

The effect of male size, age, and mating behavior on sexual selection in the seed beetle *Callosobruchus maculatus* *

U.M. SAVALLI ¹ and C.W. FOX

The Louis Calder Center and Department of Biological Sciences, Fordham University, Box K, Armonk, NY 10504, U.S.A.

Received 28 February 1998, accepted 3 June 1998

We use laboratory mating experiments to examine the effect of male size, age, and mating behavior on fecundity selection and sexual selection in the seed beetle, *Callosobruchus maculatus* (Coleoptera Bruchidae), a species in which females are larger than males. Female *C. maculatus* gain a fitness advantage, in the form of increased lifetime fecundity, from mating with large males (which contribute larger ejaculates), but the partial correlation between male size and fecundity is weaker than the partial correlation between female size and her fecundity. Large males had a mating advantage relative to small males, both when a single male was presented to a female and when two males were present. However, this did not appear to be due to females rejecting male courtship attempts, but instead may be due to male-male competition. When females were mated to two males sequentially, neither the size of the first male nor the size of the second male influenced whether or how quickly a female remated. None of the other potential bases for sexual selection — male age, male mating experience, and male courtship persistence — appeared to influence male mating success. We discuss how patterns of sexual selection on body size and sexual size dimorphism in *C. maculatus* differ from patterns of sexual selection and dimorphism in another seed beetle, *S. limbatus*.

KEY WORDS: Bruchidae, sexual dimorphism, female choice, male-male competition, fecundity selection.

Introduction	50
Methods	51
Results	54
Experiment 1: Effect of male size on female fecundity	54
Experiment 2: Effect of male size on the latency to mate	54

* Contribution No. 177 of the Louis Calder Center of Fordham University.

¹ Correspondence to : Dr Udo M. Savalli, The Louis Calder Center, 53 Whipoorwill Rd., Box K, Armonk, NY 10504, U.S.A. (E-mail: usavalli@earthlink.net; Phone: 914-273-3078; Fax: 914-273-6346).

Experiment 3: Female choice of two males	55
Experiment 4: Effect of male size on female remating	56
Experiment 5: Effect of male age on mating success	56
Experiment 6: Effect of male mating experience on mating success	56
Experiment 7: Effect of male courtship persistence on mating success	57
Discussion	57
Acknowledgements	59
References	59

INTRODUCTION

Sexual size dimorphism is common and widespread among animals. When males are larger than females, it is most commonly attributed to sexual selection (either male-male competition or female choice), especially in species in which the male is more ornamented or equipped with weaponry (DARWIN 1871, ANDERSSON 1994). In most insects, however, females are larger than males (GHISELIN 1974, SHINE 1979). This is most frequently attributed to fecundity selection favoring large females that can lay more or larger eggs than small females (DARWIN 1871, WILLIAMS 1966, GHISELIN 1974, HONEK 1993). In many species, female fecundity advantages may be sufficiently strong to lead to larger females even when there is sexual selection favoring large males (e.g. VOLLRATH 1980, PARTRIDGE & FARQUHAR 1983, FAIRBAIRN & PREZIOSI 1996).

To date there have been few attempts to quantify the relative importance of sexual and fecundity selection on male body size (ANDERSSON 1994). Still fewer studies have compared closely related species that have different patterns of dimorphism. For example, in some seed beetles, such as *Stator limbatus*, males are larger than females (SAVALLI & FOX 1998a). In seed beetles, males produce large ejaculates, nutrients from which are incorporated into female somatic and reproductive tissues (HUIGNARD 1983, BOUCHER & HUIGNARD 1987) and influence female fecundity, egg size, and larval development (FOX 1993a, 1993b; WASSERMAN & ASAMI 1985; SAVALLI & FOX 1998b). Fecundity selection favors large body size in both female and male *S. limbatus*, in the latter, via size-dependent ejaculates (FOX et al. 1995b, SAVALLI & FOX 1998a). In addition, sexual selection favors large size in males: fe-males mated to large males were less likely to remate than females mated to small males (a potentially significant benefit to males since seed beetles have last-male sperm precedence; EADY 1994) and when females were presented with two males simultaneously, large males had a mating advantage (due to male-male competition or female choice) (SAVALLI & FOX 1998a). However, most seed beetles, such as *Callosobruchus maculatus*, exhibit the typical insect pattern in which males are smaller than females, yet sexual selection on body size has not yet been studied in these species.

