TERRITORIAL AND REPRODUCTIVE BEHAVIOUR IN A SYMPATRIC SPECIES COMPLEX OF THE NEOTROPICAL DAMSELFLY *CORA* SELYS (ZYGOPTERA: POLYTHORIDAE)

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Sympatric populations of *C. semiopaca*, *C. notoxantha* and *C. obscura* were studied along a forest creek at El Rodeo Biological Reserve in Costa Rica. Territorial and reproductive behaviour of these 3 spp. are described and compared with *C. marina*, the only other *Cora sp.* studied to date. Males defended territories centered around rotting wood in the creek bed, used by females for oviposition. Territories of *C. semiopaca*, *C. notoxantha* and *C. obscura* were interspersed along the creek and were occupied simultaneously during the day. Extensive spatial and temporal overlap of resource use by the 3 spp. allowed for considerable interspecific interaction at the study site. Aggressive behaviour of males was similar among the 3 spp., with the exception of an escalated ascending spiral contest, observed only between *C. semiopaca* males. Reproductive behaviour was not elaborate; males did not perform courtship or postcopulatory site displays to females. Males of all spp. were rarely observed transferring sperm to their accessory genitalia, either while in tandem or while perched alone. The authors were unable to distinguish between females of the 3 *Cora* spp. at the study site. From records of marked individuals it also appears that *semiopaca*, *notoxantha* and *obscura* males could not distinguish between females of the 3 spp. since a high percentage (32%) of multiple mating females copulated with males of more than one *Cora* spp. Interspecific mating involved full (unshortened) copulation, often followed by oviposition. Recent sympatry of these 3 spp. is the most plausible explanation for an apparent lack of a premating reproductive isolating mechanism in these species. However, the possibility that these putative species are morphological variants of the same species is suggested.

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INTRODUCTION

The family Polythoridae was considered by MUNZ (1919) as one of the most "primitive" of extant zygopteran groups. All eight genera in the family are strictly neotropical and inhabit cool, shaded forest streams (PAULSON, 1982). The genus *Cora* Selys is the most widespread, extending from southern Mexico (18°N) to southern Bolivia (16°S) (BICK & BICK, 1990). Of the approximately twenty *Cora* species, the ecology and behaviour of only one, *C. marina* Selys, has been studied (GONZALEZ & VERDUGO, 1984a, 1984b). This represents the only study within the entire family, other than a brief note by DE MARMELS (1982) on the copulatory behaviour and microhabitat of *Euthore f. fasciata* (Hagen).

In order to broaden the base of knowledge on tropical odonates we studied territorial and reproductive behaviour of *Cora semiopaca* Selys, *C. notoxantha* Ris and *C. obscura* Ris. These species occur in Costa Rica and Panama and are generally uncommon, although *C. semiopaca* may be locally abundant (ESQUI-VEL, 1991). At our study site the three species occurred sympatrically, but differed in population density. *C. semiopaca* was by far the most abundant, while *C. notoxantha* and *C. obscura* occurred in low numbers. The latter two species rarely encountered conspecific individuals; however, there was considerable interspecific interaction among the *Cora* species.

In this paper we describe and compare activity and behaviour in *C. semiopaca*, *C. notoxantha* and *C. obscura*, and compare these species with *C. marina*. We also report on a high degree of interspecific mating among the three *Cora* species at our study site and discuss possible reasons for this.

SPECIES IDENTIFICATION

Cora semiopaca, C. notoxantha and *C. obscura* are sexually dimorphic species, with males being the more elaborately coloured of the two sexes. Males are easily distinguished from one another in the field by wing and thorax colouration. *C. semiopaca* males have metallic blue wings with a distal brown transverse band; the thoracic dorsum is black. *C. notoxantha* males have hyaline wings, and the thoracic dorsum is either blue or yellow-orange (BICK & BICK, 1990). Of these two chromatic forms (blue versus yellow-orange thoracic dorsum) we recorded 47 males of the blue form, and two of the yellow form at our study site over a 13 month period. *C. obscura* males have hyaline wings with a blue sheen that fades as the individual ages (personal observation); the thoracic dorsum is black.

Table I

Total body length of sexually mature male *Cora semiopaca, C. notoxantha* and *C. obscura*

Species	N	Mean ± S.D. (mm)	Range (mm)
semiopaca	99	44.7 ± 1.5[a]	38.0-47.5
notoxantha	12	41.7 ± 0.9[b]	40.0-43.0
obscura	16	41.2 ± 1.2[b]	39.0-43.0

One way ANOVA: F=61.28, p=0.0001; — [a,b] Tukey--Kramer multiple comparisons method: mean body length measurements not sharing the same letter differ significantly.

C. semiopaca males were significantly longer in total body length than either *C. notoxantha* or *C. obscura* males (Tab. I). Although *C. notoxantha* and *C. obscura* males did not differ in mean body length, males of *C. notoxantha* had more robust thoraces than did either *C. obscura* or *C. semiopaca* males.

