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REPRODUCTIVE BEHAVIOR OF *ENALLAGMA COECUM* (HAGEN) IN CUBA (ZYGOPTERA: COENAGRIONIDAE)

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The reproductive behavior is described from 2 populations on the outskirts of Santiago de Cuba, between June 2005 and May 2006. ♂♂ started arriving at the water body in the morning nearly 2 h before ♀♀. Sperm translocation was brief (less than 30 s), and the duration of copulation averaged about 18 min. During oviposition the ♀ was guarded in tandem by the ♂, except when she submerged under water, when non-contact guarding was observed. The mean duration of oviposition was about 10 min. Abiotic factors that interfered with the reproduction were wind, absence of sun, and rain; and the biotic interactions included conspecific ♂♂, spiders of the genus *Dolomedes*, *Gambusia punctata* fishes and the lizard *Anolis sagrei*.

INTRODUCTION

The odonates have a complex reproduction (CORBET, 1999), and this aspect of their biology has been especially well studied in the temperate zones (NOVELO & GONZÁLEZ, 1984). The genus *Enallagma* constitutes approximately 40 species (MAY, 2002), four of which are found in Cuba. Of these, *E. coecum* has the largest area of distribution, and is characteristic of slow-moving and tree-lined rivers and streams. The species also occurs in Jamaica, La Española, Puerto Rico, the Lesser Antilles (ALAYO, 1968), and Florida and Alabama in the USA (WESTFALL & MAY, 1996).

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MATERIAL AND METHODS

The study was carried out at two sites between June 2005 and May 2006. One site is a stream at "Los Gómez" farm, located North of Santiago de Cuba between 75°49'18"N and 20°02'52"W, and at 90 m asl. The second site is on the Sevilla river, located East of the city between 75°45'56"N and 20°00'54"W and at an altitude of 62 m asl. The observations (total: 176 hours) were made daily between 08:00 a.m. and 16:00 a.m. The first site is an open stream 50 cm in depth with a muddy bottom. Herbaceous vegetation with *Cyperus rotundus* L. predominates and the dominant aquatic vegetation consists of the shrubs *Dichrostachys sinerea* (L.) Wight, Arn. *Cabomba piauchiensis* L. and *Hydrocotyle umbellata* L. The Sevilla river is 20 cm deep, its bottom is composed of rocks and sand, and it is partially covered with large size trees such as *Sterculia apetala* (Jacq.) Karst., besides herbaceous vegetation with *C. rotundus* and *H. umbellata.* Water temperature in both sites oscillated between 23-28 °C.

The duration of the reproductive processes was registered with a digital 63-1126 chronometer and the temperature with a dry bulb thermometer.

Other Odonata species seen in the area were: *Enallagma civile* (Hagen), *Ischnura capreolus* (Hagen), *I. ramburii* (Selys), *Telebasis dominicana* (Selys), *Neoneura maria* (Scudder), *Coryphaeschna adnexa* (Hagen), *Aphylla caraiba* Selys, *Cannaphila insularis* (Kirby), *Crocothemis servilia* (Drury), *Dythemis rufinervis* (Burmeister), *Erythemis plebeja* (Burmeister), *E. simplicicollis* (Say), *Erythrodiplax justiniana* (Selys), *E. umbrata* (L.), *Macrothemis celeno* (Selys), *Miathyria marcella* (Selys), *Micrathyria aequalis* (Hagen), *Orthemis discolor* (Burmeister), *O. ferruginea* (Fabricius), *Pantala flavescens* (Fabricius) and *Perithemis domitia* (Drury).

