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GERONTOCRACY IN THE SOCIAL WASP, *POLISTES EXCLAMANS*

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Abstract. We observed three naturally occurring *Polistes exclamans* nests in Austin, Texas for 139 h through a succession of 13 queens. Nine of the 13 replacement queens were the oldest individuals on the nest, forming a system of queen replacement that may be described as a gerontocracy. Before becoming queen, replacement queens foraged more and were more aggressive than females who never became queen. This system of old forager supersedure was similar to that found in other temperate species but contrasted with that reported for tropical species of wasps in which younger females who are not workers occupy the higher ranks just beneath the queen.

In social wasps of the genus *Polistes*, dominance hierarchies were first described by Pardi (1948), who found that high rank as measured by who chewed on whom was correlated with age, ovarian development, and egg laying. When the queen was removed from a single *P. gallicus* nest, the oldest worker present took over as queen (Pardi 1948). Pardi also observed that older females dominated younger females and never vice versa. His findings regarding the dominance of older workers have been confirmed in studies of *P. metricus* (Dew & Michener 1981) and *P. fadigwae* (Yoshikawa 1956, 1963); in other primitively social wasps such as *Ropalidia marginata* (Gadagkar 1980) and *Mischocyttarus flavitarsis* (Little 1979), in the primitively social bee, *Lasioglossum zephrum* (Michener 1974); and in the bumblebee, *Bombus terrestris* (Van Honk et al. 1981; Van Honk & Hogeweg 1981). With the exception of *R. marginata*, which was studied in India, these are all north temperate zone species. On the other hand, studies of the neotropical social wasps *P. canadensis*, *M. drewseni*, *Synoeca surinama* and *Metapolybia aztecoides* described a very different relationship between age and dominance in which younger females occupy the ranks just below the queen (West-Eberhard 1969, 1978, 1981; Jeanne 1972). As Jeanne (1972, page 102) put it: '. . . the role of the "beta" wasp — the most dominant wasp besides the queen — constantly changed hands, passing down the line from older to younger offspring'. In these species, once a female begins foraging, she is no longer part of dominance interactions and no longer has any probability of becoming queen (Jeanne 1972; West-Eberhard 1981).

The present study was designed to investigate the role of age in dominance interactions in a species living at a latitude intermediate between tropical and temperate zones. This knowledge may help elucidate reasons for differences in dominance relations between temperate and tropical wasps. The second goal of this study was to establish whether or not dominant workers were more likely to supersede after the original queen died or was removed. This would establish a critical link between dominance rank and reproductive success by demonstrating that dominant workers have higher chances of becoming egg layers. Such a link would explain the ubiquity of dominance hierarchies among primitively social wasps. Finally, we were interested in seeing how becoming a forager influenced a worker's dominance rank.

We chose *P. exclamans* as a study organism because it is abundant in central Texas, is easily observed, and exhibits a colony cycle intermediate between temperate and tropical *Polistes*, which makes it a likely candidate for an intermediate relationship between age and dominance (Strassmann 1981a, b, c). Worker *P. exclamans* frequently supersede under natural conditions since original queens are lost from over half of all nests (Strassmann 1981a). Supersedure was the principal way for workers to become egg layers, since during hundreds of hours of observations we never saw a subordinate lay eggs in the nest, even though we routinely dissected subordinates with fully developed ovaries and no apparent resorption of oocytes (Strassmann, unpublished data; Strassmann & Thomas 1980).

Methods

We observed three naturally occurring nests of *Polistes exclamans* through a succession of 13 queens at Brackenridge Field Laboratory (BFL) in Austin, Texas. The nests were in fields of grass with *Baccharus* and mesquite (*Prosopis*) shrubs. Nest 1 was observed from 28 May to 13 June, 1980 through five new queens for a total of 43.1 h (Table I). Nest 2 was observed from 16 June to 26 June through three new queens for a total of 33.5 h. Nest 3 was observed 30 June through 20 July through six new queens for a total of 62.4 h. Wasps were marked individually using enamel (Strassmann 1981c). Six positions on the wings allowed 63 easily distinguishable numbers for each colour of enamel used. During observations we tried to record all behaviours, which was not difficult since few wasps were active at any one time. Queens were removed by covering their wings with enamel so they could not fly, and lifting them from the nest with forceps. The other wasps on the nest did not react to this procedure. All new queens matured in the current season; none were nest foundresses.