In contrast to males, we were unable to distinguish among females of the three species in the field. Only the *C. notoxantha* female has been described (RIS, 1918) and we found considerable variation in wing, thorax, facial and abdominal colouration among females at our site. Wing colouration varied from clear, to amber tinged or clear with a blue sheen. A smoky transverse band was noted on the distal portion of the wings of some females as they aged. Females of the three species are a cryptic brown colour. The thoracic dorsum ranged in colour from creamy-tan in some individuals, to dark brown in others, with blue patches on some females. The abdomen was blue-brown with a pale lateral longitudinal stripe on each side varying from indistinct to pronounced. Mean body length for females was 38.5 ± 1.0 mm (n=35). In addition to morphological variation, species identification of females was further confounded by relatively frequent observations of females copulating with males of more than one *Cora* species at our study site. Females are therefore identified only to genus in this study.

STUDY AREA

The study was conducted along a small unnamed creek (herein referred to as Quebrada Cora) on the El Rodeo Biological Reserve near Ciudad Colón, San José Province, Costa Rica (09°55'N, 84° 16'W; elevation 800 m). The area is classified as tropical humid forest (MEZA & BONILLA, 1990).

Quebrada Cora is a small, slow-flowing creek, 1-2 m wide on average and 0-30 cm deep. The creek and surrounding area were shaded by second growth forest, with only small patches of sunlight penetrating the canopy. Native bamboo, ferns, and forbs (primarily family Araceae) dominated the streamside vegetation. The creek bed was sandy and essentially devoid of vegetation.

Studies were conducted along a 150 m portion of the main branch of the creek and along a 40 m side branch. Detailed behavioural observations were carried out at three 8 m sectors in which all three *Cora* species were usually present.

Of the three *Cora* species studied, *C. semiopaca* was the most abundant ($\bar{X}$ = 1.5 males/10 m), with *C. notoxantha* and *C. obscura* occurring in low numbers ($\bar{X}$ = 0.2 and 0.1 males/10 m, respectively). Among the other odonate species on the creek, *Heteragrion erythrogastrum* Selys, *Hetaerina capitalis* Selys and several *Argia* species were most abundant.

METHODS

The study was conducted from 15 May to 27 July, 1990. It complemented a larger demographic study conducted from November 1989 to December 1990. Individuals were captured by aerial net and marked with unique identification numbers on the left hind wing using a waterproof marker. Perched individuals usually could be approached closely enough to read marks with the naked eye; otherwise compact binoculars were used.

Each mark and recapture record included the time of capture, location along the creek, and behaviour or activity at the time of capture. If the individual was perched, the perch height above water and distance from the water (measured to the nearest 10 cm) were recorded, along with the type of perching substrate. Total body length of individuals (from labrum to tip of abdominal appendages) was measured with dividers to the nearest 0.5 mm.

Arrival and departure times of individuals on the creek were obtained from hourly censuses along the main branch of the creek from 0830-1630 Central Standard Time on 12, 14, 15 February, 12, 14 March and 12, 19 July, 1990. Mean population density of each species was calculated from these

data using the mean number of males sighted between 1130-1230, divided by the 150 m length of creek censused, and then expressed as mean number of individuals/10 m of creek.

Behavioural observations were made between 0900-1500 and totaled 120 hours. Fifteen-minute focal observation sessions of individual territorial males (17 *C. semiopaca*, 11 *C. obscura* and 7 *C. notoxantha*) were made to determine durations of various activities ("activity budgets"). Each time a new behaviour was observed the behaviour and time were recorded.

A one-way analysis of variance was used to test for differences in mean body length between males of the three species and for differences in copulation durations. Kruskall-Wallis tests (corrected for ties) were used to test for differences between males of the three species for territory and copulation perch heights and the duration of various activities since these data were not normally distributed. Means are given ± S.D.

DAILY ACTIVITY PATTERNS

Each day, males began appearing along the edges of the creek before 0830 hours (Figs. 1A-C), but usually did not take up residence at their respective territories until 0930-1030. Females were also sighted on the creek by 0830, and reached peak numbers between 1030-1230 (Fig. 1D). Although females were present at the creek throughout the day, each individual remained for only one to several hours (to mate and oviposit); thus the composition of the female population continually changed.

The number of individuals (male and female) at the water began to decline after 1230 for all species (Fig. 1). *C. notoxantha* and *C. obscura* males were not present after 1430 (Figs 1B & C), although the occasional *C. semiopaca* male and *Cora* female persisted at the creek until 1630 (Figs 1A & D, respectively). When individuals left the water for the day they flew upward toward the canopy, where they presumably roosted.

Peak activity (territorial and reproductive) occurred between 1000 and 1400. Although individuals perched in shade and did not chase sunspots, they were most abundant and most active on sunny days. On cloudy days individuals descended from the canopy to elevated perches above the creek, but few took up residence at the creek bed. When rain penetrated the canopy individuals ascended out of sight. On several occasions a brief shower occurred at midday whereupon individuals ascended but returned to the water approximately 30 minutes after the shower ended. As the rainy season progressed, however, activity was increasingly preempted by afternoon rain.

No feeding behaviour was observed on the creek during the day, although females were occasionally observed feeding from elevated perches (≥ 2 m high) adjacent to the creek.

