SEXUAL SELECTION ON BODY SIZE AND SHAPE IN THE WESTERN HARVESTER ANT, *POGONOMYRMEX OCCIDENTALIS* CRESSON

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Abstract.—Mating in social insects has generally been studied in relation to reproductive allocation and relatedness. Despite the tremendous morphological diversity in social insects, little is known about how individual morphology affects mating success. We examined the correlation of male size and shape with mating success in the western harvester ant, *Pogonomyrmex occidentalis*. Larger males had significantly higher mating success in two independent collections of males at mating aggregations. We also detected significant linear and nonlinear selection on aspects of male shape that were consistent across years. These shape components are independent of size, suggesting that male mating success is a complex function of size and shape. Successful males had elongate thoraxes and short mandibles relative to males collected at random at the lek. Overall, mated males also had longer postpetioles relative to body size, but there was also evidence of nonlinear selection on relative postpetiole length in both years. We found no evidence of assortative mating based on size or multivariate shape measures in either year, but in one year we found weak assortative mating based on some univariate traits.

Key words.—Ants, assortative mating, body size and shape, *Pogonomyrmex*, sexual selection.

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The potential role of sexual selection in shaping morphological variation in social insects has been largely ignored. Instead, studies have focused on the determinants of allocation to males and queens (reviewed in Bourke and Franks 1995; Crozier and Pamilo 1996; Pamilo et al. 1997). A critical assumption of theoretical and empirical research on reproductive output and sexual investment is that the individual fitness of reproductives does not vary. If, for example, males differ in mating success, then the optimal investment ratios will need to be modified by the fitness consequences (Wiernasz et al. 1995). Reproduction in many species of social insects, especially ants, is characterized by swarm mating, often with highly skewed operational sex ratios (Wilson 1971; Hölldobler and Bartz 1985). The opportunity for sexual selection should be great in such mating systems by either female choice or male scrambles over females (Thornhill and Alcock 1983; Andersson 1994).

Sexual selection favoring large males has been reported in many insects (e.g., Elmes 1991; Carroll and Salamon 1995; Cordero 1995; Alcock 1996; Alcock and Houston 1996; Arnqvist et al. 1997; also see reviews in Thornhill and Alcock 1983; Choe and Crespi 1997), as well as in many other taxa (reviews in Clutton-Brock 1988; Andersson 1994). Although selection favoring large males appears widespread in insects, including swarm maters (e.g., Thornhill 1980); some studies have shown no difference in mating success related to male size (Alcock and Pyle 1979; Litte 1979; O'Neill 1994; Aspi and Hoikkala 1995), whereas others have found a small male advantage (McLachlan 1986; Day et al. 1987; McLachlan and Allen 1987; Steele and Partridge 1988; Neems et al. 1990; Aspi and Hoikkala 1995). For swarm-mating species, the higher mating success of small males has been attributed to better maneuverability in the swarm (MacLachlan 1986; Neems et al. 1990).

Most studies of sexual selection on body size have used a single measurement. As a consequence, conclusions about selection favoring larger size may be unwarranted if the actual target of selection is the size of a particular feature. For example, in the cerambycid beetle, *Phoracantha semipunctata,* the mating advantage of large males appears to result from more efficient mate locating ability due to longer antennae (Hanks et al. 1996). In a study of correlates of male mating success in *Drosophila buzzatii*, the actual target of sexual selection was face width rather than body size (Norry et al. 1995). The mating advantage of large males in the water strider *Aquarius remigus* is a consequence of direct selection on genital length (Preziosi and Fairbairn 1996) and forefemoral width (Weigensberg and Fairbairn 1996). A handful of studies in other taxa (e.g., frogs: Howard and Kluge 1985; lizards: Hews 1990) yielded similar results. Because most studies of sexual selection have focused on overall size or on ornaments, the effects of differences in shape independent of body size have been given less attention.

Even when large males enjoy a mating advantage, there may be selective, physiological, and phylogenetic constraints on male size. Particularly in insects there may be strong trade-offs between larval development time and final size (e.g., Roff 1981; Stearns and Koella 1986). Many species of insects have the capacity to pass through successive larval and pupal molts at a range of sizes that depend on environmental conditions such as temperature and food availability (Chapman 1982). Additionally, for females or colonies allocating resources to reproduction, large male size may come at the expense of large numbers of male offspring (Smith and Fretwell 1974). When selection on body size is constrained and variation in shape is present, shape may become the target of selection.

Studies of male variation and mating patterns in ants have focused on species with polymorphic males (*Hypoponera eduardi*: Le Masne 1956; *Technomyrmex*: Terron 1972, Yamauchi et al. 1991; *Cardiocondyla*: Kugler 1983; *Solenopsis*

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invicta: Ross and Fletcher 1985; *Formica exsecta*: Agosti and Hauschteck-Jungen 1987; *Hypoponera bondroiti*: Yamauchi et al. 1996). In such species, the morphs frequently have different reproductive roles (e.g., inbreeding versus outcrossing: Fortelius et al. 1987; Kinomura and Yamauchi 1987; Heinze and Hölldobler 1993). Little is known about species with continuous rather than discrete variation in males. An exception is the work on three species of harvester ants (*Pogonomyrmex*: Davidson 1982; Wiernasz et al. 1995), that demonstrated that larger males had greater mating success. If continuous size variation in males is common and typically affects male fitness, it will have important implications for the evolution of reproductive allocation in social insects. The common metric of reproductive allocation, relative investment in males and queens, is not valid when individual variation in size is associated with variation in fitness.

In this paper, we examine sexual selection on body size and shape in the western harvester ant, *Pogonomyrmex occidentalis*. We also tested for evidence of assortative mating based on size and shape. Harvester ants mate in large aggregations (Hölldobler 1976). The numerical sex ratio at the lek is highly male biased (Nagel and Rettenmeyer 1973; Cole and Wiernasz, unpubl. data), suggesting a high opportunity for sexual selection on male traits. In the western part of its range, *P. occidentalis* leks form at the tops of locally high hills. Males begin arriving at the lek slightly before females and attempt to copulate with females arriving at the hilltop. Mating pairs land on vegetation and are quickly surrounded by other males that attempt to copulate. These "mating balls" represent scrambles of four to 18 males over a single female. The frequency with which the copulating male is displaced is unknown. Although sexual selection for larger males has been documented previously in this genus, past studies have been based on dry mass (*P. desertorum* and *P. rugosus*; Davidson 1982) or relatively few morphometric characters (*P. occidentalis*; Wiernasz et al. 1995), which limits the ability to examine selection on shape.

