

Pairing Patterns in Japanese Beetles (*Popillia japonica* Newman): Effects of Sex Ratio and Time of Day

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*Size-related patterns between unpaired and paired individuals and between males and females of a given pair give clues about both a species' sexual behavior and the environmental factors affecting its sexual behavior. We studied the mating patterns of Japanese beetles (*Popillia japonica*) in east-central Illinois. The frequency of male–female pairs varied significantly among days and within a day, with pairs being significantly more common in the morning and the evening. The sex ratio on the food plants was significantly male biased, but although the sex ratio fluctuated among days and among time periods, the variation in the frequency of mating pairs was not explained by variation in the sex ratio. We found no assortative pairing with respect to size, but sizes of paired and unpaired individuals did differ. Paired females were larger than unpaired females at all time periods. In contrast, paired males were larger at 0700 and smaller at 1000, and little difference existed at other times of the day. The size of males and females, sex ratio, and pairing frequency also differed among days. Much of this variation in size and pairing frequency was related to a seasonal effect: later in the summer, beetles of both sexes were smaller and pairs were less common. Interestingly, pairs were also less frequent on days with higher average temperatures. This between-day variation in pairing, in combination with the within-day pairing differences, suggests that the temperature may alter the cost, and hence likelihood, of pairing in this species.*

KEY WORDS: assortative mating; Japanese beetle; sex ratio; sexual behavior; weather.

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INTRODUCTION

The basis for much of sexual behavior involves individuals of one sex competing for or preferring certain individuals of the opposite sex. As a result of this behavior, nonrandom pairings between males and females are common among a wide range of taxa. These pairing patterns can be influenced by factors such as the operational sex ratio and density of the population (Alonso-Pimentel and Papaj, 1996). The patterns are often found in relation to body size, particularly if body size is related to competitive ability (McLain and Boromisa, 1987; Lawrence, 1987; Enders, 1995) or fecundity (Thornhill and Alcock, 1983; Snead and Alcock, 1985; Lawrence, 1987; Enders, 1995). Specifically, if competition exists for mates, then size assortative mating may result if the sex ratio is not biased, while a large male (or female) advantage may exist with biased sex ratio (Harari *et al.*, 1999).

Identifying size-related mating patterns can give us clues as to the underlying mechanisms involved in mating behavior. For instance, size assortative mating can be due to similar size individuals living in the same places, constraints preventing mismatched pairs from successfully copulating, and/or mate choice with competition for the largest and best mates (Crespi, 1989; Bernstein and Bernstein, 1998). Once size-assortative mating is demonstrated, the various hypotheses can be tested with evidence of either the current patterns or with additional observations and experiments (e.g., Harari *et al.*, 1999). Alternatively, if paired individuals are larger than unpaired individuals, then several nonexclusive possibilities exist. First, environmental constraints or adult sex ratio may prevent smaller individuals from mating at that time (Lawrence, 1987). Second, larger individuals may be preferred by the opposite sex (Johnson, 1982; Ward, 1983; Svensson and Peterson, 1988; Brown, 1990; Polak and Brown, 1995). Third, larger individuals may outcompete smaller individuals of the same sex for mates (McLain, 1982; McLain and Boromisa, 1987; Polak and Brown, 1995). Thus, identifying the size-related mating patterns is an important first step toward understanding a species' underlying sexual behavior.

In this paper, we present the results of a study on mating behavior and size-related mating patterns in the Japanese beetle (*Popillia japonica*). Japanese beetles are a common, introduced species that as adults feed on over 300 species of plants (Fleming, 1972). Although hundreds of articles have been written on the biology of Japanese beetles (for a review see Fleming, 1972), relatively few studies have been conducted on their mating behavior (but see, e.g., Ladd, 1970a; Barrows and Gordh, 1978). Upon emergence, females emit a sex pheromone and usually mate; they may also mate later on food plants (Ladd, 1970a; Fleming, 1972). Adults of both sexes aggregate on the food plants, as a possible result of pheromones (Ladd,