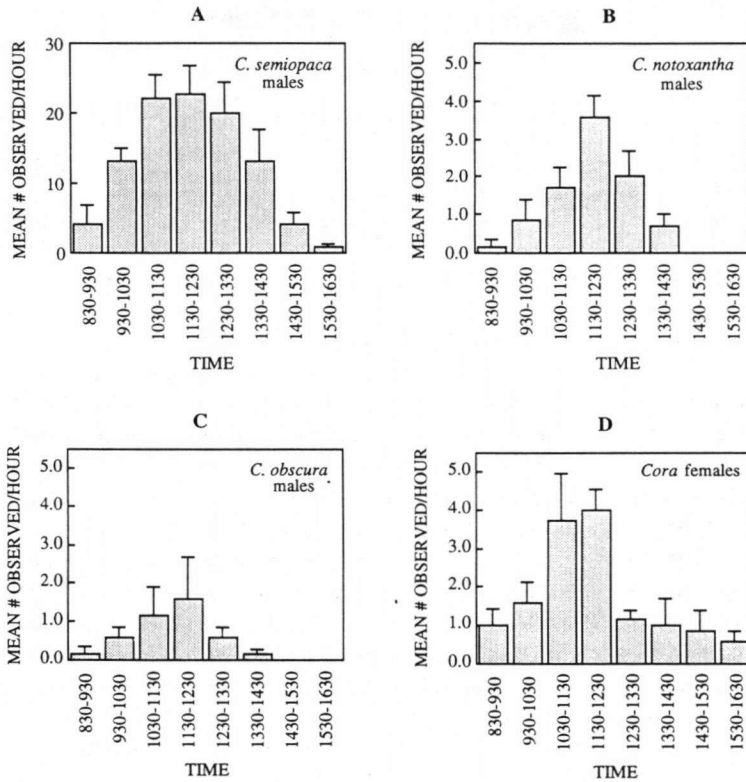Fig. 1. Mean number of indviduals (with S.E. bars) observed along Quebrada Cora during hourly census intervals (n = 7 days): (A) *Cora semiopaca* males; − (B) *C. notoxantha* males; − (C) *C. obscura* males; − (D) Females of all three species.

TERRITORIALITY

SITE ATTACHMENT

A territorial male is defined here as a male who remains in or returns to a fixed area, and is aggressive toward and dominates other males in that area (WAAGE, 1973). Males of all three species defended territories around pieces of rotting wood in the creek bed, used by females as oviposition substrate. This substrate varied in size from twigs 1 cm in diameter to portions of fallen trunks over 50 cm in diameter and 100 cm in length. Oviposition material was not distributed uniformly; site size varied from a single branch or trunk to large patches of wood covering an area of over 2 m². Territories for males of the three species were interspersed along the creek. At sites where oviposition material

Table II

Mean perch heights for territorial male *Cora semiopaca, C. notoxantha* and *C. obscura* during hours of peak activity (1000-1400 hours)

Species	N	Mean ± S.D. (cm)	Median (cm)	Range (cm)
semiopaca	60	25 ± 14	20	0-70
notoxantha	25	22 ± 13	20	10-60
obscura	25	20 ± 12	20	· 0-60

Kruskall-Wallis test: H=2.75, p=0.253.

was abundant, several males of one or more *Cora* species each controlled a portion of the site. At sites with sparse oviposition material, such as a single piece of fallen trunk or a small pile of rotting wood debris, a single male was the sole resident. Individual territory size in all species ranged from approximately 1 to 10 m².

Males showed astounding site tenacity, commonly holding a given territory for over 15 days (unpublished data). Males defended territories from slightly elevated perch sites over, or at the edge of the water, perching almost exclusively in the shade. Perch heights for males of the three species did not differ significantly (Tab. II). Planar surfaces such as rocks or broad leaves were rarely used as perching substrate. Males preferred to perch on points of twigs or branches projecting from the creek bed, or on low overhanging vegetation such as bamboo

Table III

Activity budgets for *Cora semiopaca, C. notoxantha* and *C. obscura* males during 15-minute (900 sec) runs: duration of activities

Activity	*semiopaca* (n=17)			*notoxantha* (n=7)			*obscura* (n=16)		
	Mean ± S.D. (s)	Median (s)	Mean (%)	Mean ± S.D. (s)	Median (s)	Mean (%)	Mean ± S.D. (s)	Median (s)	Mean (%)
Perching	857.5±60.9	885	95.3	887.9±8.4	886	98.7	888.6±12.9	893	98.7
Non- -interactive flight	9.4±8.7	7.0	1.1	8.4±9.3	3.0	0.9	3.9±5.3	1.0	0.4
Intraspecific aggression*	20.5±49.9	0	2.3	0	0	0	0	0	0
Interspecific aggression	6.3±8.9	1.0	0.7	3.7±6.8	0	0.4	6.7±8.3	5	0.7
Reproduction	6.4±25.7	0	0.7	0	0	0	0.7±1.3	0	0.1

Kruskall-Wallis test: *H=7.36, p=0.025

or thin branches. From these perches males made apparently spontaneous flights of several seconds around their territories, even in the absence of other individuals.

Cora males were inactive while at the creek, spending the majority of their time (95-99%) perched (Tab. III). We did not partition male perching time into categories of territorial vigilance and mate guarding since these two activities were not behaviourally distinct. *C. semiopaca* males were most active of the three species, although only the duration of intraspecific aggressive interactions was significantly greater than for *C. notoxantha* or *C. obscura* males (Tab. III).

