

Mating Behavior and Male Territoriality in *Enallagma vesperum* (Odonata: Coenagrionidae) on Ponds in Ohio and Northern Michigan

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ABSTRACT. The crepuscular damselfly *Enallagma vesperum* Calvert, was studied to document and clarify mating behavior. This paper is a descriptive synthesis of observations which answer basic questions regarding mating behavior of *E. vesperum*. Beginning in July 2004 and continuing in the summers through September 2009, approximately 140 hours of direct observation on a lake in Northern Michigan and a lake and two ponds in Ohio were logged to support the results and conclusions. The literature regarding mating behavior in *E. vesperum* provides little information about male territoriality. The results from this six-year study offer strong evidence of male territory selection and territory defense. Copulatory behavior and ovipositional behavior were also recorded. In most coenagrionid species, males remain in tandem with ovipositing females unless the females submerge. In this study, however, females were observed ovipositing in tandem or individually into surface vegetation.

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INTRODUCTION

Work with the bluet damselflies (Moody 2002) in Glotzhofer's and McShaffrey's *Dragonflies and Damselflies of Ohio* generated the impetus for this study. Individuals of the genus *Enallagma* (bluets) are predominately blue, diurnal, and non-territorial in mating behavior, however, vesper bluets (*Enallagma vesperum*) appear yellowish and are crepuscular. The question became, "could they also exhibit a different mating behavior from other *Enallagma*?" In reviewing literature for the Coenagrionidae chapter, in *Dragonflies and Damselflies of Ohio*, there was much less information about *E. vesperum* mating behavior than other *Enallagma* species (Dunkle 1990; Walker 1953; Westfall and May 1996). Furthermore, Odonata literature indicates that the genus *Enallagma* exhibit little territorial behavior (Corbet 1999; Fincke 2004; Sherratt and Forbes 2001). Westfall and May (1996) state that *E. civile* may be the only *Enallagma* species to engage in territorial behavior and Moody (2002) reported that reproductive behavior is similar to that of other *Enallagma* species. Thus began bi-weekly evening forays to observe and describe mating behavior in *E. vesperum*.

The investigation was initiated with Tom Schultz, Ph.D. at the Middleton Pond, on the Denison University campus in Granville, Ohio, 15 July 2004. Schultz's continued work with male damselfly coloration (Schultz et al. 2008) has resulted in several hours of *E. vesperum* observation. As Schultz and the author watched males land and perch on white water lily pads (leaves), Schultz speculated that we may be watching territoriality. Not only were males perching and returning to perches momentarily, but they appeared to be flying at conspecific males who came near the lily pad on which they were perched.

MATERIALS AND METHODS

A population of *E. vesperum* was essential for this research. Consequently, a survey was conducted which resulted in 23 ponds and lake areas in Northwest Ohio explored as possible *E. vesperum* habitats.

Habitat requirements were met on an interstate highway pond at the junction of Interstate 75, and State Route 25, near Cynnet,

Cedar Portage Watershed, Wood County, Ohio. Cottonwoods, black willow and silver maple overhang the bank on much of three sides. A wall of narrow-leaf cattail crowded the bank beneath the trees, and variable water weed occurred in areas stretching from the cattails to an average of 15 meters toward the pond's interior. No vegetation occurred on the interior. The depth of the pond became two-and-a-half meters approximately one-and-a-half meters from the bank. This pond was the major work site accounting for 130 of the 140 observational hours. Other areas observed in this study included: Nettle Lake in Williams County, Ohio, (approximately four hours), the Denison University pond, in Granville, Licking County, Ohio, (two hours) and Lake Ann in Benzie County, near Traverse City, Michigan, (about four hours). Table 1 shows the year, duration of time worked and site locations.

The shorelines of the ponds worked for the project were nearly impossible to walk because the banks were crowded with trees or cattails. In isolated spots, where access from the bank was possible, there was often an abrupt drop in water depth to two meters, less than a meter from shore. Therefore, a boat was necessary and the damselflies were observed from the water rather than from the bank. The view from the water provided a different perspective from most other Odonata surveys. Field notes were taken on every investigation. These field notes were descriptive; only 18 investigations allowed detailed quantitative data to be collected. On these 18 occasions, there were two observers which allowed a second pair of eyes and a second timer. A second observer also permitted one to stabilize the boat, while the other intermittently videotaped or photographed and verified observations.