1970a; Tumlinson *et al.*, 1977; Iwabuchi and Takahashi, 1983) and/or plant kairomones (Loughrin *et al.*, 1995, 1996). Japanese beetles exhibit last male sperm precedence (Ladd, 1966, 1970b), and perhaps as a consequence, males may mate guard females for hours by riding on their backs (Barrows and Gordh, 1978). The sex ratio on the food plants has been reported to change consistently throughout the day, with male-biased sex ratios in the morning and evening and relatively unbiased sex ratios in the middle of the day (Smith, 1923). These changes have been speculated to be the result of females arriving from the oviposition sites over the morning, then leaving the food plants again in the evening for oviposition sites (Fleming, 1972). Thus, Japanese beetles provide an excellent study system in which to investigate how pairing patterns are affected by the time of day and/or sex ratio.

METHODS

This study took place in a soybean field located in Coles County, Illinois, U.S.A. Only beetles found on soybeans were collected. Soybeans are a preferred food plant of Japanese beetles (Fleming, 1972), and limiting our collections to soybeans controlled for possible differences in behavior among food plants. Through the study period, portions of plants became noticeably damaged [skeletonized (Fleming, 1972)] by Japanese beetle herbivory; however, this damage did not destroy whole plants or patches of plants. Thus, large amounts of suitable forage existed for the beetles throughout the study.

We collected beetles every 3 h between 0700 and 1900 for 13 days in late July and early August 1999, for a total of 65 sampling periods. This part of the summer is in the latter half of the emergence period for Japanese beetles in this area (Van Timmeren *et al.*, in press), but adults were present for a month after the end of the study. At each collection time, we recorded the temperature, determined the frequency of pairs and the density of beetles, and systematically collected paired and solitary beetles. As expected, the mean average temperature was higher in the afternoon than in the morning or evening (time/mean temperature: 0700/24.1°C, 1000/32.4°C, 1300/33.7°C, 1600/33.1°C, 1900/27.2°C; range of average daily temperatures, 22.2/31.9°C). To obtain the pairing frequency and density, we determined the number of pairs in the first 100 beetles we encountered in the sampling area. To estimate beetle density, we measured the roughly square area occupied by these 100 beetles to the nearest 0.5 m on a side. We then collected 25 paired beetles [i.e., one beetle on top of another in a “mate guarding” position (Barrows and Gordh, 1978)] and 50 solitary beetles (i.e., not in contact with another beetle). These beetles were frozen for later sexing and measuring. To avoid effects due to our sampling, we never sampled the same area twice.

Beetle size and sex were determined in the laboratory. We recorded size as the maximum lateral body width, which occurs near the attachment point of the elytra. We had previously determined that maximum body width was positively and highly correlated with the size of six other morphological measures, including dry mass (Van Timmeren *et al.*, in press). Body width was measured using a dissecting scope with an ocular micrometer. We determined sex by using differences in the tibial spur and the first tarsal segment on the front pair of legs (Smith and Hadley, 1926). We calculated the sex ratio at each time period by combining the frequency of the paired beetles (number of paired beetles per 100 beetles) in which we assumed that the sex ratio was 0.5, with corresponding frequency and observed sex ratio of the solitary beetles.

Relationships among date, sex ratio, and pairing frequency were determined using ANOVA, as were differences between paired and unpaired individuals. We investigated assortative mating by using ANCOVA, with date and time period as factors, female size as the dependent variable and male size as a covariate (SAS Institute, 1995). We used multiple regression analyses to investigate both the factors potentially affecting pairing frequency and the effects of date and temperature. Sex ratio was arcsine transformed to meet the assumptions of the parametric tests (Zar, 1999). The significance of simple correlation coefficients was calculated using Fisher's r to z test. We report untransformed means \pm SE.

RESULTS

Pairing Frequency and Sex Ratio

The percentage of paired beetles varied from 20 to 62 (mean = 43.2 ± 1.2 per 100 individuals; $N = 65$). The number of pairs varied both among days and among time periods [date, $F_{12,65} = 3.18$, $P < 0.002$; time period (Fig. 1), $F_{4,65} = 9.53$, $P < 0.0001$], with pairing being most frequent in the morning and evening and least frequent in the late afternoon. Therefore, at a maximum, slightly more than half of the available beetles were paired.

