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WASP REPRODUCTION AND KIN SELECTION: REPRODUCTIVE COMPETITION AND DOMINANCE HIERARCHIES AMONG *POLISTES ANNULARIS* FOUNDRESSES

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Polistes wasps are ideal subjects for studies on the evolution of social organization because all females beginning nests in the spring are mated and capable of functioning as egg-laying queens on their own nests, but some do not. Why they do not is the topic of this paper, and my research investigates the evolution of social behavior.

Evolutionary theory predicts that individuals behave in ways that result in their passing as many copies of their genes on to the next generation as possible. Classical natural selection models used number of offspring as the measure of reproductive success. But Hamilton (1964 a,b) recognized that under certain circumstances it was possible to pass on more genes by raising relatives that were not offspring. For potential mothers to pass on more genes by raising the progeny of sisters, aunts or other relatives, it is necessary to raise greater numbers of them, to make up for the loss in relatedness. In *Polistes* wasps abdicating mothers—potential queens—do this.

In the spring *Polistes annularis* females form nesting groups in which some females lay more eggs than others. Marking studies have shown that the females in these groups were born on the same nest the preceding autumn (Strassmann 1979). Therefore, they may be sisters, sharing 3/4 of their genes (because Hymenoptera have haploid males[1]), if their mother (the egg layer in the autumn nest) was mated to only one male (Metcalf and Whitt 1977, Metcalf, 1980)[2]. On a spring nest a female that is helping her sister is raising nieces (3/8 shared genes) who are more distantly related than offspring (1/2 shared genes[3]). According to Hamilton's theory of kin selection, for an aunt to pass on more genes this way, she must raise at least 1/3 more nieces than offspring, had she exercised her "mother option." I have found that a female alone on a nest raises about three offspring, while each female on a nest with 2-7 females, raises about five Strassman, in prep.). This is enough more nieces to account for females joining groups and raising nieces, instead of becoming mothers and raising their own offspring.[4]

EGG LAYING BY SUBORDINATES

The female that *lays eggs* in the nest gains most, but how far is the (dominant) queen willing to escalate a fight to maintain absolute control and lay all of the eggs? The queen has the most to lose if subordinates leave (see appendix note 5 for the concept of *offspring-equivalents*, the measure central to these considerations and comparisons), and she is the one that controls subordinate reproduction. Evolutionary theory predicts that she will allow some egg-laying by subordinates.

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[1]Superscripts refer to notes in the appendix.

What proportion of the eggs should a queen allow the subordinates to lay? An equilibrium will be reached when the queen and the subordinates lose equal amounts by leaving the group (Parker 1974). If all females are able to raise identical numbers of offspring, were they to form individual nests, then all are predicted to lay equal numbers of eggs in the communal nest, unless the advantage of being in a group (measured in numbers of offspring raised) is reduced when all females lay because the efficiency that results from a division of labor is lost. However, it is likely that the queen is somewhat more physically fit than her subordinates, (since she won the fights for queenship), and therefore could probably raise more young were she alone than could her subordinates were they alone.

In this paper, I report and discuss the development of the interactions of females in a group, from nest initiation (in March) through the maturation into adult workers of the first eggs laid, to determine exactly how foundresses divide up egg laying and nest chores and what changes occur as spring progresses. The question asked is: on nests with more than one foundress do subordinates have opportunities for direct reproduction, as well as the opportunity to raise relatives? Of concern are the females born and mated in the previous autumn, that hibernated, and then in spring began nests. Worker females born in spring are not considered and their behavior is not included. Males do not participate to any extent, and there are few of them in the spring, so they are not part of this story either.

Study Site, Methods and Behavior Definitions

The study site was a limestone cliff overlooking a reservoir 48 km (30 miles) west of Austin, Texas (Fig. 1). The nests occurred right on the limestone cliffs that face west where they are protected from sun until 1400 hrs.

I marked females on the nests they emerged from in the autumns of 1976-1979 (marks were individually-coded enamel spots). Wasps were observed for 2-26 days and for 6-20 hours each day.[6] Behaviors were recorded as classified below. Two nests contained only eggs, seven had eggs and larvae, five had eggs, larvae and pupae, and four had eggs, larvae, pupae and workers. During observations on two nests containing eggs and larvae, the queens were dethroned—one by a subordinate and one by a queen from a neighboring nest that had been destroyed (Table 1).

Ideally in a study of the behavior of animals in groups, all behaviors are recorded—what each individual does at any given time, the duration of each behavior, and where it occurred—for 24 hours a day. This was not possible in this study, so I used a number of conventions: (1) It was assumed that a daytime sample of behavior that lasted 6 to 20 hours was representative. (2) All behaviors not directly involving another individual were recorded without noting where the others were at the time. Interactive behaviors were recorded as pairs, one female the subject, the other the object. If a female arrived at the nest and three others took some caterpillar meat from her, these were recorded as three separate exchanges. (3) Behavior durations were not timed, though total observation time was noted. Most behaviors took little time and did not vary much in duration. Therefore, counting the times an individual performed a given behavior allowed a comparison of nestmates and females on different nests.

