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Jessica L. Thornton
Eastern Illinois University

Paul V. Switzer
Eastern Illinois University, pvswitzer@eiu.edu

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RESEARCH

Factors Affecting the Spatial Distribution of Oviposition Sites for Tandem Black Saddlebags Dragonflies (Odonata: Libellulidae)

Jessica L. Thornton[1] and Paul V. Switzer[2]

[1]Department of Biological Sciences, Eastern Illinois University, Charleston, IL, U.S.A.
[2]Corresponding author, e-mail: pvswitzer@eiu.edu

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ABSTRACT. Oviposition site location may be affected by (1) factors influencing the costs and benefits to the offspring (e.g., resource availability, competition, predation risk) and (2) factors influencing the costs and benefits to the female (e.g., predation risk or mate harassment). In cases in which both the male and female are involved in locating a site, costs and benefits may differ for each parent and the resulting oviposition site location may represent the outcome of selection pressures on one or both of them. We studied oviposition behavior in the black saddlebags dragonfly (*Tramea lacerata* Hagen), a species in which the male and female typically remain together (i.e., in tandem) while traveling among potential oviposition locations. Oviposition sites tended to be away from pond shoreline at the outer edge of the vegetation on the water's surface. We found that tandems distributed their oviposition locations widely around the pond, and interactions with other dragonflies (typically other *T. lacerata*, either territorial males or tandems) led to a larger distance between consecutive oviposition locations. Interestingly, for 10% of the tandems, the female became separated from the male and oviposited solitarily multiple times. These solitary females spent significantly less time and traveled significantly smaller distances between successive oviposition sites than when in tandem. Our results indicate that while some aspects of oviposition behavior and site selection may be consistent between the male and female (e.g., the characteristics that make a site suitable), other aspects, such as the distribution of sites, may be a result of a differing benefits and costs for the two sexes, perhaps as a consequence of potential sperm competition.

Key Words: dispersion, egg laying, habitat selection, mate-guarding, territoriality

Behavioral decisions made during the selection of oviposition sites may have a strong effect on the fitness of both parents and offspring (Resetarits 1996). Behaviors associated with oviposition site selection are particularly interesting in animals such as odonates (i.e., dragonflies and damselflies), because the terrestrial adults must find optimal sites for the success of their aquatic offspring. Buskirk and Sherman (1985) suggested that a female's choice of oviposition site may be strongly affected by the ecology of their aquatic larvae. Furthermore, individual female odonates may concentrate most of their eggs in one location (e.g., *Perithemis tenera*; Jacobs 1955) or spread them out over a larger area within or among breeding sites (e.g., *Pantela flavescens*; Schenk et al. 2004). This spatial distribution of oviposition sites may relate to egg predation and intraspecific competition among larvae that a species experiences (Buskirk and Sherman 1985), and widely distributed oviposition sites may be a form of bet hedging, whereby the female spreads risk to cope with environmental uncertainty (Buskirk and Sherman 1985, Hopper 1999).

The particular choice of oviposition sites, and the spatial distribution of sites, may also be affected by the interactions a female has with competing individuals (Koch 2006). For some species these interactions are positive, such as the aggregating behavior in ovipositing females of *Sympetrum vicinum* (McMillan 2000) and *Argia moesta* (Byers and Eason 2009). In these species, the presence of conspecific females may indicate a good oviposition site (McMillan 2000). Interactions may also negatively affect a female's oviposition success. For example, during times of high male density, Koch (2006) observed some females adjusting by hovering closer to the water, a change that decreased male harassment but increased their risk of predation. Such male harassment is a consequence of sperm competition (Simmons 2001). Sperm competition exists in many odonates because the last male to copulate with the female prior to oviposition has a higher probability of fertilizing her eggs (Waage 1984, Alcock 1994).

