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OVIPOSITION SITE SELECTION IN *ENALLAGMA CIVILE* (HAGEN) AND THE CONSEQUENCES OF AGGREGATING BEHAVIOUR (ZYGOPTERA: COENAGRIONIDAE)

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E. civile is a nonterritorial damselfly whose males exhibit contact-guarding, and the tandem-pairs oviposit alone or in small groups. Three possible factors influencing the formation of aggregations were investigated: single-male interference, female oviposition efficiency and predation risk. Although aggregating reduced the risk of interference and may lower predation risk, for this species, oviposition efficiency was reduced under crowded conditions. This reduction in efficiency was primarily due to the incidental contact that occurred among ovipositing pairs. Because contact-guarding was effective at preventing takeovers, and males had few mating opportunities on a given day, males as well as females should prefer conditions favoring high oviposition efficiency. Future research on oviposition behaviour should include a measure of oviposition efficiency, because it can be an important factor influencing site selection.

INTRODUCTION

For oviparous animals that exhibit no parental care, the choice of oviposition sites is critically important to an individual's reproductive success. Among odonates, oviposition can be a lengthy process (CORBET, 1962) during which adults must face risks of predation. For many odonate species, males displace the sperm of a female's previous mate(s) (FINCKE, 1984; WAAGE, 1984). Aggressive behaviour from males attempting to take over the mates of conspecifics can further lengthen the oviposition period. Because longevity is a major predictor of the lifetime reproductive success of many odonates (e.g. FINCKE, 1982; BANKS & THOMPSON, 1985; McVEY, 1988), selection should favour indi-

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viduals that choose locations where they can complete oviposition quickly and in relative safety.

Despite its importance, oviposition site selection has only recently been studied in the Zygoptera (e.g. FINCKE, 1986; WAAGE, 1987; MARTENS & REHFELDT, 1989; REHFELDT, 1990; FINCKE, 1992). Selective factors that may influence oviposition behaviour include male interference (WAAGE, 1987; MARTENS & REHFELDT, 1989), predation on adults (MICHIELS & DHONDT, 1990; REHFELDT, 1990) and offspring survivorship (FINCKE, 1992).

Aggregating at oviposition sites is a common occurrence among Zygoptera (e.g. NEEDHAM & HEYWOOD, 1929; BICK & BICK, 1965; PAJUNEN, 1966; WAAGE, 1987; MARTENS & REHFELDT, 1989). A mechanism that can lead to the formation of such aggregations is a strong attraction of females to other females already ovipositing (e.g. WAAGE, 1987; MARTENS, 1989; MARTENS & REHFELDT, 1989). For *Calopteryx maculata* (WAAGE, 1987) and *Platycypha caligata* (MARTENS & REHFELDT, 1989), two territorial species that exhibit noncontact mate guarding, aggregating females oviposited with fewer disturbances by courting males than females ovipositing alone.

Enallagma civile is a common coenagrionid damselfly in Oklahoma (BICK & BICK, 1957). Males are nonterritorial and, after sighting a female, a male grasps her in tandem without prior courtship. Females oviposit above and sometimes below water on a variety of substrates, and are held in tandem except during submerged oviposition (see BICK & BICK, 1963 for details).

The goal of this study was to quantify the size and frequency of aggregations of *E. civile* at oviposition sites, and to evaluate possible advantages and disadvantages associated with grouping behaviour. I measured two interrelated factors: (1) interference from conspecific single males; and (2) time required by females to lay an egg clutch on a given day (hereafter termed "oviposition efficiency"). Because risk of predation may also influence grouping behaviour, predation on males and females was also recorded. Finally, I contrast oviposition behaviour of *E. civile* with that of two territorial species, *P. caligata* and *C. maculata*.

MATERIAL AND METHODS

Data were collected from 7 June through 10 September 1990. The field site, located on the Norman campus of the University of Oklahoma, was 1 of the 32 artificial ponds maintained for fish breeding and research. The study pond was approximately 25 x 17 m (with rounded corners) and had a maximum water depth of 1 m (Fig. 1). Various grasses and wildflowers along the banks of the pond were periodically trimmed to allow easy viewing of damselfly behaviour. Each day, I recorded air temperature at 14:00 h Central Daylight Time (CDT) and water temperature at about 16:00 h CDT.

