femora.

MALE TERRITORIALITY AND AGONISTIC BEHAVIOUR. – Territorial males perch as in *R. aurofulgens* in similar situations but usually closer to the shore where the water is slower flowing. They are active from about 0930 h to 1500 h, frequently perching in shaded places. Territorial behaviour is very similar to that described for *R. aurofulgens*, although as *cucullata* occurs at much lower densities, only 17 contests were observed. The ascending flight which may reach 2.5 m appears to be steadier than in *aurofulgens*, with fewer movements back and forth. As in *R. aurofulgens* the abdomen is cocked upwards revealing the unique terminal dorsal marking, and the undersides of the wings are turned forward to reveal the brilliant subterminal iridescent patches, especially at the point of closest approach. The legs are not displayed.

COURTSHIP AND MATING. – Courtship was observed on only two occasions and did not result in mating. Following the usual pattern of behaviour, a female arrived in a male's territory, and commenced oviposition/probing. The male flew up from his nearby perch, and performed an elegant dance about 10-15 cm in front of and to the side of the female (Fig. 6). With the wings moving in a jerky, scissor-like action, he flew back and forth around an arc of about 90°, with both wings canted to display the subterminal iridescent patch on the underside. The pale blue mid and hind legs were extended and vibrated, an action which became particularly intense as the male made little feints at the female, approaching to within 2 cm. The abdomen was slightly depressed and the ventral blue markings were probably visible to the female. On both occasions the female signalled rejection by half opening and quivering her wings. After

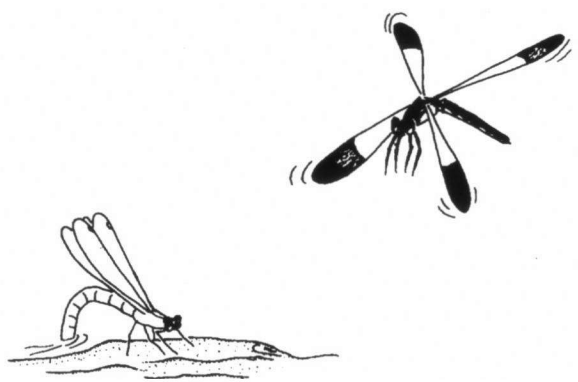

Fig. 6. Courtship display of *R. cucullata*.

two or three attempted courtships lasting 10-15 sec the male desisted, without making physical contact with the female.

RHINOCYPHA HUMERALIS

MALE ORNAMENTATION. – Abdomen dorsally unmarked, ventrally with 2 lateral lines of blue markings on either side; mesepisternum and head with extensive blue marking; wings with large terminal faintly iridescent areas; meso- and metathoracic legs with pale blue coloration on anterior face on femur and tibia but legs of normal width.

MALE TERRITORIALITY AND AGONISTIC BEHAVIOUR. – In one day of continuous observation 57 contests were witnessed. Territories about 2 to 4 m in diameter are maintained along small streams. Males perch on low vegetation about 1 m above the water, and sometimes on stones and twigs in midstream. Contests between occupants of neighbouring territories are frequent and often prolonged, contests sometimes lasting 15 min or longer (mean 3.8 min, n=194) without any eventual change in territory occupancy. As in other *Rhinocypha*, males face each other head to head, but tend to dart back and forth at one another, frequently rotating slowly in a horizontal plane, rather than ascending in a vertical flight (Fig. 7A). When a vertical ascent occurs it is rarely over 1 m and is rather slow. The abdomen is not cocked upwards, but is held straight out or even slightly depressed (Fig. 7B).