Odonate species with last male advantage often guard their females either by ovipositing in tandem (in physical contact with female), or by accompanying the female without contact (Waage 1984, Corbet 1999, Schenk et al. 2004). Some species participate in both types of mate guarding depending on environmental and social factors (Latty 2006). The type of mate guarding may also relate to the oviposition pattern of the female (Buskirk and Sherman 1985; Schenk et al. 2004). For instance, species that perform tandem oviposition typically have many widely distributed oviposition sites within a limited area (Conrad and Pritchard 1992), whereas noncontact guarding species localize oviposition sites (Schenk et al. 2004). Thus, links may exist between a species' oviposition site choice and its mating system (Buskirk and Sherman 1985, Ware et al. 2012).

Most studies of the spatial distribution among oviposition sites in odonates have focused on species that oviposit in multiple breeding sites (e.g., different ponds; Schenk et al. 2004). Relatively few studies have quantified the distribution of oviposition sites within a breeding site, especially for those species that have tandem oviposition, nor have studies typically investigated how this distribution is affected by interactions with the guarding male or other individuals. In this study, we investigated the oviposition site selection of the black saddlebags dragonfly (*Tramea lacerata* Hagen). *T. lacerata* is a widely distributed migratory species (Needham et al. 2000). The territorial males often patrol large areas along the edges of ponds or lakes, and the females arrive at the breeding site to copulate and oviposit in tandem with a male or, more rarely, to oviposit alone (Dunkle 1989). The oviposition behavior used by most *Tramea* sp. is particularly interesting because tandem formation is interrupted continually during oviposition (Young 1967, Sherman 1983). During tandem oviposition the male guides the female to a site, releases the tandem grip, and the female dips to the surface of the water to release eggs. Following oviposition the male grabs her again and the tandem proceeds to a different location (Sherman 1983, Dunkle 2000). Dunkle (1989) observed that *T. lacerata* tandems occasionally chase other dragonflies while searching for oviposition sites. Oviposition for *T. lacerata* typically occurs in open water or on algae mats (Dunkle 1989), and the larvae are often found among stems of aquatic vegetation or masses of algae (Needham et al. 2000).

Specifically, in this study, we examine the following questions: (1) Do tandems choose particular locations in which to oviposit? (2) Are these locations concentrated or dispersed at the breeding site? (3) Is oviposition site selection affected by interactions with other dragonflies? (4) Does oviposition behavior differ between females ovipositing in tandem and those ovipositing alone? Based on the answers to these questions, we speculate on how oviposition site selection represents an outcome of selection pressures on the offspring, the male, and the female.

Materials and Methods

Study Site. Observations of *T. lacerata* oviposition behavior were made at Carman Pond (39°28′34.52″ N, 88°10′18.31″ W), a small pond on the campus of Eastern Illinois University in Coles County, Illinois, during 20 d in June-August, 2013. Carman pond is "*L*" shaped with a total circumference of ~300 m. The surrounding vegetation was mowed low to the edge of the pond, facilitating observations. Vegetation in the water at the pond's edge consisted primarily of creeping primrose (*Ludwigia peploides*), growing 4-5 m out into the pond from the shoreline, as well as floating mats of green algae. Due to its small size, we were able to view the entire pond from the inside corner of the "*L*," using binoculars to help view the far sides of the pond. If necessary, the observer moved along the shoreline to better observe a tandem. The edge of the pond was marked to facilitate our recording of locations; marks were either placed on existing objects or on surveyor's flags that we placed at the edge every 5 m.

Observations were made between 1000 and 1600 hr on days, when males were active on the pond and females were most likely to copulate and oviposit (Lutz and Pittman 1970, P.V.S., unpublished data). To control for possible effects of temperature on their behavior, we only conducted observations on days above 25°C. All observations were made on unmarked individuals, but previous studies on marked individuals at this and nearby ponds indicate that turnover at a particular location is extremely high for males, with few males returning to the pond on successive days (P.V.S., unpublished data). Thus, although we do not know whether females were observed multiple times, the males of pairs were likely to be different, at least between days.

