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# TERRITORIALITY IN THE DRAGONFLY *LIBELLULA SATURATA* UHLER: MUTUAL AVOIDANCE OR RESOURCE DEFENSE? (ANISOPTERA: LIBELLULIDAE)

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2 models of territoriality were compared in an observational study. The "mutual avoidance" model predicts that males should become more territorial as densities increase. The "resource monopolization" model proposes the opposite. Because some males were territorial throughout the season, even at low densities, the mutual avoidance model was rejected and the resource monopolization was supported. However, another prediction of the resource monopolization model is that if females are easily defended in space, then males benefit by being territorial. This prediction was not met. Mate-encounter points were randomly distributed. Thus it appears difficult for males to monopolize females, and yet some males were territorial throughout the season for reasons that remain to be identified.

## INTRODUCTION

Although territoriality is generally interpreted as a behavior that functions to maximize a male's contact with receptive females, just how this maximization might be achieved is debated. Traditionally, behavioral ecologists have proposed that territorial males benefit by monopolizing copulations, which they sometimes may be able to do by monopolizing resources used by females (BROWN & ORIANS, 1970; THORNHILL & ALCOCK, 1983). I will refer to this model of territoriality as the "resource monopolization" model.

However, in some aggressive species, territoriality may benefit males in another way: by decreasing the number of costly interactions among males (POETHKE

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& KAISER, 1987). According to this model, territoriality facilitates mutual avoidance. In the "mutual avoidance" model, males that defend a particular space potentially reduce their energetic costs compared to wide-ranging nonterritorial males. Reducing energetic costs may be very important in species that operate at the extreme range of their energetic capabilities. Energy that would otherwise be used in interacting with other males can then be spent on other activities, such as mate-locating, that increase fitness more directly.

These two models of territoriality yield different predictions about how the density of conspecific males will affect the costs and benefits of territoriality. If territoriality maximizes fitness by decreasing costly interactions while at the mating site, then the benefits of territorial behavior should increase with increasing male density. Thus, the higher the density of males, the more likely it is that males should be territorial. As more males become territorial in response to increased densities, interaction rates between males should either remain constant or decrease.

If, however, territoriality maximizes fitness by allowing for the monopolization of a resource that females use, then the costs of territorial defense should increase with increased male density because of the greater number of intrusions per territory. Therefore, at higher male densities, territorial behavior should decrease, and interaction rates between males should remain constant or even fall because of decreased attempts at site defense. In addition, this model of territoriality also predicts that males will engage in territorial behavior when either females or the resources they use are easily monopolized. This will occur, for example, when the resources are clumped spatially. In contrast, resource distribution should not influence territoriality if minimizing male-male interactions drives the behavior.

I tested the predictions of these two models of territoriality in an observational study of the dragonfly, *Libellula saturata* Uhler. *L. saturata* is a large (80-90 mm) temperate zone dragonfly found mostly in the southwestern United States. One brief study (ALCOCK, 1989) and a preliminary study (DeBano, unpubl.) indicated that *L. saturata* was an appropriate subject to test these hypotheses for three reasons: males are extremely aggressive; population densities vary throughout the season; and males, at least occasionally, engage in territorial behavior. Territoriality will be defined as the defense of a fixed area and the exclusion of conspecifics from that area (KAUFMAN, 1983). This paper presents the results of tests designed to distinguish between the two hypotheses. I also describe the mating system of *L. saturata* more fully than previous studies (HEINRICH & CASEY, 1978; ALCOCK, 1989).

## MATERIAL AND METHODS

The study was conducted from 27 April to 13 November 1991 at Sycamore Creek, a small perennial stream located about 90 km northeast of Phoenix, Arizona, U.S.A. The study site included a 48 m stretch of the stream that covered sandy, rocky, and vegetated areas. This stretch of stream was selected because the density of dragonflies was higher there than in surrounding areas. Because the entire stream stretch could not be observed simultaneously by one person, only a third of the 48 m stretch was observed at one time. Each of the three observed sections of the stream was of equal length (16 m), and will hereafter be referred to as Section A, Section B, and Section C (Fig. 1). All sections included pools as well as runs and riffles, although the sections differ in the relative amounts of each type of water they contained. Streamside areas varied from bare sandy beaches to vegetation-covered, gently sloping banks.