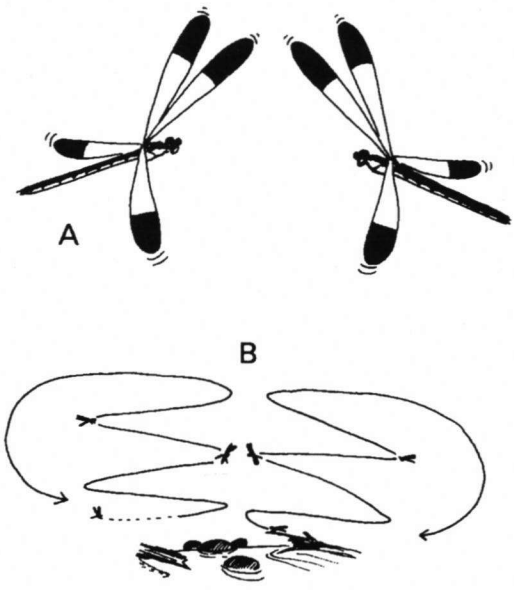

Fig. 7. Agonistic behaviour of *Rhinocypha humeralis*: (A) males at point of closest approach; – (B) general form of contest flights.

COURTSHIP AND MATING. – Courtship was observed on 14 occasions throughout the day, with two matings recorded. Females were observed ovipositing on large logs lying across the stream well above the level of the water, and on sticks and root masses along the stream margins. Ovipositing females discovered by the males were courted. The male described semicircles to one side of the female, with the abdomen depressed and the bluish legs thrust forward and vibrated. This display

lasted for 20 to 30 sec. In 2 cases the female remained quiescent, and the male landed on her thorax and copulation was achieved in about a second and lasted 62--93 sec. In other cases the female responded by signalling rejection by partially opening and vibrating her wings and the male did not attempt copulation. Following mating males did not guard closely, since they returned to high perches and the female had moved out of the territory within 10 min. Since the female of *R. humeralis* is andromorphic, with dark terminal markings on the wings, it is possible that the rejection display is more effective in dissuading males than in other species, and close guarding may be less necessary.

RHINOCYPHA STYGIA

MALE ORNAMENTATION. – Abdomen dorsal surface deep blue; hindwing with small terminal spot; otherwise unmarked.

TERRITORIALITY AND AGONISTIC BEHAVIOUR. – Males perch on sunlit foliage between 2-5 m on vegetation beside a small stream at KBFSC. Contests observed were brief (less than 1 min) and involved a rapid ascent with the pair facing one another with the hindwings held forward and canted vertically, displaying the small terminal spot. The abdomen was apparently not displayed. Only 5 such contests were observed in this rare insect, and further observations are needed.

COURTSHIP AND MATING. – Not observed.

HELIOCYPHA BISERIATA

MALE ORNAMENTATION. – Abdomen not flattened and almost completely black with insignificant blue lateral markings; almost covering the anterior half of the mesepisternum are two prominent lateral patches and a triangular median patch, coloured blue shading into crimson-magenta; head weakly marked; forewing outer third darkly shaded, hindwing with dark shading in its outer two thirds containing a series of iridescent magenta fenestrae; meso- and metathoracic legs with tibia and femora brilliant white on their anterior face, but not abnormally flattened.

MALE AGONISTIC BEHAVIOUR. – Males maintain small territories of two to three metres in length along the partially submerged logs where females oviposit. Nonterritorial males (usually those defeated in combat) sometimes perch 1-3 m above the stream on surrounding vegetation or on projecting twigs. During the course of one day 4 marked males occupying territories along a 13 m log were observed to engage in contests with each other 23 times without any changes in the pattern of occupancy. These contests usually took place when one male was attracted to a neighbour's territory by the presence of a female as revealed by the conspicuous courtship behaviour of the resident male. Seven brief contests were observed between residents and outside males, and in two cases this resulted in the resident male being displaced. Marked males were commonly seen in the area over

the next five days but frequent changes in patterns of territory ownership occurred from day to day. Contests were vigorous but usually fairly brief (mean 42 sec, n=73). Males faced one another and darted back and forth in an ascending flight approaching each other to within 1 cm. They usually ascended to about 2-2.5 m in about 1-2 sec and then returned to near the water level to repeat the performance. This rarely happened more than 10 times in succession and the sequence culminated in either a high speed chase or both males returning at once to their original perches. During contests, the legs were not displayed, but the wings were turned to reveal their undersides during the approaches, but at no stage was either wing held completely stationary. The abdomen was straight and slightly depressed.

