

Lifetime Mating Success in a Natural Population of the Damselfly, *Enallagma hageni* (Walsh) (Odonata: Coenagrionidae)

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Summary. Variance in lifetime mating success was measured for individuals of a population of *Enallagma hageni*, a non-territorial damselfly in northern Michigan. *E. hageni* is an explosive breeder with scramble competition for mates. Highly skewed operational sex ratios resulted in intense male-male competition which took the form of interference with tandem pairs. 41% of the males failed to mate in their lifetime as opposed to only 3.6% mating failure in females. The effect on mating success of size, age, longevity, and time spent at the breeding site were investigated. Intermediate sized males obtained the most matings, and male lifetime mating success was highly correlated with longevity.

Introduction

The results from a growing number of studies on sexual selection leave little doubt that both male-male competition and female choice have been important in shaping reproductive behavior of many species (see Thornhill 1979, for a review). However, much of the theory of the dynamics of sexual selection which identifies the conditions under which sexual selection should be expected to occur remains to be adequately tested. Specifically, Emlen and Oring (1977) proposed that ecological conditions limit the degree to which sexual selection can act on populations. They predicted that the intensity of sexual selection should vary across mating systems. In polygamous species where limiting resources (such as females, oviposition sites, etc.) are spatially clumped such that an individual male can effectively defend them, directly or territorially, the intensity of sexual selection should be high. Where ecological constraints prevent either sex from monopolizing more than one or a few mates, sexual selection should be minimal, as in monogamous species and polygamous explosive breeders.

Variation in male mating success which results from male-male competition and/or female choice should directly reflect the intensity of sexual selection on males (Wade and Arnold 1980). The above predictions of how the intensity of sexual selection should vary across mating systems can thus be tested by quantifying the variation in male mating success across populations or species. The few long-term measurements of mating success which have been made are on vertebrates (Le Boeuf 1974; Emlen 1976; Payne and Payne 1977; Wells 1977, 1979; Howard 1978; Gibson and Guinness 1980). While these studies collectively support the hypothesis that territorial species characteristically show higher variance in male mating success than explosive breeders, vertebrate studies have not been able to clearly distinguish between age effects and size effects on mating success in males (but see Berven 1981). This distinction is critical if one views variance in mating success as a measure of the intensity of sexual selection. What is needed is a measure of lifetime variance in reproductive success.

Insects are well suited for studies of lifetime mating success in field populations. The size of an adult insect is fixed at the time of its final molt, so that age and size effects on reproductive success can be measured separately. In addition, the lifespan of the adults is fairly short, so that measurement of lifetime reproductive success is feasible. Despite these advantages, little is known of the variance in reproductive success for the lifetime of any insect in a natural population (Thornhill 1979).

I report here on lifetime mating success of individual males and females of a population of *Enallagma hageni* in northern Michigan. This is a medium sized, sexually dimorphic damselfly which is widely distributed across eastern North America. I describe its general reproductive behavior and identify those factors which are important to male mating success.

Materials and Methods

This study was conducted from June–August, 1980, at East Point Pond, a small beach pool (110 m perimeter) on the shore of Douglas Lake at The University of Michigan Biological Station near Pellston, Michigan. The population of *E. hageni* was an isolated one, for breeding never occurred on Douglas Lake, and the closest conspecific population was 4 km away. The only other zygopteran breeding on the pond is *Enallagma carunculatum*, whose population peaks in late August, and overlaps only slightly with *E. hageni*.

The shallow pool (less than 0.5 m at the deepest point) is separated from the lake by a sand beach 10–20 m wide, and is bordered by a 5–15 m wide area of sparse grasses which ends in pine woods on three sides of the pool. The perimeter of the pool was marked off in 10-m sections so that the position of individuals could be recorded. Oviposition sites of *Chara* sp. (musk-grass) were clumped within 2 m of shore. Observation of reproductive activity was further enhanced by placing wooden dowels in the pond to serve as additional perches for single males and tandem pairs.

The sex ratio at emergence was calculated from daily collections of exuviae collected from the grasses along the pond edges. Study of the adults began July 7, 3 weeks after the first teneral were seen, and continued until the end of the flight season in early August. Because the ages of the adults initially present were not known, I deleted individuals marked on the first and second days from all calculations. Study day 1 thus represents the third day of actual marking. Thereafter, individuals seen for the first time were scored as being 1 day old, age referring to the age of sexually mature individuals. A sexually mature individual is here defined as one with adult coloration (teneral are pale in color). Beginning at 09:00 h when the first males arrived, and ending at 17:30 or 18:00 h when most of the individuals had left the breeding area, all *E. hageni* found were uniquely marked by writing a number on the forewing with an indelible 'Pilot' pen, and placing a dot of Testor's paint on the dorsum of the thorax. Because individuals marked in this manner and kept in an insectarium did not differ in mortality from unmarked individuals so kept, marking effects were assumed to be minimal. A total of 915 adults and teneral were marked over a 3-week period. Time of capture, position at the pond, activity of the individual, and forewing length were recorded for each animal. Head width, forewing length, abdomen length, front right tarsus length, and weight were measured for 20 males and 20 females to determine the correlation of wing length with other measures of body size. Means are reported with their standard errors. Since the females of this species exhibit a sex-limited color dimorphism, the color morph of the females was also noted.