In this study we examine the role of fecundity selection and sexual selection on male size in the seed beetle *C. maculatus*. *C. maculatus* is biologically very similar to *S. limbatus*. Like *S. limbatus*, *C. maculatus* males have large ejaculates (about 8% of body mass for the first mating), and ejaculate size is highly correlated with male body mass (Fig. 1; SAVALLI & FOX 1998b). However, unlike *S. limbatus*, *C. maculatus* females are larger than males (see FOX 1993a, 1993b; FOX et al. 1995a, 1995b; SAVALLI & FOX 1998a, 1998b, and references therein for a review of the natural history of these species). Thus, we expect that this species may differ from *S. limbatus* in the intensity of either fecundity selection or sexual selection acting on males.

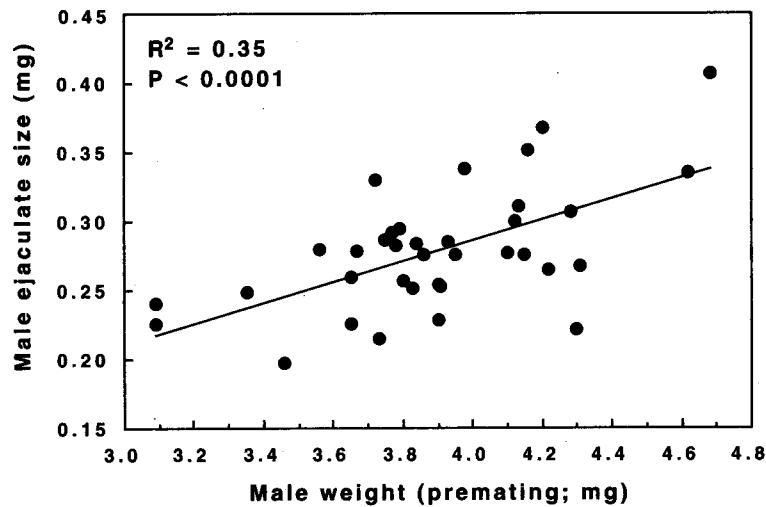


Fig. 1. — The relationship between male ejaculate size, measured as male weight loss during mating, and male size (prior to mating) in the seed beetle *Callosobruchus maculatus*. Each point represents the average for a full-sib family. Data from SAVALLI & FOX (1998b).

The goals of this study were: (1) to determine if females obtain a fitness benefit (increased fecundity) from mating with large males; (2) to determine if there is sexual selection on male body size in *C. maculatus*; (3) to investigate what mechanisms — female choice, male-male competition, or sperm competition — are influencing the evolution of male body size in *C. maculatus*; and (4) to determine if other characters besides body size — specifically, male age, mating experience, or courtship vigor — may influence male mating success via either female choice or intrasexual competition.

METHODS

Population origin, maintenance, and general methods

Callosobruchus maculatus is a cosmopolitan pest of stored legumes (Fabaceae). Females cement their eggs to the surface of host seeds (MESSINA 1991) and larvae burrow into the seeds. Larval development and pupation are completed entirely within a single seed. Emerging adults are well-adapted to storage conditions where food and water are typically not available; they require neither food nor water to reproduce. Even though one mating is sufficient to fertilize all of her eggs (EADY 1994), females may mate multiple times during their lifetime (FOX 1993a, 1993b; SAVALLI & FOX in press). All beetles used in these experiments were collected from infested pods of cowpea (*Vigna unguiculata*) in Niamey, Niger, at the University of Niamey Experiment Station, in November 1989, and maintained in laboratory growth chambers at > 1500 adults per generation, prior to this experiment.

All experiments were initiated with virgin males and females collected from isolated cowpea seeds within 12 hr of their adult emergence. Because male *C. maculatus* emerge from

their host seed with only partially filled seminal vesicles (Fox et al. 1995a), all virgin beetles were isolated in individual 30 mm petri dishes without seeds and allowed to mature for 24-36 hr before use in experiments. Thus, for all experiments, we used virgin beetles that were of similar age, between 24 and 48 hr old. Each beetle was used only once. Immediately prior to each experiment, all beetles were weighed on an electronic balance to 0.1 mg precision.

