

Alternative mate-finding tactics in a non-territorial damselfly (Odonata: Coenagrionidae)

OLA M. FINCKE*

Program in Evolutionary Biology and Behavior, Department of Zoology, The University of Iowa, Iowa City, Iowa 52242, U.S.A.

Abstract. Males of the non-territorial damselfly *Enallagma hageni* have two alternative tactics for finding mates: (1) they search the banks of the pond for unmated females (searching tactic), or (2) wait at oviposition sites for females that resurface prematurely from underwater oviposition (waiting tactic). Although the searching tactic yielded more fertilizations than the waiting tactic, for time invested, the waiting tactic became increasingly successful later in the reproductive season due to changes in female oviposition behaviour. The two tactics can be maintained in the population because males can mate by the waiting tactic during the afternoon when few females are available to searchers. Among males visiting the breeding site an equal number of times, males mating by a mixture of tactics were as successful as males mating only by the main tactic. Because marked males were found to use both tactics, these behaviours are interpreted as evidence of behavioural plasticity within individuals, representing one conditional evolutionary strategy.

Ethologists have tended to view mating behaviour as characteristically species-specific and highly stereotyped, functioning to minimize matings between similar species. Mating behaviour in natural populations, however, shows considerable intra-specific variation (reviewed by Cade 1980; Thornhill & Alcock 1983). Within a population, variation in male mating behaviour is usually ascribed to competition among males for females, in response to a single female behaviour pattern (Cade 1980; Rubenstein 1980; West-Eberhard 1985). Variation in female behaviour could also favour variation in male behaviours (e.g. Alcock et al. 1979), but this view is not often considered.

Alternative mating behaviour may arise either when age or size affects mating success, or when changing densities of males and females or environmental fluctuations enable more than one behaviour to be successful. Proximal mechanisms responsible for alternative behaviours include: (1) genetic polymorphisms, in which each genotype uses a particular behaviour (Cade 1981), (2) ontogenetic switches in behaviour as triggered by age or size (Howard 1978; Alcock et al. 1979; Arak 1983 and references therein), (3) behavioural plasticity, whereby behaviour changes in response to cues reflecting environmental conditions (Otte & Joern 1975; Thornhill 1979, 1981; Cade 1981), or (4)

probabilistic switches in behaviour, independent of context (Brockmann et al. 1979).

I identified two variants in male mate-finding behaviour in the common temperate damselfly *Enallagma hageni*, as part of a study of lifetime reproductive success in this species (Fincke 1982, in press a). I use the term 'tactic' to refer to a specific behaviour pattern, one or more of which could comprise an evolutionary strategy. Herein I address four major questions about the nature of the two variants. (1) Do these tactics represent genetic polymorphism, an ontogenetic switch, or behavioural plasticity? (2) What is the relative profit of each tactic, in number of eggs fertilized per unit time? (3) How are the relative profits affected by changes in female behaviour over the season and between habitats? (4) How are the two tactics maintained by natural selection?

Natural History of *Enallagma hageni*

Enallagma hageni is a short-lived (\bar{x} estimated lifespan = 12–13 days) coenagrionid damselfly that breeds around clumped oviposition sites on quiet lakes or ponds. Fincke (1983) has described the reproductive biology of this species in detail. To summarize, male *E. hageni* do not hold territories, and larger males show no advantage over smaller males in lifetime success (body size is fixed at emergence as adults). Males visit the breeding site every other day, whereas females spend most of

* Present address: Department of Zoology, The University of Oxford, Oxford OX1 3PS, U.K.

their time in nearby feeding areas, returning to the pond on an average of once per 5.1 ± 0.7 days ($N=69$) to deposit a clutch of eggs. They re-mate between successive clutches but may also mate with up to three different males per day while ovipositing a given clutch. The last male to mate with a female fertilizes up to 95% ($\bar{x}=80\%$) of her clutch (Fincke 1984). Females may begin oviposition in tandem with males, but eventually submerge completely to insert eggs in the base of aquatic plant stems (sedges and the arrowhead, *Potamogeton*), or in masses of the macrophytic alga, *Chara*. While a female is under water, her mate defends the perch, darting at passing males but tolerating those perched nearby, usually seizing the female when she resurfaces. Guarding males are behaviourally distinct from unmated males at the water (Fincke, in press b). Although females under water are inaccessible to males, non-contact guarding protects a male's sperm investment by preventing another male from seizing his mate should she be disturbed and resurface before laying a complete clutch of eggs. Guarding also benefits both males and females by insuring that females will live to lay an entire clutch. Females sometimes fail to resurface properly and float in the water where they are susceptible to drowning and predation (Fincke 1983). Floating females may be taken in tandem by guarding mates or lone males who then pull them up from the water. Guarding males do not re-mate with their original female unless she has been submerged for longer than about 25 min. If females still have eggs to lay, they remain receptive, and will copulate with a second male (Fincke, in press b).

Males can use two tactics to find mates because: (1) females will re-mate with more than one male on a given day, (2) a female does not always deposit a full clutch during her first oviposition bout, and (3) guarding males sometimes abandon mates (particularly those submerged for more than 25 min), or do not notice females when they resurface. A male mating by the searching tactic seizes a female in the adjacent field or around the edge of the pond, and after mating with her, away from the water, remains in tandem with her until she submerges. In contrast, a male mating by the waiting tactic flies to the pond alone, perching at oviposition sites or patrolling around them until he seizes another male's mate as she resurfaces from an oviposition bout. Waiting males usually mate at the oviposition site. Males mating by either tactic guard submerged mates.

Lone males may also harass a tandem pair until a female is accidentally released by her mate, or they may seize a female as she submerges, just after her mate has released her normally. Because such behaviour rarely succeeded (accounting for less than 2% of the pairings), I do not treat it as a significant alternative in my study populations. However, under conditions of greater male density, or where females spend more time ovipositing in tandem, this tactic may represent a successful alternative.

