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TERRITORIALITY IN *LIBELLULA JULIA* UHLER (ANISOPTERA: LIBELLULIDAE)

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Territorial behaviour of *L. julia* was studied at a sphagnum bog pond near Sherbrooke, Quebec, Canada. Males defend a 10—25 m length of shoreline by flying at, and chasing, conspecific males. Feeding was not seen to occur in these territories. Females visit shoreline areas to oviposit in water under the overhanging vegetation and males attempt to mate with any females they encounter at the oviposition sites. Following brief, aerial copulation, females resume ovipositon and are guarded by the males who hover nearby and attempt to drive away conspecific males.

INTRODUCTION

Libellula julia Uhler is a medium-sized dragonfly (total length ca 40 mm, wingspan ca 65 mm) which is basically dark brown but matures to become pruinose white (males) or grey (females) on the thoracic dorsum and basal abdominal tergites. Wings are hyaline, each with a small, dark patch at its base. Distribution is transcontinental along both sides of the Canadian-U.S. border from British Columbia and Washington to New Brunswick, Nova Scotia, Maine, Massachusetts and New York. Within this broad zone it occupies boggy, marshy and swampy areas, but is especially abundant in sphagnum bogs (WALKER & CORBET, 1975).

In spite of its broad distribution and local abundance, little is known about *L. julia* beyond general natural history and occasional observations such as: "In fine still weather the males may be seen chasing each other swiftly and erratically over the water" (WALKER & CORBET, 1975). This lack of information, together with the presence of a large breeding population of *L. julia* in a black spruce--sphagnum bog where I am currently studying the behavioural ecology of bog--dwelling dragonflies, prompted me to investigate (during the summer of 1981) the

reproductive behaviour of *L. julia*.

MATERIAL AND METHODS

The study bog is located 13 km SE of Sherbrooke, Quebec, Canada (45°20'N, 71°45'W). I have described its dragonfly fauna (HILTON, 1981) and relevant details of vegetation and physiography (HILTON, 1983).*

Dragonflies were captured at the pond with an aerial insect net, marked and immediately released at the capture point. Each individual was given an identification number consisting of dots of red nailpolish on the wings' undersurfaces. See HILTON (1983) for details of the marking system.

RESULTS AND DISCUSSION

MARKING AND PHENOLOGY

I observed *L. julia* on 28 days from June 1 — July 30 for a total of 100h, 20 min (mean 3h, 35 min/day; range 1h, 30 min — 5h,15 min). Observation began on average at 11.25 hours EST (range 09.30 — 14.45 hours) and ceased on average at 15.00 hours (range 14.45 — 16.45 hours). Males first appeared June 1 (many teneral, one mature) and were last observed July 30. Females first appeared June 10 (mating and oviposition also first seen on that date) and were last seen (and ovipositing) July 22.

Marking took place on 21 days from June 2 — July 24 (i.e. once every 2.5 days). In total, 152 males and 3 females were marked, with an average of 7.4/marking day (range 1—20). This small number of females reflects the fact that females come to the pond only for brief periods of oviposition whereas males congregate there to acquire and defend mating territories, as is typical for many dragonflies (CORBET, 1963, 1980; JOHNSON, 1964). Also, I tended not to capture females since I did not wish to interfere with opportunities to observe mating and oviposition. In many anisopteran dragonflies males are slightly less abundant than females and comprise 40—50% of the adults emerging from the larval stage (CORBET, 1963, 1980; LAWTON, 1972).

Following marking, dragonflies were released by placing them on the branches of a nearby bush and allowing them to fly away at will. This usually meant an immediate, rapid flight across the water or up and over the trees surrounding the pond. In both cases they were lost from sight. This response is like that seen for *Cordulia shurtleffi* Scudder (Corduliidae) (HILTON, 1983) and *Leucorrhinia caudalis* (Charp.) (Libellulidae) (PAJUNEN, 1964) but contrasts with the tropical *Nesciothemis nigeriensis* Gambles (Libellulidae) in which PARR & PARR (1974) observed that males usually resumed territorial behaviour immediately

* Due to an unfortunate error in the final processing, the following line has been omitted from the bottom of p. 15 in HILTON (1983):

"Study site. — This study was conducted at a black spruce-sphagnum bog located 13 km SE of"...

following similar mark and release methods.

