

**Lifetime Reproductive Success and the Opportunity for Selection in a  
Nonterritorial Damselfly (Odonata: Coenagrionidae)**



Ola M. Fincke

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LIFETIME REPRODUCTIVE SUCCESS AND THE OPPORTUNITY  
FOR SELECTION IN A NONTERRITORIAL DAMSELFLY  
(ODONATA: COENAGRIONIDAE)

OLA M. FINCKE<sup>1</sup>

*Program in Evolutionary Ecology and Behavior, Department of Biology,  
The University of Iowa, Iowa City, IA 52242*

*Abstract.*—Major components of male and female lifetime reproductive success (LRS) were quantified for a damselfly that exhibits “scramble competition” for mates. The opportunity for selection on male reproduction was potentially 2.9 times that for females. Differential fertility/clutch and survivorship each accounted for about half of the total variation in female reproductive success. Variation in fertilization efficiency accounted for 7% of the total opportunity for selection on males. Although differences in survivorship and mating efficiency each contributed to about a third of the total opportunity for selection on male reproduction, both components appeared to be influenced by random factors. Survivorship was age-independent, and the mating distributions among males with equal mating opportunities were indistinguishable from those expected if matings were random with respect to male phenotype. Because the proportion of the standardized variance ( $I$ ) in LRS that was attributed to sexual selection depended on the way the selective episodes were defined, the sample of individuals included in the partitioning analysis, and the degree of sexual selection on mated males that could be detected, my results caution against drawing conclusions about the dynamics of sexual selection on populations based on a superficial comparison of  $I$  values.

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A general prediction of sexual selection theory is that the intensity of selection on the limited sex should be greater as investment in reproduction between the two sexes becomes more unequal (Trivers, 1972) and as reproductive resources become spatially clumped and temporally predictable, such that the limited sex can sequester a disproportionate number of mates (Emlen and Oring, 1977). The test of this prediction first requires accurately quantifying variation in reproductive success over a variety of mating systems. Reproductive success may not be consistent within seasons (e.g., Fincke, 1986*a*), and age and size effects on mating success may be correlated (e.g., Howard, 1978). Thus, variation in reproductive success over the lifespan of marked individuals should provide a more accurate measure of the opportunity for selection on components of reproduction than episodic sampling (see Clutton-Brock, 1983; Arnold and Wade, 1984). Quantifying variation in reproductive success only estimates a potential for selection on reproduction. For this potential to be realized, mating or reproductive success must reflect phenotypic dif-

ferences among individuals, and for the population to respond to selection, these differences must be heritable.

Sexual selection is generally viewed as selection that acts in a frequency-dependent manner, via variation in ability to acquire mates (e.g., Darwin, 1871; Lande, 1980; Wade and Arnold, 1980) or fertilizations, given a mating (e.g., Parker, 1970), whereas natural selection acts on variation in factors affecting survivorship or fertility and usually does not depend on the relative frequency of the two sexes. The relative importance of, and covariance between, different components of natural and sexual selection can be determined by partitioning total variation in lifetime reproductive success into multiplicative episodes of selection (Wade and Arnold, 1980; Arnold and Wade, 1984). For convenience, many studies have used lifetime mating success as a correlate of reproductive success (Fincke, 1982; McCauley, 1983; Partridge and Farquhar, 1983). However, such studies cannot detect sources of variation among mated males in fertilizations/mating that potentially may be acted on by sexual selection. Furthermore, using mating success as the fitness correlate ignores variation in female fertility, which may act as a constraint on

<sup>1</sup> Current address: Department of Biology, University of Missouri—St. Louis, St. Louis, MO 63121-4499.

the opportunity for sexual selection on males (Clutton-Brock et al., 1982). Long-term studies of reproductive success have emphasized territorial or harem species (Howard, 1978; Payne, 1979; Clutton-Brock et al., 1982; McVey, 1986) for which the opportunity of sexual selection is predicted to be high.

The damselfly, *Enallagma hageni*, shows no parental care and exhibits "scramble" competition for mates. Its biology makes it a convenient insect on which to measure lifetime reproductive success, for which the opportunity for sexual selection has been predicted to be moderate (see Emlen and Oring, 1977). Both sexes return repeatedly to the same pond to mate, reproductive behavior is predictably limited to 7–8 hours a day, and oviposition sites are clumped in a few discrete areas. The size of adult insects is fixed at emergence; age and size effects on reproductive success can be clearly distinguished. Finally, because I have determined the pattern of paternity for multiple matings (Fincke, 1984) and can retrieve eggs to measure oviposition rates, I can estimate lifetime reproductive success (LRS) in terms of the zygotes produced and compare the fitness correlate of mating success with that of fertilization success. Herein, I determine the relative opportunity for selection on major components of male and female reproductive success. In so doing, I point out potential problems in using field data on LRS to assess the relative potential for natural and sexual selection on a current population and distinguish between the potential and realized opportunity for selection.

#### Theoretical Considerations

For female *E. hageni*, the number of matings is not limiting to reproductive success because females store sperm, nearly all females mate each time they return to the pond to oviposit, and many remate between bouts of egg-laying of the same clutch. Evidence argues against females gaining nutrients from multiple matings (Fincke, 1986b). Thus, lifetime reproductive success (LRS) of females is the product of the number of eggs/clutch and the number of clutches a female produces in her lifetime. Using Crow's index for the opportunity for selection (variance/mean<sup>2</sup> Crow, 1958; see

Wade and Arnold, 1980), this is expressed as

$$I_f = I_o + I_c, \quad (1)$$

where  $I_f$  is the total opportunity for selection on female reproduction,  $I_o$  is the opportunity for selection on fertility/clutch, and  $I_c$  is the opportunity for selection on the number of clutches. These values of  $I$  are additive, unless the multiplicative episodes covary, in which case a covariance term must be added (see Arnold and Wade, 1984). Because *E. hageni* females produce only one clutch/visit to the pond, the number of clutches/lifetime reflects both the frequency with which females visit the pond and survivorship.  $I_c$  could be further partitioned into components of clutches/day alive and days alive, but I chose not to because the spurious covariance made the interpretation of the results unclear (see Results).