The sex ratio on the food plants varied from 0.42 to 0.72 (mean = 0.61 ± 0.01 ; $N = 65$) and overall was significantly greater than 0.5 (one-sample t test; $t = 15.82$, $P < 0.0001$), with 62 of the 65 individual sampling periods having a sex ratio higher than 0.5. Given that the overall sex ratio was male biased, it is not surprising that the sex ratio among the single beetles was also male biased (0.70 ± 0.01 ; $N = 65$) and exceeded that of the overall ratio (on 62 of 65 sampling periods). Interestingly, though, the sex ratio of the unpaired beetles was not correlated significantly with the number of pairs ($r = 0.16$, $P = 0.20$), indicating that the sex composition of the individuals on

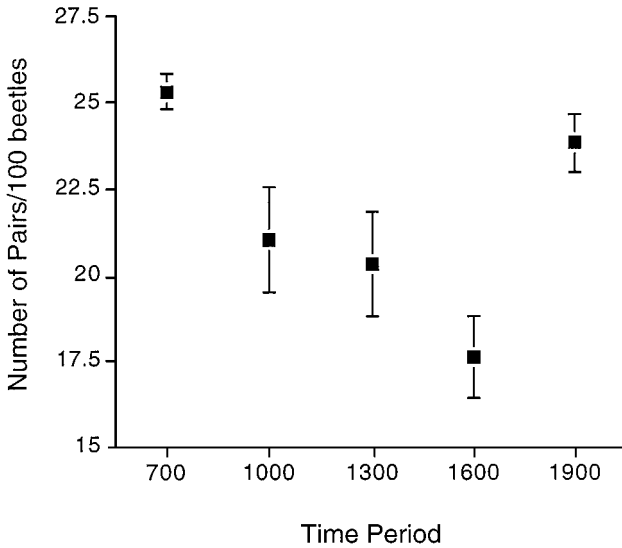


Fig. 1. Average number of pairs (\pm SE) of Japanese beetles observed at different times of day ($N = 13$ for each time period) from July and August 1999.

the food plants did vary. In fact, the sex ratio varied among days ($F_{12,65} = 2.81$, $P = 0.005$) but not among time periods ($F_{4,65} = 0.77$, $P = 0.55$). However, multiple regression analyses revealed that neither sex ratio nor density were significantly correlated with the number of pairs (β sex ratio = -14.0 , $t = 1.39$, $P = 0.20$; β density = 0.018 , $t = 0.53$, $P = 0.60$; $N = 65$). Thus, a difference among days and times caused differences in pairing, but this difference was not due to the sex ratio, even though the sex ratio also differed among days.

Size of Paired and Solitary Individuals

Females were significantly larger than males (females, 6.26 ± 0.006 mm, $N = 2572$; males, 5.82 ± 0.005 mm, $N = 3904$; $t = 55.1$, $df = 6474$, $P < 0.0001$). For females, size varied significantly among days and paired females were significantly larger than unpaired females (Table I). The disparity between paired and unpaired females was greatest at 0700 and 1900 (Fig. 2). Male size also varied significantly among days, but there were no other overall differences. However, a significant interaction exists between paired status and time period, indicating that the size of paired versus unpaired males was not consistent across the day. Inspection of Fig. 2 indicates that paired males

Table I. Results of Three-Factor ANOVA for Size of Male ($N = 3904$) and Female ($N = 2572$) Japanese Beetles Collected in July and August 1999^a

Sex	Source	df	SS	<i>F</i>	<i>P</i>
Female	Date	12	6.48	4.8	<0.0001
	Time period	4	0.79	1.77	0.13
	Paired status	1	1.20	10.7	0.001
	Date × Time period	48	6.15	1.14	0.24
	Date × Status	12	1.84	1.36	0.17
	Time period × Status	4	0.75	1.67	0.15
	Date × Time period × Status	48	5.35	0.99	0.49
Male	Date	12	4.16	4.14	<0.0001
	Time period	4	0.26	0.78	0.54
	Paired status	1	0.0001	0.0014	0.97
	Date × Time period	48	3.70	0.921	0.63
	Date × Status	12	1.16	1.16	0.31
	Time period × Status	4	1.18	3.52	0.007
	Date × Time period × Status	48	3.61	0.90	0.67

^aPaired status refers to whether the individual was single or sexually paired with another beetle.

were larger at 0700, but smaller at 1000, with minimal size difference at other times.