Only 2/155 (1.3%) returned to resume normal activities at the capture site on the same day. These were two males captured at 11.10 hours June 10 and 13.09 hours July 15 which returned at 13.01 and 13.55 hours, respectively. Of the remainder, 99/155 (63.9%) were not seen again following marking (including all 3 females) but 33/155 (21.3%) returned once, 11/155 (7.1%) returned twice, 7/155 (4.5%) returned 3 times, 2/155 (1.3%) returned 4 times, 1/155 (0.6%) returned 5 times and 2/155 (1.3%) returned 6 times during my observation periods.

The length of *L. julia's* prereproductive period is unknown but the males' mean (maximum) reproductive periods are 9.8 (40) days (Fig. 1). This compares with mean (maximum) reproductive periods of 25 (60) days for *Orthetrum cancellatum* (L.) (KRÜNER, 1977) and 9 (51) days for *O. julia* Kirby (Libellulidae) (PARR, 1980).

FEEDING

Neither sex was observed to feed at the pond. However, on two separate occasions I saw a male abruptly fly up from its shoreline perch towards a small flying insect. In both cases the male immediately returned to its perch but I was unable to see if it had captured the insect. Feeding activity (or lack of it) at the breeding site is a species characteristic and, within the Libellulidae, some feed there while others do not and periodically leave to forage for prey elsewhere. PARR (1980) summarizes the literature reporting libellulid feeding activity.

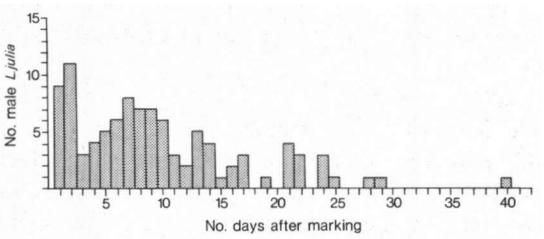

Fig. 1. Number of marked males of *Libellula julia* reappearing at the marking site.

PERCHING

L. julia males are perchers and considerably more time is spent perching than patrolling (Tab.I). Only 3/10 dragonflies for which perching and flying periods were timed showed a significantly longer time spent in flight. Long perching periods were also demonstrated for *N. nigeriensis* (PARR & PARR, 1974) and *O. julia* (PARR, 1980). However, HEINRICH & CASEY (1977) and PEZALLA (1979) have shown that for the perchers *Libellula saturata* Uhler and *L. pulchella* Drury, respectively high and low ambient temperatures increase the duration of perching whereas at temperatures of 29.5 — 33°C (*L. saturata*) or

Table I
Comparison between mean time spent patrolling or perching by territorial male *Libellula julia*

Male	Date	Patrolling					Perching					Student's t	P
		Number flights	Total flight time (min,sec)	Mean flight time (sec)	Range (sec)	SD	Number perching periods	Total perching time (min,sec)	Mean perching time (sec)	Range (sec)	SD		
8*	19 June	14	7,21	31.5	1-101	35.4	14	5,27	23.4	1-65	19.6	4.09	<0.001
30*	29 June	29	11,30	23.8	1-120	30.5	29	9,57	20.6	1-157	30.6	2.20	<0.05
41	2 July	25	10,30	25.2	2-147	38.6	25	25,05	60.2	3-206	63.3	17.34	<0.001
60	29 June	9	1,10	7.8	1-20	7.6	9	20,31	136.8	2-306	121.1	29.96	<0.001
60	3 July	7	3,21	28.7	3-57	20.5	7	4,30	38.6	16-73	19.9	4.12	<0.001
61	7 July	39	15,40	24.1	4-80	21.1	39	21,27	33.0	3-160	34.3	7.47	<0.001
77*	6 July	16	33,38	126.1	9-488	135.6	16	11,22	42.6	3-130	36.2	25.48	<0.001
77	10 July	50	19,25	23.3	3-139	27.8	50	37,15	44.7	1-238	53.2	16.80	<0.001
113	8 July	35	5,05	8.7	1-56	9.6	35	15,17	26.2	3-125	26.6	17.20	<0.001
145	17 July	62	19,32	18.9	1-98	19.4	62	42,41	41.3	1-172	37.2	23.40	<0.001
Total		*286*	*127,12*	*31.8*	*1-488*	*34.0*	*286*	*193,32*	*46.7*	*1-306*	*33.7*	*5.73*	*<0.001*

* Males which spent significantly more time patrolling.

