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Physical variability among nest foundresses in the polygynous social wasp, *Polistes annularis*

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Summary. An individual's rank in a dominance hierarchy is often based on size or weight, especially in insects. Foundresses of the social wasp, *Polistes annularis*, vary greatly in size as measured by wing length, dry weight, fat weight, and residue weight after fat has been extracted. Females that emerged from the same nest are much more similar in size to each other than they are to females that emerged from other nests. Within nests however queens are usually larger than their subordinates. Queens that emerged from one nest may be smaller than subordinates that emerged from another nest. We found no evidence of a group of females that are forced into being subordinates because of inadequate feeding as larvae. Females are also probably not attempting to begin new nests with females as different in size as possible from themselves since means and variances of winglength of females on new nests do not differ from those of all females emerging from that natal nest.

Introduction

One of the consequences of group living is increased competition for resources among group members (Alexander 1974). When individuals contest a resource, assessment of fighting abilities is likely, and assymetries in some overall measure of ability may influence the outcome of a contest (Parker 1974; Sigurjonsdottir and Parker 1981). Size and age are commonly reported correlates of dominance rank in many different organisms (wasps: Pardi 1948; Richards 1971; Noonan 1981; sweatbees: Batra 1966; Breed 1976; crickets: Alexander 1961; crayfish: Bøvbjerg 1956; Lowe 1956; frogs: Haubrich 1961; fish: MacDonald et al. 1968; mice: Ginsburg and Allee 1942). In a group the result of contests is usually a dominance hierarchy where dominant individuals have greater access to food, mates, or other resources (Wilson 1971, 1975; Richards 1974; but also see Rowell 1974; Scott and Fredericson 1951). Subordinates may also reproduce less successfully or be completely excluded from personal reproduction (insects: West 1967; Noonan 1981; Strassmann 1981a; Hermann and Dirks 1975; West Eberhard 1975a; Lin and Michener 1972; Brothers and Michener 1974; birds: Brown 1970; mammals: Rabb, Woolpy and Ginsburg 1967; Hall and DeVore 1965; Crook and Gartlan 1966; Jarvis 1981). If groups are composed of related individuals, subordinates who aid dominant relatives may increase their fitnesses above the level that they could have achieved by personal reproduction outside the group (Hamilton 1964; West Eberhard 1975a; Strassmann 1981a; Noonan 1981).

Since dominance rank frequently determines an individual's reproductive success in many instances, the basis of physical variability that results in a dominance hierarchy is of interest. In groups of relatives it may be that differences in physical size are the result of differential feeding of young that result in size classes destined to take on specific roles as adults (Alexander 1974; West Eberhard 1975a; Haggard and Gamboa 1980; Turillazzi 1980; Strassmann and Orgren 1983). This study was designed to examine physical variability and its relationship to dominance rank among group-nesting wasps. We focused on four physical measurements (wing length, dry weight, fat weight, and residue weight after fat is extracted). We looked at the relative impact of nest of origin and dominance rank on physical measurements. If wasps

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are more variable within nests than between nests, then physical variability may be said to originate to facilitate dominance hierarchy establishment by creating a pool of smaller individuals destined to function as subordinates to larger relatives. This would be a first step in the development of a worker caste. Internest differences in physical condition may be larger than intranest differences if larvae on a single nest are treated equally, and nests vary in amounts of food supplied to larvae. Females from the same nest are also genetically more similar. Females themselves may facilitate dominance hierarchy establishment regardless of the types of variability that exist by beginning nests with females as different as possible from themselves in size.

Polistes annularis, a social wasp, was chosen as a study organism because nests are begun by large groups of females near their parental nest and behavioral dominance rank is closely correlated with degree of ovarian development (Strassmann 1981a). Therefore dominance rank can be measured by ovarian condition and brief observations of behavior, making a much larger sample feasible than would be possible if extensive behavioral observations were necessary on each nest (Strassmann 1983). The proximity of new nests to their parental nest makes complete studies of all females surviving the winter from a given nest possible (Rau 1930).