COURTSHIP AND MATING. – Courtship resulting in mating was observed in 5 occasions. In every case a female landed in a male's territory and commenced oviposition, or at least probing gestures. The male flew up from his perch and darted back and forth at the female about an arc of 45°, flashing and vibrating his white legs as he approached, and at the closest point of his approach briefly hovering with his forewings while turning the underside of his hindwings to face the female and holding them in this position and vibrating them slightly for about half a second. After 10 to 20 approaches, if the female remained still and did not signal rejection, the male mounted her and copulation was effected almost at once, usually while the pair remained on the log. Copulation lasted from 56 to 95 sec (mean 73 sec, n=5). After the pair separated the female always commenced ovipositing nearby, and the male remained within about 20-30 cm of her for as long as she remained in his territory (25-45 min), during which time he drove away other males who attempted to court the female. On 13 occasions ovipositing females were courted unsuccessfully. Rejection was signalled by flashing the wings in a half open display, but if males persisted and attempted to mount the female she either flew away, or flew up with the male in pursuit, but returned to hover over the territory facing the male, who sometimes attempted to court her in midair, but eventually returned to his perch after which the female landed and recommenced oviposition. Essentially similar behaviour is reported by UEDA (1992).

INTERSPECIFIC INTERACTIONS

Significant interspecific interactions were only observed on the main stream at KBFSC, where 5 species overlap broadly in their territorial and oviposition sites, and these were to some extent limited by the slightly different habitat requirements of some species and the scarcity of *R. cucullata* and *L. stictica*. The most frequent interactions were between males of *L. semiopaca* and *R. aurofulgens*, and between *L. semiopaca* and *H. biseriata*. Very commonly males of the smaller *L. semiopaca* were attacked at their perches by males of one of the other species and were displaced either to another site, or were forced to take up a station behind the larger insect, higher up the log and further from the oviposition substrate. These interac-

tions, which sometimes included elements more normally associated with violent mating behaviour, generally rapidly escalated in a high speed chase without assuming any regular form. Persistent males of *R. aurofulgens* buffeted their rival, and *H. biseriata* males sometimes flashed their white legs at the perched *L. semiopaca*, often making physical contact. Displaced *L. semiopaca* regularly returned and hovered in front of their adversary adopting the aggressive stationary wing display and occasionally pouncing on the other insect. Both actions invariably provoked another chase, and usually the larger insect prevailed although reverses in favour of the smaller *L. semiopaca* also occurred.

Less common were contests between *R. aurofulgens* and *R. cucullata*, and *L. semiopaca* and *L. stictica*, both of which involved two very closely related species. Occasionally a male *R. aurofulgens* strayed into a *R. cucullata* territory or vice versa, and they met each other in a brief ascending flight of up to half a metre. This had the appearance of the beginnings of the ritualized combat "dance" which is of very similar form in the two species, but it always terminated rapidly and abruptly, generally with a chase and the expulsion of the intruder. Even more protracted were the head to head "out-facing" contests of *L. semiopaca* and *L. stictica*, which sometimes lasted up to 30 sec, and were always won by *L. semiopaca* even though it is the smaller insect. Brief contests involving *R. aurofulgens* and *H. biseriata* occurred sometimes, but involved only a series of rapid uncoordinated attacks followed by a chase. *L. stictica* males, which resemble females of *R. aurofulgens* slightly in overall colour, were occasionally "courted" and pounced on by males of that species.

