

## Underwater oviposition in a damselfly (Odonata: Coenagrionidae) favors male vigilance, and multiple mating by females

Ola M. Fincke\*

Program in Evolutionary Ecology and Behavior, Department of Biology, University of Iowa, Iowa City, Iowa 52242, USA

Received March 18, 1985 / Accepted July 25, 1985

**Summary.** Female *Enallagma hageni* oviposit underwater where they are inaccessible to males. I demonstrate that males guard submerged females rather than perch sites, and are behaviorally distinct from lone males at the water. In contrast to lone males, which always attempt to copulate with females presented to them, guarding males exhibit a conditional latency to remating which corresponds closely to the time required by females to oviposit a complete clutch of eggs. By ovipositing underwater, females decrease the risk that their eggs become exposed. Risks associated with submerged oviposition favor both mate guarding, and multiple, within-clutch matings by females. Both guarding mates and lone males ‘rescue’ females that float on the water surface as the result of improper resurfacing. Such behavior reduces the mortality risk to females from 0.06 to 0.02 per oviposition bout. By remating between bouts, females benefit from the additional vigilance of lone males, who rescue floating females 1.4 times as often as original mates. A second consequence of multiple mating is an increase in the selective advantage of vigilance by mates. Because receptive females become scarce by early afternoon, whereas male density remains high, a male has little (3%) chance of encountering a second receptive female that day. However, he incurs a 42% risk of losing fertilizations if he abandons a mate. For male *E. hageni* mate guarding functions in the context of both natural and sexual selection. It insures that a mate lives to lay a complete egg clutch in addition to protecting a male’s sperm investment.

---

### Introduction

A question critical to our understanding of the evolution of mating systems is why females of some

species mate more often than is necessary for sperm replenishment, while others mate only once per clutch or lifetime. Females that mate multiply may partition egg clutches or litters among a number of males, enabling males to compete for fertilizations via sperm competition (Parker 1970). Despite the numerous theoretical advantages for multiple matings to females (see Walker 1980), few data demonstrate the selective advantage accruing to females of mating repeatedly while laying a single clutch, except for species in which females derive nutritional gains from mating males (e.g. Friedel and Gillott 1977; Boggs and Gilbert 1979; Thornhill 1980; Gwynne 1984), or mate in exchange for access to a needed resource (e.g. Smith 1979; Waage 1979a; Fincke 1984a).

Upon maturing a clutch of eggs, females of the damselfly, *Enallagma hageni*, become receptive and may mate multiply, enabling males to use one of two alternative mate-finding tactics (Fincke 1985). In the morning, males search the banks for females arriving at the pond to lay eggs. By mid-afternoon, when this supply of unmated females is exhausted, males shift their search to oviposition sites at the water, waiting for females to resurface from bouts of underwater egg-laying.

Because both mated and unmated males perch around oviposition sites, it is uncertain whether mated mates are actually guarding submerged mates, or whether they remain at oviposition sites because that is where they have the best chance of encountering additional females that day. By ‘non-contact’ guarding, males might protect their sperm from displacement by a second mate, which can fertilize up to 95% ( $\bar{x} = 80$ ) of the eggs a female immediately lays (Fincke 1984b). On the other hand, submerged oviposition might free mates from guarding because females underwater are inaccessible to males.

I demonstrate that mated males are behaviorally distinct from unmated males waiting at ovipo-

---

\* Present address: Department of Biology, University of Pennsylvania, Philadelphia, PA 19104, USA

sition sites, and that mates are guarding submerged females rather than defending territories at oviposition sites. I then quantify the consequences of submerged oviposition to females and males. I suggest that sperm competition may not be a necessary pre-condition for the evolution of mate guarding in this species because guarding increases a male's fertilizations by insuring that his female lives to lay a complete clutch. Finally, I show that female damselflies benefit from mating multiply because they elicit 'rescue' services from lone males, and simultaneously favor increased vigilance by their original mates.

## Methods

The study was conducted during the summer of 1982, at East Point Pond, at the University of Michigan Biological Station near Pellston, MI, USA (site detailed in Fincke 1982). Most of the *E. hageni* were marked with numbers written on the hindwing with an indelible felt-tipped pen. The main oviposition plants of sedges and *Potamogeton* were sparsely clumped in three areas totaling roughly 60 m<sup>2</sup> at the edge of the pond, where the water was less than 30 cm deep, allowing an unimpeded view of females underwater.

### *Experiment I – Can males detect females underwater?*

Air trapped between the wings gave submerged females a silvery appearance, possibly cueing their presence to mates above, which often made short flights around the perch in the absence of other males. To determine whether males could visually detect the presence of females underwater, I noted the responses of males to live females pinned to sedge stems either 2 or 5 cm below the water surface. Control stems contained only an insect pin. I recorded the number of males perching on each of 3 experimental and control dowels during seven, 10-min replicates, between 1200 and 1500 h. Test stems were alternatively pinned with females to control for any position effects. If other females submerged within the 10 m<sup>2</sup> area during the test time, the run was excluded.

