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The social environment affects mate guarding behavior in Japanese beetles, *Popillia japonica*

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Abstract

The effect of the social environment on post-copulatory mate guarding duration in Japanese beetles, (*Popillia japonica* Newman), was examined in a laboratory experiment. The mate guarding durations of beetles in different sex ratios and densities were observed for 10 hours. Guarding duration was longer when females were larger, suggesting the presence of 'cryptic' male mate choice. Densities, but not sex ratio, affected the duration of guarding bouts, with males guarding for longer at higher densities. This result implies that males increase their guarding duration under conditions in which their female may be likely to be encountered by other males. The lack of a sex ratio effect on the duration of guarding bouts is consistent with other studies on this species that indicate males have difficulty distinguishing females from males. Consequently, because the sex ratio on food plants is typically male-biased, a paired male may react just to density, treating surrounding individuals as if they were mostly males. The total amount of time males spent guarding was lower at lower densities and at male-biased sex ratios; this suggests that after ceasing to guard one female, males were less able to find a subsequent mate under these conditions.

Keywords: density, mating behavior, sexual selection, postcopulatory mate guarding, sex ratio

Introduction

Mate guarding, which may increase a male's paternity assurance, is a commonly observed behavior in insects (Thornhill and Alcock 1983; reviewed in Alcock 1994; Simmons 2001). Some aspects of a species' mate guarding will depend on its biology. For example, last sperm precedence, which occurs when only sperm from the last mating is used to fertilize the eggs, may lead to the evolution of post-copulatory mate guarding behavior (Parker 1970a; 1970b). However, more subtle aspects of mate guarding, such as guarding duration, may change according to more variable conditions, such as sex ratios, densities of conspecifics, and the number and quality of available females.

Theoretical studies have investigated how post-copulatory mate guarding evolved and how different social environments should affect optimal mate guarding behavior (Parker 1970a; Parker 1974; Yamamura 1986). Parker (1974) used time spent as a cost of mate guarding and found that post-copulatory mate guarding would be favored by a male-biased sex ratio; this result was because of an increase in the probability of multiple mating by the female. Yamamura (1986) predicted that a male should guard his mate when the sex ratio is male-biased, when density is high, and when the female lays eggs soon after the copulation. Finally, Alcock (1994) suggested 10 conditions for the evolution of mate guarding; some of these conditions include last male advantage, high potential of taking over previously paired females, and a male-biased sex ratio.

These theoretical predictions have been tested empirically in many studies (e.g. Alcock 1991; Adolph and Geber 1995; Stoks *et al*. 1997; Schöfl and Taborsky 2002). For example, Alcock (1991) confirmed Yamamura's predictions of the effects of female availability and high intensity of sperm competition in the staphylinid beetle *Ontholestes cingulatus*. Furthermore, Stoks *et al*. (1997) demonstrated that the mate guarding behavior of the emerald damselfly (*Lestes sponsa*) supported the 10 predictions of Alcock (1994) for the evolution of mate guarding, including high density, multiple mating by females, and a male-biased operational sex ratio.

In this study, the question was whether a male's immediate social environment affected his guarding duration in Japanese beetles, *Popillia japonica* Newman. Japanese beetles are an introduced species first discovered in the United States in New Jersey in 1916. They are an important pest species; as adults they feed on approximately 300 species of plants (Fleming 1968; 1972; Potter and Held 2002).

Japanese beetles are promiscuous; both males and females may mate with multiple partners. Furthermore, evidence for male mate choice exists. In the field, paired females tend to be larger and in the lab, males tend to copulate with larger females when given a choice (Saeki *et al*. 2005). Males exhibit post-copulatory mate guarding behavior, in which a male stays in tandem formation on his mate after a brief copulation (approximately 2 minutes; Barrows and Gordh 1978). The guarding duration could last from a few minutes to several hours (Barrows and Gordh 1978; personal observation). Females periodically oviposit eggs in the soil (Smith and Hadley 1926; Fleming 1972; Van Timmeren *et al*. 2000) and