I divided the perimeter of the pond into 21 sections of 3.5 m length (Fig. 1). At the centre of each of these sections, three cattail (*Typha latifolia*) leaves, each cut to 0.5 m in length and held together with a plastic clip (5-cm length), were laid flat on the water surface along the pond bank. This arrangement provided abundant, uniform oviposition sites. Using about 0.5 m of monofilament line, I connected the clip to a numbered dowel rod on the bank to keep the cattails in position. Cattail leaves were replaced with fresh ones at approximately 10-day intervals.

An additional 42 dowel rods (4.8 mm diameter) were stuck vertically in the pond bottom and equally distributed (two per section) 25 cm from the bank to provide perches for males and tandem pairs (Fig. 1). No aquatic vegetation was present, and I kept the small amount of emergent vegetation clipped along the water's edge to encourage ovipositing pairs to use only the substrates provided.

Data were collected from 12:00 to 16:50 h CDT on a total of 62 days. To determine the distribution of ovipositing pairs, I slowly walked around the pond at approximately 45 min intervals and recorded the location of all ovipositing pairs. I conducted a maximum of six of these surveys per day, for a total of 223 surveys involving 1,961 ovipositing pairs. Frequencies of pairs that oviposited alone and in aggregations were tested against random (Poisson) distributions. Because the total number of pairs at the pond continuously fluctuated, I combined the data for only those surveys with equal sample sizes. For instance, if 10 surveys over the course of the season each included 20 pairs, I combined the pair frequencies in those 10 surveys for one test. When a test indicated a significant deviation from random, the coefficient of dispersion (CD) was used to determine whether the distribution of pairs was more uniform (CD < 1.0) or more clumped (CD > 1.0) than expected by chance. Only surveys including five or more pairs (n=153) were analyzed. During the first, middle and last surveys on a given day, I also recorded the total number of single males at the pond and the total number of tandem pairs that were not ovipositing. In all cases, means are reported ± 1 standard deviation.

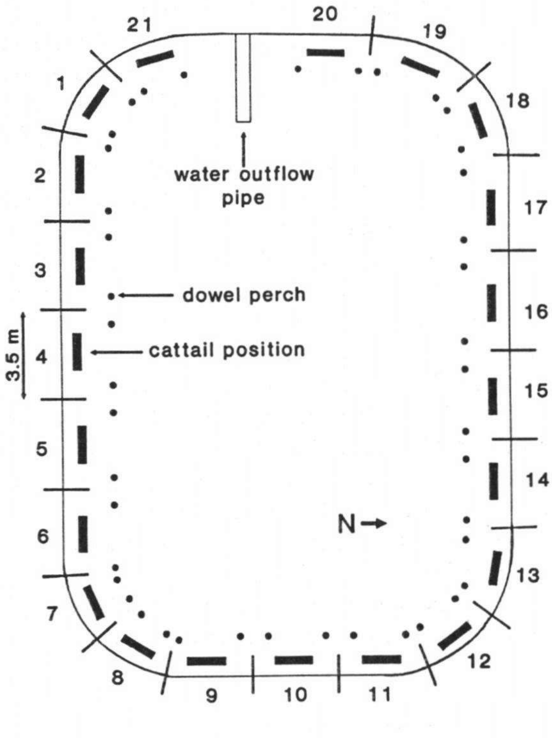

Fig. 1. Schematic representation of the 25 x 17 m study pond showing distributions of cattails and dowel rod perches.

Interference by single males directed towards ovipositing pairs was recorded during 30 min observation periods at oviposition sites where pairs were already present (57 h total observation). The rate of interference was defined as the number of interference acts . min^{-1} . pair^{-1}. For each act of interference, I recorded: (1) the number of pairs present at the pond section; (2) the type of interference; and (3) the response by the targeted pair. Interference was categorized as "flight toward" if the male flew directly toward his target without making contact, or "contact" when the male made physical contact with either member of the tandem pair. In response to the interference, ovipositing pairs: (1) displayed a wing warning (described by BICK & BICK, 1963); (2) briefly took flight and landed in the same pond section; or (3) left the section completely.