If competition were more intense for females (e.g., at more male-biased sex ratios), we might expect that the difference between paired and unpaired males would be greater as a result. Likewise, given that paired females were larger than unpaired females, the sex ratio might also relate to the magnitude of this difference in females. However, no significant pattern existed between the sex ratio and the difference in size between paired and unpaired males ($r = -0.12$, $P = 0.97$; $N = 65$) or females ($r = -0.004$, $P = 0.97$; $N = 65$).

Assortative Pairing

Because the date and time period may have affected the size of the beetles overall or the size assortative pairing, we conducted an analysis of covariance looking at the relationship between the size of the paired male and female with date and time period as factors (Table II). As in earlier analyses, date emerged as a significant effect in the model, but neither male size nor time was significantly related to female size. Thus, the Japanese beetles in our study were not size assortatively paired.

Possible Causes of the “Date” Effect

Date consistently emerged as a factor related to individual size, sex ratio, and number of pairs (see above). This pattern could have been a result

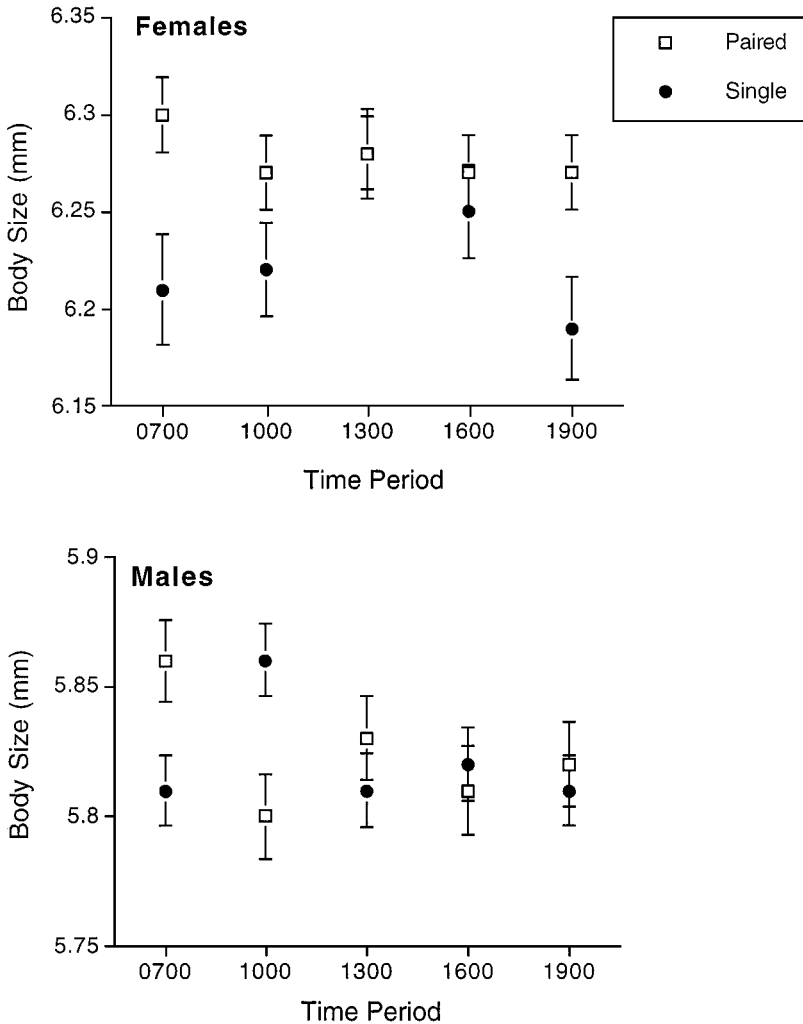


Fig. 2. Body size (maximum body width \pm SE) of paired and single female and male Japanese beetles across different time periods in July and August 1999. Sample sizes are approximately 325 for each time period for pairs and 200 for single females and 450 for single males at each time period.