Experiment 1: Effect of male size on female fecundity

To quantify the effects of male and female body size on female fecundity, we mated virgin females to males and determined the female's lifetime fecundity. Since females will usually remate several times in their life if given an opportunity to do so (FOX 1993a, 1993b; SAVALLI & FOX in press), and to maximize the effect of male size, we mated the same male to the same female on three occasions, each 2 days apart. We did not combine males and females together for the entire experiment since females could then compensate for small ejaculates by mating more often; our design thus controls for mating frequency. For the first mating we paired each virgin female with a randomly selected single virgin male until they mated and then removed the male. We then placed the females in a 60-mm petri dish containing > 70 cowpea seeds. At 2 days and again at 4 days after the initial mating, females were removed from the seeds, remated to the original male, and replaced on the seeds. If a female did not remate at one of these times, we remated her on the following day. Females were left on the seeds until they died, after which we determined the total number of eggs that she laid.

Experiment 2: Effect of male size on the latency to mate

To determine if females mated with large males were more likely to mate, mated more quickly, or mated for a longer duration than females paired with small males: that is, if females exhibited an absolute mate preference for large males in the absence of male-male competition, we confined virgin females with a single virgin male and examined the latency to mating. Randomly selected males were transferred into a 30 mm petri dish containing a virgin female (without seeds) and watched continuously until the pair mated. We scored the latency to mate and the duration of the mating. Matings were defined as beginning when the male inserted his aedeagus and stopped antennating the female and defined as ended when the female started kicking at the male to separate. We recorded any rejection behaviors by females (persistently running away from the male for at least the circumference of the dish or kicking at a male attempting to mount). Pairs that failed to mate within 15 min were classified as "unmated". We tested if females paired with large males were more likely to mate or mated sooner than females paired with small males and if female size influenced her mating behavior.

Experiment 3: Female choice of two males

To examine the potential role of relative female choice or male-male competition in obtaining matings, virgin females were paired with two virgin males. All males used in this experiment were ranked according to their size and divided into two groups, representing the largest half and smallest half of the size distribution. To assure that there was a reasonable size difference between paired males, the largest of the large males and the largest of the small males were confined simultaneously with a randomly selected female. Next, the second largest of the large males and the second largest of the small males were confined with a second randomly selected female, and so on until all males were confined with another male and a female. Thus, small males were on average 19% (\pm 5.8% SD, range 10-37%) smaller than the large males. This approach enhanced our ability to statistically detect an effect of body size and enabled us to easily determine which male successfully mated without marking the males.

The trios (2 males + 1 female) were observed continuously for 15 min or until a mating occurred. As in the previous experiment, we recorded male and female behaviors. When a male successfully mated, the length of mating was recorded and the unmated male was removed and reweighed to determine his identity. We classified the outcome of each trial as having been influenced by either female rejection behavior, male-male interference, or scramble competition. Female rejection behavior was indicated by females persistently running away from a male or by kicking at a male that attempted to mount. Male-male interference was defined as one male interfering with another that was attempting to mount, resulting in that male being knocked off the female. Finally, a trial's outcome was defined to be due to scramble competition (THORNHILL & ALCOCK 1983) if the first male to locate and contact the female mated with her in the absence of either female rejection or male-male interference. We then determined if the small or large males were relatively more successful in obtaining matings, both for all trials combined and for trials influenced by different forms of competition.

Experiment 4: Effect of male size on female remating

Although the previous two experiments provide information about sexual selection on male body size in *C. maculatus*, they do not allow us to completely distinguish female preference for large males from effects of male body size on male-male competition. In this experiment we quantified the effect of a male's body size on the tendency of a female to remate when she encountered a new male. Females were randomly paired with a single male, as in Experiment 1. Immediately following mating the male was removed. A second randomly-assigned male was placed with the female 48 hr after the first mating. This pair was monitored for 15 min. We recorded whether a female remated, the time at which the female remated, and whether she exhibited any rejection behavior. In subsequent statistical analyses we tested whether the body size of the first male, the second male or the female affected the tendency of the female to remate.

Experiment 5: Effect of male age on mating success

In addition to body size, male contributions to females are also influenced by male age. Since males were provided neither food nor water, their ejaculate declined with age (FOX et al. 1995a). Thus, females might be expected to prefer to mate with younger rather than older (depleted) males. On the other hand, greater male age may indicate genetic quality (TRIVERS 1972, HALLIDAY 1983, MANNING 1985), and thus females might benefit from mating with older males. Male age (or nutritional condition) could also affect male behavior and the ability to compete for females. In this experiment we test the effect of male age on male mating success by presenting virgin females with two virgin males, one young and one old.