By slowly walking around the perimeter of the pond 1–3 times per h, I recorded the presence of all the individuals I saw. I assume that I was able to observe most individuals visiting the beach pool area because: (1) the average mated pair spends over an hour in tandem; (2) males accompany females to oviposition sites which were centered in two areas each about 7 m²; (3) I often saw the same individuals several times on any given day. Tandems of brief duration which did not end in ovipositions could have been overlooked. If biased, my data would tend to overestimate the percentage of mated males in the population since tandem pairs are more conspicuous than single adults and could be expected to visit the oviposition sites.

Tandem pairs were captured unless both male and female had been previously marked. The difficulty of keeping captured pairs in tandem resulted in an abnormal excess of single females at the water, and artificially increased the number of matings per day (see Results). In order to determine whether single males could displace tandem males, I observed take-over attempts of tethered females. Females were tethered by tying a thread around the lower abdomen and attaching the other end of the thread to a perch.

A total of 132 h of observation were spent during the study. During very overcast or rainy weather, few or no individuals were present at the breeding site, although they could be found in the feeding area. These days are not included in the study days.

Results

Demography

Of the 870 adults marked, 389, or 45% were recaptured at least once. After the first 3 days of the study, the proportion of captures that were recaptures varied from 60–100% for males with a mean recapture of 66%. Recaptures of females were much lower, and remained more or less constant over time (\bar{x} = 32%) (Fig. 1). Daily adult sex ratios at the pool varied from 9:1 to 1.5:1.0 (males:females). This contrasts with the sex ratio at emergence which did not deviate significantly from 1:1 (113 males:124 females) over the 3 weeks studied. The Jolly-Seber estimates for population size (Jolly 1965) indicate a daily survivorship rate of 0.7 for males. Because the Jolly-Seber method requires high recapture rates, the population size and survivorship for females could not be reliably calculated since female recapture was so low.

Sex differences were found in time to maturity, recovery of teneral as adults, and adult lifespans. Using individuals marked as teneral, time between emergence and sexual maturity (as measured by return to the pond in addition to adult coloration), was estimated to be 5.6 ± 1.6 days for males ($n=5$) and 6.5 ± 0.92 days for females ($n=6$). More complete data from 1981 showed a similar though statistically insignificant trend (\bar{x} = 6.8 ± 0.52 days ($n=47$) and \bar{x} = 8.1 ± 0.79 days ($n=30$) for males and females respectively, Mann-Whitney *U*-test, $P < 0.18$). Of the 14 males and 31 females marked as teneral, 42% of the males vs only 26% of the females returned to the pond as adults. In 1981, 34% ($n=137$) of the male and 20% ($n=154$) of the female teneral were recaptured as adults ($\chi^2 = 6.26$, $d.f. = 1$, $P < 0.025$). The average reproductive span of males was twice as long as that of females (4.4 ± 0.18 days, $n=512$ vs 2.1 ± 0.14 days, $n=358$, males and females respectively, *t*-test, $P < 0.0001$).

The major cause of death at the breeding site was predation. Of the 26 deaths of marked *E. hageni* observed, 10 males were killed by web building spiders that inhabited the bushes along the water's edge. A total of six males were eaten by an asilid, a raft spider, a gomphid dragonfly, and three *Rana clamitans*. One tandem pair was caught mid-flight by a gomphid, and another pair was eaten by a grasshopper. Six male deaths were due to unknown causes. While it appears from these limited data that males suffer higher mortality at the breeding site than do females,

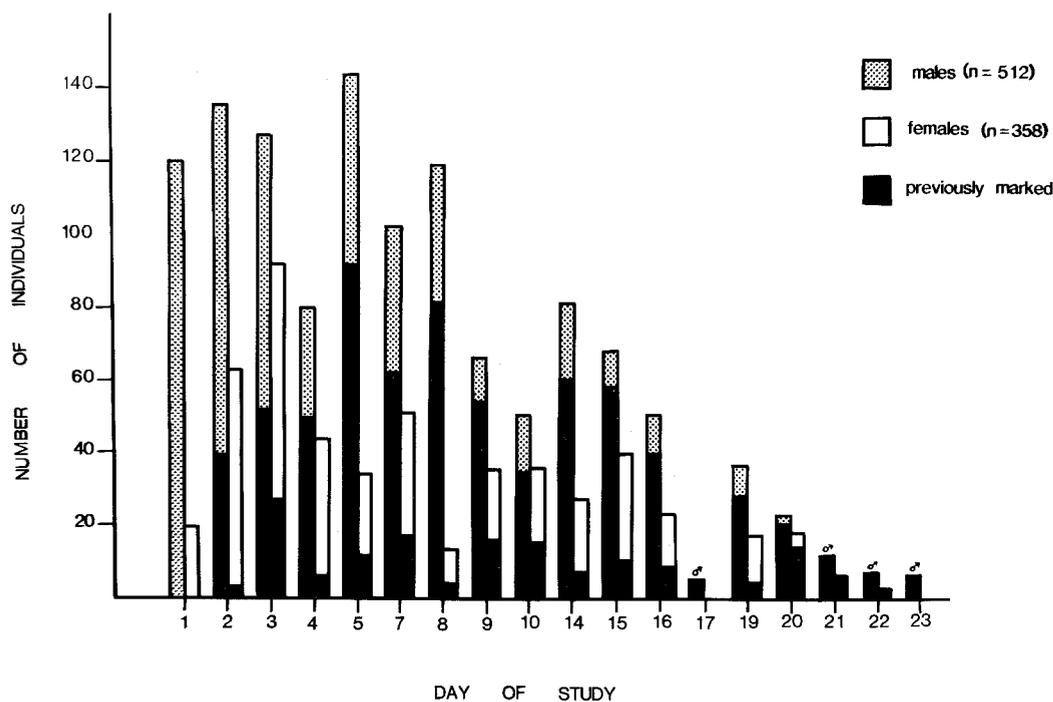


Fig. 1. Daily captures and recaptures. Days of inclement weather have been deleted

indirect evidence suggests that mortality is high for ovipositing females. Female *E. hageni* submerge to oviposit and are subjected to predation by aquatic predators such as belostomatid bugs, water scorpions, diving beetles and their larvae, fish, frogs, and raft spiders (personal observation). Of 31 marked females observed in 1981 (personal observation), 8 were found floating in the water after oviposition. Direct male-male competition is also detrimental to females. Tandem females sometimes drown in 'take-over' attempts by conspecific males. Harassment of tandem pairs may result in wing damage in females. Male interference during oviposition attempts prolongs the time females are close to the water surface, and thus exposes them to increased risk of predation by aquatic predators.