### *Experiment II – Do males guard?*

To determine whether males guarded submerged mates or simply waited at the water for additional females to resurface, I compared the behavior of marked, mated and unmated males perched in an oviposition area. On five days, a total of 14 mated males were observed from the time their female submerged for the first time until either the male left the site or until he seized his resurfacing mate. The behavior of eleven unmated males (so determined because they arrived at the oviposition site alone) was likewise recorded until the male left the oviposition area. For both groups, I recorded the frequency of the following acts:

- (1) *Wing raise*. The wings are raised and may be fluttered briefly while the insect remains perched. This display is often accompanied by a downward curling of the abdomen, and is usually in response to the approach of another individual.
- (2) *Dart*. A flight of less than 4 sec, usually towards an individual that may or may not include actual contact.
- (3) *Chase*. Following another individual beyond 0.3 m from the perch. Absences of > 1 min are scored as leaving the perch.

(4) *Perch change*. A male leaves a perch, returning to another stem in the same oviposition area.

(5) *No response*. A male is approached within 0.2 m by another male but fails to exhibit any of the above behaviors.

### *Experiment III – What are males guarding?*

If males guarded perches rather than mates, they would be expected to abandon females after they submerged, in order to mate with additional females resurfacing in the area. To test this hypothesis, I presented receptive females to 10 'attending' males whose original mates had been submerged for 5–20 min (treatment), and to 12 unmated males perched in the oviposition area (controls). Marked females were collected as they submerged for the first time, and held gently by the wings between two dowels secured by a rubber band, then submerged 4–5 cm underwater. By pulling the dowels apart, I introduced a live, floating female within 0.2 m of a perched 'attending' or control male. I recorded whether or not the female was seized by the male, and if so, whether: (1) the male mated with the female, (2) the female submerged to oviposit with or without mating with the male, (3) the male guarded. The run was excluded if additional females resurfaced in the area.

### *What are the consequences of submerged oviposition?*

To determine the consequences of submerged oviposition to females and males in terms of reproductive gains, and risks involved, 232 marked pairs were followed from the time the female submerged until after she resurfaced. I recorded whether resurfacing females floated in the water and/or were (1) abandoned, (2) grabbed by a mate or by a non-mate (noting in either case whether they mated again), (3) escaped to shore without being taken in tandem, or (4) drowned or were eaten. I determined the fertilization value of females to second mates by counting the mature eggs in females that had mated but not yet oviposited, and in females that had been submerged for varying durations.

To determine if submerged oviposition decreased interference to ovipositing females by lone males, I observed each of 24 tandem pairs continuously for 5 min, noting each time a pair was forced to move to another perch because of interference by a lone male. I determined the effect of exposure on egg hatching by placing 6 sedge stems containing *E. hageni* eggs (laid under field conditions) in aquaria (22–23° C), and noting the time to hatching. The presence of larvae, as well as emergence holes in the eggs enabled me to easily score hatching success. Three of the stems were fully submerged, and the other three were placed such that all of the eggs were exposed to air, while the lower portion of stem was underwater, stuck in sand. To determine if eggs laid at the pond were actually in risk of drying, at the main oviposition areas, I measured the distance from the water's edge to the bank at 2-week intervals from late-June to mid-August, when *E. hageni* were reproductive.

## Results

### *Female oviposition behavior*

After copula, a male remained in tandem with his mate (contact guarding) until she submerged. While females inspected oviposition plants in tandem with mates, they probed stems and, although

they occasionally laid a few eggs above water (maximum = 3 min oviposition,  $n = 24$ ), all of the 232 females observed eventually submerged in a stereotypic manner. A female first backed down the stem until her thorax was level with the water surface. She then curved around the stem, and walked headfirst underwater, at which point her mate, who never submerged more than his abdomen, released her. If lone males persisted in darting at the pair, a male prevented his female from descending by maintaining his hold on her prothorax and flying with her to another perch. Twice, I saw lone males try to grab submerging females that had just been released by mates, but both attempts were unsuccessful.

Females usually descended to the plant base, and all began egg-laying after submerging at least 5 cm (maximum depth = 22 cm). When submerged on the relatively thick sedge and *Potamogeton* stems, females usually remained on the same stem for the duration of the oviposition bout, shifting their position along the stem after inserting a band of about 10–30 eggs half encircling it. If these preferred stems were full of eggs, females walked off of them underwater and onto the thin-stemmed, macrophytic algae, *Chara*. Here, they had to walk about much more, repositioning themselves after the deposition of 1–5 eggs.

Air trapped between the wings and within tracheal airsacs made females buoyant underwater. By releasing her hold upon a stem, a female usually resurfaced with enough force to break through the surface tension and fly. Few females (3/27) resurfaced by climbing all the way up the stem upon which they descended. Females that lost their hold as the result of wave action or walking underwater, ‘popped up’ prematurely.