Virgin females were paired with two males that were matched in size to 0.1 mg but differed in age. Young males were \approx 1 d post-emergence while old males were \approx 7 d post-emergence (adult *C. maculatus* typically live \approx 10 d). To distinguish males, we marked, with a permanent marker, the elytra of the young male in half of the treatments and the elytra of the old male in the other half. This allowed us to test if marking the males influenced the outcome of the trials. Each trio was monitored for 15 min. As soon as a pair mated, the unmated male was removed. In subsequent statistical analyses we tested whether young or old males were more likely to mate.

Experiment 6: Effect of male mating experience on mating success

Previous experience with females may improve a male's ability to locate, court, and mate with a female. On the other hand, previously mated males may be less likely to remate (e.g., SAVALLI & FOX 1998a) and have smaller ejaculates (FOX et al. 1995a, SAVALLI & FOX in

press), making them less attractive to females. Here we test whether having previously mated affects a male's tendency to remate.

Virgin females were paired with two males that were matched in size to within 0.1 mg, one of which was a virgin and the other which had been mated to another female \approx 8 hr earlier. We again marked the virgin males in half of the treatments and the previously mated males in the other half. Each trio was monitored for 15 min. As soon as a pair mated, the unmated male was removed. In subsequent statistical analyses we tested whether virgin or experienced males were more likely to mate.

Experiment 7: Effect of male courtship persistence on mating success

Observations of *C. maculatus* suggest that males differ considerably in their persistence in pursuing and courting females, particularly if the female resists mating. In this experiment we first quantify male courtship persistence and then present males of high and low courtship persistence to females.

To quantify male courtship persistence, we placed single virgin males in a dish for 2 min with a female that had recently mated. Because recently mated females do not immediately remate, we could be sure that the female would reject any courtship attempts. We then counted the total number of chases (defined as a continuous pursuit of a female for one full circumference of the petri dish) and attempted mountings. The number of chases and attempted mounts were positively correlated ($r_s = 0.293$; $n = 40$; $P = 0.030$). Based on the relative frequency of these two behaviors and the duration required for each, we derived a persistence score as $2 \times (\text{no. of chases}) + (\text{no. of attempted mounts})$; scores ranged from 0-17. We then divided the males into two groups, those with persistence scores below the median (≤ 6) and those with scores above the median (≥ 7). We again marked one or the other of these two groups of males and paired them with a new, virgin female for 15 min. In subsequent statistical analyses we tested whether males that previously exhibited low or high courtship persistence were more likely to mate.

RESULTS

Experiment 1: Effect of male size on female fecundity

Larger females and females mated to larger males laid significantly more eggs over their lifetime than did small females or females mated to smaller males (Fig. 2). However, the partial effect of male body size on lifetime fecundity (squared partial correlation = 0.132; $n = 58$; $P = 0.002$) was of smaller magnitude than the effect of female body size on fecundity (squared partial correlation = 0.347; $n = 58$; $P < 0.001$), suggesting that male size is less predictive of a female's fecundity than is female size.

Experiment 2: Effect of male size on the latency to mate

Males that mated within the 15 min trial were larger than males that did not mate (mated: $\bar{x} \pm \text{SE} = 3.83 \pm 0.10$ mg; not mated: 3.20 ± 0.28 mg; Mann-Whitney test, $U = 35.5$, $n = 37$, $P = 0.047$), but there was no indication that this was due to differential rejections by females, as male weights did not differ among those trials in which females exhibited no, weak, or strong rejection behavior (Kruskal-Wallis test, $H = 0.879$, $n = 37$, $P = 0.64$). Of males that mated, there was no correlation

