

Variation in sexual selection on male body size within and between populations of the soapberry bug

SCOTT P. CARROLL* & MICHAEL H. SALAMON†

**Center for Population Biology, University of California at Davis*

†*Department of Physics, University of Utah*

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Abstract. In spite of its evolutionary importance, little is known about intraspecific variation in sexual selection. In the soapberry bug, *Jadera haematoloma*, absolute adult sex ratio varies within and between populations because of differences in mortality rates, creating natural opportunities for variation in the intensity of sexual selection. Sex ratios in Oklahoma, U.S.A., are variably male biased, but approach 1:1 in the Florida Keys. Comparisons of reproductive aggregations in Oklahoma and the Florida Keys showed a higher large-male mating frequency only in Oklahoma, mainly in aggregations with above-average male:female ratios. There was no evidence of assortative mating by size in either region. In laboratory tests, large and small males were similar in several mating characteristics, including mate-guarding ability, but large males searched for mates with a significantly greater rate of locomotion. To predict how this difference in searching rate interacted with sex ratio, the equilibrium mating frequencies of large and small males were modelled across the observed range of sex ratios. This model predicted the pattern observed in nature: with increasing sex ratio, the proportional large-male mating advantage increased and then asymptoted. Notably, the asymptotic value was close to the ratio of the average mate-searching locomotion rate of large males to that of small males, further indicating that a size-based difference in mate searching is the main cause of the large-male mating advantage. This species thus shows a mosaic pattern in the intensity of sexual selection on body size, which depends on the interaction of sex ratio and male mating competition.

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Many studies have described phenotypic correlates of mating success in animals. Less is known, however, about natural variation in the intensity of sexual selection within and between populations, or about the evolutionary consequences of such variation. This information is important because spatial or temporal variation in selection may substantially alter the phenotypic constitution of a population (e.g. Gibbs & Grant 1987; Seger & Brockmann 1987), and variation in selection between populations may lead to rapid differentiation (e.g. Carroll & Boyd 1992). In this study, we examined male mating success over a broad gradient in the intensity of male–male mating competition, within and between populations. Our goals were to characterize natural variation in

the intensity of sexual selection on male body size, to test predictions about the behavioural significance of male body size in mating competition, and, based on these findings, to test a model of the effect of sex ratio on how male body size influences the outcome of mating competition.

Theory predicts that ecological and social conditions can alter the intensity and form of sexual selection (Emlen & Oring 1977), but only a few studies have examined sexual selection in the context of natural variation in such conditions (e.g. Alcock 1979; McLain 1982, 1993; Fincke 1988; Gwynne 1990; Berglund 1994). For soapberry bugs, *Jadera haematoloma* (Hemiptera: Rhopalidae), in Oklahoma, disproportionate female mortality commonly causes male-biased adult sex ratios. These sex ratios may vary substantially within the lifetimes of individual males (Carroll 1988, 1991). In contrast, aggregations in the less seasonal habitats in the Florida Keys have unbiased adult sex ratios (Carroll 1988, 1991,

Correspondence: S. P. Carroll, Center for Population Biology, University of California, Davis, CA 95616, U.S.A. (email: spcarroll@ucdavis.edu). M. H. Salamon is at the Department of Physics, University of Utah, Salt Lake City, UT 84112, U.S.A.

1993). Based on this demographic difference, we predicted that mating competition, and the resulting sexual selection on components of mating ability, is more intense in Oklahoma than in Florida.

One such component of mating ability may be male body size, which is important in mating competition in several insect species (e.g. Borgia 1982; Partridge & Farquahr 1983; Ward 1983; Simmons 1986; McLain 1987; Partridge 1989; Fincke 1992). In the soapberry bug, males exhibit scramble mate searching, both sexes mate more than once, and males frequently use copulatory and contact mate guarding. This species forms dense mating aggregations at food plants, and male-male encounters are common (Carroll 1991, 1993). As a result of these factors, male body size may be important to fertilization success both during mate searching and mate guarding.

We examined these possibilities using a series of field and laboratory studies, as well as a simulation model. Specifically, we compared the relationship between male body size and mating frequency between aggregations in Oklahoma and Florida. We tested for assortative mating by body size, and for causal relationships between male body size and success in mate searching and in mate guarding.

METHODS

Biology of the Soapberry Bug

Adult and juvenile soapberry bugs feed on the seeds of several species of sapindaceous plants (Carroll & Loye 1987). Aggregations of up to hundreds or thousands of adult males and females and juveniles occur at host plants with large seed crops. Recruitment comes from immigration by flying adults and the maturation of juveniles that develop at a host. In the southwestern and south central United States, including Oklahoma, these hosts include the soapberry tree, *Sapindus saponaria* v. *drummondii*, and the goldenrain tree, *Koeleruteria paniculata*. From Key Largo to Lower Matecumbe Key in the Florida Keys, the host is balloon vine, *Cardiospermum corindum*. The insect populations are separated by a geographical gap in host plants across most of the Gulf Coast region. In Oklahoma, most reproductive activity occurs in late July-September when new seed crops are available from the trees; the bugs then enter a reproductive diapause in early

October. In contrast, breeding occurs year-round in the Florida Keys (Carroll 1988), whenever seeds are available.

