Male body size and mating success in swarms of the mayfly Epeorus longimanus

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Epeorus longimanus is a widely distributed mayfly in the western United States that forms relatively large mating swarms. The operational sex ratio of swarms is highly male biased and males are potentially polygynous, suggesting that male-male competition over mates may be intense. We investigated whether body size influenced male mating success in *E. longimanus*, as evidence of sexual selection. Males collected as mating pairs had significantly greater body lengths compared with males collected randomly from the swarm on each of six sampling dates examined, and had significantly greater head widths than males from random collections on two dates. There was no indication that large male advantage may be due to greater success in pursuing females. We found no evidence of size-assortative mating in *E. longimanus* indicating that males attempt to mate with every female encountered, consistent with the brief copulatory period in mayflies and overall low parental investment of males.

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1. Introduction

The mayflies (Ephemeroptera) have fascinated naturalists for centuries (e.g. Swammerdam 1675, Reaumur 1742) due to their notoriously brief adult lives and the spectacular mass emergences displayed by some species. Swarming is of almost ubiquitous occurrence amongst the Ephemeroptera. Typically, swarms are composed almost exclusively of males and therefore most of the area in which females are flying has a relatively low density of males (Sullivan 1981). Males remain near a swarm marker for a prolonged period, where they perform a nuptial dance.

Several lines of evidence suggest that sexual selection could be important in mayflies. An operational sex ratio (Emlen 1976) that is heavily biased towards males could lead to intense male-male competition and differential male mating success. In addition, males are larger than females in many mayfly species. Sexual dimorphism where males are the larger sex has long been viewed as the outcome of intrasexual selection, if large size confers some sort of advantage in a male's ability to win access to females (e.g., Darwin 1871).

At present there are no studies that have examined whether sexual selection occurs in mayflies, and only a limited number of studies exist that have documented differential mating success of males found within swarms not based on resources (e.g., Thornhill 1976, 1980, Hieber and Cohen 1983). Two of the most common indicators of sexual selection are substantial variation in mating success among males, which correlates with some phenotypic measurement, and a statistical bias that favors the males of certain phenotypes (Bateman 1948, Borgia 1979, Thornhill 1979, Thornhill and Alcock 1983, Partridge and Halliday 1984). We investigated sexual selection in the mayfly Epeorus longimanus by determining whether differential mating success of males occurred on the basis of male body-size characters. In addition, we investigated whether size assortative mating occurs in E. longimanus as a further indication of mate selection by either sex.

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Fig. 1. Size distribution of mating males (from pairs captured in copula) vs males captured randomly from swarms, based on body length, for three collecting dates in 1983. Arrows denote means.



Fig. 2. Size distribution of mating vs randomly collected males for three collecting dates in 1984. See Fig. 1 for details.

HOLARCTIC ECOLOGY 11:4 (1988)

Tab. 1. Size of adult *Epeorus longimanus*, from collections during swarm activity. Unmated males were obtained from random collections; females and mated males were captured as mating pairs. Means (x), standard deviations (sd) and sample sizes (n) are shown in micrometer units (1 unit = 0.04 mm) for total body length (TBL), length of foretibia (TIB), and head width (HW).

1983		July			August			September		
		mated males	unmated males	females	mated males	unmated males	females	mated males	unmated males	females
TBL	x	58.6	55.3	55.3	55.2	53.4	50.7	46.0	44.6	41.4
	sd	3.6	3.2	4.3	3.2	3.1	4.7	2.4	2.9	2.0
	n	21	23	20	25	43	26	25	47	23
		*	**		*			*		
TIB	x	96.0	93.4	56.3	90.8	87.6	52 3	76.5	76.2	45.0
	sd	7.3	4.5	5.3	4.4	7.3	5.1	4 4	5.5	33
	n	23	16	22	24	17	24	25	35	22
		1	1		×	1		1	1	
			ns		1	ns		1	ns	
HW	x	49.8	47.6	42.6	45.8	46.3	39.7	40.0	39.2	34.7
	sd	2.0	2.1	2.5	1.5	2.2	2.2	1.8	2.2	1.2
	n	22	21	22	26	45	26	24	48	23
		`	/		1	/		×	/	
		*	**		1	ns		1	ns	
1984		July			early August			late August		
TBL	х	57.6	55.7		57.0	54.3		54.6	49.6	
	sd	3.3	3.1		3.3	2.9		3.2	3.0	
	n	25	30		30	31		24	38	
		1	1		1	1		>	1	
		02.4	*		*	**		*	**	
TIB	x	92.4	93.1		88.1	88.9		84.0	84.5	
	sd	4.4	3.1		6.7	5.1		3.2	3.0	
	n	25	30		30	31		24	38	
		``	/						/	
HW	v	19 5	17 7		15.2	45.2		44.2	12 6	
	sd	1.9	1.9		2.0	43.3		23	42.0	
	n	25	30		30	31		24	38	
		1	1		1	/			/	
		1	ns		1	ns			*	