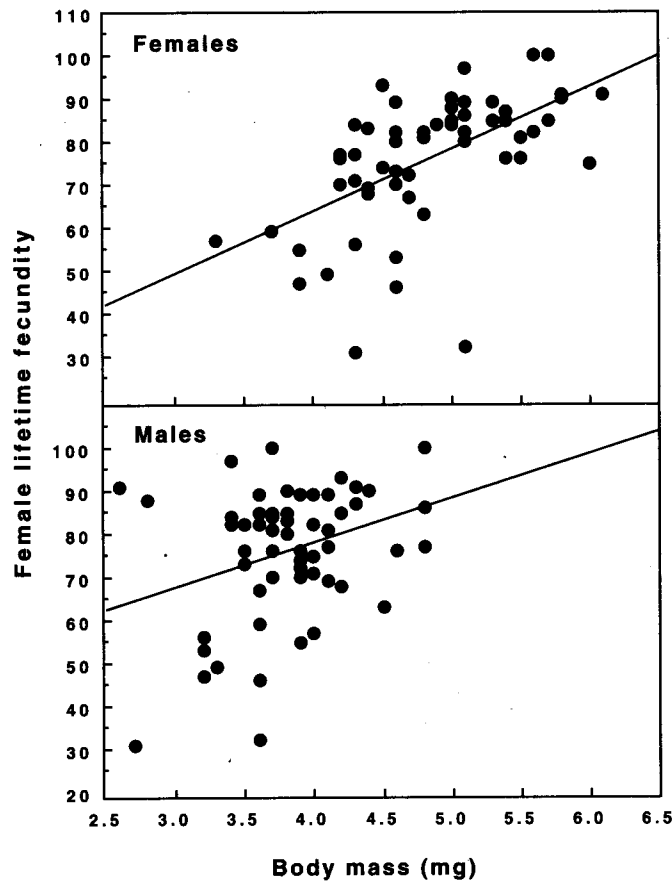


Fig. 2. — The relationships between female lifetime fecundity (no. of eggs) and male and female body size, when each female is mated to the same male 3 times.

between male size and latency to mate (Spearman rank correlation, $r_s = -0.176$, $n = 32$, $P = 0.33$).

Female size did not influence whether or not a pair mated within the 15 min trial period (Mann-Whitney test, $U = 61.5$, $n = 37$, $P = 0.41$) or how quickly they did so (Spearman rank correlation, $r_s = -0.263$, $n = 32$, $P = 0.14$), but small females were more likely to exhibit strong rejection behaviors than large females (Kruskal-Wallis test, $H = 9.42$, $n = 37$, $P = 0.009$). Neither male nor female size influenced mating duration (male size; $r_s = -0.076$, $P = 0.67$; female size, $r_s = 0.195$, $P = 0.28$).

Experiment 3: Female choice of two males

When two males were presented to a female, the larger male won 119 of 205 trials (Binomial test, $P = 0.025$). To investigate if this slight large-male advantage is

due to female choice, male-male interference competition or scramble competition, we independently analyzed each subset of trials whose outcome was attributed to these causes. In the 80 trials in which male-male interference was observed, the larger of the two males mated more often than the smaller (50 vs 30; one-tailed binomial test, $P = 0.039$). Female rejection was only rarely observed (12 trials), and neither large nor small males were more likely to mate in those trials (large males mated in 7 trials; one-tailed binomial test, $P = 0.39$). In the remaining trials in which scramble competition affected the outcome, the large male showed a non-significant tendency to be more successful (67 of 117 trials, one-tailed binomial test, $P = 0.07$).

Experiment 4: Effect of male size on female remating

Of 76 virgin females that were presented sequentially with two males, 32 (42%) remated when presented with the second male. There was no difference in the size of the first male to mate between those trials in which the female remated and those in which she did not (Mann-Whitney test, $U = 630$, $P = 0.44$). Similarly, second males did not differ between remated and unremated trials (Mann-Whitney test, $U = 677$, $P = 0.78$). The relative sizes of the males also did not affect female remating behavior: females remated in 21 of 44 trials in which the first male was larger than the second and in 8 of 24 trials in which the second male was larger (Fisher exact test, $P = 0.31$). Female body size had no detectable effect on her tendency to remate (Mann-Whitney test, $U = 688$, $P = 0.86$). Neither the size of the first male, the size of the second male, nor the size of the female, influenced how quickly a female remated (Table 1).

Experiment 5: Effect of male age on mating success

Male age did not influence male mating success (the older male mated in 20 of 43 trials; binomial test, $P = 0.76$). There was no effect of marking males on the outcome of the trials (marked males mated in 21 of 43 trials; binomial test, $P > 0.99$).

Experiment 6: Effect of male mating experience on mating success

Whether or not a male had previously mated with a female did not influence his mating success (of 140 trials, the previously-mated male succeeded in mating

Table 1.

The effect of female weight, the weight of the first male to mate to the female and the weight of the second male to mate on the latency to mate when the second male was placed with the female, $n = 32$.

