

# Male choice, fighting ability, assortative mating and the intensity of sexual selection in the milkweed longhorn beetle, *Tetraopes tetraophthalmus* (Coleoptera, Cerambycidae)

Denson Kelly McLain\* and Robert D. Boromisa

Department of Biological Sciences, University of Notre Dame, Notre Dame, IN 46556, USA

Received March 10, 1986 / Accepted November 17, 1986

**Summary.** Over five hundred adult longhorn milkweed beetles, *Tetraopes tetraophthalmus*, were individually marked and their copulatory success followed for one month in a pasture of *Asclepias syriaca* in northern Indiana, USA. Migration of beetles from the field site was greatest from areas of low population density. Dispersal was significantly greater for males experiencing low copulatory success; a similar but nonsignificant trend was observed for females. Large males, which displayed greater site tenacity than small males, copulated more frequently than small males because of their ability to displace small males from females. Both large and small males demonstrated a preference for large females in laboratory tests. Male preference in combination with aggressive displacement of small males results in size-assortative mating which was much stronger under conditions of high population density. It contributes to variance in male reproductive success since female size is known to be correlated with fecundity and offspring viability. Variance in copulatory success is similar for males and females, suggesting that both sexes experience similar intensities of sexual selection with respect to this component of reproductive success. Furthermore, comparison of this with other studies suggests that the intensity of sexual selection among males is positively correlated with the variance in body size which appears to be under both stabilizing and directional sexual selection in males but not in females.

## Introduction

Reproductive effort is partitioned into two components, mating effort and parental effort (Low

1978). Parental effort is expenditure on one offspring which reduces the ability of the parent to invest in other offspring and includes the production of large nutritive gametes by females (Trivers 1972). Generally among insects, males expend most of their reproductive effort as mating effort while females allocate relatively more time and energy to parental effort (Thornhill and Alcock 1983).

Consequently, variance in the number of females inseminated is the major component of variance in male reproductive success (Wade and Arnold 1984), and may select for male behavior that promotes the insemination of many females without concomitant selection for discrimination between potential mates (reviewed in Thornhill and Alcock 1983). Females, however, are frequently discriminating since the amount of material transferred during courtship or mating, in the form of nutritive spermatophores, access to food sources, etc., can influence female fitness through effects on fertility and longevity (Thornhill and Alcock 1983). Yet, discrimination among potential mates by males may be selectively favored if the cost of procuring a single mating is high relative to total lifetime mating effort (Thornhill and Alcock 1983).

Preference by both males and females for mates of relatively large size could result in size-assortative mating. Such preferences are selected for in the meloid beetle, *Lytta magister*, because larger males transfer larger spermatophores and larger females are more fecund (Snead and Alcock 1985). However, weak size-assortative mating may also result in the absence of any active preference as when females only mate with males capable of subduing them (McCauley et al. 1981). In such cases only large males mate large females while small and large males mate small females (e.g. McLain 1984, 1985).

\* Present address: Department of Biology, Emory University, Atlanta, GA 30322, USA

The present study examines size assortative mating in the milkweed longhorn beetle, *Tetraopes tetraophthalmus*. The objectives of the study were to determine: (1) if size is associated with copulatory success in both males and females, (2) if males or females exhibit preferences on the basis of size, (3) if there is size-assortative mating in a natural population, and (4) if males and females experience different intensities of sexual selection.

Some aspects of sexual selection and mate choice in *T. tetraophthalmus* have been examined in several other studies. For instance, in some populations size (length of the elytron) appears to be under stabilizing selection (McCauley 1979; Scheiring 1977; Mason 1964), while in others, larger males appear to be more successful at obtaining mates (McCauley 1982). The strength of sexual selection also appears to vary between populations (McCauley 1979, 1983).

## Methods

The present study was conducted in a 40 m × 160 m pasture within a wood lot on the campus of the University of Notre Dame, South Bend, Indiana. The pasture contained only grasses and milkweed, *Asclepias syriaca*. At the initiation of the study, June 19, 1985, most milkweeds were under 25 cm in height and without flowers or fruit. The study was conducted from June 19 until July 26. Most sampling was done from 1400–1900 hours.