Observations. For observations, we observed the pond until a male-female tandem was located. The tandem was then followed until it separated and the female left the pond or until its identity became uncertain. Identity uncertainty occurred occasionally when a tandem would interact with more than one additional tandem, which made it difficult to keep track of the focal tandem. We refer to the start through end of an observation on a single tandem as a 'tandem bout'. For each tandem bout, we recorded the time and location of events using a voice recorder. Recorded events included copulation, pause, oviposition, interaction, and end of bout. Copulation was recorded for those tandems in which the initial copulation was observed. Our observations of 'oviposition' for *T. lacerata* matched those cited earlier: the pair pauses over a potential oviposition site (usually about 25 cm above the water), the male lets go of the female and she dips the tip of her abdomen into the surface of the water to deposit eggs. Typically the tandem is then reinstated, with the female rising up from the water and the male dropping lower to resume contact. We used 'pause' to describe when the male and female hovered in tandem for a few seconds, as with oviposition, but the male never released the female and they changed locations without ovipositing. Both ovipositions and pauses are brief (<2 s) in duration, and thus are best represented as events rather than states with a duration. 'Interactions' were defined as the tandem chasing, or being chased by, another dragonfly or tandem. When an interaction occurred, we also recorded the species with which they interacted. Interacting species included *T. lacerata*, *Tramea carolina/Tramea onusta* [combined for our purposes because they are difficult to distinguish in flight (Dunkle 2000) and both species occur at our study pond (P.V.S., unpublished data)]), *Libellula luctuosa*, *Libellula pulchella*, and *Anax junius*. These interactions were also brief, usually lasting no more than a few seconds. We defined the 'end' of a tandem bout as when the female flew up and away from the pond. Any attempted predation events that occurred during a tandem bout were also recorded. An event location was recorded to the nearest 1 m for both its location relative to the perimeter of the pond and how far out into the pond it occurred from edge of the water. For some individuals, we also recorded the distance the perimeter 'vegetation' (i.e., primrose and algal mats) extended from the shore, to allow us to compare the location of the oviposition and pause events relative to vegetation. The vegetation extent wasn't recorded initially for tandems, and thus sample sizes are smaller when we analyze this variable.

To determine density, for most observation days we recorded the number of *T. lacerata* males that were active on the pond once an hour. The density census closest to the tandem observation was then used as its corresponding density. Density measurements were not taken on a few of the observation days, which led to some differences in sample sizes among some comparisons. Temperatures were obtained from a weather station located within 1 km of the study pond. Temperature readings were recorded by the station every 5 min, and for our data we used the reading mostly closely corresponding to the time of a specific tandem observation.

Analysis. Our data consisted of a number of events that occurred sequentially during a tandem bout. For all comparisons that required comparison of single events, we used the second event of the appropriate type (e.g., second oviposition, or second pause) to avoid pseudoreplication within tandems and to avoid any potential bias from using the first event after we initially noticed the tandem. If the second event was unusable for some reason (e.g., it was followed by interaction), we used the next event that met the criteria for the statistical comparison.

In order to examine oviposition site locations relative to vegetation, we needed to account for the fact that vegetation extended out from shore into the pond at different distances for different pond locations. Accordingly, using the second oviposition per tandem, we used a chi-square test to compare the frequency of ovipositions across tandems that occurred within 0–25%, 25–50%, 50–75%, and 75–100% of the vegetation extent at that location, with 0 and 100% corresponding to the shoreline and outer edge of the vegetation, respectively. Ovipositions beyond the vegetation were consolidated into a >100% category. To examine the relative location of a tandem's pause and oviposition sites, we conducted a pair-wise comparison with a tandem between the distance from the shoreline for a tandem's second oviposition event to the distance from shoreline for its second pause event. Because bouts differed in duration, to compare oviposition frequency, we used two relative values: 'oviposition rate' (i.e., the total number of oviposition events that occurred while being observed divided by the total time observed) and 'oviposition percentage' [i.e., 100*the number of oviposition events/(number of oviposition events + number of pause events)]. Distances and latencies between consecutive ovipositions, pauses, with or without interactions, etc. started with the second possible event that met the necessary characteristic (e.g., oviposition event followed by one interaction followed by an oviposition event). When calculating the average distance between consecutive ovipositions for each tandem, we excluded those distances during which they crossed the pond between oviposition sites because the straight-line distance between sites in those instances would not be the same as the distance determined by locations marked on the pond perimeter. Finally, to determine the distance over which an individual tandem spread its eggs, we calculated the distance between a tandem's two oviposition sites that were furthest from each other during a bout, regardless of when the oviposition events occurred relative to each other. We used JMP (v. 9; SAS Institute, Inc.) for statistical comparisons. Comparisons are nonparametric due to nonnormality in the distributions of the data. We report means as ± se.