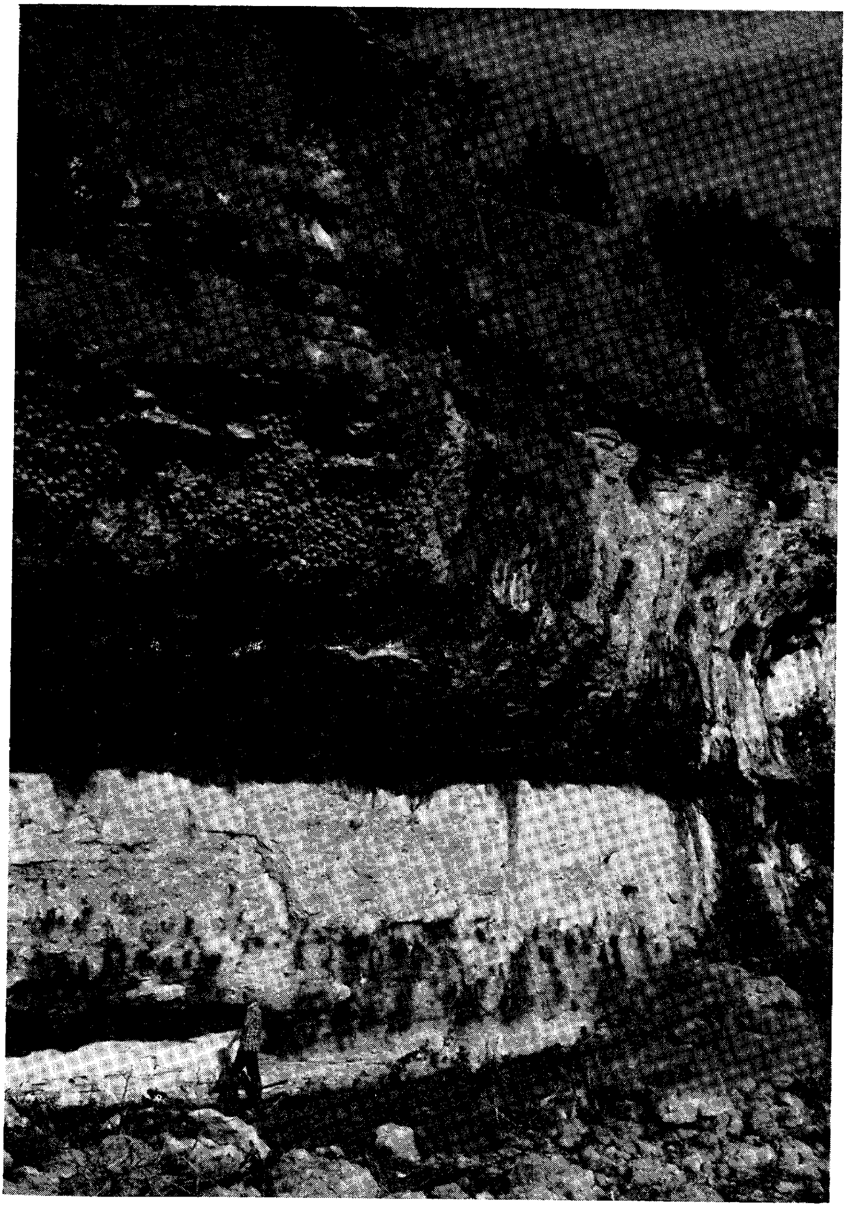

Fig. 1. Limestone cliffs where *Polistes annularis* nests were studied.

Interactions classified as aggressive ranged from touching with antennae, to chewing or climbing on another while chewing on her and attempting to sting her.[7] Chewing was by far the most common aggressive behavior. Since there were no systematic differences in which of these aggressive behaviors

TABLE 1. GENERAL CHARACTERISTICS OF *Polistes annularis* NESTS INVOLVED IN THE STUDY, AND A SUMMARY OF SOME BEHAVIORS ASSOCIATED WITH DOMINANCE.

