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Queen Succession in the Social Wasp, *Polistes annularis*

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With one figure

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Abstract

Outcomes of conflicts among social animals can strongly affect individual fitness and therefore partly determine how sociality evolves. In the social wasp, *Polistes annularis*, conflicts over egg laying result in a linear dominance hierarchy discernible from which wasps attack which others. We investigated the structure and maintenance of dominance hierarchies in colonies containing both nest foundresses and workers. We also investigated the outcome of a potential conflict between foundresses and workers over the identity of the female which becomes queen after the original queen disappears. To investigate queen replacement we recorded individuals' behavior before and after removal of the queen from 13 nests. This experiment simulated natural queen disappearance which occurs frequently. All foundresses were ranked over workers; high ranking females were most aggressive and directed most of their attacks to the female directly beneath them in the hierarchy. This hierarchy determined succession to queenship; the beta female became queen within 3 h. Therefore a foundress became the new queen whenever one was present. There was no evidence of conflict between workers and foundresses when a foundress became queen. This chance of becoming queen contributes to the expected fitness of a female that accepts a subordinate role in spring.

Introduction

Conspicuous dominance hierarchies emerge as the results of competition for limited resources or for opportunities to reproduce among animals living in groups (DEWSBURY 1982). Individuals establish their relative status by assessing the capability of other group members and sometimes by fighting. Subsequently, when individual ranks are determined, less dramatic dominance and subordinance signals replace fighting. An understanding of dominance hierarchies is critical for weighing individual costs and benefits to group living, because individuals gain access to resources or reproduction according to their rank (DEWSBURY 1982).

In the social wasps, *Polistes,* females emerging from hibernation sometimes cooperate in small groups to start new nests. Groups are usually composed of females, called foundresses, which emerged on the same nest the previous autumn and which therefore are likely to be sisters (HELDMANN 1936; WEST EBERHARD 1969; STRASSMANN 1979). Initially foundresses fight violently with others in the group; they grapple and attempt to sting each other, occasionally falling to the ground locked in combat that can result in death (WEST EBERHARD 1969; STRASSMANN 1981 a). Later, aggressive interactions typically involve less violent interactions during which the subordinate adopts a submissive crouch (PARDI 1942; ITO 1985). The most dominant animal lays most or all of the eggs and is called the queen (PARDI 1948).

Polistes annularis is of particular interest in investigating dominance hierarchies because foundress groups are unusually large and stable compared to other *Polistes* species (RAU 1928, 1929, 1930, 1940; KRISPYN 1979; STRASSMANN 1979). In a population near Austin, Texas, individual nests are begun by 1 to 28 females, $\bar{x} = 4.9$, (S.E. = 0.2, N = 114 nests in 1980) and 89 % of nests are begun by a group (QUELLER & STRASSMANN 1987). After three or more consecutive warm spring days natal nestmates form distinct groups within which they fight for dominance. One female begins the new nest by depositing pulp (masticated plant fibers) where the group has settled; most nests are started within three meters of the natal nest. Group membership on new nests is fixed; females do not switch, even to other nearby groups of natal nestmates unless their nest is destroyed (STRASSMANN 1983). On average the queen lays 55 % of eggs and the beta foundress lays most of the rest (QUELLER & STRASSMANN 1987). On a third of nests the queen lays all eggs. This proportion may increase as the season continues and the queen consolidates her dominance. Subordinate foundresses forage for plant fibers to build the nest and for caterpillars, nectar and water to feed the brood. Queens rarely leave the nest to forage and return with caterpillar meat only if they are the only female on the nest. Females raised in the first brood, called workers, take over all foraging tasks soon after they emerge; subordinate foundresses then cease foraging and remain largely idle on the nest. On roughly a third of nests the first brood contains a few males among the worker females. Such early males appear to be produced in populations where workers sometimes become queens (STRASSMANN 1981 b). To become fully functional queens, workers must mate, so they can lay female (fertilized) as well as male (unfertilized) eggs. The final brood raised before winter consists of both males and females. They hibernate in sheltered places and mate on warm winter days. In spring, female reproductives become the foundresses of the new year's nests.

