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Size and Mating Success in Males of the Western Harvester Ant, *Pogonomyrmex occidentalis* (Hymenoptera: Formicidae)

Diane C. Wiernasz,[1,2] Julie Yencharis,[1] and Blaine J. Cole[1]

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Mating success in males of the lek mating ant species, Pogonomyrmex occidentalis, *increases with increased body size. We estimated the magnitude of the selection coefficients on components of size by collecting males in copula and comparing their morphology to that of males that were collected at the lek but that were not mating. Four characters, body mass, head width, wing length, and leg length, were measured for a sample of 225 mating and 324 nonmating males and 225 females. Significant direct selection favors increased wing length and leg length. Multiple regression of transformed variables (principal components) indicated that the increased mating success of larger males is a function of all four characters. We found no evidence of positive assortative mating on the basis of any individual character or on the multivariate general size variable (the first principal component).*

KEY WORDS: mating success; male size; sexual selection.

INTRODUCTION

Information on mating in ants is relatively sparse. Various researchers have collected data on the frequency of mating by queens (reviews by Cole, 1983; Page, 1986), the ethology of mate attraction (Hölldobler, 1976; Hölldobler and Bartz, 1985), and the timing of mating flights (reviewed by Hölldobler and Wilson, 1991, pp. 150–152). Most work has focused on the allocation of reproductive investment to males and females (see reviews by Nonacs, 1986; Bourke,

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[1] Program in Ecology and Evolutionary Biology, Department of Biology, University of Houston, Houston, Texas 77204-5513.

[2] To whom correspondence should be addressed.

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1988). A critical assumption of empirical and theoretical studies of reproductive output and sexual investment is that variation in the size of the reproductives does not affect their fitness. If males vary in their probability of mating or if females vary in their probability of founding a colony as a function of body size, then the optimal investment ratios will need to be modified by the fitness consequences. Unfortunately, little is known about the effect that size has on any aspect of fitness among ants.

Davidson's (1982) study of *Pogonomyrmex barbatus* and *P. desertorum* provides one of the few data sets on the relative mating abilities of ants. Contrary to the assumption made by studies of reproductive investment, these data show that large males have higher probabilities of mating than do small males. The relevance of her observation has been neglected. If larger males have higher fitness, then colonies may gain disproportionately by investing in a smaller number of larger males. If Davidson's result is a general one, then the predicted outcome of investment strategies needs to be modified by this information. It also suggests that studies of sexual investment will be more valuable if they include information on relative mating abilities or colony establishment.

Our purpose is to examine the relative mating abilities of males in the western harvester ant, *P. occidentalis* (Cresson), as part of an integrated study of reproductive biology of this species. Like the species of *Pogonomyrmex* studied by Davidson (1982) and Hölldobler (1976), this is a lek-mating species. The potential for competition between mating males at the lek is great and intrasexual selection is expected to be intense. We show that females mate with males in a highly nonrandom way, resulting in strong selection on aspects of male morphology.

MATERIALS AND METHODS

Pogonomyrmex occidentalis is one of the most conspicuous ants of western North America. Our study was performed on Bureau of Land Management land approximately 15 km northwest of Fruita (Mesa Co.), Colorado (39°16′N, 108°45′W), at a 1470-m elevation. The land is a mixture of adobe hills, dry washes, and flat areas dominated by saltbush (primarily *Atriplex corrugata* and *A. confertifolia*) and greasewood (*Sarcobatus vermiculatus*), all Chenopodiaceae, and several introduced crucifers (Brassicaceae).

The study site covers approximately 25 ha and consists of a population of over 1300 colonies which are permanently marked with numbered aluminum tags. *P. occidentalis* is overwhelmingly the dominant ant species at the site; two species of *Myrmecocystus* (*M. mexicanus* and *M. mendax*) occur infrequently throughout the area. The dynamics of movement of workers and brood into the nest mound throughout the day (Cole, 1995), patterns of spatial dispersion, recruitment, and mortality (Wiernasz and Cole, 1995a), and population genetic structure (Wiernasz and Cole, 1995b) have been studied at this location.

In typical years, mating flights occur once, on the first sunny day following substantial rainfall from mid-July onward. In 1994 mating flights occurred twice. A partial flight (on 20 July) was triggered by rainfall of less than one millimeter. A second, larger flight (on 9 August) followed a rainfall of 6.5 mm. Mating flights begin at approximately 1300 h and continue throughout the afternoon until near-darkness (2000 h). Mating aggregations (leks) occur on the tops of adobe hills. Several leks (two to five) occurred in our study area during each mating flight. We analyzed individuals from the first flight that were collected from two lek sites on adjacent hills. Individuals from the second flight were collected from a single lek.