Other studies of social wasp foundresses have focused on differences in reproductive success of nests begun by different numbers of foundresses (Noonan 1981; Strassmann 1981a; Turillazzi et al. 1982), relatedness among foundresses (Metcalf and Whitt 1977), frequencies of usurpation (Gamboa 1978), tendencies to nest near the natal nest (Klahn 1979; Strassmann 1979; Noonan 1981), dominance hierarchies (West Eberhard 1969; Noonan 1981; Turillazzi and Pardi 1977; Pardi 1948) size differences between workers and queens (Haggard and Gamboa 1980; Turillazzi 1980) timing of brood development (Gamboa 1980), and nest fidelity (Pratte 1979, 1982; Strassmann 1983). Turillazzi and Pardi (1977) found queens were on average larger than subordinates on bigynic nests. Dropkin and Gamboa (1981) compared headwidths of subordinates, lone foundresses and queens of multiply-founded nests in *P. metricus* and found that subordinates and lone foundresses were equivalent, and that both were smaller than queens of multiply founded nests. Their study was not designed to investigate the source of these differences by looking at size differences within and between natal nests. Noonan (1981) found that subordinate foundresses in *P. fuscatus* were significantly smaller than either lone foundresses or association queens. Noonan (1981) found average sizes of females were similar from nest to nest. Association queens ranged from 13.5–15 mm winglength ($N=11$), subordinates from 12–14.5 mm ($N=22$) and single foundresses from 12.8–14.2 mm ($N=11$).

Materials and methods

All wasps were observed and collected at a study site along a cliff face overlooking a reservoir about 30 miles west of Austin, Texas. The following spring, observations of the behavior of these marked individuals indicated which foundress was queen on each new nest (Strassmann 1981a; Strassmann 1983). One hundred and twenty-nine foundresses were collected from nests on 2 collection dates (8 April, and 15 April). At this time nests were 2–3 weeks old and contained only eggs. We marked 313 females from 5 parental nests in autumn.

Winglength was measured from tip to tegulum using Helios dial calipers accurate to 0.01 mm (Strassmann 1983). This is a good measure of overall size, and winglength is highly correlated with other measures of size, such as total body length (Haggard and Gamboa 1980). Dissections were performed by pulling the last abdominal segment from the rest of the body (West-Eberhard 1975b). Total layable eggs in both ovaries, size of the largest oocyte (in micrometer units, 1 unit = 12.5 mm), and number of oocytes in a representative ovariole were recorded (Strassmann 1983). Resorbing eggs, which could be distinguished by their dull chorion and irregular shape, were not included in the counts of layable eggs.

After dissection, wasps were placed with their ovaries in numbered, weighed vials. They were then dried under vacuum in a Fisher Isotemp oven at 52° C for 10–14 days. Individuals were weighed to 0.1 mg and replaced in the oven for successive periods of 5–7 days. A hotter (80° C) non-vacuum oven was employed for the final 2–3 drying periods (of 1–2 days each). Wasps were dried to constant dry weight. At this time, weight change averaged $-0.8 \pm$ S.D. 0.7 mg, $N=154$.

A 2:1 chloroform:methanol solution was used to extract fat (Folch et al. 1957). This process does not extract structural fat, which was desirable since we were interested only in energy reserves. Individual wasps were ground by hand in a ground glass homogenizer for 5–7 min. Ground tissues were placed in approximately 12 ml of solvent and vortexed for 1 min at medium speed, then centrifuged. Three washes were performed, each using 12 ml of solvent and 30 s of vortexing. Total contact time between solvent and tissues was about 3 h, and total volume of solvent, about 48 ml. Residues were placed in weighed vials in an oven set at 80° C and dried as above. Subtracting the weight of the vial from the lowest recorded weight yielded a (dry) weight for the residue, which consisted mainly of cuticle and proteins. Gain or loss at this time averaged -0.5 mg $\pm$ S.D. 1.5 mg, $N=151$. Residue weight was then subtracted from dry weight to give fat content.

Statistical analyses follow the methods of Fisher (1932), Siegel (1956) and Sokal and Rohlf (1969). Most analyses were performed using the Statistical Package for the Social Sciences (Nie et al. 1975).