ns = not significant, * = P < 0.05, *** = P < 0.001

2. Methods

This study was conducted at Cement Creek, Gunnison Co., Colorado. Cement Creek is a third order, stonybottom stream that originates in snow melt at 3 600 m a.s.l. and joins the East River at 2 600 m. Observations were made at a site at 2700 m, where substantial swarms have been observed at the same marker for the past 10 years (personal observation). The swarm marker is a small island in the center of an open section of stream. The stream is fast-flowing and the banks are canopied by a mix of deciduous and spruce trees. A more detailed description of the study site is provided by Allan and Flecker (1988).

Observations and collections of mating pairs were made from mid-July to September in 1983 and 1984. Usually, observations were made in the late afternoon close to sunset, when swarming most typically occurred in *E. longimanus*. However, on several occasions we made observations from morning until dark. Collections are combined into 6 separate groups over the course of the 2 seasons: July 1983 (28–30 July 1983), August 1983 (8–11, 17, 22 August 1983), September 1983 (9–11 September 1983), July 1984 (17–19 July 1984), mid August 1984 (18–25 August 1984), and late August 1984 (29–31 August 1984).

Swarming typically began 1/2–2 h before dark, and was initiated at light levels between 20000 and 40000 lux. Swarming usually lasted 45–75 min. Occasionally swarms formed on cloudy afternoons, especially in 1984, when rain and wind made some evenings unsuitable for swarming. Allan and Flecker (1988) describe further details of swarming conditions.

We searched for mating pairs as soon as males began their nuptial dance. Occasionally we observed a lone female entering the swarm and pairing with a male, but more commonly we sighted a mating couple in flight after pairing had occurred. Mating pairs were captured

				Body length			
		1983				1984	
	July	August	September		July	Early August	Late August
r ² probability	0.28 0.24	$-0.02 \\ 0.92$	0.12 0.58		$-0.02 \\ 0.93$	0.03 0.89	$\substack{-0.17\\0.41}$
				Fore tibia			
		1983				1984	
	July	August	September		July	Early August	Late August
r ²	0.32	0.85	0.03		-0.05	-0.06	0.06
probability	0.15	0.71	0.89		0.80	0.73	0.77
				Head width			
		1983				1984	
	July	August	September		July	Early August	Late August
r ²	0.31	-0.31	-0.23		-0.24	-0.04	0.18
probability	0.18	0.12	0.30		0.27	0.85	0.85

Tab. 2. Relationship between male and female body size of mating pairs for each of six sampling periods. Coefficients of determination were calculated using Pearson's product-moment correlations.

by net and preserved in 70% ethanol for later measurement. Comparisons were made between males captured in copula and males captured from random samples taken from within the swarm. It was necessary to pool data from several successive dates, as generally it required 3–4 evenings of sampling to obtain a sufficient sample size of mating pairs. Total body length (TBL), foretibia length (TIB), and head width (HW) of males and females were measured using a stereo dissecting microscope. Singlefactor ANOVAs were performed to compare males from mating and random samples for each of the body characters measured.

In addition, we assessed whether size assortative mating is important in *E. longimanus*. This was determined by measuring both males and females collected as mating pairs, and testing for correlation between size of mates for each of the 3 body characters (TBL, TIB, HW).

3. Results

Males captured in mating pairs were significantly larger (body length) than males from random samples. This was found on all dates over both seasons (Figs 1–2, Tab. 1). The difference in mean body length of mated and unmated males ranged from 3.1-10.1% over all sampling periods. Mean head width of mated males was significantly larger than of random males in the collections of July 1983 (P<0.001) and late August 1984 (P<0.05, Tab. 1). Foretibia length was not significantly different between mating vs randomly collected males for any dates in 1983 or 1984 (Tab. 1).

