

SHORT COMMUNICATIONS

REPRODUCTIVE BEHAVIOR OF *CORDULEGASTER DIADEMA* SELYS
(ANISOPTERA: CORDULEGASTRIDAE)

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Received March 18, 1985 / Accepted March 26, 1985

Males of *C. diadema* are not territorial; instead they patrol long routes by streams in southeastern Arizona. Certain stream segments are visited sporadically by many different males. Females rarely appear at water and receptive females are rarer still. Males capture receptive females in flight, copulate while perched for periods of about 2 hr, after which their mates are released to oviposit unguarded. The significance of the correlation between prolonged copulation and non-territorial patrolling, which occurs in this and other unrelated dragonflies, remains to be fully understood.

INTRODUCTION

This paper presents new information on the natural history of a little-studied group, the cordulegastrid dragonflies. There are few accounts of male mating tactics for any member of the genus *Cordulegaster*. KAISER (1982) provides a review of information on a handful of European species, including *C. boltoni*; there appears to be only one paper on male behavior for a North American species, *C. dorsalis*, by KENNEDY (1917). From the limited data available it appears that males of this genus patrol long stretches of streams in search of receptive females, which are exceptionally scarce. Here I shall describe similar behavior for an Arizonan population of *C. diadema* Selys, documenting that males of this species are not territorial. In addition, I shall explore possible reasons why mating lasts such a long time in this species.

MATERIAL AND METHODS

Notes were collected on the activities of *C. diadema* from 30 July to 20 August 1984 at the middle fork of Cave Creek, a permanent stream in the Chiricahua Mountains of southeastern Arizona. The

stream flows through a juniper-oak woodland typical for elevations of about 1500 m. Cave Creek experiences sporadic flooding, but rarely exceeds more than 3 m in width and 0.5 m in depth.

In order to identify males, 20 individuals were captured and marked during the study; each male received a distinctive combination of Liquid Paper or Mark-Tex Inks on his wings. Between 15-20 August, one segment of stream about 20 m in length was monitored over six 90-min periods during which time I recorded the duration of visits by marking males to the site. Throughout the study all sightings of females and of male-female interactions were noted. These records provide information on the mate searching pattern of males as well as the frequency of oviposition and the occurrence of copulations at the study site. Means are expressed \pm 1 S.D.

MALE BEHAVIOR

Males patrolled the stream on all partly sunny and sunny days from about 0830 M.S.T. to about 1600 M.S.T. Cool weather and complete overcast depressed or ended patrol flights. Individuals cruised at heights of less than 50 cm above the stream, often going back and forth along two segments within the study area, one about 5 m in length, the other approximately 15 m long. One of the heavily patrolled segments was along the edge of the stream in an area with many shallow pools and slow-moving current; the other consisted of a small (less than 25 cm wide) side channel with water moving slowly through a depression bordered with dense grasses. Males generally made several passes over these segments, which facilitated the identification of previously marked individuals.

When two patrolling males encountered one another, they usually darted at one another and then engaged in a brief, twisting, ascending flight after which they separated. Chases were reasonably common, averaging 7.2 per hr during the 9 hr of observations.

Despite their apparent intolerance for one another, males of *C. diadema* clearly were not territorial in the sense of defending a fixed location. Individuals flew into the study area, inspected it in flight for a short time as a rule, and then departed. The maximum patrolling time for one individual within the area during any one 90-min observation period was only 30 min, with a mean patrolling duration per 90-min of 8.5 ± 7.0 min for all the marked males in the study ($N = 26$ records). Some males did visit the site more than once during a single observation period, after an absence of from 7-43 min ($\bar{X} = 26.1 \pm 12.7$ min; $N = 8$). The average number of males sighted in the study site per 90-min period was 7.7 ± 3.7 .

It was not uncommon for males to come to the study site over a period of several days (Tab. I). Of 20 marked males, 11 were seen again on another day; the mean interval between marking and last sighting for these 11 dragonflies was 5.3 days, surely an underestimate of male longevity and fidelity of individuals to patrolling routes that included the study area. For the 13 marked males present on 15 August, the probability that an individual would appear during any subsequent observation period was 19/65 (29%). Thus not only did a steady series of males visit the site, each for a short time, but there was no one male that

Table I
Duration (min) of patrolling visits by individually marked males of *C. diadema* to a 20-m stretch of Cave Creek, 15-20 August 1984

Male	Date and time of observation					
	15 Aug 0845-1015	16 Aug 1430-1600	17 Aug 1430-1600	18 Aug 0810-0940	19 Aug 1105-1235	20 Aug 0955-1125
A	8	—	—	4	3	—
B	7	10	—	—	3	1
C	3	2	3	2	—	—
D	1	13	—	4	—	13
E	11	—	—	—	—	—
F	1	—	—	—	—	—
G	1	17	30	—	13	—
H	7	—	—	—	—	—
I	1	—	—	—	4	—
J	1	—	—	—	—	—
K	1	—	—	—	—	25
L	1	—	—	—	—	—
M	1	—	6	—	7	—

returned to the location more consistently than all others. In fact, during the entire 9 hr of observation between 15-20 August the maximum total of all the visits for one male to the study site did not exceed 1 hr; the average time spent patrolling this part of the stream was only 15.5 min per male, or 3% of the total observation time (based on the sample of 13 marked males present on 15 August).