This study investigates the structure and maintenance of dominance hierarchies in colonies containing foundresses and workers, and compares responses of foundresses and workers to experimental queen removal. These responses are expected to have evolved naturally because queens disappear from 82 % of nests before all the eggs which will develop into reproductives have been laid (QUELLER & STRASSMANN 1987). The large foundress groups and persistence of subordinate foundresses after worker emergence enable the responses of foundresses and workers to queen disappearance to be compared within a colony in *P. annularis.*

If there is one once-mated egg layer per nest, foundresses and workers will be in conflict over the identity of the new queen because a foundress is more closely related to the offspring of another foundress (r = .375) than to those of a worker (r = .1875) and a worker is more closely related to another worker's offspring (r = .375) than to the progeny of another foundress (r = .1875). This conflict may be expressed as an increase in aggression between foundresses and workers following queen removal. However, when more than one foundress lays eggs the genetic interests of foundresses and workers are not so divergent. Using QUELLER & STRASSMANN's (1987) estimates of relatedness from egg laying data (r = .5) among foundresses, there is little conflict expected. This study determines whether a worker or a co-foundress takes over on nests where both are present. We compare behavior of individuals on nests with co-foundresses to the behavior of individuals on nests without co-foundresses.

Methods

The study was conducted at a 15 m high west-facing limestone cliff overlooking a reservoir 26 miles west of Austin, Texas. Nests of *Polistes annularis* are abundant on the cliff face where they are protected from direct sunlight until late afternoon. 13 nests were observed, for a total of 161 h in May, June and July, after the emergence of a number of workers but before the emergence of any reproductives (O'ROURKE 1982). All individuals on each nest were marked uniquely with Testors PLA enamel (STRASSMANN 1981a). On 7 nests observed in 1981, behavior of all individuals was recorded on microcassette. On 6 nests observed in 1978 and 1980 only the behavior of dominant wasps was recorded. First, nests were observed to determine the identity of the queen and to characterize individual behavior; then, the queen was removed with forceps and further observations were made. The 7 nests observed in 1981 were observed during three periods: 3—5 h before queen removal then for 1.2—4 h immediately following removal and 3—4 h the next day (Table 1). The 6 nests observed in 1978 and 1980 were observed for 6 h and the queen was removed late the same afternoon. The nests were then observed for 6 h the following day. We analyze data from all 13 nests to determine whether a foundress or a worker becomes the new queen. Detailed behavioral analyses were only done on the 7 nests observed in 1981 that had complete behavioral records. Nests had 10—43 workers and 0—7 foundresses (Table 1). The 1981 colonies on which detailed behavioral studies were done were of approximately the same size. Colonies in which a co-foundress became

Table 1: The times of day and duration of observation periods of the *P. annularis* nests that were used in the detailed analysis of behavior. On nests 1, 10 and X a cofoundress became the new queen, while on the remaining four nests a worker took over as the new queen

Nest	Before queen removal				After queen removal				No. of females
	Session 1		Session 2		Session 3		Session 4		
	Time	min	Time	min	Time	min	Time	min	
1	12.30	195	10.45	75	12.00	240	14.30	175	20
10	16.15	80	11.25	185	14.35	170	12.00	180	35
X	16.14	86	11.27	126	14.35	175	12.07	228	29
2	12.30	238	10.14	136	12.35	262			11
21	13.05	133	10.52	173	14.50	70	11.00	180	43
1A	12.10	160			13.15	110			33
22	12.30	170	10.55	140	14.30	120	10.55	180	44

queen contained an average of 28 females while colonies in which a worker became queen contained an average of 33 females (Table 1). Therefore colony size differences are not expected to confound comparisons of behavior between the two types of colony. After queen removal nine nests still had a foundress present and four nests had only workers remaining.

Foundresses were distinguished from workers on the basis of wing wear or by marks they had been given on their natal nest the previous year; foundresses have lusterless, rufous wings that are more worn than the blue-black shiny wings of workers. In over 100 trials, observers who did not know the actual status of marked wasps correctly categorized all of them as workers or foundresses using these criteria.