For notation, we refer to oviposition events as "*O*" and pause events as "*P*". The corresponding measure is given as a subscript. For example, oviposition percentage is notated as "$O_{\%}$" and the latency for a pause event to occur after an oviposition event is notated "$O\text{-}P_{\text{latency}}$."

Results

General Oviposition Behavior. We observed 106 total tandems, with 94 of those remaining as a tandem (i.e., contact guarding; see later) for the entire observation. These 94 tandems were observed for an average of 379.3 ± 21.7 s. Tandem bouts included 10.9 ± 0.78 oviposition events and 8.7 ± 0.64 pause events. For comparison, the three bouts that were known to be complete (i.e., watched from tandem arrival on the pond following copulation to when the female left the pond) lasted an average 555.3 s and included 15.3 oviposition events and 12.7 pause events. Individual tandems had slightly but significantly more oviposition events than pauses within a given bout (median difference = 1 event, range: – 15 to 32 events; Wilcoxon matched pairs, $S = 583$, $P = 0.01$). Most pauses were not simply attempted ovipositions that were disturbed, because only 5% (44/879) of all pauses we observed were associated with an interaction with another dragonfly. Not surprisingly, tandems that paused less often relative to oviposition events (i.e., had a higher $O_{\%}$) tended to have a higher O_{rate} (ovipositions/s; Spearman Correlation, $r_s = 0.74$, $N = 94$, $P < 0.0001$).

Following an oviposition, a tandem took longer before ovipositing again than if the oviposition were following a pause (median difference $O\text{-}O_{\text{latency}}$ minus $P\text{-}O_{\text{latency}} = 9$ s, range: −158 to 58 s, $N = 82$; Wilcoxon $S = 758$, $P = 0.0003$). However, the distance to the next oviposition location is similar following an oviposition and following a pause (median $O\text{-}O_{\text{distance}}$ minus $P\text{-}O_{\text{distance}} = 1$ m, range: −60 to 96 m, $N = 82$; Wilcoxon $S = 206$, $P = 0.29$). Male density on the pond was positively correlated with temperature ($r_s = 0.28$, $N = 73$, $P = 0.01$), but neither temperature nor density was significantly correlated with $O_{\%}$ (density: $r_s = -0.11$, $N = 86$, $P = 0.31$; temperature: $r_s = 0.08$, $N = 81$, $P = 0.45$) or O_{rate} (density: $r_s = -0.06$, $N = 86$, $P = 0.56$; temperature: $r_s = 011$, $N = 81$, $P = 0.35$).

