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REPRODUCTIVE BEHAVIOUR OF *CERIAGRION CERINORUBELLUM* (BRAUER) (COENAGRIONIDAE, ODONATA) WITH SPECIAL REFERENCE TO SUBSTRATE SELECTION

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ABSTRACT

Adults of *Ceriagrion cerinorubellum* were reproductively active between February and November in a semi-shaded freshwater wetland. Males exhibited strong territoriality, defending reproductive substrates by aggressive chases and conspicuous abdominal threat display. Courtship involved stereotyped abdominal flexion display with paired cerci acting as stimulus to female. Mating included rapid intra-male sperm translocation following tandem formation, followed by a variable pre-copulatory period and prolonged copulation. Endophytic oviposition was predominantly discontinuous which occurred under male guarding. Females deposited eggs on a wide range of aquatic plant parts, including leaves, stems, petioles and rootlets. Landing frequency differed significantly among the eight macrophyte species examined, with *Spirodela polyrhiza* and *Pistia stratiotes* receiving the highest frequencies of landing. *Eichhornia crassipes* supported the highest mean clutch size among the substrates examined. The species used both invasive and decaying plant materials, indicating high ecological plasticity. A rare instance of triple connections and an active female resistance are being reported for the first time in this species.

Key words: Zygoptera, damselfly, triple connections, female resistance, false copulatory wheel, substrate selection, host plant preference, macrophytes, oviposition, sexual harassment, male rivalry, mate choice

Ceriagrion cerinorubellum (Brauer, 1865), is a common damselfly in South and Southeast Asia spreading from Pakistan to Singapore (Subramanian, 2005; Dow and Reels, 2013; Cai et al., 2018; Kalkman et al., 2020). It is abundantly seen in the wetlands of Paschim Medinipur district of West Bengal (Jana et al., 2021). Reproductive behaviour of coenagrionid damselflies is reasonably well documented through the works of Matsubara and Hironaka (2005) on *Pseudagrion pilidorsum*, Ngiam (2009) on *P. rubriceps*, Takahashi and Watanabe (2010) on *Ischnura senegalensis*, Sanmartin-Villar et al. (2022) on *I. praematura*, Cordero-Rivera et al. (2023) on *I. hastata* and Mohamed (2024) on *Enallagma vansomereni*. These studies have addressed various aspects of reproductive biology and behaviour, including territoriality, mating interactions, post-copulatory guarding, female reproductive success, sexual conflict, and oviposition behaviour. In India various aspects of reproductive and oviposition behaviour of *C. coromandelianum* have been investigated by Srivastava and Babu (1985) and Thaokar et al. (2018). However, despite the wide spread distribution of the congeneric *C. cerinorubellum*, similar studies on this species appear to be lacking. Vegetation structure profoundly influences the reproductive strategies of damselflies (Ferreira-Perruqueti and De Marco Jr., 2002; Thaokar et al., 2018; Bota-Sierra et al., 2021; Jana et al., 2024). As most damselflies show strong fidelity towards specific macrophytes or parts thereof during oviposition, anthropogenic alteration of aquatic vegetation can compromise reproductive success by reducing substrate availability or suitability. Previous studies clearly reveal that female damselflies have a definite substrate preference for oviposition (Martens, 2001; McMillan and Arnold, 2004; Lambret et al., 2015; Thaokar et al., 2018; Jana et al., 2024). Oviposition site selection in damselflies involves a multi-step behavioural sequence comprising approach, inspection, landing, palpation, and egg insertion-each shaped by ecological constraints and evolutionary pressures (Lambret et al., 2015). Habitat degradation due to anthropogenic alteration is one of the leading causes of species loss (Paulson, 2019; Córdoba-Aguilar and Rocha-Ortega, 2019). IUCN in its Dragonfly Action Plan (Moore, 1997) has highlighted the urgent need for species-specific ecological knowledge to guide conservation strategies. In view of the afore mentioned backdrop the present investigation has been

envisaged to study the reproductive behaviour of *C. cerinorubellum* with special emphasis on the substrate selection for oviposition.

