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SHORT COMMUNICATIONS

THE MATING SYSTEM OF *LIBELLULA SATURATA* UHLER (ANISOPTERA: LIBELLULIDAE)

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Males of *L. saturata* either patrol long stretches of stream in search of mates, or perch near stagnant pools used as oviposition sites. Perched males respond to patrolling males by flying with them in ascending flights along the stream. Only one male eventually returns to the perch site. Perching males rarely defend the same location from day to day. Ovipositing females are often receptive, and after a brief aerial mating, males employ non-contact guarding. Females, however, apparently eventually lose their guarding partners, because they are rarely seen ovipositing with a male in attendance except briefly, shortly after copulation.

INTRODUCTION

The mate-locating tactics of male dragonflies in the genus *Libellula* have been described for a small number of species, including *L. julia, L. pulchella,* and *L. luctuosa.* Males of all three species have been observed defending fairly large territories at ponds (CAMPANELLA, 1974; PEZALIA, 1979; HILTON, 1983; MOORE, 1987). As is typical for territorial odonates, males defend oviposition locations that attract receptive, gravid females.

To date, no account exists on the behavior of *L. saturata,* a species that occurs in low density at streams in the Chiricahua Mountains of southeastern Arizona. Over three summers, I have accumulated notes on this species that permit me to sketch its mating system, which I do here to provide material that may ultimately facilitate comparative analyses of dragonfly mating systems.

STUDY AREA AND METHODS

The dragonfly was observed at the middle fork of Cave Creek, a permanent stream in the

Chiricahua Mountains, Cochise County, Arizona. In the course of extensive studies of another dragonfly, *Paltothemis lineatipes* (ALCOCK, 1987), I observed *L. saturata* between 15 to 22 June 1985. In 1987 from 18 June to 9 July, and in 1988 from 4 to 26 June, additional notes were taken on the times at which males and females were seen traveling along the stream and on the nature of their activities (especially, male-male interactions and female oviposition). In both years, a small number of males were captured while they perched along the stream and given distinctive marks with Liquid Paper Typewriting Correction Fluid on their wings.

MALE-FEMALE INTERACTIONS

In the middle fork of Cave Creek, neither males nor females were abundant (Tab. I). Males generally first appeared on the stream some time after 0830 M.S.T. These infrequent "transient" males were almost certainly patrolling the stream for the still less numerous "transient" females, which were moving from one oviposition site to the next. Patrolling males were most frequently seen in the late morning (Tab. I). Females were not only sighted much less often but their visits to the stream were distributed more evenly during the period from 0900 to 1230 (Tab. I). Although only sporadic observations were made on the stream after 1300, the dragonflies were occasionally seen as late as 1500, although in the afternoon males were generally perched and exhibited little or no flight activity.

The first perching males were usually seen by mid-morning when a male would rest on vegetation near a small pool created behind a dam on Cave Creek. This individual would change perches occasionally and travel out along the stream before turning back to resume perching.

Table I
The frequency per hour of different behavioral categories of individuals of *L. saturata*

Period	Total hr observation	Transient females	Transient males	Chasing males	Ovipositing females	Copulating pairs
0800-0859	15.5	0	0.65	0	0	0
0900-0959	25.0	0.24	1.16	0.08	0	0
1000-1059	25.0	0.28	2.12	0.68	0.24	0.04
1100-1159	17.5	0.17	1.26	0.40	0.32	0.12
1200-1259	7.0	0.29	0.00	0.00	0.14	0
Total	*90.0*	*0.20*	*1.27*			

Both perched males and those patrolling the stream apparently were attempting to locate mates, because when they encounted an ovipositing female they were quick to pursue her. Receptive females flew up a short distance from the water, were grasped in mid-air by the male with a brief (< 10s) copulation following ($N = 5$; another four matings were first observed when the copulation had already begun). After sperm transfer, the male released the female but

remained near her for between 45 to 90 sec in the six cases in which the pair remained in view for a few minutes. The female eventually left the male by flying into the riparian woodland or the pair was lost to view when the male went with the female along the stream, the female ovipositing in several locations as she travelled away from the copulation site. The five matings observed in 1985 occurred between 1012 and 1158, and the same pattern persisted in 1987 and 1988 (Tab. I).

Fifteen (45%) of 33 unaccompanied females seen moving along the stream in 1987 and 1988 were observed ovipositing, which they did by forcefully flipping the abdomen tip into the water surface while hovering. Females only oviposited at the edge of still pools in the stream, particularly those with ample decayed plant material lying on the bottom of the stream. Only one female whose mating was not seen had a guarding male with her when she came into view. I conclude that gravid females generally oviposit for some time over a wide area, with the result that they usually lose contact with the male that mated with them originally.

MALE-MALE INTERACTIONS

Males were sometimes seen flying with a "companion" male in a generally straight, slightly ascending line that took the pair directly up- or downstream. The two individuals were usually side by side and only a few cm apart, although one male might trail the other by a short distance. The two rivals covered dozens of meters in one direction before turning to retrace the route they had just traversed.