Temporal Pattern of Reproduction and Reproductive Behavior

On sunny days, males began to move from the feeding area to the pond around 09:30 h. All individuals were usually gone from the pool by 18:30 h. Feeding occurred primarily in a marshy, open field adjacent to the breeding site but separated from it by a narrow band of pines. Marked individuals visiting the beach pool could be found in the feeding area later the same day.

Before 13:00 h, most of the males present were unmated. Tandem pairs increased until 15:00 h, re-

maining high until 17:30 h. On all but three of the 18 study days, males present at the pond which did not mate on a particular day outnumbered those that did. Since nearly 100% of the females seen at the pool were in tandem, this resulted in an operational sex ratio which was highly male biased at the breeding site. Not only were males more abundant at the water, they visited the pool more frequently than did females (Fig. 1).

Few seizures of females by males were seen around the beach pool. Seizures were seen to occur in the feeding area, and I suspect that most females were taken in tandem there or on their way to the pond, although more data is needed to verify this. Virtually all the seizures seen to occur over the water were with females which had come up from ovipositing, or which had been disrupted from a previous tandem. The sequence of reproductive behavior is as follows. Copulation time (exclusive of interruptions which may occur spontaneously) averaged 22.4 ± 3 min ($n = 12$). After mating, pairs remained in tandem for an average of 58 ± 5.7 min (excluding copulation) before oviposition occurred. Oviposition is endophytic and was usually in the patches of *Chara* near shore. In all of the cases observed, females completely submerged to oviposit, and remained under water an average of 28.5 ± 3.4 min ($n = 11$) for the first oviposition. The majority of first ovipositions resulted in the deposition of a full clutch of eggs (personal observation), although if disturbed under water, a gravid female would resurface. While females oviposited,

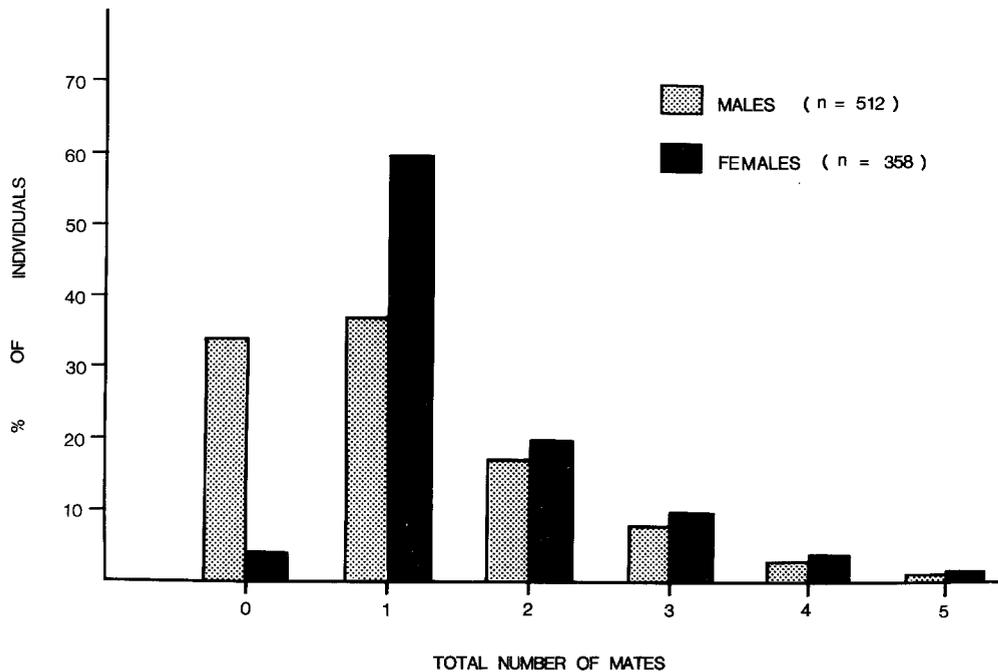


Fig. 2. Total number of matings by males and females over their lifetimes

their mates usually (15/22) guarded them from a perch. Upon resurfacing, approximately half of the females (19/31) were grabbed by males, usually non-mates (74% nonmates, 26% mates). These females usually resisted the male's attempt at copulation by holding their abdomens stiff. Females resisted tandem flight by hanging onto a perch. After several minutes of such resistance, the males would release them. Remating a second time was uncommon (3/31) and of short duration (7, 2, 7 min copulation times). Second ovipositions rarely occurred and were also shorter than first ovipositions (e.g. 8, 15, 20 min). Females that were not caught by males either escaped to shore (4/31) or floated in the water (8/31). Floating females may (1) eventually reach a perch upon which to climb, (2) be grabbed by a male and pulled from the water in tandem or (3) drown or be eaten by predators.