MATERIALS AND METHODS

The investigation was conducted from January 2021 to December 2023 in a freshwater pond measuring 10.7 x 13.7 m and having a maximum depth of 1.5 meters at Madhabchak village (22°15′54.0″N, 87°32′47.2″E). Behavioural observations on *C. cerinorubellum* were conducted weekly on each month between 06:00 and 17:00 hr by following nearest focal individuals or tandems. Reproductive activities from courtship to post-tandem separation were recorded. Observations including territoriality, courtship, mating, and oviposition were recorded continuously from the onset of interaction until its termination. Durations were recorded using a mobile phone timer. To minimise observer bias, observation distance of 1.5 to 2m were maintained throughout the study. Events of sexual harassment were also recorded during the study period. A male making repeated attempts to approach, grasp or disrupt a female or an established tandem, followed by avoidance or resistance by the female or disengagement of the interfering male was considered as sexual harassment. A total of hundred focal behavioural observations were made for each category such as territoriality, courtship and mating. Observations were distributed across the active season (February to November) in each year depending upon the actual occurrence of the concerned behaviour in field conditions.

Detailed observations on oviposition, including clutch size and host plant selection, were conducted in September of each study year. For evaluating host preference, eight single-species vegetation patches, each measuring 1.22 m² and maintained at >95% vegetation cover, were established in the study pond. Each patch was regularly monitored throughout the study period, and vegetation cover was maintained at >95% by allowing natural vegetative growth to fill minor gaps and manually removing unwanted or encroaching vegetation. Vegetation cover was assessed visually during routine field monitoring. The patches were arranged in two rows, with four adjacent patches in each row separated by a gap of 1 m in between. The vegetation comprised of *Spirodela polyrhiza* (L.) Schleid, *Pistia stratiotes* L., *Eichhornia crassipes* (Mart.) Solms, *Nymphaea alba* L., *Alternanthera philoxeroides* (Mart.) Griseb., *Commelina diffusa* Burm.f., *Marsilea quadrifolia* L. and *Colocasia esculenta* (L.) Schott. Water depth was comparable among the patches. To reduce potential spatial bias, the three floating macrophytes (*S. polyrhiza*, *P. stratiotes* and *E. crassipes*) were rotated among designated positions annually, whereas the positions of the other five vegetation patches remained unchanged. *Spirodela polyrhiza* and *P. stratiotes* patches were separated from the adjacent patches using bundles of paddy straw to minimize movement of the free-floating plants between experimental units. The experimental patches were monitored throughout the study period, and unwanted vegetation encroaching into the experimental area was manually removed. Natural vegetation along the pond bank was retained throughout the study period. The annual arrangement of the eight vegetation is presented schematically in Fig. 1.

For the host-preference observations, fifty distinct tandems were followed continuously during their oviposition sequence. As a tandem could visit more than one plant species before selecting an oviposition substrate, individual landings within a tandem sequence were treated as repeated observations associated with that tandem rather than as observations from independent individuals. After oviposition, tandems were briefly captured during their post-ovipositional resting period, gently marked on the lateral side of the thorax using water resistant red marker, and released to prevent the same tandem from being unknowingly counted as a new tandem in subsequent oviposition-following observations. Landing frequency on each plant species was used as the measure of host choice. Landing observations from the three study years were pooled for the primary host-preference analysis. Statistical analyses were performed in SPSS v26. Landing counts were first tested using the Kruskal-Wallis *H* test to assess differences among plant species. When found significant, Bonferroni-adjusted pairwise

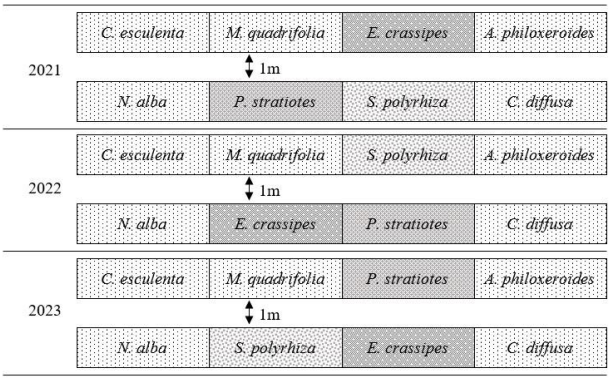


Fig. 1. Scheme of spatial arrangement of the eight experimental vegetation patches

comparisons were done to identify the specific contrasts. Oviposition duration was measured from the female's first abdominal contact during egg insertion up to the final withdrawal. To determine clutch size, plant parts bearing eggs were collected after completion of oviposition, and all visible eggs were counted under a stereoscopic binocular microscope (Leica DM3000). Clutch-size estimates were therefore based on recovered egg-bearing plant parts from completed oviposition events.