In Oklahoma, adult sex ratios vary widely among aggregations and average approximately 2.5 males per female, but in the Florida Keys, sex ratios vary little and average 1:1 (Carroll 1988, 1993). In both populations many individuals mate with several different partners during their lifetimes; adults survive for up to 2 months of reproductive activity (Carroll 1991). About half of the copulations last until the female lays her next clutch of eggs (oviposition takes place within the aggregation), and some pairings last for more than one oviposition (pairs have been observed to remain together for up to 250 h). Prolonged pairings function as mate guarding by males: in sperm competition experiments, the second male fertilized 60-70% of the subsequent offspring, on average (Carroll 1991, 1993).

Locomotion by males functions principally as mate searching (Carroll 1993). Adult males are actively searching for mates in about 50% of instantaneous observations in reproductive aggregations, and attempt to mount most other adult conspecifics encountered. Detection of potential mates appears to be primarily visual within aggregations. Although single males sometimes attempt to displace mating males, there are no specialized organs of combat.

A large proportion of males remains within a single aggregation for most of their life span; although a small proportion of marked males moves to other aggregations (Carroll 1988), many histolyse their flight muscles early in adulthood and are incapable of flying thereafter (S. P. Carroll, unpublished data).

Females are larger-bodied than males, on average, and Florida Keys bugs are larger-bodied than Oklahoma bugs, on average (Carroll 1988). Male and female body size distributions overlap considerably less in Florida than in Oklahoma (S. P. Carroll, unpublished data).

Body Size, Mating Frequency and the Intensity of Sexual Selection in Nature

The pronotum is a dorsal thoracic plate that covers the muscles of locomotion. We used maximum pronotum width as our measure of body size in both populations. Compared to other size measures (e.g. wing length, hind tibia length),

pronotum width correlated well with both log-transformed live weight at the time of moult to adulthood (Oklahoma, males: Pearson's $r=0.80$, $N=37$, $P<0.001$; females: $r=0.82$, $N=40$, $P<0.001$; Florida, males: $r=0.78$, $N=40$, $P<0.001$; females $r=0.83$, $N=40$, $P<0.001$) and log-transformed body length (distance from anterior tip of the clypeus to the posterior tip of the folded wings, short-winged morph individuals excluded; Oklahoma, males: $r=0.85$, $N=50$, $P<0.001$; females: $r=0.86$, $N=50$, $P<0.001$; Florida, males: $r=0.87$, $N=50$, $P<0.001$; females: $r=0.83$, $N=50$, $P<0.001$). Pronotum width is normally distributed in both sexes.

We sampled aggregations in central and west-central Oklahoma in 1982–1987, and in the upper Florida Keys during 1985–1989 (detailed in Carroll 1988). We measured aggregation sex ratios by counting all adult males and females (distinguished by visual inspection of the genitalia) encountered within 20 min. This included censusing both the ground beneath the host plant and the host plant itself. We sampled each area systematically to avoid re-sampling. Accurate sampling was also facilitated by the 'tame' demeanour and slow locomotion of the bugs. Our censusing did not cause mating pairs to separate.

Immediately after censusing sex ratio, we collected data to estimate the mean body size of males, the body sizes of mating and single males, and in some cases, mating females. To do so, we quickly captured a haphazard sample of single adult males and mating pairs (N s varied; see Table I), held them separately and measured their pronotum width to the nearest 0.02 mm with dial calipers. We then released the bugs in their aggregations. These data were used to calculate mean male size. In some aggregations in which mating males were uncommon, we also captured and measured additional mating males to augment the sample for this category.

In investigating sexual selection, we defined mating frequency as the probability of being sampled while mating. For each aggregation, we divided males into two classes, 'large' and 'small', consisting of individuals above and below the aggregation mean for pronotum width, respectively. We defined the 'large-male mating advantage' as the ratio of mating frequencies of large and small males, calculated as the proportion of large males mating divided by the proportion of small males mating. This measure showed whether

the males comprising each size class were mating in proportion to their relative abundance in an aggregation. For example, a value of 1.0 means that each size class was mating in proportion to its abundance, values greater than 1.0 indicate that large males were mating at a disproportionately high frequency, and values less than 1.0 indicate that small males were mating at a disproportionately high frequency. Similarly, we estimated the 'relative mating success' of large males as their mating frequency in each aggregation divided by the average male mating frequency in that aggregation.