A mark-recapture experiment was conducted in order to follow the copulatory success of individuals through time and thereby permit an estimation of the relative intensity of sexual selection on males and females. Using a dissecting needle, males and females were marked with individually distinguishing spots of model airplane paint at the field site. For each beetle, paint was applied at two of ten possible points on the elytra or pronotum with one or two of ten colors of paint. This paint is fast drying, water insoluble, and highly resistant to scratching or flaking off (Southwood 1966).

Beetles were marked and released where they were encountered at each end of the field. The south end of the field had a much higher density of beetles than the north end, although *A. syriaca* were distributed over the entire area. Beetles at the southern edge were marked on June 19 (67 males and 53 females) and June 20 (140 males and 154 females). Beetles at the northern edge were marked on June 22 (73 males and 48 females). On all 18 sampling dates (between June 20 and July 26) every *A. syriaca* in the field was inspected for beetles. The status of each beetle, marked or not marked, was recorded as mating, guarding(male)/guarded(female), or single. The length of the right elytron was determined to the nearest 0.5 mm for each beetle and represents an index of size. The strength of assortative mating is measured by the Pearson's linear correlation between the size of the elytra of paired males and females.

Tests were conducted in the laboratory to determine if males exhibit a preference for females on the basis of size. Twenty tests were conducted in which one male was housed with two females, one large (elytron > 9.0 mm) and one small (< 8.0 mm). In ten instances each, the males were small (elytron < 7.5 mm) or large (> 8.5 mm). Tests were conducted in 1 l cartons covered with a nylon mesh at 1400 h and terminated when the first female was mated.

The intensity of sexual selection, defined as  $I = \sigma^2/x^2$  where  $\sigma^2$  is the variance in the number of copulations and  $x^2$  is the square of the mean (Wade and Arnold 1984), was calculated for marked males and females captured four times. The significance of the measured intensity of sexual selection was tested by comparing the variance in the number of copulations between null and real data sets (McLain 1986). A null data set is constructed by assigning copulations to individuals at random until the number assigned equals the number observed. The only constraint is that the number of copulations received is not greater than the number of sightings. Since the mean is preserved in the null data set, but the variance need not be conserved, equality of variance between real and null data sets can be tested with Levene's test (Schultz 1985).

## Results

### Population size

The marking and recapture of beetles permits the estimation of population size. Population size was estimated for both the low density end of the field, representing 0.75 of the total area, and the high density end, using the formulae reviewed in Southwood (1966). At the high density end where beetles were marked on two consecutive days the appropriate formula is  $P_2 = (a_2 n_3 r_{31}) / (r_{21} r_{32})$  and the standard deviation of the estimate is  $SD = (P_2^2 (1/r_{21} + 1/r_{32} + 1/r_{31} - 1/n_3))^{1/2}$  where  $P_2$  is the population estimate,  $a_2$  is the number marked on the second day,  $n_3$  is the total number of beetles sighted on the day following marking, and  $r_{ij}$  is the number of recaptures on day  $i$  that were marked on day  $j$ . The observed figures were:  $a_2 = 294$ ,  $n_3 = 305$ ,  $r_{31} = 16$ ,  $r_{21} = 23$  and  $r_{32} = 84$ . This gives a population estimate of 742.6 on 1600 m<sup>2</sup> (density: 0.464/m<sup>2</sup>) (SD = 85.1). At the low density end the population size is estimated by  $P = a_1 n_2 / r_{21}$  (SD =  $(a_1^2 n_2 (n_2 - r) / r^3)^{1/2}$ ), with the observed values being  $a_1 = 121$ ,  $n_2 = 35$ , and  $r_{21} = 16$ . Thus, the estimated size of the population is 264.7 (SD = 48.8) on 4800 m<sup>2</sup>, resulting in a density of 0.055 individuals/m<sup>2</sup>. Thus, at high density there were over 8.4 times as many beetles per unit area.

In the high density area the number of recaptures of males versus females was very similar (Fig. 1). For both sexes most individuals were sighted only once or twice with progressively fewer individuals sighted from 3–11 times. Thus, there was no significant difference ( $P > 0.05$ ; Mann-Whitney  $U$ -test) between the sexes in the distribution of the number of sightings for marked males and females. A similar result was obtained in the low density area (Fig. 1).