In addition to the stream, observations were made at two large pools adjacent to the 48 m stretch (Fig. 1). Each pool was about 16 m long and 3 m wide. These pools, herafter referred to as Pool A and Pool C, were located off the main flow of the stream. Pool A was near Section A of the stream; Pool C, near Section C. The physical features of the pools were very similar to the adjacent stream areas. Behavior at the pools did not appear to differ from behavior at the stream; males were territorial in both places, and females copulated and oviposited in both places.

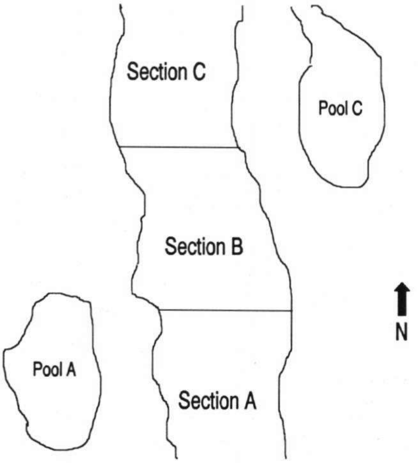

Fig. 1. Map of the study site showing three sections and two pools.

Because behavior did not appear to differ between the main stream and the pools, observations of territorial males were made at the pools, and data on oviposition and copulation were along the main stream. Female activity was measured along the stream because data on spatial distribution were more easily measured in this area, and female activity began at the same time in the pools and stream sections. Territorial behavior was measured at the pools because males consistently occupied these areas, even early in the season, when Sections A, B, and C held few or no territorial males.

In order to follow individual males, I either marked males after they were netted, or marked them without capture. To mark males without capture, I approached males quietly from behind, and used a long stick with marking fluid on the end to dab them on the wings. This method was quite effective, and caused minimal disturbance to the animal. Males were marked throughout the study on days when no data were to be collected or in the afternoon after observations for the day were over. With both methods, a male's wings were marked with unique combinations of colors and shapes using Liquid Paper Typewriter Correction Fluid or enamel paints. Two females and 135 males were marked between 27 April and 26 Ocotober. One male died because of handling associated with capture and marking; all other males appeared to be unaffected by the marking procedure.

I measured male territoriality by observing focal males at Pools A and C on 42 irregularly spaced days from 22 May to 12 November. Males were observed for 20 min periods, alternating between the two pools every hour from 800 to 1600. Whenever possible, marked males were observed as focal males. Otherwise, observations were made on unmarked males. I recorded duration of all flights, outcomes of all flights, identity of all marked individuals involved, location of perches, and any copulations or mate-guarding by focal males. Male densities were measured by taking a census of all males at the study site each hour from 800 to 1600 on each day of the study, before observations on territorial males were made.

I gathered data on the distribution of copulations (a measure of receptive females), and ovipositions (a measure of female-used resources), by observing one of the three sections for 20 min every hour from 800 to 1600 on each day of the study. Observations were made so that each section was observed equally. During the 20 min observation periods, the location within each section of every copulation and oviposition bout was recorded on a map. The map of each section was divided into 8 sectors, each representing a 2 m length of the stream. The distribution of sites of copulations and ovipositions were compared to a Poisson distribution using a G-test to see if they differed significantly from random. Coefficients of dispersion (C.D.) are given for those distributions that differed significantly from a Poisson distribution. A C.D. greater than 1 indicates a clumped distribution and a C.D. less than 1 indicates a uniform distribution (SOKAL & ROHLF, 1981).

Means in the text are reported ± one standard deviation and error bars in figures show 95% confidence intervals. All correlation coefficients are Pearson's product-moment correlation coefficients and were calculated using the SPSS statistical package.