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approximately 70% of eggs are fertilized by the sperm from the last male with which she mated (Ladd, 1966; 1970a). Interestingly, in the field and the laboratory, males have been observed to "voluntarily" end their guarding (personal observation) apparently prior to female oviposition. However, male behavior while in tandem, such as fights with other males (Kruse and Switzer, unpublished data), indicate that their tandem formation does have a mate guarding function. The intensity of sperm competition in this species is likely high because of the male-biased sex ratio (Switzer *et al*. 2001), and because local density may be quite high on food plants; although some beetles may be solitary, extreme aggregations in which thousands of beetles are on the same food plant frequently occur (Fleming 1972; personal observation). Accordingly, in this study the sex ratio, density, and male and female sizes were examined to see if they would affect the mate guarding duration of Japanese beetles.

Materials and Methods

The effects of densities and sex ratios on guarding durations

Japanese beetles were collected from peach trees (Rosaceae: *Prunus persica* (L) Batsch) in Coles County, IL. and brought to the laboratory. The same morning they were collected, they were sexed and each beetle was marked with a numbered bee tag (Thorne Ltd.) on its pronotum to facilitate individual identification. The colors of the bee tags were different for each sex. They were kept overnight at a constant density (14 individuals/container) with the same sex in small containers (diameter 7 cm; depth 10 cm) with sassafras leaves (Lauraceae: *Sassafras albidum* Nutt) for food.

The next morning, they were randomly placed, with a single grape leaf (*Vitis cinifera*), in petri dishes at 2 densities (4 or 8 individuals/petri dish) and 3 sex ratios (male: female = 1: 1, 3: 1, and 1: 3) for a total of 6 treatments. Each treatment had 10 replicates. All groups were placed in an environmental chamber where the temperature was maintained at 28°C. Pair formations were recorded every 15 minutes for 10 hours (from 0900 to 1900). Some replicates were observed continuously for a period of time; during these observations, males were never observed leaving a female and then remounting the same female within the 15 min observation period. After the experiment, the body size of each individual was measured. We defined body size as the maximum width of thorax, which occurs at the anterior portion of the elytra; this measure is a good overall indicator of body size (Van Timmeren *et al*. 2000).

Analysis

The data were analyzed in four ways. In three cases, averages were calculated from each trial, so each trial only contributed one data point. First, the number of pairs was counted for each male in 10 hours, regardless of which female he was paired with, and pairings for the males in each trial (hereafter "number of pairs") were averaged. Second, the duration of the longest pairing for each male during a trial was taken, and an average for the males in each trial was calculated (hereafter "longest pairing"). In this case, males were not included who did not pair during the trial. Third, the duration of all pairs was summed for each male regardless of which female he was paired with (hereafter "total pairing") and an average of those totals was determined for the males in each a trial. Finally, in order to analyze whether the size of the male or female affected their pair duration, the pair exhibiting the longest pair duration was used from each trial, regardless of which male was paired with which female. This latter method, while not valid for sex ratio and density analyses (because of potential sample size effects; larger numbers of males may lead to longer durations just by chance), avoided pseudoreplication while being consistent in the use of data from different trials.

To analyze differences among treatments in number of pairings, longest pairing, and total pairing, 2-way ANOVA was used. For examining the possible effects of male and female size on longest pair duration, a 2-way ANCOVA was used, with the covariates of absolute body size of the female who were guarded for the longest period, the relative body size of the female compared with the average of the females' body size in the treatment group, and the body size of the male that exhibited the longest pairing. Sample sizes differ slightly for some analyses because in one replicate a male died during the experiment and two other beetles (one male and one female) were lost prior to measurement. SPSS version 12.0 (SPSS Inc. Chicago) was used for all analyses, and LSD (Least Significant Differences) for post hoc comparisons. All means are presented with SE.