Nest Number	Dates Observed	No. of Hrs. Observed	Most Advanced Brood Type	No. of Females	No. of Eggs Laid	% Eggs Laid by Queen	Tailwags Per Hr.	% of Tailwags Performed by Queen	Smears Per Hr.	% of Smearing Performed by Queen	Aggressive Acts Per Hour	Aggressive Acts Per Female Per Hr.	% Aggression Performed by Queen	% Aggression by Subordinate on Dominants
59	III/19-IV/1	20	eggs	3	7	57	2.9	100	3.3	65	5.7	1.9	92	0
55	III/19-IV/1	20	eggs	4	4	75	4.1	95	7.9	61	3.1	0.8	92	2
49	III/30-IV/11	10	larvae	10	1	100	10.8	92	2.2	9	7.1	0.7	63	4
50	III/31-IV/10	10	larvae	8	5	80	7.2	83	1.8	89	8.5	1.1	66	8
44	III/19-IV/16	20	larvae	15	6	33	5.5	59	1.7	0	1.6	0.1	13	13
179	IV/2-IV/10	11	larvae	3	2	100	1.3	100	2.6	71	1.7	0.6	95	0
Tony	III/30-IV/12	15	larvae	6	2	50	24.1	92	2.1	50	22.1	3.7	69	5
65	IV/2-IV/10	10	larvae	7	1	100	7.7	100	3.1	77	6.2	0.9	76	10
2	IV/8-IV/23	20	pupae	23	11	36	14.3	29	3.3	45	14.5	0.6	23	4
W75	IV/19-IV/20	06	pupae	7	2	100	19.2	68	0.3	50	4.7	0.7	64	4
P18	IV/19-IV/20	06	pupae	4	0	—	15.0	80	1.8	55	5.0	1.3	93	0
60	IV/13-IV/30	08	pupae	6	0	—	8.8	62	0.3	0	1.9	0.3	64	14
Q1	V/9-V/10	06	pupae	3	1	100	9.7	93	0.3	100	3.2	1.1	95	5
Q2	V/9-V/10	06	workers	7*	1	100	12.7	75	0.2	0	0.2	0.0	100	0
Q3	V/19-V/20	06	workers	6*	2	100	5.0	57	0.0	—	1.3	0.2	38	13
Q4	V/19-V/20	06	workers	5*	0	—	8.0	98	0.0	—	0.3	0.1	0	50
55	V/16-V/20	10	workers	2*	2	100	13.6	70	0.5	0	1.6	0.8	100	0
102†	III/22-IV/2	06	larvae	11	2	50	24.3	53	0.8	0	30.4	2.8	55	8
102‡	IV/2-IV/8	04	larvae	12	3	33**	72.0	82**	4.2	28**	70.8	5.9	60**	13
24#	III/17-IV/11	12	larvae	9	3	33**	27.0	68**	9.4	48**	27.3	3.0	46**	2

*These nests have workers not included in table.
**Calculated for new queen.
†Before subordinate takeover.
‡After subordinate takeover.
#After takeover by females from another nest.

occurred among females, all were combined for this analysis and their total for each female was used to establish a linear dominance hierarchy.[8]

Data on 12 behaviors are considered here. Other behaviors occurred but these 12 cover the important activities including dominance interactions, egg laying and brood care.

(1) *Tailwagging* is vibrating the abdomen from side to side across the nest. Since only dominant females do this it may spread a "dominance pheromone." (See Lloyd, this Symposium). This behavior is usually performed repeatedly as the female walks across the nest antennating cells containing eggs. Each tailwag takes less than a second. (2) *Check cells* is often performed in conjunction with tailwagging. It is also performed by a female with a load of pulp in her mandibles as she searches for a cell to enlarge, or for a place to begin a new cell. Cells that are antennated usually contain eggs and not larvae. The female may be checking for empty cells in which to lay an egg. (3) To *lay an egg,* a female inserts her abdomen into a cell, extrudes her sting, and holds it out of the way. Laying an egg takes about 2 min. (4) *Smearing* is a slow-motion version of tailwagging and is directed to the nest pedicel about 70 percent of the time. Smearing deposits an ant-repellent chemical on the pedicel (Jeanne 1970). (5) *Pedicel nibbling* consists of depositing a secretion on the pedicel, and the back of the nest and substrate near the pedicel, by moving the mandibles over the surface for 2-3 minutes. When this secretion dries, it is hard and transparent like lacquer. (6) *Building* is either adding onto an existing cell, or building a new cell. A ball of pulp is tamped into place with the mandibles while the female touches both sides of the wall under construction with her antennae. Building typically takes about 4 min. Here beginning a new cell is not distinguished from adding onto a cell. However, all eggs were laid in cells that had just been built by that female except the listed cases of egg eating, so egg laying and building a new cell occur at the same frequencies. (7) *Arriving with pulp.* Common sources of pulp are weathered wood, and weed stems. The average length of a trip for pulp is 11 (S.D.=10, N=29) min. and the median trip length is 9 min. (8) *Arriving with caterpillar.* Caterpillars are the principal food of the larvae, and hunting for them takes 30 (S.D.=21, N=18) min.; the median trip length is 27 min. This is probably the most difficult and risky task for wasps (since they are most vulnerable to predators while off the nest walking on vegetation), and involves the longest time away from the nest. (9) *Arrive with nothing visible* includes returns when females bring back nectar or water (which are usually carried in the crop and therefore not visible), or nothing. Such trips average 19 (S.D.=19, N=23) min., and the median trip length is 8 min. The difference between the mean and the median is probably the result of mixing different types of trips since trips for water which are included here because the water is not usually visible, usually take very little time. (10) *Leave* is always by flight and is usually preceded by a quick walk across the nest face. (11) *Exchange with larvae* usually means an adult wasp is feeding a larva, but larvae will sometimes spit up a drop of liquid for the adult, and it is often not possible to tell who is feeding whom, unless the wasp just returned to the nest with caterpillar or just exchanged with someone who did. Therefore, both behaviors are grouped here. Each exchange takes several seconds. (12) *Fan nest* is done by buzzing the wings when standing on the nest. This cools

the nest by evaporation when water has been deposited on the cell walls. Fanning is usually done on very hot days when the sun is on the nest, and lasts from 1-7 min.