METHODS

The main population of *E. hageni* described here reproduced at East Point Pond, a small isolated beach pool (110 m perimeter, 0.5 m deep) on the shore of Douglas Lake at the University of Michigan Biological Station near Pellston, MI. In order to distinguish genetic polymorphism from ontogenetic switching or behavioural plasticity, I followed marked tandem pairs for as long as possible throughout the day. Pairings involving 84 marked females and 105 marked males were followed on 17 days, spanning a 28-day reproductive period. Individuals were marked by writing a number on the forewing with an indelible felt-tip pen. Wing numbers could be read easily at close range, since an observer could move slowly around the edges of the oviposition areas without disturbing the insects. I used binoculars to identify numbers on more distant pairs. Forewing length, an indicator of body size, was measured with calipers to determine if use of the two tactics was size-dependent (and controlled by an ontogenetic switch during larval development). Reproductive span was estimated as the number of days spanning first and last sightings of a sexually mature individual.

The relative success of each tactic over the season was analysed using a modified version of Parker's (1974) optimization model which maximizes the gains (eggs fertilized) per investment (time spent searching for, mating with, and guarding mates). I calculated the total gain per *E. hageni* female taken in tandem by a searching male as:

$$G_s = P_m[(1 - P_t)(y_0) + P_t(y_1 + 0.2(y_0 - y_1))]$$

P_m is the probability of successfully mating with a female taken in tandem, $1 - P_t$ is the probability that

a male fertilizes a female's entire clutch, and y_0 is the average number of eggs per clutch. The probability of intervention, P_i , is the frequency with which a female re-mates with another male after resurfacing. In this case, the first male fertilizes 0.2 of her remaining clutch (due to incomplete sperm displacement by the second male). y_1 is the number of eggs deposited in the first oviposition bout by females that mate with another male upon resurfacing, and $y_0 - y_1$ is the average number of eggs such females carry when they resurface; y_0 is the average number of eggs a male fertilizes if no other male intervenes, and $y_1 + 0.2(y_0 - y_1)$ is the average number of eggs fertilized by a first male (searcher) if the female mates again before completely laying her clutch.

The profit of the waiting tactic was calculated only for males seizing a female after her first bout because too few waiting males seized females after their second or third bout for me to calculate an estimate of gains. The gain per female taken in tandem by a waiting male was calculated as:

$$G_w = P_m[0.8(1 - P_i)(y_0 - y_1) + P_i\{y_2 + 0.2(y_1 - y_2)\}]$$

The maximum number of eggs that a waiting male could fertilize is $y_0 - y_1$; y_2 is the average number of eggs laid in the second oviposition bout by females who re-mate upon resurfacing; $y_2 + 0.2(y_1 - y_2)$ is the number of eggs fertilized by a waiting male if his female re-mates with another male after she resurfaces.

Investments for each tactic were calculated as:

$$I = e + P_m(T_i) + (1 - P_m)T_r$$

Encounter time, e , is the time required to find and take a female in tandem. T_i is the total time spent on a successful mating from the time tandem begins to the time a male abandons his guarding post. $1 - P_m$ is the probability that a male is rejected by a tandem female, and T_r is the time from initiation to abandonment of tandem when a male's mating attempt is unsuccessful. T_r , assumed to be constant for each tactic throughout the reproductive season, was 4.8 ± 0.9 min ($N = 17$) for the searching tactic and 7.2 ± 1.7 min ($N = 24$) for the waiting tactic. For each tactic, I calculated the profit per unit effort as G/I .

Values used in the above equations were obtained from 25 complete (i.e. from initial pairing of a female until her release after her final oviposition bout of the day) and 240 partial sequences with

different pairs of individuals. I noted the duration of unsuccessful and successful mating attempts, the duration of copulation and oviposition, the type of plant used for oviposition, guarding duration and success of males, and the fate of resurfacing females. Means are given with their standard errors; mean durations of behavioural acts were calculated using only those cases for which the beginning and end were seen.

For the purpose of analysis, I made the assumption that after a female's first mating, all subsequent males mating with her on a given day used the waiting tactic, except when the first male was rejected by the female (i.e. he failed to mate with her and/or did not accompany her to the oviposition site). Of the 449 pairings seen, only 3% involved females who were found in tandem with another male within 50 min of a pairing by the first male (and thus may have rejected the first male). If a female was not seen ovipositing but was known to have been in tandem for more than 50 min with the same male, she was assumed to have mated and to have had at least one oviposition bout. Any subsequent male with whom she was seen was assumed to be a 'waiter'. I assumed that females escaping to shore after laying eggs oviposited no more that day (none of the 54 females seen to fly to shore did so). While I noted the position of as many single males as possible, it was not feasible to follow them continuously and still get data on tandem pairs. The two tactics are thus discussed in terms of the successful use of each, rather than in terms of attempted but unsuccessful use (which was estimated as a function of encounter rates, see below).

Each submergence by a female was considered an oviposition 'bout' regardless of the time a female remained under water. I estimated the number of eggs a given male fertilized by multiplying the duration of submergence of mates by the rate of oviposition. I calculated oviposition rate by timing the duration of egg laying on unused *Potamogeton* stems and counting the number of eggs deposited. Thirty seconds after a female began to oviposit under water, I transferred her (still under water) to a fresh *Potamogeton* stem positioned next to the original stem. Only transferred females that began to oviposit on fresh stems within 10 s were used. Water temperature was measured in the shade at a depth of about 5 cm from the pond bottom in the centre of the oviposition area. To measure the effect of seasonal and/or daily changes in water temperature on the rate of egg laying, I submerged

females by hand on fresh stems placed in water-filled 1-litre jars (23–37°C), timed them for 10 min of continuous oviposition, and then counted the number of eggs deposited.