23—31°C (*L. pulchella*) they flew more than 50% of the time.

Meteorological conditions also affect perching and flying behaviour in *L. julia* and cloudy periods cause males to cease their patrolling flights. For example, on June 12 some *Epitheca canis* McLachlan (Corduliidae) and many *C. shurtleffi* (both fliers) and *L. julia* were patrolling the pond's shore. However, at 13.25 hours it became cloudy with a light sprinkle of rain and all the *L. julia* stopped patrolling whereas the two corduliids continued their flights. At 13.35 hours the clouds dispersed and *L. julia* began patrolling again. Disappearance from the water during cloudy periods has also been noted for *Leucorrhinia rubicunda* (L.) (Libellulidae) (PAJUNEN, 1966).

Perching time is reduced when many dragonflies (species and individuals) are present at the pond because males repeatedly leave their perches to fly at passing males (normally conspecific, but occasionally other species.)

A male usually employs the same few perches for all perching periods. These perches were frequently branches of ericaceous shrubs that projected conspicuously above the adjacent branches. Such perches were 1—2 m from the pond margin and 20—30 cm above the sphagnum mat. Occasional males perched at random and up to 5 m from the water's edge. Males didn't seem to preferentially face the water and were oriented at various compass directions from one perching period to another. A percher's body is usually angled with the head up, abdomen slanting slightly downwards and the wings drooping (front pairs more than hind). These are postures MAY (1976) illustrates for perching libellulids maximizing their exposure to the sun. He considers such dragonflies heliotherms since they rely largely on insolation for body heat.

During prolonged perching periods males sometimes fly up from the perch in a short, looping flight of several cm—0.5 m and immediately resettle on the same perch. In addition, they periodically rotate and twist their heads at various angles while rubbing it with their forelegs.

PATROLLING

Male *L. julia* flying along the shoreline are of two types: those with, or without, territories. Both fly at a height of 1—2 m and either directly above the overhanging shoreline vegetation or 1—2 m from it over the water. They periodically intersperse their flights with short (1—3 sec) periods of hovering. Non-territory holders, however, continue to fly in one direction for long distances without stopping to localize at a particular site. It appears as though attacks by territory holders cause them to continue moving along the shoreline for they have a tendency to restrict their movements to back and forth flights and hovering in an area of shoreline where they are not attacked. For example, male 61 patrolled and defended a territory July 7 from 10.49—11.55 hours at which time I removed it. During this period it flew at passing male *L. julia* and chased them for several metres along the pond's margin. None of these trespassers ever stayed for more than a few sec. At 11.56 hours male 26 entered the zone formerly defended by 61 and, not being attacked, localized there until 12.25 hours during which time it became the territory holder and defended it against passing conspecific males. On another occasion (July 17) male 145 had been defending 10 m of shoreline for about 2 h when male 151 flew in and landed 1 m away from 145's perch. It was not clear whether they saw each other, but it appeared to me that the leatherleaf (*Chamaedaphne calyculata* [L.] Moench) branches could easily have hidden them from one another's view. Thirty sec later 151 flew from its perch. Male 145 saw it, left its own perch and chased 151 towards the surrounding forest. Male 145 returned to its perch after a flight of 12 sec. About 1 min later, 151 flew past the shoreline of 145's territory and the latter left its perch to chase 151 for several m along the shore. Male 151 did not reappear but 145 returned within a few sec to continue its territorial perching and patrolling activities. As with *Pararge aegeria* (Lepidoptera: Satyridae) (DAVIES,1978), these observations suggest that in territorial disputes the resident usually wins.

Patrolling flights of territory holders are different from those of non-holders in that the former tend to spend more time perching than flying. Passing dragonflies are the most obvious stimuli causing them to leave their perches. If these are of other anisopteran species the flights (if any) are brief (a few sec) and consist of short approach flights followed by turning away when within a few cm (before body contact is made) to return to the perch. However, if the trespasser is a conspecific male flights are more prolonged (usually greater than 10 sec) and consist of a chasing flight for many m along the shore (or out over the pond) with occasional body contact and wing clashing. The defending male always returns to perch in its territory.