Results

One hundred and sixty-six of 313 wasps from 5 parental nests survived the winter. Of these, 36

Table 1. Means and standard deviations of dry weight, residue weight and fat content, for queens and subordinates from each parental nest

Variable	Parental nest	Queens			Non queens		
		$\bar{x}$	S.D.	N	$\bar{x}$	S.D.	N
Dry weight (mg)	1	109	–	1	122	15	16
	2	103	4	4	98	17	15
	3	83	23	4	71	8	17
	4	103	12	3	103	12	27
	5	101	5	7	84	13	33
Residue weight (mg)	1	90	–	1	95	12	16
	2	81	6	4	80	18	13
	3	65	21	5	58	7	17
	4	86	9	3	84	10	26
	5	83	5	7	67	11	32
Fat content (mg)	1	19	–	1	27	10	16
	2	23	5	4	17	5	13
	3	21	10	4	13	4	17
	4	17	2	3	19	3	26
	5	18	3	7	17	5	32

Table 2. Analysis of variance of the effects of parental nest and rank (queen or subordinate). * $P<0.05$, ** $P<0.01$, *** $P<0.001$

Variable	Degrees of freedom	Parental nest % of variance explained	Rank (queen or subordinate) % of variance explained
Dry weight	4	52***	2**
Residue weight	4	44***	1
Fat content	4	33***	2*
Wing length	4	56***	2*
# of Oocytes	4	4	20***
# of Oocytes with Yolk	4	4	20***
# of layable eggs	4	14***	18***
Length of largest Oocyte	4	5	8***

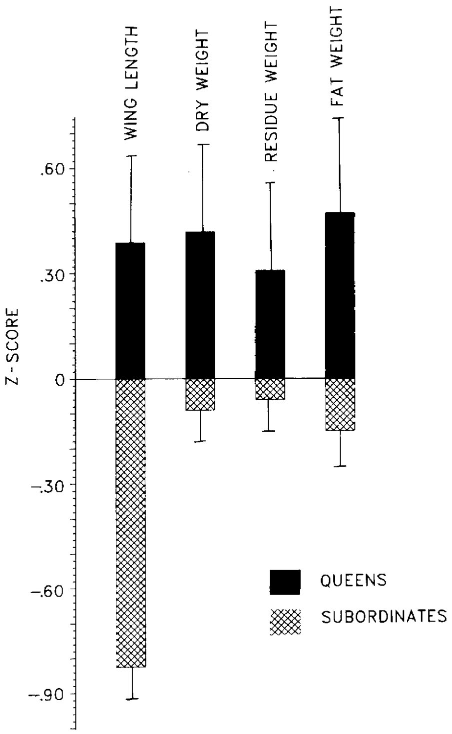

Fig. 1. Z scores and standard deviations for wing length, dry weight, residue weight and fat weight for queens and subordinates

were present on nests but not caught. All females were caught on 13 nests, all but 1 on 7 nests, all but 2 on 2 nests and on one nest each 4, 7 and 14 females were missed (Strassmann 1983). The females founded a total of 25 nests in groups of 1 to 16 ($\bar{x}=5.1\pm$S.D. 3.2), with two larger groups of wasps (21 and 28 females, respectively) reusing parental nests (see Strassmann 1983 for details). New nests were built within a few meters of their parental nest. All marked nestmates came from the same parental nest, indicating that nest founding occurs exclusively with relatives.

Females from different parental nests differed greatly in dry weight, residue weight, wing length, and fat content (Tables 1 and 2). Number of layable eggs was the only ovarian measurement that differed among parental nests (Table 2). Since wasps from different parental nests differed in size, weight, and fat content and females begin new nests only with others from the same parental nest, the effects of nest of origin must be controlled for before differences in dominance can be evaluated. For females from each parental nest, Z-scores were obtained for the dry weight, residue weight, fat content, and winglength of each individual, where $Z=(x-\bar{x})/\text{S.D.}$, and these scores were used in place of raw numbers in the following analyses. This method eliminates variation between parental nests by transforming the data into standardized deviations from the mean of each parental nest group (Fig. 1). Fisher's (1932) method of combining probabilities from independent samples gives similar results, and the Z-score method is applicable over a wider selection of analyses.