To estimate the strength of sexual selection on male traits in *P. occidentalis,* we assessed mating success of males at the lek and measured 17 morphological traits throughout the body, in two different leks in different years. In agreement with earlier studies of *Pogonomyrmex,* our results suggest a mating advantage for larger males. We also find evidence for directional and nonlinear sexual selection on certain aspects of male shape that are consistent across years.

MATERIALS AND METHODS

Pogonomyrmex occidentalis was studied in Mesa County, Colorado, at the same site used for long-term studies of this species (for site description see Cole 1994; Wiernasz and Cole 1995; Wiernasz et al. 1995). In this area, mating flights occur once or twice a year, on the first sunny day after considerable rainfall from mid-July onward. Mating flights start at about 1500 hr and continue until dusk (about 2000 hr). In 1994, a single mating flight occurred on 14 August; in 1996 a partial mating flight occurred on 26 June, and a second, larger mating flight took place on 17 July. In 1994 we collected 200 mating pairs and 239 random males from about 1500 hr to 1630 hr, and on 17 July 1996 we collected 550

mating pairs and 599 random males from about 1445 hr to 1540 hr. Mating pairs were collected by removing all noncopulating males from the mating ball (see Wiernasz et al. 1995). After we collected 50 mated pairs, we collected a similar number of "random" males by scooping them off of the vegetation. Although it would have been preferable to compare successful and unsuccessful males directly, this was not possible. Attempts to collect intact mating balls resulted in separation of the mating pair when the entire ball was placed in a vial, and one could not distinguish which male had been copulating. Attempts to remove nonmating males from the ball individually always resulted in the loss of some nonmating males. Finally, because males can mate multiply (Nagel and Rettenmeyer 1973), currently unsuccessful males might be successful at a later time. Ants were placed in plastic vials, shipped overnight to the University of Houston, and frozen at $-20°C$ until the specimens were dried, weighed, and mounted on pins for the morphological measurements.

Dry body weight was measured to the nearest 0.1 mg (1994) or 0.01 mg (1996) after the ants were dried at least five days at 55°C. Dry weight did not change after four days at this temperature (Wiernasz et al. 1995). Body part lengths were measured using a dissecting microscope fitted with an ocular micrometer (50 μm divisions = 1 mm at 40×; 25 μm divisions = 1 mm at 20×). Seventeen body parts were measured in 1994: eye length, head length, head width, scape length, mandible length, thorax width, thorax length, gaster length, gaster width, postpetiole length, petiole length, fore femur length, mid femur length, hind femur length, fore tibia length, mid tibia length, hind tibia length (Table 1). Seventeen body parts were also measured in 1996: gaster length, fore femur length, and fore tibia length were not measured, but mandible width, pronotum length and thorax depth were measured in addition to the 1994 traits (Table 1). All traits were measured at 40×, except for thorax length and pronotum length, which were measured at 20×. Body parts present on both the left and right sides of the body were measured on the left side. If the left side was deformed or missing, the right side was measured. Either the left or right mandible was measured, depending on which was on top. One or more morphological measurements could not be taken for some individuals, due to a missing or deformed body part or to excess glue on the mounted specimen. All measurements were made by one person in each year (RR in 1994, AJA in 1996). In 1996 some male traits were measured slightly differently than in 1994, because of differences in the perception of landmarks.

Females were measured in a manner similar to that described for males of that year. Scape length and mandible length were not measured in females from 1996. For 1996 females, postpetiole length was measured from a lateral view. In both years, petiole length was measured laterally from the tip of the petiole to the suture of the petiole and postpetiole.

The natural-log (ln) transformation was applied to all variables to enhance the normality of the distribution and the homogeneity of the variances. Dry weight was cube-root transformed before the log transformation. Log transformation substantially reduced the nonhomogeneity of variances and the degree of kurtosis of most variables. Visual inspection of the frequency distributions and Q-Q plots suggested that

TABLE 1. Description of male traits. Years in parentheses denote differences in landmarks or traits measured in a single year.

Character	Description
EL, eye length	distance from the top to the bottom of the eye across the long axis
HL, head length	head-on as the distance from the vertex of the head to the anterior margin of the clypeus near the mandible (1994)
	distance from the anterior edge of the medial ocellus to the anterior margin of the clypeus near the mandible (1996)
HW, head width	across the eyes at the widest part of the head
SL, scape length	distance from the proximal edge to the distal edge of the scape
ML, mandible length	distance from the suture between the mandible and head to the tip of the apical tooth of the mandible
MW, mandible width	distance from the basal tooth of the mandible to the apical tooth of the mandible (1996)
PR, pronotum length	dorsally as the distance from the anterior to the posterior margins of the pronotum (1996)
TW, thorax width	distance from the suture of the mesopleuron and the promesonotum to the suture of the mesonotum and the propodeum
TL, thorax length	laterally as the distance from the suture between the mesonotum and the pronotum to the tip of the propodeal spine (1994)
	distance from the suture between the mesonotum and pronotum to the anterior of the suture between the propodeal lobe and the petiole (1996)
TD, thorax depth	dorsally as the distance from the left to right suture of the pronotum and the mesonotum (1996)
GW, gaster width	dorsally at the widest point of the abdomen
GL, gaster length	dorsally as the length of the first tergite from the postpetiole to the second tergite
PPL, postpetiole length	dorsally as the distance from the suture with the petiole to the suture between the main part of the postpetiole and the smooth posterior segment (1994)
	dorsally as the distance from the suture with the petiole to the suture with the gaster, at the tip of the smooth posterior segment that includes the stridulatory scraper (1996)
PL, petiole length	distance across the ventral surface from the petiole tooth to the suture with the postpetiole
FL, femur length	laterally on the anterior surface from the proximal to distal tips (1994)
	dorsally from the suture of the trochanter with the coxa to the distal tip of the femur (1996)
TL, tibia length	laterally on the anterior surface from the proximal to distal tips (1994)
	dorsally from the proximal to distal tips (1996)