Using the number of progeny from a single season (analogous to a single day for an annual insect), Wade and Arnold (1980) partition the opportunity for selection on male reproduction into two episodes which they treat as components of natural and sexual selection. They express the relationship between the two as

$$I_m = RI_f + I_s, \quad (2)$$

where  $I_m$  is the total opportunity for selection on male reproduction,  $R$  is the sex ratio of breeding adults,  $I_f$  is the opportunity for selection on female fertility (equivalent to  $I_o$  above), and  $I_s$  is the opportunity for sexual selection on males, as measured by variation in mating success. Because the above model defines variation in males' offspring in terms of variation in female fertility, it underestimates the opportunity for sexual selection for many animals. First, the model assumes that reproduction among females is independent, thereby implying that males mating with females do so independently as well. This is not the case if mate choice by either males or females occurs, such that some males mate nonrandomly with the more fertile females, or if a male can influence the fertility of the female with whom he mates (as might occur for males offering nutritious nuptial gifts). In such cases, even if there was no variance in mating success and  $R$  was unity, the variance in fertilizations/mating of males could be greater than

eggs/mating of females. Second, the model is inappropriate for species in which females mate with more than one male before producing a clutch or litter, thereby partitioning their offspring among several males. Such partitioning is not analogous to the case of sperm mixing discussed by Wade and Arnold (1980) because multiple mates may not necessarily get equal representation in fertilizations.

I adapt the derivations of Wade and Arnold (1980) to species in which the females partition clutches among males by the following analogous reasoning. In the derivation of  $I_s$ , Wade and Arnold use the sex ratio of breeding adults ( $R$ , males/females) to calculate mean mates/male (i.e.,  $1/R$ ). If the number of matings (leading to fertilizations) per clutch is greater than one, then the ratio necessary to calculate mean mates/male becomes males/matings, or, for mated males,  $R/M$  where  $M$  is mean matings/clutch. The unit by which female fertility is calculated must likewise be changed from eggs/clutch to eggs/mating. The need for these modifications is eliminated by replacing  $RI_f$  with the term  $I_{fm}$ , the opportunity for selection on fertilizations/mating, which is specific to males and independent of  $R$ .

In order not to confound components of natural and sexual selection for lifetime data,  $I_s$  must be partitioned into the opportunity for selection on survivorship ( $I_1$ ) and the opportunity for selection on mating efficiency ( $I_e$ ) (see McCauley, 1983). For male *E. hageni* then, lifetime reproductive success (LRS) can be described as the product of the number of fertilizations/mating, the number of matings/day alive, and lifespan. This is expressed as

$$I_m = I_{fm} + I_e + I_1. \quad (3)$$

The opportunity for selection on total mating success, which I shall denote as  $I_t$ , should equal the sum of  $I_e$  and  $I_1$  (plus a possible covariance term). For animals for which measurement of  $I_m$  under field conditions is impractical or impossible, the ratio of  $I_e/I_1$  is the appropriate estimate of the relative opportunity for sexual selection on males.

If males mated randomly with respect to female clutch size, and females mated only once/clutch,  $I_{fm}$  for mated males would equal  $R_1(I_o)$ , where  $R_1$  is the ratio of first mates/

mated females (i.e., the sex ratio given  $M = 1$ ). Assuming that the sample of mates of males is identical to the sample of females used to calculate  $I_o$ , any difference between  $R_1I_o$  and  $I_{fm}$  must result from nonrandom mating of males with females of different fertility. For species whose females divide clutches among males, the difference could also be due to differences among males in their fertilization efficiency, which I here define as the proportion of a female's clutch that a male fertilizes, given that he mates. Considering the biology of the animal and how fertilizations/mating was actually measured, fertilization efficiency would depend on such variables as guarding duration of males, type of alternative mating tactic, sperm displacement ability, or effectiveness of sperm plugs. Variation in these forms of male-male competition for fertilizations constitutes an additional source of variation on which sexual selection could act. Thus, the total opportunity for sexual selection on males ( $I_s$ ) is

$$I_s = I_e + |I_{fm} - R_1I_o|. \quad (4)$$

Although I retain the original interpretation of  $I_s$  as the standardized variance on which sexual selection could act, the value of  $I_s$  in equation (2) (which ignores variation in lifespan and the opportunity for sexual selection on mated males) is equivalent to  $I_e$  above. I express the relative importance of both pre- and postcopulatory sexual competition as  $I_s/I_m$ .

If female clutch size is more variable than the bouts of eggs/mating into which they are divided,  $R_1I_o$  may be larger than  $I_{fm}$  of mated males. Thus, the opportunity for sexual selection on mated males that is detectable by the above method is a minimum value. For example, in species whose females mate multiply per clutch, nonrandom fertilizations by mated males may result in a positive difference between  $I_{fm}$  and  $R_1I_o$ , while clutch partitioning could conceivably result in a negative difference, in which case the absolute difference may be zero, in spite of real variation on which sexual selection could potentially act.

#### MATERIALS AND METHODS

The univoltine study population is an isolated one which breeds at a small pond (100

m perimeter, <1 m depth) at the University of Michigan Biological Station, near Pellston, MI (for details see Fincke, 1982, 1986a). After overwintering as aquatic larvae, adults emerge during mid-late June and breed until early August. The sex ratio at emergence is 1:1. Both sexes are clear-winged and differ only moderately in body coloration. Females, which are slightly larger than males, require more time to reach sexual maturity than do males ( $\bar{x} \pm \text{SE} = 8.8 \pm 1.1$  days,  $N = 21$  females;  $\bar{x} \pm \text{SE} = 6.1 \pm 0.6$  days,  $N = 29$  males).