Oviposition efficiency of females under different crowding conditions was determined by conducting a series of 30 min focal samples (17.5 h total), watching a female and recording: (1) the number of ovipositing pairs present at the pond section; and (2) the total amount of time the female oviposited during the sampling period. Oviposition occurred when the female moved her ovipositor against the cattail in a series of thrusting motions. If the original focal pair left the section I began a new focal sample with another pair until the 30 min period ended. Efficiency was calculated as the proportion of time a female oviposited while at an oviposition site. For statistical analysis, proportions were subjected to the arcsine (or angular) transformation (SOKAL & ROHLF, 1981).

To observe the entire oviposition event in detail, I first placed dots of enamel paint on the wings of individual males and females. I then looked for a copulating pair that included a marked individual, and followed the pair throughout the oviposition period. This period began when the pair made its first flight after copulating, and ended when the male released the female. For each stop the pair made I recorded: (1) the duration of the stop; (2) the number of pairs present at the pond section; and (3) whether the female oviposited or not. Thirteen pairs were observed for a combined total of 32 h. For 12 of these pairs, I also noted the number of times single males interfered with the pair while the pair was perched or in flight. The same categories of interference ("flight toward" and "contact") were used.

Any predation on damselflies during the study period was recorded. In addition, on six days I observed only predation behaviour and searched for cases of predation.

RESULTS

During the field season, the temperature of the water just below the surface remained fairly constant ($\bar{x}$ = 30.7°C ± 1.3°), while daily air temperature showed some fluctuation ($\bar{x}$ = 32.2°C ± 2.9°). There were always more males than females at the pond, and the operational sex ratio (males:females) remained fairly consistent ($\bar{x}$ = 4.9 ± 1.9).

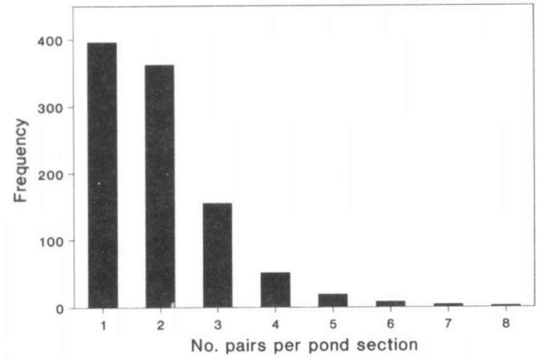

Fig. 2. Frequencies of pairs ovipositing alone and of different-sized aggregations (1961 pairs from 223 surveys).

AGGREGATION

The frequencies of pairs that oviposited alone and in aggregations significantly deviated from random (Poisson) distributions (Tab. I). For all sample sizes, the coefficients of dispersion were > 1, suggesting that pairs were forming aggregations. The average number of pairs per pond section was 2.0 ± 1.1 pairs (n=995, Fig. 2). Eighty percent (n=1,565) of the pairs oviposited in the presence of at least one other pair.

Table I

Results of goodness-of-fit tests for 153 ovipositing pair surveys to determine if the distributions of pairs among the 21 pond sections deviated from random (Poisson) distributions. A significant p-value, combined with a coefficient of dispersion value > 1, indicates aggregating.

No. pairs/survey	No. surveys	Coefficient of dispersion	G-value
5	17	1.57	29.70**
6	4	1.57	15.60**
7	14	1.57	45.90**
8	16	1.68	59.18**
9	13	1.91	69.60**
10	12	1.88	55.92**
11	12	2.01	80.39**
12	9	2.22	55.62**
13	9	2.06	73.06**
14	9	1.80	72.85**
15	7	1.90	76.26**
16	3	1.64	23.33**
17	2	2.00	19.45**
18	4	2.53	36.02**
19	7	2.00	72.71**
20	5	2.49	58.73**
21	4	2.36	48.84**
23	1	2.37	6.65**
24	1	2.65	13.90**
26	1	2.17	19.87**
28	1	3.85	18.40**
29	1	2.35	10.14**
31	1	1.26	8.77*

* $p < 0.05$
** $p < 0.01$

SINGLE-MALE INTERFERENCE

Observations of single-male interference directed toward ovipositing pairs showed that the most common type of interference was "flight toward" (n=914 occurrences). When single males made contact (n=88), they usually perched on the tandem female or briefly grasped either member of the tandem pair. During these observations, no single male was successful at separating a tandem pair and taking over possession of the female. Tandem males and/or females usually responded to the interference by flashing a wing warning at the approaching male (response 1, n=884). In some cases, the pairs would briefly take flight in tandem and land in the same section (response 2, n=97) or leave the section completely (response 3, n=21). Only response 2 or 3 resulted in the interruption of oviposition. Consequently, the data for those two responses were combined and analyzed. The rate of interference (number of interference acts . min^{-1} . $pair^{-1}$) by single males that caused response 2 and 3 was negatively correlated with the number of ovipositing pairs present (Fig. 3).