Results

The number of pairings

The mean number of pairings was significantly different among three of the different sex ratios (Figure 1; $F_{2, 53} = 13.3$, $R^2 = 0.37$, $P < 0.01$). Not surprisingly, post hoc tests showed that males in the female-biased sex ratio paired more, on average, than other sex ratios (1m: 1f vs. 1m: 3f: $P = 0.22$; 1m: 1f vs. 3m: 1f: $P < 0.01$; 1m: 3f vs. 3m: 1f: $P < 0.01$). There was no significant difference in the number of pairs between the two densities ($F_{1,53} = 0.75$, $P = 0.39$), and no interaction between sex ratio and density ($F_{2, 53}$ =

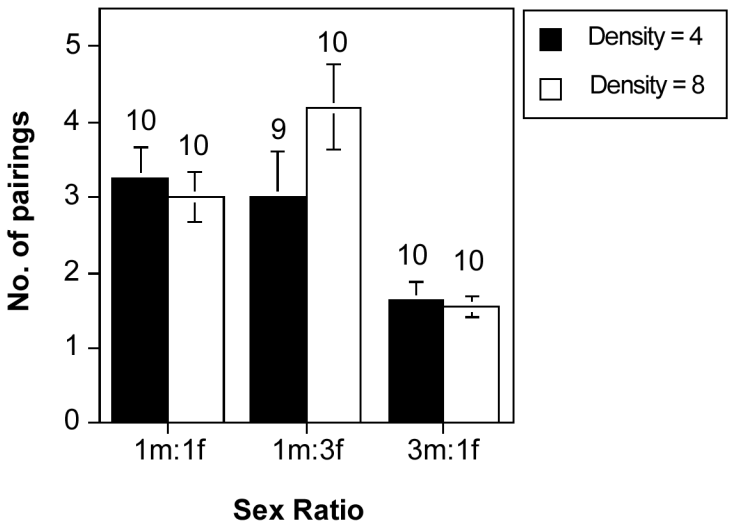


Figure 1. Number of pairings (mean ± se), averaged across males for each trial, for Japanese beetles at different sex ratios and densities. Number above bars refers to sample size.

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1.86, $P = 0.17$). Thus, when relatively more females were present, males tended to pair more.

Longest pairing

Mean longest pairing duration significantly differed between the two densities (Figure 2; $F_{1, 53} = 4.1$, $R^2 = 0.11$, $P = 0.49$), indicating that the pairing duration was longer in higher density. Sex ratio, however, did not affect the mean longest pairing duration significantly (Figure 2; $F_{2, 53} = 0.10$, $P = 0.90$) and post hoc tests did not show any significant difference in the mean longest pairing among the sex ratio treatments (1m: 1f and 3m: 1f: $P = 0.87$; 1m: 3f and 3m: 1f: $P = 0.60$; 1m: 1f and 1m: 3f: $P = 0.72$). Moreover, no interaction existed between sex ratio and density ($F_{2, 53} = 1.08$, $P = 0.35$).

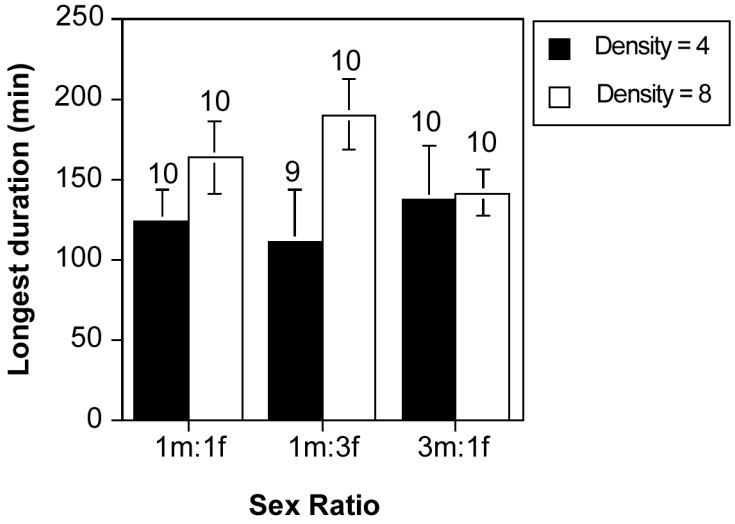


Figure 2. Mean duration of guarding (mean ± se), averaged across males for each trial, for Japanese beetles at different sex ratios and densities. Number above bars refers to sample size.