Although there is greater mortality and/or dispersal of females before their first visit to the pond, mature females live slightly longer than do males, making the adult sex ratio nearly equal to one (1.3 females per male, Fincke, 1986a). Because females visit the pond only after maturing a clutch of eggs every 2–7 days ( $\bar{x} = 5.2$ ,  $N = 73$ ), whereas mature males visit the pond on average once every 2.5 days, the operational sex ratio at the breeding site is male biased ( $\bar{x} = 3:1$ , range = 1.5–9:1). On days when individuals are not at the pond, they can be found in an adjacent field where adults and teneral feed and roost at night.

In the morning, males search the banks of the pond for gravid females arriving from the feeding areas. After copulation, the male flies in tandem with the female to an oviposition site, and remains in tandem until the female completely submerges to lay eggs in plant stems. The male (above water) guards the submerged female. Females may submerge up to four times ( $\bar{x} = 1.6$  times) per day. Because females will remate if they have a substantial portion of a clutch left to lay (Fincke, 1986b), males failing to find a female earlier in the day have additional mating opportunities by waiting at oviposition sites for females that resurface prematurely. Males are behaviorally plastic in their use of the two alternative mating tactics (Fincke, 1985).

All data reported refer to sexually mature adults (distinguishable from immatures by body coloration and presence at the breeding site). When first seen at the pond, mature individuals were marked by writing a number on the wing with an indelible felt-tip pen. I measured lifetime mating success (LMS) of marked individuals over the re-

productive season in 1980 ( $N = 870$ ; on 18 days of a 23-day season; methods described in Fincke, 1982) and in 1982 ( $N = 213$ , 17/28 days). *E. hageni* do not breed on very overcast or rainy days; such days were excluded from analysis in both years. In 1982, I measured lifetime reproductive success (LRS) as the number of eggs laid by females or fertilized by males. I followed tandem pairs throughout the day, recording copulation duration, the number and duration of oviposition bouts, guarding success of males, and the fate of resurfacing females for as many of the 265 observed tandems as possible. Of the matings by marked males for which I report fertilization data, 22% were in tandem with unmarked females, while 24% of the matings by marked females for which data are given involved unmarked males. Although paternity by second mates was experimentally determined to be 80% (maximum = 95%, Fincke, 1984), irradiated sperm used to determine paternity were less competitive than were normal sperm, making detection of 100% precedence impossible. I thus credited a male in tandem with a female as she submerged with 100% of the fertilizations from her subsequent oviposition bouts that day, unless she remated with another male between bouts, in which case the intercepting male gained a portion of her clutch. Although egg-laying rates increased with water temperature, water temperature of the beach pool remained fairly stable throughout the afternoon when most ovipositions occurred (Fincke, 1985). Oviposition duration was thus used as a measure of the number of eggs laid by females (rate = 13 eggs/min at 27°C, the average afternoon water temperature).

Fertilizations/mating was measured as the unintercepted oviposition duration/mate, averaged over each mated male. I estimated lifespan as the span between first and last sightings of mature adults. Mating efficiency was measured directly as the number of matings leading to ovipositions per visit to the pond. This measure was compared to mating efficiency calculated by dividing total mates by days alive (mates/day). Individuals were scored for only one visit on a given day at the pond because it was impossible to detect brief absences from the

TABLE 1. Daily reproductive success of males and females visiting the pond summed over the 17 study days in 1982.  $I = \text{variance}/\text{mean}^2$ . Means for mated males and females are slightly different for the two sexes because unmarked females in tandem with males are excluded from values for females (see text). Matings/visit do not include redundant matings by a male that remated with his original female after she resurfaced.

Source of variation	<i>N</i>	Mean	Variance	<i>I</i>
Eggs laid or fertilized daily				
Females	114	361	48,841.0	0.37
Mated males	182	365	85,556.3	0.64
All males	451	147	66,522.7	3.08
Matings/visit				
Females	114	1.14	0.136	0.10
Mated males	182	1.12	0.129	0.10
All males	451	0.45	0.354	1.75
Eggs/mating				
Females	114	330	30,345.6	0.28
Mated males	182	334	49,417.3	0.44
All males	451	129	45,565.2	2.74

pond within the day. Female LRS was measured as total oviposition duration/lifetime. Eggs/clutch was measured as oviposition duration/visit, and the number of clutches was measured as the number of visits a female made to the pond to lay eggs.

In order to distinguish the potential for selection on mating efficiency from the realized selection on the current population, I compared the observed mating distribution of males with equal numbers of visits with the Poisson distributions expected if matings were independent events. A significant deviation from the Poisson, coupled with significant covariance between mating success and a phenotypic character(s), would suggest that mating success was nonrandom with respect to male phenotype.

## RESULTS

### Daily Reproductive Success

Herein, I designate "daily" reproductive success as that calculated only for individuals at the breeding site on a given day (as distinct from success measured as mates/day alive which is averaged over the lifespan of individuals). The daily opportunity for selection on male mating efficiency ( $I_e$ ) varied from 0.67–13.6 ( $\bar{x} \pm \text{SE} = 1.8 \pm 0.8$ ,

TABLE 2. Multivariate partitioning of the total opportunity for selection on male ( $N = 132$ ) and female ( $N = 76$ ) *E. hageni* (after Arnold and Wade, 1984).