One wasp, the queen, was the major egg-layer on each nest and was the most dominant individual. Behaviors correlated with dominance included abdomen-wagging, frequent checking of cells containing eggs, building new cells, laying eggs and aggression (STRASSMANN 1981a). Abdomen wagging is a rapid side to side vibration of the gaster performed most frequently by dominant females (WEST EBERHARD 1969). We call interactions 'aggressive' when one wasp appears to be attacking another and 'non-aggressive' when wasps appear to be interacting non-violently. Aggressive acts ranged in severity from chewing the thorax of another wasp to fights in which the wasps fall from the nest, biting and attempting to sting each other. Non-aggressive interactions between wasps included antennation, chewing mandibles and exchanging food. We determined dominance ranks from tabulating which wasps attacked which others. The dominance rank of the three to five most dominant females could be determined for the 1981 nests.

The frequencies of behavioral acts were highly skewed so we used non-parametric statistics, mainly the Wilcoxon matched-pairs signed-ranks test for comparisons among sessions described below (LEHNER 1979). Data from the six nests observed before 1981 are only analyzed to determine the identity of the new queen because behavior of subordinate workers was not recorded. For analysis of behavior three sessions were recognized for the 1981 data: 1. before queen removal (sessions 1 and 2 of Table 1 combined), 2. immediately after queen removal, and 3. the next day. Sessions were compared in pairs (1 and 2, 2 and 3, 1 and 3) using all wasps present during both sessions. One nest could be included only in the first of these comparisons. Since original queens were only present during session 1 they are not included in any of the comparisons.

Results

A dominance hierarchy headed by the queen exists among the females of a *Polistes annularis* colony. Dominant wasps were more often aggressive than lower ranking wasps (Table 1). This is not circular reasoning since dominance ranks were determined only from tabulations of who attacked whom. Between 6.8 and 262 aggressive interactions occurred per h so frequencies of aggressive acts were

Table 2: Mean proportion of all aggressive acts on the nest performed by females of identified rank. Higher ranking wasps perform significantly more aggression than lower ranking wasps. Proportions are shown because the rate of aggression varied widely (from 6.8 to 262 acts/h) between colonies making comparison difficult. Dominance rank is a significant predictor of the proportion of aggressive acts an individual performs; $F = 13.2$, $r^2 = .31$, $p < .001$ before queen removal; $F = 11.9$, $r^2 = .36$, $p < .01$ after queen removal

Dominance rank	1 highest	2	3	4	5 lowest
Aggressive acts before queen removal	0.28 (N = 7)	0.18 (N = 7)	0.10 (N = 7)	0.10 (N = 6)	0.06 (N = 5)
Aggressive acts after queen removal	0.42 (N = 7)	0.10 (N = 6)	0.07 (N = 6)	0.08 (N = 3)	

converted to proportions of all aggressive acts during the recording period to facilitate comparison between nests. Queens performed .03 to .59, $\overline{X}$ = .28, of all aggressive acts occurring on a nest before queen removal; new queens performed .14 to .78, $\overline{X}$ = .42, of aggressive acts after queen removal (Table 2). The dominant 3 wasps performed .36 to .73, $\overline{X}$ = .56, of aggressive acts before and .09 to .78, $\overline{X}$ = .60 of aggressive acts after queen removal (Table 2). On average each female which could be ranked directed most of her aggression to her immediate subordinate and declining amounts to successively lower ranking females (Table 3).

The most dominant female remaining after queen removal became the new queen. Two of the new queens laid one and three eggs respectively. Since all foundresses on a nest were dominant over all workers, on all 9 nests which had at least one subordinate foundress, it was a foundress that became queen (Table 4). On the 4 nests where no foundresses remained after queen removal, the most dominant worker became queen (Table 4). In every case but one the new queen had ranked second to the original queen; on the exceptional nest the second-ranked (beta) female disappeared after queen removal and the third-ranked (gamma) female became the new queen.

There was more aggression on nests which had no subordinate foundresses and on which a worker took over (Fig. 1). Females rarely attacked higher ranking wasps on nests which had subordinate foundresses. On three nests where a

Table 3: Average proportion of aggressive acts that a female of identified dominance rank directs to victims of identified rank. Females are significantly more aggressive toward immediate subordinates than to more distant individuals. The position of a subordinate in the dominance hierarchy relative to an aggressor is a significant predictor of the proportion of attacks the aggressor directs towards the subordinate; $F = 16.5$, $r^2 = .23$, $p < .0001$ before queen removal; $F = 5.7$, $r^2 = .18$, $p < .05$ after queen removal