The proportion of marked individuals sighted only once was significantly higher in the low density area than in the high density area for both males (low = 0.71,  $n = 73$ ; high = 0.47,  $n = 207$ ;  $P <$

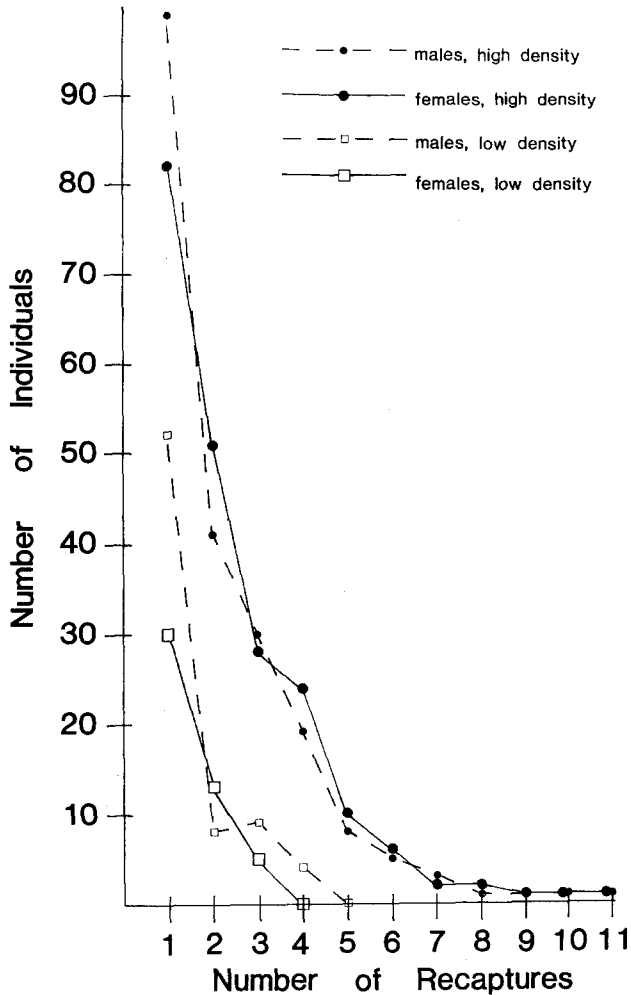


Fig. 1. Distribution of the number of recaptures for males and females in the high and low density areas

0.05;  $t=3.8$ ) and females (low=0.63,  $n=48$ ; high=0.39,  $n=207$ ;  $P<0.05$ ;  $t=3.0$ ). For both low and high density areas the proportion of females sighted only once was lower than the proportion of males sighted only once, but the differences were not significant ( $P>0.05$ ; low,  $t=1.0$ ; high,  $t=1.7$ ).

McCauley (1983) defines mating efficiency (ME) as the number of times an individual is observed mating divided by the total number of observations of that individual. In the present study, males observed on three or four occasions had a mean ME=0.26 (SD=0.28,  $n=62$ ) while males observed on five or more occasions had a mean ME=0.40 (SD=0.23,  $n=19$ ;  $P<0.05$ ,  $t=2.1$ ). Females observed on five or more occasions (ME=0.28, SD=0.20,  $n=23$ ) had slightly larger, but not significantly different ( $P<0.05$ ;  $t=0.7$ ) mating efficiencies than females sighted three or four times (ME=0.25, SD=0.23,  $n=57$ ).

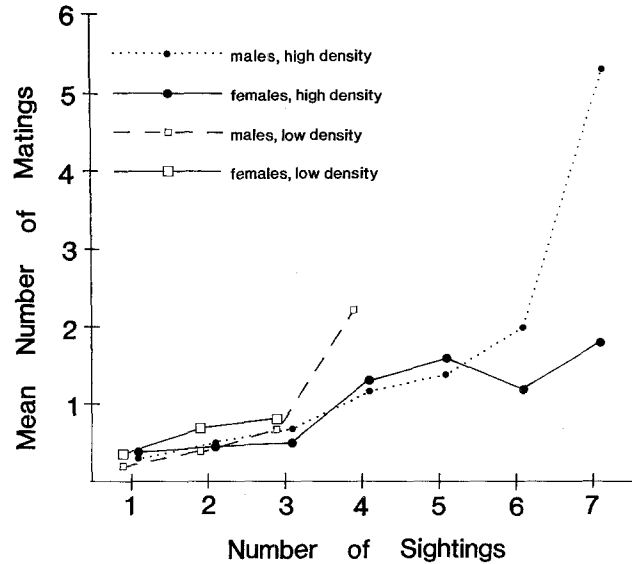


Fig. 2. Mean number of matings as a function of the number of times sighted. Sample sizes are presented in Fig. 1

#### Correlates of mating success

For both males and females in both low and high density areas there was a significant correlation between the number of times a marked beetle was sighted and the number of times the beetle was observed mating (Fig. 2).

