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BREEDING BEHAVIOUR OF THE COROMANDEL DAMSELFLY *CERIAGRION COROMANDELIANUM* (FABRICIUS) (ZYGOPTERA: COENAGRIONIDAE) IN CENTRAL INDIA: COPULATION

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Abstract: The Coromandel Damselfly *Ceriagrion coromandelianum* can be easily identified because of its bright yellow abdomen, greenish thorax and eyes. In females, the abdomen is darker with light brown colouration extending to dark brown towards the terminal end. The documentation of the reproductive behaviour of *Ceriagrion coromandelianum* was carried out at the botanical garden of Hislop College, Nagpur, India. The males of *C. coromandelianum* arrive early in the morning by 07:00hr at the ovipositing site. They belong to “sit and wait” type of mate-location. While perched and waiting for the female to arrive they at times exhibit abdominal bobbing, and oviposition posture. The territorial area of male *C. coromandelianum* is very small, within a range of about 45cm around his perch. There is no precopulatory courtship display and the male move toward the arriving receptive female and directly tries to form a tandem link. The other males of the group follow the pair. The tandem pair flies towards the safety of the surrounding vegetation to copulate. Before copulation, the male fills his penis vesicle with sperm material by the process of “intra male sperm translocation” which lasts for 30±8 seconds. The female curves her abdomen ventrally forward so that her gonopore which is located between the eighth and ninth sternite comes to lie before the secondary copulatory apparatus of the male and forms a strong genital link, to form the copulatory wheel. The copulation duration can be long (34–55 min) or short (12–15 min). Two stages of copulation depending upon the pumping movement of the couple can be differentiated. During the first stage, the male rhythmically and forcefully depresses and stretches the first two abdominal segments, vigorously pumping the penis inside the female vagina which accounts for 72% of the copulation duration. The second stage starts with rapid short thrusting movement which are not forceful but exhibit shallow movements of the first two abdominal segment of the male. The tandem pairs after copulation may directly move for oviposition or settle around the surrounding foliage and exhibit “post-copulatory resting” (PCR) behaviour. It is noted that 23.3% females immediately commence oviposition, 53.4% exhibit brief, while 23.3% display prolonged PCR behaviour.

Keywords: Intra male sperm translocation, mate-location, post-copulatory resting.

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Authors Contribution: Nilesh R. Thaokar and Payal R. Verma contributed in field work and documentation of the oviposition behaviour. Raymond J. Andrew set up the project and evaluated the findings.

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INTRODUCTION

In Odonata, the mating system has the following components—encounter, recognition, copulation, sperm transfer and oviposition. The encounter for a majority of odonates is near the oviposition site and is therefore the water body (Waage 1984). Encounter leads to territoriality and aggressive interaction between males. Recognition of sex and species is based predominantly on visual signals (Mokrushov & Frantsevich 1976). In many odonates the phenomena of male courtship follows recognition during which the female can exhibit “refusal display” to unwelcome approaches by male. Courtship leads to pre-copulatory tandem formation where the male grasps the female’s thorax and head with his anal appendages. Intra-male sperm translocation generally occurs during tandem and is followed by copulation. Copulation is achieved by the “wheel” formation where the female’s genital aperture is secured to the male’s secondary genitalia. Copulation in Odonata is unique among pterygote insects since the primary genitalia of the two sexes do not meet during sperm transfer (Carle 1982; Matsuda 1976). Sperm competition occurs widely among insects and the discovery that the odonate penis both inseminates the female and displaces rival sperm (Waage 1986) has indeed proved to be an invaluable aid in interpreting odonate reproductive behaviour (Corbet 1999). Sperm competition as found in Odonata benefits the female by reducing their energy expenditure, lowering risk of harassment from conspecific males and predators, survival of genetic diversity of progeny and fertility backup.