Source of variance in fitness	Sym- bol	Contribution to total opportunity for selection	
		Value	Percentage
<b>Males</b>			
Reproductive span ( $w_1$ )	$I_1$	0.866	62%
Matings/day ( $w_2$ )	$I_2$	1.098	78%
Cointensities and change in covariance (12)	—	-1.096	-66%
Subtotal ( $w_1w_2$ ) (total matings)	$I_{12}$	1.040	74%
Fertilizations/mating ( $w_3$ )	$I_3$	0.224	16%
Cointensities and change in covariance (123)	—	0.135	10%
Total selection ( $w_1w_2w_3$ )	$I_{123}$	1.402	100%
<b>Females</b>			
Reproductive span ( $w_1$ )	$I_1$	1.150	224%
Clutches/day ( $w_2$ )	$I_2$	0.540	105%
Cointensities and change in covariance (12)	—	-1.315	-256%
Subtotal ( $w_{12}$ ) (total clutches)	$I_{12}$	0.375	73%
Eggs/clutch ( $w_3$ )	$I_3$	0.279	54%
Cointensities and change in covariance (123)	—	-0.141	-27%
Total selection ( $w_1w_2w_3$ )	$I_{123}$	0.513	100%

$N = 17$  days) while  $I_e/I_m$  ranged from 0–1 ( $\bar{x} \pm \text{SE} = 0.46 \pm 0.07$ ). There was an inverse relationship between the operational sex ratio and the proportion of males present at the breeding site that mated ( $r = -0.87$ ,  $N = 17$  days). Table 1 shows the daily variation in reproduction of mated males and females present at the breeding site. Not only were mated males more variable than were mated females, but the opportunity for selection on female fertility was less than that on fertilizations/mating of males. Covariance between daily mating efficiency and fertilizations/mate was not significant ( $r = 0.05$ ,  $N = 182$  day males). On a daily basis, the opportunity for sexual selection on fertilization efficiency was 18%

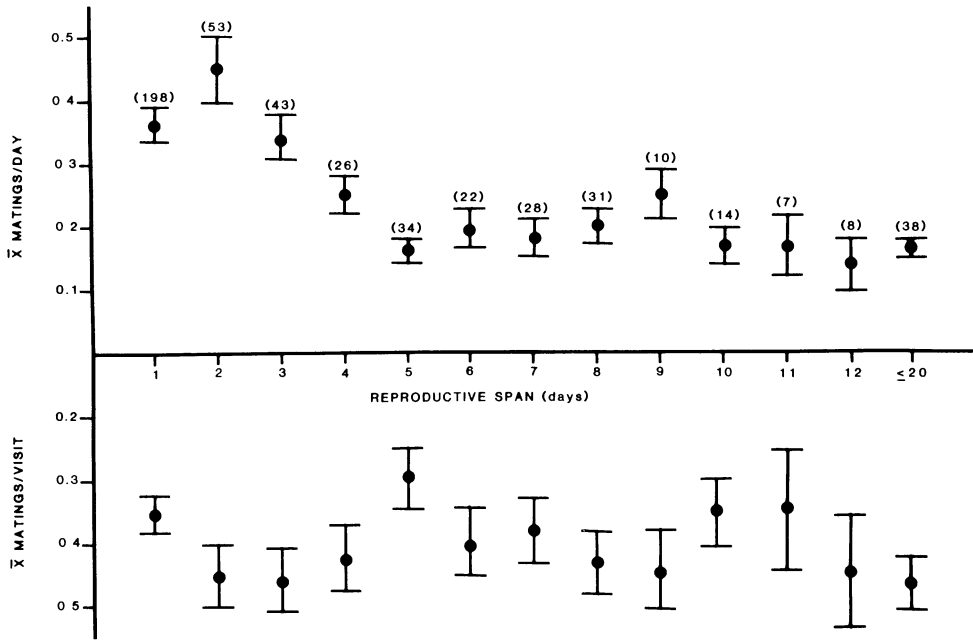


FIG. 1. Mean  $\pm$  SE of mating efficiency, measured as mates/day alive and mates/visit to the breeding site of males with different reproductive spans. Sample sizes are in parentheses (1980 data).

of the total daily opportunity for selection on mated males ( $I_{\text{m}} - R_1 I_o = 0.11$ ).

#### *Practical Problems in Partitioning Variance in LRS*

For lifetime data, the relative importance of major components of LRS and the meaning attributed to the covariance between them depended on my treatment of the following problems: 1) mating efficiency could be defined in more than one way, 2) the partitioning analysis restricted data to that subset for which each selective episode was known, thereby artificially increasing the percentage of unmated males, 3) assigning a value of "fertilizations/mating" to unmated males was artificial, 4) a marking and/or capture effect resulted in sampling error in the estimate of lifespan and 5) selective episodes defined in terms of days alive had artificially high values for individuals seen only once. By cross-checking the results of the partitioning (Table 2) with additional analyses on appropriate subsets of individuals, I adjusted the results (Table 3) to more accurately reflect the relative importance of components of LRS in *E. hageni*.

The results of the multivariate partitioning analysis shown in Table 2 suggested there was an evolutionary "trade-off" between survivorship and mating efficiency of males, and survivorship and reproductive effort of females, as indicated by the large negative covariance components between those episodes. Rather, these results were a statistical artifact resulting from artificially high values for matings/day or clutches/day for individuals seen only a few times (Fig. 1). Because male *E. hageni* were not present at the breeding site every day of their reproductive lifetime, for this species, the more appropriate measure of mating efficiency was mates/visit. In contrast with mates/day, mates/visit did not significantly covary with lifespan ( $r = 0.10$ ,  $N = 156$ ). However, for the product of the episodes to remain total eggs fertilized, an additional episode, the proportion of reproductive days spent at the pond, which theoretically should reflect the interval between visits, had to be included in the equation for male LRS (i.e.,  $I_p$ , Table 3).

As shown in Figure 2, restricting the analysis to the 88 mated, 43 unmated males,

and 76 mated females for which I had complete data, increased the percentage of unmated males from 27% to 33% (and changed  $I_e/I_m$  from 0.40 to 0.44). I did not consider this to be a serious problem because the proportion of unmated males was underestimated in the original data from 1982, when I concentrated on following tandem pairs. In 1980, when I recorded all individuals present at the pond, unmated males accounted for 41% of the sample (complete data for 1980 and 1982 are given in Fincke, 1986a).