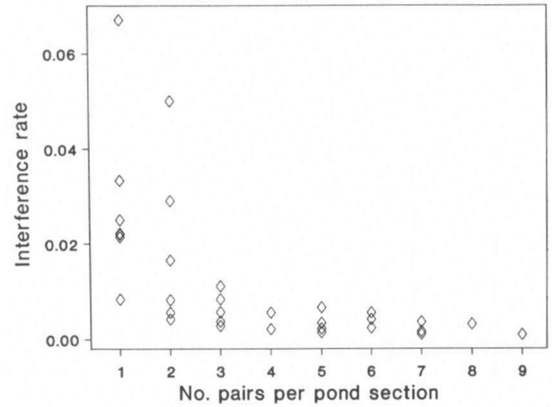

Fig. 3. Rate of single-male interference (no. interference acts • minute $^{-1}$ • pair $^{-1}$) for different-sized groupings that caused a targeted pair to take flight (r= -0.497, n-47, p < 0.01).

The rate of interference directed toward ovipositing pairs that elicited any type of response was found to be higher when the pair was in flight ($\bar{x}$ = 0.60 ± 0.28 interference acts/min) than when perched ($\bar{x}$ = 0.07 ± 0.04; t-test = 6.30, df=11, p<0.001). Pairs frequently received multiple attacks from males as soon as they took flight. Furthermore, of the 13 takeover attempts involving physical clashes that I witnessed, 9 occurred when the targeted pair was in flight.

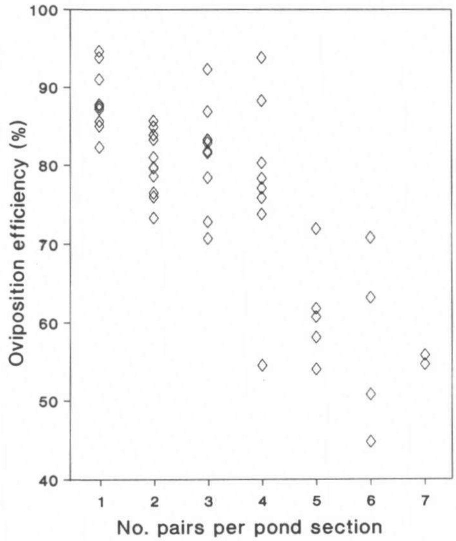

Fig. 4. Efficiency of ovipositing females in different-sized groupings (r= -0.767, n=50, p < 0.01), defined as percentage of time female oviposited while at an oviposition site.

OVIPOSITION EFFICIENCY

Although interference rates were lower in larger aggregations, female oviposition efficiency decreased as the size of the aggregations increased (Fig. 4). This resulted from the "incidental contact" of ovipositing pairs under crowded conditions, which caused repeated interruptions of ovipositing females. Once oviposition was interrupted, pairs frequently walked a few centimeters along the cattail or briefly flew and landed on the same cattail before resuming oviposition.

OVIPOSITION BEHAVIOUR

Females used 98-199 min ($\bar{x} = 142.1 \pm 29.7$) to oviposit on a given day. All 13 females used as focal animals began oviposition above water. Of these, 6 (46%) completely submerged one or more times to oviposit. The time spent under water per bout was 2-78 min ($\bar{x} = 31.8 \pm 30.4$, $n=10$), and the average number of bouts was 1.7 ± 0.82. Four of the females that submerged to oviposit were seized by non-mates upon resurfacing. Three of these females refused to copulate and were soon released. The oviposition period for those three females was already over 2 h each when the second male attempted copulation, suggesting that these females had finished laying their clutches.