MATERIAL AND METHOD

The documentation of the reproductive behaviour of *Ceriagrion coromandelianum* was carried out at the botanical garden of Hislop College, Nagpur, (21.166°N & 79.033°E) where small underground cement tubs are used to grow macrophytes. The garden houses aquatic plants in a large circular tub surrounded by six smaller circular tubs followed by a row of three rectangular cement containers. These tubs contain free floating *Nymphaea nouchali*, *Lemna paucicostata* and submerged *Hydrilla verticillata*. The tubs are surrounded by grasses and bushes of flowering plants (*Mussaenda laxa*, *Chrozophora* sp., *Catharanthus roseus*, *Phyllanthus amarus*, *Ageratum conyzoides*, *Bougainvillea* sp.) (Images 1 a,b). Post-noon this area is in shadow of the college building. Adult *C. coromandelianum* are found

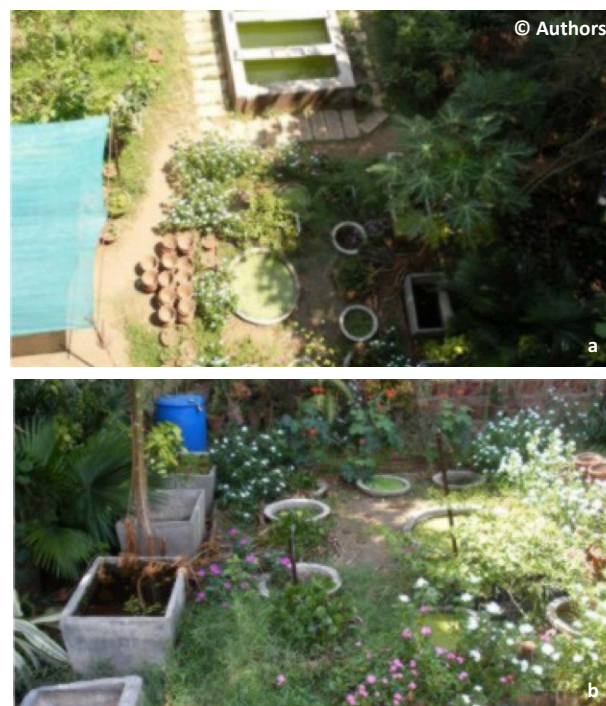


Image 1. The study site: Location of oviposition sites at the Botanical garden of Hislop College, Nagpur.

almost all round the year breeding in these water-bodies.

To study the reproductive behaviour of *C. coromandelianum*, field observations were carried out mostly during the months of August to November and March to May from 2008–2013. These observations were carried out in the morning and/or afternoon and the reproductive behaviour was documented, noted and/or photographed, videotaped while the duration of different behaviour was timed with a stop-watch.

RESULTS

On a typical breeding day, the males of *C. coromandelianum* arrive early in the morning by 7am and move between the bushes and grasses around the ovipositing site (water tubs). Within an hour, they can be spotted perched all around the bushes surrounding the water-body. The male belong to “sit and wait” type of mate-location. They occupy a base perch which is about 10–60 cm above the ground and not more than 120cm away from the water tubs. The base perch is commonly a floating/emerging water plant or any other object on water or shrubs and grasses bordering the water-body. While perched and waiting for the female to arrive, they at times exhibit two peculiar behaviors. The first is “abdominal bobbing” when a wave of motion

passes from the first to the last abdominal segment while the second is copying the “oviposition posture of the female” when the male bends the abdomen down along the fourth-fifth segment (Image 2 a,b).

Territoriality

The territorial area is determined by the range of distance beyond which the resident territorial male does not respond to an intruder. The territorial area of male *C. coromandelianum* is very small. It gets disturbed only if an intruder comes within a range of about 45cm near his perch. Many a times, two to three males can be seen perched within a vicinity of 120cm.

Whenever an intruder (conspecific or heterospecific male or any other insect) enters his territory, the resident male flies behind the intruder, follows it up to around 600cm and chasing it away. The male returns to his territory either at the same base perch or a few inches around it. If the intruder persists in his territory, then the resident male moves to a new perch about 70–120 cm away but returns as soon as the intruder leaves. If the intruder (generally a conspecific male) is persistent, he chases the resident male away from the ovipositing site into the surrounding bushes. The male later moves to a new location around the water-body. The territorial male also undertakes small patrolling flights. This flight is of not more than 500cm from his perch. The female arrives from 07:30hr onwards (upto noon) when most of the male have demarcated their territory.