We collected pairs in copula from the mating swarm from 1400 to 1800 h, placed them in plastic vials where they completed copulation, and then froze them. Throughout the mating flight, we also collected males from the swarm that were not mating. During the first flight we collected a total of 75 pairs in copula and during the second mating flight we collected 150 pairs. We measured 160 nonmating males from the first mating flight and 164 nonmating individuals from the second flight. The data from the two mating flights were initially analyzed separately.

Four measurements were made on each male and female collected. The dry body weight was measured to the nearest 0.1 mg on specimens dried for 4 days at 60°C. Preliminary tests showed that dry weight did not change after 3 days at this temperature. We measured three length parameters: head width across the eyes, forewing length, and length of the second femur. Length characters were measured with an ocular micrometer that allowed measurements to the nearest 0.01 mm (50 micrometer units = 1 mm). Head width across the eyes was the width through the eyes at the widest part of the head. Forewing length was the distance from the point of insertion on the thorax to the apex of the forewing. Femur length was the distance from the trochanter to the tibia along the inner margin of the leg.

Differences in multivariate characters between mating and randomly chosen males may result from direct selection on the trait or from a correlated response due to selection on other traits. We first analyzed characters singly, using one-way analysis of variance, to test whether mating males differed from a random sample of males. We then analyzed the data using the multiple regression method of Lande and Arnold (1983) to estimate the strength of sexual selection acting directly on each character. For the combined data set, each character was standardized to a mean value of zero with a standard deviation of one. We extracted principal components from the standardized morphological measurements to obtain independent morphological variables. Male fitness was assigned as a step function: Males that were mating had a relative fitness of one and males that were sampled randomly from the lek site had a relative fitness of zero. Since it is possible that some of the randomly collected males either had mated previously or would have mated, any difference between the groups conservatively estimates the difference between males that mate and those that do not. We used multiple regression of fitness on the principal components to determine the strength of direct selection on each of the principal components.

We tested for positive assortative mating between males and females using Pearson product-moment correlation analysis. Mating pairs were compared on the basis of each of the four morphological variables as well as the principal component that represents overall size.

RESULTS

Considerable variation in alate size, as measured by all four characters, was present in both flights (Table I). Because the mean as well as the range for each character was similar in both flights ($P > 0.15$ in all cases), we combined data from the two flights. The univariate regressions indicate that mating success is significantly affected by male size (Table II). Males collected in copula had significantly longer femurs ($P < 0.001$), longer wings ($P < 0.001$), and wider heads ($P = 0.02$) than did randomly collected males, but did not differ in dry weight ($P > 0.3$). The multiple regression indicates that significant sexual selection is acting directly on several characters; all of the partial selection coefficients are significant with the exception of head width (Table II). Both femur length and, more strongly, wing length are under strong positive selection. Because the univariate and multiple regressions yield very similar coefficients for wing length and femur length, we can conclude that virtually all selection

Table I. Summary Statistics for the Male Morphological Measurements (None of the Means Differed Between Flights)

	Mated males	Random males	Females
Flight 1			
Weight (mg)	4.4 ± 0.6 (2.5–5.9)	4.4 ± 0.8 (1.9–6.4)	12.5 ± 1.5 (7.2–15.4)
Head width (mm)	1.90 ± 0.08 (1.60–2.08)	1.87 ± 0.10 (1.42–2.14)	2.26 ± 0.09 (1.90–2.42)
Leg length (mm)	1.88 ± 0.09 (1.66–2.00)	1.85 ± 0.10 (1.54–2.22)	1.86 ± 0.10 (1.54–2.22)
Wing length (mm)	7.08 ± 0.32 (6.22–7.70)	6.94 ± 0.42 (5.78–7.70)	8.02 ± 0.24 (7.33–8.52)
N	75	160	75
Flight 2			
Weight (mg)	4.3 ± 0.8 (1.8–5.9)	4.3 ± 0.9 (1.6–6.3)	12.2 ± 1.7 (6.7–15.3)
Head width (mm)	1.89 ± 0.10 (1.46–2.04)	1.88 ± 0.10 (1.52–2.08)	2.25 ± 0.11 (1.90–2.44)
Leg length (mm)	1.86 ± 0.09 (1.50–2.20)	1.83 ± 0.10 (1.54–2.18)	1.85 ± 0.10 (1.50–2.20)
Wing length (mm)	7.01 ± 0.38 (5.63–7.67)	6.87 ± 0.45 (5.33–7.89)	8.01 ± 0.39 (6.96–8.67)
N	150	164	150

Table II. Univariate and Multivariate (Lande–Arnold) Regression of Mating Success on Morphological Characters[a]

	Univariate regression		Multivariate regression	
	s	*t*	*β*	*t*
Body weight	0.012	0.29	−0.357	−4.77***
Head width	0.095	2.22*	0.121	1.45
Leg length	0.139	3.27**	0.148	2.33*
Wing length	0.151	3.48***	0.325	3.15**

[a] The univariate coefficient (*s*) gives the total strength of selection on each character, while the partial coefficient (*β*) gives the direct selection component. The overall multiple regression is highly significant ($F = 8.43$, df = 4,513, $P = 0.0001$).