<div align="center">TERRITORIAL DEFENCE</div>

A perched male responded agonistically to disturbance from another individual flying in his vicinity in the following ways:
(1) the male remained perched but w i n g w a r n e d (BICK & BICK, 1963) an intruder flying overhead. The male splayed his wings and held them horizontally for one to several·seconds. The wing warn response was rarely observed and was elicited by disturbance from other odonates and insects as often as from conspecific individuals.
(2) the male flew from his perch toward the detected movement and performed one of the following:
  (a) a l i n e a r c h a s e in which the male pursued the intruder from a distance of approximately 10 cm. Linear chases were brief (1-6 s) and never involved physical contact.
  (b) a f r o n t a l c h a l l e n g e in which the two interacting males hovered head to head while remaining approximately 10 cm apart, although head--on collisions between contestants occurred occasionally. In brief (1-3 s) frontal challenges males remained hovering in one location. In longer bouts (up to 10 s) the males sawed back and forth or gradually ascended while facing one another.
  (c) an a s c e n d i n g s p i r a l c o n t e s t in which the two interacting males rapidly chased one another in a tight ascending spiral, approximately 30 cm in diameter. Physical contact occurred during these contests as an interaction changed from a spiral contest to a frontal challenge. These prolonged aggressive interactions lasted up to 30 seconds and 8 of 11 continued until both individuals were lost in the canopy above; in these instances males returned to the water approximately two minutes later.

Linear chases and frontal challenges occurred between conspecific males of all three species, as well as between heterospecific *Cora* males. However, the ascending spiral contest was only observed between *C. semiopaca* males. Five of eleven prolonged *C. semiopaca* contests involved males guarding ovipositing females. In one instance the ovipositing female mated with a neighbouring male while the guarding male was engaged in an escalated contest with another male.

Six spiral contests involved a resident male and a non-neighbour; three involved neighbouring males; males were not identified in the other two cases.

OTHER BEHAVIOUR

Perched individuals of both sexes w i n g c l a p p e d (BICK & BICK, 1965a) infrequently. In wing clapping, an individual slowly opened its wings approximately half-way, then closed them. This behaviour was apparently unsolicited by outside disturbance and was frequently performed following flight activities.

Grooming behaviour was performed by both males and females in our study. Grooming involved pulling the abdomen downward between the closed wings. This was repeated up to twenty times per grooming bout, and usually followed copulation; in *C. semiopaca* males this was also observed following prolonged aggressive encounters.

REPRODUCTION

Reproductive behaviour was similar in all three *Cora* species and followed the sequence shown for *C. semiopaca* in Figure 2.
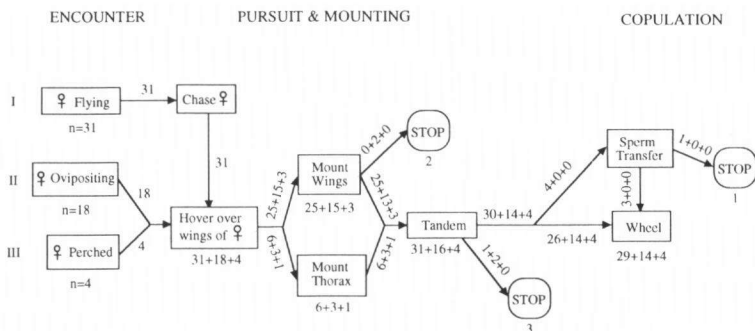

Fig. 2. Sequences of reproductive behaviours leading to successful copulations for *Cora semiopaca, C. notoxantha* and *C. obscura* males. Numbers refer to responses by *C. semiopaca* males only for Type I, II and III encounters respectively with *Cora* females. − [Note: the frequency of mating attempts aborted prior to the male mounting the female were not recorded].

FEMALE ENCOUNTER

A male encountered a female as the female flew within or adjacent to the male's territory, or as the female oviposited or perched within the male's territory. In the latter two cases, movement by the female (such as pivoting on her perch) was necessary to elicit a response by the male.

PURSUIT AND MOUNTING

A flying female was pursued by the male until she perched or flew out of his territory. If the female perched, the male usually hovered above and slightly behind the female's wings for one to several seconds. While in this posterior hovering position, the male's thorax and tarsi sometimes contacted the apex of the female's wings. On several occasions a *C. semiopaca* male hovered head-on or facing the thorax of the female before moving to the usual posterior position. Since this frontal approach was rarely observed, we consider courtship in these *Cora* species to be lacking.

A female usually responded to a male hovering over her wings by w i n g f l i p p i n g. This behaviour consists of the female rapidly and repeatedly opening her wings halfway, then closing them. We consider wing flipping to be different from wing clapping since wing flipping is a rapid, repeated motion, performed only by females in response to a disturbance (i.e. a hovering male). Wing clapping is a much slower motion, is usually not repeated, and is apparently an unsolicited behaviour. Wing flipping is distinct from wing warning in that the wings are not splayed and held open as they are in wing warning. Although the majority of females seemed to respond to hovering males by wing flipping, not all females wing flipped. Males were observed mounting both wing flipping and silent females, while abandoning others. Neither the female's response to a hovering male, nor the male's response to the female were recorded; thus we were unable to determine the significance of wing flipping behaviour by females.

The male usually mounted the female at the distal end of her folded wings and walked down the outer edge of her wings to the prothorax. In some cases, however, the male simply mounted the female's prothorax directly (Fig. 2). Tandem formation quickly followed, with the male bringing his abdomen forward to clasp the female's prothorax with his anal appendages. Once in tandem the pair flew briefly to an elevated perch, usually within the male's territory, where copulation occurred. Mean copulation perch heights for the three species did not differ significantly (Tab. IV).