Marked males observed mating three or more times were significantly larger (elytron length[mm],  $x=7.9$ , SD=0.3,  $n=10$ ) than marked males mating less than three times ( $x=7.4$ , SD=0.5,  $n=37$ ) ( $P<0.05$ ;  $t=4.1$ ). Similarly, females mating two or more times ( $x=8.6$ , SD=0.6,  $n=22$ ) were larger than females mating once or not at all ( $x=8.4$ , SD=0.5,  $n=47$ ). However, in the case of females the difference was not significant ( $P>0.05$ ;  $t=1.1$ ). In the high density area mating and guarding males were significantly larger than singletons (Table 1a). However, there was no difference in size between mating and guarding males (Table 1a). The variance in size was significantly greater for guarders than for maters ( $t=2.9$ ;  $P<0.05$ ; Levene's test, Schultz 1985). Among females in the high density area there were no significant differences in size (Table 1a) or variance in size ( $t<1.4$ ;  $P>0.05$ ; Levene's test) between singletons, guarded females, and maters.

In the low density area male singletons were significantly smaller than mating males but not smaller than guarding males (Table 1b). There was no significant difference in the size of guarding and mating males. Nor was the variance in size significantly different between guarding males and mating males ( $t=0.4$ ;  $P>0.05$ ; Levene's test).

**Table 1.** Average length of elytra in mm ( $\bar{x}$ ), standard deviation (SD), and sample size ( $n$ ) for males and females as a function of copulatory status under conditions of high density. Values of  $t$ , for comparisons among means, are significant ( $P < 0.05$ ) where  $t > 1.96$ . Subscripts of  $t$  refer to the means being compared where S = singleton, G = guarder (or guarded), and M = mater

Sex		Singletons	Guarders/ Guarded	Maters
<b>a High density</b>				
Male	$\bar{x}$	7.5	7.48	7.8
	SD	0.6	0.6	0.6
	$n$	502	123	235
	$t_{S/M}$	4.0	—	—
	$t_{S/G}$	—	2.7	—
	$t_{G/M}$	—	—	0.3
Female	$\bar{x}$	8.5	8.3	8.5
	SD	0.7	0.7	0.7
	$n$	224	121	235
	$t_{S/M}$	1.6	—	—
	$t_{S/G}$	—	1.8	—
	$t_{G/M}$	—	—	0.2
<b>b Low density</b>				
Male	$\bar{x}$	7.6	7.8	8.0
	SD	0.6	0.6	0.5
	$n$	181	42	68
	$t_{S/M}$	3.9	—	—
	$t_{S/G}$	—	1.7	—
	$t_{G/M}$	—	—	0.9
Female	$\bar{x}$	8.5	8.5	8.4
	SD	0.6	0.7	0.7
	$n$	86	43	68
	$t_{S/M}$	0.7	—	—
	$t_{S/G}$	—	0.1	—
	$t_{G/M}$	—	—	0.6

There were no significant differences in size among females on the basis of copulatory status in the low density area.

Males were frequently observed fighting, both in the presence and absence of females. Males would interlock their mandibles and push until one male either retreated or was thrown from the host plant. The average size of the victor in these contests (elytron length[mm],  $\bar{x} = 8.2$ ,  $SD = 0.3$ ,  $n = 14$ ) was significantly larger ( $P < 0.05$ ;  $t = 5.2$ ) than the average size of the loser ( $\bar{x} = 7.3$ ,  $SD = 0.5$ ,  $n = 14$ ). The average difference in size between the winner and loser was 0.9 mm ( $SD = 0.5$ ,  $t = 5.2$ , paired-difference  $t$ -test). The winner was larger than the loser in every instance.