L. semiopaca females were sometimes courted briefly by *R. aurofulgens* males and on several occasions the male pounced on the female and attempted mating. Conversely, males of *L. semiopaca* were on three occasions observed to court and attempt mating with a *R. aurofulgens* female. In each case the female was guarded by a male of her own species who attacked the importunate *L. semiopaca* and drove him off. *L. stictica* very frequently courted females of *L. semiopaca*, which signalled strong rejection. *Libellago* females are very similar in appearance and it is doubtful if males are able to distinguish those of their own species. Females subjected to intergeneric courtship did not at first respond with strong rejection signal. Possibly they did not appreciate that the overtures were directed at them as it is usual for groups of *L. semiopaca* and *R. aurofulgens* females to oviposit in close proximity and all are exposed to courting males of either species very near to them. On the other hand *L. semiopaca* females courted by *L. stictica* males signalled strong rejection at once and flew away if the males persisted.

DISCUSSION

Species examined exhibit considerable variation in the extent of male ornamentation even within genera, which is largely congruent with the incidence of ritual-

ized display. This in turn is probably influenced by environmental conditions, such as density and distribution of female oviposition sites defended by males and the range of other, similar species encountered. Displays include both morphological and behavioural components; i.e. ornaments per se and the actions which reveal them. Both ornaments and actions may be generalized, occurring in nearly identical form among closely related species and bearing broad similarities among many members of the family – e.g. display of terminal wing markings during territorial disputes or the flashing of pruinescent legs during courtship – or (usually) similar actions may display corresponding ornaments which differ sharply between close species and presumably are critical in establishing species identity. However even among generalized display elements there is considerable interspecific variation in the precise form of the display, particularly with respect to such qualities as tempo, rhythm and scale of movements, and clearly such slight differences may also play an important role in species recognition.

In agonistic displays, there is a common pattern of ritualized display in the close mutual frontal threat employed by males of all species except *L. hyalina* (which alone among species studied lacks markings on the wings). However the form of the behaviour is variable; among *Libellago* species, especially *L. semiopaca*, there is a tendency to hover for long periods, ascending very slowly if at all, whereas *L. stictica* is considerably more aerobatic with a more regular and rapid vertical component. All three species for which information is available adopt a stationary wing display and do so only during territorial disputes, displaying the dark

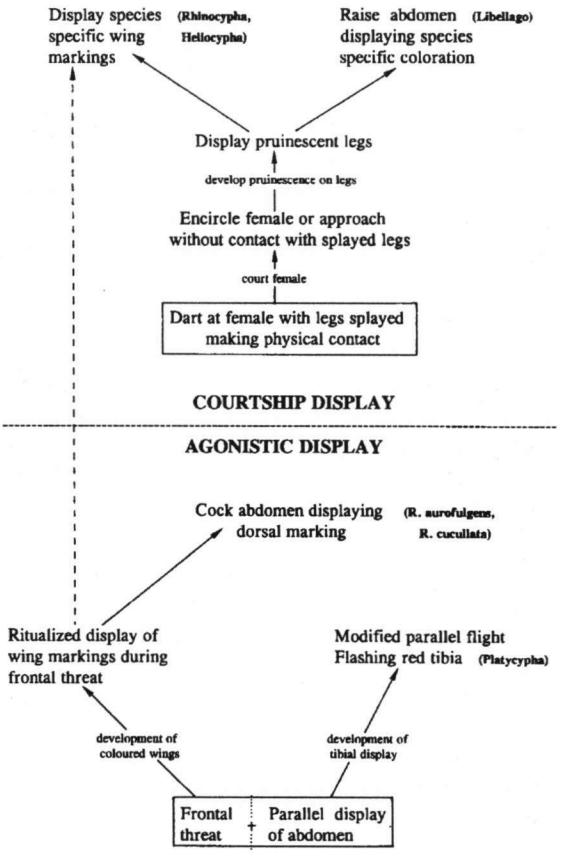

Fig. 8. Possible evolution of ornaments and their display in courtship and agonistic interactions.