Table IV

Mean heights of copulation perches for *Cora semiopaca*, *C. notoxantha* and *C. obscura* males

Species	N	Mean ± S.D. (cm)	Median (cm)	Range (cm)
semiopaca	76	77 ± 66	60	10-300
notoxantha	11	45 ± 47	40	10-140
obscura	11	55 ± 44	60	10-130

Kruskall-Wallis test: H=3.00, p=0.224.

COPULATION

The copulatory (wheel) position was formed directly after the tandem pair perched. Although in Zygoptera sperm transfer usually occurs while the pair is in tandem, and immediately prior to copulation (BICK & BICK, 1965b), we rarely observed this in the three *Cora* species at our study site. Sperm transfer (inferred from contact between a male' s second and ninth abdominal segments) was observed in only 6 of 125 pairings involving *C. semiopaca* males, 1 of 12 pairings involving *C. obscura* males, and none of the 21 pairings involving *C. notoxantha* males. Sperm transfer was observed in males perched alone, but this too was rare. Throughout the study only 11 *C. semiopaca* males were observed transferring sperm while perched alone; 8 of these were males guarding mates following copulation. The mean elapsed time from the break of the wheel until the male transferred sperm was 5.7 min (range = 3.1-10.0 min; n=5). One *C. notoxantha* male was observed transferring sperm 6 minutes postcopulation; no lone *C. obscura* males were observed transferring sperm.

Copulation durations among the three species did not differ significantly (Tab. V). During copulation, abdominal pumping by males was observed.

Table V

Duration of copulation (from formation to break of wheel) for *Cora semiopaca*, *C. notoxantha* and *C. obscura* males

Species	N	Mean ± S.D. (s)	Range (s)
semiopaca	61	212.2 ± 67.9	118-455
notoxantha	4	192.0 ± 19.5	169-211
obscura	3	259.0 ± 10.4	252-271

One way ANOVA: $F=0.951$, $p=0.392$.

INTERSPECIFIC MATING

Both males and females were observed mating more than once within a day. From lifetime mating records of marked females we found that a surprising 32% (12/37) of these females copulated with two or more species of *Cora* males; two of these females copulated with males of all three species. In these interspecific matings the reproductive sequence shown in Figure 2, including complete, unshortened copulation, was observed. Interspecific matings were sometimes followed by oviposition, but the total number of times this was observed was not recorded.

POST-COPULATORY BEHAVIOUR

Following the break of the wheel the male released the female and, in order of decreasing frequency:
(a) immediately returned to his territory perch site,
(b) returned to his territory perch site after a brief flight around his territory,

(c) returned to his territory perch site after perching at the copulation site.

We observed no subsequent site display by the male to the female following copulation and preceding oviposition by the female.

The female flew to an oviposition site within the male's territory either immediately following copulation or after perching at the copulation site for some time. Of 63 females observed ovipositing following copulation, the time lag ranged from 0 to 17.5 min ($\bar{X}$ = 1.6 ± 3.2 min, median = 0.6 min).

A male responded to his mate's arrival at the oviposition site by hovering slightly above her, then perching nearby, usually within 15 cm. The male did not maintain this close proximity throughout the female's oviposition bout; rather, he returned to his territory perch site which was generally within 30 cm of the female. The postcopulatory male sometimes perched with the last few segments of his abdomen sharply downturned. This posture was not maintained for the duration of time the female oviposited however, and was therefore not a reliable indicator of a guarding male.

Females oviposited in spongy, barkless rotting wood protruding above the water ($\bar{X}$ height above water = 10 ± 9 cm, n=67). The yellow to grey-black wood effectively camouflaged ovipositing females. Females probed several pieces of rotting wood within a small area before beginning oviposition. Oviposition appeared prolonged (personal observation, and one timed oviposition sequence lasting 51 min). Females at our site were sometimes observed ovipositing without first mating with resident males, but oviposition durations are unknown.

Each time an ovipositing female moved, the guarding (resident) male responded by hovering over the female's wings. Females usually wing flipped in response to hovering males. We observed several *C. semiopaca* males recopulating with their previous mates and guarding non-mates. *C. semiopaca* males were observed guarding as many as five females at one time.

DISCUSSION

COMPARISONS AMONG *CORA* SPECIES

RESOURCE USE & ACTIVITY. − Sympatric populations of *Cora semiopaca*, *C. notoxantha* and *C. obscura* were studied along a shaded, forest creek at El Rodeo Biological Reserve in Costa Rica. These three species broadly overlapped in their resource use and exhibited striking similarity in their activity patterns. *C. semiopaca* was the largest of the three species in terms of total body size. This size asymmetry may give *C. semiopaca* a competitive advantage over the two smaller species (MAYNARD SMITH, 1982), and thus explain its greater abundance.

Abundances and activity levels of *Cora* species appear to be affected by ambient light levels, even though these species perch almost exclusively in shade,

and do not chase sunspots. The moist, shaded environment of the creek buffered temperature fluctuations (daily fluctuations were in the order of 2°C), in sharp contrast to the open field habitat near our site where daily temperatures fluctuations could exceed 10°C. Although both light levels and temperature may play an important role in regulating activity in sun-seeking species (e.g. *Hetaerina* and *Argia*), light levels are probably the more important of the two factors for shade-seekers such as *Cora*.