of environmental or seasonal effects. To investigate the possible causes of these patterns, we related the average male and female size, sex ratio, and number of pairs to both the average temperature that day and the Julian date (Table III). Julian date, and hence seasonal effects, seemed to explain much of the variation among days for male and female size and part of the

Table II. Results of ANCOVA Investigating Size Assortative Pairing in Japanese Beetles Collected in July and August 1999, with Female Size as the Dependent Variable ($N = 1560$ Total Pairs)^a

Source	df	SS	F	P
Male size	1	0.0532	0.488	0.49
Time	4	0.195	0.447	0.77
Date	12	4.11	3.14	0.0002

^aNone of the interactions were significant (i.e., testing for separate slopes), so we report here the final model with only main effects included.

variation in pairing frequency; males and females were smaller and pairs were less frequent as the season progressed. Pairing frequency was also negatively related to the average temperature during a day. The variation in sex ratio among days, however, was not explained by either Julian date or temperature.

DISCUSSION

Pairing Frequency

The Japanese beetles in this study paired, and thus most likely mated, more frequently in the morning and the evening. This pattern could reflect changes in the availability of females at these times. However, in contrast to earlier reports (Smith and Hadley, 1926), the sex ratio of Japanese beetles on

Table III. Results of Multiple Regression Analyses for Japanese Beetles Collected in July and August 1999, with Averages of Either Number of Pairs, Male Size, Female Size, or Sex Ratio as Dependent Variables and Julian Date and Average Temperature that Day as Independent Variables^a

Dependent variable	R^2	Intercept/independent variable	Coefficient	t	P
No. of pairs	0.69	Intercept	48.9	4.7	0.001
		Average temperature	-0.27	2.3	0.047
		Julian date	-0.63	5.1	0.0005
Male size	0.71	Intercept	5.90	45	<0.0001
		Average temperature	-0.0003	0.21	0.83
		Julian date	-0.006	3.8	0.004
Female size	0.60	Intercept	6.51	26	<0.0001
		Average temperature	-0.002	0.72	0.49
		Julian date	-0.01	3.3	0.008
Sex ratio	0.08	Intercept	.77	3.0	0.014
		Average temperature	0.001	0.48	0.64
		Julian date	-0.001	0.25	0.80

^aThe whole model R^2 is given for each ($N = 13$ for each test).

food plants did not change consistently over the course of the day, and unpaired females existed in all samples. These results suggest that females were as available in the afternoon as they were in the morning and the evening.

Alternatively, the difference in pairing frequency may have been because males and/or females may not have been receptive to mating or mate guarding at these times. This lack of receptivity or mate guarding may relate to the cost of guarding or being guarded. Such costs may include decreased mating opportunities (e.g., Travers and Sih, 1991; Dickinson, 1996), increased predation risk (e.g., Travers and Sih, 1991), or increased physiological stress. In Japanese beetles, copulation lasts for only a few minutes (Barrows and Gordh, 1978) but males may remain mounted on females for hours (Barrows and Gordh, 1978; Switzer *et al.*, unpublished data), possibly with the function of counteracting the last male sperm precedence in this species (Ladd, 1966, 1970b). When guarding a female, males do not eat and are generally exposed to the sun (Moore and Cole, 1921; Smith and Hadley, 1926; Hawley and Metzger, 1940; Potter *et al.*, 1996; Rowe and Potter, 1996). Exposure to sun may cause dehydration, and Japanese beetles are sensitive to water loss (Ludwig, 1936; Ludwig and Landsman, 1937). Japanese beetles can use water from food for evaporative cooling (Oertli and Oertli, 1990). But because guarding males do not feed, mate guarding will likely be more costly physiologically for males in the afternoons (Oertli and Oertli, 1990), which tend to be hotter and drier than the morning and evening. In support of the “cost of mate guarding” hypothesis for temporal patterns in pairing, we found that pairs were less frequent during relatively hot days.