Assigning a value of zero to fertilizations/mating for unmated males resulted in an artificially high  $I$  value (Table 3) and a spurious correlation between eggs/mating and mates/visit ( $r = -0.549$ ,  $N = 156$ ), simply because of the large number of males with no mates. In contrast, for mated males, fertilizations/mating and mating efficiency were not significantly correlated ( $r = 0.10$ ,  $N = 88$ ). I therefore used the  $I_{fm}$  value for mated males to estimate  $I_{fm}/I_m$  (Table 3).

The probability of seeing a male or female after the day of marking ( $P = 0.48$ ) was considerably less than daily survivorship on subsequent days (Fig. 3). Individuals with a lifespan of one day were thus over-represented in my sample, exacerbating the negative correlations between visits/day alive (i.e., clutches/day for females) and lifespan ( $r = -0.90$ ,  $N = 89$  females;  $r = -0.84$ ,  $N = 132$  males). These negative correlations were statistical artifacts. Females seen only once were those seen on their first return to the pond to oviposit, and thus their score for clutches/day was 1.0, the maximum possible. Any female maturing a second clutch would automatically have a score of less than one, because the interclutch interval was greater than one day. Likewise, for males seen only once at the pond, the score for visits/day was 1.0, artificially high because males did not visit the pond every day. Further evidence that the correlations were spurious was that the inter-clutch interval, measured directly from the females seen more than once, was positively correlated with lifespan ( $r = 0.61$ ,  $N = 44$ ) (and was not significantly correlated with LRS,  $r = -0.26$ ,  $N = 44$ ). Likewise, for the 62 males seen more than once in 1982, the interval between visits to the pond, measured di-

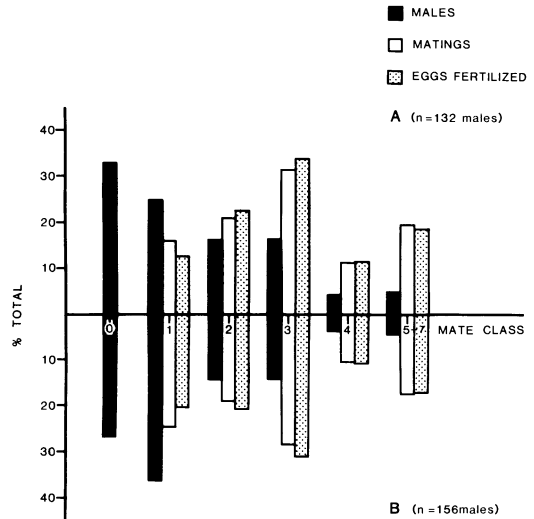


FIG. 2. Contribution to total matings and eggs fertilized by males with 0–7 mates (no male achieved more than seven matings/lifetime). A: Males for which all selection episodes were known. B: All males. Total eggs fertilized was estimated by crediting the 26 unmated males whose fertilizations were not known, with the mean fertilizations/mating for mate class 1.

rectly, was positively correlated with lifespan ( $r = 0.34$ ) (and was not significantly correlated with LRS,  $r = -0.1$ ).

Consequently, the value of  $I_m$  was larger than the sum of its components (Table 3), resulting in an overestimate of the relative value of  $I_1$  (62%). Fertilizations/mating was not significantly correlated with lifespan ( $r = 0.15$ ,  $N = 87$ ). Excluding males seen only once decreased the relative value of  $I_1$  (39%, Table 2) but did not eliminate the negative covariance between visits/day and lifespan ( $r = -0.66$ ), and consequently, the relative contribution of  $I_e$  was overestimated (58%). I thus ignored the spurious covariance component by estimating the combined value of  $I_1 + I_p$  by subtraction of  $I_{fm}$  and  $I_e$  from  $I_m$ . This method ignores the small, but as shown above, statistically insignificant covariance components between the selective episodes.

#### *Opportunity for Selection on Males and Females*

As predicted by Bateman (1948), males were more variable than females in both the number of matings obtained and the total number of zygotes produced. Tables 3 and

TABLE 3. Variation in components of male LRS in 1982.  $I$  = variance/mean<sup>2</sup>.  $I/I_m$  values assume no significant covariance between the episodes (see text). Values for "fertilizations" are given in oviposition duration (fertilizations = mean duration  $\times$  13 eggs/min).

Variable	Symbol	$N$	Mean	Variance	$I$	$I/I_m$
Total fertilizations (LRS)	$I_m$	132	40.7	2,323.24	1.40	
		85 <sup>a</sup>	56.3	2,683.24	0.85	
Fertilizations/mate	$I_{fm}$	132	16.9	268.96	0.94	
		88 <sup>b</sup>	25.4	193.21	0.30	0.21
		60 <sup>a</sup>	27.2	146.41	0.20	
Mates/visit	$I_e$	132	0.63	0.25	0.62	0.44
		85 <sup>a</sup>	0.67	0.22	0.49	
Lifespan	$I_l$	132	6.24	33.76	0.87	0.23–0.34
		85 <sup>a</sup>	9.19	28.09	0.33	
Visits/day alive	$I_p$	132	0.64	0.11	0.26	<0.11
		85 <sup>a</sup>	0.42	0.05	0.26	
Total mates (LMS)	$I_t$	132	1.56	2.53	1.04	
		85 <sup>a</sup>	2.09	2.92	0.67	
Visits to pond		132	2.38	2.31	0.41	
Days between visits	(intervals) (males)	146	2.7	10.45	1.43	
		62	3.1	9.30	0.97	
Fertilizations/day alive		132	10.0	262.44	2.62	
Mates/day alive		132	0.41	0.18	1.09	
				0.06 <sup>c</sup>	0.36 <sup>c</sup>	

<sup>a</sup> Males seen once are excluded.