The behaviours we observed were defined previously (Strassmann 1981d). In this analysis we focussed on foraging for caterpillars, aggression, and abdomen wagging. A female that arrived on the nest one or more times with caterpillar meat in her mandibles was classified as a forager. Aggressive acts included chewing on any part of another wasp except her mandibles, climbing on another wasp, climbing on another wasp while chewing on her and attempting to sting her, crashing to the ground in this position (a falling fight), and grappling forelegs while reared up on the nest. Aggressive chewing was easily distinguished from grooming behaviour such as was reported by Maher (1976) because in our population social grooming occurred only during or after rain and was directed towards noticeably wet wasps. During grooming behaviour the mandibles of the groomer were opened and closed more slowly, covered a larger area of the body of the wasp being groomed, and continued for several minutes longer, than did aggressive chewing (Strassmann, unpublished data). Abdomen wagging involved vibrating the abdomen laterally across the nest surface as the wasp walked around the nest. It was performed most often on cells containing eggs and was positively correlated with dominance, at least in *Polistes* of the subgenus *Aphaniloptera* (Strassmann 1981d; unpublished data).

We used two-tailed non-parametric statistics for analyses of data containing large numbers of zero values and we corrected for ties. Kendall Tau correlations were calculated for aggression with foraging rates and for all behaviours with reign of supersedure. Mann–Whitney *U*-tests were used to compare behaviours of females that superseded with those of females that never superseded. Wilcoxon matched-pairs signed-ranks tests were used to compare the behaviours of females before and after superseding. Discriminant analysis was used to distinguish overall behaviour of females who subsequently superseded from that of females who never did. All statistical tests followed Siegel (1956) and were performed using SPSS (Nie et al. 1975).

Results

Age and Size of New Queens

Females that became queens were the oldest females present on the nest in 9 of 13 (69 %) cases (Table I). In five of these nine cases, there were other females equally old on the nest. In three of the four cases where the female that became queen was not the oldest female on the nest, an older female superseded subsequently. In the four cases in which the queen was not the oldest female on the nest, she was among the older females (numbers of females older than the queen were only 1 of 25, 5 of 18, 4 of 17, and 3 of 19, Table I). At the time of supersedure new queens varied from 7 to 32 days in age ($\bar{x} = 17 \pm$ SD, 7.4 days, Table I). There was no evidence that females beyond a certain age lose their ability to become queens.

Most of the supersedures did not involve a great increase in aggression. A notable exception involved the last takeover on nest 3. Y01 and Y04 fought vigorously for control of the nest and had many falling fights. Eventually Y01 took over and dominated Y04 every time Y04 landed on the nest.

Size was secondary in determining which female became queen (Table I). On nest 1, queens 3, 4 and 5 were of similar ages and were ranked in order of supersedure by size, queen 3 being largest. Queens 2 and 3 on nest 2 were also ranked by size, but no pattern involving size was apparent among the queens on nest 3 (Table I). Since most of the older females that did not supersede died naturally before the end of the experiment, their size could not be ascertained.

Behaviours of Queens and Non-queens

Eight of the 13 females that superseded foraged for caterpillars during observation sessions before becoming queens. Of the 24 other females present on the nests that were as old as or older than a queen, 11 foraged and 13 never foraged. This indicated that foragers and non-foragers superseded equally often ($\chi^2 = 0.83$, $P > 0.05$). Females that became replacement queens were generally much more active than their con-