Variable	Spearman rank partial correlation coefficients	P
First male weight	- 0.053	0.8
Second male weight	- 0.125	0.5
Female weight	0.055	0.8

74 times; binomial test, $P = 0.55$). As in the previous experiment, there was no effect of marking males on the outcome of the trials (marked males mated in 65 of 140 trials; Binomial test, $P = 0.45$).

Experiment 7: Effect of male courtship persistence on mating success

Males that exhibited a high degree of courtship persistence (persistence score ≥ 7) when paired with a non-mating female were not more likely to mate when subsequently presented to a virgin female than were males with low courtship persistence (15 matings for high-persistence males vs 12 for low persistence males; binomial test, $P = 0.70$). There was no relationship between male size and courtship persistence (Spearman rank correlation, $r_s = -0.098$, $n = 40$, $P = 0.54$). As in the previous experiment, there was no effect of marking males on the outcome of the trials (marked males mated in 15 of 27 trials; binomial test, $P = 0.70$).

DISCUSSION

Our results demonstrate that female *Callosobruchus maculatus* gain a fitness advantage, in the form of increased lifetime fecundity, from mating with large males (Experiment 1). Thus, fecundity selection acts on male as well as female body size. However, the effect of male size on fecundity is clearly much weaker than the effect of female size on fecundity.

Since females benefit from mating with large males, we might expect that they should preferentially mate with large males. As expected, large males had a mating advantage relative to small males, both when a single male was presented to a female (Experiment 2) and when two males were present (Experiment 3). In both of these experiments, the results could be due to female choice or some form of male-male competition. We could find no direct evidence for female choice of large males: in neither experiment was female rejection behavior related to male size. We cannot, however, exclude more subtle forms of female influence, such as females using pheromonal signals to deter or attract males (e.g. BOPPRÉ 1984, MOORE & BREED 1986).

In the single-male experiment (Experiment 2), overt male-male competition was not possible, but the large male advantage could be because large males may be more active and may locate females more rapidly. In the two-male experiment (Experiment 3), both scramble competition and more overt interference competition were possible among males, and in those trials in which male-male interference was observed, large males continued to have an advantage. On the other hand, in those trials in which either female rejection was observed or that were attributed to scramble competition, neither large nor small males had a clear advantage (there was a non-significant trend for large males to be more successful in the scramble competition trials, suggesting that this form of competition may also have a weak influence). Neither the size of the first male nor the size of the second male influenced whether or not or how quickly a female remated (Experiment 4). Thus, there is no advantage of large body size in reducing the risk of sperm competition in *C. maculatus*, although it is possible that large size can affect sperm number and thus success at sperm competition.

Although male size can influence mating success, none of the other potential bases for sexual selection — male age, male mating experience, and male courtship persistence — appeared to influence male mating success (Experiments 5-7). We were particularly surprised by the lack of any effect of courtship persistence, since males are so variable in this trait. One possible explanation is that females, especially virgin females, simply do not exhibit any mate choice, and any male mating advantage is due to differences in the male's ability to encounter females rather than being due to variation in courtship abilities.

It is not clear why virgin females were apparently unselective when presented with males. It is possible that there is simply no cost to multiple mating, but this is unlikely, since females exhibit a long refractory period after mating. Potential costs of mating include reduced mobility (increasing risk of predation), transmission of diseases, and interference with other activities such as egg-laying. If mating has some cost, as seems likely, then females should be selective when mating. One possible reason why females were not selective in these experiments is that the cost, in terms of lost reproductive opportunities, of forgoing a mating exceeds the benefits of obtaining larger ejaculates, especially for a species in which the adult stage lives only about one week. Any cost of mating with a small male may be easily recouped by simply remating at a later time. Only by determining the available mating opportunities in the field can this issue be resolved.

