Odonatologica 12(1): 15-23 *March 1, 1983*

REPRODUCTIVE BEHAVIOR OF *CORDULIA SHURTLEFFI* SCUDDER (ANISOPTERA: CORDULIIDAE)

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Received May 11, 1982/Accepted September 2, 1982

The reproductive behaviour of *C. shurtleffi* was studied at a sphagnum bog pond near Sherbrooke, Quebec, Canada. No feeding occurred at the pond, only mating and oviposition. Males briefly patrol about 15 m of shoreline and attempt to drive away any conspecific males. Females visit shoreline areas to oviposit in water overhung by shrubs. When detected by patrolling males, ovipositing females are grasped in tandem and the pair flies into the surrounding forest where copulation occurs.

INTRODUCTION

Cordulia shurtleffi is a medium-sized (total length ca 45 mm, wingspan ca 60 mm), dark-bodied, clear-winged dragonfly with brilliant-green eyes whose preferred habitats are sphagnum bogs. WALKER & CORBET (1975) consider it "to be the commonest and most widely distributed species of its family in Canada", ranging from British Columbia to Newfoundland and as far north as the Yukon and North West Territories. In the U.S.A. the species has been recorded from Alaska, California, Colorado, Connecticut, Maine, Massachusetts, Michigan, Nevada, New Hampshire, New Jersey, New York, Oregon, Pennsylvania, Utah, Washington and Wyoming (NEEDHAM & WESTFALL, 1954).

In spite of such abundance and wide distribution, *C. shurtleffi* has not received much attention and, aside from its general natural history, little is known. Because of its abundance in sphagnum bogs, I investigated its reproductive behavior as part of a broader study on the behavioral ecology of bog-dwelling dragonflies.

MATERIAL AND METHODS

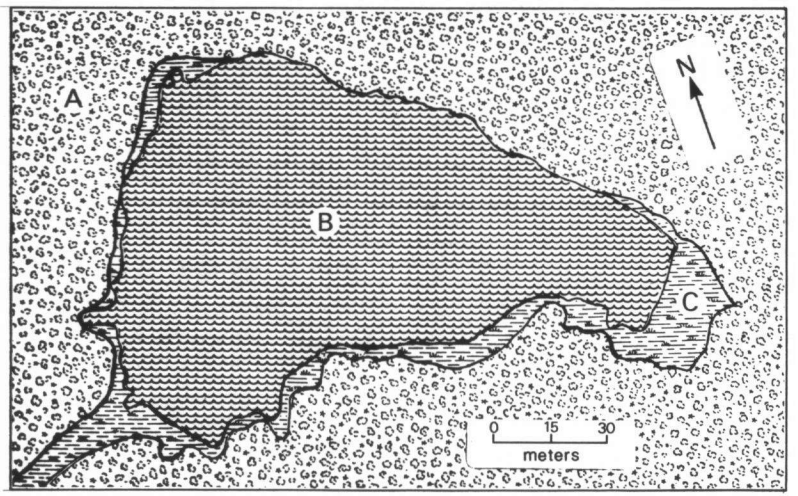

Fig. 1. Acidic, brown-water pond in the sphagnum bog where a breeding population of *Cordulia shurtleffi* was studied. A: coniferous forest composed primarily of black spruce (*Picea mariana* [Mill.] BSP.) and tamarack (*Larix laricina* [Du Roi] K. Koch); — B: open water area of pond; — C: sphagnum mosses and ericaceous shrubs.

Sherbrooke, Quebec, Canada (45°20'N, 71°45'W). The dragonfly fauna of this bog has been previously described (HILTON, 1981) and references in that paper will provide details of the bog's vegetation and physiography.

There are 3 acidic, brown-water ponds within this bog area and my study dealt only with the population of *C. shurtleffi* breeding in the northern pond (Fig. 1). This has an open-water surface area of 8950 m² and a circumference of 470 m. Shoreline vegetation consists primarily of various ericaceous shrubs, especially leatherleaf (*Chamaedaphne calyculata* [L] Moench), which overhang the water's edge.

