

PRELIMINARY RESEARCH NOTE

**NOTES ON TANDEM OVIPOSITION AND OTHER
ASPECTS OF REPRODUCTIVE BEHAVIOUR IN
SYMPETRUM VICINUM (HAGEN)
(ANISOPTERA: LIBELLULIDAE)**

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Tandem oviposition (contact guarding) in low-density populations was observed at a small pond in New York State. Oviposition generally occurred between 1200-1430, during which time pairs appeared at the water already in tandem. Searches of the surroundings failed to reveal aggregations of tandem pairs; hence pairs may have flown immediately to the water or may have come from greater distances. Many arriving tandems performed dipping movements over potential oviposition sites along the shoreline. This behaviour resembled oviposition, was often followed by copulation, and may have functioned to show the ♀ oviposition sites and thereby induce mating. During tandem oviposition, the ♂ alternately dipped the ♀'s abdomen into the water and struck it against the pond bank or other surface; such actions probably deposited eggs both in the water and on mud or shore vegetation. As many as 10 pairs occasionally oviposited 5-10 cm from one another at the same site. Occasional lone ♂♂ were present near oviposition areas, but rarely disrupted tandem pairs; no takeovers or rematings of ovipositing ♀♀ were recorded. Guardians stayed in tandem for the duration of oviposition and never switched to non-contact guarding. The adaptive significance of contact guarding in *S. vicinum* is discussed with reference to other members of the genus.

INTRODUCTION

Tandem oviposition, or male contact guarding, is well known for many members of the genus *Sympetrum*. Depending on the species, this behaviour may occur together with oviposition by unattended females, non-contact guarding of ovipositing females, and/or pre-copulatory guarding in the tandem position (e.g. MILLER et al., 1984; VAN BUSKIRK, 1986; SINGER, 1987; CONVEY, 1989). To date, little has been reported on tandem oviposition in *S. vicinum*, a late-season species of

Canada and the United States. In this species, the female's abdomen is struck alternately against the water surface and the bank of ponds or slow streams; during this process, eggs are released from her large funnel-shaped vulvar lamina (WALKER & CORBET, 1978). Over the course of four years I accumulated behavioural data on low-density populations of *S. vicinum* in central New York State. In this paper, I expand earlier accounts of oviposition in this species, describe related aspects of reproductive behaviour, and raise points of comparison with other members of the genus.

STUDY AREA AND METHODS

Most observations were made at a small artificial pond (Pond 1) 4 km East of Hamilton, Madison County, New York, U.S.A. The pond was lined with black plastic covered with sand and sediment, and measured ca 8 × 5 m. Along the shoreline were grasses, sedges, and small shrubs (*Salix*); open water areas were predominated by patches of *Typha latifolia* and floating mats of *Myriophyllum*. The south side of the pond was bordered by woodland, the east side by lawn, and the remaining sides by meadows. Occasional observations were also made at a second artificial pond (Pond 2) lined with mud and bentonite clay and measuring ca 16 × 14 m. Pond 2 was located 66 m from Pond 1. Some dragonflies were seen flying between the two ponds, but it was not possible to monitor the extent of such movements in the present study. Unless noted otherwise, results reported here refer to Pond 1, although the general behaviour of *S. vicinum* was similar at both locations.

Data were collected during late August and early October 1992-1995, generally between 1100-1500, when tandem pairs were present at the water. Most observation sessions lasted 1-4 h, totaling over 130 h. In addition, in 1992, on 3 days from 1000-1600, Pond 1 was censused every 30 min for pairs and individuals within 1.5 m of the water. In 1993-95 I captured a total of 96 males and 84 females within 2 m of Pond 1 and marked them uniquely with enamel paint. An additional 35 males and 55 females were marked at Pond 2 or in the adjacent meadows. Only 14% (39) of all marked dragonflies were sighted again; thus most data came from unmarked individuals. Since unmarked tandems often joined others at the same oviposition site and/or left the pond temporarily, most pairs could not be observed continuously from time of appearance to end of oviposition. Direct observation of behaviour was supplemented by the use of binoculars and a video camera, and reproductive acts were timed with a stopwatch.

OBSERVATIONS AND DISCUSSION

PAIR FORMATION AND LONE MALES

Reproductive activity at both ponds was restricted to a period of several hours around midday, generally 1200 - 1430. During this period, pairs already in tandem arrived at the pond from the surrounding areas, and many proceeded to mate or oviposit. Unpaired males were also present for short periods (e.g., several minutes to 1 h) and at low densities (generally 1-3 males at Pond 1). These males rested on vegetation around the shoreline or over shallow water, and spent most of their time perching. Some showed weak localization around their perch sites and chased other males flying near them. However, most marked males were never re-sighted: of 96

males captured and released at Pond 1 in 1993-95, only three returned to the pond the same afternoon, and only eight returned on one or more subsequent days.