Given that both fecundity selection and sexual selection appear to favor large males in *C. maculatus*, why are males nonetheless smaller than females in this species? The most common explanation for the large female size in insects (and many other organisms) is that large females are favored by fecundity selection (DARWIN 1871, WILLIAMS 1966, GHISELIN 1974, HONEK 1993) while there is little or no selection for large size in males. In addition, there may be selection favoring small males, such as through greater agility (ANDERSSON & NORBERG 1981), more rapid development (e.g. selection for protandry; SINGER 1982, BULMER 1983), more efficient searching for females (GHISELIN 1974, FAGERSTRÖM & WIKLUND 1982, VOLLRATH 1998), less time spent foraging (BLANCKENHORN et al. 1995) or female preferences for small males (PETRIE 1983, STEELE & PARTRIDGE 1988). Fecundity selection does favor large female size in *C. maculatus*, since large females lay more and larger eggs in their lifetime than small females (FOX 1993a, 1993b, 1993c; SAVALLI & FOX in press). However, fecundity selection also favors large male size, although it is weaker than fecundity selection on females. In contrast to *C. maculatus*, in *S. limbatus* — in which males are larger than females — large males are favored by fecundity selection that appears to be nearly as strong as the fecundity selection acting on females (FOX et al. 1995b, SAVALLI & FOX 1998a). Furthermore, in *S. limbatus*, females that mated to large males were less likely to remate than females mated to small males (SAVALLI & FOX 1998a). As a consequence, large *S. limbatus* males gain an advantage over small males in that they are less likely to suffer sperm competition; this advantage can be considerable since seed beetles, like most insects, have last-male sperm precedence (EADY 1994). Large *C. maculatus* males do not enjoy a similar advantage.

We have argued that the combination of fecundity selection acting on both males and females and the effect of male size on female remating may explain why in *Stator limbatus* males are larger than females. The reduced fecundity selection and absence of an effect of male size on female remating may likewise explain why *C. maculatus* males are small. We suggest that female-biased sexual dimorphism in *C. maculatus* is due to fecundity selection acting more strongly on females than

males, with sexual selection only weakly favoring large males. It is possible that in natural conditions sexual selection may favor small males via an increased mobility or reduced time spent foraging resulting in a greater ability to locate females (GHISELIN 1974, BLANCKENHORN et al. 1995, VOLLRATH 1998), but in our laboratory conditions (and probably also in the seed stores from which these populations were derived; MESSINA 1991) there is little advantage to efficient searching.

ACKNOWLEDGEMENTS

This research was funded in part by a Fordham University Faculty Research Grant to C.W. Fox. Frank Messina provided the beetle populations. We thank John Wehr and Berish Rubin for providing space and support to U.M. Savalli. We are grateful to Mary Ellen Czesak for assistance and to Laura Beani, Mary Ellen Czesak, Daphne Fairbairn, Paul Spinelli and an anonymous reviewer for helpful comments on earlier versions of this manuscript.

REFERENCES

- ANDERSSON M. 1994. Sexual selection. *Princeton, NJ: Princeton University Press.*
- ANDERSSON M. & NORBERG R.Å. 1981. The evolution of reversed sexual size dimorphism and role partitioning among predatory birds, with a size scaling of flight performance. *Biological Journal of the Linnean Society* 15: 105-130.
- BLANCKENHORN W.U., PREZIOSI R.F. & FAIRBAIRN D.J. 1995. Time and energy constraints and the evolution of sexual size dimorphism — to eat or to mate? *Evolutionary Ecology* 9: 369-381.
- BOPPRÉ M. 1984. Chemically mediated interactions between butterflies, pp. 259-275. In: Vane-Wright R.I. & Ackery P.R., Edits. *The biology of butterflies. New York: Academic Press.*
- BOUCHER L. & HUIGNARD J. 1987. Transfer of male secretions from the spermatophore to the female insect in *Caryedon serratus* (Ol.): analysis of the possible trophic role of these secretions. *Journal of Insect Physiology* 33: 949-957.
- BULMER M.G. 1983. Models for the evolution of protandry in insects. *Theoretical Population Biology* 23: 314-322.
- DARWIN C. 1871. *The descent of man and selection in relation to sex. London: J. Murray.*
- EADY P. 1994. Sperm transfer and storage in relation to sperm competition in *Callosobruchus maculatus*. *Behavioral Ecology and Sociobiology* 35: 123-129.
- FAGERSTRÖM T. & WIKLUND C. 1982. Why do males emerge before females? Protandry as a mating strategy in male and female butterflies. *Oecologia* 52: 164-166.
- FAIRBAIRN D.J. & PREZIOSI R.F. 1996. Sexual selection and the evolution of sexual size dimorphism in the water strider, *Aquarius remigis*. *Evolution* 50: 1549-1559.
- FOX C.W. 1993a. The influence of maternal age and mating frequency on egg size and offspring performance in *Callosobruchus maculatus* (Coleoptera: Bruchidae). *Oecologia* 96: 139-146.
- FOX C.W. 1993b. Multiple mating, lifetime fecundity and female mortality of the bruchid beetle, *Callosobruchus maculatus* (Coleoptera: Bruchidae). *Functional Ecology* 7: 203-208.
- FOX C.W. 1993c. Maternal and genetic influences on egg size and larval performance in a seed beetle (*Callosobruchus maculatus*): multigenerational transmission of a maternal effect? *Heredity* 73: 509-517.
- FOX C.W., HICKMAN D.L., RALEIGH E.L. & MOUSSEAU T.A. 1995a. Paternal investment in a seed beetle (Coleoptera: Bruchidae): influence of male size, age, and mating history. *Annals of the Entomological Society of America* 88: 101-103.