Males of all *Cora* species so far studied defend territories around pieces of rotting wood in the creek bed, used by females as oviposition substrate (GONZA-LEZ & VERDUGO, 1984a, 1984b; this study). ROBERTSON (1982) describes the use of rotting wood for oviposition as an adaptation to living on streams with little or no emergent vegetation. The conditions at our study site support this hypothesis. A list of species known to oviposit in rotting wood is provided by GONZALEZ & VERDUGO (1984b). The probing we observed by *Cora* females prior to oviposition may be a means of testing the sponginess of the wood. We found that females sometimes probed wood with bark, but quickly abandoned it, perhaps due to its hardness.

TERRITORIAL BEHAVIOUR. — *Cora* males perch on the tips of twigs and branches within or adjacent to their territories, flying out to intercept intruding males and receptive females. *C. semiopaca, C. notoxantha* and *C. obscura* males all perched close to the water, in sharp contrast to the long distance vigilance *C. marina* males exhibit (X perch height = 74 cm; GONZALEZ & VERDUGO, 1984b). This difference may simply reflect differences in resource defence strategies between species, or it may reflect behavioural plasticity in response to population density. GONZALEZ & VERDUGO (1984b) reported low densities of *C. marina* at their site, but did not quantify this. The collective male *Cora* density at our site was relatively high (X = 1.9 males/10 m). If a male's probability of failing to detect an intruder, or of losing a mate to another male increases with population density, then males may show some plasticity in their territory and mate-guarding defence strategies. Density manipulation studies could help distinguish between the species-specific and density-dependent hypotheses.

Males engaged in ritualized aggressive behaviours in defence of their territories. Linear chases and frontal challenges were performed by males of all three *Cora* species at our study site, and occurred between both conspecific and heterospecific individuals. We attribute the rarity of intraspecific aggression within *C. notoxantha* and *C. obscura* (absent in Tab. III and rarely observed otherwise) to the low population densities of these two species at our study site. *C. notoxantha* and *C. obscura* rarely encountered conspecific males and interacted most frequently with *C. semiopaca* males. The high relative density of *C. semiopaca* males allowed for considerable intraspecific interaction in this species, and probably explains the significant difference between species in the amount of time spent in intraspecific aggression (Tab. III).

C. semiopaca was similar to *C. marina* in aggressive behaviour. Both of these species engage in escalated aggression in the form of an ascending spiral contest (GONZALEZ & VERDUGO, 1984b; this study); *C. notoxantha* and *C. obscura* were never observed in these escalated contests. If the ascending spiral contest is part of the behavioural repertoire of *C. notoxantha* and *C. obscura*, but is only performed between conspecific males, then the absence of this behaviour in these two species may be due to the low population densities of these two species at our study site. If this escalated aggression is not a strictly conspecific interaction, then its absence between *C. semiopaca* and *C. notoxantha* or *C. obscura* males may be explained by the larger body size of *C. semiopaca*. The size asymmetry may give *C. semiopaca* a competitive advantage over *C. notoxantha* and *C. obscura*, enabling disputes to be settled quickly, without escalation (MAYNARD SMITH, 1982).

C. semiopaca and *C. marina* males resemble *Calopteryx maculata*, a well studied temperate calopterygid, in their territorial interactions. Most disputes last only a few seconds, but prolonged contests of several minutes, and up to hours in *Calopteryx maculata* (WAAGE, 1988) occur. WAAGE (1988) attributed these escalated territorial disputes between *C. maculata* males to confusion over residency, where two males became residents in the same territory. The context in which ascending spiral contests occurred between conspecific *Cora semiopaca* and *C. marina* males differ from one another, but neither seems to fit the confusion hypothesis. GONZALEZ & VERDUGO (1984b) noted that up to 5 *C. marina* males were involved in ascending spiral contests, while we never observed more than 2 *C. semiopaca* males engaged in these contests. In *C. marina* the large number of interacting males makes it unlikely that all males mistakenly become residents of the same territory. In *C. semiopaca* guarding males were involved in almost half of the interactions, and over half of these interactions involved fights with non-neighbouring males. Not all oviposition sites attracted females equally, and thus intense fighting may be a result of nonresident males trying to take over particularly attractive sites, especially those with females present. This 'valuable resource' hypothesis could be tested in the future by manipulating the amount of oviposition material at a site, and by altering the number of females present at the site using pinned specimens.

Wing clapping was performed by males and females at our study site. BICK & BICK (1978) hypothesize that wing clapping serves to communicate the presence of a territorial male to his potential competitors, and when performed between a male and a female, it serves to communicate their presence to each other. ERICKSON & REID (1989) suggest that wing clapping may further serve a thermoregulatory function, aiding in heat reduction. Since wing clapping behaviour by *Cora* was unsolicited by outside disturbance and usually followed flight activities, our observations tend to support the thermoregulatory hypothesis. The tropical shade-dwelling habit of *Cora* suggests that these species prefer

stable temperature environments, and their low activity levels reinforce this. Thus, wing clapping could be a means of thermoregulation. However, without further study we cannot discount a social function.