Field work for this project was done from approximately 15 June to 15 August, each year following the distribution pattern of *E. vesperum* activity (Moody 2002), and from 7 p.m.-midnight. The nocturnal activity of the vesper bluet (*E. vesperum*) required artificial lighting; however, bright light drove the males away. After much trial and error, it was discovered that the best illumination was a six-volt general utility lantern. In 2004, a digital camera was used by Shane Myers to record the contact interaction of males. Although, with flashlight illumination these interactions, which occurred quickly, were difficult to visually register. From 2005-2008, Myers used a video camera to provide a sequential picture of *E. vesperum* behavior. A problem that persisted was the inability to get a "stop action" shot of males during an interaction. In 2009, photographs of interactions which show males on territories, and

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male-to-male contact were taken with a Canon EOS Digital Rebel XT camera by Ryan Smith.

RESULTS

Enallagma vesperum was found in four of the 23 sites surveyed. *E. vesperum* was found when a combination of trees surrounding much of the pond and overhanging the banks and some floating vegetation was present. Dunkle (1990) described trees as roosting sites for females. In addition to trees, floating plants also provided a necessary platform for reproductive activity. In this project, white water lily (*Nymphaea odorata*) and variable water weed (*Potamogeton gramineus*) were the only plants observed as perching sites by males and oviposition sites for females. On three sites, Middleton Pond, and Nettle Lake in Ohio, and Lake Ann in Michigan, the floating plant surfaces were lily pad leaves. In the pond near Cygnet, Ohio, variable water weed provided the floating vegetative surface. Other floating vegetation may be suitable, but a solid, fairly defined surface seems important for landing and perching. If the floating vegetation was amorphous, as algal clumps tend to get in middle to late summer, *E. vesperum* males were not found during the hours of maximal activity. Further, in three eutrophic ponds it was observed that algal or lily pad growth was very dense. On these ponds few odonates were observed and no *E. vesperum* were seen.

Males guarding leaves of *Potamogeton gramineus* was recorded by Myers on digital camera. Each male perched on a leaf, generally in a discrete mass of four to seven leaves. While variable in size, depending on weather and hours of daylight, these masses or territories were usually no larger than 50 centimeters in diameter.

Table 1
Sites, Year, Duration and Total of Investigations

Sites Worked	No. of Observation Hours	No. of Investigations
2004		
Middleton Pond	2	1
Nettle Lake	4	1
Cygnet Pond	21	7
2005		
Cygnet Pond	26	8
Lake Ann	4	2
2006		
Cygnet Pond	18	5
2007		
Cygnet Pond	16	4
2008		
Cygnet Pond	36	10
2009		
Cygnet Pond	13	4

Perched males, if approached by a conspecific male, resulted in the resident flying directly at the intruder. Table 2 shows the number of male-to-male interactions recorded from 18 investigations. The time duration for these interactive flights was seconds and seldom more than a minute and the length of these flights varied, but was often less than a meter and seldom more than three meters from their territory. In 2005, and the through the next four summers, Myers used a video camera to capture the activity occurring on the *Potamogeton* leaves. When edited, a total of 30 minutes of territorial guarding and male-to-male interaction, including physical contact, copulation and oviposition was recorded.

From 2004 through 2009, in each body of water with an *E. vesperum* population, male territorial mating behavior continued to be observed. Generally, the same male could be observed occupying the same leaf or adjoining leaves in the leaf mass. Site fidelity, the length of time males occupy the same site (Corbet 1999), averaged approximately 18 minutes, n=145. Table 2 shows male time on territory. Identity verification of the individuals was possible in this work because males remained on leaves or made a horizontal circular flight almost directly above and very close (10 centimeters) to the leaf mass allowing constant observation. Lefevre and Muehler (2004) categorized these seemingly unprovoked flights as loop flights. During observation for this study, loop flights were not timed and the actual number of loop flights was not recorded. Loop flight duration, a few seconds, was common when several males were perched in an area. On most nights, males were on territories for about 12-24 minutes; however, on 5 August 2009, a male was observed holding a territory for 49 minutes and on 2 September 2009, a male was observed holding territory for 74 minutes. These timed territorial durations were interspersed with loop flights and interactive flights which were generally always less than a minute each. Of the total time on territory, a great majority was spent perching. While times and lengths of interactive flights were not recorded, descriptive observations and videotape indicates *E. vesperum* males may be classed as perchers, as opposed to fliers. According to Parr (1983), perchers spend less than 20 percent of their territorial time in a flight pattern of some type.