The intensity of sexual selection was very similar and significant ( $P < 0.05$ ; Levene's Test) for both males ( $I = 0.55$ ,  $n = 45$ ) and females ( $I = 0.57$ ,  $n = 53$ ). The distribution of the number of matings for individuals sighted four times was nearly identi-

cal for males and females (0 matings,  $\delta = 9$ ,  $\phi = 11$ ; 1 mating,  $\delta = 12$ ,  $\phi = 16$ ; 2 matings,  $\delta = 12$ ,  $\phi = 14$ ; 3 matings,  $\delta = 7$ ,  $\phi = 8$ ; 4 matings,  $\delta = 5$ ,  $\phi = 4$ ).

#### Assortative mating

The strength of positive assortative mating on the basis of size was much greater in the high ( $r = 0.46$ ;  $P < 0.05$ ;  $n = 271$ ) than in the low density area ( $r = 0.08$ ;  $P > 0.05$ ;  $n = 65$ ). The least squares regression equation in the high density area was  $y = 0.5x + 4.3$  where  $y$  is female size (elytron length) and  $x$  is male size. The least squares equation in the low density area was  $y = 0.1x + 7.6$ . Combining low and high density areas the regression was  $y = 0.4x + 5.5$  ( $r = 0.36$ ;  $P < 0.05$ ;  $n = 321$ ).

The strength of assortative mating varied from day to day in both the low and high density areas (Table 2). However, assortative mating was invariably stronger in the high density area.

Unlike mating, guarding was not assortative in the high density area (Table 2). Frequently, correlation coefficients were negative for guarding in the high density area. Guarding was similarly non-assortative in the low density area. It was not possible to distinguish between pre- and postcopulatory guarding in the present study.

#### Mate choice tests

In seventeen of twenty trials in which a single male made a choice between one large and one small female the large female was mated first. Thus, there was a significant preference by males for large females ( $P < 0.05$ ; Chi-square = 8.45 with a correction for continuity, Sokal and Rohlf 1981). Small males ( $n = 10$ ) always chose large females while large males ( $n = 10$ ) chose large females in 70% of their trials ( $P > 0.05$ ; Chi-square = 3.53 for difference in preference for large females between males of different size).

#### Size and longevity

There was no significant difference ( $P > 0.05$ ;  $t = 0.4$ ) in average size between males sighted late in the seasonal activity of adult *T. tetraophthalmus* (July 26,  $\bar{x} = 7.7$  mm,  $SD = 0.6$ ;  $n = 70$ ) and those sighted earlier in the season (July 9 and prior dates,  $\bar{x} = 7.6$  mm,  $SD = 0.6$ ;  $n = 860$ ). By early August very few adult beetles were still active in the field. The average size of all marked males was 7.6 mm ( $SD = 0.6$ ) while the average size of marked males observed at least 10 and 15 days after marking was, respectively, 7.6 mm ( $SD = 0.6$ ;  $n = 48$ ) and 7.6 mm

**Table 2.** Daily variation in strength of assortative mating or guarding ( $r$ =Pearson's linear coefficient) and sample size ( $n$ ) at low and high density

Date	High density				Low density			
	Mating		Guarding		Mating		Guarding	
	$r$	$n$	$r$	$n$	$r$	$n$	$r$	$n$
6-27	0.37*	45	—	—	—	—	—	—
6-28	0.46*	25	-0.63*	10	—	—	—	—
6-29	0.30*	46	0.01	22	—	—	—	—
6-30	0.79*	35	-0.05	18	0.21	10	—	—
7- 1	0.50*	20	0.25	14	-0.20	7	0.38	5
7- 2	0.74*	24	0.06	8	0.37	7	-0.60	5
7- 3	—	—	—	—	-0.76*	11	-0.40	5
7- 4	0.77*	8	-0.68	4	0.99*	3	—	—
7- 5	0.61*	19	0.35	12	-0.17	13	0.26	7
7- 6	0.79*	14	0.01	4	-0.37	7	—	—
7- 8	0.51*	25	0.06	9	0.37	11	-0.94*	5
7- 9	0.83*	20	0.19	25	0.32	6	-0.03	8

\* Correlation is significant ( $P < 0.05$ )

(SD=0.6;  $n=23$ ). The differences between the means are not significant. There was, however, a significant difference ( $P < 0.05$ ;  $t=4.7$ ) in size between those marked males observed on 5 or fewer occasions ( $x=7.4$  mm; SD=0.6;  $n=266$ ) and those observed more than 5 times ( $x=8.1$  mm, SD=0.5;  $n=12$ ). The correlation between male size and the number of occasions observed was significant ( $P < 0.05$ ;  $r=0.30$ ).