REPRODUCTIVE BEHAVIOUR. — Reproductive behaviour in *C. semiopaca, C. notoxantha* and *C. obscura* was not elaborate. No form of courtship display to the female was recognized. This is in contrast to *C. marina* in which the male faces the female and hovers for several seconds with his abdomen elevated, thereby displaying its bright blue dorsum (GONZALEZ & VERDUGO, 1984b).

Another distinct difference between *C. ·marina* and the three species at our study site concerned sperm transfer. We rarely observed males transferring sperm to their accessory genitalia, either while in the tandem position, or while perched alone. GONZALEZ & VERDUGO (1984b) observed tandem males transferring sperm in 15 of 18 observed matings. We are puzzled by its general absence in our study species and are unsure of its possible significance. Copulation durations of *C. marina* (X = 186s; GONZALEZ & VERDUGO, 1984b) are similar to those we recorded for *Cora* species at our site.

The multiple mating capacity and territorial nature of *Cora* males, combined with the prolonged oviposition duration of females (*C. marina*: $\bar{X}$ = 56.8 min; GONZALEZ & VERDUGO, 1984b) select for non-contact mate guarding. Natural selection may also act on male mate-guarding distance if population density and the conspicuousness of an ovipositing female affect the probability that a male's mate will be detected and approached by a rival male. Females of all *Cora* species are brown, which effectively camouflages them against the background of rotting wood in which they oviposit. *Cora* males appear to have difficulty detecting ovipositing females since movement on the part of the female is necessary to elicit a response by the male. Thus there may be little advantage for *Cora* males to guard females from close proximity if female camouflage is effective in significantly reducing the probability that an ovipositing female will be discovered by an intruding male. This 'camouflage' hypothesis may explain why *Cora* males guard mates from their territory perch sites. This strategy is most striking in *C. marina* males where males guard mates from a considerable distance ($\bar{X}$ territory perch height = 74 cm; GONZALEZ & VERDUGO, 1984b); *Cora* males at our site generally remained within 30 cm of a mate. These differences in territory perch heights and guarding distances may be due to differences in male population densities and could be tested by manipulating population density at a site.

The significance of the lag time exhibited between copulation and oviposition by *Cora* females is unclear. GONZALEZ & VERDUGO (1984b) noted that *C. marina* females ($\bar{X}$ lag time = 6.2 min) used this time to rub an unidentified white substance from the terminal part of the abdomen. The substance covered the genital pore and they postulated it was the rest of the spermatophore, and possibly a mating plug. No such excretion was noted on *Cora* females at our

site, although postcopulatory abdominal grooming by females was occasionally observed. Possible explanations for this lag time are (1) female assessment of the oviposition site in her mate's territory, or (2) female assessment of her mate before committing her eggs. Since *Cora* males presumably practice sperm removal, postcopulatory assessment of males by females is a possible, albeit inefficient means of female mate choice. Further study is needed before the significance of the lag time is clear.

Finally, *C. semiopaca*, *C. notoxantha* and *C. obscura* males responded differently than *C. marina* males toward females descending from the copulation perch site to the oviposition site. GONZALEZ & VERDUGO (1984b) describe an occasional wing clapping site display by *C. marina* males as their mates descend to the oviposition sites. We did not recognize any conspicuous site display by *C. semiopaca*, *C. notoxantha* and *C. obscura* males to their mates.

COMPARISONS WITH CLOSELY RELATED GROUPS

The strong territorial behaviour exhibited by *Cora* resembles that of some members of two closely related families, Chlorocyphidae and Calopterygidae. Males of *Platycypha caligata* (Chlorocyphidae) centre their territories around driftwood and treeroots in streams (ROBERTSON, 1982); males of *Calopteryx* species defend territories around patches of emergent stream vegetation (e.g. PAJUNEN, 1966; WAAGE, 1973). All three groups exhibit highly ritualized aggressive behaviours. However, reproductive behaviour is much simpler in *Cora* than in *Platycypha* and *Calopteryx*. *Cora marina* is the only *Cora* species known to exhibit courtship behaviour. However, this behaviour is rudimentary compared to the elaborate tibial flashing display of *Platycypha caligata* (ROBERTSON, 1982) and the cross display and courtship flight of *Calopteryx* (e.g. WAAGE, 1973; MIYAKAWA, 1982). Comparisons of Polythoridae with its more advanced relatives, Chlorocyphidae and Calopterygidae, will help enhance understanding of the evolution of territorial and reproductive behaviour among Zygoptera.

SIGNIFICANCE OF INTERSPECIFIC INTERACTIONS

Because *C. semiopaca*, *C. notoxantha* and *C. obscura* were sympatric along Quebrada Cora we were able to study both intra- and interspecific interactions within this species complex. The broad spatial and temporal overlap of resource use created the potential for considerable interaction among these three species. Males were aggressive toward both conspecific and heterospecific *Cora* males. This interaction is expected given the high percentage of multiple mating females that mated with males of more than one species of *Cora*, and assuming that *Cora* males practice sperm removal (see WAAGE, 1986).