Because behavioral data are not normally distributed, the statistical analyses presented here are nonparametric. Means between two categories are compared using the Mann-Whitney U test, and Kendall Tau correlations are used (Siegel 1956). For the sake of space values of Mann-Whitney U's are not given. Whenever two means are stated to be different, they are significant < 0.05 level. All correlations are also significant < 0.05 level.

Nest Initiation

Females return to their parental nest in the spring, just as they do on warm days all winter (Strassmann 1979). They then leave the nest and walk about on the cliff usually within 3 m of the nest and antennate the substrate. Before new nests are begun, small groups form on the cliff face. Females in these groups are always from the same parental nest and interact extensively, chewing and antennating each other, and remaining close together. When a flying wasp approaches a group all group members spread their wings. They chase away non-nestmates, but allow nestmates to land. Antennal battles take place within these groups, and I have observed them at no other time. Females facing each other clash antennae, first those of one female contact the other's from above, then vice-versa. These confrontations may go on for several minutes before the females separate. Sometimes they escalate into grappling and both females rear up on their hind legs, grab at each other with the first two pairs of legs, and slap antennae. These grouped females return to hibernacula (protected cracks in the cliff where they hibernated) at night. After a few days one female in the group begins a nest. A load of pulp is used for the nest base, another load or two for the pedicel and then the first cell is built. This females begins as the principal egg layer in the new nest. In general, females do not switch from one new nest to another, and do not join other nests begun by females born on the same parental nest (Strassmann, in prep.).

Table 1 presents data on the nests observed in this study. Some of the nest variables in Table 1 were correlated. Number of females on the nest was positively correlated with number of eggs laid per hour ($\tau = 0.28$), number of tailwags per hour ($\tau = 0.37$) and number of aggressive acts per hour ($\tau = 0.36$). Number of females was negatively correlated with percent eggs laid by the queen ($\tau = -0.31$), percent tailwags by queen ($\tau = -0.47$), percent smears by queen ($\tau = -0.51$) and percent aggression by queen ($\tau = -0.53$). Queens control larger nests less absolutely than they control smaller nests.

Dominance Hierarchies

I ranked females on each nest in "dominance hierarchies" according to who chewed on (or otherwise attacked) whom.[8] It was easy to rank the top five individuals but toward the lower end of the hierarchy (on nests with more than five females) individuals are less clearly differentiated, and neither initiate nor receive much aggression. Some of the time females of ranks above (>) 5 could not be ranked among themselves according to aggression. A female was assigned a lower numbered rank if she had laid an egg or tailwagged more. This only involved a few of the 38 percent of all females of ranks above five. Individuals of ranks 1 through 5 were compared pairwise to see if females of different ranks also performed different frequencies of other behaviors. Comparisons were done among nests with the same brood types so changes in behavior over time would not add confusion.

The top ranking female (rank 1), the queen, differed in many behaviors in pairwise Mann-Whitney U comparisons with her subordinates (ranks 2-5), and will be discussed in more detail below. Females of ranks 2-5 varied in aggressive rank, but not consistently in frequency of performance of other behaviors as determined by Mann-Whitney U comparisons; therefore in the comparisons of subordinate ranks with queens, ranks 2 and higher were combined (Tables 2-3).[9] Mean frequency of each behavior is given for queens (Table 2) and non-queens (Table 3) on nests with different brood stages.

Queens laid more eggs and tailwagged more often than their subordinates on nests of all stages. Queens checked more cells and were more aggressive than subordinates on nests with larvae, pupae or workers. Queens smeared more often on nests with larvae or pupae. No queen ever foraged for caterpillars. On nests with workers, subordinate foundresses did not forage for caterpillars. On nests with larvae and nests with pupae, all caterpillar foraging was done by subordinate foundresses. On nest 2, four of the eggs laid were eaten by others. On this nest, all eggs eaten were laid by subordinates and all egg eating was done by subordinates. On nest 55, the queen ate one egg laid by a subordinate and replaced it with her own. This is the only egg eating I observed in this study.

TABLE 2. MEANS AND STANDARD DEVIATIONS OF BEHAVIORS PERFORMED PER HOUR BY QUEENS ON NESTS WHOSE MOST ADVANCED BROOD ARE A. EGGS B. LARVAE C. PUPAE, AND D. WORKERS.