#### Experiment I – Can males detect females underwater?

Nineteen males perched on the dowels containing females pinned 2 cm below the water surface, whereas only 11 males perched on the control dowels ( $\chi^2 = 5.5$ ,  $P < 0.025$ ). However, there was no significant difference in the frequency with which males perched on dowels with and without females pinned at 5 cm below the surface (10 males on experimental dowels, versus 16 males on control dowels,  $\chi^2 = 1.4$ , ns).

#### Experiment II – Do males guard?

Mated males ‘attending’ underwater females were behaviorally distinct from unmated males perched in the same area (Fig. 1). Males whose mates were submerged were much more likely to dart at, or

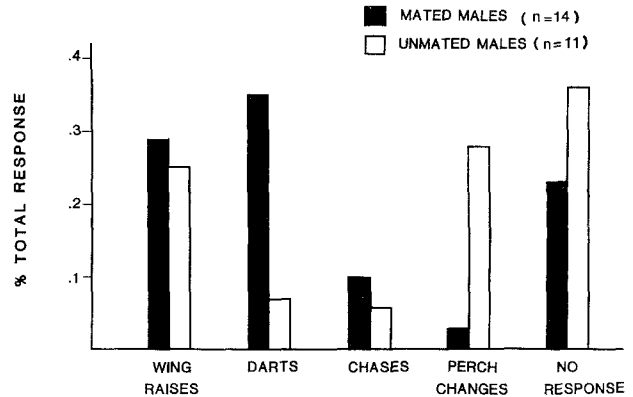


Fig. 1. Response to passing males by perched, mated and unmated males in the same oviposition area

chase other males than were unmated males (darts + chases averaged  $1.0 \pm 0.4$ /min/mated male versus  $\bar{x} = 0.1 + 0.07$ /min/unmated male,  $t$ -test,  $P < 0.05$ ). Mated males rarely changed perches (range 0–2 during total observation/male); unmated, waiting males changed perches repeatedly. In addition, mated males remained in the oviposition areas significantly longer ( $\bar{x} = 22.8 \pm 5.2$  min,  $n = 15$ ) than did unmated males ( $\bar{x} = 6.3 \pm 1.4$  min,  $n = 10$ ,  $t$ -test,  $P < 0.001$ ). Responses by mated males declined the longer a female remained underwater, and males strayed ever more widely from their original perch. Darts plus chases during the first 10 min of guarding averaged  $1.8 \pm 0.7$ /min, dropping to  $0.4 \pm 0.1$ /min during the second 10 min ( $t$ -test,  $P < 0.05$ ). There was no difference between mated and unmated males in their use of wing raising, which was a common response of both sexes when individuals approached too closely.

#### Experiment III – What are males guarding?

Although both the guarding males and the unmated waiting males seized all of the introduced females upon detecting them, their subsequent behavior differed markedly (Table 1). Guarding males treated the experimental females as if they were their original mates. During the time they were observed in tandem, none of the 10 previously mated males copulated or even attempted to copulate with the experimental females presented to them. However, these males guarded experimental females that later submerged (33%). The remaining experimental females did not attempt to submerge during the time they were observed.

In contrast to the previously mated males, 9 of the 12 (75%) unmated control males copulated with females presented to them within  $19.3 \pm 6.7$  min of seizing the females in tandem. The remaining 3 unsuccessful males tried to mate within less than a min after tandem, as evidenced

**Table 1.** Response by males to additional females 'popped up' experimentally

	<i>n</i>	Time observed (min)	Mated	Guarded but did not mate	No. of females resisting
Males with mates underwater	10	221	0	3	3 <sup>a</sup>
Unmated males at the water	12	236	9	0	3 <sup>b</sup>

<sup>a</sup> None tried to copulate<sup>b</sup> All tried to copulate (see text)**Table 2.** Fate of 232 resurfacing females. The fate of an additional 31 females (of which 3 floated), was not known

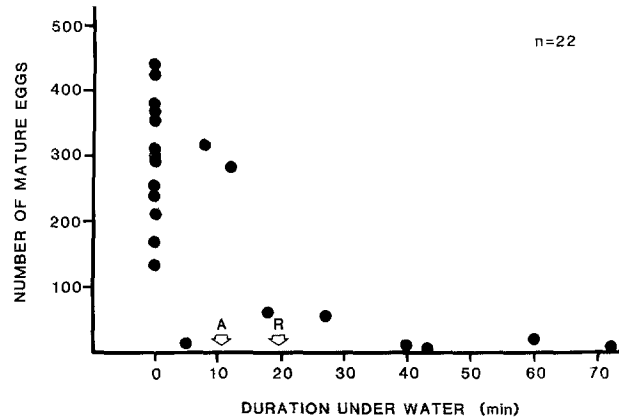
	Seized by		Flew to shore	Died
	Mate	Non-mate		
Floating females	13	19	9	4
Non-floating females	94	46	45	2

Of floating females taken in tandem, more were 'rescued' by non-mates than by mates ( $\chi^2 = 14.8$ ,  $df = 1$ ,  $P < 0.005$ )

by their characteristic jerking on the female's prothorax. The wings of these resisting females had become soaked while floating, and such females typically were unresponsive to males until their wings dried. In contrast to the previously mated, guarding males, none of the waiting control males allowed tandem females to submerge unless they first mated with them.