Male *E. vesperum* were observed flying from 7:30 p.m. until after dark in the middle of the summer. The daylight flights appeared more random and were likely feeding flights, rather than courting behavior. However, in later August and into September, males appeared sooner, and by 7 p.m. often appeared on perches. This earlier active time may be explained by a change in light intensity and corresponding spectra utilized by *E. vesperum* (Schultz et al. 2008). By 8:30 p.m. from June through early August, males had restricted the area of flight and proceeded to settle on leaves. If a male conspecific came within a half-meter or less of an occupied leaf mass, the resident flew up and directly at the intruder. These confrontations may have been close inspections, but in several of the interactions contact was observed. Most notably on 30 June 2005, nine physical contacts were recorded within 45 minutes, one of which was so intense that it was described in the field notes as a "dogfight". From each summer's work (2004-2009), pictures or video showing interactions were recorded. The photographs by Smith are among the first-ever reproduced showing male *E. vesperum* defending a territory. These images were first shown, 8 August 2010, in a "Dragonflies & Damselflies" presentation for the Hancock County Parks, Findlay, Ohio. An interaction showing two males locked in combat, with one of the males inverted in midair, was exhibited through videotape at the Ohio Odonata State Meeting, Columbus, Ohio, in February 2006.

Males only left their perches to interact with other males, to capture females, or perform a loop flight. Evidently loop flights were not near enough to males perched on leaves to cause an immediate attack. However, resident males did respond to a nearby loop flight, with a loop flight. The loop flight also occurred if the flashlight beam was too bright or when a nearby territorial dispute took place. It's possible this was a display to roaming males and perhaps to females watching the territorial acquisitions and battles. When the weather was cooler (approaching 70 degrees) or if there was a breeze, there were fewer males, fewer interactions and fewer tandem couples observed. On these nights males spread out with two to three meters between territories. On warm, still nights in July, the distance between territories was often as little as a meter, and the most dense territorial congregation was observed on 30 June 2005. There were 14 males in a four-by-four meter area. Each territory was no larger than four or five leaves, and in two territories, only a half-meter separated two males. Both males in this more intimate arrangement appeared agitated and exhibited a greater number of loop flights. After about 15 minutes the male who arrived secondarily flew away.

In midsummer, females were not observed before sundown, which was about 9:15 p.m. and in August/September they appeared nearer 8 p.m. They emerged from the dark most likely from perches in the trees. Video recordings and observations were made of males flying up from their perches and grasping females. Although on most occasions, the females and males simply appeared in the light already in tandem, and it is likely they connected nearer shore. Copulation may occur on shore or on lily pads (Dunkle 1990), or as observed in this research, on Potomageton and cattail leaves. Dunkle (1990) reported that copulatory activity occurs for 15-20 minutes which was also found in this work. However, this study did produce a videotape of a pair in copula for 48 minutes.

Following copulation, couples normally remained in tandem to oviposit. A ratio of 6:1, tandem oviposition to single female oviposition, $n=56$, was found. Table 2 shows the data used to calculate the ratio of tandem oviposition to single female oviposition. The literature generally agrees that oviposition is a tandem effort of males and females in coenagrionid damselflies (Corbet 1999; Dunkle 1990; Westfall and May 1996). Most often oviposition was into the horizontal Potomageton stems, which floated near

Table 2
Male and Female Reproductive Behavior

Date	No. of Males	Male to Male Interactions	Time on Territory	No. of Females	Tandem Oviposition	Lone Oviposition
2004: July 15	15	18	13 min.			
19	7	4	10 min.			
20	12	15	11 min.			
28	9	8	12 min.	17	15	2
August 12				8	7	1
2005: June 30	14	30	14 min.			
July 8	8	9	13 min.	5	3	2
10	7	12	21 min.			
11	5	7	13 min.			
24	6	4	19 min.			
2006: July 12	11	10	18 min.			
13				4	3	1
2007: July 22	13	10	22 min.	8	7	1
2008: July 24	7	5	11 min.			
September 11	11	9	21 min.	14	12	2
2009: July 7	9	7	12 min.			
August 5	4	11	37 min.			
September 2	7	8	47 min.			