Queens had significantly more layable eggs, oocytes and oocytes with yolk, and the largest oocyte of queens was longer than that of subordinates (Strassmann 1983). This result is commonly observed, and relative ovarian development is often used as an indicator of dominance (Pardi 1948; Hermann and Dirks 1975; West-Eberhard 1975a; Strassmann 1981a). Queens, including single foundresses, were larger, heavier, and had more fat than subordinates (dry weight: *t*-test, $t=2.2$, $P<0.03$; fat content: *t*-test, $t=2.59$, $P<0.01$; and winglength: *t*-test, $t=2.09$, $P<0.04$, Fig. 1, sample sizes are given in Table 1). Differences in dry weight explained 6% of the variance between queens and subordinates. Differences in residue weight explained 5% of the variance; differences in winglength, 6% and differences in fat content, 3%. The queen was not always larger than her subordinates on individual nests (Table 1).

The measures of physical condition and ovarian development were analyzed to see to what extent they were intercorrelated ($P<0.05$ for all reported correlations). Dry weight was correlated with both residue weight ($r=0.92$) and fat content ($r=0.52$). Fat content was only slightly correlated with residue weight ($r=0.17$). Winglength was strongly correlated with dry weight ($r=0.85$) and with residue weight ($r=0.90$). Winglength was correlated with fat content ($r=0.45$). Winglength, dry weight, and residue weight may be indicators of overall body size. There were moderately high correlations among the measures of ovarian development, ranging from 0.44 to 0.76.

In addition to the differences between queens and subordinates, trends across ranks (from most subordinate to most dominant) can be examined when females are ranked according to degree of ovarian development. Dry weight was moderately correlated with all ovarian measures ($r=0.23$ to 0.43). Residue weight was similarly correlated, as was winglength. Fat content was moderately correlated with the number of oocytes ($r=0.32$), number of oocytes with yolk ($r=0.32$), and size of largest oocyte ($r=0.31$). Larger wasps and wasps with more fat were somewhat more likely to have more developed ovaries, however some of this fat comes from the oocytes themselves.

Since dry weight, fat content, residue weight and winglength are intercorrelated, partial correlations were performed to examine the independent effects of size and fat content. The correlation of fat content with ovarian measures is partly dependent on the association of fat with size measures, but the converse is not true. When fat content was controlled for, dry weight, residue weight and winglength were still correlated with the four measures of ovarian development ($r=0.25$–0.41). When residue weight was controlled for, the correlations of fat with number of oocytes ($r=0.23$), number of oocytes with yolk ($r=0.24$), number of layable eggs ($r=0.06$, N.S.) and size of largest oocyte ($r=0.26$) were less. Controlling for winglength reduced the correlations of fat with each of the four measures of ovarian development, so only the correlation with oocytes with yolk remained significant ($r=0.16$). No asymmetries in the effects of partial correlations were noted among the remaining variables (dry weight, residue weight and winglength). Controlling for one of these variables always greatly reduced the association of the others with ovarian measures; most partial correlations were not statistically significant. For example, the effect of controlling for winglength on the partial correlation of residue weight with number of oocytes ($r=0.15$) was similar to the effect of controlling for residue weight on the partial correlation of winglength with number of oocytes ($r=0.14$, N.S.).

Since correlations exist among most physical and ovarian variables, calculations of principal components were performed to examine differences in overall condition with dominance. Principal components analysis groups variables into factors which are not correlated with each other. The pattern of association of variables with factors may indicate that variables measure some common attribute. Additionally, tests using factor scores provide a way to separate differences due to rank from those due to correlations among variables. A principal components analysis of dry weight, fat content, winglength, number of oocytes, oocytes with yolk, layable eggs, and size of largest oocyte was performed using quartimax rotation (Nie et al. 1975).

Measures of ovarian development were highly correlated with the first factor, which explained 55% of the variance (Table 3). Measures of size (dry weight, residue weight, and winglength) were highly correlated with the second factor, which explained 20% of the variance. Fat content and number of oocytes with yolk characterize the third principal component, which explained 11% of the variance. Since yolk is fatty, this result was expected. Since fat content, size measures, and ovarian measures loaded high on separate factors, they were separate sources of variation since by definition principal components factors are not correlated.