most log-transformed variables were approximately normally distributed. Two characters, dry weight and gaster width, exhibited substantial bimodality, which was not associated with a simple division into mated and random males. We independently calculated normal curves using the sample means and standard deviations for the low mass (≤ 3.65 mg) and high mass (> 3.65 mg) groups. The region of overlap of the two normal curves is approximately 7% of the area under the low-mass curve and 4% of the area under the high-mass curve, suggesting substantial bimodality. This bimodality was present in the males collected in the first half hour of sampling, as well as in the entire sample. We omitted these two variables from the multivariate analyses.

The sample of randomly collected males probably included individuals that had mated earlier in the day or that would have mated later. Multiple mating is known to occur in males of several species of *Pogonomyrmex* (Nagel and Rettenmeyer 1973; Hölldobler 1976; Mintzer 1982) as well as in *Myrmica rubra* (Woyciechowski 1990). The frequency distribution of number of matings is not known for males of any *Pogonomyrmex* species; in *M. rubra* more than half of mating males copulated only once or twice (Woyciechowski 1990). Thus, any differences between the mated and random males conservatively estimate the differences between mated and unmated males.

We used principal components analysis to examine size and shape variation between random and mated males. Overall size was estimated as the linear combination of characters (ln-transformed) having as coefficients F_1, the first eigenvector of the variance-covariance matrix of the characters centered at zero separately by mating status (Rohlf and Bookstein 1987). Subsequent principal components were sheared by regressing out F_1 so we could examine shape independent of size (Bookstein et al. 1985; Rohlf and Bookstein 1987). To visualize the form of selection, we estimated fitness functions (Schluter 1988) for overall size (F_1) and the first several sheared principal components. Logistic regression (Hosmer and Lemeshow 1989) was used to test the significance of differences between mated and random males in overall size, as well as in subsequent sheared principal components. We also calculated linear and nonlinear sexual selection gradients by performing linear and quadratic regressions of standardized principal components on relative mating success (Lande and Arnold 1983; Brodie et al. 1995).

We used a path analytical model to examine sexual selection on individual size-adjusted traits (Crespi and Bookstein 1989; Crespi 1990; Kingsolver and Schemske 1991). Path analysis is a method of partitioning correlations among variables; it is related to multiple regression and partial correlation, but path analysis allows for more comprehensive testing of direct and indirect effects. The selection coefficients in our path analysis represent the differences in the size-adjusted mean trait values of mated and random males. Significance of the selection coefficients was tested by analysis of covariance (Snedecor and Cochran 1980), using the ln-transformed morphological traits as response variables and overall size (F_1 scores) as the covariate. The assumptions of homogeneity of residual variances and homogeneity of slopes were tested and met except where otherwise specified.

We also performed principal components analysis (using

TABLE 2. (a) Mean phenotypic values of males and females in 1994. (b) Mean phenotypic values of males and females in 1996. All traits are in mm except dry weight (in mg). F, fore; M, mid; H, hind.

(a)

Trait	Random males			Mated males			Females		
	Mean	Range	n	Mean	Range	n	Mean	Range	n
Dry weight	4.19	1.90–6.20	239	4.19	2.20–5.90	200	12.22	7.80–15.20	200
Eye length	0.58	0.44–0.70	230	0.60	0.48–0.70	197	0.49	0.42–0.56	199
Head length	1.22	0.94–1.44	238	1.26	1.00–1.40	200	1.83	1.40–2.00	200
Head width	1.86	1.48–2.14	239	1.89	1.54–2.08	200	2.29	1.94–2.42	200
Scape length	0.73	0.50–0.90	235	0.76	0.60–0.94	199	1.50	1.26–1.62	197
Mandible length	0.95	0.70–1.14	238	0.96	0.76–1.16	200	1.59	1.38–1.88	187
Thorax width	1.38	1.00–1.66	199	1.40	1.10–1.60	196	1.51	1.24–1.64	198
Thorax length	2.82	2.16–3.28	218	2.88	2.24–3.32	198	2.94	2.48–3.32	199
Gaster width	2.19	1.60–2.54	239	2.23	1.70–2.70	198	2.37	1.94–2.62	192
Gaster length	1.28	0.84–1.94	217	1.28	0.96–1.74	194	1.60	1.24–2.12	200
Postpetiole length	0.75	0.56–1.00	217	0.79	0.54–0.98	196	0.87	0.62–1.04	200
Petiole length	0.81	0.56–1.04	203	0.84	0.50–1.12	185	0.70	0.60–0.82	200
F femur length	1.81	1.46–2.02	232	1.83	1.50–2.00	187	1.93	1.58–2.08	196
M femur length	1.82	1.50–2.02	227	1.84	1.50–2.04	197	1.94	1.70–2.10	195
H femur length	2.12	1.42–2.42	229	2.16	1.74–2.36	196	2.28	2.02–2.44	194
F tibia length	1.45	1.20–1.66	235	1.46	1.22–1.62	198	1.52	1.30–1.64	179
M tibia length	1.43	1.20–1.62	223	1.44	1.22–1.62	196	1.51	1.30–1.66	193
H tibia length	1.88	1.60–2.12	225	1.91	1.62–2.14	196	2.01	1.80–2.24	188

(b)