The intensity of selection is the mean deviation of the selected individuals, in units of phenotypic standard deviations (Falconer 1981). In this study, we made the simplifying assumption that male fitness may be equated with mating frequency. Therefore, to estimate the intensity of sexual selection on male body size (i), we first calculated the selection differential, S , as the mean pronotum width of mating males minus the aggregation mean. The intensity of selection is S divided by the standard deviation from the mean pronotum width (i.e. $i=S/SD$; Falconer 1981). Male pronotum width is normally distributed, such that i -values are measured in standardized units that are independent of the mean value of each aggregation. Thus their magnitudes may be directly compared.

To judge whether the intensity of selection was significant in a given aggregation, we also compared the mean pronotum widths of mating and single males in each aggregation with t -tests. We judged the intensity of selection to be significant if the t -value was significant ($\alpha=0.05$; Price et al. 1984).

In eight aggregations in Oklahoma, we tested for a correlation between the pronotum widths of males and females in mating pairs. Such a correlation could result from a body size influence on male for female mate choice or mate retention ability, or on an interaction of these factors (e.g. large males might be better able to overcome resistance to mating in large females than are small males, resulting in a positive correlation between male and female body size in mating pairs).

Large-male Mating Advantage

Several hypotheses could explain a relationship between male body size and mating frequency. We

Table 1. The relationship between aggregation sex ratio and body size of mating versus single mates in the soapberry bug in Oklahoma and Florida

Site	Sex ratio†	N mating/ N single‡	Mean (\pm SD) size mating/single§	Mean size††	<i>i</i>	Mating frequency large/mean‡‡	Mating frequency large/small§§
Oklahoma							
A	1.30	20/24	2.86 \pm 0.12/2.91 \pm 0.21	2.88	-0.13	0.67	0.49
B	1.80	41/48	2.99 \pm 0.22/2.96 \pm 0.22	2.98	0.05	0.95	0.92
C	2.10	28/39	3.16 \pm 0.19/3.08 \pm 0.19	3.11	0.26*	1.24	1.55
D	2.15	34/48	3.12 \pm 0.20/3.14 \pm 0.20	3.13	-0.05	0.98	0.95
E	2.31	23/86	3.11 \pm 0.18/3.12 \pm 0.23	3.12	-0.05	1.05	1.00
F	2.48	71/83	3.16 \pm 0.19/3.12 \pm 0.18	3.13	0.19	1.13	1.29
G	2.56	45/45	3.13 \pm 0.18/3.02 \pm 0.20	3.06	0.37*	1.19	1.50
H	2.58	24/117	3.10 \pm 0.17/3.04 \pm 0.17	3.06	0.24*	1.20	1.53
I	2.83	55/52	2.99 \pm 0.17/2.89 \pm 0.20	2.93	0.32**	1.17	1.43
J	3.04	52/41	3.17 \pm 0.17/3.09 \pm 0.20	3.12	0.27*	1.21	1.69
K	3.10	45/50	3.14 \pm 0.19/3.03 \pm 0.20	3.08	0.31**	1.43	1.73
L	3.17	61/60	3.19 \pm 0.22/3.10 \pm 0.22	3.14	0.23*	1.08	1.20
M	3.30	20/53	3.17 \pm 0.19/3.11 \pm 0.16	3.14	0.18	1.25	1.71
N	3.81	60/60	3.17 \pm 0.20/3.07 \pm 0.19	3.12	0.26**	1.12	1.26
O	4.02	51/51	3.09 \pm 0.17/3.00 \pm 0.21	3.03	0.32**	1.25	1.79
P	4.71	32/28	3.05 \pm 0.19/2.87 \pm 0.22	2.94	0.54***	1.29	2.14
Florida							
AA	0.87	20/30	3.20 \pm 0.18/3.25 \pm 0.20	3.22	-0.11	0.97	0.95
BB	0.89	27/25	3.19 \pm 0.20/3.23 \pm 0.19	3.21	-0.10	0.93	0.86
CC	0.96	23/34	3.08 \pm 0.19/3.05 \pm 0.19	3.07	0.05	1.04	1.07
DD	1.01	18/19	3.21 \pm 0.24/3.23 \pm 0.21	3.22	-0.04	0.96	0.94
EE	1.17	30/30	3.15 \pm 0.20/3.11 \pm 0.19	3.13	0.10	1.03	1.05
FF	1.28	74/99	2.96 \pm 0.25/2.92 \pm 0.25	2.94	0.18	1.12	1.31

i is the standardized intensity of selection, presented in units of the standard deviation of male pronotum width, as estimated statistically for each aggregation. Negative values indicate that mating males were smaller than the mean. *P*-values (**P* \leq 0.05; ***P* \leq 0.01; ****P* \leq 0.001) are from *t*-tests comparing pronotum width of mating and single males within each aggregation.