When many males are flying along the shore perching periods can be very brief because the territory holder often has only just returned to its perch when 1—2 sec later it lifts off to chase another male. Frequently passing males of other species

are ignored but this is not the case for male *L. julia* unless: (a) they are further than 3 m away, or (b) the perching male's view of the pond is obstructed by vegetation. The latter situation does not happen often because males usually select perches that command a good view of the shore.

Territorial males defend and patrol a 10—25 m length of shoreline. In some other libellulids territory size varies from 0.5—2.0 m for *Acisoma panorpoides inflatum* Selys (HASSAN, 1978) to 3—20 m for *N. nigeriensis* (PARR & PARR, 1974) and 10—50 m for *O. cancellatum* (KRÜNER, 1977). Although territory size is a species characteristic, in general for these and other species (e.g. CORBET, 1963, 1980; GREEN, 1974; PEZALLA, 1979), smaller territories occur if more males are present to compete for available shoreline.

When males possessing adjacent territories are patrolling and happen to meet at the common border, they briefly (1—3 sec) grapple wih one another while flying in tight circles with their wings clashing. They then separate and fly back to patrol, or perch in, their respective territories. The clashes are too short and rapid to determine the nature of the physical contact. However PAJUNEN (1962), using cinematography, has illustrated what appear to be similar aggressive clashes between males of *Leucorrhinia dubia* (Vander L.).

Males may return and hold the same territory on different days over a many-day period. On each occasion a territory is occupied (by perching) and defended (by patrolling, hovering and chasing) for 30 min to over 2 h. These times of possession compare with 8—42 min for *A. p. inflatum* (HASSAN, 1978), 10 min—3 h for *Pachydiplax longipennis* Burm. (Libellulidae) (JOHNSON, 1962), 5 h for *N. nigeriensis* (PARR & PARR, 1974), 6—8 h for *O. julia* (PARR, 1980) and 7 h for *Libellula pulchella* (PEZALLA, 1979).

Late in *L. julia*'s flight season, both perching and patrolling behaviour change. There are not many males present at this time and those few remaining usually fly for long distances down the shoreline without localizing, or perch for several min well back (many m) from shore where vegetation obstructs their view of the pond.

MATING, GUARDING AND OVIPOSITION

The location and timing of intra-male sperm transfer differs for various species and CORBET (1963, 1980) reviews the major variations. Except for one occasion I never saw evidence of such transfer in male *L. julia* at the pond. In this instance (July 2, 13.10 hours) a male was flying about 20 cm above the pond and 4—5 m from shore with its abdominal tip curved under and forward making contact with the copulatory organs. Normally intra-male sperm transfer probably occurs before the males arrive at the pond as is the case for *Leucorrhinia dubia* and *L. rubicunda* (PAJUNEN, 1963).

Females seem to be present at the pond only for oviposition. I never observed mating to occur except with females that were ovipositing or flying to the

shoreline in an apparent oviposition attempt. This was also the case for *L. dubia* and *L. rubicunda* (PAJUNEN, 1963). Since territorial males control access to oviposition sites they are practicing resource defence polygyny (EMLEN & ORING, 1977).

When a patrolling male (territory holder, or not) detects an ovipositing female he swoops down, grasps her behind her head with his anal appendages and they fly up from the shoreline vegetation in tandem. Almost immediately they adopt the wheel position but sometimes may stay in tandem while flying low over the water for several metres before entering the wheel position. The mean duration of 31 timed wheel positions was 4.97 sec (range 3—9 sec, sd 1.72). This places *L. julia* at the low range of those dragonflies considered to have short-duration copulation (CORBET, 1963). During this brief period the pair usually flies as far as 10 m over the pond at a height of a few cm—1 m above the water. They may disengage at this point or return to the shoreline vegetation before separating. Sometimes copulation occurs while hovering 1—2 m inland. In contrast to these observations, FURTADO (1973) says "...copulation occurs outside the territory on a perch." If separation occurs over water the female flies directly back to shore, sometimes repeatedly touching her abdominal tip to the water surface and the male follows about 20 cm behind. Upon reaching the pond's margin the female begins oviposition. This involves a rapid dipping of her abdominal tip into water overhung by the shoreline vegetation and slowly moving along while hovering and flying her way through the branches. Her movements are often hidden by the shrubbery but her position is indicated by the rustling, buzzing noise her wings make against the twigs. During oviposition the male guards her (also reported by FURTADO, 1973) by hovering within 20 cm—1 m with occasional, brief flights of 1—3 m along the shore. While hovering the male yaws in various directions and may fly at other dragonfly species that pass by but is particularly aggressive in its chasing flights towards conspecific males. Similar guarding behaviour following copulation has been demonstrated for various libellulids (e.g. CAMPANELLA, 1977; CAMPANELLA & WOLF, 1974; HASSAN, 1978; JACOBS, 1955; KRÜNER, 1977; PAJUNEN, 1963, 1966; PARR, 1980; PARR & PARR, 1974; PEZALLA, 1979; WILLIAMS, 1977).