Trait	Random males			Mated males			Females		
	Mean	Range	n	Mean	Range	n	Mean	Range	n
Dry weight	3.99	1.45–6.10	599	4.00	1.88–6.73	550	12.25	7.13–16.15	550
Eye length	0.59	0.46–0.72	599	0.60	0.46–0.70	550	0.52	0.42–0.58	550
Head length	1.12	0.90–1.34	598	1.14	0.92–1.32	550	1.55	1.34–1.70	549
Head width	1.85	1.44–2.22	597	1.86	1.44–2.16	550	2.29	1.88–2.50	547
Scape length	0.75	0.58–0.94	599	0.76	0.54–0.92	548	—	—	—
Mandible length	0.95	0.72–1.30	599	0.96	0.76–1.16	550	—	—	—
Mandible width	0.42	0.28–0.60	599	0.42	0.28–0.56	550	0.81	0.56–0.92	549
Thorax width	1.37	0.96–1.68	596	1.38	1.02–1.76	550	1.58	1.28–1.78	550
Thorax length	2.87	2.20–3.56	599	2.94	2.32–3.52	550	3.18	2.64–3.52	549
Pronotum length	1.50	1.12–1.84	599	1.51	1.16–1.84	549	1.63	1.32–1.80	550
Thorax depth	1.18	0.84–1.50	486	1.19	0.84–1.56	490	1.34	1.06–1.50	546
Gaster width	2.12	1.56–2.56	590	2.14	1.66–2.56	543	2.72	2.22–2.98	547
Postpetiole length	0.89	0.54–1.20	597	0.92	0.66–1.20	549	0.91	0.64–1.14	549
Petiole length	1.17	0.90–1.46	427	1.19	0.82–1.40	376	0.67	0.56–0.80	546
M femur length	1.98	1.58–2.32	596	2.01	1.66–2.30	547	2.16	1.84–2.38	543
H femur length	2.29	1.84–2.62	599	2.31	1.94–2.66	548	2.47	2.12–2.70	549
M tibia length	1.42	1.12–1.74	597	1.43	1.18–1.68	546	1.54	1.30–1.74	550
H tibia length	1.89	1.42–2.22	599	1.90	1.52–2.24	548	2.05	1.72–2.30	550

the variance-covariance matrix) on the female morphological data (ln-transformed) to obtain measures of female size and shape. To test for assortative mating, we calculated Kendall's rank correlation coefficient for the relationship between male and female estimates of overall size (first principal components, PC1s) and shape (subsequent principal components having comparable loadings in the two sexes). We also tested for assortative mating on size by comparing the F_1 scores of males mated to small females ($\leq$ median female PC1 score) and large females ($>$ median female PC1 score).

Most statistical analyses, including nonlinear regressions and matrix manipulations, were performed with SYSTAT 6.0 (SPSS 1996). Cubic spline fits for the fitness functions were estimated with the FORTRAN program described in Schluter (1988), with estimates of standard errors based on 1000 bootstraps. Exact P-values for the logistic regression were obtained by integrating the appropriate probability density function (Beyer 1991) with Mathematica (Wolfram 1991). The sequential Bonferroni method (Rice 1989) was applied within

tables to adjust an overall significance level of 0.05, but exact P-values are listed for comparative purposes.

RESULTS

Variation in Male Traits

There was considerable variability in all traits measured (Table 2). For example, the heaviest male collected was more than four times heavier than the lightest male. Within each sex in each year, each variable was positively correlated with every other variable (Table 3).

Random and mated males differed significantly in morphometric size in 1994 (Wilks' $\lambda = 0.759$, df = 16 and 259, $P < 0.0001$, canonical correlation 0.491, 71% of the 276 males classified correctly). Because there were only two groups, the significance testing is exactly the same as discriminant function analysis for multivariate analysis of variance (Pedhazur 1982), showing that there is significant separation between groups. Two characters could not be mea-

TABLE 3. (a) Principal component loadings of male morphological traits in 1994. (b) Principal component loadings of male morphological traits in 1996. Notation follows that of Rohlf and Bookstein (1987). F_1 is the overall size factor, or the first eigenvector of the variance-covariance matrix of ln-transformed traits centered at zero separately by mating status group. H_i is the ith sheared principal component. F, fore; M, mid; H, hind.

(a)

Trait	F_1	H_2	H_3	H_4	H_5
Eye length	−0.26	0.02	0.03	0.16	−0.29
Head length	−0.25	−0.04	−0.03	0.12	−0.13
Head width	−0.24	−0.04	−0.03	0.09	−0.11
Scape length	−0.22	−0.14	0.01	0.21	0.85
Mandible length	−0.30	−0.04	−0.07	0.18	−0.10
Thorax width	−0.34	−0.04	−0.00	0.09	−0.31
Thorax length	−0.31	−0.05	−0.03	0.06	−0.14
Gaster length	−0.29	0.70	0.60	−0.19	0.11
Postpetiole length	−0.31	0.26	−0.66	−0.61	0.12
Petiole length	−0.22	−0.62	0.43	−0.61	−0.00
F femur length	−0.20	−0.03	−0.03	0.11	0.07
M femur length	−0.21	−0.04	−0.03	0.12	0.04
H femur length	−0.20	−0.05	−0.01	0.11	0.06
F tibia length	−0.19	−0.07	−0.02	0.11	0.05
M tibia length	−0.20	−0.07	−0.02	0.13	0.04
H tibia length	−0.19	−0.08	−0.02	0.11	0.06
% variance	61.10	9.97	7.70	7.01	4.30

(b)

Trait	F_1	H_2	H_3	H_4
Eye length	−0.23	−0.07	−0.18	−0.27
Head length	−0.24	−0.04	−0.10	−0.11
Head width	−0.23	−0.05	−0.12	−0.09
Scape length	−0.18	−0.14	−0.27	0.84
Mandible length	−0.27	−0.15	0.13	0.00
Mandible width	−0.37	−0.41	0.77	0.11
Thorax width	−0.34	−0.05	−0.14	−0.25
Thorax length	−0.30	0.02	−0.12	−0.17
Pronotum length	−0.32	−0.02	−0.16	−0.21
Postpetiole length	−0.36	0.87	0.26	0.16
M femur length	−0.21	−0.05	−0.18	0.06
H femur length	−0.20	−0.05	−0.15	0.05
M tibia length	−0.19	−0.07	−0.20	0.10
H tibia length	−0.18	−0.06	−0.17	0.10
% variance	74.56	7.79	5.15	3.72

sured on more than 15% of males in 1996: petiole length (because the petiole tooth was sometimes absent or not pronounced) and thorax depth (because glue sometimes obscured the edge). These variables had significant partial correlations with other variables, so they were dropped from subsequent 1996 analyses to increase the number of males with measurements for all variables in the analysis. When discriminant function analysis was performed on the remaining 14 variables, 63% of the 1131 males were classified correctly as mated or random (Wilks' λ = 0.915, df = 14 and 1116, P < 0.0001, canonical correlation 0.291).