Table I. Characteristics of Nests and Queens Involved in Experiments†

Nest	Reign (order of supersedure)	Dates	No. hours nest observed	ID of queen	Was queen a caterpillar forager?	Queen's winglength	Females on nest	Age of queen at takeover	Females as old as queen	Females older than queen	Females later becoming queen as old or older than current queen
1	1	28 May–29 May	8.0	W04							
	2	30 May–3 June	4.0	Y09	no		12	12+	4 (1)*	0	0
	3	4 June–5 June	7.1	Y02	no	12.79	18	13+	1	0	0
	4	6 June–9 June	8.0	Y24	yes	11.94	25	18	0	1 (1)*	1
	5	10 June–11 June	8.0	Y18	yes	10.84	32	23+	0	0	0
	6	12 June–13 June	8.0	O32	yes	12.47	31	13+	0	0	0
2	1	16 June–18 June	9.5	Y16		14.77					
	2	19 June–23 June	12.0	W07	yes	13.84	18	7	3 (1)*	5 (3)*	1
	3	24 June–25 June	8.0	W04	yes	11.84	20	16+	3 (2)*	0	0
	4	26 June	4.0	B08	no	14.27	17	9	2 (1)*	4 (3)*	0
3	1	30 June–7 July	18.3	B04							
	2	8 July–9 July	8.0	Y17	no		26	13+	13 (4)*	0	0
	3	10 July–14 July	12.1	B01	yes	14.41	23	25+	5 (1)*	0	0
	4	15 July–16 July	8.0	Y06	yes	14.76	19	15	0	3 (1)*	2
	5	17 July–18 July	8.0	B09	yes	12.77	16	32+	0	0	0
	6	19 July–20 July	8.0	Y01	no	15.41	18	26	0	0	0

*Asterisked numbers in parentheses are numbers of those females that had foraged for caterpillars.
†Blank spaces in columns indicate data were not available.

Table II. Behavioural Rates per Hour for Pre-queen Behaviour of Females that Became Queens, Behaviour for Females as Old as Queens that Never Superseded, and Behaviour of All Females that Never Became Queens†

Behaviour	Replacement queens ($N = 13$)	Non-queens as old or older than queens ($N = 24$)	(A)	All non-queens ($N = 102$)	(B)
	$\bar{X}$ (SD)	$\bar{X}$ (SD)	Z	$\bar{X}$ (SD)	Z
Aggressive acts	0.25 (0.05)	0.06 (0.02)	3.4***	0.08 (0.01)	3.7***
Abdomen wag	0.36 (0.18)	0.20 (0.07)	1.4	0.12 (0.03)	3.2**
Arrive with caterpillar	0.13 (0.04)	0.05 (0.02)	1.7	0.04 (0.01)	2.5*
Check cell	0.34 (0.14)	0.29 (0.08)	0.6	0.18 (0.03)	2.1*

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

†Mann–Whitney U calculations of Z are used to compare: (A) behaviour of pre-queens to contemporaries and older females that never became queen, and (B) behaviour of all non-queens compared to replacement queens.

temporaries who never superseded (Table II). In 12 of 13 cases, the new queen was the most aggressive non-queen on the nest before she superseded. Future queens did not forage significantly more often for caterpillars than did their contemporaries; however they did so significantly more often than did all non-queens (foraging trips per hour: pre-queens $\bar{X} = 0.13 \pm$ SE 0.04, $N = 13$; contemporaries $\bar{X} = 0.05 \pm$ SE 0.02, $N = 24$; $Z = 1.7, P > 0.1$; non-queens $\bar{X} = 0.04 \pm$ SE 0.01, $N = 102$; $Z = 2.5, P < 0.001$).

Aggressive acts by the 13 queens toward all other individuals were tabulated according to whether the victim had foraged for caterpillars. On all nests there were more attacks on foragers, significantly so on nests 2 and 3 (Table III). Foraging was correlated both with performing aggressive acts and being victim of aggressive acts (Table IV). Foraging (or something correlated with it) appeared to increase a female's chances of becoming queen and increased the queen's perception of her as a threat.