- FOX C.W., McLENNAN L.A. & MOUSSEAU T.A. 1995b. Male body size affects female lifetime reproductive success in a seed beetle. *Animal Behaviour* 50: 281-284.
- GHISELIN M.T. 1974. The economy of nature and the evolution of sex. *Berkeley: University of California Press*.
- HALLIDAY T.R. 1983. The study of mate choice, pp. 3-32. In: Bateson P., Edit. *Mate choice. Cambridge, UK: Cambridge University Press*.
- HONEK A. 1993. Intraspecific variation in body size and fecundity in insects: a general relationship. *Oikos* 66: 483-492.
- HUIGNARD J. 1983. Transfer and fate of male secretions deposited in the spermatophore of females of *Acanthoscelides obtectus* Say (Coleoptera: Bruchidae). *Journal of Insect Physiology* 29: 55-63.
- MANNING J.T. 1985. Choosy females and correlates of male age. *Journal of Theoretical Biology* 116: 349-354.
- MESSINA F.J. 1991. Life-history variation in a seed beetle: adult egg-laying vs. larval competitive ability. *Oecologia* 85: 447-455.
- MOORE A.J. & BREED M.D. 1986. Mate assessment in a cockroach, *Nauphoeta cinerea*. *Animal Behaviour* 34: 1160-1165.
- PARTRIDGE L. & FARQUHAR M. 1983. Lifetime mating success of male fruitflies (*Drosophila melanogaster*) is related to their size. *Animal Behaviour* 31: 871-877.
- PETRIE M. 1983. Female moorhens compete for small, fat males. *Science* 220: 413-415.
- SAVALLI U.M. & FOX C.W. 1998a. Sexual selection and the fitness consequences of male body size in the seed beetle *Stator limbatus*. *Animal Behaviour* 55: 473-483.
- SAVALLI U.M. & FOX C.W. 1998b. Genetic variation in paternal investment in a seed beetle. *Animal Behaviour* 56: 953-961.
- SAVALLI U.M. & FOX C.W. (in press). The effect of male mating history on paternal investment, fecundity, and female remating in the seed beetle *Callosobruchus maculatus*. *Functional Ecology*.
- SHINE R. 1979. Sexual selection and sexual dimorphism in the Amphibia. *Copeia*: 297-306.
- SINGER M.C. 1982. Sexual selection for small size in male butterflies. *The American Naturalist* 119: 440-443.
- STEELE R.H. & PARTRIDGE L. 1988. A courtship advantage for small males in *Drosophila subobscura*. *Animal Behaviour* 36: 1190-1197.
- THORNHILL R. & ALCOCK J. 1983. The evolution of insect mating systems. *Cambridge: Harvard University Press*.
- TRIVERS R.L. 1972. Parental investment and sexual selection, pp. 136-179. In: Campbell B., Edit. *Sexual selection and the Descent of Man, 1871-1971. London: Heinemann*.
- VOLLRATH F. 1980. Male body size and fitness in the web-building spider *Nephila clavipes*. *Zeitschrift für Tierpsychologie* 53: 61-78.
- VOLLRATH F. 1998. Dwarf males. *Trends in Ecology and Evolution* 13: 159-163.
- WASSERMAN S.S. & ASAMI T. 1985. The effect of maternal age upon fitness of progeny in the southern cowpea weevil, *Callosobruchus maculatus*. *Oikos* 45: 191-196.
- WILLIAMS G.C. 1966. Adaptation and natural selection: a critique of some current evolutionary thought. *Princeton, NJ: Princeton University Press*.