The first principal component of the variance-covariance matrix of ln-transformed traits centered at zero separately by mating group accounted for most of the morphological variance in males (61.10% in 1994, Table 3a; 74.56% in 1996, Table 3b). This component had all loadings of the same sign and could reasonably be interpreted as a general size factor. The first five principal components of the variance-covariance matrix in 1994 and the first four principal components of the variance-covariance matrix in 1996 accounted for more than
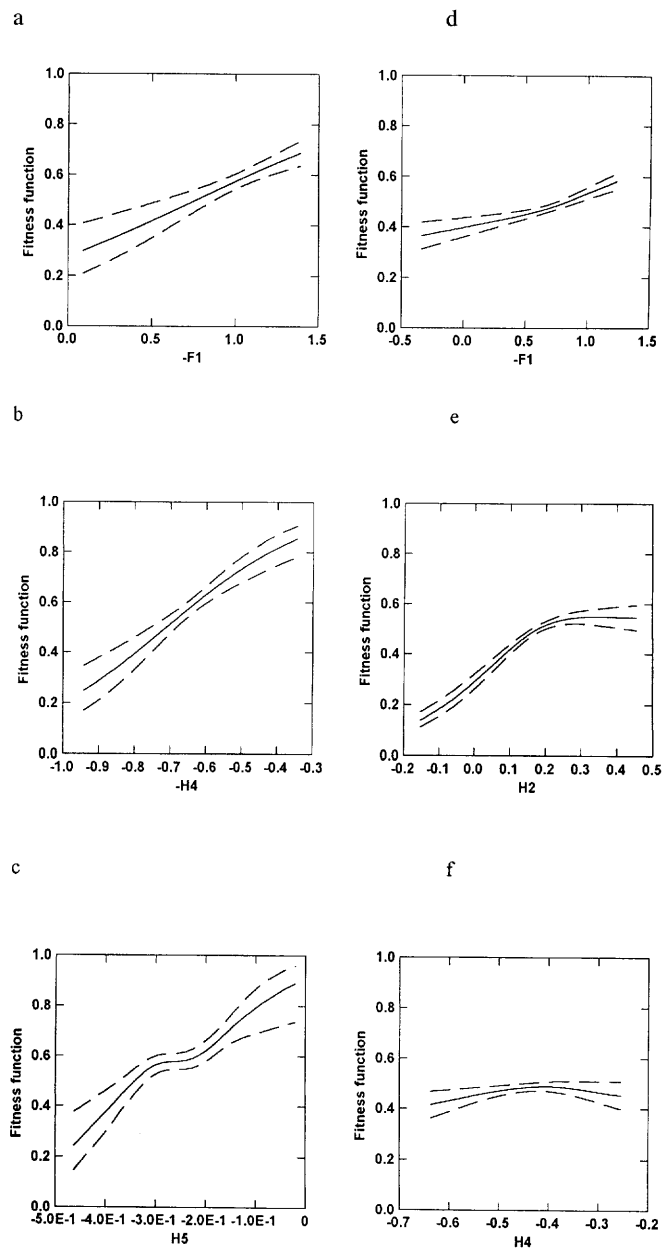

FIG. 1. Fitness functions (solid lines) and bootstrap standard errors (dashed lines) calculated with the cubic spline technique for overall body size ($-F_1$) and two subsequent sheared principal components in 1994 (a–c, left column) and 1996 (d–f, right column). Figures aligned next to each other represent principal components with comparable loadings in both years of the study. Figures 1b and 1e show the principal components for postpetiole length relative to mandible size, and figures 1c and 1f show the principal components for scape length relative to thorax and head size.

90% of the morphological variance (Table 3). Subsequent principal components accounted for less than 3% each.

Sexual Selection on Male Size and Shape

The fitness functions indicated selection with a large directional component on most principal components (Figs. 1, 2). However, the fitness functions deviated most from line-
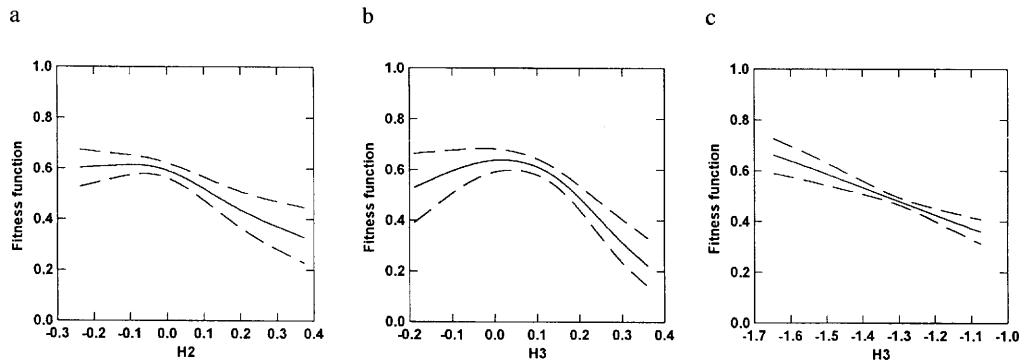
FIG. 2. Fitness functions (solid lines) and bootstrap standard errors (dashed lines) calculated with the cubic spline technique for sheared principal components unique to 1994 (a, b) or 1996 (c).

arity for H_2 and H_3 in 1994 (Fig. 2a, b) and for H_2 in 1996 (Fig. 1e). The graphical analysis of selection agreed well with the linear and nonlinear gradients described below.