The amount of time invested for each tactic was more difficult to estimate than the gains because it was impractical to watch males before they had a female in tandem. I calculated the time to encounter a female as the time over which receptive females were available to males (roughly 4 h for each tactic), multiplied by the number of males seeking mates on a given day, divided by the number of receptive females available to such males. For searchers, the number of males/receptive females was estimated using the average total number of males and mating females visiting the pond per day. To estimate the operational sex ratio for waiters, I counted, at hourly intervals, the maximum number of single males, females and tandem pairs seen within a 5-min period in a 20-m² sector at the water (representing 30–40% of the total oviposition area, depending upon the time of season) and in two 20-m² sectors on the bank of the pond (roughly 60% of the bank area through which females arrived at the pond). By dividing the average number of males/female/20-m² at the water by the average number of males/female/20-m² on the bank, I estimated, on 10 days over an 18-day span, the proportion of males visiting the pond that later waited at oviposition sites on a given day. This estimate assumes that all females seen on the bank moved later to oviposition sites. The number of receptive females available to waiters was calculated by multiplying the total number of receptive females by the proportion of females that neither escaped to shore nor were seized by mates upon resurfacing. Because my estimates of encounter times are the least direct estimates in the model, the data for gains/investments are presented with and without encounter times.

I assessed seasonal trends in reproductive behaviour by dividing the season from June 26 to July 23 into three roughly equal periods: early = days 1,2,3,6,10; mid = days 11,13,14,18,19; and late season = days 20,21,22,23,24,26,28, and compared the gains/investments by period. An additional 31 mated pairs from a second population at Lake Cathleen (12 km away) were used to compare the success of the two tactics under different environmental conditions. At this site, oviposition was limited to a quiet bay (about 500 m²) where females

submerged to a greater depth (1–1.5 m) than was possible in the shallow beach pool. Finally, to determine how the two tactics are maintained by natural selection, I compared the total number of matings and eggs fertilized by males mating only by the searching tactic with those of males mating by a mixture of tactics.

RESULTS

The Use of Tactics by Individual Males

Thirteen per cent of the males mating by the searching tactic mated successfully by the waiting tactic on the same day. Of the 55 males which I saw

Table I. Number of matings by searching and waiting tactics performed by males of different ages

	Relative age of male (days)			
	1–4	5–10	11–16	> 16
Searching tactic	47 (47.6)	29 (27.0)	18 (20.6)	9 (7.8)
Waiting tactic	20 (19.4)	9 (11)	11 (8.9)	2 (3.2)

Expected values are in parentheses. There was no significant use of one or the other tactic with respect to relative age of the male ($\chi^2 = 2.3$, $df = 3$, NS).

Table II. Pattern of successful use of searching and waiting tactics

Initial tactic used	Subsequent tactic used	
	Searching	Waiting
Searching	53 (53.5)	39 (38.4)
Waiting	36 (35.5)	25 (25.5)

Expected values are in parentheses. There was no significant effect of the initial tactic used successfully on the subsequent tactic used successfully ($\chi^2 = 0.03$, $df = 1$, NS).

mate at least twice in their lifetime, 41 (75%) obtained mates by both tactics while one male mated only by the waiting tactic and 13 males (24%) mated only by the searching tactic. All of these last 13 males were seen perching at oviposition sites on days when they were unsuccessful in obtaining a mate. Of the 50 males seen to mate only once, 30 mated by searching and 20 used the waiting tactic to seize resurfacing females.

The relative success with which a male used a given tactic was unaffected by its body size. First mates (of 71 females remating again that day) were no larger (\bar{x} wing length = 17.6 ± 0.06) than subsequent mates using the waiting tactic ($\bar{x} = 17.4 \pm 0.06$, *t*-test, NS). Nor did use of a tactic depend on a male's age (Table I) or the tactic by which it last mated (Table II).

As seen in Table III, the searching tactic was generally used earlier in the day than was the waiting tactic (which could only be successful after some males had found females by searching). Although the average time of first pairing of mates was 1400 and 1530 hours for searchers and waiters respectively, the use of the two tactics was not strictly time-dependent. On any given day, some

marked males (26–47%, $\bar{x} = 35.5\%$) were repeatedly found on the bank throughout the day. During the first half of the season, few unmarked males (1.6 ± 0.4 males/day, *N* = 6 days) were seen waiting at the oviposition sites before 1200 hours, while during the second half an average of 4.8 ± 1.1 males/day (*N* = 6) were perched there as early as 1000 hours.

Relative Profit of Each Tactic

The mean total oviposition duration of the mates of males using the searching tactic was not significantly different from that of males mating by the waiting tactic (Table V; ANOVA, *P* > 0.05). Waiting males were less likely to seize a gravid female (which had submerged less than 10 min and would thus still have most of a clutch left to fertilize) over a spent one (submerged for > 30 min) than would be expected by chance (Table IV).

The similarity in gains of males mating by each tactic does not account for differences in the investments, nor the number of males that tried using a tactic before one was successful. From the optimization model, one sees that the gain/invest-

Table III. Time of day of first tandem pairings in early, mid-, and late season by males using the two tactics

	Proportion of males pairing by:			
	1200 hours	1400 hours	1600 hours	1800 hours
Early season				
Searching tactic (<i>N</i> = 70)	0.28	0.52	0.82	0.99
Waiting tactic (<i>N</i> = 13)	0.08	0.23	0.69	1.00
Mid-season				
Searching tactic (<i>N</i> = 65)	0.19	0.54	0.84	1.00
Waiting tactic (<i>N</i> = 26)	0.0	0.27	0.69	0.96
Late season				
Searching tactic (<i>N</i> = 49)	0.02	0.08	0.59	0.94
Waiting tactic (<i>N</i> = 14)	0.0	0.0	0.64	0.86
Mean				
Searching tactic (<i>N</i> = 184)	0.18	0.41	0.78	0.98
Waiting tactic (<i>N</i> = 53)	0.02	0.19	0.68	0.94

Table IV. Seasonal differences in oviposition duration frequencies of resurfacing females seized by males

	Duration of oviposition bout before being seized by male (min)			
	1-10	11-20	21-30	> 30
Season				
Early	9 (13.8)	4 (6.4)	8 (7.3)	16 (9.5)
Mid-	20 (18.2)	4 (8.5)	15 (9.7)	10 (12.6)
Late	16 (13.0)	13 (6.1)	1 (6.9)	5 (9.0)
Total resurfacing females seized by males	45	21	24	31
Females seized by males using waiting tactic	7 (12.6)	4 (5.9)	6 (6.7)	17 (8.7)

Expected frequencies are in parentheses.

The longer the oviposition bout duration, the fewer eggs a resurfacing female carried.