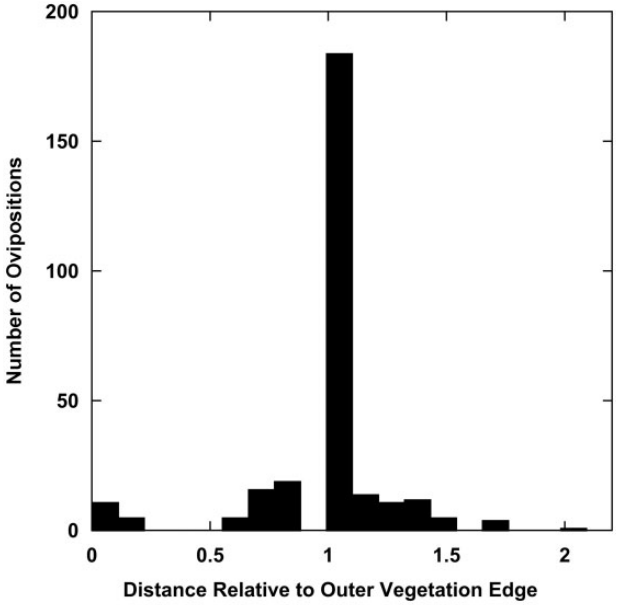

Fig. 1. Distribution of oviposition events relative to the vegetation edge. A value of 0 represents the shoreline, and a value of 1.0 represents the outer edge of the vegetation. Proportions > 1.0 represent ovipositions that occurred in the water beyond this outer edge. Data are from all ovipositions by all tandems for which we had data on the extent of vegetation ($N = 286$ oviposition events).

Oviposition locations averaged 4.0 ± 0.06 m into the pond from the shore edge ($N = 1066$ oviposition events pooled across tandems), with the vegetation extending out into the pond an average of 4.4 ± 0.03 m ($N = 513$) at the oviposition sites. The locations tended to occur toward the outer edge of the vegetation or algae on the surface of the water, with most of the oviposition sites within the last 25% of the vegetation or in the water just beyond the edge of the surface vegetation (Fig. 1, ovipositions within 0-25% vegetation extent: 1/24 tandems, 25-50%: 0/24, 50-75%: 0/24, 75-100%: 16/24, >100%: 7/24, $\chi^2 = 39.8$, df = 3, $P < 0.0001$). Furthermore, a tandem's successful ovipositions were significantly farther out (relative to the vegetation) than their pauses (median difference ovip to pause location = 0 m, range: −0.25 to 1.13 m, Wilcoxon matched pairs, $S = 26$, $P = 0.04$, $N = 22$). Consecutive ovipositions were spread 7.8 ± 0.6 m apart ($N = 91$) along the shoreline (Fig. 2), and as a consequence, a tandem's ovipositions for the entire bout were spread widely around the pond (mean distance between a tandem's furthest oviposition sites = 60.1 ± 4.9 m, range = 1-145 m; $N = 91$). Tandems for which we observed more ovipositions had a larger maximum spread between oviposition sites ($N = 91$, $r_s = 0.52$, $P < 0.0001$).

Predators (primarily largemouth bass, *Macropterus salmoides*) attacked 14 of the 106 total tandems at some point during the bout, and one tandem was attacked twice. Four of the 15 predation attempts were on the female while she was ovipositing, four occurred while the tandem was paused at a site, six were on the tandem as it was flying between locations, and one occurred on the male while he was guarding the ovipositing female (this was the only successful predation we observed).

Solitary versus Tandem Females. During our observations, we never observed a female to only oviposit alone. However, 11/106 (10%) tandems had a period of time in which the female did not return to the male between ovipositions. This typically occurred if the male either began chasing another male during her oviposition or she left the male after she oviposited but before he could grab onto her again. We never observed these solitarily ovipositing females return to the male, but in two cases (18%), they were grabbed by another male and she copulated with him prior to leaving the pond. Density of males on the pond did not differ significantly between bouts in which the pair remained in tandem and those that included some solitary oviposition (median density for solitary = 5 males, range: 4-11 males, $N = 6$; median for tandem = 6 males, range: 3-11 males, $N = 86$; Wilcoxon $S = 229$, $P = 0.43$), although the sample size is small for solitary females for which we had corresponding pond densities.