The indistinguishability of *C. semiopaca*, *C. notoxantha* and *C. obscura*

females, and the high percentage of interspecific mating we recorded at our site raise some interesting questions regarding reproductive isolating mechanisms and species integrity in these species. It appears that males are unable to distinguish between females of their own species and of other *Cora* species. Species and sex recognition in odonates is based primarily on visual and tactile stimuli (PAULSON, 1974; TENNESSEN, 1982). Flight pattern, morphology, and wing and body colouration are the main visual stimuli. However, accounts of heterospecific pairing have been recorded in species with colourful wing patterns, such as *Calopteryx* and *Libellula* (BICK & BICK, 1981). *Cora semiopaca, C. notoxantha* and *C. obscura* males are morphologically distinct. *C. semiopaca* has bright blue colouring in the wings and *C. notoxantha* is the only species with a blue (rather than black) thoracic dorsum. However, how these species are perceived in the odonate visual spectrum is unknown. Regardless, the lack of courtship in these species largely precludes species recognition by the female prior to the male taking her in tandem.

Tactile stimuli may provide opportunities for males or females to discriminate between species, as has been demonstrated in several *Enallagma* species (PAULSON, 1974; ROBERTSON & PATERSON, 1982). However, incompatibility of genitalia as a reproductive isolating mechanism has not been demonstrated convincingly for any odonate species (TENNESSEN, 1982; WAAGE, 1984). We noted several cases of failed tandem or wheel formation in *Cora* species at our study site, but due to the overwhelming numbers of successful matings among species it does not appear that mechanical reproductive isolating mechanisms are well developed in *Cora*.

We presume that sperm was transferred to females during interspecific matings since we never observed any noticably short (aborted) copulations. Thus, reproductive isolation in *Cora* is probably occurring via a post-mating isolating mechanism. Female odonates store sperm transferred during copulation, and fertilize their eggs as they oviposit. Therefore, if a *Cora* female recognized her mate as a heterospecific male, she could delay oviposition until she remated with a conspecific male. However, we found that females usually oviposited after copulation; thus females do not appear to use discretion in sperm usage. Mistakes made by females attempting to fertilize eggs with sperm from a heterospecific male may be costly if egg production is expensive (in terms of time and energy).

Assuming *Cora* females do fertilize eggs indiscriminately, inviability of hybrids may still act as a reproductive isolating mechanism between these species. We did not recognize any male hybrids at our site, and female morphological variability precluded the identification of species, not to mention of hybrids. Therefore, if *C. semiopaca, C. notoxantha* and *C. obscura* are indeed good biological species (sensu MAYR, 1942), then reproductive isolation is probably occurring via a postmating, and more specifically, a postzygotic isolating mechanism.

The high costs of interspecific interactions in this system, and the lack of

ecological, behavioural or female morphological divergence among these species strongly suggest that sympatry of the three species is a recent phenomenon. Until the distribution of *Cora* is more fully known, it is impossible to say how frequently these species coexist, or how long they have done so. SINGER (1990) studied three sympatric species of *Leucorrhinia* that exhibit broad spatial and temporal overlap of their mating habitat and found that males frequently attempted to mate with heterospecific females. However, tactile stimuli seemed to be operating as reproductive isolating mechanisms in *Leucorrhinia* since interspecific matings were very brief in comparison to intraspecific matings (SINGER, 1990). Singer rejected recent sympatry as an explanation for failed species discrimination because the three *Leucorrhinia* species have broadly overlapping geographic ranges. Instead, he proposed that neurological constraints restrict species discrimination in the *Leucorrhinia* complex. A resident male would lose his competitive advantage of being the initiator in a contest if he delayed approaching a congeneric intruder until the intruder was identified as a conspecific (SINGER, 1990). This hypothesis may also be important in *Cora*, especially if sperm competition among species is occurring. Males were aggressive toward both conspecific and heterospecific *Cora* males, but the apparent lack of prezygotic reproductive isolation in these species suggests that the geographic ranges of *C. semiopaca*, *C. notoxantha* and *C. obscura* have only recently overlapped.

Members of the genus *Cora*, and Polythoridae in general, are poorly collected, and their distributions are not well known. Species ranks are based on males, and females of only a few species have been described. The high degree of interspecific mating (i.e. unshortened copulation, often followed by oviposition) among *C. semiopaca*, *C. notoxantha* and *C. obscura* suggests that more detailed taxonomic work is required on this species complex. We are presently considering the possibility that *C. semiopaca*, *C. notoxantha* and *C. obscura* are actually morphological variants of the same species. We plan to investigate the taxonomic status of these three putative species using both morphological and allozyme analyses. A final step in this examination would be to rear eggs from mixed matings in the lab. However, a previous attempt by C. Esquivel and his student A. Ramirez to rear eggs in the lab from wood we gathered from our study site proved unsuccessful.

We began this study with the aim of describing territorial and reproductive behaviour in a poorly known neotropical group of forest stream-dwelling odonates. From our study we were able to document a perhaps unprecedented level of interspecific mating among a sympatric odonate species complex. TENNESSEN (1982, p. 260), wrote: "Very little has been published on behavior and isolation of neotropical Zygoptera, in which many unusual strucural and color differences exist between related species. Intriguing problems and discoveries await investigators who undertake studies of Polythoridae, Megapodagrionidae, Pseudostigmatidae, Platystictidae and Protoneuridae, as well as the Chlorocyphi-

dae and Epallagidae of other parts of the world." This prediction has been realized by our study of *Cora*, a member of the Polythoridae. We look forward to hearing of more cases like this as our knowledge of tropical odonate fauna grows.

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