#### *Fate of ovipositing females*

Females remained underwater on average,  $18.4 \pm 1.3$  min ( $n = 219$ , range 1–128 min), submerging up to 4 times/day ( $\bar{x} = 1.55 \pm 0.4$ ), in order to lay an entire clutch of eggs. As seen in Table 2, upon resurfacing, about a quarter (23%) of the females avoided capture by males and left the pond. Of the 232 females seen to resurface, 19.4% floated in the water, of which two thirds were pulled from the water surface by males. Lone males pulled 42% of the floating females from the water surface, 1.4 times as many as were 'rescued' by original mates. In the absence of vigilant males, a minimum estimate of 31% (4/13) of the floating females (or 0.06 of the total ovipositing females) would die. This represents a risk of 0.09 chance of dying for each clutch a female matured, and a risk of 0.16 per lifetime ( $\bar{x}$  clutches/lifetime = 1.8,



**Fig. 2.** Number of mature eggs in females as a function of the time they had been underwater. Females at time 0 had not yet oviposited that day. 'A' indicates the average time at which females accepted a second mating, and 'R' is the average time at which they rejected males

Fincke 1986a). In the presence of males, females risked only 0.026 chance of dying/clutch. Together, both guarding and waiting males decreased potential female mortality by 71%, while guarding males alone decreased it by 29%.

#### *Fertilization value of resurfacing females*

Roughly half of the resurfacing females (58%) oviposited again the same day. The number of eggs a female carried decreased as a function of the time she had spent underwater (Fig. 2). Upon resurfacing from an oviposition bout, a female either remated or rejected additional males that took her in tandem, depending upon the number of mature eggs she still carried. Once in tandem, a male jerked his point of attachment on the female's prothorax. Only if the female responded by curving her abdomen upward to touch his secondary genitalia, did he transfer sperm to his sperm vesicle, after which he again jerked the female, and copulation occurred when she again raised her abdomen to engage her genitalia with the male's. Unreceptive females maintained a straight abdomen, and were released within 10 min.

Females that accepted a second mate had previously been submerged for  $10.5 \pm 2.2$  min ( $n = 31$ ), while those that rejected second males had been submerged for  $19.5 \pm 3.0$  min ( $n = 18$ ,  $t$ -test,  $P < 0.05$ ). As seen in Table 3, lone males did not differentially seize resurfacing females of high fertilization value. Second mates of females resurfacing after their first bout had a 0.53 (18/34) chance of fertilizing a partial clutch, and a 0.26 (9/34) chance of fertilizing greater than 50% of a clutch.

A mated male recopulated with his original mate only if she had been submerged for more than 27 min ( $\bar{x} = 38.5 \pm 5.4$  min,  $n = 15$ ), which cor-

**Table 3.** Fertilization value of females seized by a second male. Percentage of clutch available for fertilization was estimated from an average rate of oviposition of 13 eggs/min, and total clutch size of 400 eggs (Fincke 1985)

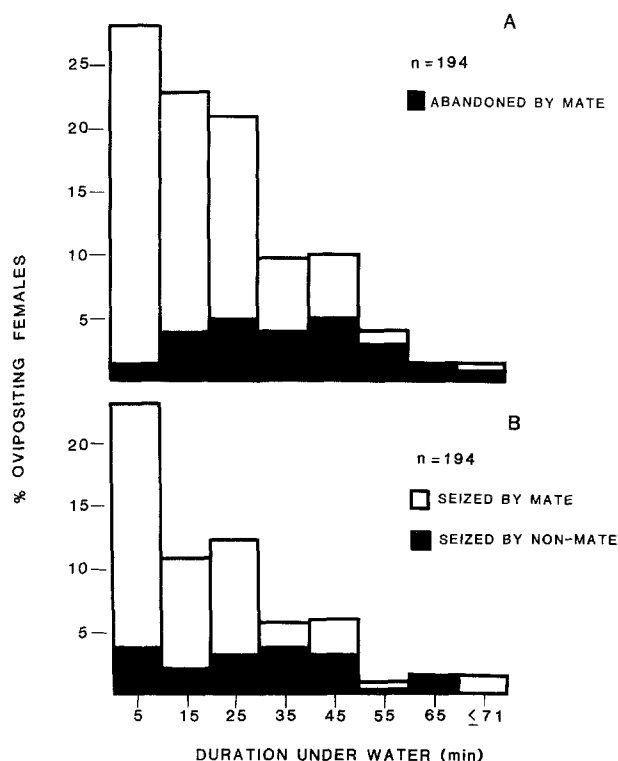
Duration of oviposition (min)	No. of second males seizing females	% of clutch available for fertilization
1-10	9	64-94
11-20	3	32-63
21-30	6	0-31
>30	16	0