Male-Male Competition

Male-male competition was intense. Since nearly all mated males were paired before arriving at the water, competition at the pool took the form of interference with tandem pairs. Single males arriving early at the pond spent the morning searching for females on the grassy banks. They made darting movements at conspecifics as well as at objects resembling females (such as black and green striped *Equisetum* lying on the ground). That these were investigatory movements rather than defensive ones is clear from the fact that

males were not site specific, and once investigated, conspecifics were tolerated in the area. While I consider *E. hageni* to be non-territorial since individuals never remained long in one area, certain males did defend perches at the water for up to 20 min, as did males which were guarding ovipositing mates.

Copulation occurred on the banks away from the water where the density of single males was lower. Males interfered with mating and ovipositing pairs by darting at them, and if possible, displacing the tandem male. On one afternoon of intense activity for example, tandem pairs observed for 5 min each were harassed 2–14 times/min ($\bar{x}=7.4$, $n=24$ pairs). The average number of oviposition attempts was 1.4/min. Harassment sometimes (2/24) resulted in the uncoupling of the tandem pair. I have observed up to two additional males actually attached to a tandem pair, but such extreme interference was rare, and most pairs were successful in evading single males by flying to another area. That such agonistic behavior is sometimes successful is suggested by the fact that males were seen to displace other males in tandem with tethered females. Late in the afternoon, single males perched around oviposition sites, and attempted to displace males of tandem pairs or else tried to grab females as they resurfaced from ovipositing. Resulting tandems could be distinguished by a characteristic 'zig zag' flight pattern (as described by Bick and Bick 1963), presumably due to resistance to flight by the females.

Mating Success and Correlates of Male Mating Success

Of the 512 marked adult males, 338 were responsible for the 578 matings observed involving 358 marked and 20 unmarked females. Thus 34% of the males sampled never mated. Disruption of tandem pairs during marking artificially increased the chance of a male finding a solitary female at the beach pool. Because females spend a relatively long time in tandem and ovipositing, it is unlikely that females mate more than once in a day under normal conditions. Of the total matings by marked females, 121 were second matings by females on the same day. Of the 103 marked males responsible for these second matings, 35 never obtained another mate. If it is assumed that these males would not have mated if pairs had not been disturbed by capture, the percentage of marked males obtaining at least one mate in their lifetime drops from 66% to 59%. In sharp contrast, only 13 or 3.6% of the marked females failed to mate. Marked females averaged 1.56 ± 0.06 matings/lifetime ($n=358$, $c.v.=67.5$) while males averaged 1.13 ± 0.05 matings/lifetime ($n=512$, $c.v.=104.63$) (Fig. 2). If one excludes the above second tandems, the average lifetime matings drop to 0.89 for males and 1.22 for females. These figures represent maximum ones since it was impossible for me to follow all pairs until the female oviposited. In some cases (2/35), a female found early in the morning in tandem with one male was found later in the afternoon ovipositing with a different male. It is possible that the event represented a second oviposition, though this seems unlikely since most females are unreceptive to males after one oviposition. A second male could have displaced the first mate, or the female could have resisted the first mate and subsequently been seized by a second male.

Daily variation in mating success over the breeding season was considerable. The proportion of males present at the breeding site which succeeded in mating varied from 0–0.77. Average mating success of males per day was 0.39 ± 0.05 . Male mating success did not differ significantly among days of high, medium, and low density of individuals at the breeding site (Table 1).

The effects of size, age, longevity, and time spent at the breeding pool were examined to determine if any of these factors are correlated with mating success in males. Correlations of wing length with abdomen length, tarsus length, and body weight were 0.80, 0.75, and 0.85 respectively. As wing length was found to be an accurate indicator of general body size, size will hereafter refer to forewing length. Females were

Table 1. Daily variation in male mating success. Each density group comprises a sample of 6 days. ANOVA on arcsine transformed data indicated that density levels had no significant effect on mating success ($P=0.51$)

Proportion of males mating under different densities of individuals in the breeding area		
High (131–225)	Medium (63–124)	Low (7–53)
0.69	0.57	0.77
0.50	0.55	0.55
0.47	0.53	0.47
0.23	0.44	0.43
0.16	0.28	0.00
0.11	0.26	0.00

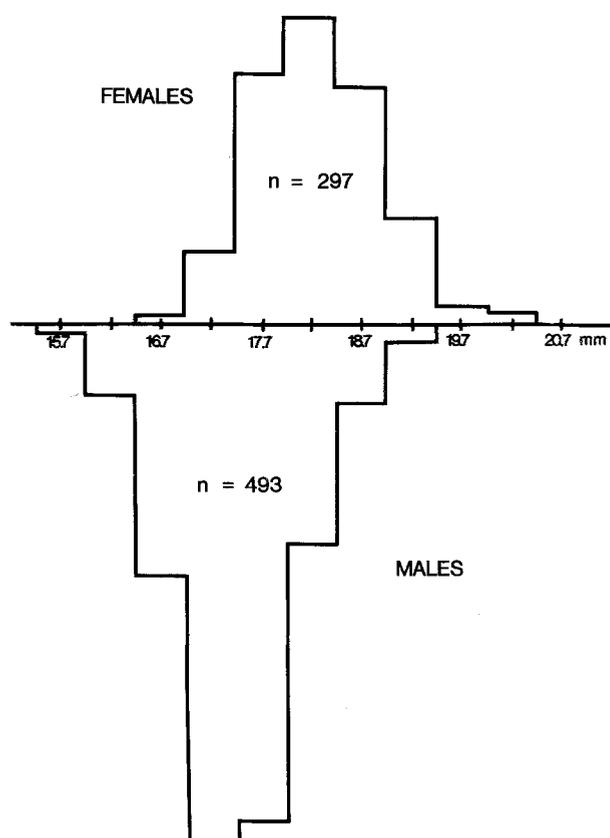


Fig. 3. Size frequency histograms (wing length) of males and females. \bar{x} of females = 18.2 ± 0.036 ; \bar{x} of males = 17.4 ± 0.027

slightly larger than males (Fig. 3). There was no significant correlation between male size and mating success ($r = -0.03$, $P < 0.57$). While the mean size of mated males was not significantly different from that of unmated males (t -test, $P < 0.28$), the variance of mated males was significantly smaller than the variance of unmated males ($F = 1.36$, $P < 0.019$) (Fig. 4). Mating was not found to be assortative by size (corre-