For directional selection, we emphasize the results of the logistic regression, although the results obtained with standard linear regression were almost identical, with the P-values differing by less than 0.01 in every case (Table 4). There was significant sexual selection for larger males in both years (F_1 in Table 5; Fig. 1a,d). Mated males also had significantly larger postpetioles relative to their mandible sizes and scape lengths (H_4 in 1994, Table 5a, Fig. 1b; H_2 in 1996, Table 5b, Fig. 1e). In 1994 mated males had relatively large scape lengths (H_5, Table 5a, Fig. 1c), but the corresponding principal component in 1996 was not significant (H_4, Table 5b, Fig. 1f). In 1996 mated males had relatively narrow mandibles (H_3, Table 5b, Fig. 2c), but there was no corresponding principal component in 1994.

The third sheared principal component in 1994 was a contrast of postpetiole length with gaster length and petiole length; males with highly negative H_3 scores had long postpetioles relative to gaster length and petiole length, and males with highly positive H_3 scores had long gasters and petioles relative to postpetiole. There was significant nonlinear selection on the third sheared principal component in 1994, indicating maximal mating success for males with intermediate H_3 scores (Table 4a, Fig. 2b). The mating success curve

dropped off more sharply above than below the inflection point, and the inflection point was somewhat below the population mean H_3 score (0.096), which suggests some selection for males with relatively long postpetioles. This agrees with the nonsignificant trend detected in the analysis of linear selection (Table 4a). There was also significant nonlinear selection on the second principal component in 1996, suggesting that the advantage of a long postpetiole relative to mandible size and scape length tapers off for males with very large postpetioles (Table 4b, Fig. 1e). The corresponding principal component in 1994 (H_4) was not subject to significant nonlinear selection, although in that year the principal component also had high loadings on two traits not included in the 1996 analysis (gaster length, petiole length). A nonsignificant trend for nonlinear selection on H_4 was present in 1996, suggesting higher fitness of intermediate values of scape length relative to thorax size and eye length (Table 4b, Fig. 1f).

The path analytical model yielded similar results to those described above for regression analysis on the principal components. In 1994, analysis of covariance indicated a significant difference in size-adjusted means of random and mated males for three traits (Table 5a). Mated males were significantly lighter and had significantly narrower thoraxes and longer postpetioles relative to overall body size. Because the residual variances of thorax length, postpetiole length, and

TABLE 4. (a) Sexual selection gradients on overall size (F_1) and on sheared principal component scores (H_i) in 1994. (b) Sexual selection gradients on overall size (F_1) and on sheared principal component scores (H_i) in 1996. B, logistic regression coefficients; β, linear selection gradients; γ, nonlinear selection gradients. Values in bold type were significant after sequential Bonferroni corrections.

(a)

PC	B ± SE	P	β ± SE	P	γ ± SE	P
F_1	**−1.265 ± 0.495**	0.0097	**−0.133 ± 0.051**	0.0095	−0.020 ± 0.088	0.8165
H_2	−1.650 ± 1.214	0.1722	−0.070 ± 0.051	0.1737	−0.098 ± 0.071	0.1654
H_3	−2.841 ± 1.403	0.0405	−0.105 ± 0.051	0.0415	**−0.240 ± 0.070**	0.0007
H_4	**−4.829 ± 1.533**	0.0011	**0.166 ± 0.051**	0.0012	−0.026 ± 0.058	0.6516
H_5	**4.499 ± 1.908**	0.0163	0.122 ± 0.051	0.0171	0.002 ± 0.068	0.9775

(b)

PC	B ± SE	P	β ± SE	P	γ ± SE	P
F_1	**−0.577 ± 0.221**	0.0087	**−0.081 ± 0.031**	0.0089	0.074 ± 0.059	0.2137
H_2	**3.345 ± 0.705**	< 0.0001	**0.149 ± 0.031**	< 0.0001	**−0.144 ± 0.040**	0.0003
H_3	**−2.182 ± 0.841**	0.0091	**−0.081 ± 0.031**	0.0092	0.028 ± 0.019	0.4633
H_4	0.476 ± 0.981	0.6273	0.015 ± 0.031	0.6277	−0.084 ± 0.044	0.0568

TABLE 5. (a) Directional sexual selection on size-adjusted traits of males in 1994. A positive direction of selection indicates that the size-adjusted mean trait value is higher in mated males than in random males. Significance of selection was tested by analysis of covariance, using F_1 scores as a measure of overall body size and ln-transformed trait values. The assumption of homogeneity of slopes was met for all traits except scape length and head length, and the assumption of homogeneity of residual variances was satisfied for all traits except head length, thorax width, and postpetiole length (see text). Values marked with an asterisk were significant after sequential Bonferroni corrections. (b) Directional sexual selection on size-adjusted traits of males in 1996. The assumption of homogeneity of residual variances was met for all traits except postpetiole length and dry mass; the assumption of homogeneity of slopes was met for all traits.

(a)

Trait	Direction of selection	$F_{1,273}$	P
Dry mass	−	40.87	< 0.0001*
Eye length	+	0.81	0.3687
Head length	+	3.49	0.0629
Head width	−	2.22	0.1378
Scape length	+	3.98	0.0471
Mandible length	−	5.35	0.0215
Thorax width	−	11.41	0.0008*
Thorax length	−	3.67	0.0565
Gaster length	−	2.48	0.1168
Postpetiole length	+	11.50	0.0008*
Petiole length	+	3.95	0.0479
Fore femur length	−	2.57	0.1098
Mid femur length	−	8.00	0.0050
Hind femur length	−	0.17	0.6841
Fore tibia length	−	2.01	0.1578
Mid tibia length	−	5.02	0.0259
Hind tibia length	+	0.41	0.5224

(b)