## RESULTS

### MATING BEHAVIOR

All females observed at the creek (n=188 observations), except one, were either ovipositing or copulating. The exception, a marked female, returned on 5 sampling days, each time perching inconspicuously in the brush near Pool C for at least 20 min and for as long as 3 hours. All other females, after arriving at the creek, generally flew low to the water and oviposited by dipping their abdomens in the water while flying. Although many females began to oviposit before approached by a male, only a few females oviposited and left the site without being detected by a male. The failure to detect females most often occurred in the late afternoon, when ovipositing activity peaked, but male densities were low (Fig. 2). After a male detected a female, he always attempted to copulate with her and was generally successful (n=148 copulations), although females occasionally rejected males, even when grasped by the male (n<5).

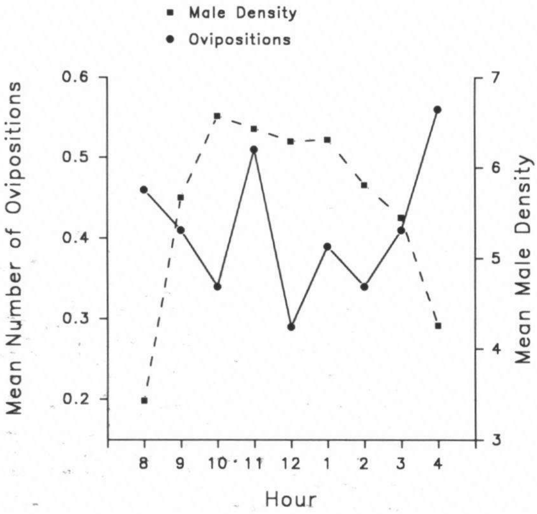

Fig. 2. Mean number of ovipositions and mean male density for each hour of the day. Each point is an average of 41 days of observation.

If a female was receptive, the male grasped her and immediately assumed the wheel position. Copulations were completed in the air and lasted on average

9.1±2.02 s (n=148). When released, the female attempted to oviposit while the male hovered nearby, guarding her. Forty-three percent of these ovipositions (n=71) ended when other males harassed the pair so much that the female was driven away. The average time a female oviposited in the observer's view by dipping her abdomen repeatedly (average oviposition duration) was less than a minute (57.6±56.03 s, n=188). With four exceptions, a male attempted to guard the female during the entire observed oviposition. However, the total duration of all oviposition bouts is probably much longer than that recorded since I could only measure oviposition duration while the female remained in view. Oviposition may have continued elsewhere after the female flew from the study site.

## TERRITORIALITY

*L. saturata* males were territorial under some circumstances. While at the creek, males either perched on nearby vegetation, or flew over the water. Two types of flights were observed: patrol flights and interaction flights. If a male made a brief flight away from and then back to the same or a nearby perch, without encountering and interacting with another male, I counted that flight as a patrol. These flights were typically horizontal, slow-moving flights, and were usually confined to a male's territory or, in the case of nonterritorial males, to a nearby area. The typical duration of these flights was 16.8±30.96 s (n=3191). Any patrol flight that ended with an encounter with another male, or any flight that was initiated by another male was considered an interaction flight. These flights were almost always of a back and forth horizontal pattern, often over the same general area, with one male chasing the other. The average duration of these flights was 37.3±43.24 s (n=1288)

Table I

Territorial males present throughout the study. – [Only males that were observed 80 min or more are listed]

| Month | Individual | Total time observed (in min) | Number of interactions | Wins | Precent wins |
|---|---|---|---|---|---|
| May | #5 | 520 | 26 | 26 | 100 |
| June | #19 | 80 | 4 | 4 | 100 |
| July | #35 | 220 | 18 | 18 | 100 |
| August | #39 | 180 | 32 | 27 | 84 |
| August | #33 | 100 | 7 | 7 | 100 |
| August | #53 | 220 | 90 | 87 | 97 |
| August | #74 | 80 | 50 | 47 | 94 |
| September | #79 | 80 | 29 | 29 | 100 |
| September | #95 | 80 | 36 | 30 | 83 |
| October | #99 | 200 | 56 | 52 | 93 |

To document territoriality I measured the frequency that resident males were displaced after interacting flights. A total of 27 marked resident males were observed at Pools A and C. They were involved in a total of 408 interactions, 91% of which were won by the resident. The outcomes of interactions involving marked males observed for more than 80 minutes are shown in Table I. These data support the contention that some males were able to monopolize a perch and patrolling area through defense of the site.