Marking technique. — Although a number of marking techniques have been employed with the Odonata (CONNOR, 1971; HINNEKINT, 1974; LABEDZKI & SAWKIEWICZ, 1979; and references therein) none suited my purpose exactly. I had to identify rapidly-flying individuals without the disturbance of recapture. I adapted LABEDZKI & SAWKIEWICZ's (1979) method by using only bright-red nailpolish and applying dots of this on one or more positions [designated as A (base), B(nodus), and C(tip)] on the right-front (RF), right-hind (RH), left-front (LF), or left-hind (LH) wings. This provides up to 12 marking points and allows for the identification of 5018 individuals if all 12 locations are employed. I never needed more than 4 spots since this yields 793 individuals.

Dragonflies were netted for marking at the pond shoreline while they were patrolling (males) or ovipositing (females). They were restrained by bringing the left and right pairs of wings together over the thorax and holding them in this position (with their dorsal surfaces in apposition) utilizing a thin, flexible pair of forceps. Single dots of polish were then applied to the appropriate locations on the wings' undersurfaces. Following marking, each dragonfly was released by placing it on the branch of a nearby bush and allowing it to fly away at will. In almost all cases this immediately involved a rapid flight up and over the trees surrounding the pond. None ever resumed its patrolling flight.

RESULTS AND DISCUSSION

MARKING

Marking began on 26 May and ended 24 July 1981. During this 60-day period, marking and observation occurred on 31 days with a mean of 3 hr 30 min/day (range 1 hr — 5 hr 15 min; total 108 hr 30 min). Observation time began each day at an average time of 11.12h Est (range 09.30 — 14.45) and finished at an average time of 14.42h (range 11.15 — 16.45).

Out of the 375 marked, 4 (all males) had difficulty flying immediately after release, never did recover and were found dead the next day at the release points. Another 27 (all males) had difficulty flying (or flew awkwardly with their wings making a buzzing noise) for up to 30 sec, but then recovered and seemed to fly normally. However, none ever reappeared at the pond during the observation periods. These flight difficulties seemed to occur when the nailpolish got too thick in the bottle as a consequence of solvent evaporation. Keeping the polish thin by diluting with ethyl acetate solved the problem.

ANALYSIS OF THE FEMALE POPULATION

Very few females were captured for marking since they were much scarcer than males and I did not wish to interfere with the comparatively few opportunities to observe mating and oviposition. However, females first appeared at the pond 27 June and the last one observed was 22 July. Five females were captured (for marking and release) as well as 10 others kept for spermathecal examination. None of the 5 marked females ever reappeared at the pond during my observation periods.

Cordulia aenea amurensis Sel. also exhibits a very low percentage of females (1.4%) at the pond during the reproductive period even though the emergence sex ratio is 1:1 (UBUKATA, 1975). He attributes this relative scarcity of females to their lower visiting frequencies, and shorter stays, at the pond.

ANALYSIS OF THE MALE POPULATION

Males first appeared 26 May and the last one seen was 24 July. All males were teneral 26 May and some were still teneral for the next few days. In 1980, the flight period did not commence until 5 June but ended 24 July, the same date as in 1981 (HILTON, 1981).

Males were marked an average of once every 2.1 days including 26 May and 24 July. A total of 370 were marked with a mean of 13.2/marking day (range 1-29). Only one returned to the same site on the same day (27 May). This occurred 1 hr 35 min following marking and release. Sixty-one (16.7%) of the 365 surviving,

marked males reappeared at the pond one or more times (Fig. 2). This involved a mean of 2.2 marked individuals/observation day (range 0-10). Forty-four of the 61 (72.1%) were observed once, 13 (21.3%) twice, 1 (1.6%) three times and 3 (4.9%) four times.