†Ratio of adult males to adult females in the aggregation.

‡Numbers of mating and single males measured.

§Pronotum widths (mm) of mating and single males.

††Mean pronotum width of all males in the aggregation.

‡‡The relative large-male mating success, calculated as the cross-product of the mating frequency of mating in males above the aggregation mean for male pronotum width and the mating frequency in all males in the aggregation.

§§The large-male mating advantage, calculated as the cross-product of the mating frequency in males above the aggregation mean for male pronotum width and the mating frequency in males below this mean. These values are plotted against sex ratio for each Oklahoma aggregation in Fig. 2.

tested the possibilities that relatively large males (1) are more active in mate searching and thus encounter females more frequently, (2) are more successful in mate guarding, (3) are more successful in combat for mating females, (4) are faster and more successful in pre-copulatory interactions with single females and (5) mate for longer periods than smaller males (and are thus more likely to be mating when sampled). Related considerations regarding other selection on male body size, such as possible association between male size and life span, are important to the overall evolutionary outcome of sexual selection on male body size (see

Discussion). Our aim here, however, is restricted to describing the behavioural patterns significant in selection involved with mating competition.

We tested these hypotheses with individually marked adults in the laboratory, where soapberry bugs appear to show their full normal repertoire of mating behaviour. Bugs were collected as advanced nymphs in central Oklahoma (Cleveland County). We studied groups at two sex ratios, 2:1 and 3:1 (male:female). Each group consisted of 24 sexually mature virgins that had moulted to the adult morph on the same day. We chose these two sex ratios to bracket the most

common field ratios in Oklahoma (Carroll 1988). To ensure that a broad range of male sizes was included, each group included approximately 25% 'small' adults (pronotum widths >1 SD below the mean for their sex), 50% 'medium' adults (within 1 SD of their mean), and 25% 'large' adults (>1 SD above their mean). We marked individuals with numbered plastic tags attached to the dorsal pronotum with balsam gum.

We housed and observed the bugs in $60 \times 25 \times 6$ -cm high enamel pans. Densities were within the range common in nature (e.g. Carroll 1991). We coated the pan walls with Sigmacote silicon to prevent escape, and coated the floors with an absorbent mixture of plaster of Paris and ground charcoal. A 13.5:10.5 h L:D photoperiod with 'Daylight' fluorescent tubes, and 33°C daytime and 26°C nighttime temperatures, matched concurrent (midsummer) external conditions. We provided food (seeds of the goldenrain tree) and water in cotton stoppered shell vials ad libitum.

Observation periods of 30 min began every 2 h, six times each day per diel period. We instantaneously sampled (Altmann 1973) the mating status (single or paired) of all individuals in the arena at the beginning of each observation period. We then recorded the activities of each male for 1 randomly chosen min in each observation period. Activities included locomotion rate (recorded as the number of lines crossed on a grid of 5×5 -cm squares drawn on the pan floor) as a measure of mate searching activity, and the number of pre-copulatory mounts made on single males, on mating pairs and on single females. We continued observations for 2 weeks. We replaced individuals that died during the course of the study with virgins of the same size class.

In a separate experiment to observe direct competition or combat among Oklahoma males for receptive females, we introduced 34 virgin females one at a time to a group of 70 individually marked virgin males, of known size, in an observation arena as described above. We used this high density experiment to explore male mating ability directly around the female, rather than in 'long distance' mate searching. These conditions reflected those found in natural aggregations, where males may accumulate in large numbers on the tree trunks that females walk up or down when commuting between feeding and oviposition sites (Carroll 1988, 1991). We introduced females at random into one of the 60 grid sections in the

arena. These females had been held in isolation from males for more than 1 week after eclosion, ensuring sexual receptivity. For each female, we recorded the number and order of males attempting copulation, the time between initial contact and mating for the first male to mount, and the identity of the male that mated.

Model of the Scramble Competition Hypothesis

We constructed a model to investigate whether size-mediated scramble competition could account for both the higher mating success of large males and the increase in large-male advantage with increasing sex ratio. The model calculates the equilibrium mating frequencies of large and small males based on their observed proportions in each aggregation, the sex ratio in each, and, as free parameters, the rates with which each class encounters (and mates with) females. For each sex ratio we searched with a computer for the encounter rates for which the relative mating success of large versus small males best matched the relative mating success observed in the field. We were interested in (1) whether this model generated a relationship between sex ratio and large-male advantage similar to that observed in nature, and if so (2) whether the relative encounter rates that produced the best agreement between the model's calculations and our field observations were similar to the relative rates of locomotion and female encounter rates measured in captive populations. Details of the model are presented in the Appendix.