RESULTS

DAILY ACTIVITY

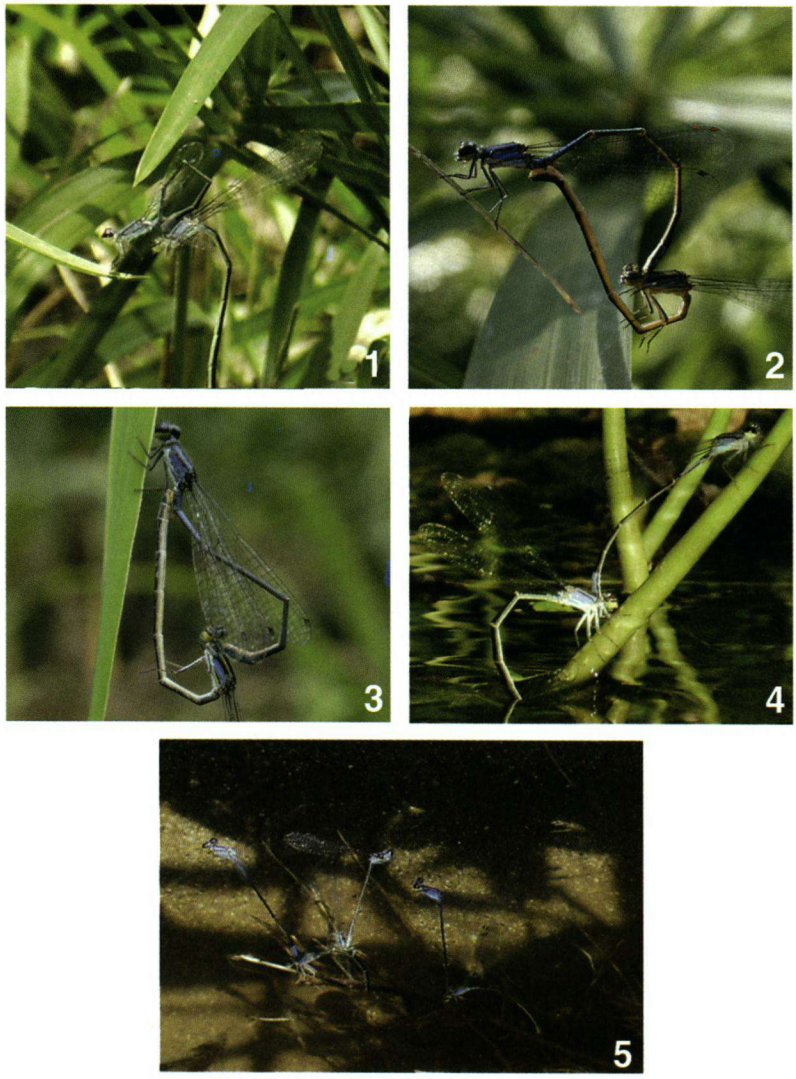
The first males to arrive were detected at 08:15 a.m., perching close to the water and flying among the vegetation. This combined activity was maintained until 09:50 a.m. During flight some males maintained the abdomen slightly curved downwards with segments eight and nine slightly expanded. Confrontations were observed with a duration of 6 ± 1.6 s (4.3-9.0 s, N = 16), among 11 conspecific males and among *E. coecum* and five *Ischnura capreolus*. These interactions involved short flights in a position always inferior to the intruder until the latter had moved for at least 40 cm from the perching site.

REPRODUCTIVE BEHAVIOR

Arrival of females began at about 10:00 a.m. When a male detected a female he grabbed her with its legs to form a precopulatory tandem without any apparent preceding courtship. In both locations the sudden rupture of the precopulatory tandem was observed on five occasions, possibly due to non receptive behavior by the females. Sperm translocation occurred on herbaceous vegetation exposed to the sun and had an average duration of 22 ± 13 s (14-50 s, N = 7). During this event, the male's abdominal segments 4-6 formed an angle of 90° (Fig. 1). On two occasions, during precopulatory tandem and before translocation, the female was

observed swinging her abdomen and making contact with the secondary genitalia of the male for one or two seconds (cf. "genital touching" of ROBERTSON & TENNESSEN, 1984).

Copulation occurred immediately after translocation. It was observed between 10.00 a.m and 04.00 p.m. and had an average duration of 18 ± 10 min (2-32 min, N = 23). While in precopulatory tandem the female began a series of waves with



Figs 1-5. Reproductive behaviour in *Enallagma coecum*: (1) sperm translocation; – (2) stage I of copulation; – (3) stage II of copulation; – (4) oviposition; – (5) aggregations for oviposition.

her abdomen until making contact with the secondary genitalia of the male. The male's abdomen formed an arc (Fig. 2) that corresponds to Stage I of copulation, during which sperm removal from the bursa and/or spermatheca from preceding copulas probably occurs. This first stage had an average duration of 14 ± 5.1 min, and the transference of sperm presumably began shortly afterwards, with an average duration of 7 ± 1.6 min (4-9 min, N = 9) (Fig. 3). At the end of this stage, the male arched his abdomen as in Stage I. The couple remained in tandem for a few minutes, usually in the place where they had copulated, before heading to the water to oviposit.

Oviposition under water took place in tandem and lasted on average of 10 ± 8,7 min (3-40 min, N = 39). The substrata were the plants of *H. umbellata* and *C. piauchiensis* (Fig. 4), where some females (N = 7) submerged under the water for up to 12 min. The tandem separated when the water reached the male's thorax and the male flew to a branch close to the immersion site, recapturing the female when she left the water. Remaining ovipositions were in *C. piauchiensis* and roots of *C. rotundus*, where no immersion was observed. Communal ovipositions of a duration of 17 min (Fig. 5) involving up to five couples were observed (8-26 min, N = 5).

According to the classification of WAAGE (1984) on the variation in the postcopulatory behavior in odonates, *E. coecum* is classified as category A "oviposition in tandem" with the exception in some cases of a secondary behavior of solitary submerged oviposition. After oviposition some couples (N = 4) stayed in tandem for approximately 90 minutes without apparent sexual intercourse, far from the water and among the vegetation. Major reproductive activity in *E. coecum* is concentrated in hours around noon (Fig. 6).