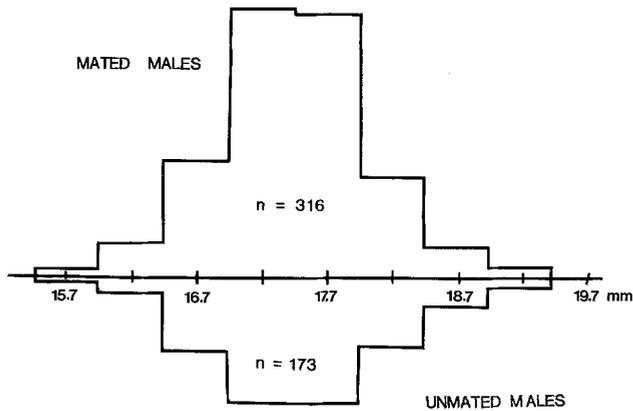


Fig. 4. Size frequency histograms (wing length) of mated and unmated males. \bar{x} of mated males = 17.39 ± 0.032 ; \bar{x} of unmated males = 17.45 ± 0.049

Table 2. Effect of age on mating males. Older males tend to be less successful on a daily basis than younger males ($\chi^2=155.4$, $d.f.=14$, $P<0.005$). Expected values were generated from the assumption that the number of matings obtained by any age group should be proportional to the number of males of that age in the total population

Number of males in the population	Age (in days)	Number of matings	
		Observed	Expected
512	1	229	133.2
313	2	91	81.4
261	3	78	67.9
218	4	19	56.7
192	5	23	49.9
158	6	21	41.1
134	7	40	34.9
106	8	15	27.6
75	9	16	19.5
64	10	5	16.6
50	11	5	13.0
43	12	5	11.2
35	13	7	9.1
38	14-15	19	9.9
23	16-20	5	6.0

lation of male size with female size, $r=0.036$, $P<0.54$).

If one compares males in the total marked population, older males obtained fewer matings/day than expected than younger males (Table 2). However, if only the marked males visiting the beach pool area are compared (i.e. receptive males), no consistent effect of age on mating success is apparent (Fig. 5).

The total number of matings per lifetime was highly correlated with lifespan ($r=0.55$ for males, $P<0.0001$). In addition, mating rates when young (1-2 days old) were not significantly higher for males which were short-lived (less than 4 days) than for males which were long-lived (greater than 7 days) ($\chi^2=0.36$, $d.f.=3$, n.s.). This indicates that mating

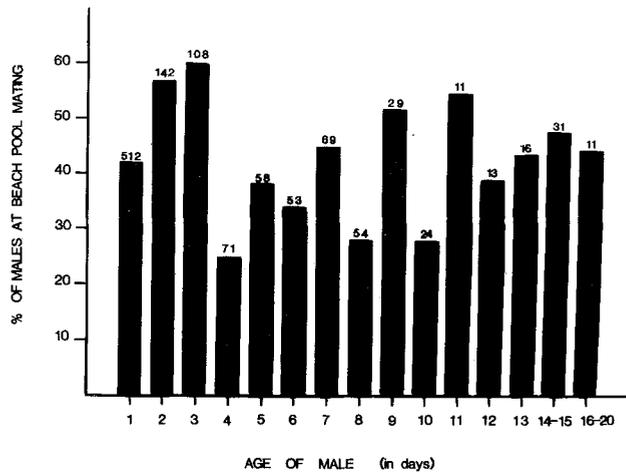


Fig. 5. Age distribution of males which mated at the breeding site. Numbers at the top of the columns indicate the total number of males of each age present. Younger males (1-2 days) present at the pool were no more successful than older males (≥ 2 days) which were present ($\chi^2=1.01$, $d.f.=1$, n.s.)

Table 3. Effect of mating on return to the pond. Males present at the pond which mated on a particular day remained away from the breeding site more days than those which failed to mate ($\chi^2=5.8$, $d.f.=1$, $P<0.025$). Expected values are in parentheses

	Days between return	
	0-2	≥ 3
Males present at pond that didn't mate	232 (220)	53 (65)
Males present at pond that mated	203 (215)	75 (63)

frequency did not have adverse effects on male survivorship.

The number of days a male was captured at the breeding site was compared for mated vs unmated males to determine whether time spent at the breeding site (as opposed to time spent in the feeding area) was a factor in male mating success and to determine whether the act of finding a female and mating had an effect on a male's probability of returning to the pond to breed on successive days. There was a significant negative correlation between the total lifetime matings achieved and the fraction of his reproductive span that a male spent at the beach pool ($r=-0.395$, $P<0.0001$). Of mated males whose reproductive spans were greater than or equal to 3 days, those which mated on a particular day spent significantly more time away from the pond ($\bar{x}=1.7 \pm 0.1$ days) than those which did not mate but were present at the breeding site ($\bar{x}=1.3 \pm 0.1$) (Table 3). Non-mated males with spans of greater than three days stayed away from the pond the longest time between visits ($\bar{x}=1.9$ days). There was a slight but significant correlation between the fraction of the reproductive span

spent at the beach pool and wing size in males ($r = 0.11$, $P < .01$). Such correlation for females was not significant.