Table III. Average Numbers of Aggressive Attacks by Queens on Individual Foragers and Non-foragers

	Attacks on foragers			Attacks on non-foragers			
	$\bar{X}$	SD	N	$\bar{X}$	SD	N	Z
Nest 1	1.7	2.7	60	1.0	1.7	55	1.6
Nest 2	2.3	3.3	26	0.8	2.7	37	3.4***
Nest 3	2.1	3.4	56	0.8	2.2	90	3.2**

**$P < 0.01$; ***$P < 0.001$.

The age of each female in all aggressive interactions was calculated for the day the interaction occurred to see whether older females were more aggressive than younger females. Aggressors were older than their victims on the average on all three nests although the average age of aggressors and victims varied from nest to nest (Wilcoxon matched-pairs, signed-ranks test, nest 1: $N = 226$, $Z = 10.7$, $P < 0.001$; nest 2: $N = 219$, $Z = 2.7$, $P < 0.01$; nest 3: $N = 257$, $Z = 6.8$, $P < 0.001$ (Fig. 1)).

Discriminant analysis was performed to contrast behaviour of pre-queens with the behaviour of females that never became queens (Table V). The 13 most common behaviours and the date of birth were entered as discriminating variables. We found that a function which correlated positively with abdomen wagging (0.60), aggression (0.69) and foraging for caterpillars (0.92), and correlated negatively with foraging for pulp

Table IV. Correlations between Aggression, Receiving Aggression and Foraging; All Wasps Are Included

Variables		Kendall Tau	N
Caterpillar foraging, Aggression	Nest 1	0.28**	48
	Nest 2	0.49**	27
	Nest 3	0.20	40
Caterpillar foraging, Receiving aggressive attacks	Nest 1	0.36***	48
	Nest 2	0.40**	27
	Nest 3	0.20	40
Aggression, Receiving aggressive attacks	Nest 1	0.36***	48
	Nest 2	0.56***	27
	Nest 3	0.45***	40

**$P < 0.01$; ***$P < 0.001$.

(− 0.95), most clearly differentiated between the behaviour of pre-queens and non-queens. This discriminant function was highly significant ($\chi^2 = 45.2, P < 0.0001$). When this function was used to match actual groups (pre-queen, non-queen) to predicted groups, it was correct for 89% of the wasps. Interestingly, the three pre-queens that were not predicted to become queen became queen 4th, 6th and 6th on nests, 1, 2 and 3 respectively, indicating they were late in superseding. Ten females that were never queens were predicted to become queens. No other discriminant functions were significant.

Changes in Behaviour after Becoming Queen

Females increased the frequency with which they performed most behavioural acts after becoming queen. The single behaviour that decreased significantly was foraging for caterpillars (Table VI). As queens, females laid eggs, sometimes on the first day of their reign, indicating that their ovaries were already fully developed. Kendall Tau correlations were calculated between reign of supersedure and behaviour to see