The fertilization value of resurfacing females to males increased across the season ($\chi^2 = 28.3$, $df = 6$, $P < 0.05$). Waiting males seized females of lower fertilization value than would be expected by chance ($\chi^2 = 11.1$, $df = 3$, $P < 0.025$).

ment of the searching tactic was always higher than the profit from the waiting tactic, but that the relative profit of waiters increased considerably from early to late season (Table V). This relative increase was coupled with an increase in the proportion of males successfully finding mates by waiting at the oviposition site.

Factors Affecting Relative profits

Factors affecting gains for both tactics are presented in Table VI. The probability of mating (P_m) was much lower for males using the waiting tactic because many of the females that resurfaced had finished laying eggs and were unreceptive to mating. In contrast, nearly all of the females seized by searching males were receptive, because only females that had matured clutches moved from the adjacent field to the pond where they encountered searching males. The probability that searching males would lose mates to waiters (P_l), doubled in mid-season, due to the higher density of males at

the pond at this time, coupled with shorter oviposition bouts of females.

The sex ratios of all individuals visiting the pond were 3.6, 4.3, 1.7 (males/female) for early, mid-, and late season respectively. The density of individuals at the pond fluctuated inversely with the density on the banks from 1100 to 1800 hours. The density of both males and females on the banks increased from 1000 to 1200 hours, after which the density of males at the water increased from 1100 to 1800 hours ($r = 0.80$, $N = 8$, $P < 0.025$), while density on the banks decreased ($r = -0.82$, $N = 8$, $P < 0.025$).

From 1100 to 1500 hours, the average density of receptive females in the searching sector was $1.7 \pm 0.6/20 \text{ m}^2$ whereas male density was $14.6 \pm 1.2/20 \text{ m}^2$. During the time of peak activity at the water (1500-1900), the average density of ovipositing females was $3.9 \pm 0.3/20 \text{ m}^2$, and that of males was $11.2 \pm 1.9/20 \text{ m}^2$. Comparison of sex ratios at the water (2.8:1) with that on the banks (8.5:1) indicated that approximately 30% of all the males eventually became waiters. Virtually all of the females at the oviposition site arrived in tandem with mates, and of the resurfacing females, only a small proportion (23%) were available to waiting males because 49% were seized by their guarding males and 28% either escaped to shore or died. The realized sex ratio at the water was thus 10.4:1.

Females ovipositing a second time had, on the average, fewer eggs available for males to fertilize than did females ovipositing for the first time on a given day (ANOVA, $P < 0.06$; Table VI). They were also less likely to resurface prematurely because they submerged for a shorter time. Thus one might predict that, unless the chance of encountering additional receptive females is very low, males mating by the waiting tactic should abandon submerged mates more frequently than males mating by the searching tactic. However, males in general guarded persistently, occasionally remaining on their perches long after (up to 117 min) their mates had re-emerged unnoticed and had either escaped to shore or had been seized by another male. Guarding duration did not differ between the two tactics; the correlation between guarding and oviposition durations was actually higher for waiting males ($r = 0.61$, $P < 0.05$) than for searching males ($r = 0.34$, $P < 0.01$). Further evidence indicated that the realized encounter rates for either tactic must be quite low. No male obtained matings with more than three different

Table V. Frequency of matings by searching and waiting males, and relative success of the two tactics over the season

	Reproductive season			
	Early	Mid-	Late	Mean
Matings by:				
Searching tactic	0.80 (70)	0.75 (65)	0.72 (49)	0.76 (184)
Waiting tactic	0.20 (17)	0.25 (22)	0.28 (19)	0.24 (58)
Mean oviposition duration of mates				
Searching tactic	28.1 ± 3.5 (34)	19.6 ± 2.3 (56)	16.0 ± 3.4 (27)	22.0 ± 1.8 (117)
Waiting tactic	17.3 ± 7.1 (3)	33.3 ± 6.3 (11)	12.0 ± 5.5 (5)	25.2 ± 6.5 (19)
Mean fertilizations/mate*				
Searching tactic	423	313	289	335
Waiting tactic	58	125	78	80
Fertilizations/min invested/ female encountered*				
Searching tactic	4.8	5.4	5.1	4.9
Waiting tactic	0.8	2.0	1.9	1.4
Gains/investment* (eggs/min)				
Searching tactic	0.52	0.40	0.25	0.37
Waiting tactic	0.04	0.17	0.06	0.07
Relative profit of waiting/searching				
	0.08	0.43	0.24	0.19

Sample sizes are given in parentheses.

* Estimated from the optimization model.

females on any given day, and mated males averaged only 2.5 successful matings (range 1–8) over the 28-day period. Of females that mated, the mean oviposition time was 27.6 ± 1.6 min/day and the mean number of tandems with different males/day was 1.2 ± 0.02 . The estimated mean total oviposition time by females was 63.1 ± 6.9 min (equivalent to 819 eggs fertilized/lifetime and comparable to a female's total egg production).

Seasonal Effects on Oviposition Behaviour

Early in the season, 86% of all females seen to oviposit on a given day had already begun oviposition by 1600 hours. By late season, only 60% of the females had begun to oviposit by that time. This shift meant that the time over which females were available to searching males increased by 2 h,

resulting in longer encounter times for searchers at the end of the season.

A second seasonal effect was a progressive decrease in the total oviposition duration per female per day (Table VI; ANOVA, $P < 0.05$). The proportion of females that escaped, died, were seized by mates or non-mates, or had unknown fates did not differ across early, mid-, or late season ($N = 284$ females, $\chi^2 = 8.1$, $df = 8$, ns). But there was a significant tactic \times period interaction in which the oviposition duration for mates of waiting males was longer than that for mates of searching males during mid-season, but not in early or late season. The duration of individual bouts also decreased late in the season (ANOVA, $P < 0.05$). The mean number of bouts/female increased slightly, ($\bar{x} = 1.5$, 1.6 and 1.7 for early, mid- and late season respectively), but not significantly (ANOVA, $P > 0.05$).