I saw no unpaired females at the water except those that had recently deposited eggs and were unreceptive to further matings. Hence I conclude that pairing occurred away from oviposition sites. However, searches of the woods edge and meadows surrounding both ponds (an area of ca 3 ha) yielded only scattered, perched individuals of both sexes, and no pairs. I occasionally saw dragonflies in tandem or in copula perched on vegetation as far as 5 m from Pond 1, but most pairs were within 2 m of the water or else in transit, sometimes flying at heights of 8-10 m. Therefore pairs, once formed in the surroundings, may have flown immediately to the water, or they may have come from greater distance, as occurs in some other *Sympetrum* species (MILLER et al., 1984; WATANABE & TAGUCHI, 1988; MICHIELS & DHONDT, 1989; MIYAKAWA, 1994).

In an attempt to witness pair formation, I captured, marked, and separated 68 pairs in tandem and 12 pairs in copula, then released them near the water. Most females were chased by lone males, and seven were taken into tandem. Of these, five formed the copulatory wheel within 30 s with their new partners. One female was released after 1 min; the others flew off still in copula, and one female was seen 20 min later ovipositing in tandem.

Unpaired males also chased females that left the pond after completing oviposition, and they sometimes approached or hovered near tandem pairs. Such behaviour suggested that they were searching for females, perhaps through a "sit-and-wait" strategy similar to that described for *S. danae* (MICHIELS & DHONDT, 1988). Since some of these males had arrived alone, they may have been unable to locate mates earlier in the day away from the water. Other males came initially in tandem, but stayed for variable periods of time after their partners oviposited. However, under natural conditions I saw no lone males acquire mates at the pond. MICHIELS & DHONDT (1989, 1991), studying dense populations of *S. danae*, found that most pairings occur away from oviposition areas in the early morning, but towards noon males move to the water, where they may intercept still unmated (undetected) females. If a similar situation applies in *S. vicinum*, then pairings near the pond may be more likely than my observations in these low-density populations suggest.

PRE-COPULATORY DIPPING

Some tandem pairs oviposited soon after arriving at the water. However, others cruised 1-2 m above the pond or fluttered along the shoreline 20 cm - 1 m over the water surface. Pairs flying close to the water often performed dipping movements resembling those of oviposition; however, the female's abdomen rarely touched the surface, and the pair moved quickly from one area to another. Many pairs copulated after such behaviour. Others left the pond after several minutes, turned in mid-air, and returned to make more circuits of the shoreline accompanied by dip-

ping movements; many of these pairs also eventually copulated. Still other tandems flew rapidly towards Pond 2 or out of sight.

Pre-copulatory dipping in *S. vicinum* seemed to be a means by which males allowed females to sample potential oviposition sites, and females may have delayed copulation until suitable areas were located. Very similar behaviour has been described and interpreted as in-tandem courtship for *S. depressiusculum* (MILLER et al., 1984) and *Orthetrum coerulescens* (LEE, 1991; MILLER, 1991).

COPULATION

At the pond, tandems formed the copulatory wheel as they flew over the water or near the shore; they then settled on one or more perch sites usually within 3-4 m of the water. Pairs were rarely disturbed by unpaired males, and females in copula were never seized and re-mated. Mean copulation duration for 19 pairs observed from start to finish was 5 min 48 s (minimum = 3 min 16 s, maximum = 12 min 20 s). Eight of 10 females captured within 2 min of the onset of copulation all had at least one egg visible at the tip of the abdomen; the remaining two females began to release eggs several seconds after I dipped their abdomens into pond water. Batch size for three females caught in copula and dipped until no further eggs emerged was 305, 418, and 445 eggs.

After copulating, pairs stayed in tandem. Some moved directly to the water and soon began ovipositing, while others flew rapidly away and were lost from view. One marked female was seen in tandem investigating sites at Pond 1 and then tandem ovipositing at Pond 2 several minutes later, and other marking records showed that individuals and pairs could shift between the two ponds. I surmise that the many unmarked pairs which arrived at Pond 1 and began ovipositing without first copulating had mated there earlier in the day, or had mated at Pond 2 but come to Pond 1 to oviposit.