RESULTS

Sex Ratio and Mating Frequency of Large and Small Males

In Oklahoma, adult sex ratios varied widely between aggregations, ranging from approximately 1:1 to 5:1 in reproductive aggregations (i.e. those sampled in the March–September breeding season; $N=28$), and averaged (\pm SD) 2.64 ± 0.99 males/female. In contrast, Florida sex ratios were restricted to approximately 1:1, and averaged 1.09 ± 0.26 males/female ($N=19$; Fig. 1).

In Oklahoma, the ratio of the proportion of large males mating to the proportion of small males mating (see Methods for definitions of large and small males) increased with sex ratio (linear

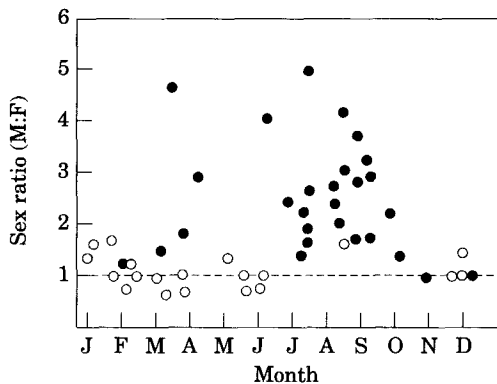


Figure 1. Adult male:female ratios in aggregations of soapberry bugs in Oklahoma (●) and the Florida Keys (○). The dashed line indicates the 1:1 primary sex ratio (Carroll 1988).

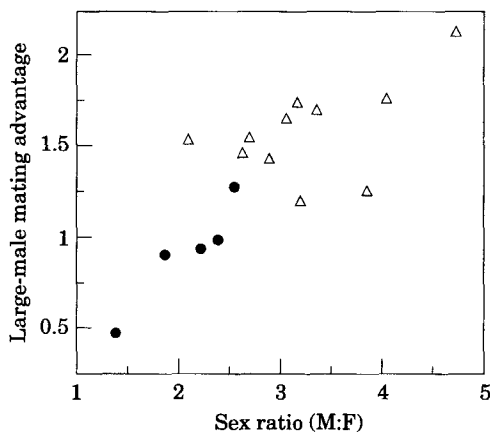


Figure 2. Large-male mating advantage (mating frequency of large males divided by the mating frequency of small males) as a function of aggregation sex ratio in Oklahoma. Δ : Aggregations in which mating males were significantly larger than non-mating males ($P < 0.05$).

$r^2 = 0.69$, $P < 0.001$, quadratic $r^2 = 0.76$, with $F_{2\text{nd term}} = 4.338$, $P = 0.07$, for log-transformed values of sex ratio and pronotum width; Table I and Fig. 2). The results of the quadratic regression suggest that the relationship may be non-linear. It models a curve that asymptotes at a large-male to small-male mating ratio of 1.65, a value that is important for evaluating the results of the simulation model (below).

Also in Oklahoma, mating males were significantly larger than single males in 10 of the 16 aggregations sampled (Table I). Size differences

Table II. Tests of assortative mating by body size (pronotum width) in males and females of mating pairs of soapberry bugs from eight aggregations in Oklahoma

Aggregation	N pairs sampled	r^*	P
C	28	0.37	0.05
D	24	-0.14	0.53
E	22	0.02	0.91
F	71	0.16	0.18
I	54	-0.07	0.59
J	52	0.18	0.19
K	44	0.20	0.19
M	20	-0.24	0.06

Aggregations have the same identifying letters as in Table I.

*Pearson product-moment correlations.

between mating and single males were more common at higher sex ratios: significant differences were found in nine of the 10 aggregations with sex ratios above 2.5 but in only one of six aggregations below this ratio (Fisher's exact test: $P < 0.005$). The mean (\pm SD) mating frequency of large males was 1.37 ± 0.40 times greater than that of small males. The mean relative mating success of large males (compared with all males) was 1.14 ± 0.17 .

In contrast, in the Florida Keys population, there was no significant difference between the size of mating and single males in the six aggregations sampled (Table I). The mean mating frequency of large males was 1.03 ± 0.16 times greater than that of small males, and the mean relative mating success of large males was 1.01 ± 0.07 .

Assortative Mating

In the eight Oklahoma aggregations sampled, the body sizes of male and female partners in mating pairs showed no consistent correlation across a range of sex ratios (Table II). In the two aggregations with the strongest correlations ('C' and 'M'), one correlation is positive and the other is negative.