There was no significant correlation between body size of males and females captured while copulating (Tab. 2). This was true for all body characters examined body size of *E. longimanus* declined sharply from July to September over both 1983 and 1984 (Tab. 1). This decrease in size was observed for each of the body characteristics (TBL, TIB, HW) and in both mated and randomly collected males, as well as in females captured while mating. The decline in body size over the time course of emergence is commonly reported in mayflies, and likely is caused by increased water temperature resulting in faster metabolic and developmental rates, and thus smaller size attained at maturity (Sweeney and Vannote 1982).

(TBL, TIB, HW) and over all sampling periods. Mean

4. Discussion

A considerable amount of variation exists among mayfly species in swarming behavior, including male density, complexity of the nuptial dance, time and length of the swarming period, etc. (see Brodskiy 1973, Fischer 1984 for behavioral classifications). In spite of the widespread nature of swarming in mayflies, there have been few attempts to examine the significance of swarming in this insect order. Edmunds and Edmunds (1980) and Sweeney and Vannote (1982) considered the role of predation in the evolution of a short adult lifespan and synchrony of emergence, and Allan and Flecker (1988) investigated the benefits of swarming to mating.

In *E. longimanus*, males in copula consistently were larger than males from random samples (Tab. 1). This should represent a conservative estimate of the differences in mean body size between mated and unmated individuals, because the random samples are a composite of males that may never mate, males that have mated in the past and males that will mate in the future.

Sexual selection based on body size has been reported

in other species of insects (see Thornhill and Alcock 1983). However, for most species studied, large males gain an advantage because they are better able to defend prime sites of emergence, oviposition or feeding, or sites otherwise important to mating, such as leks. In contrast, mayflies do not defend locations. Furthermore, males do not search for females, but instead aggregate at swarm markers where females later arrive to mate.

Assortative mating has been used to assess whether mate choice is operating (see Johnson 1982, Hieber and Cohen 1983, Burley 1983), although other factors such as mechanical constraints also may result in assortative mating (Adams and Greenwood 1983, Partridge and Halliday 1984). In lovebugs (*Plecia nearctica*), for example, size assortative mating has been attributed to male choice (Hieber and Cohen 1983). Larger males apparently are able to out-compete smaller males for access to female emergence sites, and males exercise choice because of the long time (>2 days) spent in copulation.

Unlike in lovebugs, we found no evidence of size assortative mating or male mate choice in *E. longimanus*. However, the presence of male mate choice within insect species may depend on male reproductive investment and the potential for polygyny. In species where male investment is large because of length of time spent in copula (lovebugs) or for some other reason such as providing nuptial gifts (some dance flies, Svensson and Petersson 1987), males are more likely to exercise mate choice. Because male *E. longimanus* mate rapidly (5–30 s) and immediately rejoin the swarm, the likelihood is small that they will encounter a more preferred mate during the time spent in copulation (Borgia 1980). Therefore, mate rejection by males would not be expected.

The mechanism whereby large males obtain a disproportionate share of matings remains unknown. Sullivan (1981) suggested that males may attempt to occupy positions where females are most likely to enter the swarm. At present we know little about the flight patterns of females into the swarm, but reports suggest that females approach at or near the height of the top of the swarm (Brodskiy 1973). By following focal males during nuptial displays it appeared that individual males occupied the full vertical range encompassed by the swarm itself. When collections were made from different sectors of a swarm, males did not differ in body size. Futhermore, swarms that were depleted by repeated captures rapidly reestablished with males no different in body size than those present previously (Allan and Flecker 1988). Thus we believe that positional effects do not explain the mating advantage of large males in E. longimanus.

A second possibility, not investigated by us, is that large males are most successful in chasing females (Partridge et al. 1987). In mayflies, the well developed compound eyes of males include laterally directed ommati-

dia that apparently serve to orient to vertical structure at the swarm location, and upwardly directed ommatidia thought to function in mate location (Brodskiy 1973). Brodskiy (1973) further suggested that males detect females during the downward portion of their flight, in which case speed of upward flight may be critical to mating success. Evidence that large male mayflies are faster in flight and pursuit would help to evaluate this currently untested possibility. Finally, if large males enjoyed a higher probability of displacing the male from copulating pairs, that also could explain the observed size advantage. However, although males frequently darted at one another within swarms (Allan and Flecker, unpubl.), we rarely observed apparent take-over attempts, and fewer than 5% of the captured copulating pairs were instances of two males grasping a single female. Thus we doubt that large size allows one male to displace another, and favor the hypothesis that the benefit instead is associated with initial capture of the female.

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HOLARCTIC ECOLOGY 11:4 (1988)

284

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