The side-by-side flight appeared to occur when one male met another, particularly when a male perched by the pool behind the dam detected an incoming male. Invariably only one individual would return eventually to perch again by the pool after flights that could last as long as 5 min. In six occasions when a marked male had been perching by the pool and flew off with an unmarked intruder, the previous resident "won" three times, and the intruder returned to perch by the pool alone the three other times.

The side-by-side flights appeared to establish which individual would have sole access to a perching location or stretch between near a site especially suitable for oviposition by females. But males were not site tenacious, because only 4 of 14 males that were marked while perching by the pool ever returned in 1988. (In 1985 one male did return every day between 16-22 June for periods that ranged from a little over an hour to nearly 6 hr, but this male was the exception to the rule). Of those marked males seen again in 1988, one came back on the same day and remained for over 90 minutes by the pool. Three others came back one or two days after marking and remained for periods ranging from 34 min to 144 min.

DISCUSSION

The mate-location behavior of males of *L. saturata* is interpretable in light of the behavior of females, which are often receptive during the time they are searching for oviposition sites. Gravid females are scarce and they apparently traval considerable distances along the stream, ovipositing in a variety of locations without a guarding male in attendance. The low density of males means that not all possible oviposition sites are kept under continuous surveillance, enabling some males to secure mates by patrolling long stretches of stream. This pattern is common for riverine and stream dwelling dragonflies, particularly those that occur in low densities and whose females generally oviposit alone (WAAGE, 1984; POETHKE & KAISER, 1987).

As the morning progresses, some individuals begin to wait at and before what may be particularly good egg-laying spots likely to attract incoming females. The prime oviposition sites are large stagnant pools, and these can be easily identified by males. Perching males sit by pools and apparently attempt to repel intruders via ritualized flights while they wait for a female to appear.

The differences between male behavior in *L. saturata* and that of the territorial libellulid *Paltothemis lineatipes* that occupies the same stream habitat (ALCOCK, 1987) match the expectations of the model of POETHKE & KAISER (1987). Females of *P. lineatipes* lay an entire clutch of eggs in a few minutes at one small oviposition site, suitable sites are moderately scarce, and conspecific males are moderately abundant. As a result, males fiercely defend all oviposition sites, appearing to invest far more in aggressive interactions than do males of *L. saturata.* Males of *P. lineatipes* are able to guard their mates with considerable effectiveness given the localized and brief oviposition bout.

In contrast, females of *L. saturata* are evidently more difficult to guard, given the longer period of oviposition which may occur in many widely separated locations. Because females often oviposit alone in more than one location and because conspecific males are relatively scarce, it is possible for a wide ranging, patrolling male to encounter accessible, receptive females, whereas this option is closed to males of *P. lineatipes.*

SITE TENACITY

Another striking difference between the two libellulids on Cave Creek is the high site tenacity of *P. lineatipes* and the very low probability that a male of *L. saturata* would return to the same perching location from day to day. One untested hypothesis for the difference is that very low frequency of encounters between males and females of *L. saturata* at all locations means that most perching and patrolling sites are essentially equal in value, and therefore little is to be gained by returning to precisely the same place day after day.

An alternative possibility is that males of most (or all) *Libellula* lack site tenacity as a result of phylogenetic inertia. Males of the three previously studied members of the genus are reported to return only rarely after marking (*L. julia,* HILTON, 1983) or to be site faithful for only one day as a rule (*L. pulchella,* PEZALLA, 1979; *L. luctuosa,* CAMPANELLA, 1975; MOORE 1987). Given that all three pond species reach moderate densities and males defend odonate territories, one might expect males of these species to return on consecutive days to the same site. They do not, suggesting that for some reason members of the genus are locked into a pattern in which some individuals may exhibit territoriality but do not return day after day to the same location in the manner of many other odonates. The differences among odonates in the degree of site tenacity is a problem worth additional investigation.

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REFERENCES

ALCOCK, J., 1987. Male reproductive tactics in the libellulid dragonfly Paltothemis lineatipes: Temporal partitioning of territories. *Behaviour* 103: 157-173.

CAMPANELLA, P.J., 1975. The evolution of mating systems in temperate zone dragonflies (Odonata: Anisoptera) II: Libellula luctuosa (Burmeister). *Behaviour* 54: 278-310.

HILTON, D.F.J., 1983. Territoriality in Libellula julia Uhler (Anisoptera: Libellulidae). *Odonatologica* 12: 115-124.

MOORE, A.J., 1987. The behavioral ecology of Libellula luctuosa (Burmeister) (Anisoptera: Libellulidae): I. Temporal changes in the population density and the effects on male territorial behavior. *Ethology* 75: 246-254.

PEZALIA, V.M., 1979. Behavioral ecology of the dragonfly Libellula pulchella Drury (Odonata: Anisoptera). *Am. Midl. Nat.* 102: 1-22.

POETHKE, H.J. & H. KAISER, 1987. The territoriality threshold: a model for mutual avoidance in dragonfly mating systems. *Behav. Ecol. Sociobiol.* 20: 11-20.

WAAGE, J.K., 1984. Sperm competition and the evolution of odonate mating systems. *In:* R.L. Smith, [Ed.], Sperm competition and the evolution of animal mating systems, pp. 251-290. Academic Press, New York.