Behavior	A. Eggs, N = 2 $\bar{X}$	S. D.	B. Larvae, N = 6 $\bar{X}$	S. D.	C. Pupae, N = 5 $\bar{X}$	S. D.	D. Workers, N = 4 $\bar{X}$	S. D.
Tailwags	3.40	0.71	8.36	7.39	8.65	3.98	7.42	3.16
Check cells	4.63	4.77	4.82	4.53	2.88	2.50	2.94	2.16
Lay eggs	0.18	0.04	0.16	0.13	0.14	0.14	0.13	0.16
Smear	3.48	1.87	1.18	0.94	0.59	0.63	0.00	0.00
Nibble pedicel	0.75	0.00	0.19	0.35	0.13	0.22	0.00	0.00
Build	0.78	0.18	0.63	0.32	0.52	0.56	0.10	0.20
Arrive with pulp	0.53	0.18	0.07	0.13	0.17	0.24	0.00	0.00
Arrive with caterpillar	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Arrive	0.30	0.07	0.15	0.18	0.14	0.16	0.00	0.00
Leave	0.80	0.21	0.11	0.21	0.28	0.34	0.04	0.08
Feed larvae	0.00	0.00	2.31	2.27	3.00	3.50	0.38	0.29
Fan	0.30	0.42	0.67	1.59	0.03	0.08	0.03	0.05
Attack wasp	4.00	1.70	5.32	5.29	3.02	1.26	0.57	0.72
Be attacked by a wasp	0.00	0.00	0.12	0.21	0.06	0.09	0.00	0.00

BEHAVIORAL DIFFERENCES AMONG FEMALES ON NESTS WITH DIFFERENT STAGES OF BROOD

The behavior of queens and subordinate foundresses changed as the season progressed and brood developed from eggs to workers (Tables 2, 3). Queens were more active on younger nests. They smeared more, pedicel-nibbled more, built more, arrived with pulp more frequently, arrived and left more often, and were more aggressive (Table 2). Behaviors that most distinguished queens from subordinates, such as tailwagging, cell checking and egg laying did not change significantly over the season. In general, queens on younger nests were less specialized and did more work than queens on older nests.

Subordinates laid more eggs on nests with only eggs than they lay on later nests (Table 3). Subordinates also smeared more, built more, arrived with pulp more often, and left more frequently on nests with eggs than they did on nests with other stages of brood. Subordinates worked more on nests with pupae, and arrived with caterpillars and pulp more often, than when on nests with larvae. Then, when workers emerged, subordinate foundresses dramatically decreased many behaviors and did less smearing, pedicel nibbling, building, arriving (behaviors 7-9), leaving, and feeding of larvae, and were involved in less aggression than subordinates on earlier nests.

Kendall τ correlations among all behaviors were calculated for females

TABLE 3. MEANS AND STANDARD DEVIATIONS OF BEHAVIORS PERFORMED PER HOUR BY SUBORDINATE FOUNDRESSES ON NESTS WHOSE MOST ADVANCED BROOD ARE A. EGGS B. LARVAE C. PUPAE, AND D. WORKERS. SAMPLE SIZE FOR 'ARRIVE WITH PULP' AND 'ARRIVE WITH CATERPILLAR' IS 27 FOR NESTS WITH LARVAE AND 16 FOR NESTS WITH PUPAE.

	A. Eggs, N = 5		B. Larvae, N = 43		C. Pupae, N = 38		D. Workers, N = 16	
Behavior	$\bar{X}$	S. D.	$\bar{X}$	S. D.	$\bar{X}$	S. D.	$\bar{X}$	S. D.
Tailwags	0.05	0.09	0.15	0.33	0.61	1.42	0.49	0.66
Check cells	2.28	2.76	0.82	1.16	0.32	0.48	0.87	1.14
Lay eggs	0.04	0.04	0.01	0.03	0.01	0.04	0.00	0.00
Smear	0.85	0.52	0.15	0.20	0.08	0.12	0.02	0.05
Nibble pedicel	0.15	0.14	0.04	0.11	0.07	0.11	0.00	0.00
Build	0.54	0.23	0.22	0.22	0.34	0.30	0.07	0.17
Arrive with pulp	0.46	0.25	0.06	0.10	0.22	0.16	0.06	0.13
Arrive with caterpillar	0.00	0.00	0.08	0.11	0.26	0.31	0.06	0.15
Arrive	0.33	0.21	0.31	0.28	0.36	0.39	0.08	0.15
Leave	0.79	0.39	0.36	0.29	0.44	0.44	0.20	0.29
Feed larvae	0.00	0.00	0.70	1.10	2.20	2.36	0.17	0.14
Fan	0.70	1.48	0.44	1.09	0.10	0.30	0.10	0.38
Attack wasp	0.14	0.19	0.35	0.66	0.37	1.11	0.07	0.15
Be attacked by a wasp	1.74	1.21	1.08	1.66	0.75	0.89	0.21	0.40