The mean size of females observed on and prior to July 9 ( $x=8.5$  mm, SD=0.6;  $n=777$ ) was not significantly different ( $P > 0.05$ ;  $t=1.1$ ) from the mean size of females observed on July 26 ( $x=8.6$  mm; SD=0.6;  $n=19$ ). However, there was a significant difference ( $P < 0.05$ ) in size between marked females sighted at least 10 ( $x=8.6$  mm; SD=0.4;  $n=47$ ;  $t=3.0$  for difference between means) and 15 ( $x=8.6$  mm; SD=0.4;  $n=17$ ;  $t=2.5$ ) days after marking and the average size of all marked females ( $x=8.3$  mm; SD=0.6;  $n=252$ ). As with males, the size of females observed five or fewer times ( $x=8.3$  mm, SD=0.6;  $n=239$ ) was significantly smaller ( $P < 0.05$ ;  $t=2.3$ ) than the size of females observed more than five times ( $x=8.7$  mm, SD=0.6;  $n=13$ ).

## Discussion

### *Size and copulatory success*

Both males and females dispersed from the low density area at a higher frequency than from the high density area. Within either the low or high density area, males and females dispersed at ap-

proximately the same rate. However, larger males display more site tenacity than smaller males. This does not appear to be a function of longevity because: (1) there was no difference in the mean size of all males initially captured and the subset of marked males captured 10 or 15 days later (adult lifespan in the field is 16 days, McCauley 1983), and (2) the mean size of males was the same early and late in the season of adult activity. Larger males may disperse less than smaller males since size is associated with mating success. Selection might favor site tenacity where males are experiencing reproductive success (e.g. McLain 1984). In the present study, the greater mating efficiency of males sighted five or more times versus males sighted only 3–4 times suggests that local migration is reduced in males experiencing greater copulatory success. Larger females also appear to disperse less than smaller females, perhaps for the same reason as males. However, site tenacity is more difficult to evaluate for females since larger females also live longer than smaller females.

Two observations substantiate the claim that larger males experience greater copulatory success than smaller males. First, among marked males, those of greater size mated more frequently. Second, among all males, in both high and low density areas, copulating and guarding males averaged significantly larger than singletons. The effect of size on copulatory success is also observed in some other populations of the milkweed longhorn beetle (e.g. McCauley 1982) but not others (e.g. Scheiring 1977).

The relatively greater copulatory success of

larger males results from their greater prowess in combat with smaller males. Fights were frequently observed in the field, both in the presence and absence of females, with the larger male invariably forcing the retreat of the smaller male. Occasionally, guarding males which sit atop their females, were displaced from their females. The greater copulatory success of larger males does not result from female choice as evidenced in laboratory choice experiments (McCauley 1982). In the present study, females in the field were entirely passive, allowing any male to assume the guarding position.

The mean size of guarding and copulating males did not differ in either the low or high density area. However, the variance in the length of the elytron was significantly greater for guarding than copulating males at high density. Thus, there is stabilizing sexual selection on male size (also see Scheiring 1977; Mason 1964; McCauley 1979). Yet, the smaller size of singletons also suggests directional selection on male size. Thus, directional selection may be occurring through stabilizing selection around a shifting mean (Charlesworth 1984).

#### *Male preference and assortative mating*

Even though larger males copulated more frequently than smaller males, mating was significantly positively assortative, on the basis of elytron length in the high density area. Assortative mating was weak or nonexistent in the low density area. Guarding, however, was not positively assortative at low or high density. This suggests that most guarding males observed were precopulatory guarders. Assortative mating occurs because (1) males, regardless of their size, prefer large females, generating nonassortative or weakly negatively assortative guarding, (2) some large males displace smaller males from large females while other large males maintain access to their large females when challenged by smaller males, and (3) small males losing access to large females mate with smaller, less attractive females.

Since female fecundity is correlated with size (Price and Wilson 1976), size-assortative mating increases the relative reproductive success of larger males (which already copulate more frequently) through the greater fecundity of their mates. Since the opportunity for sexual selection to effect phenotypic change is a function of both variation in the number of mates and their fecundity (Wade and Arnold 1984; Arnold and Wade 1980), assortative mating may have important evolutionary consequences (reviewed in McLain 1983b).