Precopulatory behaviour

The males move toward the arriving receptive female when she is at a distance of 70cm from the water body. The males follow the female and directly try to form a tandem link. This link is also formed when the female has entered the oviposition site and is settled on a low lying bush. There is no precopulatory courtship display. It is a common site to find 2–3 males following a female to form a link. Although there is no visible fight amongst the males, the quickest male holds the female just below the head with his anal appendages and forms the tandem linkage. The other males of the group follow the pair but do not try to physically dislodge the male. Once the link is formed, the remaining males may follow the pair keeping a distance of 6–12 cm. The tandem pair moves away from the water-body and flies towards the safety of the surrounding vegetation where they form the copulatory wheel. Before forming the copulatory wheel, the male charges his penis with sperm material by the process of “intra male sperm translocation”.

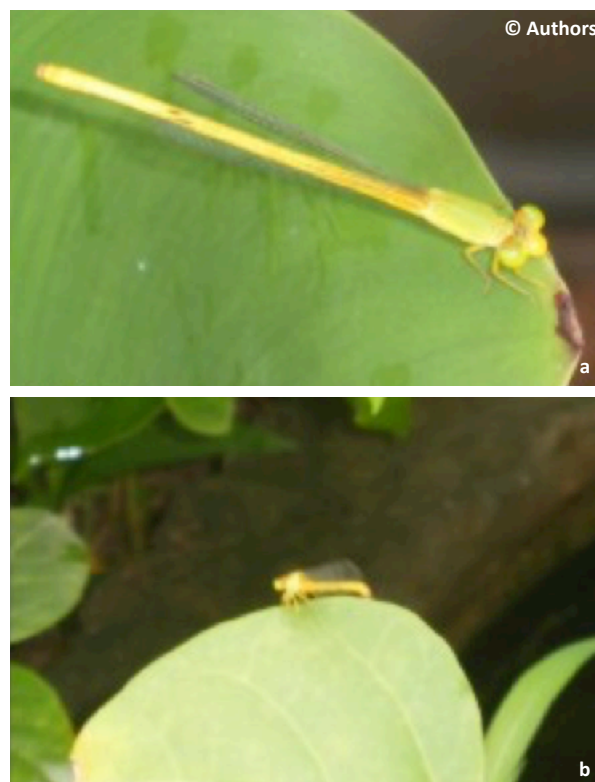


Image 2. *Ceriagrion coromandelianum* male at his perch (a) and (b) exhibiting oviposition posture along the rim of the leaf blade

Intra male sperm translocation

The male transfers the sperm material from the sperm sac which is located in the ninth abdominal segment to the penis of the secondary copulatory apparatus located on the second abdominal segment. The male gonopore and paired coxites of the primary genitalia located on ninth abdominal sternum and penis vesicle of the secondary copulatory apparatus play a key role during this process of intra male sperm translocation (IMST). During this translocation, the position of the male is precarious, since it has to grip the substrate with his legs, hold the female with his terminal anal appendages and curve and bend the abdomen to bring the gonopore in contact with the penis vesicle with the female suspended vertically. The female hangs passively with folded wings and the abdomen is either straight or slightly curved inwards. IMST in *C. coromandelianum* lasts for 30±8 seconds (N=28). During this translocation, the male's gonopore pumps sperm material in the penis vesicle which acts as a sperm reservoir during copulation.

Copulatory wheel

After IMST, the female curves the abdomen ventrally forward so that her gonopore which is located between

Table 1. Duration (in minutes) of copulation observed in 10 pairs of *Ceriatrion coromandelianum*.