TANDEM OVIPOSITION

During oviposition, the male clasped the female in tandem and alternately dipped her abdomen into the water and struck it against the pond bank or other surface. Dipping movements were often irregular, but pairs dipped roughly once per second. During dipping, the wings of both partners beat vigorously, and the female's abdomen was extended more or less horizontally. Ovipositing pairs tolerated the presence of other pairs in close proximity, and newly arrived pairs often joined others already using a particular site. It was not uncommon to see 2-3 pairs, and occasionally as many as 10 pairs, dipping without apparent interaction within 5-10 cm of one another.

Typical oviposition sites were areas of shallow water adjacent to wet mud, moss, matted vegetation, or protruding plant roots on the bank. However, some pairs

dipped into open water containing mats of *Myriophyllum*, and on two occasions, pairs dipped onto clumps of wet moss 1 m from the water. In 1995, during an unusually dry season, large numbers of dragonflies oviposited over a portion of the bank of Pond 1 where the plastic lining had been exposed; here, eggs could be seen with the unaided eye on the black plastic. Heavy rains in late fall subsequently flooded this area; however, other odonates have often been seen ovipositing on reflective substrates that are biologically unsuitable (e.g., MIYAKAWA, 1994; see also UTZERI, 1991). In *S. vicinum*, as in other *Sympetrum* species, such apparently aberrant behaviour due to low site selectivity may reflect a potential for wide-spread exploitation of varied habitats (UTZERI, 1991).

S. vicinum pairs often investigated several sites before localizing at a single area. As tandems fluttered along the shoreline, the female sometimes raised her abdomen briefly, perhaps indicating an unwillingness to oviposit. UTZERI (1989) observed similar behaviour by *S. striolatum* females ovipositing in tandem, and interpreted it as a signal to the male to change oviposition sites. During site selection, many *S. vicinum* pairs also performed tentative or ill-defined dipping movements above the water or other surface, and sometimes in contact with it. I could not determine if eggs were released at such times, but such behaviour often led to more regular dipping at the same site, and thus to what I considered normal oviposition. Post-copulatory dipping without apparent egg release occurs in *S. depressiusculum*, and MILLER et al. (1984) have suggested that it represents the male's attempts to induce the female to oviposit. Such may also be the case in *S. vicinum*, since females captured in tandem that had not yet begun to release eggs did so several seconds after I dipped their abdomens into pond water. Preliminary dipping during site selection may also have allowed the female to inspect the substrate more closely.

Most tandem pairs settled at a single site within several minutes and dipped more or less continuously unless disturbed. These dipping bouts were usually brief: the mean duration for 12 pairs observed from the beginning of dipping until pair separation was 1 min 52 s (minimum = 1 min 16 s, maximum = 1 min 44 s). Oviposition could take several minutes longer, however, if a pair moved to two or three different sites, as sometimes happened even in the absence of any apparent disturbance. In addition, sometimes pairs interrupted a dipping bout to perch on the shore, then resumed oviposition several minutes later, usually near the same location. I attributed perching bouts to (male) fatigue, as contact guarding in flight is considered to be energetically expensive (cf. SINGER, 1987).

When I captured 26 females during oviposition, they continued to extrude eggs freely. In the absence of dipping movements, the eggs adhered to the tip of the abdomen, often forming a clump of 20 or more. If the female was then dipped by hand into a vial of pond water, the clumped eggs separated and fell to the bottom, to which they adhered. Eggs of hand-dipped females also became attached to mud and associated vegetation. Thus, under natural conditions, tandem oviposition probably deposited eggs both in the water and onto the substrates contacted by the

female's abdomen.

Although unpaired males sometimes approached or hovered near ovipositing pairs, they rarely attempted to seize the female. Occasionally lone males contacted females briefly, and once a tandem separated and left the pond when a male clashed with it. However, during 1992-95 I saw no other pair separations due to male harassment, and no takeovers and re-matings of ovipositing females. Generally, tandem pairs showed little response to the approach of a male, scarcely breaking stride as they continued dipping; sometimes they moved a short distance down the bank or left the pond briefly. *S. internum* males also flew at *S. vicinum* pairs, usually with little apparent response, although once a pair separated after the approach of a male aeshnid (*Aeshna* sp.).