Effect of Female Morph Color on Mating

As in many coenagrionid damselflies, *E. hageni* females exhibit a color dimorphism which persists throughout their lives. The andromorphic females have a blue and black color pattern similar to the males but distinguishable from it by a darker abdominal dorsum. Heteromorphic females vary in color from bright green to olive brown. The ratio of andromorphs: heteromorphs was 1:2.9 in the beach pool population. No significant differences between the morphs with respect to wing length, total number of matings, duration of reproductive span, or number of days at the breeding site were found (t -tests). Individual males showed no consistent preference for one morph over the other (χ^2 -test, n.s.).

Discussion

In this study, reproductive success is measured as mating success. Although mating success is several steps removed from individual fitness (see Howard 1978), it was not feasible to collect the eggs of mated pairs. Wade and Arnold (1980) showed that the variance in reproductive success of males is comprised of two factors: the variance due to differences in fertility among females and the variance due to differences in the number of mates a male acquires over his lifetime. While I measured only the latter component, it is this variance which is mainly responsible for the intensity of sexual selection on males.

My estimates of the variance in mating success must be interpreted in light of two assumptions. The first of these is that the male accompanying an ovipositing female has fertilized her clutch. This assumes that *E. hageni* males can displace sperm of a previous mate. There is good evidence that many odonates can displace sperm by using the penis to scoop out sperm masses from the female's reproductive tract (Waage 1979a, 1982). Miller and Miller (1981) present evidence for such ability in *Enallagma cyathigerum* which supports my findings for sperm displacement in *E. hageni* (personal observation). Such ability would explain why males attempt to copulate with females that have previously mated, or that have oviposited a partial clutch. Guarding an ovipositing mate would thus serve to protect a male's sperm investment should the female resurface before depositing a full clutch of eggs.

I cannot distinguish between dispersion and mortality in this study, but I assume that dispersal of adults is minimal and/or dispersing adults do not successfully reproduce elsewhere. By the end of the breeding season, I had marked approximately 1 1/2 times as many adult males as females. Such an absolute preponderance of males in the adult population (as distinct from a biased operational sex ratio) has been found in other mark-recapture studies of coenagrionid damselflies (Parr and Palmer 1971; Garrison 1978), and could be explained either by greater dispersal of teneral females or by higher female mortality in the teneral stage, or both. My data indicated that 14–16% fewer females returned as adults to the beach pool than males. If one assumes that these females are dispersing and reproducing elsewhere, then one would expect the adult sex ratio in populations to be close to 1:1 due to similar rates of emigration of females from neighboring areas. Since this was not the case for my population, and because females took on the average, one more day to mature than males, the likeliest explanation is that of greater mortality among females in the teneral stage. My estimates of 4.4 and 2.1-day male and female reproductive spans compare favorably with such estimates for other *Enallagma* (4.7 days for male *E. cyathigerum*, Garrison 1978; 3.3 days for male and 3.1 days for female *E. civile*, Bick and Bick 1963). *E. hageni* are relatively weak flyers, and it is unlikely that adults that left the beach pool could fly the 4 km to the closest conspecific breeding site before dying.

As predicted by sexual selection theory (Bateman 1948), the variance of mating success of male *E. hageni* was higher than that of females. Females of this species are the limiting resource; they are relatively rare at the breeding site, as well as absolutely rare in the adult population. The implications of higher variance in male mating success has not often been considered in past studies of odonate breeding behavior (but see Jacobs 1955; Waage 1979b). Attempts to explain skewed operational sex ratios have focused on group selection arguments for efficient breeding success of the species (Johnson 1964; Campanella and Wolf 1974). My results show that at best, only 59% of the males mated at least once. These results corroborate those of Bick and Bick (1963) for *Enallagma civile*. They reported that 76% of the males observed never mated (as opposed to 40% mating failure in females) but attributed low mating success in males to a short lifespan rather than to sexual selection.

Mating success among males varied greatly between days. In addition, mating success did not vary consistently with the density of males and females in the breeding area. The average daily mating success was lower than the average lifetime mating success

(39% vs 59%). These results illustrate why it may be impossible to characterize general trends in mating behavior of insects based on a sample of one or two days.

While *E. hageni* would best be described as an 'explosive' breeder by the criteria of Emlen and Oring (1977), its breeding system differs from that of a vertebrate explosive breeder in that the lifetime of an individual is short relative to the seasonal span of the population. Since numerous females are synchronously receptive on any one day, the effect on a short-lived male is similar to that of a long-lived vertebrate male restricted to a very short breeding season (i.e. an 'explosive' breeder). Oviposition sites of muskgrass are highly clumped and male density is high, making it ineffective for *E. hageni* males to try to exclude conspecific males from the oviposition patches. Such a population should show less variance in male mating success than one in which males are territorial, lifespan is long relative to the reproductive season, and females are asynchronous in receptivity. While there are some field data on mating success of territorial odonates (Jacobs 1955; Campanella and Wolf 1974; Waage 1979b), comparisons are difficult to make since these studies did not report total lifetime matings by individual males.