on nests of each of the four brood stages, for convenience here named for the most advanced stage only. Nests with larvae also have eggs, etc. A significantly correlated pair of behaviors means a female performing one behavior frequently is also likely to perform the other behavior frequently. Higher values of the variable "rank" indicate a more subordinate female. Only nests without takeovers were used. Correlations are given in parentheses in this order: (1) nests with eggs, (2) nests with larvae, (3) nests with pupae, (4) nests with workers. Among females on nests of each brood stage, rank was negatively correlated with tailwagging (-0.79, -0.53, -0.70, -0.74); egg laying (-0.70, -0.46, -0.39, -0.41); aggression (-0.90, -0.65, -0.59, -0.39); cell checking (-0.41,n.s., -0.59, -0.67, -0.51); smearing (-0.62, -0.38, -0.37, -0.03,n.s.); and building (-0.58, -0.32, -0.36, -0.22,n.s.). On nests with larvae and pupae, more subordinate females foraged more for caterpillars (0.35, 0.60). The conclusion from these results is that highly ranked females (ranks 1-3) behave more like queens than do subordinate females (ranks $\geqq 4$). This is not a circular argument since it is *who chewed on whom* that is used to rank almost all females. Who chewed on whom is not the same as how many times any one female chewed on other females. The correlations indicate whether other behaviors vary predictably with rank.

The Mann-Whitney U comparisons between pairs of ranks (other than 1 i.e. queen) disclosed few differences in contrast to these results. Probably the differences were not large enough to be clear in 2-category comparisons even though the trends across ranks were significant as seen in the correlations.

DISCUSSION

Reproductive competition is clearly intense among these females, and they establish a linear dominance hierarchy on the nests. The queen and dominant females laid more eggs, tailwagged more, checked more cells, and were more aggressive, while subordinate females foraged more for caterpillars and were the victims of aggression more often. Queens differed more from all subordinates than subordinates of different ranks varied among themselves. Subordinates behaved more like queens on nests with eggs and nests with workers, and differed most from queens on nests with larvae and pupae. This is probably because subordinate work was most vital on nests with larvae and pupae, where subordinate foundresses alone were responsible for raising the brood.

Queens laid a mean of 80 percent of the 47 eggs laid in the 16 nests without takeovers that were observed 190 hours. On the two nests with takeovers, the new queens laid only two of the six eggs, so new queens do not immediately attain control (Table 1). The queen was overthrown on two of 18 nests, once by a subordinate and once by a group of intruders from a neighboring nest. Thus subordinates lay eggs when they can, sometimes overthrow the queen and they perform dangerous work such as caterpillar foraging only when it is essential to the success of the nest, i.e. before any workers have emerged. This is consistent with a view of subordinates that considers direct reproduction very important. Additional chances to take over the nest also occur later in the season, beyond the period of this study. When queens die in the presence of workers and subordinate foundresses, a subordinate foundress and not a worker always takes over (Strassmann in prep.).

Offspring Equilvalents Raised by Females of Various Ranks

Using the data obtained here, calculations of numbers of offspring equivalents can be made for females of different ranks on nests of different sizes. It is necessary to make several estimates from the data that may not always hold. First, we assume that foundresses are all related to each other as full sisters. Each foundress on a multiple foundress nest produced a mean of five young; on a one-female nest, three young were produced. The queen laid a mean of 80 percent of eggs. In this study one of the seven nests with larvae was taken over by a subordinate, and the queen fell then to bottom rank. In addition, at least 20 percent of all nests lost their queens after the period of this study (Strassmann, in prep.), so we will assume the second-ranked female takes over the queenship on a total of 35 percent of the nests, the queen then dropping to the bottom and everyone else moving up a notch. Since rank is negatively correlated with egg laying, I will assume that the second ranked female lays 15 percent of the eggs and the third ranked female lays 5 percent of the eggs, and more subordinate females lay no eggs. Using methods outlined in the introduction and detailed in the appendix, Table 4 gives numbers of offspring equivalents produced on nests with 1, 2, 4, 7 and 15 founding females.[10] All females produce more offspring equivalents than the three they would have produced on a lone nest, but the queen and the second ranked female do much better than more subordinate females. The top two females also are attributed with more offspring equivalents, the more females there are on the nest. Under this model it is easy to see why a female joins a queen since the joiner will have 4.77 offspring equivalents, 1.77 more than she could have produced alone and only 0.46 less than the queen produces, supporting the theory of kin selection. Both females will encourage additional females to join because their inclusive fitnesses rise, but the females ranked ≧ 3 do not produce many more offspring than they would have produced alone, thus, they have less "incentive" to join large groups.

All of these calculations assume all females on a nest are full sisters. However, a queen laying 80 percent of the eggs, using 90 percent sperm

TABLE 4. Numbers of offspring equivalents produced by females of given ranks on nests with 1, 2, 4, 7 or 15 females. See text for assumptions made in calculations, and see appendix for calculations.

Number of females on nest	Female rank						
	1	2	3	4	5	6	7
1	3.00	—	—	—	—	—	—
2	5.23	4.77	—	—	—	—	—
4	6.68	5.57	3.96	3.79	—	—	—
7	9.11	6.88	3.96	3.79	(Females 5-7 3.75 each)		
15	15.61	10.38	3.96	3.79	(Females 5-17 3.75 each)		

from one male means 72 percent of all females likely to nest together are actually full sisters. Direct reproduction becomes much more important in calculating the offspring equivalents raised by subordinates on nests where the queen is their half sister (r = 1/4), cousins (r = 3/8), or half cousin (r = 1/8). Calculations of offspring equivalents produced under these circumstances are not included in this paper.