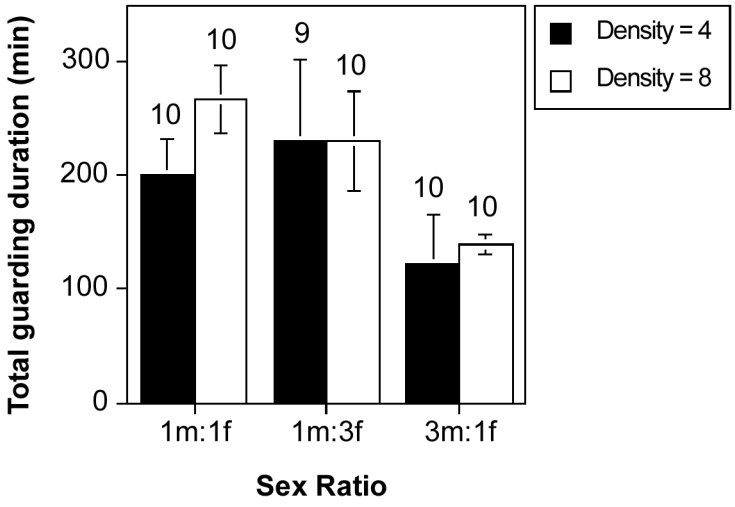


Figure 3. Duration of total guarding (mean ± se) for Japanese beetles at different sex ratios and densities. Number above bars refers to sample size.

Total pairing

Total pair duration significantly differed between the two densities (Figure 3; $F_{1, 53} = 5.35$, $R^2 = 0.34$, $P = 0.03$), with each individual spending more total time pairing at a higher density. In addition, sex ratio also significantly affected the total pairing duration (Figure 3; $F_{2, 53} = 9.8$, $P < 0.0001$). In post hoc tests, total pairing duration was longer in the sex ratio 1m: 1f than in 3m: 1f ($P = 0.01$), and it was longer in the sex ratio 1m: 3f than 3m: 1f ($P < 0.01$), but the difference between the sex ratios 1m: 1f and 1m: 3f was not significant ($P = 0.09$). No interaction existed between sex ratio and density ($F_{2, 53} = 1.13$, $P = 0.33$).

Effect of male and female size

The longest pairing duration of each treatment was significantly affected by female absolute body size, but not the relative body size of females or male body size (Figure 4; female absolute body size: Slope = 7.85, $F_{1, 48} = 10.1$, $P = 0.003$; female relative body size: Slope = -5.6, $F_{1, 48} = 2.7$, $P = 0.11$; male body size: Slope = -0.57, $F_{1, 48} = 0.091$, $P = 0.76$). Therefore, males guarded larger females for longer periods.

Discussion

Female size and density affected male pairing behavior. Although pairing status was recorded in this study, we consider the pairing as post-copulatory mate guarding because copulation typically occurs a few seconds after mounting a female (unpublished data) and lasts for approximately 2 minutes (Barrows and Gordh 1978; unpublished data;). Therefore, the paired males are referred to as "mate guarding."

At higher densities, a longer duration for both longest pairing and total pairing occurred. For the sex ratio, however, only total pairing was significant, with males guarding for less total time at male-biased sex ratios. This density pattern is consistent with theoretical predictions (Parker 1974; Yamamura 1986) and with results from some previous empirical studies (e.g. Andrés and Rivera 2000). Ultimately, the density pattern may be explained by higher densities increasing the likelihood of other males encountering a female that a male is no longer guarding (Parker 1974). Thus, a male benefits by guarding his current female longer because it is likely that another male will find her. Proximately, longer durations may be explained by the lowered stability of the social environment. When the density was higher, more individuals disturbed the pairs by crawling over them or attempting to mount on them (personal observations). Likewise, Koshio (1997) reported that the gypsy moth (*Lymantria dispar*) prolonged the duration for which a male stayed with the female when the pair was disturbed, and suggested that the paired male sensed the density of other males by the degree of disturbance. In terms of total pairing duration, after leaving one female, at male-biased sex ratios the male is less likely to find another female; under these conditions, the male is therefore less likely to begin mate guarding as quickly and thus spend less total time guarding.