responded closely to the time required for females to lay a complete clutch ( $\bar{x}=32.3 \pm 2.2$  min,  $n=11$ ). In contrast, females that were not re-mated, but that were subsequently guarded by their original mate, had been submerged for shorter durations ( $\bar{x}=14.4 \pm 1.3$  min,  $n=47$ ,  $t$ -test,  $P<0.001$ ). The duration of second copulations did not significantly differ from that of first copulations ( $\bar{x}=26.2 \pm 3.1$  min,  $n=22$ ; versus  $\bar{x}$  of second copula =  $28.4 \pm 4.4$  min,  $n=18$ ,  $t$ -test, ns). This is contrary to earlier results based on 3 observations (Fincke 1982).

#### *Success of guarding and its benefit to males*

As seen in Fig. 3A, few males abandoned their mates. First mates were successful in seizing their female 75% of the time, and 50.2% ( $n=194$ ) of the males seized their females between all of their bouts on a given day. Some males persisted in guarding for up to a total of 117 min ( $\bar{x}=71.7 \pm 9.2$  min,  $n=25$ ), even after their mates had resurfaced unnoticed. Of the 48 males (25%) that abandoned females before they resurfaced, 6 accepted other resurfacing females as their own mates, one was eaten by a frog, and the remaining left after guarding for an average of  $24.1 \pm 2.6$  min. Although 34% of the abandoning males seized additional females later that day, only 9% of these females were still receptive to mating, resulting in a 0.03 chance of securing additional fertilizations that day.

As seen in Fig. 3B, 14.6% of first mates lost some fertilizations to waiting males. Twenty-eight percent of the resurfacing females were seized by a second male, and of these, 52% remated. If males did not guard at all, they risked losing fertilizations either by death of a mate before she completed egg-laying ( $0.06 \times 18/34 = 0.03$  risk), or to another male ( $0.39$  risk,  $172/232 \times 0.52$ ). The average duration of a first oviposition bout was  $20.5 \pm 2.2$  min, or 70% of the average total oviposition by a female on a given day ( $\bar{x}=29.4$  min,  $n=86$ , Fincke 1985). Thus, by guarding a fully gravid female until she



**Fig. 3A, B.** Frequency distribution of ovipositing females. **A** The proportion of females that were abandoned by their original mates increased from 2% after <10 min of oviposition, to 75% after 60 min of submergence. **B** The proportion of the total ovipositing females that were seized by non-mates increased from 4% after <10 min submergence, to 50% after 40 min submergence. The difference in total females represented in **A** and **B** are those that avoided capture by males and flew to shore

had finished oviposition, a male was insured of fertilizing a maximum of 30% more eggs than he would have if he abandoned his mate immediately after she submerged.

#### *Costs and benefits of submerged oviposition*

Even in the presence of males, resurfacing females risked a 0.02 chance of dying/bout from floating after resurfacing, and the toll on others was not immediately apparent. In one case, a female emerged from the water exhausted, crawled up a perch, and died there within a few hrs. Of the 263 ovipositing females observed, 10.6% of the females, most of which were hidden from view in clumps of *Chara*, were not seen to resurface. If all lost females were assumed to have died, the risk to females per oviposition bout would increase to a maximum estimate of 0.13 ( $34/263$ ).

By submerging to oviposit, females reduced the likelihood that their eggs would dry out before hatching. Between June and August, the shoreline receded 1.5 m from the bank. By late July, roughly half of the original oviposition areas were com-

pletely exposed. Although eggs in the lab normally hatch within two to three weeks (Fincke 1984b), none of the eggs ( $n=637$ ) in the stems exposed in the lab had hatched after 45 days, whereas 96.3% ( $n=712$ ) of the eggs in the submerged stems hatched successfully during this time.

In addition to allowing most females to oviposit continuously on the same stem, submergence also prevented interruptions of oviposition by unmated males at the water. Tandem females that attempted to probe stems and/or oviposit above water were interrupted by lone males on average 7.4 times/5-min observation period (range 2–14 times,  $n=24$ ).

### Discussion

Even though males appear unable to detect females underwater, except those just beneath the surface, two results support the conclusion that male *E. hageni* non-contact guard submerged mates. The response of a mated male to approaching males decreases as the fertilization value of his mate declines, the longer she has been submerged. If males defended territories at perch sites rather than mates, one would expect the guarding response to remain high even after the females left the area. Secondly, 'attending' males do not mate with additional females presented to them at the water within 20 min from the time their original mate submerges. If such males were waiting at oviposition areas in order to seize additional females at the water, they would be expected to mate with additional females presented to them, as do lone males.