<sup>b</sup> Mated males.

<sup>c</sup> Variance of males with lifespan of 3 days (after McCauley, 1983).

4 show the opportunity for selection on the components of male and female reproductive success respectively. Selection on male reproduction was potentially 2.9 times as great as that on females (assuming no difference in the variation of offspring survivorship to hatching between males and females). If the 1982 data are adjusted to make the proportion of unmated males the same as it was in 1980, the ratio of  $I_m/I_f$  increases to 3.6.

The combined opportunity for selection on lifespan and visits/span was 0.48, or 34% of  $I_m$ . Because variation in visits/span accounted for 11% of the total variation in LRS ( $r = -0.33$ ,  $N = 132$ ),  $I_l/I_m$  must be greater than 23% but less than 34%. The opportunity for selection on fertilizations/mate accounted for 21% of total  $I_m$ . This included 7% that resulted from the opportunity for selection on fertilization efficiency of mated males ( $I_{fe}$ ) [ $0.39(77/76) - 0.30 = 0.095$ ], with the remaining 14% resulting from variation in female fertility. Because  $I_o$  from lifetime data used in the above calculation could not include oviposition data

on the unmarked females mating with marked males (22% of the mates of marked males, assuming mean number of clutches did not differ between marked and unmarked females), the estimate for lifetime  $I_{fe}$  was less reliable than the daily value.

Variation in mating efficiency, the main source of potential sexual selection, accounted for about half ( $I_e/I_t = 60\%$ ) of the opportunity for selection on lifetime mating success (LMS) and 44% of the total opportunity for selection on male LRS. Over the lifetime of individuals, opportunity for sexual selection on males ( $I_e$ ) accounted for 51% of  $I_m$  (7% + 44%). Although total mates/lifetime (LMS) was highly correlated with total eggs fertilized ( $r = 0.89$ ,  $N = 156$  males;  $r = 0.80$ ,  $N = 76$  females), using LMS rather than LRS as a fitness correlate overestimated the relative contribution of  $I_e$  by 16%.

The relative opportunity for selection on mating efficiency among mated males ( $I_e/I_m = 0.08/0.62$ ) was only 13%, about 1/3 of that for all males. The comparison indicates that one mating for an *E. hageni* male was relatively valuable, considering that many

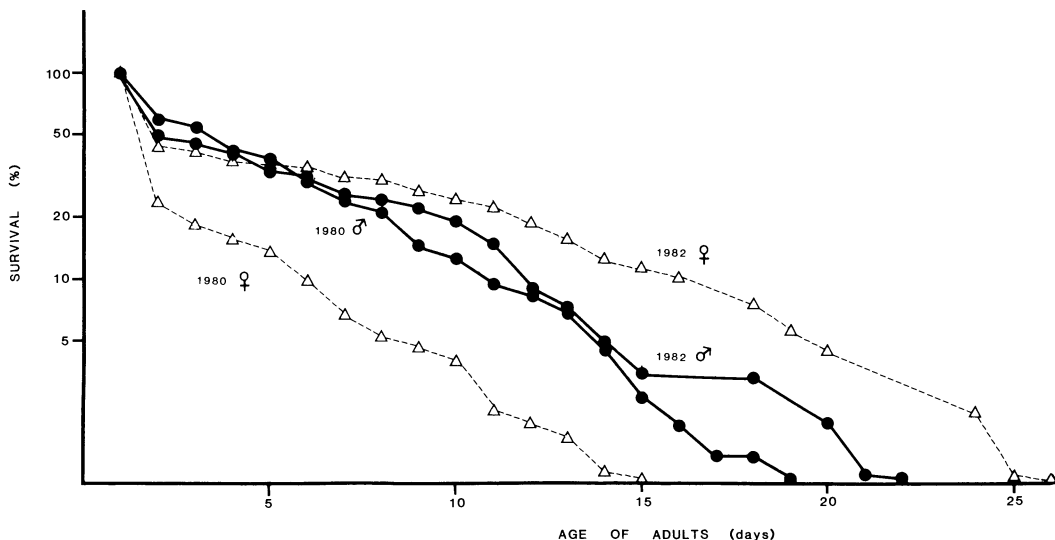


FIG. 3. Survivorship curves of adult *E. hageni* for two years (log scale). 1980:  $N = 512$  males, 358 females; 1982:  $N = 156$  males, 89 females. In 1980, individuals were only censused at the breeding site, while in 1982, the adjacent field was also searched, accounting for differences between the two curves for females. Probability of resighting after day 1 (1982 data):  $\bar{x} \pm SE = 0.85 \pm 0.03$  for females,  $0.83 \pm 0.03$  for males.

males did not mate, and 72% of all eggs laid were accounted for by males with 1–3 mates (Fig. 2).

Means and variances of components of female LRS are shown in Table 4. The opportunity for selection on female fertility,  $I_o$ , plus the opportunity for selection on total clutches,  $I_c$ , was greater than  $I_f$  because eggs/clutch covaried slightly but insignificantly with the number of clutches ( $r = -0.10$ ,  $N = 76$ ). The relative contribution of the opportunity for selection on survivorship ( $I_s$ ) remained obscured by the spurious negative covariance component between  $I_1$  and  $I_p$  (see above) and was underestimated by  $I_c$ . Eggs/clutch accounted for about a third of the total variation in female LRS ( $r^2 = 0.31$ ,  $N = 76$ ), while the number of clutches accounted for about half of the total variation ( $r^2 = 0.49$ ,  $N = 76$ ).