Trait	Direction of selection	$F_{1,1128}$	P
Dry mass	−	46.73	< 0.0001*
Eye length	−	0.03	0.8574
Head length	+	0.05	0.8190
Head width	−	0.05	0.8175
Scape length	+	0.10	0.7485
Mandible length	−	10.60	0.0012*
Mandible width	−	21.26	< 0.0001*
Thorax width	−	1.25	0.2466
Thorax length	+	37.88	< 0.0001*
Pronotum length	−	3.36	0.0671
Postpetiole length	+	15.68	0.0001*
Mid femur length	+	1.44	0.2308
Hind femur length	+	1.00	0.3170
Mid tibia length	−	1.53	0.2162
Hind tibia length	+	0.37	0.5427

head length were significantly higher for random than mated males, the finding of a difference in size-adjusted means must be interpreted cautiously. Higher variances might be expected, however, because the random group is composed of both successful and unsuccessful males. The assumption of homogeneity of slopes was met for all 16 variables (relative to body size) except scape length and head length. In 1996 mated males were lighter and had shorter and narrower mandibles, longer thoraxes, and longer postpetioles relative to body size (Table 5b). As in 1994, the residual variance of postpetiole length was significantly higher in random males than in mated males. Random males also had a higher residual

variance of dry mass, although this trend was less marked for dry mass than for postpetiole length. The assumption of homogeneity of residual variances was met for all other traits, and the assumption of homogeneity of slopes was met for all traits.

For the 1996 data, we examined the robustness of the results by dividing the data into four random subsets and repeating the analysis of covariance within each subset. In every subset, mated males had relatively narrow mandibles and long thoraxes (P < 0.05). Mated males were lighter in three of four subsets (P < 0.05), and in the other subset there was a marginal trend in the same direction (P = 0.0630). The tendency for mated males to have shorter mandibles and longer postpetioles was less consistent, being found at P < 0.05 in only one (mandible length) or two (postpetiole length) of the four random subsets; in other subsets P > 0.10 for these comparisons.

Assortative Mating

We performed principal components analysis on the female data, using the same variables as in the analysis of male data, except that scape length and mandible length were not included for 1996 females because these traits were not measured that year. The first principal component accounted for 51.6% of overall variance in 1994 and 48.4% in 1996. It had loadings of the same sign on all variables. Unlike Davidson (1982), we found no evidence of assortative mating. For individuals in mated pairs, Kendall's rank correlation coefficient between overall size (F_1) of males males and the first principal component (E_1) of females was not significantly different from zero (1994: $\tau = -0.0476$, $n = 122$ pairs, $t_s = -0.777$, two-tailed $0.40 < P < 0.50$; 1996: $\tau = -0.0548$, $n = 526$ pairs, $t_s = -1.878$, two-tailed $0.05 < P < 0.10$). The nonsignificant trend in 1996 was in the direction of assortative mating by size. In both 1994 and 1996, there was a nonsignificant tendency for males mating with small females ($\leq$ median female PC1 score) to be smaller in overall size than males mating with large females ($>$ median female PC1 score) (1994: $t_{120} = -1.6788$, $P = 0.0958$; 1996: $t_{524} = -1.7576$, $P = 0.0794$).

In 1994, principal components after the first were not similar in males and females. In 1996, the second and third principal components had similar interpretations in males and females: a contrast of postpetiole length with mandible width and other traits and a contrast of mandible width with eye length and other traits. Kendall's rank correlation coefficient between male and female values was not significant for either the second ($\tau = 0.0421$, $t_s = 1.445$, two-tailed $0.10 < P < 0.20$) or third ($\tau = -0.0097$, $t_s = -0.334$, two-tailed $0.50 < P < 0.90$) principal component.

In contrast to the multivariate results, analyses of individual morphological traits suggested some degree of assortative mating in one of the two years. In 1994, there was a significant positive correlation between the petiole lengths of females and their mates ($\tau = 0.156$, $t_s = 3.15$, $n = 185$ pairs, $0.001 < P < 0.01$, at borderline significance with $\alpha_{adj} = 0.05/18 = 0.028$), suggesting significant assortative mating for petiole length. Several other traits had similar positive correlations in females and their mates, although these cor-

relations were not significant with the Bonferroni correction (thorax length: $\tau = 0.138$, $t_s = 2.88$, $n = 197$, $0.001 < P < 0.01$; thorax width: $\tau = 0.130$, $t_s = 2.69$, $n = 194$, $0.001 < P < 0.01$; head width: $\tau = 0.106$, $t_s = 2.23$, $n = 200$, $0.02 < P < 0.05$; mandible length: $\tau = 0.103$, $t_s = 2.09$, $n = 187$, $0.02 < P < 0.05$). In 1996, there was no evidence for assortative mating on the basis of single traits. Only one trait had a correlation coefficient of $P < 0.10$ between females and their mates (mandible width: $\tau = 0.048$, $t_s = 1.69$, $n = 549$, $0.05 < P < 0.10$).

DISCUSSION

Our results taken together with those of Davidson (1982) on *P. desertorum* and *P. barbatus* indicate that sexual selection consistently favors increased male size in harvester ants. Mating males were significantly larger than males collected at random from the lek. In this population of *P. occidentalis*, larger males consistently have greater mating success than smaller males. Large size may be favored because of overall endurance at the lek, giving large males more opportunities to attempt copulation (Andersson 1994). Large males may be less susceptible to desiccation and may be able to spend more time flying, thus increasing the probability of encountering females. They also may be better able to exclude other males while copulating and gain access to females that are mating with other males.

Unlike Davidson's (1982) study of *P. barbatus*, we found no evidence that mating advantage tapered off among the very largest males. This difference may be a consequence of the use of dry weight (Davidson 1982) versus a composite of linear measurements (F_1) as a measure of body size. In both years of our study, we found a highly significant positive correlation between F_1 and dry mass, both within each mating class and for all males combined. Despite the fact that dry mass was a good predictor of composite linear size, use of dry mass alone masks some size differences between the two mating classes. In both this and the previous study of *P. occidentalis*, there was a highly significant tendency for mated males to be lighter than random males of comparable morphometric size (Table 5). This pattern of dry mass differences is consistent with the idea that mated males are losing sperm, accessory gland secretions, and perhaps thoracic muscle mass disproportionately to unmated males (Wiernasz et al. 1995). If dry mass decreases as a function of mating frequency and/or duration, both mated and random males that are large should be more variable for dry mass than for morphometric size. Because the random group of males contains some males that have mated previously, whereas the mated group contains some males that have only mated once or whose mating has been interrupted, the variance in dry mass should be high for both groups. Because we can only compare successful and random males, the relationship between mating success and dry mass is confounded. It is possible that the heaviest males at the lek have not mated and therefore have not released any of their sperm and accessory gland secretions.