The length of the oviposition period did not differ between pairs in which the female stayed above water and those in which the female submerged (t-test=0.61, df=12, $p>0.05$). There were also no differences between these two groups in the total time spent in flight (t-test=0.69, df=12, $p>0.05$) and the total time spent perched while not ovipositing (t-test=0.15, df=12, $p>0.05$). However, the rate at which ovipositing pairs were interfered with for females that stayed above water ($\bar{x} = 0.14 \pm 0.06$ interference acts/min, $n=6$) was significantly lower than that toward pairs in which the female spent some time submerged ($\bar{x} = 0.22 \pm 0.04$, $n=6$; t-test=2.78, df=11, $p<0.05$). Consequently, a high rate of interference from males may have been an important factor determining whether or not a female submerged.

While above water, most tandem pairs made frequent stops at various oviposition sites to deposit eggs ($\bar{x} = 23.5 \pm 15.7$ stops), and the average time spent at each oviposition stop increased as aggregation size increased ($r=0.50$, $n=47$, $p<0.01$). For all aggregation sizes, the average oviposition stop lasted 3.0 ± 4.2 min ($n=299$).

PREDATION

Over the course of the season, I saw evidence of predation on three damselfly species (Tab. II). In most cases (63%), I saw which predator ate a damselfly and, in 29% of the cases, I witnessed the actual capture. The two major predators

Table II

Summary of 35 cases of predation (0.56 per day) on damselflies.

Prey species	Sex of prey ♂	 ♀	 Unknown*
Enallagma civile	19	3	2
Argia apicalis	3	0	1
Ischnura verticalis	4	1	1
Unknown	--	--	1

* 3 were tenerals.

were robber flies (Asilidae; n=18 predation acts) and *Erythemis simplicicollis* (Libellulidae; n=13). On one occasion, I saw a diving beetle (Dytiscidae) eating a damselfly, and I saw three tandem pairs in which the male had been decapitated by an unknown predator. Although the frequency of predation on *E. civile* males was 6.3 times that of females, prey captures were proportional to the number of males and females present (χ^2=0.25, n=22, p>0.05).

I saw 10 cases of predation during the six days in which I focused primarily on searching for evidence of predation. This rate was 3.9 times greater than the rate for data I collected opportunistically over the field season (0.4/day), suggesting that predation on damselflies was probably more common than my occasional observations implied.

DISCUSSION

SINGLE-MALE INTERFERENCE

Although *E. civile* males rarely, if ever, displace the mates of tandem females (BICK & BICK, 1963; this study), their attempts to do so can result in an increase in the total time needed to oviposit. Such interference by lone males that caused a pair to take flight was lower in larger aggregations. While in flight, interference rates were greatly increased. As MARTENS (1989) found for another coenagrionid, *Coenagrion pulchellum,* single males seemed to be attracted to a moving pair, especially right after the pair took flight. Furthermore, most takeover attempts occurred on the wing, so it appears that tandem pairs are most vulnerable to aggressive acts while in flight. Consequently, an individual attempting to better its odds against interference and a possible takeover attempt should prefer a large aggregation over a small one, and should avoid flying as much as possible.

OVIPOSITION EFFICIENCY

MARTENS & REHFELDT (1989) suggested that aggregated *P. caligata* females, whose aggregations lowered male interference on any given pair, could potentially lay more eggs than solitary females. For *E. civile* I found that, despite the lower rate of interference in large aggregations, tandem females were most efficient at ovipositing while by themselves or in small aggregations. The reduction of efficiency under crowded conditions was principally due to the incidental bumping and jostling that occurred between pairs, and not to single-male interference. With a contact-guarding species like *E. civile*, tandem males at an aggregation can hinder the ability of females to lay their eggs. Not only do tandem males take up valuable space on the substrate, but they reduce a female's mobility and, when trying to rest on neighbouring males or females, cause repeated interruptions of oviposition. To lay eggs as quickly as possible, then, preference should be given to small aggregations or ovipositing alone where other pairs cannot get in the way. The fact that pairs spent longer periods of time ovipositing at large aggregations can be accounted for by the reduction in efficiency under crowded conditions.