My estimate of clutch size assumed a constant rate of oviposition. This assumption was generally valid, because females oviposited during early–late afternoon when the water temperature (which was correlated with egg-laying rate) was fairly constant (Fincke, 1985). However, oviposition rates were probably lower on the thin filaments of the alga, *Chara* (16% of total ovipositions), than on the preferred, thicker-

stemmed sedges and *Potamogeton*. Failure of egg-laying rates to be constant would decrease both the variance and the mean of clutch size, overestimating  $I_o$  and consequently, underestimating the relative importance of survivorship on LRS.

#### The Role of Chance

The two major components of LRS appeared to be influenced by stochastic factors. The survivorship curves for both sexes were characteristic of age-independent mortality (Fig. 3), and maximum lifespan was 25 days, about five times the average. Although variation in mates/visit was potentially attributable to differences among males in their ability to monopolize females, the observed mating distributions for males visiting the pond on two or more days were not significantly different from those expected if matings were random with respect to male phenotype (Table 5). Of males visiting the pond only once, fewer obtained two or more matings than was expected by chance. This discrepancy resulted because the Poisson distribution did not account for “handling” time given a mating, which, for *E. hageni*, was more than two hours, making it nearly impossible for a male to acquire more than one mating/visit. The mating

TABLE 4. Variation in components of female LRS in 1982.  $I$  = variance/mean<sup>2</sup>. Values for "eggs" are given in oviposition duration (eggs = mean duration  $\times$  13 eggs/min).

Variable	Symbol	$N$	Mean	Variance	$I$	$I/I_f$
Total eggs (LRS)	$I_f$	76	44.5	961.00	0.49	
Eggs/clutch	$I_o$	76	24.2	228.01	0.39	0.79
Total clutches (visits)	$I_c$	76	1.9	1.23	0.34	0.69
Lifespan (days)	$I_l$	76 39 <sup>a</sup>	6.2 11.1	43.82 35.64	1.15 0.29	
Clutches/day alive	$I_p$	76	0.66	0.14	0.32	
Total mates (LMS)	$I_t$	76	1.84	1.17	0.35	
Interclutch interval	(intervals) (females)	73 44	5.2 5.7	21.16 20.88	0.78 0.64	
Eggs/day alive		76	16.4	278.89	1.04	

<sup>a</sup> Females seen once are excluded.

distribution of males with equal lifespans likewise did not differ from the expected Poisson distribution, except for males seen only once ( $X^2 = 16.6$ ,  $d.f. = 3$ ,  $P < 0.005$ ).

#### DISCUSSION

Several findings of this study have important implications for field studies of reproductive success. Daily ratios of  $I_c/I_m$  varied greatly, making it unlikely that episodic sampling would accurately reflect the opportunity for sexual selection in similarly short-lived species. Second, using only the variation in male mating success or the proportion of both sexes that mated over their lifetime (e.g., Fincke, 1982), would overestimate the potential opportunity for sexual selection on mating efficiency and could not detect the opportunity for sexual selection on mated males. Variation in longevity, and to a lesser extent, female fertility, decreased the relative opportunity for selection on male mating efficiency ( $I_c/I_m$ ). Third, random encounters with females may explain variation in the mating "efficiency" of males (see also Sutherland, 1985), and thus the potential opportunity for sexual selection must be distinguished from the realized opportunity for selection. Finally, because statistical artifacts affecting covariances resulted from sampling error and/or the way a selective episode was defined (see Fig. 1), spurious relationships must be distinguished from real evolutionary "trade-offs"

and/or positive covariance between the components of reproductive success.

Contrary to an assumption often made in theoretical models (e.g., Wade and Arnold, 1980; Arnold and Wade, 1984), I have shown that for males that mated with females that produced offspring, variation in female fertility was not the only source of variation in the number of zygotes produced by males. The number of eggs an *E. hageni* male could potentially fertilize depended on whether he mated with her before she had oviposited that day or after she resurfaced from laying a partial clutch (Fincke, 1986b). After mating, the number of fertilizations a male achieved depended on the duration and effectiveness of mate guarding (Fincke, 1985, 1986b). These additional sources of variation in eggs fertilized were less detectable over the lifetime of males than on a daily basis, because individuals mating more than once per lifetime usually used two mate-finding tactics (Fincke, 1985). In addition, males exhibited a conditional latency to re-mating, equal in duration to the time required for females to lay a complete clutch, and few males abandoned mates. For species in which the use of alternative tactics depends on male phenotype (e.g., Alcock et al., 1979), oviposition occurs long after mates separate, or the potential profit from abandoning a mate is high, such variation in fertilization efficiency may constitute a substantial portion of total opportunity for

TABLE 5. Comparison of the observed mating distribution with the Poisson distribution (expected values in parentheses) for males visiting the pond an equal number of days (1980 data).

Total visits (days at pond)	$\bar{x}$	Total matings/lifetime					P
		0	1	2	3	4-7	
1	0.36	126 (137.5)	73 (50.4)	0 (9.2)	0 (1.1)	0 (0)	<0.005
2	0.88	48 (54.8)	56 (48.2)	24 (21.2)	4 (6.2)	0 (1.6)	ns
3	1.17	15 (21.7)	32 (25.4)	19 (14.9)	4 (5.8)	0 (2.1)	ns
4	1.48	7 (11.4)	22 (16.9)	14 (12.5)	5 (6.2)	2 (3.1)	ns
5	2.43	2 (2.5)	7 (6.0)	5 (7.3)	7 (5.9)	7 (6.4)	ns
6	2.37	1 (1.8)	4 (4.2)	4 (5.0)	7 (3.9)	3 (4.1)	ns
7-9	3.20	0 (0.4)	0 (1.3)	4 (2.1)	3 (2.2)	3 (3.8)	ns

sexual selection on males. However, using  $I$  values to detect this form of sexual selection in insects may be difficult because it requires long-term data on marked females as well as males.