To avoid confusion in cross-species comparisons, it is important to clearly distinguish mate-guarding, and/or localization for mate-searching, from territoriality associated with resource-defense polygyny (see Emlen and Oring 1977). For example, 'territoriality' has been ascribed to a damselfly which guards submerged mates (Utzeri et al. 1983), as well as to a coenagrionid whose females oviposit in tandem with mates (Harvey and Corbet 1985). Yet none of these authors have provided evidence that coenagrionid males repeatedly exclude others from an oviposition area even in the absence of females. In contrast, such behavior is characteristic of territorial odonates which obtain matings by defending resources needed by females (e.g. Heymer 1972; Waage 1979a; Fincke 1984a; McVey 1986). Contrary to Waage (1984), who describes non-contact guarding as found only in territorial, 'behaviorally advanced' odonates (e.g. *Calopterygidae* and *Libellulidae*), and absent in damselflies that submerge, non-contact guarding is common in non-territorial coenagrionids that oviposit underwater. Females of *Enallagma bor-*

*eale*, *E. ebrium* (personal observation), *E. civile* (Bick and Bick 1963), *E. aspersum* (Jacobs 1955), and *E. cyathigerum* (Robert 1958), all submerge, and their mates exhibit behavior similar to that of guarding *E. hageni* (although mate guarding for these species has not experimentally demonstrated).

Mate guarding is considered to have evolved in the context of sexual selection, to protect a male's sperm investment from conspecific males competing for fertilizations (e.g. Parker 1970; Alcock 1979; Waage 1979b; Sillen-Tullberg 1981). As a consequence of multiple mating by females, mate guarding allows females to oviposit uninterrupted by additional males trying to mate with them (e.g. Sherman (1983). In species such as *E. hageni*, where the chance of encountering a female is low, and where, after mating, males protect females from *other* than conspecific males, sperm competition may not have been a necessary precondition for the evolution of mate guarding. Even if female *E. hageni* mated only once per lifetime, guarding by their mates would be selectively favored because a male that 'rescued' his female would insure that she lived to lay the maximum number of eggs he could fertilize per mating. Once females began to mate multiply, the selective advantage of vigilance to males would have been even greater, because males that abandoned mates would then also risk losing fertilizations to competing males.

Unlike territorial species, where some males acquire a disproportionate number of matings/day, but usually guard a mate for only a portion of her total oviposition duration/day (e.g. Campanella and Wolf 1974; Waage 1979a; Fincke, unpublished observation), successful *E. hageni* males rarely obtain more than one mate per lifetime (Fincke 1986a). For *E. hageni*, where the relatively high density of males around few available oviposition sites makes territoriality inefficient, submergence by females favors males that maximize the number of fertilizations/mate, because females occasionally resurface prematurely, and the probability of encountering a second receptive female is low (see also Alcock 1982). Mate fidelity, at least until a female has laid her clutch, is insured by a conditional latency to remating, which is much longer than the physiological refractory period. In an insectary, males successively mate at a minimum of 4-min intervals (personal observation). Other non-territorial damselflies whose females submerge, exhibit an equally extreme variation of guarding by following their mates in tandem underwater (e.g. *Lestes sponsa*, *Erythromma nais*, Robert 1958).

Remating increases the time a pair is at the

water where the risk of predation is relatively high (Fincke 1982). For guarding *E. hageni* males, remating between oviposition bouts is advantageous only after guarding for greater than about 20 min. After this time, mated males begin to wander further and further from the perch on which their females descended and are thus more likely to seize non-mates. Most of the resurfacing females that a male encounters have laid all of their eggs and are unreceptive. Thus, males conserve sperm and seminal fluids by not translocating sperm to their sperm vesicles unless they receive a signal of receptivity from tandem females. This test of female receptivity allows unwilling females to be released with a minimum waste of time.

If underwater oviposition is risky, why do females submerge? Submergence is not a physiological prerequisite for egg-laying because some *E. hageni* females lay a few eggs in tandem with mates (and lay into moistened filter paper in a cage). For species laying non-diapause eggs, the benefits of submerged oviposition may vary as a function of: (1) oviposition substrate, (2) the density of above, versus underwater predators, and (3) water temperature and/or the amount of vegetation present, (4) the density of lone males at the water. Many damselflies that oviposit above water do so on mats of floating vegetation (e.g. *Ischnura verticalis*, *Platycnemis pennipes*, personal observation), or into flexible stems that bend over in streams (e.g. *Calopteryx virgo*, personal observation). Either type of substrate would rise and fall with the water level, and eggs would not be in danger of drying if the water level dropped. In contrast, females that submerge to oviposit primarily use either upright stems of emergent vegetation, or submerged algae. By submerging, *E. hageni* females decrease the chance of egg desiccation.