Sometimes a passing male notices the ovipositing female and manages to get past the guarding male. When this happens, the intruder grasps the female with his anal appendages and they fly out of the shoreline vegetation in tandem with the guarding male in pursuit. A chasing flight with frequent clashes ensues as they all fly swiftly over the pond, along the shoreline or into the surrounding forest. If the intruder is unsuccessful in assuming the tandem position with the ovipositing female, she escapes by flying into the forest with intruding and guarding males in pursuit.

I do not know where or when virgin females are first mated. However in an attempt to answer this question, I captured and dissected five, unattended

females that had come to the shoreline for oviposition. Each had large masses of sperm in the spermatheca. Consequently, ovipositing females probably do not need to adopt the wheel position with any male that successfully grasps them in tandem. The fact that they do may result from: (a) a need for periodic sperm replenishment, (b) the likelihood of body damage or increased chances for predation that could result by struggling with the male, or (c) the benefits of an uninterrupted oviposition period that a guarding male ensures. The latter is definitely a benefit because oviposition periods are significantly ($P<0.01$) longer when the female voluntarily leaves (mean 22.5 sec, sd 9.6, range 10—33 sec) than when she is disturbed by an intruding male (mean 15.4 sec, sd 14.7, range 2—45 sec). Due to this interference oviposition periods are shorter when many patrolling males are present because one is likely to grasp the female while the guarding male is chasing yet another intruder. Excessive interference with oviposition when large numbers of competing males are present has also been recorded for *Leucorrhinia rubicunda* (PAJUNEN, 1966), *Libellula pulchella* (PEZALLA, 1979) and *Plathemis* (=*Libellula*) *lydia* (Drury) and *Perithemis tenera* (Say) (Libellulidae) (JACOBS, 1955).

Females of *C. shurtleffi* (HILTON, 1983) also contain sperm when appearing at the oviposition site and JACOBS (1955) noted that females of *Perithemis tenera* ovipositing at a pond from which all males had been experimentally removed nevertheless produced fertile eggs. This means that copulation took place previously and therefore mating during oviposition is of greatest evolutionary benefit to the male because, as with most insects exhibiting multiple matings, sperm precedence probably occurs (PARKER, 1970). This is undoubtedly why males guard females with which they have just copulated. In fact, males will attempt to recopulate with a female they are guarding if they are forced to leave her for too long as a result of a prolonged chasing flight (in one case 8 sec) and another male is guarding her (and therefore has copulated) when the original male returns. Due to the brief copulation period it is unlikely that males remove sperm stored in the female from a previous mating before depositing their own as MILLER & MILLER (1981) and WAAGE (1979a) showed occurs in *Enallagma cyathigerum* (Charp.) (Coenagrionidae) and *Calopteryx maculata* (P. de Beauv.) (Calopterygidae), respectively. The benefits to both sexes of an uninterrupted, extended oviposition period provided by guarding behaviour are discussed in general by PARKER (1970) and by WAAGE (1978, 1979b) for *C. maculata.*

When a female finishes a bout of oviposition without being interrupted she flies out of the shoreline vegetation and usually into the surrounding forest but occasionally rapidly along the shoreline at a height of about 2 m.The guarding male follows her for a few m but then returns and patrols the shoreline where the female used to be for about 1 min before flying elsewhere along the shore or resuming normal territorial behaviour.

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