RESULTS AND DISCUSSION

Adults of *Ceriagrion cerinorubellum* were observed to be reproductively active from early February to late November in each year, thereafter, adults were not observed in the semi-shaded study area. Males were distinctly territorial and exhibited pronounced aggression toward conspecific males. Territorial area ranged between 0.89 and 1.91 m^2 (1.37 ± 0.03 m^2, median 1.39 m^2) which were defended vigorously through threat displays and aerial pursuits. They typically perched on emergent vegetations, establishing base perches that were defended through aggressive chases and characteristic formal threat displays. The threat display, triggered by sudden intrusion of the intruding male, conspecific or heterospecific, consisted of the display of the slightly bent red abdominal tip by raising the abdomen and slightly spreading the wings. The display continued till the intruder retreated and lasted for 3-7 sec (5.25± 0.09 sec). Similar threat display has also been previously reported by Gorb (1998) for *Coenagrion puella* and similar territorial defence has also been observed by Thaokar et al. (2018) in *C. coromandelianum* (Fabricius, 1798). Territory switching was frequent. Males held territories for an average duration of 32 min 25 sec± 1 min 31 sec. However, when male density was low territories were maintained even for 2 to 6 hours (n=17). Territorial males occupied areas rich in oviposition substrates, thereby potentially combining resource defence with access to receptive females.

Courtship involved a stereotyped abdominal flexion display ("courtship flexions"), performed on a fixed perch. On the perch, males partially spread their wings and repeatedly flexed their abdomen upwards and downwards, usually for 4-7 successive flexions (Fig. 2). Each flexion sequence lasted for 4-7 sec (5.54± 0.09 sec) and acted as a visual signal to approaching females. Such courtship displays occurred at a frequency of 2-7 h^{-1} (3.52± 0.28 h^{-1}), mostly between 09:00 and 14:00 h. Males used their abdominal paired cerci as part of their courtship signalling repertoire. In the presence of a conspecific female, male bends its straight paired abdominal cerci into a claw-like configuration to stimulate the female. The combination of abdominal movement and cercal display suggests that courtship involves visual signalling. Visual cues are known to contribute to mate recognition in coenagrionid damselflies, including *C. puella* (Gorb, 1998). Mating began when male seized female either while perched (n=74) or during flight (n=26); on eight occasions females were seized while engaged in feeding activities and were subsequently brought into tandem formation. Intra-male sperm translocation (IST) took place immediately after tandem formation and lasted for 4-9 sec (6.71± 0.10 sec) (Fig. 3). The interval between tandem formation and copulatory wheel formation varied from 9-46 min depending probably upon female receptivity. On rainy days, tandem-holding period was prolonged to 16-94 min, during which male maintained a firm grip on female, suggesting that adverse weather conditions could delay the transition to wheel formation.

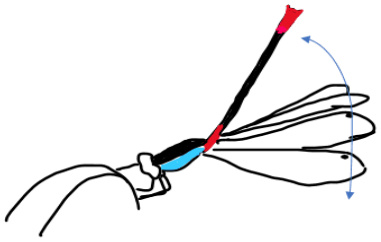


Fig. 2. Diagrammatic representation of the courtship flexion

Prior to wheel formation, males exhibited pre-copulatory rhythmic movements, alternately arched and relaxed the abdomen at a slow pace of one cycle every 3-5 sec, with their wings partially spread. Female responded by rhythmically flexing and relaxing their abdomen, with a slight temporal lag relative to the male's movement. The frequency of male abdominal movement subsequently increased to approximately one cycle every 2-3 sec, culminating in formation of the copulatory wheel. Copulation then proceeded through alternating thrusting and resting phases and lasted for 34-82 min (54 min 56 sec ± 1 min 12 sec). Breaking of the wheel position marks the end of the copulation. The copulatory period was, therefore, longer than that reported for *C. coromandelianum*, where copulation lasts for 12-55 min (Thaokar et al., 2018). The difference might be due to differences in the duration of resting phase during copulation, although comparative observations under standardized conditions would be required to test this possibility.