Another indication of territoriality was the strong site tenacity exhibited by some males. Overall site tenacity was measured by recording the total number of sites occupied by marked males during hourly censuses in a month and dividing this figure by the number of census hours in that month for each section and pool (Tab. II). The mean number of census hours that resighted males were seen in the entire season was 5±8.1 hrs.

Table II

Measures of site tenacity. – ["Total census hours resighted" is the total number of times males were resighted in any of the 3 sections or 2 pools during the month]

| Month | Number of times ♂ was resighted | | | Total census hrs resighted | Total resighted/total census hrs possible | No. ♂♂ marked in month |
|---|---|---|---|---|---|---|
| | 1-5 | 6-10 | > 10 | | | |
| May | 6 | 1 | 1 | 71 | 71/225<br>(0.32) | 17 |
| June | 4 | 2 | 1 | 44 | 44/225<br>(0.20) | 6 |
| July | 6 | 0 | 1 | 40 | 40/315<br>(0.13) | 28 |
| August | 9 | 2 | 3 | 94 | 94/450<br>(0.21) | 30 |
| Sept | 12 | 1 | 2 | 61 | 61/315<br>(0.19) | 22 |
| October | 10 | 2 | 1 | 64 | 64/315<br>(0.20) | 19 |
| Nov | 2 | 0 | 0 | 2 | 2/135<br>(0.01) | 0 |

## MALE DENSITY AND TERRITORIALITY

Data on variation in male density and territoriality were needed to distinguish between the two models of territoriality. As expected, male density of *L. saturata* at Sycamore Creek varied throughout the season (Fig. 3A). The highest daily mean male density over the entire study site was 10.7±2.73 males per hour. The lowest daily mean density was 1.2±1.30 males per hour. The mean hourly density per month increased significantly (as shown by 95% confidence intervals) from

July to August, and from August to September, and then decreased significantly from October to November.

The tendency for males to be territorial was measured by the likelihood that marked males remained on a territory for the entire 20 min observation period. Males that remained at the pool for the full 20 min were considered "territorial residents". As male density increased, the proportion of territorial residents decreased. The highest percentage of resident males occurred in May, a month of low male density (Fig. 3B). The lowest proportion of resident males occurred in September, the month with the highest densities. A negative correlation exists between the proportion of territorial males each day and the mean male density per hour (r=-0.15; p=0.17; n=42), although this correlation is not significant. However, I repeated the analysis excluding the last 3 days of data, when males behaved atypically, wandering widely and engaging in very little aggressive or territorial behavior. Under the condition of this post-hoc test, the negative correlation becomes significant (r=-0.34; p=0.02; n=39). This correlation cannot be explained simply in terms of the number of males marked in the month; no statistically significant correlation exists between the number of males marked in a month and the proportion of territorial males observed (r=0.20; p=0.10; n=42).

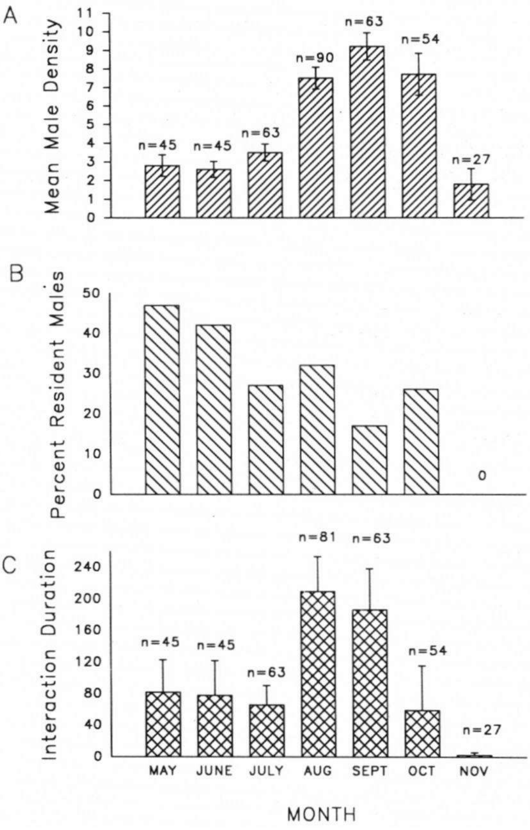

Fig. 3. (A) Mean hourly male density of the study site per month; — (B) Percent 20 min observation periods each month with resident marked males present; — (C) Mean total interaction time in seconds for each 20 min observation on focal males. — [The number of 20 min observation blocks per month is indicated by n].