	1	2	3	4	5	6	7	8	9	10	Total	Mean	SD	SE
Stage I	34	34	25	25	27	22	12	12	13	8	215	21.5	9.62	3.21
Stage II	21	7	15	10	8	12	3	2	1	4	83	8.3	6.36	2.12
Total	55	41	40	37	36	34	15	14	14	12	298	29.3	14.93	4.97

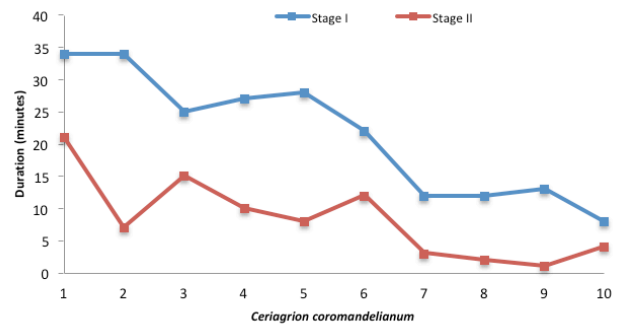
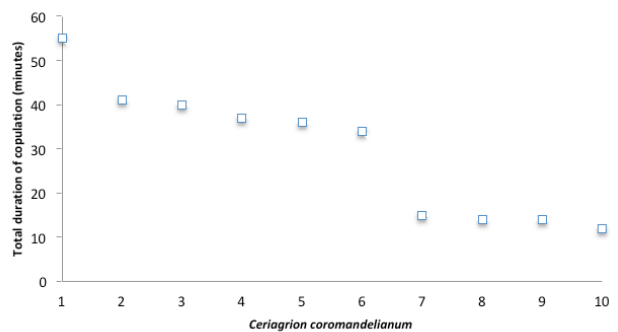
the eighth and ninth sternite comes to lie before the secondary copulatory apparatus of the male and forms a strong genital link, in the form of a copulatory wheel. The wheel is always formed when the male is holding a supporting substrate and never in flight. Copulation takes place within 5m around the oviposition site and not more than 500cm above ground level. Copulation lasts for 29.3 ± 4 m (N=10, Max - 55 min: Min - 12 min, SD - 14.93).

Copulation

Copulation of *C. coromandelianum* is initiated when the male starts pumping the penis inside the female's vagina. Two types of pumping movement can be differentiated (which can be observed from a distance) by recording the variation in the periodic movements of the first two abdominal segments of the male, the change in the shape of the copulatory wheel and the pressure exerted on the head of the female by the anal appendages of the male.

During the first stage, i.e., stage I, the male rhythmically and forcefully depresses and stretches the first two abdominal segments, vigorously pumping the penis inside the female genitalia. At this stage, there is a rapid and energetic movement of the male's abdomen which in turn exerts heavy pressure on the females head held by the anal appendages. The female's head generally wobbles with every thrusting movement. This movement is interspaced with very short (<14 seconds) resting periods when there is no movement of the abdomen. This stage lasts for 21.5 ± 3 min (N = 10, Max - 34 min: Min- 8 min, SD - 9.62) and covers 72% of the copulation duration.

The Stage II starts with rapid short thrusting movement which are not forceful as found in Stage I. Along with the rhythmic but shallow movements of the first two abdominal segment of the male, the third abdominal segment too exhibits periodic synchronised movements. The abdomen of male exhibit angular bending along the fourth- seventh abdominal segment. The frequency of movements decrease until all movements stop and the couple is immobile. This is followed by the breaking of the copulatory wheel, when

**Figure 1. *Ceriatrion coromandelianum* copulation. Duration (in minutes) of Stages I and II.****Figure 2. *Ceriatrion coromandelianum* copulation. Total duration (in minutes).****Table 2. *Ceriatrion coromandelianum* post copulation. Duration (in seconds) of post copulatory resting behavior.**

Sno	PCR	Sno	PCR	Sno	PCR
1	0	11	184	21	249
2	0	12	185	22	253
3	0	13	187	23	253
4	0	14	196	24	577
5	0	15	208	25	590
6	0	16	221	26	602
7	34	17	226	27	628
8	136	18	229	28	632
9	152	19	232	29	650
10	174	20	244	30	652



Image 3. *Ceriatrion coromandelianum* - Copulation. Stage I (a,b), Stage II (c,d).

the female extricates her genitalia from the secondary copulatory apparatus of the male. This stage lasts for 8.3 ± 2 min (N = 10, Max - 21 min: Min. - 1 min, SD - 6.36). The duration of Stage I is always greater than Stage II (Image 3a-d; Table 1; Fig. 1).