Secondly, females may be safer by ovipositing underwater on large stems on which they move minimally, than if they repeatedly reposition themselves on mats above water, where they attract the attention of frogs or other aquatic predators. Very shallow pools clogged with vegetation and/or with high water temperatures may effectively preclude the possibility of submergence. *E. hageni* females do not remain submerged at water temperatures of 37° C or above (Fincke 1985). Thus, some species, such as *Erythromma viridulum*, may persist in ovipositing above water in spite of high rates of predation by an aquatic hemipteran (M. Eldridge, personal communication).

Submergence enables females to minimize the time needed to oviposit a clutch, because females can use a continuous section of stem, and avoid interruptions due to wind, and wave motion at the water surface. Furthermore, submerged female

*E. hageni* oviposit more or less continuously underwater, whereas those attempting to oviposit in tandem above water are often interrupted by lone males. Assuming that females ovipositing above water would not be harassed unless they mated multiply per day, protection from conspecific harassment is best viewed as an incidental effect of, rather than the primary impetus for, submerged oviposition by females.

I suggest that for *E. hageni*, the risks associated with submergence favor multiple mating by females. Mating in excess of that needed for sperm replenishment should not be considered a neutral activity for these females. Unwilling females cannot be forced to mate, and within-clutch matings carry additional costs to females of increased risk of predation and/or physical damage by competing males, who occasionally force mated pairs into the water. None of the previously hypothesized benefits of multiple mating (Walker 1980; Waage 1984), can sufficiently explain rematings in *E. hageni*. Remating between oviposition bouts on the same day is not necessary for sperm replenishment, because females carry nearly full sperm load after oviposition (Fincke 1984b). For *E. hageni* whose females remate between clutches, additional genetic diversity gained by mating within clutches is probably minimal, and unlikely to outweigh the risks accompanying additional submergings. Nutritional gains from multiple matings are improbable because males remove sperm from the previous mating (Fincke 1984b). My data argue against remating as a form of mate choice for *E. hageni*. Rejection of a male by a tandem female can be predicted by knowing her egg load, females do not discriminate among males on the basis of size or age, and second mates are not significantly larger than first mates (Fincke 1986a). Finally, the argument that remating gives ovipositing females protection from harassment by unmated males, is a circular one. If females were monogamous, they would not need protection from unmated males (e.g. Fincke 1986b).

My results support the hypothesis that female *E. hageni* effectively 'exchange' fertilizations for vigilance and 'rescue' service by males. Females that resurface improperly benefit from the vigilance of unmated, waiting males as well as guarding mates, because 1/4 of their mates leave the area while they are still submerged. Unless females mated again, selection would not favor lone males that pull previously-mated females from the water. Assuming that females originally mated only once/day, selection would have favored unmated males that continued their search for females at the water because unmated females occasionally arrive at the pond before being discovered by a male (per-

sonal observation). Despite their lower fertilization value, resurfacing females are the only receptive females available to males that fail to mate earlier in the day, and contribute substantially to total lifetime reproductive success of males (Fincke 1985). The inability of males to discriminate between receptive and unreceptive females before pulling them from the water, enables even unreceptive females to benefit from this male service.

Other female insects gain similar services from males by mating multiply within a clutch. For example, normally unreceptive female soldier beetles that carry few or no eggs will mate repeatedly in the presence of aggressive wasps. Mating females are 3–9 times less likely to be forced off their food source by wasps than are single females (McLain 1981). Apterous female phorid flies (Miller 1984) and other dipterans (e.g. Borgia 1981) benefit by remating because they may then be carried to additional oviposition sites by their winged mates. A closer examination of insect mating systems from a female perspective should uncover other such male services gained by females in exchange for fertilizations.

*Acknowledgements.* I am grateful to R. Drapcho for field assistance, and to the University of Michigan for logistical support. E. Leigh, L. Loveless, S. Mulkey, D. Schemske, J. Waage, H. Wolda, and two anonymous reviewers provided helpful comments on the ms. Financial support was provided by a grant-in-aid from the Arco Corp., and a Teaching-Research Fellowship from the University of Iowa. This work was conducted in partial fulfillment of a Ph.D. degree from The University of Iowa.