Selection has apparently promoted a preference for larger females because they produce more ovarioles and larger eggs (Price and Wilson 1976). Thus, males choosing and mating larger females experience greater fitness provided the cost of choice is not high. If larger eggs result in larger progeny (e.g. Johnson 1982), then genes for preference would be favored through the production of larger, more competitive or fecund progeny. Also, larger female milkweed longhorn beetles live longer than smaller females which may result in a greater number of egg fertilizations for males mating these females.

The strength of assortative mating varied greatly from day to day. This may represent daily variation in the ability of large males to locate large females. In the low density area, where the ability of males to detect and locate females is, presumably, relatively reduced, assortative mating is much reduced.

Thus, local population density has a large effect on the strength of assortative mating. A few other studies have also shown that population density can affect the strength and direction of sexual selection (McLain 1982) and the selective advantage of male versus female choice (Gwynne 1984). Thus, when the cost of exercising choice is high, mate choice may not be advantageous (Wilson and Hendrick 1982; McLain 1984). In the present case, low population density may increase the costs of selective mating by increasing the average search time for males seeking large females. Thus, a strategy of copulating with the first available female, regardless of size, may provide greater long-term gains, especially if lower densities of competing males reduce the necessity of lengthy periods of postcopulatory guarding to prevent sperm displacement (see Parker 1970).

Precopulatory guarding, under conditions of high population density where male-male fights are frequent, may permit female passivity in mate acquisition. Females will frequently be inseminated by large males since small males are not good competitors. Thus, females have more time and energy to allocate to feeding, egg production, and the like since little or no allocation need be made to mate choice. A few other studies indicate a relaxation of female involvement in mate choice under conditions of intense inter-male rivalry (McLain 1982; McLain and Boromisa 1987). Presumably, the larger males which win access to females deliver more nutritious spermatophores or other material benefits (Thornhill and Alcock 1983), obviating the potential selective advantage of active female choice.

### *Intensity of sexual selection*

The mark-recapture data permitted an estimation of the intensity of sexual selection on both males ( $I=0.55$ ) and females ( $I=0.57$ ; see Trail, 1985 for a discussion of the relevance of this index to females). Since the intensity of sexual selection was calculated for individuals recaptured the same number of times, migration or death do not contribute a variance component. This is important since migration and death could not be distinguished (some marked beetles were found over 200 m away from the study site). In the present study, population mating efficiency contributed much more to variance in reproductive success than in the population of McCauley (1983; where  $I=0.14$ ; see McLain (1986) for the methodology for comparing selection intensities between different populations or experimental designs). Thus, the intensity of sexual selection can vary greatly between populations. McCauley (1979) found that sexual selection was more intense in populations where the variance in size (elytral length) was greater. In fact, sexual selection was detectable only in populations where the ratio of variance in elytral length to length of the elytron was 0.05–0.06 but not where the ratio was 0.03–0.04 (McCauley 1979). In our study population the ratio is 0.11. Thus, it appears that the intensity of sexual selection is greater when phenotypic diversity is greater.

It is very interesting that the intensity of sexual selection on females is as large as that on males. It appears to be generally true that females do not compete for males (Thornhill and Alcock 1983). However, in the milkweed longhorn beetle sexual selection on females arises from: (1) variation in the attractiveness of females to males, which probably ultimately derives from variation in fecundity and egg size, and (2) a presumed high cost of mating for males including energy expenditure and risk of injury through guarding and fighting. However, sexual selection on female morphology was not detected in either the size or variance in size of mating versus nonmating females (but see Scheiring 1977). Sexual selection on female morphology may be less intense than in males since there is relatively little direct competitive interaction between females. Instead, sexual selection may enhance cues which attract males, such as pheromones associated with ovariolo maturation.

In conclusion, the data reveal that both males and females compete for mates and experience similar intensities of sexual selection. Females apparently compete through differential attractiveness

to males who prefer the larger, more fecund females. Males compete through direct aggression, with large males experiencing greater copulatory success than small males. Consequently, the intensity of sexual selection on males is greater where phenotypic variance is greater. Variance in male reproductive success results in stabilizing sexual selection around a moderately extreme phenotype. Under high population density, male choice and male-male aggression result in size-assortative mating. Size-assortative mating contributes to variance in overall reproductive success among males, at least, since larger males which mate more frequently also mate the more fecund females.

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