Because no effect of sex ratio on longest pairing duration was found and no interaction existed between density and sex ratio, Japanese beetles seemed to respond to the increase in both extra females and males by increasing their guarding duration when the

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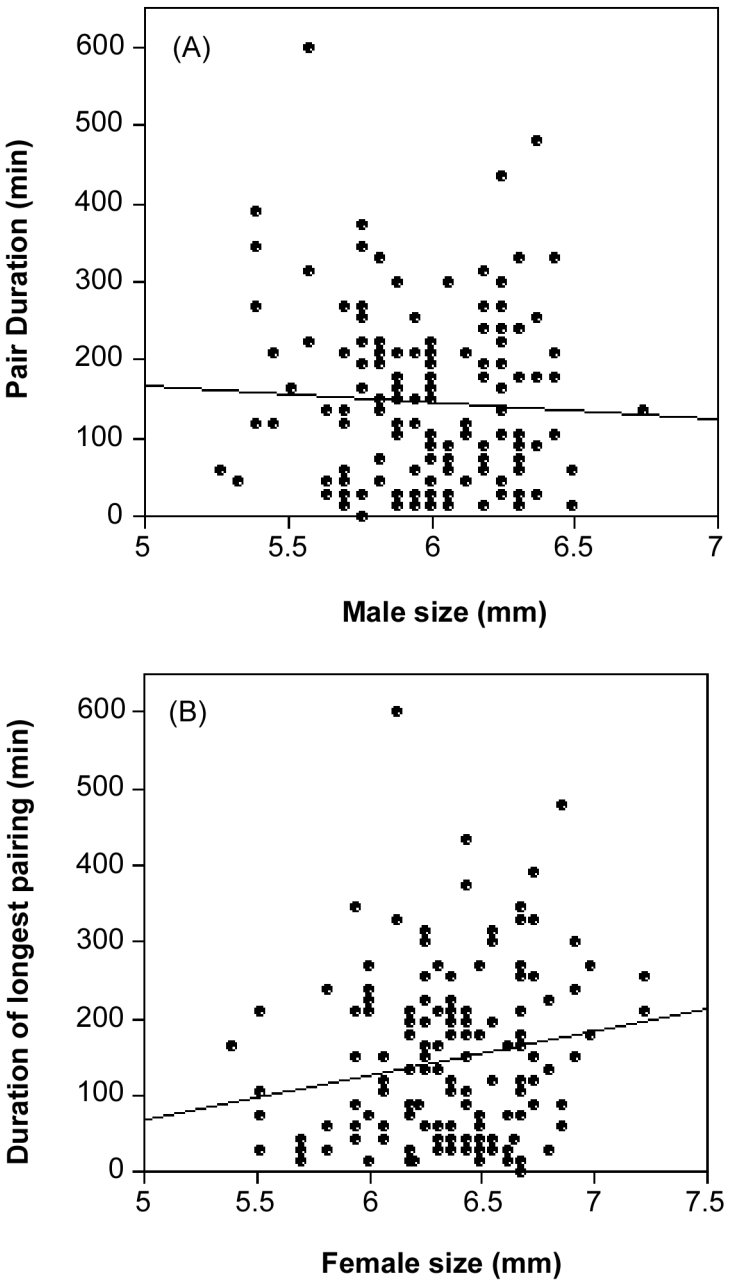


Figure 4. Relationship between body size and duration of longest pairing for (A) male and (B) female Japanese beetles for all treatments combined (N = 151). Line represents a simple linear fit to the data.