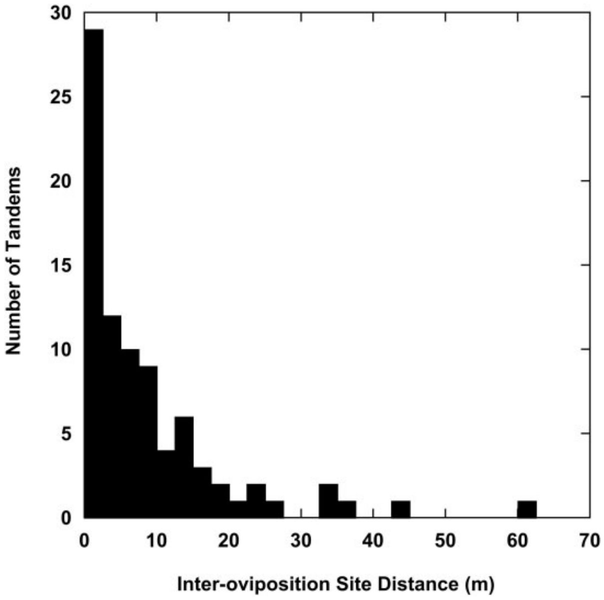

Fig. 2. Distribution of distance between consecutive (second to third) oviposition sites for an individual tandem.

The change in oviposition behavior from tandem to solitary affected the spatial and temporal patterns of oviposition. For instance, when not returning to the male, the female took significantly less time between ovipositions than when returning to the male in tandem (median latency solitary minus tandem = −13 s, range: −32 to −4 s, $N = 9$; Wilcoxon $S = 22.5$, $P = 0.004$), moved a significantly shorter distance (median distance solitary minus tandem = −3 m, range: −68 to 0 m, $N = 9$; Wilcoxon $S = 18$, $P = 0.008$), and had a significantly higher $O_{\%}$ (median solitary minus tandem = 35%, range: 8.3-100%, $N = 11$; Wilcoxon $S = 33.0$, $P = 0.001$) and O_{rate} (median solitary minus tandem = 0.18 events/s, range, 0.08 to 0.35 events/s, $N = 11$; Wilcoxon $S = 33.0$, $P = 0.001$).

Interactions. 102/106 (96%) of the tandems interacted at least once with another dragonfly during the tandem observation, with tandems averaging 5.5 ± 0.4 ($N = 106$) interactions per tandem observation. These interactions typically lasted <5 s and involved either the tandem pair pursuing a nearby dragonfly or a nearby dragonfly pursuing the tandem. Interactions occurred mostly with other black saddlebags; 309/535 (58%) of all interactions (pooled across all tandems) in which the other dragonfly could be identified were with a single black saddlebag male and 13% were with other black saddlebag tandems. Of the remaining interactions, 18% were with a *L. luctuosa* male, 8% were with an *A. junius* male or tandem, 1.5% were with a *L. pulchella* male or tandem, and 1% were with *T. carolina/T. onusta* male or tandem. The frequency at which a tandem had interactions (number of interactions/s) was positively correlated with density, but the pattern was not statistically significant ($r_s = 0.19$, $N = 86$, $P = 0.07$).

These interactions did affect some aspects of a tandem's behavior. For example, interactions seemed to cause a tandem to travel farther between ovipositions; the distance between consecutive ovipositions was greater if the tandem had an interaction between oviposition events rather than just having an oviposition event followed by another oviposition event (Fig. 3; median difference = 3 m, range: −46 to 79 m, $N = 45$, Wilcoxon matched-pairs, $S = 216$, $P = 0.007$). However, we found no significant difference in latency between consecutive oviposition events with and without an intervening interaction (median difference = 3 s, range: −55 to 105 s, $N = 45$, Wilcoxon matched-pairs, $S = 125.5$, $P = 0.13$). Tandems had a smaller average distance between consecutive oviposition sites when the rate of interactions was higher ($r_s = -0.22$, $P = 0.03$, $N = 91$). Those tandems that interacted at a higher rate also had significantly lower $O_{\%}$ ($r_s = -0.20$, $N = 94$, $P = 0.048$) but the negative correlation between interaction rate and O_{rate} was not significant ($r_s = -0.17$, $N = 94$, $P = 0.09$).