A number of testable adjustments in the model may explain the occurrence of large groups of foundresses, although testing them is beyond the

TABLE 5. COMPUTATION OF OFFSPRING EQUIVALENTS RAISED BY FEMALE OF EACH RANK.

	% Eggs laid	No. offspring raised	Proportion shared genes	Offspring equivalency factor	
Queen					
A= direct reproductive success	= 0.8	(5)	(1/2)	(2)	=4.00
B= indirect reproductive success	= 0.2	(5)	(3/8)	(2)	=0.75
C= credit for nieces rank 2 female raised					=1.06
D= credit for nieces rank 3 female raised					=1.19
E= credit for nieces rank 4 females & up raised (where x = total number of foundresses)					(x-3) (1.25)
Total offspring equivalents raised (nest with at least 3 foundresses):					= 7.0 + 1.25 (x-3)
Rank 2 Female					
A= direct reproductive success	= 0.15	(5)	(1/2)	(2)	=0.75
B= indirect reproductive success	= 0.85	(5)	(3/8)	(2)	=3.19
C= credit for nieces raised by queen					=0.19
Total offspring equivalents raised:					=4.13
Rank 3 Female					
A= direct reproductive success	= 0.05	(5)	(1/2)	(2)	=0.25
B= indirect reproductive success	= 0.95	(5)	(3/8)	(2)	=3.56
C= credit for nieces raised by queen					=0.06
Total offspring equivalents raised:					=3.87
Females of Ranks 4 and Up					
B= indirect reproductive success	= 1.00	(5)	(3/8)	(2)	=3.75
Total offspring equivalents raised:					=3.75

scope of this paper. (1) Perhaps all parameters of the model are correct, and low ranking subordinates join and lay no eggs because they are in fact of much lower physical fitness than the top two females. This could be tested by comparing size, weight, fat and nitrogen content of females of different ranks, and by determining whether numbers of offspring produced by lone foundresses varies according to the lone foundress's size, dry weight, etc. (2) In this model it is assumed that all nests with more than one foundress produce five offspring per foundress. Perhaps larger groups of foundresses actually produce more reproductive offspring, so this number should be increased for larger groups of females. This could be determined more precisely by counting offspring produced at the end of the season, and not just at the end of the foundress period. This change may increase the subordinates' number of offspring equivalents raised. (3) Perhaps takeovers by subordinates and egg laying by subordinates increases on nests of larger size. In this study it was only possible to assign an overall level of egg laying by subordinates because of the small sample sizes. However, queens have less control on nests with more females, since number of females is negatively correlated with percent of eggs laid by queen (—0.31), percent tailwags by queen (—0.47), percent smears by queen (—0.51), and percent aggression by queen (—0.53), and number of females is positively correlated with number of eggs laid (0.28). Perhaps increased egg laying by subordinates on larger nests increases the numbers of offspring produced by subordinates and decreases the number attributed to the queen.

Polistes wasps have been extensively studied and inclusive fitness has been tested using other species, (West Eberhard 1969, Metcalf and Whitt 1977, Gibo 1978, Noonan 1981, Strassmann 1981). Pardi (1948) first described dominance hierarchies in *Polistes* and related high rank to egg laying, a finding supported by West (1967). Egg laying by subordinates is common in other *Polistes* species. Noonan (1981) found subordinates lay enough eggs so a second-ranked female on a two-female nest raised more offspring equivalents than she could have raised alone. Noonan also found aggression increased when eggs that would be reproductives instead of workers were laid. Gamboa (1978) found that subordinates helped deter takeovers by non nestmates, but that subordinate foundresses were chased off the nest by workers when workers emerged, a marked contrast to the situation in *P. annularis*.

SUMMARY

Polistes annularis foundresses can be ranked in a dominance hierarchy

TABLE 6. CALCULATION OF OFFSPRING EQUIVALENTS RAISED BY FEMALES OF DIFFERENT RANKS, FROM TABLE 5 AND ASSUMING THE QUEEN IS OVERTHROWN BY RANK 2 FEMALE 35% OF THE TIME, AND THEN THE QUEEN SUBSEQUENTLY BECAME A BOTTOM-RANKED FEMALE.