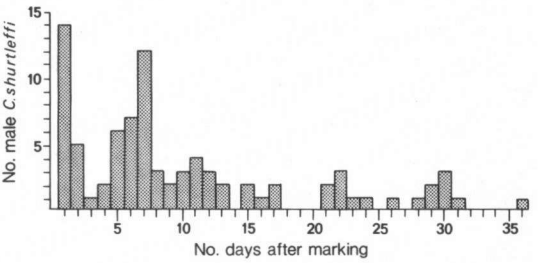

Fig. 2. Number of marked male *Cordulia shurtleffi* reappearing at the breeding site.

If *C. shurtleffi* is similar to *C. aenea amurensis,* it leaves the immediate environs of its emergence site for a pre-reproductive period of feeding and maturation. Following this, it returns for the reproductive period. Male *C. aenea amurensis* have an average pre-reproductive period of 10 days (UBUKATA, 1973) and mean (maximum) reproductive periods of 10.3 (45) days (UBUKATA, 1975). *C. shurtleffi*'s pre-reproductive period is unknown but the mean (maximum) reproductive periods are 10.4 (36) days (Fig. 2), very similar to *C. aenea amurensis.*

FEEDING

I never observed any *C. shurtleffi* (male or female) feeding at the pond during their reproductive periods. This was also usually the case for *C. aenea amurensis* and UBUKATA (1975) rarely saw feeding activity. Adults are assumed to leave the pond periodically during their reproductive periods and forage for prey in surrounding habitats. I only saw 2 *C. shurtleffi* away from the pond. One was a marked male flying slowly along the edge of a dirt road that passed through a mixed hardwood-coniferous forest. This male was sighted at 14.56h on 19 June 300 m from the pond and it made several attempts to catch a small fly that was flying among the top branches of a shrub growing along the roadside. Another marked male was seen near the same location at 10.15 h 10 June perched on a bush beside the road. This male was not observed feeding but may have been resting during a hunting foray. PRITCHARD (1964) records teneral Zygoptera, teneral *Leucorrhinia hudsonica* (Sel.), Trichoptera and Diptera (Chironomidae, Culicidae) as prey of adult *C. shurtleffi* near Flatbush, Alberta, Canada but does not mention specific feeding sites, nor whether feeding occurred at the breeding localities.

MALE PATROLLING BEHAVIOR

Patrolling males fly back and forth along 10-25 m of shoreline, 1-1.5 m above the water and just over the overhanging vegetation or up to 1 m from it on the pond side. This flight is interspersed with frequent periods (a few sec) of hovering during which the male periodically yaws to face various directions and his abdomen is angled slightly upwards with the legs tightly folded against the thorax (for a photograph of similar hovering posture in *Hemicordulia ogasawarensis* Oguma cf. SAKAGAMI et al., 1974). Usually males do not patrol a particular length of shoreline for more than about 5 min before flying elsewhere along the shore for further patrolling periods.

While patrolling they will often fly towards other passing dragonflies but stop short of actual contact unless the dragonfly is another male *C. shurtleffi*. In this case, there is a brief (1-3 sec) aerial clash which often results in both flying swiftly along the shoreline in a chasing flight. The original, patrolling male usually, but not always, returns in a few sec to continue patrolling. Some typical observations of *C. shurtleffi* patrolling behavior along the shoreline are:

Male 78	3 June	— patrolling 15 m at 11.25h for 3 min and again at 12.57h for 2 min.
Male 100	3 June	— patrolling about 10 m at 13.51h for 30 sec.
Male 237	23 June	— patrolling about 10 m at 14.37h for a few sec.
Male 243	24 June	— patrolling 10 m at 11.00h for 1-2 min.
	3 July	— patrolling 10 m at 12.34h for 1-2 min; flew by observation point at 12.42h but did not stop to patrol; returned at 12.45h and made 2 patrol flights along 10 m for a few sec.
Male 276	29 June	— patrolling 18 m at 12.30h for 8 min.
	2 July	— patrolling 25 m at 10.50h for 7 min.
Male 304	6 July	— patrolling 15 m at 14.06h for 3 min and again at 14.43h for 1-2 min.