A. Before queen removal Victim: Aggressor:	1 (7)	2 (7)	3 (7)	4 (6)	5 (5)
1	—	0.29	0.21	0.10	0.10
2	0.01	—	0.41	0.10	0.08
3	0.0	0.0	—	0.24	0.08
4	0.0	0.4	0.01	—	0.46
5	0.0	0.23	0.0	0.03	—
B. After queen removal Victim: Aggressor:	1 (7)	2 (6)	3 (6)	4 (3)	
1	—	0.33	0.22	0.10	
2	0.02	—	0.36	0.26	
3	0.13	0.0	—	0.37	
4	0.0	0.0	0.02	—	

foundress took over there were 0, 0.3 and 0 attacks per h on the dominant 4 females by their subordinates. But, on the four nests on which a worker took over there were 0.7, 0.8, 1.6 and 7.5 attacks per h on the dominant four females by their subordinates.

Following queen removal, aggressive and non-aggressive interactions were more frequent on all nests; abdomen-wagging was more frequent during takeover by a foundress (Fig. 1). On 6 of 7 nests the new queen abdomen-wagged much more frequently than had the original queen. On nests upon which a worker became queen, larvae were fed more frequently than they were before queen

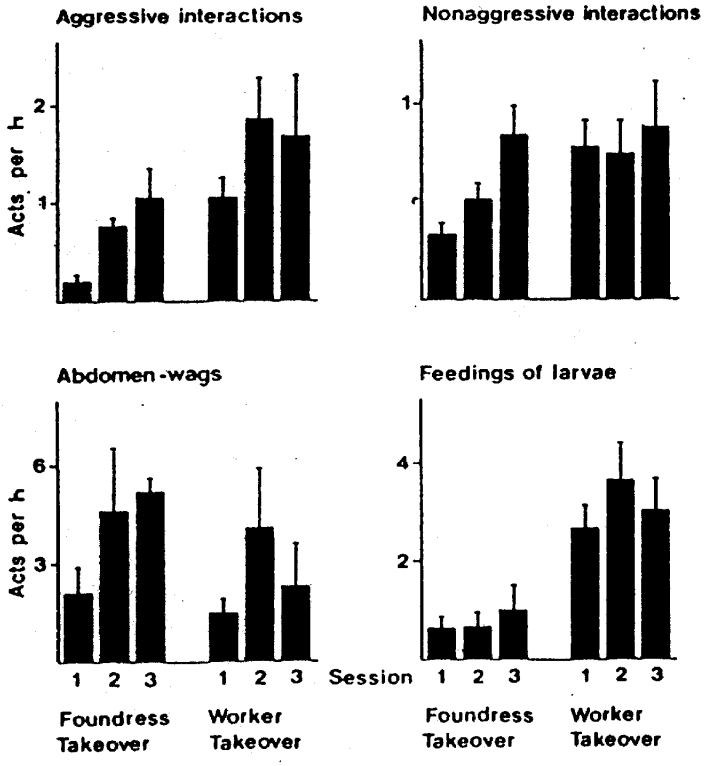

Fig. 1: Means and standard errors of four behaviors per wasp, per h. Session 1 was before queen removal, session 2 immediately followed queen removal and session 3 was the day after queen removal. On 3 nests a subordinate foundress took over and on 3 nests a worker took over. The frequency of aggressive acts increased during foundress takeover, from session 1 to 2 ($z = -4.2$, $p < 0.001$) and from session 1 to 3 ($z = -3.5$, $p < 0.001$) and during worker takeover from session 1 to 2 ($z = 3.0$, $p < 0.001$) but not from session 1 to 3 ($z = -0.5$, n.s.). The frequency of non-aggressive interactions increased during foundress takeover (from session 1 to 2, $z = -2.2$, $p < 0.05$, from session 1 to 3, $z = -3.5$, $p < 0.001$, from session 2 to 3, $z = -2.4$ $p < 0.05$) but not during worker takeover. Abdomen wagging increased during foundress takeover (from session 1 to 2, $z = -2.4$, $p < 0.05$, from session 1 to 3, $z = -2.3$, $p < 0.05$) but not during worker takeover. The frequencies of larval care behaviors did not change significantly between sessions. The frequencies of behaviors did not change significantly between sessions 2 to 3 other than mentioned above. All comparisons are Wilcoxon matched-pairs signed-ranks test

removal. Behavior indicative of competition among females increased, but there was no significant decrease in the amount of care given to the brood, indicating constraints on the extent of this competition.