*$P < 0.05$.

**$P < 0.01$.

***$P < 0.001$.

on these characters is direct. In contrast to the univariate results, body weight appears under strong negative selection; males with greater body weight have a lower probability of mating when the other aspects of male morphology are held constant.

Because the morphological characters are correlated with each other, it is more meaningful to perform the same regression analysis on the principal components extracted from the data. The loadings of the characters on the principal components were similar in males and females and are shown in Table III. The first component is a generalized size score; all traits show large positive correlations. It accounts for the bulk of morphological variance in both sexes (80% in males, 77% in females). The second component contrasts femur length with the other measures of body size; individuals with large PC2 scores have proportionately longer legs for their size. It accounts for about 9% of the variance in males and 11% in females. The third component contrasts wing length with

Table III. Principal Component Analysis of Morphological Measurements[a]

	PC 1		PC 2		PC 3		PC 4	
	Males	Females	Males	Females	Males	Females	Males	Females
Body weight	0.918	0.930	−0.233	−0.091	−0.129	−0.170	−0.295	−0.313
Head width	0.920	0.909	−0.123	−0.109	−0.259	−0.321	0.265	0.244
Femur length	0.842	0.811	0.537	0.568	−0.011	0.136	0.074	0.027
Wing length	0.900	0.858	−0.139	−0.323	0.407	0.395	−0.048	0.054
Percentage of variance	80.2	77.1	9.4	11.2	6.2	7.7	4.1	4.0

[a] The principal components were extracted from the correlation matrix of the characters.

head width and dry weight. Individuals with high PC3 scores have disproportionately longer wings. It accounts for approximately 6% of the variance in males and 8% in females. The fourth component contrasts head width and dry weight; males with larger PC4 scores have disproportionately large heads for their mass. The last component accounts for 4% of the variance in both sexes.

All of the principal components are significantly associated with mating success. Overall size (PC1: $\beta = 0.12$, $t = 2.83$, $P = 0.005$), relative length of the second femur (PC2: $\beta = 0.12$, $t = 2.68$, $P = 0.008$), and relative wing length (PC3: $\beta = 0.11$, $t = 2.55$, $P = 0.011$), and relative head width (PC4: $\beta = 0.15$, $t = 3.46$, $P = 0.001$) are all positively associated with mating success. However, because PC1 accounts for the majority of the phenotypic variance in males, and because relatively few morphometric characters were used, it is difficult to interpret the importance of significant selection on these components. The results of the principal-components regression are similar to those obtained when using the original characters. Femur length, wing length, and head width have significant and positive direct selection components, while mass (dry weight) shows a correlated response to selection on size of other characters.

We found no evidence of positive assortative mating on the basis of any individual morphological character. Forewing length exhibited the largest correlation between mating pairs, but was not significant ($r = 0.15$, $P = 0.096$). Mass [dry weight ($r = 0.06$, $P > 0.5$), head width ($r = 0.07$, $P > 0.4$), and leg length ($r = -0.01$, $P > 0.9$] exhibited very low correlations between males and females, as did the multivariate measure of overall size (principal component 1: $r = 0.08$, $P > 0.4$).

DISCUSSION

Competition among males at the lek results in intense sexual selection on male size in *P. occidentalis:* Large males have much greater mating success than smaller males. It is somewhat puzzling that there was no significant direct or correlated positive selection on dry weight (Table II). There are two possible explanations. The first is that we did not measure mass with sufficient precision; real differences exist but we did not detect them. The second possibility is that dry weight is not a good predictor of real differences in male mass, if cuticular weights are similar but wet weights are not. All mating males in this study were allowed to finish copulation before being frozen, therefore depleting their sperm and accessory gland secretions. Consequently the dry weight of these males may be considerably less than if they had been collected prior to mating.