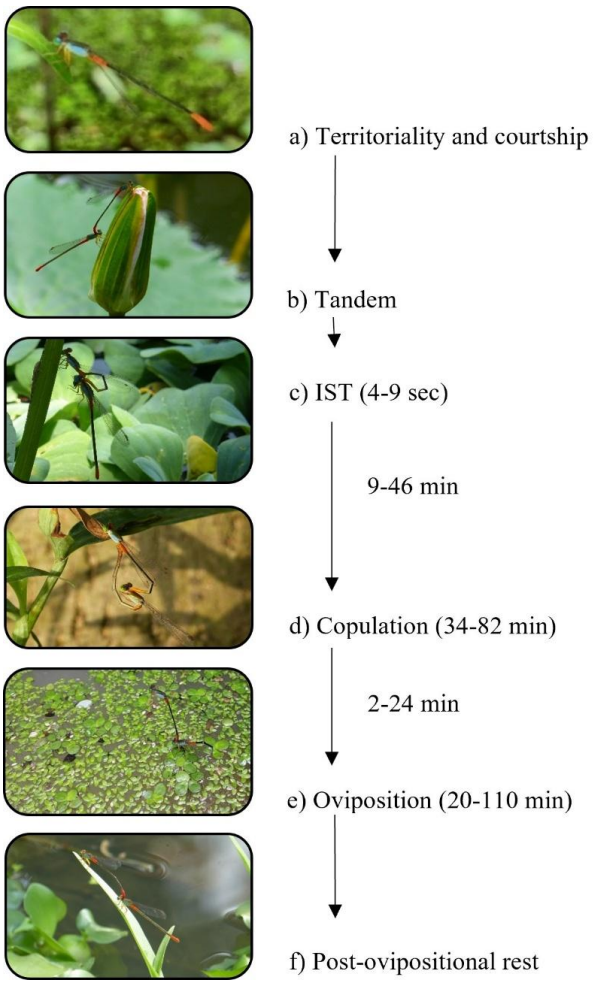


Fig. 3. Schematic representation of the reproductive events: (a) territoriality and courtship; (b) tandem formation; (c) intra-male sperm translocation (IST); (d) copulation; (e) oviposition; (f) post-ovipositional rest. Time intervals between major stages are indicated.

Following copulation, the pair rested either at the copulation site or near oviposition substrate. The post-copulatory resting phase lasted for 2-24 min (9 min 20 sec ± 26 sec) followed by oviposition. The pair subsequently explored potential oviposition substrates, frequently shifting between perches. Emergent oviposition always took place under male guard. Guarding males displayed lateral wing-flapping if challenged by a conspecific or a heterospecific male. Once a suitable site was selected, females commenced endophytic oviposition in a zigzag pattern also known as Coenagrionidae -type, *sensu* Hellmund and Hellmund, 1991 (Romero-Lebrón, et al., 2023). Oviposition took place continuously (4%, n=2) or discontinuously (96%, n=48) in nearby substrates. Continuous oviposition was limited to large floating substrates such as the leaves and petioles of *N. alba* and the broken floating petioles of *C. esculenta*, which provided enough space for complete clutch deposition. On all other macrophytes examined the oviposition was consistently discontinuous. Discontinuous bouts typically lasted 6-241 sec (1 min 40± 12 sec), separated by 5-80 sec (39± 3 sec) pause, required for shifting to adjacent substrates. The entire egg-laying sequence lasted for 20-110 min (63 min 5 sec± 3 min 27 sec). The discontinuous strategy required less energy compared to the submerged oviposition strategy (Šigutová et al., 2020) employed by other species. Additionally, it had a reduced risk of drowning even though it faced a higher likelihood of being taken over by a conspecific male as well as being more vulnerable to predation (Miller, 1994). Upon completion of oviposition, the female ceased egg laying and raised her abdomen in a straightened position. After approximately 3 to 5 seconds, the male released his grip and flew away. The female also left the oviposition site, retreated to the adjacent terrestrial vegetation, selected a sunny perch for post-copulatory grooming activities.

Landing frequency differed markedly among the eight macrophyte species examined. *S. polyrhiza* was the most preferred substrate followed by *P. stratiotes* accounting for 37.1% and 32.7% of landings respectively, whereas the remaining six species each accounted for less than 9% of total landings (Table 1). The Kruskal-Wallis test indicated that the landing frequency varied significantly across the eight macrophyte species ($H = 195.407$, $df = 7$, $p < 0.001$). This confirms that the landing behaviour was non-random and strongly vegetation-specific. Such non-random habitat selection may reflect the use of visual or environmental cues associated with suitable reproductive habitat, as demonstrated experimentally in tropical odonates by Ensaldo-Cárdenas et al. (2021). Bonferroni-adjusted pairwise comparisons showed that *S. polyrhiza* differed significantly from all other species except *P. stratiotes* (adjusted $p = 0.829$), which also experienced significantly more landing as compared to other macrophytes investigated.