Occasionally when an easily defined portion of shoreline was being patrolled, I observed more prolonged territorial behavior:

Male 1	28 May	— patrolling the shoreline of a bay that extended inland 10 m and was 4 m wide. From 10.50-11.05h it had 19 encounters with intruding conspecific males (number of different individuals is unknown) and won them all from the point of view that it returned to the inlet while the trespasser did not. Each encounter consisted of both males flying in tight circles around each other and frequently clashing while spiralling upwards the surrounding woods. From the moment 8 clashes started until the male first returned to the inlet took 3, 5, 5, 9, 11, 14, 45 and 60 sec. The two longer periods occurred when 3 or 4 males entered the inlet simultaneously and, together with the resident male, flew around one another in a clashing, upward-spiralling flight.

Such prolonged defence of a site, while infrequent, occurred more often earlier in *C. shurtleffi*'s flight season when fewer males were patrolling.

UBUKATA (1975) describes two types of patrolling behavior for *C. aenea amurensis*, 'patrol flight' and 'unstable patrol flight.' The former is very similar in most respects to the typical patrolling behavior of *C. shurtleffi* except that with

C. aenea amurensis it usually lasts longer (mean 7 min, range 1-40 min). Ubukata considers this true territoriality because it demonstrates 'localization and spacing by defense behavior'. Similarly, *Hemicordulia ogasawarensis* performs patrolling and defensive behavior but also includes occasional instances of female guarding (after they have copulated and while the female is ovipositing) (SAKAGAMI et al., 1974). These authors (like UBUKATA, 1975) quote NOBLE's (1939) definition of a territority as a 'defended area' and consider *H. ogasawarensis* territorial for the same reasons put forward for *C. aenea amurensis* by UBUKATA (1975), nevertheless acknowledging that these corduliids exhibit ephemeral territoriality with frequent replacement of owners throughout the day.

BROWN & ORIANS (1970), reviewing the literature on territoriality, conclude that 'the essential characteristics of a territory are (1) a fixed area, which may change slightly over a period of time, (2) acts of territorial defence by the possessor which evoke escape and avoidance in rivals so that (3) the area becomes an exclusive area with respect to rivals. All of these conditions must be satisfied for an area to be recognized as a territory'.

I do not consider *C. shurtleffi*'s patrolling behavior, nor that of the Japanese corduliids (cf. above), to be truly territorial because they do not conform to characteristic 1. The 'fixed area' changes frequently both spatially and temporally. Their defended areas might better be described as ephemeral, or moving, territories.

MATING AND OVIPOSITION

Because females oviposit (by repeatedly dipping their abdominal tips into the water) in water overhung by shoreline vegetation, they are difficult to see and patrolling males presumably have increased chances of detecting, and mating with, ovipositing females. Male *C. shurtleffi* are consequently practicing resource defence polygyny (EMLEN & ORING, 1977). Upon discovering an ovipositing female, the male quickly flies into the shoreline vegetation and grasps her with his anal appendages. They immediately fly upward in tandem formation from the overhanging branches and within a few meters have usually assumed the wheel position and continue in flight up and over the surrounding trees. Because they are lost from sight I do not know how long copulation lasts nor whether the male accompanies the female back to the pond for oviposition. I have not observed guarding behavior during oviposition. UBUKATA (1975) describes, and illustrates, similar mating behavior for *C. aenea amurensis*. He also could not time copulation but MÜNCHBERG (1932) recorded 10-15 min for *C. a. aenea* (L.).