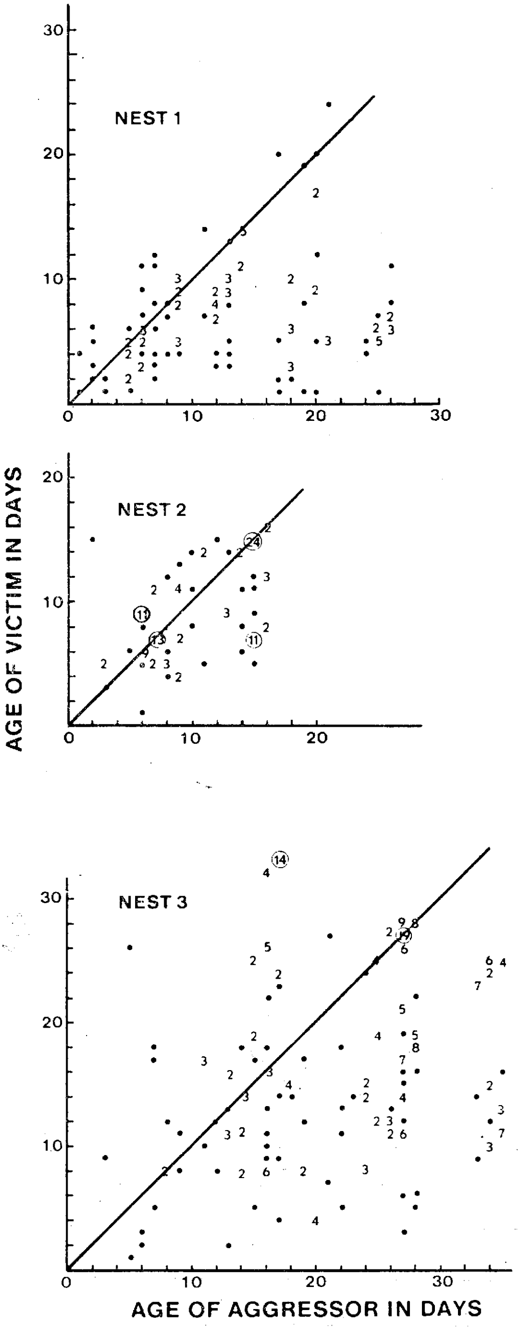

Fig. 1.

Table V. Discriminant Analysis Contrasting Behaviour of Pre-queens ($N = 13$) with that of Females that Were Never Queens ($N = 102$)

Behaviour	Standardized canonical function coefficients
Aggressive acts	0.69
Wag abdomen	0.60
Smear abdomen	0.31
Arrive with paper	−0.95
Arrive with caterpillar	0.92
Arrive with nothing	−0.48
Leave	0.54
Exchange caterpillar	−0.44
Chew on mandibles	−0.21
Feed larva	−0.37
Check cell	0.06
Build	−0.16
Fan	0.01
Date of birth	0.02

	Eigenvalue	Canonical correlation	χ^2	*df*	*P*
Function 1	0.54	0.59	45.2	15	0.0001

Fig. 1. Aggressive acts plotted by age of aggressor and age of victim at time act occurred. All wasps are included, assuming wasps who were tan-eyed when marked were then 7 days old, grey-eyed wasps were 4 days old and black-eyed wasps were one day old when marked. All points below the diagonal represent aggressors older than their victims. Circled numbers on the graph distinguish two-digit numbers from one-digit numbers. Average ages in days of aggressors and victims on nests were: Nest 1 aggressors 13.7 ± SD 6.7, $N = 226$, victims 7.4 ± SD 4.4, $N = 226$; Nest 2 aggressors 10.5 ± SD 4.1, $N = 129$, victims 9.6 ± SD 3.7, $N = 129$; Nest 3 aggressors 23.1 ± SD 7.6, $N = 257$, victims 18.3 ± SD 8.2, $N = 257$.

whether females that superseded later in the sequence of queens behaved differently from earlier queens. Since only two of 23 behavioural acts were significantly correlated with reign (abdomen wagging and chewing on wings), queens of later reigns were not very different behaviourally from earlier queens.

Discussion

We found that in *P. exclamans*, the relationship between age and dominance followed that of temperate wasps. Older females were more aggressive, foraged more often for caterpillars, and were more likely to supersede when the queen was removed. *P. exclamans* is most like temperate species of wasps in its relatively low numbers of females per nest, and in its lack of swarm founding (Wilson 1971; Strassmann 1981a). Perhaps these two characteristics result in greater plasticity of roles for old foragers. If a female loses all chances of becoming queen upon beginning foraging, she might delay foraging to an older age. Such a delay is probably intolerable for small *P. exclamans* nests, where each worker is very important to the success of the nest. In fact, loss of all females on the nest was the