C. cerinorubellum exhibited a broadly euryecious oviposition strategy, utilising a wide range of macrophytes that included free-floating hydrophytes, submerged rooted plants, and emergent vegetation. Among the vegetation used, *E. crassipes, P. stratiotes*, and *A. philoxeroides* are regarded as invasive species in India (Kumar, 2011). In the present study various plant parts were used for oviposition which included dead and fresh plant materials like stems, leaves, petioles, and rootlets (Table 1). The observed flexibility in substrate

Table 1. Landing preference and oviposition characteristics of *Ceriagrion cerinorubellum* on eight macrophyte species

Plant species	Number of landings	Preferred substrate (submerged) for oviposition	Oviposition attempts n (%)	Clutch size Mean± SE (range), n
S. polyrhiza	412	Underside of frond	412 (37.1)	4.3± 0.23 (2-6), 30
P. stratiotes	364	Upper leaf surface	186 (16.7)	8.5± 0.78 (3-21), 30
		Lower leaf surface	178 (16.0)	14.6± 0.89 (4-26), 30
E. crassipes	68	Petiole	68 (6.1)	61.3± 3.38 (14-94), 30
N. alba	43	Leaf	18 (1.6)	54.11± 18.23 (11-358*), 18
		Petiole	25 (2.2)	47.64± 5.01 (12-148), 25
A. philoxeroides	32	Leaf	23 (2.1)	24.3± 2.63 (9-64), 23
		Stem	9 (0.8)	42.7± 7.41 (18-89), 09
C. esculenta	37	Petiole	20 (1.8)	25.25± 15.95 (3-328*), 20
		Underside of floating leaf	12 (1.1)	12.83± 2.21 (5-35), 12
		Floating rootlets	5 (0.4)	1.6± 3.3 (3-21), 5
C. diffusa	61	Leaf	37 (3.3)	47.16± 3.87 (12-98), 30
		Stem	24 (2.2)	25.83± 2.36 (6-54), 24
M. quadrifolia	95	Upper leaflet surface	22 (2.0)	8.72± 0.92 (2-16), 22
		Lower leaflet surface	34 (3.1)	13.2± 1.06 (2-26), 30
		Petiole	39 (3.5)	13.43± 1.27 (4-35), 30

*High values were due to oviposition in a single effort without changing substrate

use has potential implications on the conservation of *C. cerinorubellum*. This flexible plant use resembles the pattern reported for *C. coromandelianum* by Thaokar et al. (2018). However, it differs from *C. coromandelianum* in its ability to deposit eggs on the decaying petioles of *Colocasia esculenta.* Srivastava and Babu (1985) observed that *C. coromandelianum* does not oviposit on decaying materials. This indicates that *C. cerinorubellum* has a broader substrate selection ability as compared to *C. coromandelianum*. Aquatic vegetation is an important component of odonate breeding habitats because it provides oviposition substrates and contributes to the structural complexity of reproductive microhabitats (Kolar et al., 2021). Consequently, removal, simplification or seasonal alteration of aquatic vegetation may reduce habitat heterogeneity and the availability of suitable reproductive microhabitats, even when the water body itself remains present (Kolar et al., 2021). At the same time, the use of several widespread and invasive macrophytes, such as *E. crassipes*, *P. stratiotes* and *A. philoxeroides*, indicates that the species can exploit structurally diverse vegetation. This flexibility may allow the species to exploit alternative oviposition substrates when the availability of particular plant species varies. However, it should not be interpreted that invasive macrophyte proliferation, as beneficial for the species should be encouraged. High abundance of invasive aquatic plant can adversely alter habitat structure by reducing the native plant diversity, potentially affecting the freshwater community composition and ecosystem functioning (Tasker et al., 2022). Therefore, conservation and management of breeding ponds should favour heterogeneous aquatic vegetation rather than dominance by any single macrophyte species, while retaining a diverse assemblage of native and non-invasive plant species (Kolar et al., 2021).