These data indicate that males of *C. diadema* patrol very long stretches of stream, briefly and sporadically returning to previously inspected spots, perhaps several times in one day and repeatedly at intervals over a span of many days. One male does not take up residence at a particular location, although males may chase conspecifics when their patrol routes happen to coincide.

MALE-FEMALE INTERACTIONS

Ovipositing females were sighted at the study area on only eight occasions, and they never remained for more than a few minutes. They behaved in the manner typical of their genus, plunging the tip of the abdomen repeatedly into the stream bottom at selected points before slipping off to go elsewhere. On five of the eight visits, females entered and left the area without being detected by males. The other three ovipositing females were chased by males when they flew from an oviposition site, but the females raced away and were not captured.

In addition to visits by ovipositing females, I recorded a total of ten matings during the study, never more than two on any one day. I observed the initial stages of a mating encounter only twice. Both times a female flew down low over

the stream just in front of a patrolling male. The male pursued the female in horizontal flight, capturing her after a short chase of only a few meters in one case, and after a much longer pursuit in the other. Once the male had grasped his partner, the interaction took the same form as the other eight cases in which the pair was detected only after the male had already grasped the female and assumed the tandem position. After they were linked in tandem flight, the pair cruised slowly back and forth 3-6 m above the stream or adjacent hillside. Copulation began in flight after a few minutes of tandem flight (when sperm translocation took place) before the pair settled on a streamside or hillside tree some 4-8 m above the ground. Eight of the ten copulations began between 0845-0945 M.S.T. The five copulations that could be timed in their entirety lasted from 74-145 min ($\bar{X} = 104.4 \pm 29.1$ min). Upon termination of copulation, the pair separated; the male did not accompany the female to the stream while she oviposited and no females were ever seen guarded by a male.

DISCUSSION

Male behavior in *C. diadema* closely resembles that of *C. boltoni* (KAISER, 1982) and *C. dorsalis* (KENNEDY, 1917). In all these species males do not defend plots of stream against intruders, but instead probably travel long distances up and downstream, patrolling a route and visiting various spots at considerable intervals. Many males share overlapping routes, interacting with brief rising flights when they meet, but making no effort to gain exclusive rights to any particular section of stream. Instead males seem to be attempting to be the first to locate a receptive female when she flies to the stream to mate.

The rarity of observed matings and the lack of receptivity of ovipositing females suggests that females mate just once (or at most a few times at long intervals). A low density of receptive (virgin?) females, coupled with their widely scattered distribution along the stream, may make territorial behavior unprofitable for males of *C. diadema* and other similar species. If there are no relatively small areas in which fairly large numbers of receptive females will appear, then males will gain by avoiding the time and energy costs of territoriality (cf. also KAISER, 1982).

The mating system of *C. diadema* falls neatly into category A of WAAGE (1984), a group of species with males that (1) patrol widely and non-territorially, (2) copulate infrequently but for a prolonged period when successful in finding a receptive female, and (3) release their mates upon completion of copulation rather than guarding them while they oviposit. The 1-2 hr copulations of *C. diadema* fall on the long end of the spectrum of copulation duration among odonates and they stand in sharp contrast to the very brief couplings typical of the highly territorial dragonflies (WAAGE, 1984). Although there are several possible benefits for prolonged matings (MILLER, 1983), such as the transfer of

large amounts of sperm, or the complete removal of rival ejaculates, or the prevention of remating by a partner, none of these seems likely to apply strongly to a species whose females mate once or at long intervals, as is probably the case for *C. diadema*. One can point to a strong reduction in the costs of lengthy copulations for category A species. Unlike the territorial odonates, whose males may have many opportunities to copulate in one day, a male of *C. diadema* is not likely to miss an opportunity to find another female in a 1-2 hr hiatus in patrolling, given the rarity of receptive females. Moreover, because males of *C. diadema* do not have territories to defend, they run no risk of territory usurpation while copulating for a prolonged time. What remains to be discovered is how males of *C. diadema* benefit sufficiently from prolonged copulation to outweigh the costs of reduced searching time, however slight these costs might be.

ACKNOWLEDGEMENTS

Help with the field work was provided by SCOTT SNEAD and BRUCE PETERSON. The manuscript was carefully reviewed by J.K. WAAGE. The study was supported by NSF Grant BNS-821 9791.

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