Cause of the Large-male Mating Advantage in Oklahoma

Mate searching

In both groups of captive bugs (2:1 and 3:1 sex ratios), large males mounted other individuals at

Table III. Pronotum width and reproductive behaviour of large and small males at two sex ratios

Size/behaviour	Group			
	2:1 sex ratio		3:1 sex ratio	
	$\bar{X} \pm \text{SD}$	U^\dagger	$\bar{X} \pm \text{SD}$	U
Pronotum width (mm)				
Large [‡]	3.12 ± 0.17	—	3.17 ± 0.10	—
Small	2.82 ± 0.28		2.74 ± 0.23	
Movement rate [§]				
Large	7.43 ± 3.70	15*	12.28 ± 4.60	13**
Small	4.94 ± 3.24		7.27 ± 4.50	
Males mounted/min				
Large	0.55 ± 0.29	11*	0.94 ± 0.31	17*
Small	0.27 ± 0.16		0.55 ± 0.40	
Pairs mounted/min				
Large	0.52 ± 0.25	19	0.62 ± 0.25	21*
Small	0.34 ± 0.19		0.41 ± 0.30	
Females mounted/min				
Large	0.16 ± 0.08	16*	0.040 ± 0.03	21*
Small	0.08 ± 0.06		0.013 ± 0.02	
Mating frequency (% or observations)				
Large	39.32 ± 11.85	24.5	34.7 ± 26.96	21*
Small	30.33 ± 20.63		18.4 ± 27.16	

[†] U -values are from Mann-Whitney U -tests of two pronotum width classes.

[‡]Members of the large class were those above the group mean pronotum width, and members of the small class were those below this mean. Seven large and nine small males were in the 2:1 sex ratio group, and nine large and nine small males were in the 3:1 sex ratio group.

[§]Number of grid lines (5-cm interval) crossed per min.

* $P \leq 0.05$; ** $P \leq 0.01$.

higher rates than did small males (Table III). Large males were more than 50% more active in locomotion than small males. Males of both size classes nearly doubled their locomotion at the higher sex ratio. Based on mount rates of other adults, large males showed no greater ability to distinguish females than did small males, so that the greater mounting frequencies resulted mainly from greater rates of encounter with other adults (but see Discussion). Larger males were mating in a significantly greater proportion of observations than were small males in the 3:1 sex ratio group.

Guarding and combat

Direct physical contests between males occurred when one male attempted to displace another that was already mating. However, displacements of mating males were rare ($N=2$ in 476 mounts on mating pairs in captivity), so that any body size effects in this context should be of comparatively minor selective importance. When

receptive females were introduced to a group of males, significant interference occurred when more than one male simultaneously attempted to mate with a single female: in 29 of 34 such cases the first male to mount copulated, but in the five cases in which he was not successful, the number of contemporaneously mounting males was significantly greater (Mann-Whitney U -test: $U=121$, $z=2.50$, $P<0.01$).

Mating speed

In observations of captive bugs in which no interference from other males occurred, there was no correlation between male size and the time between encounter and mating ($r=0.07$, $N=23$, $P>0.05$).

Mating duration

No significant correlation was found between male pronotum width and copulation duration in

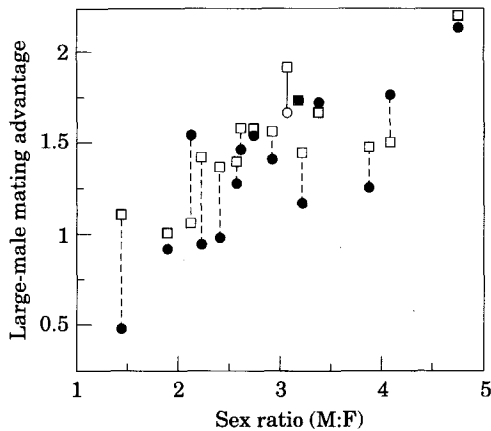


Figure 3. Observed values of large-male mating advantage (●: large-male to small-male mating rate) compared with modelled equilibrium values (□) for each Oklahoma aggregation. Dashed lines connect some of the modelled and observed values for clarity.

either sex ratio group (2:1 group: $r=0.22$, $N=14$ males making 91 copulations, $P>0.05$; 3:1 group: $r=0.29$, $N=14$ males making 34 copulations, $P>0.05$).

Modelled Difference in the Mate Encounter Rates of Large and Small Males

Of the hypotheses tested in the captive groups, only the size-linked difference in male mate-searching ability might explain the relationship between male body size, mating frequency and sex ratio in nature. Our model of the equilibrium numbers of single and mating large males and small males predicted a negative exponential curve similar to the quadratic regression of observed large/small mating ratio on sex ratio (above): both asymptote at a large-male/small-male mating ratio of 1.65. The minimum chi-squared differential from the observed values (i.e. the best fit) was 18.3 ($df=15$, $P>0.05$; Fig. 3). As the statistical test reflects, there is scatter of the observed values around the predicted values, although for many aggregations the model closely predicts the large-versus small-male mating ratio, and the overall trend in variation with sex ratio is similar.