Table VI. Seasonal changes in factors affecting gains and investments of searching and waiting tactics

	Seasonal period			
	Early	Mid-	Late	Mean
Probability of mating (P_m)				
Searching tactic (184)	0.97	0.97	0.97	0.97
Waiting tactic (58)	0.35	0.64	0.53	0.52
Probability of intervention (P_i)				
Searching tactic (184)	0.17	0.35	0.18	0.24
Waiting tactic (58)	0.08	0.13	0.44	0.18
Oviposition duration (min)				
\bar{x} total/day/female*	35.7 (17)	30.1 (39)	24.9 (30)	29.4 (86)
Bout 1	26.5 ± 3.6 (17)	21.9 ± 4.0 (39)	15.2 ± 2.7 (30)	20.5 ± 2.2 (86)
Subsequent bouts**	15.7 ± 5.2 (10)	18.8 ± 4.2 (17)	10.4 ± 2.3 (28)	13.9 ± 2.0 (55)
Total time with female (min)				
Searching tactic	87.9 ± 9.9 (65)	58.0 ± 9.8 (60)	56.9 ± 8.3 (38)	70.3 ± 5.2 (163)
Waiting tactic	72.9 ± 3.9 (11)	61.9 ± 14.0 (21)	42.0 ± 6.4 (8)	60.9 ± 10.6 (40)
Time to encounter a female (min)				
Searching tactic	720	720	1080	840
Waiting tactic	1270	679	1320	1090

Sample sizes are given in parentheses.

* Calculated from weighted means of bout 1 and subsequent bouts.

** Because of small sample sizes of bout 3 in periods 1 and 2, the combined mean of bout 3 ($\bar{x} = 15.1 \pm 5.2$, $N = 12$) was used in calculating gains for each period.

The effects of these changes on male behaviour were seen in the duration of male defence and total time spent in tandem, both of which decreased later in the season (ANOVA, $P < 0.05$).

Accompanying the shorter oviposition bouts was a shift in females' use of oviposition plants. Early in the season, females oviposited directly in the sedge or arrowhead stems on which their guarding mates perched. As these stems became full of eggs (indicated by the brown oviposition scars), females moved off these plants onto mats of submerged macrophytic algae (*Chara*). Before day 10, *Chara* was used during only 1 of 18 (6%) observed ovipositions, and females rarely left the stem on which they descended. After day 10, 43% (10/23) of the ovipositions observed involved the use of *Chara*. Because the thickness of sedge and

and arrowhead stems is much greater (3–8 mm) than that of *Chara* (< 1 mm), females on the larger stems could deposit up to 30 eggs by moving only their abdomens. In contrast, females on *Chara* were forced to walk about to insert eggs in the tiny stems, whose diameter would hold only one egg. Females ovipositing into the algae were more likely to lose their hold or to 'pop up' owing to disturbance by dytiscid larvae, tadpoles, or fish which swam through the *Chara*. Consequently, the potential fitness gain that a resurfacing female represented to a patrolling male (inversely proportional to the amount of time a female had been submerged) increased in mid- and late season (Table IV).

The average rate of oviposition under field conditions was 13.3 ± 1.02 eggs/min (range = 6–29/min, $N = 18$) at an average water temperature

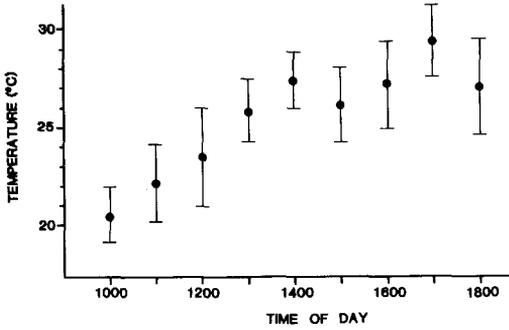


Figure 1. Water temperature in the oviposition area during the day. Means are given with 95% confidence levels.

of $27.1 \pm 0.5^\circ\text{C}$ (range = 25.6 – 35.6°C). Water temperatures changed consistently with time of day, reaching a plateau from 1400 to 1800 hours (Fig. 1). Oviposition rate (measured in jars) was positively correlated with water temperature (Fig. 2). The three females tested at 37°C would not remain submerged and were not used in the calculation. Mean afternoon water temperatures did not vary significantly across the season ($\bar{x} = 25.5 \pm 1.7^\circ\text{C}$, $N = 5$; $\bar{x} = 28.1 \pm 1.5^\circ\text{C}$, $N = 6$; $\bar{x} = 27.6 \pm 1.2^\circ\text{C}$, $N = 7$, for early, mid-, and late season respectively; ANOVA, ns). I thus used the average oviposition rate of 13 eggs/min to estimate the number of eggs fertilized by males, although the oviposition rate

was probably slightly lower on *Chara*, where females required more time moving about the filaments to insert the same number of eggs as on *Potamogeton* stems. There was no significant difference in the mean clutch size of two samples of pre-oviposition females dissected early versus late in the season ($\bar{x} = 344 \pm 27.2$ eggs, $N = 5$, and $\bar{x} = 319 \pm 35.4$ eggs, $N = 5$, early and late season respectively).

Site Effects

Factors influencing gains/investments were found to differ between the two populations. Oviposition sites in L. Cathleen were located in fairly deep (1–1.5 m) water, where there were few perch sites available for males. Guarding males were forced to hover over the oviposition area where females submerged on *Potamogeton*. Thirty-two per cent ($N = 31$) of the males at this site abandoned mates before they resurfaced, in contrast with E. Point Pond, where only 9% ($N = 232$) of the males abandoned mates. Thus, at L. Cathleen, males using the waiting tactic had nearly a four-fold greater chance of finding a female at the oviposition site than they did at E. Point Pond. At East Point, 74% ($N = 232$) of the ovipositing females, whose fates were known, were taken by males upon resurfacing; 62% of these were mates. In contrast, at L. Cathleen, of the 61% ($N = 31$) of

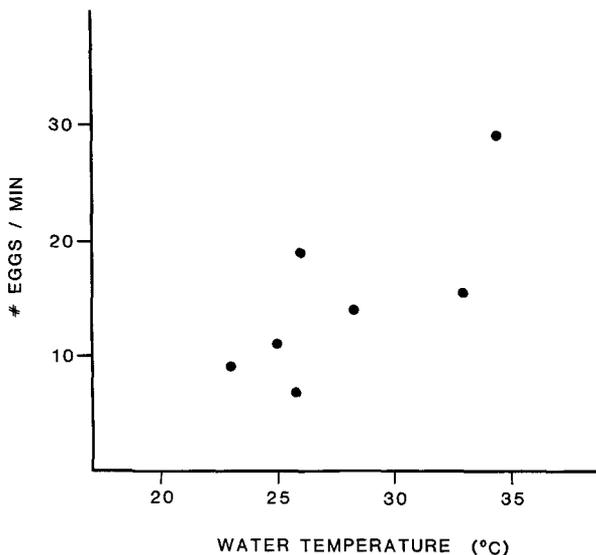


Figure 2. Effect of water temperature on oviposition rate. $r = 0.73$, $N = 7$, $P < 0.05$.