The copulation duration can be long (34–55 min) or short (12–15 min) distinctly divided into division. The long copulation which clocks between 55 to 34 minutes and short copulation which completes between 15 to 12 minutes (Fig. 2)

Post copulatory resting behaviour

The tandem pairs after copulation may directly move for oviposition or settle around the surrounding foliage and exhibit “post-copulatory resting” (PCR) behavior (Image 4 a,b,c). After monitoring and timing the PCR behavior of 30 pairs, it is found that PCR can be divided into three types. In Type-1, the pair directly moves for oviposition immediately after copulation. In Type-2, the PCR is brief (208 ± 90 sec) and in Type-3 the PCR is prolonged (619 ± 11 sec). Post copulation, 23.3% females immediately commence oviposition, 53.4% exhibit brief, while 23.3% display prolonged PCR behavior (Table 2, Fig. 3).

DISCUSSION

Habitat selection based on the oviposition site is practiced by females and by males of many species of Odonata for which the oviposition site, that is mostly a water-body, forms the focus for reproductive activity (Corbet 1999). The choice of such sites mostly depend upon the plant community present in and around the

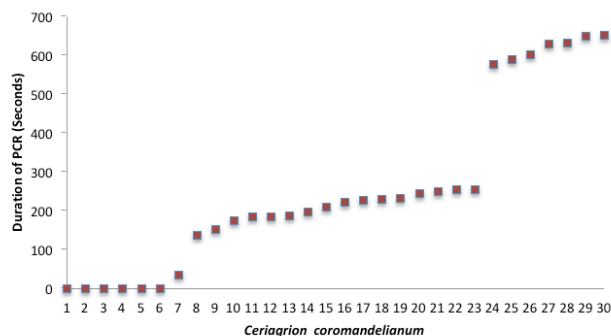


Figure 3. *Ceriatrion coromandelianum* post copulation. Graphical representation of post-copulatory resting (PCR) behavior (in ascending order).

water-body and therefore a link between the odonate and composition and structure of vegetation is evident in most odonates (Buchwald 1991). *Ceriatrion coromandelianum* is one of the most common damselflies from the Indian sub-continent found around banks of large and small perennial and weedy ponds and lakes and small garden tanks or any shallow water body with profuse growth of vegetation with floating and/or submerged vegetation (Fraser 1933; Andrew et al. 2008). *C. coromandelianum* is found breeding year around in the small tanks and tubs of the college botanical garden used for the propagation of aquatic macrophytes (*Nymphaea nouchali*, *Hydrilla verticillata*, *Lemna paucicostata*). These plants are used as substrate for egg deposition by this endophytic species. In a few odonate species, copulation occurs away from the oviposition site during roosting and foraging (Fincke 1987; Miller 1987a).

In Odonata, territoriality is functionally related to site attachment and aggressive behaviour to protect the territory. The area defended by a territorial male in Odonata varies from 1800m (*Hemianax papuensis*) to 0.2m (*Copera marginipes*) (Furtado 1974; Rowe 1987). Prasad (1990) and Sharma (2009) observed that the male of *C. coromandelianum* selects a small oval/circular territory (40–80 cm radius) and defends this area against any intrusion by other males by abdominal raising display (threat display) but Srivastava & Babu (1985) found lack of territoriality in this species. In the present investigation, it is found that the territoriality area of *C. coromandelianum* is small (Max - 45cm radius) but not a single case of threat display was detected. The “sit and wait” type search mode behaviour of male as found in *C. coromandelianum* is also found in the damselfly *Ceriatrion melanurum* (Mizuta 1988) *Enallagma nigridorsum* (Samway 1994) and the