Table VI. Behaviours per Hour of Queens Before and After They Become Queens†

Nest	Wasp	Reign (order of supersedure)	Before (B) After (A)	Aggressive acts	Abdomen wags	Arrive with caterpillar	Check cells
1	Y09	2	B	0.25	2.50	0.00	1.88
			A	3.25	10.25	0.00	3.25
1	Y02	3	B	0.58	0.58	0.00	0.42
			A	2.82	14.93	0.00	9.01
1	Y24	4	B	0.31	0.26	0.21	0.58
			A	3.86	5.73	0.00	3.24
1	Y18	5	B	0.18	0.15	0.15	0.15
			A	1.83	3.48	0.00	1.53
1	O32	6	B	0.00	0.00	0.09	0.00
			A	5.74	22.08	0.00	6.36
2	W07	2	B	0.00	0.42	0.31	0.31
			A	3.41	6.74	0.00	4.66
2	W04	3	B	0.28	0.14	0.14	0.14
			A	3.63	3.00	0.00	8.50
2	B08	4	B	0.30	0.13	0.00	0.08
			A	1.98	4.69	0.00	5.43
3	Y17	2	B	0.55	0.22	0.00	0.11
			A	2.99	1.37	0.00	0.87
3	B01	3	B	0.27	0.11	0.34	0.34
			A	4.38	6.44	0.00	4.63
3	Y06	4	B	0.13	0.03	0.42	0.08
			A	4.13	9.50	0.00	6.13
3	B09	5	B	0.34	0.11	0.06	0.22
			A	3.63	12.13	0.00	8.25
3	Y01	6	B	0.07	0.04	0.00	0.11
			A	3.12	8.23	0.00	5.99
Z				3.2**	3.2**	3.1*	3.2**

$*P < 0.01$; $**P < 0.001$.

†Wilcoxon matched-pairs signed ranks calculations of *Z*. Number of hours of observation are given in Table I.

second most common cause of nest failure in this population of *P. exclamans*. It accounted for the failure of 13 to 76% ($\bar{X} = 45\%$, $N = 4$ years) of all nests, depending on the year (Strassmann 1981b). Given the small number of workers, all females must contribute optimally in providing food for larvae, which probably leaves no room for a non-working caste. While having been a forager is not a prerequisite to becoming queen, it is correlated with dominance; foragers are more often victims of the queen's attacks than are non-foragers, and more than half of the queens were previously foragers.

The traits *P. exclamans* shares with tropical wasps include high rates of nest predation and parasitism and an increased colony cycle length (Wilson 1971; Strassmann 1981b). Apparently these traits alone do not result in selection for supersedure of young females in *P. exclamans*.

Since a majority of original *P. exclamans* queens are lost from their nests through natural circumstances, the workers probably responded to our queen removal experiments as they would have to natural episodes of queen death (Strassmann 1981a). Our research establishes a clear link between dominance and probability of becoming an egg layer, thus providing an evolutionary reason for dominance hierarchies in primitively social insects. In more highly eusocial insects such as *Apis* and *Polybia*, where dominance is less pronounced, the workers' low probability of becoming queens may explain the absence of dominance hierarchies (Wilson 1971). Studies of the bumblebee, *Bombus terrestris*, by Van Honk et al. (1981) and Van Honk & Hogeweg (1981), indicate that older workers are more likely to lay eggs, but these older workers forage less than average, a situation counter to that found in *P. exclamans*. This difference might be expected from the higher levels of caste and greater numbers of colony members exhibited by *Bombus* as compared to *Polistes*. Age is not the only factor involved in dominance. Dominance hierarchies based at least partly on size have been described for the temperate species *P. metricus* (Haggard & Gamboa 1980), *P. fuscatus* (Noonan 1981), *P. gallicus* (Turillazzi & Pardi 1979), and for a central Texas population of *P. annularis* (Sullivan & Strassmann, unpublished data). The results of the present study are not inconsistent with a secondary role for size in dominance in *P. exclamans*.

Dominance hierarchies among workers reduce conflict regarding which worker supersedes when the queen dies. Age may be a more important factor than size in this determination because the age of replacement queens affects the overall relatedness of females to the brood they raise. Queen succession and sperm precedence may result in contemporaries being more closely related to each other than to individuals of different ages (Metcalf 1980 Strassmann 1981a;). Dominance may be associated with age in all primitively social insects with small colony sizes because it is intrinsic to a system lacking castes, where no female ever entirely loses the chance to become queen.

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