The highest mean clutch size was recorded on *E. crassipes* petioles (61.3± 3.38 eggs), followed by *N. alba* leaves (54.11± 18.23 eggs) and petioles (47.64± 5.01 eggs). In contrast, the two most frequently visited species, *S. polyrhiza* and *P. stratiotes*, showed relatively small mean clutch sizes. This contrast between landing frequency and clutch size suggests that initial substrate selection and the suitability of a substrate for egg deposition may represent different stages of host selection. Variation in reproductive performance associated with oviposition substrate has also been demonstrated in *C. coromandelianum*, in which the substrate influenced hatching success (Verma et al., 2022). Previous studies have demonstrated that damselflies can discriminate among plant species and plant parts during oviposition (Martens, 2001; McMillan and Arnold, 2004; Lambret et al., 2015; Verma et al., 2022; Jana et al., 2024). Matushkina and Gorb (2007) found that coenagrionid damselflies predominantly

choose Nymphaeaceae for oviposition. This is in agreement with the present findings. Srivastava and Babu (1985) opined that *C. coromandelianum* avoids *S. polyrhiza* and *E. crassipes* for oviposition. Present investigation on the contrary revealed that *S. polyrhiza* was the most preferred species for oviposition by *C. cerinorubellum,* which also oviposited on *E. crassipes*. This is a clear indication of its greater ecological plasticity in oviposition over *C. coromandelianum.*

A solitary case of triple connection during sexual harassment was observed. A secondary male of *C. cerinorubellum* attempted to mate with a female already held in tandem by a primary male leading to the formation of a transient 'type-A', *sensu* Eda (1970), triple connection (Fig. 4a). In this configuration, the secondary male grasped the primary male while the latter maintained his hold on the female. The secondary male subsequently attempted intra-male sperm translocation. During this phase, the primary male remained attached to the female and repeatedly attempted to disengage the secondary male by its vigorous wing flapping.

The secondary male then made pronounced undulatory abdominal movements, apparently attempting to reposition the female's abdomen anteriorly so that female's genitalia could be aligned with his own. Despite repeated attempts, the female resisted and prevented successful genital alignment. She subsequently elevated her abdomen and formed a false copulatory wheel with the primary male, which was similar to 'type AB' triple connection, *sensu* Eda (1970). The primary male facilitated this configuration by grasping the female's abdomen using his thoracic legs (Fig. 4b). Following formation of the false wheel, the secondary male released his grip on the primary male, apparently misinterpreting the configuration as a completed copulatory wheel between the primary male and the female. Triple connections and female takeover attempts are not uncommon in damselflies and have been documented by several authors, including Eda (1970), Eda et al. (1973), Corbet (1999), Wada (2000), Miller and Fincke (2004), Córdoba-Aguilar (2009), Guillermo-Ferreira and Del-Claro (2011) and Jana et al. (2022). However, to date, no such behaviour has been reported for *C. cerinorubellum*. Additionally, by forming a false copulatory wheel females may employ a tactic to reduce the landing area for additional incoming males (Rüppell and Hilfert-Rüppell, 2024).



Fig. 4. (a) Triple connection; (b) false copulatory wheel formation

An instance of female resistance was also observed when the female repeatedly avoided an approaching male by maintaining a lowered head position, apparently to destabilise the male's upright position, firmly gripping the perch and engaging in vigorous struggling till he relinquished his hold. Such behaviour of female *C. cerinorubellum*, as recorded here, appears to function as effective female counter-strategies against male coercion. Similar resistance to male mating attempts by female has been documented by Khelifa (2021) in *Rhionaeschna multicolor* that disrupted the mating attempts. Such behaviours are likely to enhance female mate choice by preventing copulation with persistent or lower-quality males and by terminating energetically costly or risky mating attempts, or by controlling copulation duration (Rivas-Torres et al., 2023). Moreover, by inducing disengagement of secondary or harassing males, these strategies might reduce predation risk (Rowe et al., 1994), physical injury (Crudgington and Siva-Jothy, 2000, Jana et al., 2022), and fecundity (Sakurai and Kasuya, 2008). Nevertheless, because the present observations are based on rare events, these interpretations should be regarded as behavioural hypotheses requiring confirmation through additional observations. The observations nevertheless extend the known repertoire of reproductive interactions in *C. cerinorubellum* and provide a basis for further investigation of male competition and female resistance in this species.

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AUTHOR CONTRIBUTION STATEMENT

PKJ designed and conducted field work, analysed and interpreted the data, and prepared the initial manuscript. PHM supervised the study and reviewed the manuscript. TB critically reviewed the manuscript

and prepared the final version. All authors read and approved the final manuscript.

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CONFLICT OF INTEREST

No conflict of interest.

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