Table VII. Class means for males mating only by the searching tactic versus those mating by a mixture of tactics

Days at pond	Tactic	N	Number of mates	Oviposition duration	Total time	Eggs/min*
1	Searching	29	1.0	18.7	63.6	3.8
	Mixed	24	1.6	25.6	70.5	4.7
2	Searching	7	2.4	53.8	202.0	3.5
	Mixed	15	2.6	51.2	112.4	5.9
3	Searching	3	3.7	31.4	113.0	3.6
	Mixed	12	3.7	75.7	251.8	3.9
4	Searching	2	5.0	103.1	316.5	4.2
	Mixed	12	4.8	90.9	243.0	4.9

None of the differences was statistically significant (*t*-test, $P > 0.05$).

* Fertilizations/min invested by a male with an encountered female (differences do not reflect differences in encounter rates).

females that were taken in tandem upon resurfacing, only 26% were taken by mates.

Other factors countered this potential four-fold increase in the success of the waiting tactic at L. Cathleen. The average duration of the first oviposition bout at L. Cathleen was 42.6 ± 6.1 min ($N = 14$, range = 8–76 min), twice as long as that at the beach pool. Most (65%) of the females at L. Cathleen

remained submerged for over 40 min without ovipositing again that day. The water temperature at L. Cathleen was significantly lower ($\bar{x} = 21.9 \pm 0.4^\circ\text{C}$) than at the shallow beach pool ($\bar{x} = 27.1 \pm 0.8^\circ\text{C}$). Using the predicted oviposition rate of 8 eggs/min, the total eggs deposited per day per female at 22°C would be 340, which is close to the estimated total of 353 eggs per day per female at E. Point Pond. Thus, while encounter rates for waiting males at L. Cathleen were about four times as high as those at E. Point, waiting males at the former site had only a 0.35 chance of finding a resurfacing female who was receptive to re-mating, versus a 0.6 chance at E. Point. The waiting tactic would be slightly more advantageous at L. Cathleen than at E. Point Pond, all else being equal. In addition, the more highly clumped oviposition sites at L. Cathleen may have resulted in an increased operational sex ratio at the water which would make non-contact guarding less successful than at E. Point Pond.

Table VIII. Comparison of lifetime statistics of males mating by the searching tactic only versus males mating by a mixture of tactics

Parameter	Tactic	N	Mean \pm SE	<i>P</i> *
Number of mates	Searching	41	1.6 ± 0.19	***
	Mixed	73	3.3 ± 0.25	
Total oviposition duration of mates	Searching	29	34.3 ± 6.0	***
	Mixed	61	69.2 ± 6.4	
Total time/mate (min)	Searching	34	109.9 ± 16.8	***
	Mixed	71	182.8 ± 18.2	
Eggs/min/female	Searching	29	5.2 ± 0.07	
	Mixed	61	5.3 ± 0.04	NS
Total days at pond	Searching	41	1.5 ± 0.13	***
	Mixed	73	2.7 ± 0.2	
Reproductive span (days)	Searching	41	2.2 ± 0.37	**
	Mixed	73	7.3 ± 0.75	

* *t*-test; ** $P < 0.01$. *** $P < 0.001$.

Maintenance of Tactics by Natural Selection

Comparing males with equal lifespans, or males seen at the breeding site for the same number of days, the total number of matings obtained by a male using only the searching tactic, or the total time its mates spent laying eggs before their next mating, did not differ significantly from the corresponding totals for males using both tactics (Table VII). Males successfully using both tactics on the

same day had the highest reproductive success of any in the population ($\bar{x}=6.6 \pm 1.1$ matings; \bar{x} number of visits to pond = 4.6 ± 0.9 , $N=5$). The increased reproductive success of males mating by a mixture of tactics, compared to males mating only by the searching tactic can be accounted for by the artefact that longer-lived males were more likely to use both tactics successfully (Table VIII). No male mating by the searching tactic only was seen for more than 4 days, or had a reproductive span of greater than 11 days. For males mating by both tactics, the maximum lifespan was 26 days and the maximum number of days at the pond was 8.

DISCUSSION

Because individual males mated by both tactics, sometimes within the same day, the two mate-finding variants in *E. hageni* are best described as a single, conditional strategy reflecting behavioural plasticity within individuals. Males switched from searching to waiting if they did not encounter a female after a while. The use of the tactics was independent of age, size, and previous tactic successfully used, implying that neither an ontogenetic switch nor experience functions as the mechanism controlling their use. Nor is it likely that the two variants result from two discrete phenotypes because only a few males that mated more than once per lifetime were found to mate using only a single tactic.

The factors influencing a male's 'decision' to switch from searching on the banks to patrolling the oviposition sites remain unclear. There are several possible explanations. (1) It may be that no decision is made, because the two apparent tactics are actually one continuous tactic: males may begin searching at the site where they spent the night, and continually move towards the pond, eventually searching for females around oviposition sites. (2) Males may switch tactics on the basis of a time threshold, searching the banks for a certain period of time after which, if they have not seized a female, they go to the oviposition site. (3) Males may use the increased activity of tandem pairs at the water as a cue to switch tactics.