Queen	[7.00 + 1.25 (x-3)] 0.65 + (3.75) 0.35	= 5.86 + 0.81 (x-3)
Rank 2 female	(4.13) 0.65 + [7.0 + 1.25 (x-3)] (0.35)	= 5.13 + 0.44 (x-3)
Rank 3 female	(3.87) (0.65) + (4.13) 0.35	= 3.96
Rank 4 female	(3.75) 0.65 + (3.87) 0.35	= 3.79
Rank 5 female and up	(3.75) 1.00	= 3.75

according to aggressive behaviors. Females at the top of the hierarchy lay more eggs, tailwag more, and smear more while females at the bottom of the hierarchy forage for caterpillars more. The top-ranked females or queens differ more from all their subordinates than the subordinates differ among themselves. Subordinates are most different from queens on nests with larvae and pupae as the most advanced brood stages. On nests with only eggs, queens forage and differ little from subordinates. When workers emerge from the nest, subordinate foundresses stop working. On average queens lay 80 percent of all eggs, and subordinates overthrow queens on about 35 percent of all nests: thus, highly ranked subordinates have opportunities to lay eggs. When reproductive success is calculated using the concept of offspring equivalents, it is found that subordinates produce more offspring equivalents as subordinates than they would have by nesting alone. The larger the group of foundresses, who are assumed to be sisters, the greater the number of offspring equivalents attributed to the queen and the second-ranked female. These findings support the theory of kin selection.

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APPENDIX

[1]Since males are haploid, all the sperm they produce is identical, and sisters have 100 percent of their father's genes in common. Mothers are diploid, and so sisters share half of their mother's genes, just as in all other diploid organisms. Half of a female's genes come from her mother and half come from her father, so sisters are related by 1 x 1/2 (father) plus 1/2 x 1/2 (mother) equals 3/4 shared genes.

[2]If sisters share the same father (as they must do to be full sisters), they share 3/4 of their genes. If they have different fathers, they will be related as half sisters and will share only 1/4 of their genes, all through the mother. However, in two species of *Polistes*, Metcalf has shown that queens usually mate twice but use one male's sperm to father 90 percent of their daughters, (the other male fathers only 10 percent), so most sisters are full sisters and share 3/4 of their genes.

[3]In most cases a niece will be the daugther of her aunt's full sister, and will therefore be related to her aunt by 3/8, which is exactly half the amount sisters are related to each other (3/4). A mother contributes only half the genes to an offspring, and the father contributes the other half. An aunt is related to her niece by 3/8, which is 1/8 less than the relatedness of a mother to her own daughter, which is 1/2.

[4]Numbers of offspring a female raises is calculated at the end of the foundress period in May. Subsequently, young are raised by both workers and foundresses. Most but not all of the females and males who mate and become queens are raised by workers at the end of the season, in August.

Numbers of young raised at the end of the foundress period are correlated with the numbers of reproductive progeny that eventually emerge in August. A female alone raises 3 offspring (3 x 1/2 x 2) while a female raising nieces is raising 3.75 offspring equivalents, or 5 x 3/8 x 2, where 3/8 is her relatedness to nieces, 5 is the number of nieces she raises, and 2 is the constant all terms are multiplied by to get offspring equivalents. (see next note).

[5]Offspring equivalents equal the product of the number of young raised twice the fraction of shared genes, so an offspring is 1/2 x 2, (West Eberhard 1975). In the simple case of a 2-female versus a lone-female nest, the lone female raises 3 offspring-equivalents (3 x 1/2 x 2), a subordinate raising nieces 3.75 (5 x 3/8 x 2), while the egg-laying queen raises 6.25 (5 x 1/2 x 2) + 1.25, where the 1.25 is the queen's credit for the extra needed for the worker's 3.75 offspring equivalents to make up the 5 females raised by that worker. Thus if the association breaks up, the worker loses 0.75 offspring equivalents and the former queens loses 3.25 offspring equivalents. If there are more than 2 females on the nest, the offspring equivalents for any one worker stays the same while the offspring equivalents attributed to the queen goes up by 1.25 for every additional subordinate assuming the queen is the only egg layer. So on a nest with 10 females—a queen and 9 subordinates—3.75 offspring equivalents are produced by each subordinate and 11.25 offspring equivalents are attributed to the queen.

[6]Eighteen nests were observed for a total of 212 hours. Nest 55 was observed when it contained only eggs and again with workers. Nest 102 was observed before and after a subordinate overthrew the queen. Nest 24 was observed just after a group of females took over the nest when their own nest had been destroyed.

[7]One wasp touching another with her antennae is included with aggressive behavior because this behavior occurs in the same manner as more aggressive behaviors. Females who were chewed on were also antennated.

[8]All subordinates ranked as such by this method chewed on their superiors an average per nest for all subordinates combined of only 8 $\pm$ S.D. 11 percent of the time. The rarity of subodinates chewing on dominants indicates that the dominance hierarchies in these wasps are much stricter than those found in primates.

[9]Significant differences between pairs of ranks 2-5 include that on nests with larvae, ranks 2 and 3 did more cell checking than rank 5. On nests with pupae, rank 2 females did more tailwagging than ranks 4 or 5. Rank 2 also did more building than rank 4 while rank 3 arrived more often than rank 4. On nests with workers, rank 2 females checked more cells than rank 4 or 5 females.

[10]Numbers of offspring equivalents produced by females of different ranks under the constraints of the model given in the discussion were calculated as shown in Tables 5 and 6. Since the queen has a 35 percent chance of being overthrown the value assigned the queen in Table 4 is calculated as shown in Table 6.

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