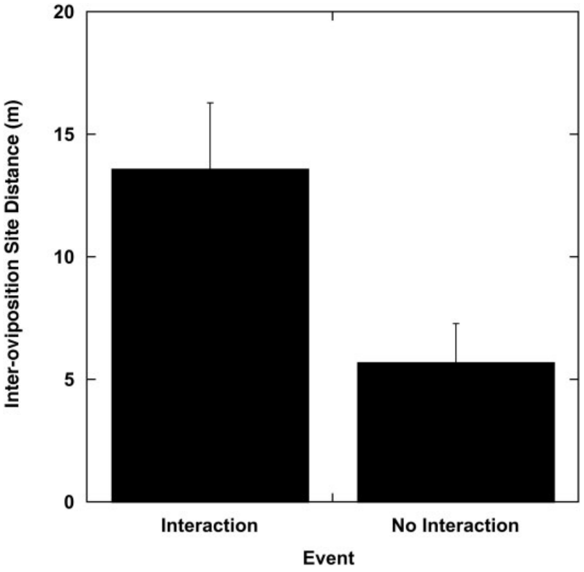

Fig. 3. Average distance (± se) between a tandem's consecutive oviposition sites with and without an interaction (i.e., chase by or chasing another dragonfly or dragonfly tandem) occurring between the oviposition events ($N = 45$ tandems).

Discussion

We found that sequential ovipositions by *T. lacerata* tandems were spread spatially. As such, their behavior matches descriptions of oviposition behavior of some other odonates (e.g., *Sympetrum fonscolombii*; Schenk et al. 2004) as well as some species in other insect taxa (e.g., butterflies; Root and Kareiva 1984). In the case of *T. lacerata*, the ovipositions were spread around a single breeding site (i.e., the pond) during an oviposition bout (e.g., *Hetaerina vulnerata*; Alcock 1982). Furthermore, we found that these locations were dependent on the presence of the male and on interactions with other odonates.

For *T. lacerata* tandems, the spread between oviposition sites around the pond typically seemed to be "voluntary." Most consecutive oviposition site locations were at least a few meters apart, and tandems often continued to move around the pond between ovipositions, resulting in a distribution of eggs over a relatively large area. Spreading out oviposition sites is often suggested to be either a result of selection to avoid the risk of putting all the reproductive output in one location (Hopper 1999), or an attempt to decrease competition among offspring (e.g., Averill and Prokopy 1987). In odonates, spatial risk spreading has been suggested previously for species that oviposit in different ponds (e.g., *P. flavescens*; Schenk et al. 2004), but it might apply to locations within a pond as well. Avoiding competition among offspring is also plausible, especially given the effects of predation and cannibalism among odonate larvae (Crumrine et al. 2008), and the fact that we found that tandem *T. lacerata* frequently chased other tandems supports this idea, although other possible explanations for tandem chases exist (e.g., avoiding harassment while ovipositing).

In contrast to *T. lacerata*, some odonate species lay all of their eggs in one location during their pond visit (e.g., *P. tenera*; Jacobs 1955, Switzer 1997), and others lay them all in a restricted area (e.g., different locations within a male's territory (e.g., *Erythemis simplicicollis*; McVey 1988)). Because it is not immediately apparent how risk and competition would be different for the larvae of these species, other factors besides those affecting larvae may also be involved. One possibility is provided by Buskirk and Sherman (1985), who suggested that spatial distribution among oviposition sites may be correlated with a species' mating system. They found support for the hypothesis that females that oviposit in tandem tend to choose more widely distributed oviposition sites (Buskirk and Sherman 1985, Ware et al. 2012).

Interestingly, our observations of *T. lacerata* suggest that the benefits of spreading ovipositions spatially may not be the same between males and females. When females were no longer reforming a tandem with their male, their oviposition behavior changed: they oviposited more rapidly and moved a shorter distance. Although we don't know whether the total number of eggs released was altered, we do know that the change in a female's oviposition behavior had two primary consequences: she laid multiple batches of eggs in the same confined area and she spent less time on the pond. Similarly, Sherman (1983) found that female *T. carolina*, when ovipositing without a male guarding them, had oviposition bouts of shorter duration than tandem females.