mark at the tip of the forewing. The mark is considerably enlarged in *L. semiopaca*, and it is notable that this species spends more time in territorial disputes than any other, perhaps because the oviposition resource is more concentrated relative to population density than in other species. Very similar behaviour occurs in *Rhinoneura villosipes*, except that in this case the hindwing, which bears the terminal marking, is thrust forward and kept almost stationary while the male flies with his forewings. Among *Rhinocypha*, there is no obvious stationary wing display but the forewings are thrust forward and apparently canted towards the opponent. In *R. aurofulgens* and *R. cucculata* the vertical component of the contest is particularly pronounced, and as well as the iridescent underside of the forewing, the dorsal markings at the tip of the abdomen are displayed. The latter may be primarily a species recognition signal, given the taxonomic affinity of the species and their general similarity in behaviour and ecology. In *R. humeralis* and *Heliocypha biseriata* the dorsal surface of the abdomen is unadorned, and significantly, the abdomen is not cocked upward and displayed. In these two species males thrust the forewing forward as they approach one another, and this appears to be the most significant signal in agonistic displays, although the role of the more highly ornamented hindwing in *H. biseriata* needs clarification. Thus in all species in which there is a ritualized agonistic display, it is always the wing bearing a terminal mark which is held in a stationary or almost stationary posture, and if both wings are pigmented the forewing appears to be displayed more prominently than the hindwing. Only two species display the abdomen, and the legs are almost never displayed. The display of wings bearing a terminal dark marking, particularly the wide spread stationary wing display of *Libellago*, presumably would enable another male to accurately gauge the size of his opponent but it may serve primarily to accentuate a signal conveying other information relating to the vigour of the displaying male.

Ascending flights by facing antagonists have also been reported in some Libellulidae, including species with coloured wings (JACOBS, 1955; WILDERMUTH, 1994). However at least some libellulids engaging in this flight pattern are physically very aggressive, and any threat display probably serves to enhance rather than replace escalated conflict. The behaviour as it occurs in the Chlorocyphidae, is distinctive, lacking as it does any physical contact, and involving the ritualized display of wing markings. This form of symbolic contest perhaps serves the function of saving energy during protracted disputes which are very common in the family and may have resulted from the extreme concentration of oviposition sites defended by males. Interestingly, territorial contests in *Platycypha caligata* although complex and ritualized, are of a completely different form. In this species the wings are uncoloured, but the tibia are exceptionally expanded and coloured white on one side and red on the other. Agonistic displays involve flashing the red side of the tibia and waggling the blue abdomen with the antagonists flying in parallel, rather than head to head. The (red) tibial signal is used only in agonistic displays, whereas

the abdominal coloration is also displayed during courtship.

Courtship patterns also show considerable specialization which may be related to the display of specific male ornamentation and species recognition is probably an important factor given the high frequency of mistaken identity in courtship. However there are also common elements found in most species which find parallels in *P. caligata* and in the Calopterygidae. The most generalized behaviour is shown by the fully ornamented *Libellago* species (*aurantiaca, stictica, phaeton*), and the major differences among them result from the species specific colour and pattern of the dorsal surface of the raised abdomen. The vibrating white legs appear to be a generalized excitatory signal, and there are slight differences in the tempo and scale of movements as the hovering male swings to and fro in a semicircle about the female. Surprizingly, although *L. semiopaca* lacks white coloration on its legs, it still employs them in courtship. Given the irregular occurrence of this trait within the genus and elsewhere it is uncertain if the lack of pruinescence on the legs is a primitive or derived condition. Hence the display of non-pruinescent legs may be an evolutionary forerunner of the fully developed display (with pruinescent legs) or it may be a vestigial behaviour remaining from a time when the legs were pruinescent. *L. hyalina*, lacking ornamentation (except faint pruinescence on the legs), does not court, and a study of sexual interactions in this species might shed light on how courtship evolved in other species. A similar generalized pattern of courtship is found in the ornamented *Rhinocypha* and *Heliocypha*. Unlike *Libellago*, however the dorsal surface of the abdomen is not displayed, (although the ventral surface might be in *R. cucullata* and *R. humeralis*), and species recognition seems to be largely dependent on differences in the patterns of the wings. In *R. cucullata* and *R. humeralis* the undersides of both wings are strongly displayed, which may partly account for the rather jerky flight about the female. Both these species also display their specialized pale blue legs. *Heliocypha biseriata* appears to display the hindwing (which is the one bearing the most striking ornamentation) as well as its white legs. *R. aurofulgens* adopts a quite different posture, (usually) standing on the substrate and vibrating its wings thereby displaying the species specific terminal iridescent patches, behaviour which may be related to the lack of white coloration on its legs.