The first two possibilities are not supported by the finding that certain individuals remained on the banks throughout a given day, even though they never paired with a female. On other days however, many of these same individuals were found waiting

at the water. Late in the season, some males waited at oviposition sites as early as 1100 hours, but most spent more time searching on the bank than they did earlier in the season. These results indicate that an individual's movement is not controlled by an inflexible time threshold that requires it to research for a fixed duration or until a certain time of day before beginning the waiting tactic. Although males appear to be unable to detect females under water (Fincke 1983), they may use the increased activity of tandem pairs or lone males at the water as a visual cue to switch behaviours. Observational data indicate that males may respond to such cues. On the banks, males occasionally were found in small clusters because they oriented to the movements of conspecifics (presumably in order to determine the sex of the individual). A plausible rule for switching might be: 'search for a female until activity at the water reaches a certain level, and then move to the oviposition site if the density of localized males there is not too great'. Other factors, such as a male's general physical condition and the time since its last mating, may play a role in whether it uses only one or both tactics on a given day.

The searching tactic was always superior to the waiting tactic. At East Point Pond, the waiting tactic was 8–43% ($\bar{x}=19\%$) as profitable as the searching tactic. Because I lacked data on the density of males on the bank and at the water during very early and very late season, I assumed a constant 30% of the total males became waiters on a given day. However, time to encounter a female is density-dependent; profits for waiters may be somewhat higher than my calculations indicate for early season. Likewise, some of the increase in profits in mid-season may have been counterbalanced by a greater proportion of males competing via the waiting tactic then. The encounter rate also depends in part on the number of searching males relative to waiting males at a given time of day; thus the gains from the tactics are probably frequency dependent during the time when tactic usage overlaps.

It is difficult to assess the possible additional 'costs' of each tactic in terms of predation risk and energetic expenses. Searching males spent more time than waiters flying in tandem with mates over the water until females submerged. Such pairs risked being eaten by gomphid dragonflies, whereas males waiting at oviposition sites risked predation by frogs and aquatic invertebrates. The

fact that so few males successfully used both tactics on the same day suggests that energy and/or predation risk, rather than time, may be a more important limitation to male mating success in *E. hageni*.

Female behaviour dramatically influenced the relative profit of the two tactics. Because oviposition rate correlated positively with water temperature, females would minimize their time under water by waiting until 1400 hours to submerge when water temperature levelled near its maximum for the day. Although water temperatures remained high even after most females had left the pond, females resurfacing after 1800 hours (when the pond was shaded), may have suffered from evaporative cooling as air temperatures dropped around the pond. On a daily basis, these apparent constraints on females in the timing of oviposition resulted in two consequences to males: (1) profits from searching decreased as the day progressed while those from waiting increased, and (2) searching males invested more time flying in tandem with mates before they submerged than did waiters, whose mates usually submerged immediately after copulating.

Seasonal changes in female behaviour resulted in profits from the waiting tactic increasing five-fold in mid season. Because the shorter oviposition durations later in the season could not be accounted for by either an increase in water temperature or a decrease in clutch size late in the season, I conclude that they were the consequence of disturbances to females as they oviposited on algae mats. Shorter oviposition bout durations increased the chance that a male's mate would prematurely resurface, thus increasing the opportunity for males waiting at oviposition sites to capture females that still had eggs to lay. The risk of drowning and/or predation a female incurs each time she submerges (Fincke, in press a) may limit the number of bouts/day she should make. If females are so constrained, one would expect that late in the season they might leave the pond before depositing a full clutch, returning within the next few days to complete egg-laying. The inter-clutch intervals of females laying on or before day 10 did tend to be longer ($\bar{x} = 5.6 \pm 0.8$ days) than those of females laying after day 10 ($\bar{x} = 4.4 \pm 0.7$ days), but the difference was not statistically significant (Wilcoxon test, $P < 0.2$, $N = 69$).

Differences between oviposition sites also resulted in differences in the relative profit of the

two tactics. The location of oviposition plants in the deeper water at L. Cathleen decreased the effectiveness of guarding males, resulting in a potential increase in profits for waiters. Taken together, these daily, seasonal, and site effects on female behaviour may favour the use of more than one male mating tactic.

The theory of evolutionarily stable strategies (ESSs, Maynard Smith 1982) explains how two or more variants can be maintained in the same population if the success of one variant depends upon the frequency with which the other variant is used. Contrary to what would be expected if the two *E. hageni* variants represented a 'mixed' evolutionarily stable strategy, the average profits of the tactics were not equal. The frequency of successful use multiplied by the gain/investment was always lower for the waiting tactic than for the searching tactic. It appears clear however, that the waiting tactic was not a 'losing' tactic, since it enabled males to mate in late afternoon when the chance of finding a mate by searching was low. Both tactics can be maintained in the population because, when differences in lifespan or visits to the pond are controlled, those males that mated by a mixture of tactics did not significantly differ in reproductive success from those mating only by the searching tactic. Since all males seen more than four times used a mixture of tactics, it appears that the searching tactic may be preferred, but if a male happens to live long enough, he will eventually use the waiting tactic successfully.

It has been suggested that territorial odonates show alternative mating behaviours in which satellite males coexist with territory holders. Waltz (1982) modelled this variation in a manner similar to a 'mixed' ESS for libellulid dragonflies, while Waage (1979) suggested that satellite behaviour in the stream-breeding damselfly *Calopteryx maculata* may be ontogenetic, used by young males, or older males no longer able to hold territories. Without knowing the pattern of use by individuals, however, an equally plausible explanation for such satellite behaviour would be behavioural plasticity, which would enable odonates to respond to unpredictable fluctuations in the density of conspecifics or territory sites (e.g. Uéda 1979), or to behave as territorial males when their energy levels remain high, switching to the less energetically expensive satellite behaviour later.