What may differ between males and females that results in this change in behavior? For males, one likely possibility is the threat of sperm competition. Males may leave a location and move about the pond in response to the presence a competing male. We found that following an interaction, tandems moved significantly farther before their next oviposition. The predominant interaction was with single male conspecifics, as Young (1967) noted for tandem *T. onusta*, and thus tandems may be avoiding conspecific males to avoid the risk of female takeover. In our study, when a female was ovipositing solitarily after being separated from her tandem male, she was occasionally grabbed by a different male and subsequently copulated with that new male. Therefore, sperm competition seems to represent a real risk for male *T. lacerata*. Tandems that experienced higher rates of interactions had a smaller average interoviposition site distance overall, which, in combination with the result that individual interactions increase distance, suggests that distances between sites may decrease once a tandem has found an area relatively free from conspecific harassment. Females, on the other hand, may experience higher predation risk than the males during oviposition (e.g., Convey 1992, Rehfeldt 1996). Consequently, the female may adopt a strategy to avoid lengthy mate guarding, instead choosing spend less time laying eggs in a relatively small area and leave the pond. Unfortunately, our observations of predation attempts are too limited to test this idea, and regardless, alternative hypotheses exist, and obtaining a better understanding on whether the male, female, or both have "control" of the tandem and oviposition locations will be critical to interpreting differences in solitary and tandem behavior.

Although our sample size was small for solitary females, male density did not differ between those tandems that remained together and those that included some solitary ovipositions by the female. As such, our results differed from studies of species in which males change guarding behavior based on density (e.g., from contact to noncontact guarding; Latty 2006) as well as from those of Sherman (1983) on *T. carolina*. Sherman (1983) found that female *T. carolina* only oviposited alone when few males were present at the breeding site (such as occurred in the early morning or on overcast days); in these cases, females were alone for the whole oviposition bout. In contrast, our observations were taken in the middle of the day on sunny days and females started their bout in tandem with a male, so although we cannot determine whether female *T. lacerata* oviposited alone during other times of the day, we can conclude that the solitarily ovipositing females we observed were not simply avoiding male harassment by choosing times of day without males (cf. Sherman 1983).

Our observations also yielded some clues as to the selection of particular oviposition sites by *T. lacerata*. We were able to compare a tandem's oviposition events to occurrences when the pair paused, but didn't actually oviposit, at the location. For many of these pauses, the lack of oviposition was not a result of interference from other odonates, suggesting that the tandem may have been rejecting the location for some reason. And, while they did not move further following a pause compared with following an oviposition, we did find evidence that sites chosen for oviposition were farther out from shore than sites at which the tandem simply paused. In addition, oviposition sites overall tended to be located at or just beyond the outer edge of vegetation.

Combined, these observations suggest that *T. lacerata* prefer to oviposit in relatively deep water at the edge of surface vegetation and algal mats or just beyond that edge, over submerged vegetation. This site choice may be a result of selection pressures on eggs and larvae. In order to avoid predation of larvae, females tend to oviposit in dense vegetation, and to avoid desiccation a female may oviposit in open water (Buskirk and Sherman 1985). The black saddlebags may achieve a balance between the dual selection pressures of predation and desiccation by ovipositing within the vegetation near the edge of open water.

Overall, this study has furthered the understanding of tandem oviposition and has given light to the events and possible tradeoffs associated with and affecting oviposition site selection. Future studies would benefit from focusing on whether a tandem's oviposition sites tend to occur in areas with relatively little harassment from single males, as predicted if males in tandem are adjusting their site choice in response to interactions. In addition, comparing the number and size of eggs laid by females, when solitary versus in a tandem, could help determine more definitively the consequences of a female changing the spatial distribution of eggs under those conditions (Schenk et al. 2004).

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