Factor scores were obtained for all individuals on factors 1–3. Queens were then compared to subordinates for the three factors. Queens and subordinates differed significantly only on factor 1 (Mann-Whitney, $U=280$, $Z=4.93$, one-tailed $P<0.001$). The two groups did not differ significantly on factor 2 or factor 3, although the mean score of queens ranked above that of subordinates on both factors (Table 3).

Number of females on a nest showed no corre-

Table 3. **A** Principal Components Analysis Factor loadings after Quartimax rotation with Kaiser normalization for variables from all females. **B** Comparison between queens and subordinates from each factor. Mann Whitney U test for difference between queens and subordinates, *** $P < 0.001$; NS not significant

	Factor 1 (ovarian development)	Factor 2 (size)	Factor 3 (fat)
A.			
Dry weight	0.28	0.92	0.22
Residue weight	0.24	0.95	0.14
Fat content	0.22	0.29	0.93
Wing length	0.24	0.90	0.19
# Oocytes	0.83	0.28	0.03
# Oocytes with Yolk	0.90	0.16	0.85
# Layable eggs	0.65	0.14	−0.07
Size of largest Oocyte	0.86	0.18	0.07
Eigen value	4.42	1.58	0.86
% of variance explained	55	20	11
B.			
Mean Rank of each factor for:			
Queens	98.3	69.8	64.8
Subordinates	54.7***	60.0 NS	61.9 NS

lation with residue weight, dry weight, or winglength, indicating that there was no tendency for smaller females to form larger foundress associations ($r = 0.04$ to 0.09, N.S.). Number of females on a nest was uncorrelated with the queen's residue weight, dry weight, or winglength, so larger queens did not attract more subordinates. Fat content and the queen's fat content were also uncorrelated with number of females on a nest. Factor 1 was significantly correlated with number of females on the nest ($r = 0.24$, $P < 0.05$). *Polistes annularis* nests with more females are often observed to have subordinates with greater ovarian development (Strassmann 1983). There were no other significant correlations of number of females per nest with factors 2–3.

It is possible that females choose to begin new nests with natal nestmates that are as different as possible from themselves in size. This behavior would facilitate dominance hierarchy establishment, and can be detected by comparing variance in size of individuals on new nests as compared to variance in size among all females from the natal nest. Variances in winglength were calculated for females from each natal nest and each new nest, and no differences were found between any new nest and its natal nest (F tests). This indicates that females are grouping randomly with respect to size on new nests, a finding contrary to West-Eberhard's hypothesis that smaller subfertile females join larger, more fertile relatives.

Discussion

The purpose of this study was to investigate the role of size as measured by wing length, dry weight and fat content in foundress associations of *Polistes annularis*. *P. annularis* queens are larger and have more fat than subordinates emerging from the same nest, but these differences are small compared to inter-parental nest differences. Queens on some nests are smaller than subordinates from other nests, and queens are not invariably the largest female on a nest. Size of females has no relation to numbers of females from the natal nest or new nest. Variability in size between queens and subordinates is not great enough to indicate that larval feeding programs a female to be either a queen or a subordinate; also size is not bimodal.

Females from a given natal nest group on new nests randomly with respect to size. Taken together, these findings are inconsistent with the hypothesis that foundress associations occur when less fertile females join their more fertile sisters. These findings instead support the hypothesis that females group for reasons entirely independent of individual condition or size, but that a hierarchy based on ability (of which the measurements taken here are correlates) develops after associations are formed. The reasons for grouping of females may be quite independent from those which result in dominance hierarchy establishment in the group. Foundresses grouped together may be better able to resist nest or nest site usurpation which may be most critical when nest sites are scarce (hollow trees, etc.) (Gamboa 1978). Groups of females may be better able to defend the nest against predators, or to rebuild after predators have attacked (Gibo 1978; Strassmann 1981b). By increasing nest size early, foundress groups may be better able to produce workers early (Gamboa 1980) and avoid nest failure due to loss of all caretakers, the second most common cause of nest failure in *P. exclamans* (Strassmann 1981b). It is common for 5% or fewer of all nests begun to survive to produce reproductives (Strassmann 1981b). Larger foundress associations may increase the females' chances of having a nest in the 5% that produce any reproductives at all (Strassmann, Hughes and Lutz, unpublished).