The models also predicted the effect of increasing male density on interaction rates. Interaction rates followed the same trend as male densities (Fig. 3A and 3C). Mean interaction time (the average total time males spent interacting per 20 min) increased significantly in August and decreased significantly in October, even though mean male densities did not decrease significantly until November. Mean interaction duration is correlated with mean hourly density (r=0.80; p<0.001; n=41).

## THE DISTRIBUTION OF FEMALES AND OVIPOSITION SITES

One prediction of the resource monopolization model was that females or their resources would be spatially clumped and therefore economically defendable. In fact, the distribution of ovipositions suggests that females are non-random in their selection of oviposition sites. Most of the 273 oviposition bouts occurred in only a few sectors (Fig. 4B). Oviposition distribution was significantly clumped (C.D.=5.91), differing from a random (Poisson) distribution (G=22.0; df=3; p<0.05). However, copulations were not clumped (Fig. 4A), and did not differ significantly from a Poisson distribution (G=6.82; df=3; p<0.05). Nevertheless, there was a significant positive correlation between copulations and oviposition bouts in each sector (r=0.72; p<0.001; n=24). Even though ovipositions were clumped in space and copulations were randomly distributed, the significant correlation between ovipositions and copulations is not surprising because most females oviposited at least briefly in the same section where they copulated. To search for a possible seasonal pattern in the distribution of oviposition or copulation sites, every 6 days of oviposition and copulation

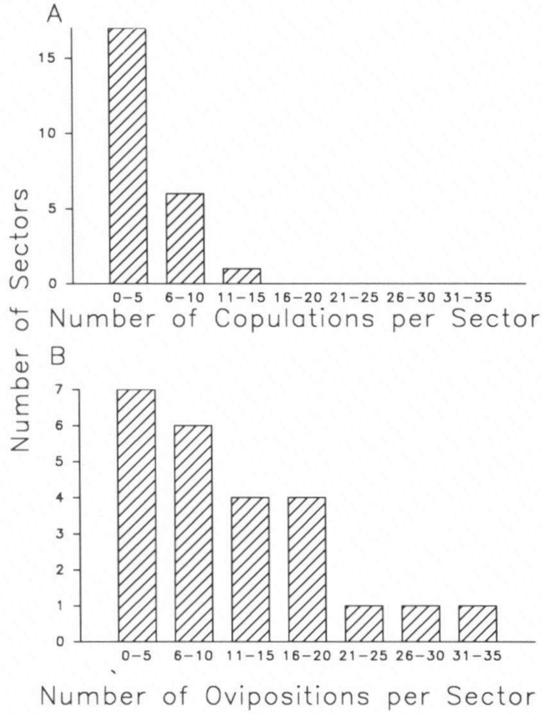

Fig. 4. Number of copulations (A) and ovipositions (B) in each of the 24 sectors of the stream throughout the 42 days of the season.

data were combined and the resulting distribution was compared to a randomly distributed pattern of ovipositions and copulations. Six day intervals were used in order to have an equal number of observations at each section and this division approximated a monthly schedule most closely. Ovipositions were spatially clumped until 21 September 1991 after which the distribution of ovipositions became random (Tab. III). Copulation distributions alternated between random and clumped throughout the season (Tab. III).