Emlen and Oring predicted low that variation in male mating success would be found in explosive breeders, in which the operational sex ratio was assumed to be 1:1. The highly skewed operational sex ratio found in *E. hageni* (and odonates in general, Corbet 1962) results in a greater intensity of sexual selection on males than would be expected either from the sex ratio at emergence which was 1:1, or from the sex ratio of adults in the population (1.4:1.0). Since female *E. hageni* mate the same day they oviposit, and usually deposit a full clutch of eggs, the population of receptive females is small relative to the population of adult males. The factors which determine the degree of synchrony among females in a population are as yet unknown. For odonates, such factors would most likely include the risk involved during mating and oviposition and the relative success of larvae developing from clumped egg clutches versus eggs which are temporally and spatially scattered. The fact that *E. hageni* females are highly susceptible to predation during oviposition would select for females which oviposited with minimum frequency.

An unexpected result of this study was the lack of a significant correlation between body size of males and mating success. In the few field studies on insects which have examined size effects on reproductive success in species showing male-male competition, male size has been positively correlated with mating success

(Alcock 1981; Borgia 1981; McLain 1981; Severinghaus et al. 1981; Thornhill 1980; Johnson 1982). The fact that the variance in size of unmated males in my study was significantly greater than that of mated males suggests that stabilizing selection for size is operating on *E. hageni*. Only a few studies have found stabilizing selection for size with reference to mating success (Mason 1964; Scheiring 1977) and these refer to a beetle with relatively non-aggressive males.

Apparently, a small *E. hageni* male is just as capable as a larger male in flying in tandem with a female. Female odonates in tandem do use their wings and thus flying in tandem is less costly for odonate males than for those species in which males must carry females without help from their mates. Borgia (1981) for example, showed that larger *Scatophaga* males had greater mating success than smaller dung flies, and that large males were better able to carry mates in flight than were smaller conspecifics. There is only a slight suggestion from my data that larger males may be better competitors under certain circumstances. Larger males tended to spend a greater amount of time at the beach pool than did smaller males. This difference could be explained if larger males were more successful in acquiring a mate at the water (methods 3 and 4 below).

Male *E. hageni* may acquire a mate in four different ways: (1) by searching for receptive females at the feeding site, before they enter the beach pool area; (2) by searching for receptive females around the beach pool; (3) by 'taking over' females from tandem males or (4) by waiting at oviposition sites to grab females as they emerge from oviposition. The first method involves the least direct competition with other males, since damselflies in the feeding area are highly dispersed. The disadvantage of this method would seem to be the difficulty in locating a receptive female, since females give no behavioral indication of receptiveness other than moving toward the breeding area and not refusing to mate once they are grabbed. (A female odonate must lift her lower abdomen to engage the male's penis which is located on his second abdominal segment; a male cannot 'force' a female to mate). The second method would thus insure that most of the females a male encounters would be receptive, but the density of single male competitors would be much greater around the beach pool. While larger males may be more successful at take overs than smaller males, the selective advantage seems to be in successful searching since males cannot easily break a tandem male's grasp on a female, and harassment of tandem pairs exposes single males to predation near the water. Obtaining females as they emerge from ovipositing is a less favorable tactic since

such males would at best fertilize only a fraction of the female's clutch (the proportion being dependent on the length of time the female had been submerged).

Studies of mating success have tended to focus on vertebrates, where male competitive ability is related to male age, and where older males are often larger and more experienced. In insects, age effects may be related to experience, but not to size, since size is fixed at the final molt. Contrary to the predictions that older males in highly polygynous mating systems should have increased mating success (Alexander et al. 1978; Howard 1978), experience did not improve mating success for *E. hageni* since the majority of older males (>2 days) were less successful on a daily basis in obtaining mates than younger (≤ 2 days). This suggests that either older males are poorer competitors and/or that males incur substantial 'costs' in mating which older males take longer to 'make up'. While older males were less likely to visit the breeding area, if they did visit the pond they were as likely to be mated as younger males. This suggests that age does not have a direct effect on a male's ability to compete, but that older males are receptive less often than are younger males. If a male mated, he subsequently spent more days away from the breeding site than if he were present at the breeding site but did not mate. Males which have spent most of a day flying in search of a mate, in tandem, and guarding a female have incurred significant energetic 'costs'. Alternatively, multiple matings may use up a male's supply of sperm or accessory gland secretions and results in temporary sterility (Lefevre and Jonsson 1962; Kvelland 1965) (but see Jacobs 1955). Such costs would tend to decrease male-male competition by limiting the number of potential male breeders in the mating arena on any given day. These possible costs of mating to males are currently under investigation.

While sexual selection has been used to explain the evolution of male secondary sex characteristics and sexual behavior, sexual selection (here measured as the variance in male mating success) has additional implications in isolated populations with low dispersion. One effect of sexual selection in this study was to decrease the effective population size by a quarter relative to the actual population size (since roughly half of the males failed to pass on any genes). The amount of genetic change due to random sampling increases as the effective population size decreases (Crow and Kimura 1970). While the level of reduction in effective population size is probably insignificant in reducing the effective number of alleles during most breeding seasons, population crashes during unfavorable years, coupled with intense sexual selection on

males would intensify the effects of random genetic drift in the population. Local genetic divergence due to random factors alone could thus result from such genetic bottlenecks (Templeton 1980). Over evolutionary time, sexual selection in such a context might have considerable implications for the potential for speciation within the genus.