Foundress associations in *P. annularis* are very interesting because they are especially large, highly variable, and females do not switch from nest to nest. Something appears to sort females into discrete groups of variable size. Females may be sorting into groups of closely related individuals. At any one time there is usually only 1 queen but queens often change over the season, and resulting broods may be mixtures of full sibs and more distant relatives (Strassmann 1981a). Recognition could be facilitated by age of female, or area of nest from which females emerged.

Previous speculations on dominance hierarchies in *Polistes* include the idea that dominant and subordinate females are fundamentally different and that these differences determine dominance rank. Gibo (1974) found in a laboratory study that some females of *Polistes fuscatus* failed to start nests and suggested that these females may be inferior to their sisters. Noonan (1981) found that *P. fuscatus* females varied more within than between nests and that queens were larger than subordinates, which supports West-Eberhard's (1967, 1969) concept of inferior individuals joining superior siblings in preference to attempting to start their own nests. Dropkin and Gamboa (1981) found that subordinate foundresses of *P. metricus* were similar in size to lone foundresses and that queens were significantly larger than either. No study has demonstrated a bimodal distribution in any measure of size which is what we would expect if larval feeding programmed individuals into two castes.

Haggard and Gamboa (1980) investigated size differences among workers, gynes and males over the season in *P. metricus*. They tested the hypothesis that queens might force some gynes into subordinate roles by comparing size variance among workers and gynes. Their finding that gynes did not vary more in size than workers argues against the hypothesis.

Craig (1983) states that the key area in which foundresses must vary for the subfertility hypothesis of West Eberhard (1975a) to work is in their egg-laying ability and not in their ability to work. In Craig's first model, subfertile females give up all their progeny to rear siblings. This resulted in selection for altruism only if altruists could rear sufficiently greater numbers of siblings. Subfertility would presumably be even more pronounced (or worker efficiency strikingly greater) before a female would give up her personal reproduction to raise her sister's offspring ($r = 3/8$). Subfertility itself seems unlikely to limit reproductive output; ability to feed and protect larvae is probably much more important. In the second model, females gave up no progeny, rearing all the eggs they could lay, and helping to rear the progeny of a relative after the needs of their own young were met. Since there is no cost in this model, relatedness between altruist and brood can be distant and variability in fertility can be slight and altruism will still occur. Because of these attributes Craig (1983) considers this second model to be a likely first step on the path to eusociality. However, a basic problem with this second model is that subfertile females must be on the same nest as their more fertile siblings before they can use their excess effort (if it exists!) to rear relatives. Queens of *Polistes* have not been observed to abandon a successful nest to join another nest as a subordinate. If a subfertile female joins a nest before laying any eggs, it is likely that she will be dominated and forced into laying few if any eggs. This will greatly increase the cost of helping. It is not necessary to assume that organisms are already partly social before they can exhibit dominance because this behavior is similar to territoriality contests found in many solitary organisms (Parker 1974). Also there is no obvious reason why presocial wasps should have had a greater variability in fertility than organisms that are solitary. This is especially true since variability in fertility is least likely of any trait to have a genetic basis (Falconer 1960). On the other hand, wasp nests may be particularly vulnerable to extrinsic factors such as nest predation which could be combatted by groups more effectively than by lone individuals. These factors, along with opportunities to become queens later in the season or to lay a few eggs on a successful nest, are likely to be important in the maintenance of foundress associations.

Röseler et al. (1980) conducted an elegant examination of the causes of variability in reproduction in *P. gallicus*. They found that the variability in ovary size, corpora allata size, and juvenile hormone synthesis increased greatly *after* dominance hierarchies were established. "... The lowered reproductivity of subordinated females is rather a consequence of dominance relations than the basis for its origin." (Röseler et al. 1980, p. 106). These findings contradict the assumption central to both of Craig's (1983) models – that subordinates are initially of lower fertility. It is interesting that Röseler et al. (1980) find no evidence for the subfertility hypotheses looking at physiological measures, corroborating our study which was based on physical measures of size.

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