Table III

Changes in the distribution of ovipositions and copulations through the season. Each distribution is the result of six days of observation and was compared to a Poisson distribution with a G-test goodness of fit test. – [Coefficients of dispersion are listed for those distributions that differed significantly from a Poisson distribution]

| Time | Ovipositions | G statistic | Copulations | G statistic |
|---|---|---|---|---|
| 5-21-91 to 6-7-91 | None | NA | None | NA |
| 6-8-91 to 7-13-91 | Insufficient data | NA | None | NA |
| 7-21-91 to 8-3-91 | Clumped<br>C.D.=3.29 | G=15.42;<br>df=3;<br>P<0.05 | Random | G=0.24;<br>df=1;<br>P>0.05 |
| 8-4-91 to 8-23-91 | Clumped<br>C.D.=3.62 | G=14.84;<br>df=3;<br>P<0.05- | Clumped<br>C.D.=1.378 | G=4.08;<br>df=1<br>P<0.05 |
| 8-29-91 to 9-15-91 | Clumped<br>C.D.=2.09 | G-10.86;<br>df=3;<br>P<0.05 | Random | G=0.95;<br>df=2;<br>P>0.05 |
| 29-91 to 10-15-91 | Random | G=6.94;<br>df=4;<br>P>0.05 | Clumped<br>C.D.=2.12 | G=10.34;<br>df=1;<br>P<0.05 |
| 10-21-91 to 11-11-91 | Random | G=4.70;<br>df=2;<br>P>0.05 | Random | G=1.24;<br>df=1;<br>P>0.05 |

## DISCUSSION

The two models of territoriality discussed here are based on the premise that males should defend territories if the benefits of the behavior outweigh its costs. However, the models propose different costs and benefits for male territoriality. The mutual avoidance model emphasizes the benefits to males of avoiding costly interactions with rivals. The population at Sycamore Creek seems to have met the three key conditions of the model: males were aggressive even when nonterritorial, female encounter points were randomly distributed in space, and the probability of an individual male encountering a female remained constant throughout the season because male and female densities were correlated. However, this model of territoriality must be rejected for *L. saturata* because males were most successful at being territorial at low male densities. As densities increased, the proportion of territorial males decreased. These results contrast with other studies that are consistent with the mutual avoidance model's prediction about male density and territoriality (POETHKE & KAISER, 1987). Increased territorial behavior with increasing density has been found in several dragonfly species, including *Cordulia aenea amurensis* Sel. (UBUKATA, 1975), *Nesciothemis nigeriensis* Gambles (PARR, 1983), *Libellula julia* Uhler (HILTON, 1983), and *Aeshna cyanea* (Müll.) (POETHKE & KAISER, 1987).

An alternative explanation for the apparent decrease in the proportion of territorial male with increasing density is that as male numbers increase, available territories do not. This explanation does not prevent the rejection of the mutual avoidance model. Under the mutual avoidance model, there is no reason to expect the number of available territories to be constant, because males should decrease the size of their territories with increasing male density in order to facilitate mutual avoidance.

The resource monopolization model was supported to the extent that males were less likely to defend territories as densities rose through the season. These results are consistent with studies of other dragonflies that show decreased territoriality with increased male density (PAJUNEN, 1962; CONVEY, 1990; MOORE, 1987). Because interaction rates reflect the cost of territoriality, and because interaction rates rose with increasing male densities, it seems likely that some males attempted to be territorial throughout the season, but were unable to control sites for prolonged periods under conditions of intense competition.

However, the fact that the observed decrease in proportions of territorial males may be a result of increased male density in an environment with a fixed number of territories presents some difficulties in testing the resource monopolization model. The inability to determine whether the decrease in proportion of territorial males reflects a general decline in the readiness of males to defend territories prevents a definitive conclusion about whether the resource monopolization model applies to *L. saturata*.

In addition, contrary to the predictions of this model, the spatial distribution of copulations was indistinguishable from random. Why should males attempt to be territorial under these circumstances? One possible explanation is that even though the distribution of copulation sites was random overall, the occasional clumping that occurs during certain parts of the season provides benefits great enough to outweigh the costs of territoriality. In addition, clumped oviposition sites suggest that certain small, potentially defendable sites contain useful resources for females. The distribution of desirable oviposition sites does not change throughout most of the season providing a potential clue for territory defenders, sometimes yielding a reproductive advantage during parts of the flight season.

This study enables us to reject the mutual avoidance hypothesis, but provides only weak support for the resource monopolization hypothesis. *L. saturata* therefore presents a continuing puzzle, especially with regard to male territorial behavior in areas without clumped resources.

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