The asymptotic limit of the function is set by the ratio of the modelled large-male searching rate ($B=0.051 \pm 0.075$) to the small-male searching rate ($A=0.031 \pm 0.054$). Notably, the B:A ratio (1.65) is very near the observed ratios of move-

ment (mate searching) rates of large and small males in the two captive arenas (Table III): 1.50 in the 2:1 sex ratio treatment, and 1.69 in the 3:1 sex ratio treatment. Thus the model, based on the relationship between sex ratio and mating frequencies in nature, closely predicted the size differences in mate searching rates observed in captivity.

DISCUSSION

Our basic findings were that sexual selection on male body size varies significantly both within and between soapberry bug populations, and that it is the interaction of aggregation sex ratio with the correlation between mate searching and body size that generates the pattern. In particular, sexual selection favouring large body size in males was found in the majority of the aggregations studied in Oklahoma (those with higher male/female ratios), but not at all in the Florida Keys.

These findings have both general and specific implications. First, for soapberry bugs and possibly other organisms, estimates of the intensity of sexual selection made from single samples within a population may not be reliable indicators of the overall selective environment. Second, estimates from a single population may not be representative for a species. Third, in spite of such variability, metapopulation differences in mean selection intensity may be consistent. Population differences in sexual dimorphism (with the body size of Oklahoma males, relative to females, being larger than that of Florida males; S. P. Carroll, unpublished data) may be a result of such consistent regional differences in sexual selection.

Within Oklahoma populations, the relative mating success of large males increased as a function of sex ratio (Table I and Fig. 2), and the intensity of sexual selection on male size potentially varies within the lives of most males (Carroll 1988, this paper). Selection was significant in almost all aggregations with above-average sex ratios, and although the intensity of selection was not perfectly correlated with sex ratio, it was highest in the aggregation with the highest sex ratio (aggregation P). Although the large number of statistical comparisons that we made increases the chance that we estimated a significant effect in an aggregation where in fact none occurred, the

repeatability of the pattern at higher sex ratios, and its overall pattern in relation to sex ratio, indicate that the effect is real.

Body size was related to movement rate and therefore to the frequency with which potential mates were encountered (Table III). We are not certain why large males move faster, but it may occur simply because they are stronger and have longer legs. In contrast to mate searching, the rarity of mate take-overs suggests that there is little variation between males in mate guarding ability, regardless of sex ratio. In addition, although mate choice could influence the relationship between body size and mating patterns, the absence of assortative mating by body size (Table II) suggests that neither males nor females exerted significant size-based mate choice, and/or that body size did not affect mate retention ability. Non-assortative mating by size does not prove that there is no mate choice in this species, but instead indicates that we can examine size-based mating patterns mainly with reference to other characters.

Why was large body size increasingly advantageous as the scramble for mates intensified at higher sex ratios? Such a result makes sense in light of the difference in movement rate between small and large males. Generally, when females are common (and pairing duration is not brief relative to the typical time required to find a female), roughly equivalent proportions of large and small males will be mating in any given sample. When females are more scarce, the higher mate-searching rates of large males will cause them to be over-represented in the mating sub-population. Given that we found little evidence of size-linked differences in other aspects of male mating behaviour, however, this advantage should not, on average, exceed the proportional difference in the mate-searching rates of the two male size classes. This was the result obtained in our model of equilibrium mating frequencies and in the quadratic regression of field mating frequencies on sex ratio (in which the second, non-linear term approached statistical significance): both asymptoted at a value similar to the ratio of mate-searching rates observed in the two size classes of captive males. This result implicates the size-based difference in the rate of locomotion during mate searching as the primary cause of the size effect on mating frequency observed across sex ratios.

The data on rates of locomotion matched the modelled values better than did the data on mating frequencies in captivity. This difference may result, in part, because we observed comparatively few matings (average mating duration being long relative to the time span of the experiments), but had copious data on rates of locomotion during mate searching. None the less, the male size difference in mounting rate on single females was even greater than that for movement rate in captive males. This result implies that size may increase mating effectiveness in ways additional to movement rate, although no such effect was evident in the experiment on 'handling time', and no size effect was found on mating duration. One possibility is that large males are more likely to mount females upon encountering them. Regardless of which data (searching rates or mounting rates) best reflect the modelled encounter rates of 'A' (small males) and 'B' (large males), however, the large standard errors of the terms indicate that equivalent results will obtain under a range of rate values, as long as their ratio remains similar.

In this comparative context, it is therefore especially interesting that movement rate appears to be a plastic trait: single males of both size classes nearly doubled their movement rates at the 3:1 sex ratio, compared to 2:1. The movement rate of small males at 3:1 was the same as that of large males at 2:1. Thus, it appears that even though small males could have searched as actively as large males at the 2:1 ratio, males of all sizes may gauge their allocation to searching as a function of the level of mating competition. Analogous changes in guarding behaviour were observed in experiments manipulating sex ratio with Oklahoma, but not Florida, bugs (Carroll & Corneli 1995).