density was higher. Therefore, regardless of the sex, higher densities caused their guarding duration to lengthen compared to the lower density group. This lack of a sex ratio effect is in contrast to theoretical predictions (Parker 1974; Yamamura 1986) and other empirical studies (e.g. Clark 1988; Carroll 1991; 1993; Shivashankar and Pearson 1994; Kaitala 1997; Bateman and MacFadyen 1999; Schöfl and Taborsky 2002). These theoretical studies, however, assume that males can distinguish males from females, which may not be valid for Japanese beetles, at least in some circumstances. Switzer *et al.* (2004) found that a small frequency of pairs in the field were male-male (homosexual) rather than male-female, and that homosexual pairs readily formed in the laboratory. Available evidence suggests that this homosexual pairing may be a result of males not being able to distinguish males from females. Only virgin females produce the sex pheromone. The females on food plants, as was the case in the current study, have already mated and thus have ceased pheromone production (Ladd 1970b). These non-virgin females may differ from males only by being, on average, larger, and by allowing males to copulate (i.e. males paired with another male do not copulate) (Switzer *et al.* 2004; unpublished data). Consequently, paired males may react to active individuals as males because the sex ratio on food plants is usually male-biased (Switzer *et al.* 2001).

Males were found to guard larger females longer. This pattern is similar to that found in other studies. For example, Brown and Stanford (1992) demonstrated that male blister beetles (*Nemognatha nitidula*) guarded for longer durations when females were larger. By guarding for a longer duration, a male increases the probability that his sperm will be used to fertilize the eggs because the probability that other males will copulate with the female before she lays her eggs decreases (Parker 1974). Because larger females tend to have more and larger eggs (Saeki *et al.* 2005), this increased time cost to the male may be repaid in terms of increased reproductive success.

These results therefore support the hypothesis that male Japanese beetles exhibit mate choice. In a previous study, we found evidence for "direct" mate choice by male Japanese beetles; males preferred to pair with larger females and larger females were more fecund (Saeki *et al*. 2005). The current study suggests that Japanese beetles may also exhibit "cryptic" mate choice by males, in which males vary the amount they invest with the female depending on her quality (Bonduriansky 2001). In our study, males invested more time, in terms of mate guarding, with larger females. Bonduriansky (2001) stated three conditions for the evolution of male mate choice: high male investment, high variation in female quality, and small cost to find mates. In the Japanese beetle mating system, mate guarding may be costly in terms of lowered thermoregulation ability or increased energy expenditure (Saeki *et al*., in press); furthermore, variation in female fecundity exists (Saeki *et al*., 2005). Data on mate searching is not available, but Japanese beetles do frequently exist at very high densities. Therefore, the conditions for male mate choice seem to be met in this species and, although the role of the female in determining mate guarding duration cannot be ruled out, our studies indicate that both direct and cryptic male mate choice may occur.

Somewhat surprisingly, male body size was not correlated with guarding duration. Male body size is often related to the ability to take over a female or to resist against being taken over, or the ability to subdue a resisting female (Dodson and Marshall 1984; Castillo 1999). Crespi (1989) found that larger male thrips (*Elaphrothrips tuberculatus*) are more capable of guarding their mates, and larger males were selected to guard while smaller males were selected to "sneak". In contrast, Harari *et al*. (1999) found that smaller males guarded for a longer duration, and suggested that smaller males compensate for their low chance of mating by lengthening their guarding duration, thus increasing their probability of paternity. In Japanese beetles, in which fighting outcome may be positively related to male body size (Kruse and Switzer, unpublished

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data), one might expect male body size to be an important factor for determining their guarding duration. However, fighting frequency appears to be negatively related to density in this species (Kruse and Switzer, unpublished data); therefore, one possible explanation for the lack of a male body size effect may be that the densities in the current study were high enough that fights were relatively rare and thus of minimal importance in determining guarding duration.

In conclusion, a male's mate guarding behavior was affected by his social environment, specifically density, and the size of the female he was guarding. Future studies, specifically examining (1) the proximate mechanisms underlying the observed density patterns, (2) whether the mate guarding was terminated voluntarily or by disturbance from another male, and (3) mate guarding under field conditions, would help to understand the effect of social conditions on mate guarding in this species.

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