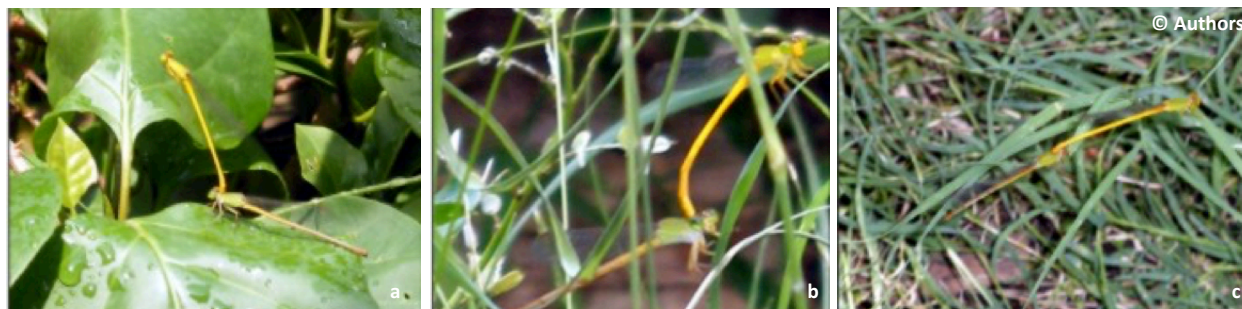


Image 4. *Ceriagrion coromandelianum* exhibiting “Post Copulatory Resting” behaviour.

gomphid, *Onychogomphus forcipatus unguiculatus* (Miller & Miller 1985). The male odonate may seize the female while she is flying or perched and often while she is ovipositing. *C. coromandelianum* always seize the female in flight and never when she is perched or ovipositing. *Pantala flavescens* executes tandem formation and wheel formation always in flight followed by oviposition (R.J. Andrew pers. obs. 2010–2017), while some odonates form the wheel in air and then perch to complete copulation (Sakagami et al. 1974; Miller & Miller 1989). In *C. coromandelianum* wheel formation is achieved in perched condition. According to Corbet (1999) long bodied odonates will always perch for copulation.

Copulation in most zygopteran species is divided into two to three stages. The first stage, i.e. Stage I can cover upto 95% of the total duration (*Nososticta kalumburu* Thompson, 1990) while in *C. coromandelianum* it covers 72%. In *Enallagma cyathigerum* the Stage II and Stage III is brief whereas in *C. coromandelianum* the Stage II and Stage III cannot be differentiated as reported in many other zygopterans (Cordero & Miller 1992; Tajima & Watanabe 2014). During Stage I the penis removes the pre-deposited sperm of previous mating from the sperm storage organ of the female and during Stage II the now empty sperm storage organs are inseminated (Waage 1982, 1984, 1986, 1988; Miller 1987a,b; Corbet 1999; Andrew 2001; Cordero-Rivera et al. 2004; Cordoba-Aguilar 2010; Tajima & Watanabe 2014). During the present investigation it is found that in *C. coromandelianum* the copulation duration is divided into short copulation which completes between 12–15 minutes and long copulation of 34–55 minutes. The probable reason for this variation is the condition of female. While copulating with virgin females and/or females with a smaller amount of sperm in their storage organs the male needs less time to displace sperm and therefore the Stage I gets over quickly which reduces the copulation duration.

In Odonata, more than 50 species exhibit post copulatory resting (PCR) behaviour, which in damselflies can fluctuate from 01 (*Calopteryx maculata* Meek & Herman, 1990) to 180 minutes (*Argia vivida*, Conrad & Pritchard 1988). Srivastava & Babu (1985) reported that PCR by *C. coromandelianum* is for 50–60 seconds followed by post copulatory flights in tandem for 54–90 minutes; such short post copulatory flights were not recorded in the present study. Prasad (1990) and Sharma (2009) observed that PCR occurs for about six minutes in this species. In the present study it is found that *C. coromandelianum* PCR is clearly differentiated into two categories, the brief PCR ranges from 136–253 seconds while the prolonged one from 577–652 seconds. Disturbance during copulation, temperature and sunlight are few factors that may increase the duration of PCR, but in the present study no specific relationship between these factors and the duration of PCR is noticed. As postulated by Miller & Miller (1989) “sperm handling” appears to be the only feasible reason for PCR in *C. coromandelianum*. Perhaps it implies that there is variation in the PCR of virgin and non-virgin females or maybe, long copulation leads to prolonged PCR as found in *Orthetrum caledonicum* (Alcock 1988).

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