OVIPOSITION BEHAVIOUR

My observations of oviposition behaviour in *E. civile* concur with the findings of BICK & BICK (1963) on the same species in southern Oklahoma, but my results suggest that interference from single males may be at least one important factor inducing a female to submerge. PAJUNEN (1966) and FINCKE (1987) also noted that male interference could result in submergence. Frequent harassment can delay oviposition by causing a pair to change its location and ward off takeover attempts while in flight. Although a female can avoid all male interference by going under water, other factors may discourage submergence. Females are very vulnerable to predation while under water and are at risk of drowning unless "rescued" from the water's surface by a male (FINCKE, 1986). In addition, oviposition efficiency does not necessarily increase while submerged (FINCKE, 1985), which may help explain why the females in my study who submerged did not have shorter oviposition periods than the females who remained above water.

The function of making frequent oviposition stops may be to enhance egg survival. MILLER & MILLER (1985) thought that in the libellulid *Tholymis tillarga* females moved from one area to another while ovipositing to reduce the loss of eggs to fish predation. For a treehole-breeding damselfly, FINCKE (1992) concluded that females partition a clutch among various treeholes as a "bet-hedging" strategy against con- and heterospecific predation.

PREDATION

Compared to other odonates, species that contact guard may be at higher risk of predation, because with tandem flight there comes a reduction of speed and maneuverability (WAAGE, 1984). For *Enallagma hageni*, FINCKE (1982) found that predation was a serious cause of death at the breeding site, and this seems to be true for *E. civile* as well.

I found that the predation frequency on *E. civile* males and females did not statistically differ. For all individuals, remaining in a group is perhaps the best way to reduce the chances of being preyed upon. It has been proposed that, although groups may be more conspicuous than solitary individuals, in some cases large numbers of prey can "dilute" the predation risk from certain kinds of predators (REHFELDT, 1990; TURCHIN & KAREIVA, 1989).

CONCLUSIONS

It seems that some of the benefits of aggregating that WAAGE (1987) and MARTENS & REHFELDT (1989) found for *C. maculata* and *P. caligata*, respectively, may also apply to *E. civile*. Tandem pairs could lower their risk of male interference, and possibly predation as well, by joining other pairs at an oviposition site. However, I found that the crowded conditions caused by the tandem-pair aggregations produced a serious negative effect that the noncontact-guarding species did not experience: reduced oviposition efficiency. *Enallagma civile* pairs should prefer ovipositing in small aggregations or alone, because, under these conditions, females can complete oviposition quickly and efficiently despite any increase in interference risk.

Neither MARTENS & REHFELDT (1989) for *P. caligata*, nor REHFELDT (1990) for *Pyrrhosoma nymphula* considered female efficiency, though it appears that this factor may be affecting oviposition site choice for the two species they studied. For instance, MARTENS & REHFELDT (1989) found that the duration of time spent at an oviposition site increased with group size. As with *E. civile*, this increase may have resulted from lowered efficiency under crowded conditions. REHFELDT (1990) showed that pairs of a contact-guarding species that first landed in a group did not stay at their initial locations for as long as pairs that initially landed alone. Furthermore, pairs that initially perched near others spent only 16.5% of the total oviposition period in groups. MARTENS & REHFELDT (1989) suggested that pairs may not remain in a group very long due to a lack of space for eggs, but reduced efficiency is perhaps a more logical explanation for these results. In addition, the results of these two studies and mine showed that the average aggregation size was less than three, so it appears that there is some pressure to keep aggregations small.

While the reproductive behaviour of *C. maculata* and *P. caligata* may promote a sexual conflict with respect to oviposition site selection, the evidence for *E. civile* suggests that male and female preferences for oviposition sites should coincide. Contact guarding is very effective at preventing takeovers, so the threat of interference from single males is not as serious as it would be for noncontact-guarding species. Perhaps the only drawback of contact guarding is that a male cannot mate as frequently as noncontact-guarding males on a given day, because he must devote long periods of time to each female. However, when the chances of encountering more than one female per day are low, such as in my study, the cost of this drawback is greatly reduced.

Undoubtedly, oviposition site selection is complex, and my results suggest that, along with male interference and predation risk, oviposition efficiency may be another important factor influencing the selection process, especially in contact-guarding species. To gain a clearer understanding of oviposition behaviour, future investigators should include a measure of oviposition efficiency. Furthermore, when distributions of ovipositing females/pairs are not tested for randomness (e.g. MARTENS & REHFELDT, 1989; REHFELDT, 1990), arguments for the existence of aggregations are weakened. Assertions that females/pairs are aggregating at oviposition sites should be properly evaluated statistically.

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