Table 4: The identity of the replacement queen on nests with and without at least one cofoundress

	Identity of new queen	
	cofoundress	worker
No. of nests		
with cofoundresses	9	0
Without cofoundresses	—	4

Discussion

Dominance hierarchies discerned from aggressive interactions between *P. annularis* nestmates seem to result from competition to lay eggs. The alpha female, called the queen, lays most eggs and when she disappears the highest ranking female that remains becomes the new queen. Similarly determined dominance hierarchies also predict which female will become the next queen in studies of other *Polistes* species, for example *P. gallicus* (PARDI 1948), *P. exclamans* (STRASSMANN & MEYER 1983), *P. instabilis* (HUGHES & STRASSMANN in prep.), *P. fuscatus* (KLAHN 1981), *P. canadensis* (WEST EBERHARD 1969), and *P. jadwigae* (YOSHIKAWA 1963). Aggression was more frequent after queen removal suggesting that competition to lay eggs is more intense when females' chances of becoming an egg layer are greater.

There was no evidence of conflict between foundresses and workers on nests where a foundress became the new queen. There was actually more aggression on nests where workers replaced the original queen; perhaps because the dominance hierarchy was less well established on these nests, as evidenced by the greater number of attacks by subordinates on dominants. Either relatedness among females is such that workers are not in conflict with foundresses over the identity of the queen in *P. annularis,* or foundresses are winning the conflict with workers. Resolution of this question awaits more accurate assessments of relatedness among females on *P. annularis* nests.

When wasps of similar ages establish a hierarchy, as *P. annularis* foundresses do in the spring, fighting plays a large part in determining ranks and the largest female most often becomes queen (SULLIVAN & STRASSMANN 1984). However among workers the oldest, or one of the oldest females becomes the new queen when the original queen dies (e.g. *P. gallicus,* PARDI 1980; *P. exclamans,* STRASSMANN & MEYER 1983; *P. instabilis,* HUGHES & STRASSMANN in prep.). In this study the major age difference separated workers from foundresses. Subordinate foundresses are older, higher ranking and usually larger than workers on a *P. annularis* nest. Therefore it is no surprise that co-foundresses and not workers took over after queen removal.

Though *P. annularis* females were more aggressive after queen removal there was no detectable decrease in brood care suggesting that colony productivity did not decrease. When REEVE & GAMBOA (1983) removed queens from *P. fuscatus* nests they found that worker activity decreased and became less synchronized. They concluded that the queen was the pacemaker of the colony, stimulating and coordinating worker activity. But, unlike their colonies, all *P. annularis* colonies had a new queen within 3 h of queen removal. New queens of *P. annularis* were very active and may have stimulated the general increase in colony activity that followed queen removal.

Dominance hierarchies based on the frequency of abdomen-wagging match those constructed from aggressive interactions. In *P. annularis* abdomen-wagging occurs from the first day of the nest. This suggests that abdomen wagging in *P. annularis* is likely to be involved in dominance interactions in contrast to 'abdominal-wagging' in *P. metricus* which may be involved in adult larval interactions (GAMBOA & DEW 1981; STRASSMANN 1981a). During abdomen-wagging females may be depositing a dominance pheromone on the surface of the nest (WEST EBERHARD 1969). The sternal glands, located on the ventral surface of the gaster, are ideally positioned to be rubbed over the nest surface during abdomen-wagging. The glands are more active in dominant females which abdomen-wag more frequently (DOWNING & JEANNE 1983). This would explain the high frequency of abdomen-wagging by new queens and give the behavior a role in dominance even if performed when other females are not present.

P. annularis foundresses do not surrender all chances of laying eggs by becoming subordinate helpers because they lay a few eggs while the original queen is alive and because they remain at the head of the dominance hierarchy. Since so many queens die during the season, a significant number of subordinate foundresses become new queens and lay eggs that develop into reproductives. In other species of *Polistes*, subordinate foundresses are unlikely to lay eggs that become reproductives because they are driven away from the colony when the first workers emerge (e.g. PFENNIG & KLAHN 1985). Foundress dominance over workers increases the fitness of subordinate foundresses that become queens and may also increase the inclusive fitness of foundresses that never become queens over their expected fitness had workers become queens.

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