Wade and Arnold (1980) consider the effects of sperm competition as a source of variation in female fertility, and consequently they are led to the biologically incorrect conclusion that last male precedence decreases the relative opportunity for sexual selection on males by increasing the value of  $I_f$  [see equation (2)]. By similar reasoning, these authors conclude that sperm mixing increases the relative opportunity for sexual selection on males by decreasing the value of  $I_f$ , and thereby increasing  $I_s/I_m$ . Because my modification allows for the partitioning of fertilizations/mating into components due to variation in males as well as females, it corrects the problem, reversing the above conclusion. Last male precedence increases the value of  $I_{fm}/I_o$ , and thus increases the relative opportunity for sexual selection, while sperm mixing decreases the variation in fertilizations/male, thus decreasing  $I_{fm}/I_o$  (note that the means remain the same).

Although the comparison of the mating distribution with a null model suggests that mating success is random, the potential opportunity for selection on mating success in *E. hageni* is probably realized as stabilizing selection. Of the phenotypic traits I measured, only guarding duration, a post-mat-

ing behavior, was positively correlated with total eggs fertilized by males (Fincke, 1986a). Males of intermediate size obtained significantly more mates/lifetime and visited the pond more often than did larger or smaller males (Fincke, 1986a). No such trend was found for females. Mating was not assortative by size, and there was no evidence for mate choice based on male phenotype (Fincke, 1982, 1986a).

Given that in short-lived species with scramble mate competition it may be difficult to discern variation in phenotypic traits or behaviors important to sexual selection, does the relative opportunity for sexual selection have any meaning? I argue that even if the potential opportunity for sexual selection is not realized, the ratio of  $I_c/I_m$  should theoretically still reflect a potential selection differential on traits increasing mating efficiency, because the ratio is indicative of differences in the reproductive biology and ecology of the sexes which act as the driving force for sexual selection. Three characteristics of breeding systems could generate variance in mating success in the absence of phenotypic differences among males: 1) differences in the duration between periods of sexual receptivity (latency), or age of first mating between the sexes, 2) differences in survivorship between the sexes, and 3) the degree to which ecological factors enable males to control access to limiting reproductive resources

other than mates. Environmental perturbations such as weather or disease might also affect variation in LRS of adults, but unless it affected the reproductive success of one sex much more than the other, it should not change the predictive value of  $I_c/I_m$ . Factors (1) and (2) both reflect differential investment in reproduction (either in energetic investment or in risk-taking), which is a principal precondition for sexual selection (Bateman, 1948; Williams, 1966; Trivers, 1972). Variance in mating success due to a male-biased operational sex ratio, resulting from (1) and/or (2) above, would be modified according to factor (3), which is also a major determinant of mating systems.

In *E. hageni*, the greater age at first reproduction and longer latency to sexual receptivity of females generate variance in male mating efficiency ( $I_c$ ), whereas environmental and behavioral constraints related to the mating system act to decrease this variance. Even when operational sex ratios approached 1:1, less than 20% of the males present at the pond obtained a second mating. The inefficiency of territorial defense of large, clumped oviposition sites when male density is high, coupled with multiple matings by females and sperm removal by males, require that a male *E. hageni* guard his mate if he is to protect his sperm investment. Non-contact guarding increases the time a male must invest per mating and decreases the time he could spend searching for additional mates. Guarding also decreases the total number of matings possible by the breeding population per day, because it decreases the probability that a female partitions her clutch among several males.

Comparisons of the relative opportunity for sexual selection on species with different mating systems are only valid using analogous data sets analyzed by similar methods.  $I_c/I_m$  calculated from seasonal data for breeding territorial blackbirds (excluding one-year-olds that never mated) ranged from 0.59–0.81 (from Payne's 1979 data, cited by Wade and Arnold, 1980), higher than my lifetime value of 0.43 for nonterritorial *E. hageni*. These values for the blackbird were no higher than the analogous value calculated from daily RS for *E. hageni* ( $I_c/I_m = 0.56$ ).

Even when the data are analogous, trends between territorial and nonterritorial species may depend on the method used to estimate relative opportunity for sexual selection. For example, in a territorial dragonfly, McVey (1986), using eggs/day as a measure of  $I_m$  (and  $I_s = I_m - RI_i$ ), reported  $I_s/I_m$  to be 0.79–0.89, which is three times higher than the analogous value for *E. hageni* (0.31). Using eggs/lifetime to calculate  $I_m$ , she determined  $I_s/I_m$  to be 0.39–0.42, about the same as the analogous value for *E. hageni* (0.39). My measure of  $I_c/I_i$  for *E. hageni* was 0.60, 1.7–2.0 times greater than that measured for a nonterritorial beetle whose operational sex ratio was 1:1 ( $I_c/I_i = 0.29$ –0.35, McCauley, 1983). However, using McCauley's method of: 1) defining mating efficiency as mates/day alive, 2) estimating variance in mating efficiency, and 3) ignoring covariances, the analogous value from my data was 0.29 (see Table 3:  $0.36/[0.36 + 0.87]$ ), about the same as that for the beetle. To determine whether differences in  $I$  values are statistically significant, confidence intervals, which may be difficult to generate for lifetime data on long-lived species, are obviously needed.

The above examples clearly illustrate the practical difficulties involved in making cross-species comparisons, even using long-term field studies with relatively large data sets. The values that most appropriately reflect the opportunity for sexual selection on one species may not be those best-suited for another. In some animals one can measure LRS in terms of offspring produced, while in others such data may be impossible to collect under field conditions. The goal of testing hypotheses about the dynamics of sexual selection in different mating systems by using measures of variance in LRS may remain an elusive one, simply because the pragmatic definition of sexual selection may vary from one species to another, some forms of sexual selection may not be detectable using  $I$  values, and substantial sampling error may be impossible to eliminate for some types of studies.

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Corresponding Editor: P. H. Harvey