Behavioural plasticity quite similar to that found in *E. hageni* has been reported in a cactus fly,

Odontoloxozus longicornis, which showed both territorial and satellite behaviour, the latter occurring in the presence of territorial males, but also during times when no males could hold a territory (Mangan 1979). Although the territorial tactic resulted in greater egg gains, the encounter rate, which was not calculated, was argued to be much higher for the satellites. Mangan concluded that the gain/investment ratios were probably equal, enabling both tactics to be maintained in the population. An alternative explanation that would not necessitate that the success of both tactics be equal would be that males using the two tactics conditionally would have equal or greater fitness than males using only the territorial tactic, because the secondary tactic could be used successfully at times when the main tactic was inefficient. Such was the case for *E. hageni* males. Behavioural plasticity or ontogenetic switches, both of which allow responses to the current environment, are likely to be responsible for many of the alternative mating behaviours observed, and are most likely to occur in animals which encounter perceptible changes within their lifetimes.

While I interpret the searching versus waiting behaviours used by *E. hageni* as two components of a single mating strategy, the finding that certain unmated males waited at oviposition sites early in the day suggests that there may be differences between individuals in the time spent in one tactic over the other (e.g. if males differed in the threshold for cues causing them to switch tactics). If such differences were heritable, individuals spending more time waiting at the oviposition sites later in the season should be selected for, while earlier in the season such males would be selected against. Likewise, any differences in the propensity to guard which were due to genetic differences would be subjected to different selective pressures between L. Cathleen and the beach pool. Both seasonal and population differences in selective pressures could result in additive genetic variance being maintained in the face of relatively strong (see Fincke, in press a) sexual selection.

ACKNOWLEDGMENTS

I am grateful to S. Franson, E. Leigh, R. Thornhill, J.K. Waage and an anonymous reviewer for critical comments on the manuscript. I thank R. Drapcho and C. Segrillo for assistance in the field. I am

grateful to the University of Michigan Biological Station for use of their facilities. This work was funded by a grant-in-aid from the Arco Foundation, and by a Teaching-Research Fellowship from The University of Iowa. The study was conducted in partial fulfilment of requirements for a Ph.D. in zoology at the University of Iowa.

REFERENCES

- Arak, A. 1983. Male-male competition and mate choice in anuran amphibians. In: *Mate Choice* (Ed. by P. Bateson), pp. 181-120. Cambridge: Cambridge University Press.
- Alcock, J., Jones, C.E. & Buchmann, S.L. 1979. Male mating strategies in the bee *Centris pallida* Fox (Anthophoridae: Hymenoptera). *Am. Nat.*, **111**, 145-155.
- Brockman, H.J., Grafen, A. & Dawkins, R. 1979. Evolutionarily stable nesting strategy in a digger wasp. *J. theor. Biol.*, **77**, 473-496.
- Cade, W. 1980. Alternative male reproductive behavior. *Fla Entomol.*, **63**, 30-45.
- Cade, W. 1981. Alternative male strategies: genetic differences in crickets. *Science, N.Y.*, **212**, 563-564.
- Fincke, O.M. 1982. Lifetime mating success in a natural population of the damselfly *Enallagma hageni* (Walsh) (Odonata: Coenagrionidae). *Behav. Ecol. Sociobiol.*, **10**, 293-302.
- Fincke, O.M. 1983. Lifetime mating patterns and reproductive success in the damselfly *Enallagma hageni* (Walsh) (Odonata: Coenagrionidae). Ph.D. thesis, University of Iowa.
- Fincke, O.M. 1984. Sperm competition in the damselfly *Enallagma hageni* (Odonata: Coenagrionidae): benefits of multiple mating to males and females. *Behav. Ecol. Sociobiol.*, **14**, 235-240.
- Fincke, O.M. In press a. Sources of variation in lifetime reproductive success in a non-territorial damselfly. In: *Reproductive Success* (Ed. by T. Clutton-Brock), in press. Chicago: University of Chicago Press.
- Fincke, O.M. In press b. Underwater oviposition in a damselfly favors male vigilance, and multiple mating by females. *Behav. Ecol. Sociobiol.*
- Howard, R.D. 1978. The evolution of mating strategies in bullfrogs, *Rana catesbeiana*. *Evolution*, **32**, 850-871.
- Mangan, R.L. 1979. Reproductive behavior of the cactus fly, *Odontoloxozus longicornis*; male territoriality and female guarding as adaptive strategies. *Behav. Ecol. Sociobiol.*, **4**, 265-278.
- Maynard Smith, J., 1982. *Evolution and the Theory of Games*. Cambridge: Cambridge University Press.
- Otte, D. & Joern, A. 1975. Insect territoriality and its evolution: population studies of desert grasshoppers on creosote bushes. *J. Anim. Ecol.*, **44**, 29-54.
- Parker, G.A. 1974. Courtship persistence and female-guarding as male time investment strategies. *Behaviour*, **48**, 157-184.
- Rubenstein, D.I. 1980. On the evolution of alternative mating strategies. In: *Limits to Action* (Ed. by J.E.R. Staddon), pp. 65-100. New York: Academic Press.
- Thornhill, R. 1979. Adaptive female-mimicking behavior in a scorpionfly. *Science, N.Y.*, **205**, 412-414.

- Thornhill, R. 1981. *Panorpa* (Mecoptera: Panorpidae) scorpionflies: systems for understanding resource-defense polygyny and alternative male reproductive efforts. *Ann. Rev. Ecol. Syst.*, **12**, 355–386.
- Thornhill, R. & Alcock, J. 1983. *The Evolution of Insect Mating Systems*. Cambridge, Massachusetts: Harvard University Press.
- Uéda, T. 1979. Plasticity of the reproductive behaviour in a dragonfly, *Sympetrum parvulum* Barteneff, with reference to the social relationship of males and the density of territories. *Res. Pop. Ecol.*, **21**, 135–152.
- Waage, J.K. 1979. Adaptive significance of postcopulatory guarding of mates and nonmates by male *Calopteryx maculata* (Odonata). *Behav. Ecol. Sociobiol.*, **6**, 147–154.
- Waltz, E.C. 1982. Alternative mating tactics and the law of diminishing returns: the satellite threshold model. *Behav. Ecol. Sociobiol.*, **10**, 75–83.
- West-Eberhard, M.J. 1985. Sexual selection, competitive communication and species-specific signals in insects. In: *Insect Communication* (Ed. by T. Lewis), pp. 283–324. London: Academic Press.

(Received 16 January 1984; revised 15 October 1984; MS. number: A4216)