We also discerned selection on several components of male shape. In both years, some significant sheared principal components were unique (Fig. 2) because the variable that was most highly correlated with the component was only measured in that year. Such results are frequent in multivariate, correlative studies of selection (Mitchell-Olds and Shaw 1987). Although these components have no equivalent in the other year of the study, they suggest patterns of selection consistent with components present in both years.

Three aspects of male shape were consistent across years (Fig. 1). Mated males had longer scapes than unmated males in both years, although the difference was not significant in 1996. The thorax of mated males was long relative to overall body size in 1996, and in 1994 the thorax was narrow relative to overall body size. In both years mated males had relatively elongate thoraxes compared to randomly collected males. Within the mating ball, relatively narrow bodies may confer an advantage in male-male competition for access to reproductive females.

Mandible length (both years) and mandible width (1996) were shorter relative to body size in mated males. Males of *P. occidentalis* often grasp the queens with their mandibles before mating (Nagel and Rettenmeyer 1973); Hölldobler (1976) has suggested that gripping strength is an important component of male competition in this genus. For a given head size, and therefore adductor muscle mass, the mandibles of a successful male have a smaller moment arm than do those of a random males (see, e.g., Elner and Campbell 1981). The result is that the mandibles of mated males are expected to apply greater force than those of males collected at random. Additional data on mandible width from 1996 indicate that the greater force is applied over a smaller area, further increasing the gripping strength. Such males may be better able to retain their hold on a female during copulation as other males attempt to wrest the mating pair apart, thus gaining copulations of longer duration.

Mated males also had large postpetioles relative to body size, although selection on postpetiole length appeared to be nonlinear in both years. In 1994 males with intermediate postpetiole lengths (relative to gaster length and petiole length) had higher mating success, and in 1996 there was apparently a threshold after which larger postpetioles (relative to mandible size, scape length, and other traits) conferred no further advantage. Males with relatively large postpetioles may be more flexible, which may enable them to gain access to females better than other males as well as to maintain copulation in the mating ball. Nonlinear selection on postpetiole may result from males with extremely long segments being easily displaced from the queen. Overall, mated males with their elongate thoraxes, short mandibles, and relatively long postpetiole segments for their body size appear to be built for successfully probing into the mating ball and holding onto the queen once mating has been achieved.

Analysis of selection on shape when the effects of size are controlled is rarely performed. The components of shape important for male mating success in this study are not simply a function of larger size, but rather of successful males independent of size. Moreover, the pattern is upheld in data from different years measured by different individuals. Although one must be cautious in interpreting patterns of selection in correlative studies of selection, particularly for composite variables such as principal components (Mitchell-

Olds and Shaw 1987), the consistency of these results argues that they are biologically meaningful.

There was no significant assortative mating based on overall size or on multivariate shape measures. Univariate analyses suggested weak assortative mating in one of the two years. In 1994 females mated with males with similarly high or low petiole lengths and there were also nonsignificant trends for assortative mating based on thorax length, thorax width, and mandible length. Interestingly, these traits are the same regions of the body identified as important for male mating success.

The results presented here demonstrate that even in the absence of pronounced male dimorphism, males may not have equivalent roles or reproductive success. Large males consistently had greater mating success. Nonetheless, small males were present in every sample taken from a mating swarm. At the level of the individual male, it is possible that the sexual selection for larger size may be offset by some other advantage for small size, such as dispersal ability (Fortelius et al. 1987) or sperm production (Fjerdingstad and Boomsma 1997). Whether small males of *P. occidentalis* have a mating advantage in another context is unknown. If males from one size class are relatively poor dispersers, they may sometimes mate within the natal nest (Fortelius et al. 1987). Intranidal mating is not known to occur in this species, but there is a substantial level of inbreeding (Cole and Wiernasz 1997).

With its extremely short-lived breeding period, the mating system of *P. occidentalis* resembles that of explosively breeding amphibians with scramble competition polygyny (Sullivan et al. 1995). The spatial and temporal concentration of females in explosive breeding systems is predicted to limit multiple mating by males because each mating takes time (Emlen and Oring 1977). The asynchronous arrival of females, the short duration of copulation relative to the time over which reproductive animals are present, and the highly male-biased operational sex ratio make the mating swarms of *P. occidentalis* also resemble leks (Emlen and Oring 1977). A large male mating advantage has been observed frequently, but not invariably, in many amphibians and other species with scramble competition polygyny or lek polygyny (reviews in Olsen et al. 1986; Sullivan et al. 1995). In mating balls similar to those formed by *Pogonomyrmex* ants, large males of some natricine snakes have a mating advantage even though these snakes do not engage in overt male-male aggressive behavior such as biting or wrestling (Madsen and Shine 1993; Luiselli 1996). From our studies of *P. occidentalis* and similar studies of explosive breeders, we predict that in other species of ants with a swarm-mating system, sexual selection will favor large male size as well as morphological structures that aid in combat or in maintaining a secure connection with the female during copulation.

If variation in male mating success and thus male fitness as a function of morphology is common in swarm-mating species, it will have implications for studies of reproductive allocation at the level of the colony. Studies of reproductive allocation in social insects have focused on the relative investment in males and queens while ignoring variation within each group (reviewed in Bourke and Franks 1995). The assumption has been that each queen or male is equivalent to

any other. If the individual fitness of queens or males is variable, this simplified view of reproductive allocation may no longer apply. Interestingly, although our results suggest that individual mating success of males varies with size, the strong linearity of this function (Fig. 1a,c) suggest that, from the perspective of the colony, a sufficiently large number of small males may produce fitness gains equal to a smaller number of large males. When size no longer matters to the colony due to size versus number trade-offs, then selection on shape may be especially important.

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