Guarding in tandem probably involves predation risks, since dragonflies at the water surface may be captured by frogs, fish, aquatic insects, or other predators (e.g. SHERMAN, 1983; MICHIELS & DHONDT, 1990; CONVEY, 1992). Approaches by bullfrogs (*Rana catesbeiana*) often prompted *S. vicinum* pairs to change oviposition sites, although tandems apparently could not detect motionless frogs and sometimes dipped only 5-10 cm away from them. Many pairs also returned to sites from which they were recently frightened away by a frog, despite the continued presence of the predator. I did not systematically record predation; however, during 1992-95 I observed only three successful captures of ovipositing dragonflies, all by bullfrogs.

Tandem oviposition continued for the duration of egg-laying. When I captured seven females immediately after pair separation and hand-dipped them for 30 s, they released no further eggs. It was the female who seemed to break the tandem connection at the end of oviposition, abruptly twisting free from her partner's grasp. In one case, a female was observed after an unusually long (12 min 20 s) copulation, followed by 10 min of perching in tandem. While she perched, eggs streamed from her abdomen and clumped together in a conspicuous mass. When the pair then began dipping, oviposition lasted only 10-15 s, presumably long enough to dislodge the egg mass, after which the female twisted free. On one occasion a pair separated prematurely when the female's abdomen became stuck in wet mud and the male was unable to continue dipping motions. The female subsequently flew away. *S. vicinum* females were never seen ovipositing alone.

When partners detached after oviposition, the female perched briefly, then left the pond. Many females rose slowly and vertically upward from their perch sites to heights of 4-5 m, after which they flew rapidly away. Such flight behaviour was never performed by males or by pairs, and it may have rendered females less conspicuous as they left the pond. If detected and chased by lone males, females responded by dropping quickly down into vegetation, or by flying rapidly and erratically, often to perches high in trees.

SIGNIFICANCE OF CONTACT GUARDING IN *S. VICINUM*

Compared to non-contact guarding, contact guarding offers a male greater security against takeovers of the female, and thus possible sperm displacement, by rivals (UEDA, 1979; WAAGE, 1984). However, remaining in tandem prevents the male from clasping other females during the guarding period and may also hinder or preclude territorial defense (ALCOCK, 1979a; SHERMAN, 1983; WAAGE, 1984). In this context, the prominence of contact-guarding in *S. vicinum* is interpretable in light of other aspects of the mating system. Pairing occurred away from the water, after which males brought females to potential oviposition sites. Thus males did not maintain territories at the pond, and guarders were unlikely to encounter other receptive females while with a current mate. In addition, since tandem guarding eliminates the need for mate recognition (ALCOCK 1979a, 1979b), it should be adaptive where many pairs oviposit simultaneously within a small area, as was often the case for *S. vicinum*.

Guarders never abandoned their mates during oviposition or switched from contact to non-contact guarding. This was true despite the frequent absence of interference from unpaired males. Thus, *S. vicinum* differs from some other libellulids in which the occurrence or duration of contact guarding is related to the frequency of male harassment, and thus the likelihood of female takeover. For example, in *S. parvulum*, territorial males perform contact-guarding, but "wandering" males contact-guard when there is a high density of rival males and non-contact guard at lower densities (UEDA, 1979). In *S. sanguineum*, contact guarding persists when there is a high degree of male interference early during an oviposition bout; otherwise males switch to non-contact guarding (CONVEY, 1989; see also MARTENS, 1991).

Why do *S. vicinum* males remain in tandem throughout oviposition? Although unpaired males were not abundant near oviposition sites, they were sexually receptive and quickly left their perches to pursue females released after oviposition. Thus, guarders that broke the tandem connection prematurely may still have risked sperm displacement if their partners re-mated. In this respect it will be important to observe *S. vicinum* under high-density conditions, as the frequency of harassment by lone males may be higher in other populations than I recorded here.

Nonetheless, a more important factor underlying persistent contact guarding in this species may be a low probability of individual males acquiring multiple matings. If receptive females are scarce or spatially unpredictable, then males may be selected to invest heavily in their current mate because searching for others that day may yield low reproductive returns or even prove fruitless (ALCOCK, 1979a). Strong mate investment is the case, for example, in dense populations of *S. depressiusculum*; here, males face intense competition for females and stay in tandem not only during oviposition, but also for as long as several hours prior to mating (MILLER et al., 1984). Whether a prolonged pre-copulatory tandem phase

exists for *S. vicinum* is not yet known. Further studies are needed to clarify mate-searching, female availability, and pair formation in this species in the broader context of its postcopulatory behaviour.

ACKNOWLEDGEMENT

I am very grateful to ROBERT ARNOLD for assistance with field work during periods of peak activity, and for helpful comments on the manuscript.

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