## References

- Alcock J (1979) Multiple mating in *Calopteryx maculata* (Odonata: Calopterygidae) and the advantage of non-contact guarding by males. *J Nat Hist* 13:439–446
- Alcock J (1982) Post-copulatory mate guarding by males of the damselfly *Hetaerina vulnerata* Selys (Odonata: Calopterygidae). *Anim Behav* 30:99–107
- Bick G, Bick J (1963) Behavior and population structure of the damselfly *Enallagma civile* (Hagen). *Southwest Nat* 6:57–84
- Boggs CL, Gilbert LE (1979) Male contribution to egg production in butterflies: Evidence for transfer of nutrients at mating. *Science* 206:83–84
- Borgia G (1981) Mate selection in the damselfly *Scatophaga stercoraria*: female choice in a male-controlled system. *Anim Behav* 29:71–80
- Campanella PJ, Wolf LL (1974) Temporal leks as a mating system in a temperate zone dragonfly (Odonata: Anisoptera) I. *Plathemis lydia* (Drury). *Behaviour* 51:49–87
- Emlen ST, Oring LW (1977) Ecology, sexual selection, and the evolution of mating systems. *Science* 197:215–223
- Fincke OM (1982) Lifetime mating success in a natural population of the damselfly *Enallagma hageni* (Walsh) (Odonata: Coenagrionidae). *Behav Ecol Sociobiol* 10:293–302
- Fincke OM (1984a) Giant damselflies in a tropical forest: Reproductive biology of *Megalopterus coeruleatus* with notes on *Mecistogaster* (Odonata: Pseudostigmatidae). *Ad Odonatol* 2:13–27
- Fincke OM (1984b) Sperm competition in a non-territorial damselfly (Odonata: Coenagrionidae): benefits of multiple mating to males and females. *Behav Ecol Sociobiol* 14:235–240
- Fincke OM (1985) Alternative mate-finding tactics in a non-territorial damselfly (Odonata: Coenagrionidae). *Anim Behav* 33:1124–1137
- Fincke OM (1986a) Sources of variation in lifetime reproductive success in a non-territorial damselfly (Odonata: Coenagrionidae). In: Clutton-Brock T (ed) *Reproductive Success*. University of Chicago Press (in press)
- Fincke OM (1986b) Female monogamy in the damselfly *Ischnura verticalis*. *Odonatologica* (in press)
- Friedel T, Gillot C (1977) Contribution of male produced proteins to vitellogenesis in *Melanoptus sanguinipes*. *J Insect Physiol* 23:145–151
- Gwynne DT (1984) Courtship feeding increases female reproductive success in bushcrickets. *Nature* 307:361–362
- Harvey IF, Corbet PS (1985) Territorial behavior of larvae enhances mating success of male dragonflies. *Anim Behav* 33:561–565
- Heymer A (1972) Comportements social et territorial des *Calopterygidae* (Odonata: Zygoptera). *Ann Soc Entomol Fr* 8:3–53
- Jacobs ME (1955) Studies on territorialism and sexual selection in dragonflies. *Ecology* 36:566–586
- McLain DK (1981) Interspecific interference competition and mate choice in the soldier beetle *Chauliognathus pennsylvanicus*. *Behav Ecol Sociobiol* 9:65–66
- McVey ME (1986) The opportunity for sexual selection in a territorial dragonfly *Erythemis simplicicollis*. In: Clutton-Brock T (ed) *Reproductive Success*. University of Chicago Press (in press)
- Miller PL (1984) Alternative reproductive routines in a small fly, *Puliciphora boringuenensis* (Diptera: Phoridae). *Ecol Entomol* 9:293–302
- Parker GA (1970) Sperm competition and its evolutionary consequences in the insects. *Biol Rev* 40:525–567
- Robert PA (1958) Les libellules (Odonates). Delchaux et Niestle SA, Neuchatel
- Sherman KJ (1983) The adaptive significance of postcopulatory mate guarding in a dragonfly, *Pachydiplax longipennis*. *Anim Behav* 31:1107–1115
- Sillén-Tullberg B (1981) Prolonged copulation: a male post-copulatory strategy in a promiscuous species *Lygaeus equestris* (Heteroptera: Lygaeidae). *Behav Ecol Sociobiol* 9:283–289
- Smith RL (1979) Repeated copulation and sperm precedence: paternity assurance for a male brooding water bug. *Science* 205:1029–1031
- Thornhill R (1980) Mate choice in *Hylobittacus apicalis* (Insecta: Mecoptera) and its relation to some models of female choice. *Evolution* 34:519–538
- Utzeri C, Falchetti E, Carchini G (1983) The reproductive behaviour in *Coenagrion lindeni* (Selys) in central Italy (Zygoptera: Coenagrionidae). *Odonatologica* 12:259–278
- Waage JK (1979a) Adaptive significance of postcopulatory guarding of mates and nonmates by male *Calopteryx maculata* (Odonata). *Behav Ecol Sociobiol* 6:147–154
- Waage JK (1979b) Dual function of the damselfly penis: Sperm removal and transfer. *Science* 203:916–918
- Waage JK (1984) Sperm competition and the evolution of odonate mating systems. In: Smith RL (ed) *Sperm competition and the evolution of animal mating systems*. Academic Press New York, pp 251–290
- Walker WF (1980) Sperm utilization strategies in nonsocial insects. *Am Nat* 115:780–799