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References

- Alcock J (1981) Lek territoriality in the tarantula hawk wasp *Hemipepsis ustulata* (Hymenoptera: Pompilidae). *Behav Ecol Sociobiol* 8:309-317
- Alexander RD, Hoogland JL, Howard RD, Noonan KM, Sherman PW (1978) Sexual selection and breeding systems in pinnipeds, ungulates, primates, humans. In: Chaquon NA, Irons WG (eds) *Evolutionary biology and human social behavior*. Duxbury Press, North Scituate, Massachusetts
- Bateman AJ (1948) Intra-sexual selection in *Drosophila*. *Heredity* 2:349-368
- Berven KA (1981) Mate choice in the wood frog, *Rana sylvatica*. *Evolution* 35:707-722
- Bick GH, Bick JH (1963) Behavior and population structure of the damselfly *Enallagma civile* (Hagen) (Odonata: Coenagrionidae). *Southwest Nat* 8:57-84
- Borgia G (1981) Mate selection in the fly *Scatophaga stercoraria*: female choice in a male-controlled system. *Anim Beh* 29:71-80
- Campanella PJ, Wolf LL (1974) Temporal leks as a mating system in a temperate zone dragonfly (Odonata: Anisoptera) I. *Platheimis lydia* (Drury). *Behaviour* 51:49-87
- Corbet PS (1962) *A biology of dragonflies*. Witherby Press, London
- Crow JF, Kimura M (1970) *An introduction to population genetics theory*. Burgess Press, Minneapolis
- Emlen ST (1976) Lek organization and mating strategies in the bullfrog. *Behav Ecol Sociobiol* 1:283-313
- Emlen ST, Oring LW (1977) Ecology, sexual selection, and the evolution of mating systems. *Science* 197:215-223
- Garrison RW (1978) A mark-recapture study of imaginal *Enallagma cyathigerum* (Charpentier) and *Argia vivida* (Hagen) (Zygoptera: Coenagrionidae). *Odonatologia* 7:223-236
- Gibson RM, Guinness FE (1980) Differential reproduction among red deer (*Cervus elaphus*) stags on Rhum. *J Anim Ecol* 49:199-208
- Howard RD (1978) The evolution of mating strategies in bullfrogs, *Rana catesbeiana*. *Evolution* 32:850-871
- Jacobs ME (1955) Studies on territorialism and sexual selection in dragonflies. *Ecology* 36:566-586
- Johnson C (1964) Mating expectancies and sex ratio in the damselfly *Enallagma praevarum* (Odonata: Coenagrionidae). *Southwest Nat* 9:297-304
- Johnson LK (1982) Sexual selection in a brentid weevil. *Evolution* 36 (in press)
- Jolly GM (1965) Explicit estimates from capture-recapture data

- with both death and immigration-stochastic model. *Biometrika* 53:225-247
- Kvelland I (1965) Some observations on the mating activity and fertility of *Drosophila melanogaster* males. *Hereditas* 53:281-306
- LeBoeuf BJ (1974) Male-male competition and reproductive success in elephant seals. *Am Zool* 14:163-176
- Lefevre G Jr, Jonsson UB (1962) Sperm transfer, storage, displacement and utilization in *Drosophila melanogaster*. *Genetics* 47:1719-1736
- Mason LG (1964) Stabilizing selection for mating fitness in natural populations of *Tetraopes*. *Evolution* 18:492-497
- McLain DK (1981) Interspecific interference competition and mate choice in the soldier beetle, *Chauliognathus pennsylvanicus*. *Behav Ecol Sociobiol* 9:65-66
- Miller PL, Miller CA (1981) Field observations on copulatory behavior in zygoptera with an examination of the structure and activity of the male genitalia. *Odonatologica* 10:201-218
- Parr MJ, Palmer M (1971) The sex ratios, mating frequencies and mating expectancies of three coenagriids (Odonata: Zygoptera) in northern England. *Entomol Scand* 2:191-204
- Payne RB, Payne K (1977) Social organization and mating success in local song populations of village indigobirds, *Vidua chalybeata*. *Z Tierpsychol* 45:113-173
- Scheiring JF (1977) Stabilizing selection for size as related to mating fitness in *Tetraopes*. *Evolution* 31:447-449
- Severinghaus LL, Kurtak BH, Eickwort GC (1981) The reproductive behavior of *Anthidium manicatum* (Hymenoptera: Megachilidae) and the significance of size for territorial males. *Behav Ecol Sociobiol* 9:51-58
- Templeton AR (1980) The theory of speciation via the founder principle. *Genetics* 94:1011-1038
- Thornhill R (1979) Male and female sexual selection and the evolution of mating strategies in insects. IN: Blum MS, Blum NA (eds) *Sexual selection and reproductive competition in insects*. Academic Press, New York
- Thornhill R (1980) Sexual selection within mating swarms of the lovebug, *Plecia neartica* (Diptera: Bibionidae). *Anim Behav* 28:405-412
- Waage J (1979a) Dual function of the damselfly penis: sperm removal and transfer. *Science* 203:916-918
- Waage J (1979b) Adaptive significance of postcopulatory guarding of mates and nonmates by male *Calopteryx maculata* (Odonata). *Behav Ecol Sociobiol* 6:147-154
- Waage J (1982) Sperm competition and the evolution of odonate mating systems. In: Smith RL (ed) *Sperm competition and the evolution of mating systems*. Academic Press, New York (in press)
- Wade ML, Arnold SJ (1980) The intensity of sexual selection in relation to male sexual behavior, female choice, and sperm precedence. *Anim Behav* 28:446-461
- Wells KD (1977) Territoriality and male mating success in the green frog (*Rana clamitans*). *Ecology* 58:750-762
- Wells KD (1979) Reproductive behavior and male mating success in a neotropical toad, *Bufo typhonius*. *Biotropica* 11:301-307