I never saw a female *C. shurtleffi* that was not ovipositing when at the pond. Ten females were captured during oviposition and before a patrolling male had

detected them (at least during the observation period). All females had sperm in the bursa copulatrix and spermathecae. As a result, I do not know when, or where, mating of virgin females occurs. For *C. aenea amurensis,* UBUKATA (1975) believes it happens at the pond following the pre-reproductive period. However, he does not mention whether he examined (for sperm) any females appearing at the pond before he saw them mate.

Sperm competition obviously occurs within mated female *C. shurtleffi* since patrolling males copulate with any ovipositing females they see. As with many insects exhibiting multiple matings, sperm from the last insemination is probably going to fertilize most of the eggs (PARKER, 1970) and, if so, it would be to the male's advantage in an evolutionary sense, to mate with any ovipositing female he encounters. There is also the possibility that copulating males remove sperm from previously inseminated females before depositing their own as has been demonstrated by WAAGE (1979) for the damselfly *Calopteryx maculata* (P. de Beauvois), but I have no evidence of this.

Frequent mating by ovipositing females with patrolling males continually disrupts oviposition. In the case of species of dragonflies which exhibit brief copulation followed by guarding behavior (for references cf. PARR, 1980), a female might benefit evolutionarily from repeated matings because each guarding male provides her with an oviposition period uninterrupted by the attacks of searching males (PARKER, 1970). Such is not the case for *C. shurtleffi* and the fact that mated females adopt the wheel position and copulate with any males that detect and grasp them may simply be a matter of allowing copulation to be completed as quickly as possible so they can return to the pond and resume oviposition.

Ovipositing females are not obvious in their movements and slowly proceed along the pond margin, hidden by the shoreline vegetation. Having finished a bout of oviposition they fly quickly out of the overhanging shrubs and directly into the surrounding forest. Almost all females I detected were first noticed via the rustling-buzzing noise their wings made among branches of the shoreline vegetation. Only rarely did I see a female approaching the pond and in each instance she flew quickly from the forest and directly into the overhanging vegetation to commence oviposition.

Additionally, a female refusing to copulate (and therefore struggling) with the male loses valuable energy as well as risking injury in the clashing and battering of wings and other body parts. Predation by birds may increase during such a struggle since the pair's flight is slow and abnormal and their attention is diverted.

However, it is also possible that sperm from the initial mating is insufficient for the entire oviposition period and continual disruptions of many matings are tolerated because of a periodic need for sperm replenishment.

INTERSPECIFIC, HETEROSEXUAL MATING ATTEMPTS

Very occasionally a male *C. shurtleffi* attempted to grasp a female of another species. These mating efforts did not result in proper tandem formation or the wheel position. After grappling with the female for one to a few sec they separated, the female flying away and the male returning to shoreline patrol. All attemps at copulation between species involved males swooping down among shoreline vegetation to grasp females ovipositing in the same general manner and location as female *C. shurtleffi.*

The species (and number of separate occasions observed) in these encounters are: *Dorocordulia libera* (Sel.) (1), and *Epitheca canis* MacL. (3) (both Corduliidae), and *Leucorrhinia glacialis* Hag. (1) (Libellulidae). In addition, I twice saw 2 male *C. shurtleffi* simultaneously fly down into the shoreline vegetation in an apparent attempt to grasp an ovipositing female *Libellula julia* Uhler (Libellulidae). However, they did not actually make contact with her and left to resume patrolling. Of the above species, *Libellula julia* is least like *C. shurtleffi* in general appearance and this may have enabled the males to make the necessary discrimination at closer quarters. On another occasion when I attempted to catch a male *C. shurtleffi,* it hit the net rim and fell, stunned, about 1 m from shore. It weakly fluttered its wings and other male *C. shurtleffi* and *Leucorrhinia glacialis* repeatedly tried to grasp, unsuccessfully, the struggling male with their anal appendages. Presumably, this male, in fluttering its wings on the water so close to shore, superficially resembled an ovipositing female. BICK & BICK (1981) summarize all references to interspecific, heterosexual pairings but none of these involved the above species pairs.

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