The higher relative mating frequencies of large males, and thus the implications of sexual selection favouring larger male body size, in Oklahoma, must be viewed in terms of regional biology. Females are larger than males in all soapberry bug populations, and Florida adults of both sexes average larger than their Oklahoma counterparts (Carroll 1988). Our preliminary data, however, indicate that male size overlaps more with that of females in Oklahoma than in Florida. Other findings show no obvious constraints on the evolution of male body size: there is no strong relationship between male adult size and development time or longevity, and there is

significant additive genetic variation for male body size in Oklahoma, and to a lesser extent in Florida (S. P. Carroll, unpublished data). One possibility for the maintenance of small male size in Oklahoma (relative to females), is that small males achieve reproductive advantages that we have not detected (cf. Kaitala & Dingle 1993).

Within a species, variation in the intensity of sexual selection will have important ramifications both in the evolution of male mating tactics and in population differentiation (e.g. Carroll & Corneli 1995, in press). In a comparison of populations of the milkweed beetle, *Tetraopes*, in a west-east transect across the eastern United States, McCauley (1979) found general uniformity in sexual selection on male body size. In that case, however, there was no a priori reason to predict differentiation other than geographic and presumed genetic distance. In contrast, McLain (1993) documented within-population variation in the intensity of sexual selection with density in a seed-feeding bug, as did Fincke (1988) in a damselfly population that experienced seasonal variation in the availability of oviposition sites. Similarly, in the soapberry bug, sex-ratio variation generates consistent variation in sexual selection within and between populations. Variable sex ratios are probably common during breeding in many taxa, and variable, absolute male biases in sex ratio may be common in insects other than the soapberry bug as well (Carroll & Loye 1990). No one value of selection intensity can characterize these species. Yet, at present, we have little empirical knowledge of the sampling intensity needed to accurately characterize selection in nature.

APPENDIX

We calculated equilibrium mating frequencies for each size class as the sum of the rate of transition of individuals from a non-mating to a mating state, plus the rate of re-entry of males into the mate searching pool after the end of a mating.

For small males at equilibrium, this sum is

$$ds/dt = -\alpha sf + (s_0 - s)/\tau = 0 \quad (A1)$$

where, for an aggregation, α is the mating frequency for small males, s is the number of single (searching) small males, f is the number of single females, s_0 is the total number of small males, and

τ is the mating duration (time spent out of the mate searching pool while with a female).

Similarly, for large males at equilibrium,

$$ds/dt = -\beta bf + (b_0 - b)/\tau = 0 \quad (A2)$$

where β is the mating frequency for large males, b is the number of single large males, b_0 is the total number of large males in the aggregation, and f and τ are as above.

Our empirical studies allowed us to give values to these parameters. First, from our field studies, we knew that the numbers of small and large males were essentially equal in each aggregation. In addition, we found that the mating duration (τ) did not differ between large and small males, but that the rate of mate encounter (α or β) did. This difference in the rate of mate encounter appeared to result mainly from a size-related difference in rates of locomotion in mate searching (see Results).

Because of the dependence of female availability on male mating frequencies, the next step was to model the equilibrium number of free females, which is

$$df/dt = -(\alpha s + \beta b)f + (f_0 - f)/\tau = 0 \quad (A3)$$

where f_0 is the total number of females in an aggregation.

Then, with the empirical data in hand, we were prepared to calculate, across all aggregations, the values of large- versus small-male mating frequencies (equivalent, for our purposes, to the rates of locomotion or mate encounter) that best fit the field data on large- versus small-male mating frequencies. To do this, we solved equations (A1) and (A2) simultaneously, with respect to female availability (A3). To simplify notation, we defined $A = \alpha\tau$ (for small males), $B = \beta\tau$ (for large males), and the frequency of mating in females $f/f_0 = p$. We then combined the three equations, as a function of absolute female availability, as the cubic equation in p

$$[ABf_0^2]p^3 + [ABf_0 + (s_0 - f_0) + (A + B)]p^2 + [A(s_0 - f_0) + B(b_0 - f_0) + 1]p - 1 = 0 \quad (A4)$$

With the computer, we searched numerically for the roots of this equation. Once p was found, the number of free females was $f = f_0 p$, the number of mating small males was $s = s_0/1 + Af$, and the number of mating large males was $b = b_0/1 + Bf$. The free variables in A and B are the mating

frequencies of small and large males respectively, which depend on their respective success in mate searching. Accordingly, directly varying the values of A and B varied the equilibrium mating frequencies of the two size classes. As a function of increasing sex ratio, the model predicted a negatively exponential increase in the large- to small-male mating frequency that asymptoted at the hypothetical ratio of the large- to small-male rates of mate encounter. We then compared this 'best fit' ratio to the one that we measured between large and small males to judge whether the pattern in nature could realistically be generated by the size-based differences in male mate-searching behaviour that we observed.

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