The basic pattern of courtship seems to have a broad phylogenetic base, and deviations such as *L. hyalina* (lacking courtship) or *R. aurofulgens* probably represent derived states. For example, semi-encircling flights occur in *Calopteryx* sp. (WAAGE, 1973) and in *Platycypha caligata* (ROBERTSON, 1982). Courtship in the latter is quite similar in general form to that occurring in *Libellago*. Specifically, it vibrates its legs while exposing the white surface of the tibia. ROBERTSON (1982) thought that this behaviour may have originated in agonistic displays but comparative evidence suggests that it is exclusively employed in courtship, and hence presumably evolved in that context. *P. caligata* is reported as exhibiting well defined recruitment behaviour, in which the female is intercepted and led to the

oviposition substrate (ROBERTSON, 1982), behaviour analogous to the well known cross display of *Calopteryx* sp. (WAAGE, 1973). By contrast, none of the Bornean chlorocyphids interacted with females before they commenced oviposition behaviour. The reasons for this difference are not clear, although it appears that none of the Bornean species mates as frequently as *P. caligata*, in which case it may be more cost effective for a male to passively advertize his presence and attract only receptive females, rather than soliciting on a general basis. It is possible that short flights made by *Libellago aurantiaca* and *L. stictica* may serve the same function as active recruitment by advertizing the presence of the male to a receptive female. Also, prolonged contests in several species, especially *L. semiopaca*, could potentially attract females by virtue of the conspicuousness of the males, so functioning as a sort of "mini-lek". These suggestions need to be subjected to critical scrutiny, but it is clear that, exhibiting the diversity in behaviour that they do, these animals offer ideal subjects to test hypotheses on the evolution of courtship and the significance of female choice.

Present knowlegde does not permit the construction of a fully coherent scheme of evolution of chlorocyphid displays but it does suggest possible relationships among the various behavioural and morphological elements involved. Assuming the ancestral form exhibited a frontal threat and parallel flight in territorial disputes and seized females as they oviposited (as occurs as a probable derived trait in *L. hyalina*), all known states can be logically traced. Terminal wing markings could have evolved to accentuate the frontal threat which became so protracted that the parallel flight disappeared. These markings could subsequently be augmented and used in courtship displays as well. In another line, *Pachycypha caligata* has augmented the parallel flight and lost the frontal threat display. Male *L. hyalina* approach females with splayed legs preparatory to seizing them. This could be modified to form a courtship display where males approach or encircle females signalling their intention to mate but refraining from physical contact as long as females signal rejection. Further evolution of this display could be the development of pruinescence on the legs, accentuating the display and conveying information about the male's vigour. The widespread occurrence of this trait suggests its early evolution within the family. Finally, in species rich communities, courtship displays could have also developed species recognition signals, either the abdominal display of *Libellago* or the display of wing markings in *Rhinocypha* and *Heliocypha*. Specialized species recognition signals in agonistic displays are probably uncommon and are expected to occur only in closely related syntopically occurring species such as *R. aurofulgens* and *R. cucullata*.

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