* All observations were recorded on Cygnet Pond, except 15 July at Middleton Pond.

** Male data was not recorded for 12 August 2004 and 13 July 2006.

*** Female data was only recorded for those date shown above.

the surface. On two occasions the female was nearly submerged while the attached male appeared to be sitting on its tail in the water. However, observations also included couples separating and females ovipositing. An unattached female was videotaped as she oviposited for 37 minutes, much of the time above the surface. This female was also videotaped for at least 18 minutes, seven centimeters underwater. Schultz (personal communication, 5 June 2007) and students found only single females, $n=10$, all of which were ovipositing, and no males after 1 a.m. Single females most often oviposited into *Potamogeton* stems, but were also observed ovipositing into the variable water weed leaves. In Lake Ann, Michigan and Nettle Lake, Ohio, where there is primarily white water lily, females appeared to oviposit into the lily leaves (pads).

Toward midnight in July, reproductive activity decreased and copulation was not observed. Near midnight there were few males left on perches. There were, however, several couples flying in tandem and ovipositing in tandem, mostly into the floating *Potamogeton* stems. The latest observations, made at 12:30 a.m., were notable because there were no other odonates and only a few tandem pairs of *E. vesperum*.

SUMMARY AND CONCLUSIONS

Direct observation by the author and colleagues, with video and pictures taken by colleagues, identified the height of mating activity from approximately 8:30 p.m. to 12:30 a.m. during the first two weeks of July. During this time males were observed guarding territories. Territorial sites were groups of *Potamogeton* (variable water weed) leaves isolated by a half-meter or more from other leaf masses. Males occupied a leaf in a leaf mass of about five, which measured approximately 50 centimeters in diameter. They remained on the leaf or a nearby leaf in the mass for an average of 18 minutes. Holding the territory consisted of perching for several minutes, loop flights and occasional flights to encounter male conspecifics. Male-to-male interactions occurred as conspecific males came into close proximity of the territorial site. Site fidelity was evident to allow determination that a territory had been established (Corbet 1999). Males began to establish territories near 8:30 p.m., with females appearing shortly after sundown. Trees are roosting sites (Dunkle 1990), and apparently observational stages for the females. Presumably, females watch males acquire and defend territories and subsequently fly into the territory of a potential mate. It has been established that females of some Odonata species, many dragonflies and pseudostigmatid and calopterygid damselflies, for example, utilize female mate choice (Corbet 1999; Dunkle 1990; Fincke 2004; Glotzhober and McShaffrey 2002; Westfall and May 1996). However, in the coenagrionid damselflies and specifically the *Enallagma* genus, much theory and research on coloration indicates that female choice may be rare or nonexistent (Fincke et al. 2005). Copulation occurred on *Potamogeton* and cattail leaves. Oviposition was accomplished by lone females and with males in tandem. Oviposition took place into *Potamogeton* leaves and most

often into the partly submerged water weed stems. Underwater oviposition was observed with lone females and with females partly submerged while in tandem.

Enallagma vesperum, is a crepuscular species with much of its mating activity occurring nocturnally. Habitat requirements also make observation more difficult than observing many other odonate species. For these two reasons this paper is describing what may be new information regarding the male behavior which precedes mating. Questions were raised, however, which need to be explored to accurately complete the picture of *E. vesperum* mating behavior. These questions include: Where do males and females form their tandem connections? What categories of male-to-male interaction can be observed and stated? Do males occupy the same territories on successive days, and if they do, how many days? Is oviposition more often accomplished in tandem or as a process most often carried out by a single female? Might the late afternoon flying orange bluet (*E. signatum*) also exhibit territorial behavior?

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