Some climatic factors seemed to interfere in the reproduction of *E. coecum*, among them wind, which could result in the separation of the tandem. Partial or total absence of sun made the damselflies inactive, and rain caused them to aban-

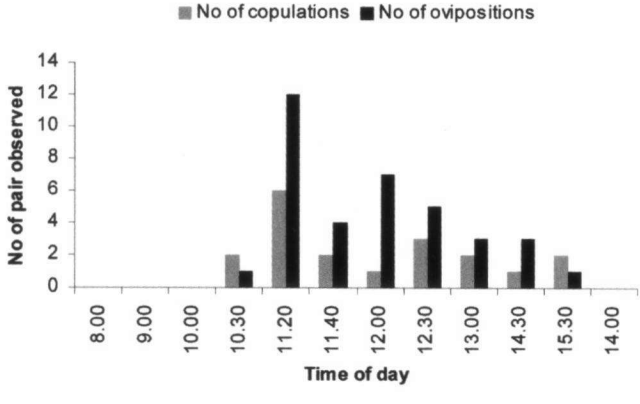


Fig. 6. Copula frequency and daily oviposition in *Enallagma coecum*.

don mating altogether. Biotic factors such as competition of conspecific males for the females (N = 11) or heterospecific interactions (N = 10), lasted only a few seconds, but were observed to slow down the sequence of reproductive behaviour. The fish, *Gambusia punctata* Poey, was observed (N = 7) to bite off the distal part of the abdomen during a spawn, and also to jump out of the water to eat individuals in copula or in tandem near the water. Spiders of the genus *Dolomedes* were observed feeding on females (N = 5) that were in copula previously, and 12 dead specimens of this species and of *Telebasis dominicanum* were found in their webs. A lizard, the Cuban Brown Anole, *Anolis sagrei* (Duméril & Bibron), was also observed (N = 8) feeding on individuals in copulation.

DISCUSSION

The mean duration of spermatic translocation in *E. coecum* (22 ± 13 s) is long compared with that known for other species in the genus. In *E. civile* it lasts 16 s (BICK & BICK, 1965), in *E. aspersum* 17.8 s and in *E. exsulans* 25.2 s (BICK & HORNUFF, 1966) (Tab. I). Copulation in *E. coecum* has an average duration of 18 min which is similar to those of *E. civile* (18.7 min) (BICK & BICK, 1965), *E. aspersum* (13.5 min) (BICK & HORNUFF, 1966), *E. hageni* (22.4 min), but different from *E. exsulans* (75.8 min), and other species in the Coenagrionidae (Tab. I). Prolonged reproductive events in *E. coecum* could reduce the chances of the female mating with other males.

Stages I and II of copula could be related to sperm removal from previous copula and insemination, respectively, as it has been demonstrated for other species of the genus. For example, in *E. cyathigerum* removal of sperm was observed during the first part of copula, while the last 200 s were destined to insemination (MILLER & MILLER, 1981). In *E. hageni* the male could eliminate 87% of the stored sperm from the spermatic bag (FINCKE, 1984).

Table I

Duration of sperm translocation (in seconds) and copulation (in minutes) in species of the genera *Enallagma* and *Ischnura*

Species	Reproductive process		Reference
	Sperm translocation	Copulation	
Enallagma coecum	22	18	This study
E. aspersum	17.8	13.5	BICK & HORNUFF, 1966
E. civile	16	18.7	BICK & BICK, 1965
E. exsulans	25.2	75.8	BICK & HORNUFF, 1966
E. hageni		22.4	FINCKE, 1982a
Ischnura denticollis		32	CÓRDOBA, 1992
I. elegans		324	MILLER, 1987
I. graellsii		74	CORDERO, 1989
I. ramburii		202	ROBERTSON, 1985

As in *E. coecum*, *E. hageni* females submerge to oviposit; oviposition in the latter species always takes place under water, with the male remaining close for safekeeping (FINCKE, 1982b, 1984). Submergence could be hazardous for females, for on occasions they have been known to die (FINCKE, 1984), but it has the advantage of reducing the chances of the eggs desiccating as a result of a lowering of the water level (FINCKE, 1984) and avoids interference with males (FINCKE, 1984; WAAGE, 1984). Conspecific males were observed in the area where the females were submerged.

The tendency to form congregations during oviposition has been noted in various species of the suborder, and some authors suggest that this behavior reduces the risk of predation by amphibians (REHFELDT, 1990). In the present study the observed congregations might reduce the risk of predation by *Anolis sagrei* lizards (MACMILLAN, 2000). The concentration of the reproductive activity toward hours of the midday apparently related to air temperature, as has been found in *Protoneura capillaris* (Rambur) in the form of a positive correlation between temperature and oviposition frequency (TRAPERO et al., 2005).

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