It may be useful to employ multivariate measures when measuring the effect of selection on body size during male–male competition during mating in social insects. The picture of selection that is obtained from looking at univariate measures of selection on morphology can be misleading compared to that obtained from multivariate measures if the chosen characters are correlated. The large positive selection coefficient for PC1 (generalized size) indicates that large males will be favored. Size is probably better estimated by the first principal component in this study than it is by dry weight. While overall size is important to male mating success, the shape of successful males is also important. The significant regression with PC2 tells us that males with long femurs relative to their overall size appear to have a mating advantage. Longer legs may be one way to make a male larger without significantly increasing wing loading. Relatively long legs may also be advantageous in male–male competition for access to queens. The magnitude of the selection coefficients is 0.12 for PC1 and 0.11 for PC2. These values are similar to other estimates of selection coefficients for mating (Endler, 1986).

The strength of sexual selection can be computed from the data presented by Davidson (1982) for *P. desertorum* and *P. barbatus*. Davidson measured dry body weight and showed that larger males have a higher probability of mating than smaller males. The selective coefficients estimated from the data presented by Davidson are 0.25 for *P. desertorum* ($P < 0.001$) and 0.08 for *P. barbatus* ($P > 0.2$), (estimates obtained by applying multivariate regression to the data from her Figs. 1 and 2). While the effect of body mass is highly significant in *P. desertorum*, it is not significant in *P. barbatus*. Large body size in this species may not appear selectively favored for the same reasons it does not in *P. occidentalis*; it would be interesting to see if multivariate measures of size indicated a significant selective coefficient in *P. barbatus*. Since in both species there is also significant positive assortative mating for body size, it is clear that the relationships between body size and mating are complex in these species.

With one exception (Heinze and Hölldobler, 1993), male ants are not known to be capable of replenishing sperm after mating (Page, 1986; Tschinkel, 1987). The frequency of mating by males of *P. occidentalis* is unknown but presumed to be once. Given the overwhelming numerical bias toward males at the leks, the probability that any given male will mate is low even though the queens are known to mate more than once (C. Heymann, B. Cole, and D. Wiernasz, unpublished electrophoretic data). The low probability that a male has of mating with any female and the intense competition among males means that a male should not discriminate among potential mates. This expectation could change if there is also intense selection for large females who may be better at founding colonies successfully. Although we found no evidence of size-based assortative mating, Davidson (1982) found positive assortative mating in *P. desertorum*, suggesting that large males may preferentially mate with large females. If we assume that a male mates once, then a male should not mate with a given female if the product of the probability of finding another female times the ratio of the fitness of the second female to the first female is larger than one. If, as seems likely, there is less than a 10% chance that a male will mate, then it will rarely be to a male's advantage to pass up mating, even if it is to a female with low relative fitness.

Male size clearly influences mating success in three species of *Pogonomyrmex*; no studies have examined the consequences of male size on male mating success in other species. Male size may be important for male fitness, particularly in swarm mating species, where male competition is characteristically great. For the species studied by Davidson (1982) the standard deviation in weight among males of *P. desertorum* is 11% of the mean, while in *P. barbatus* the standard deviation is 7.5% of the mean. In *P. occidentalis* we found that variation in weight was about 18% of the mean. While there is substantial variability in the size of reproductives in *Pogonomyrmex*, there is little comparative data on variation in size among reproductives in ants in general and still less on the significance of this variation (although see Fortelius *et al.*, 1987).

If larger males have higher mating success, it is interesting to consider why so much variation in male size exists in this population. One possibility is that while large males are favored at the lek, smaller males are favored in some other context. In *Formica exsecta*, two distinct size classes of males represent alternative male reproductive patterns at the colony level (Fortelius *et al.*, 1987): Monodomous nests produce queens and large males (macraners) that inbreed locally, while polydomous nests produce exclusively males that are significantly smaller (micraners) and more highly dispersive. Male wing dimorphism occurs in the genus *Cardiocondyla* (Heinze and Holldober, 1993): Winged males disperse and reproduce during mating flights, while wingless males mate within the nest. Because in *P. occidentalis* males must fly to the mating swarm, the upper boundary on male size may be constrained by a physiological factor such as wing loading. Smaller males may fly faster or disperse farther and may represent a bet-hedging strategy by colonies between local and distant reproduction. Small males might also inbreed with sisters within the nest before the mating flight occurs. Evaluating these adaptive explanations will require quantifying male movement and size variation within and between colonies.

Other nonadaptive explanations for this size variation exist. Body size may not be heritable. Colonies may commit to an initial number of reproductives relatively early in the yearly cycle but adjust the investment in this number based on food availability in the current season. A time delay in the production of reproductives may result in reduced size. The development time hypothesis predicts lower variance in male size in poor years and is testable with longitudinal data.

Our study emphasizes the importance of looking beyond simple definitions of reproductive investment either as sex ratio or as male versus female biomass.

This consideration will not affect studies of sexual investment based on differences in the pattern of investment between, for example, monogynous and polygynous colonies. We suggest, however, that it will be informative to include male mating success when fitness components are measured.

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