Size Relationships

The sex ratio was biased toward males on the food plants; our ratios were similar to those found in other studies (e.g., Iwabuchi and Takahashi, 1983). As would be predicted from the male-biased sex ratio (Harari *et al.*, 1999), we found that pairs were not assorted by size; rather, we found evidence of a large male and female advantage in mating. For males, though, this size bias only existed in the morning. These results suggest that either size confers a competitive advantage (Thornhill, 1980; Partridge and Farquhar, 1983; Ward, 1983; Juliano, 1985), that males and/or females prefer larger members of the opposite sex (Thornhill and Alcock, 1983; Polak and Brown, 1995), or both. Unfortunately, behavioral data allowing us to determine the causal factor(s) are lacking. Male beetles do attempt to take over, and occasionally succeed in taking over, guarded females (Switzer *et al.*, unpublished data). However, whether size influences the outcome of these takeover attempts, or whether any size preference for the opposite sex occurs, is unknown. We can also speculate only when explaining the interesting temporal pattern

in male size. For example, all males may prefer to mate in the morning for the physiological reasons explained above; however, because of competition, only the large males actually pair. Following copulation and feeding, the large males' females leave the food plants. The large males then feed to restore energy and to rehydrate, leaving the females that remain, or perhaps newly arriving females, available for the less competitive, smaller males to pair with later in the morning. Other explanations certainly exist, and clearly, data on female behavior and mate guarding duration at different times during the day are needed before any conclusion can be made.

One consistent result was that samples differed among days as to the size of the beetles and the sex ratio on the food plants. For sex ratio, the cause of the variation remains obscure: neither temperature nor a seasonal trend explained any significant variation in sex ratio among days. Potentially, some other climatic factor (e.g., wind, relative humidity, or amount of direct sun) or habitat variable (e.g., quality of food plant in a particular location) may have affected males differently than females and, hence, altered the sex ratio. In contrast to variation in sex ratio, however, we found that much of the variation in the size of the beetles among days could be explained by a seasonal effect: days later in the summer had smaller beetles on average than those earlier in the summer. This result is consistent with previous studies on beetles trapped as emerging adults (Van Timmeren *et al.*, in press) or captured as older adults in pheromone traps (Vittum, 1986). In combination with the size-related pairing patterns we found, the seasonal effect suggests that over the course of their lives Japanese beetles, which may live for well over a month in the field (Smith and Hadley, 1926), may experience changes in the competitive environment they face for mating or in the opportunities for size-based mate choice. The potential consequences of these changes remain to be explored.

Finally, we must mention two caveats to our conclusions. First, our study investigated pairing patterns, not copulation patterns. While the relationships we observed may hold for copulation patterns, they also may not (e.g., Ward, 1983; Otronen, 1993; Enders, 1995). For example, Otronen (1993) found that males and females of the dung fly *Scatophaga stercoraria* that were copulating were size assortatively paired, but those initiating copulation were not. This situation may occur when females are capable of resisting copulatory attempts by the male (e.g., Harari *et al.*, 1999). In Japanese beetles, females may be able to resist the male, even if the male is mounted in copulatory position on her back. We have observed males attempting to copulate for many minutes without success (Switzer *et al.*, unpublished data), which suggests that females may be able to resist indefinitely. Future studies, investigating the relationship among female "acceptance," copulation, and mate guarding should help us resolve this issue. Second, our measure of beetle density was

at a fairly broad scale among plants; however, Japanese beetles may be very patchy even within an individual plant, with (for example) a dozen beetles on a single leaf and few beetles elsewhere on the plant (Fleming, 1972; Switzer *et al.*, personal observations). Examining density effects at a finer scale (e.g., within individual leaves) may yield different patterns of mating behavior.

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