

DOMINANCE RELATIONS IN *POLISTES CANADENSIS* (L.),
A TROPICAL SOCIAL WASP *

MARY JANE WEST-EBERHARD

Smithsonian Tropical Research Institute, Balboa, Panama

Received 20 August 1985

I. Introduction	page 264
II. Materials and methods	» 264
III. Results	» 266
A. Aggressive behaviors associated with social dominance	» 266
1. Approach	» 266
2. Lateral vibrations	» 267
3. Territorial guarding of empty cells and newly laid eggs	» 267
4. Physical attack	» 268
B. Foraging by subordinate females	» 268
C. Results of tethering a despotic queen	» 269
D. Reproductive potential of subordinate foundresses	» 273
E. Hierarchy in a newly founded colony lacking a despotic queen	» 274
F. Dominance in mature colonies	» 274
IV. Discussion	» 275
Summary	» 278
Riassunto	» 279
References	» 279

* It is a pleasure to dedicate this paper to Professor L. Pardi, whose ingenious, careful and perceptive work I have long admired as a model to be emulated in behavioral zoology, on the occasion of his 70th birthday.

I. INTRODUCTION

Social wasps of the genus *Polistes* have come to represent a prototype of dominance/subordination behavior in invertebrate animals. Social hierarchies such as that first demonstrated by PARDI (1942, 1946, 1948) in *Polistes gallicus* (L.) were subsequently found in other *Polistes* species (reviewed by WEST-EBERHARD, 1969; AKRE, 1982). Indeed, *Polistes*-like dominance relations now appear to be crucial determinants of social organization and reproductive success in a wide variety of social organisms from insects to higher vertebrates (PARDI, 1950; WEST-EBERHARD, 1975a; WILSON, 1975).

Preliminary observations of *Polistes canadensis* (L.) in the eastern llanos (Meta) of Colombia in 1978 indicated the absence of a hierarchy in at least some foundress associations (colonies prior to the emergence of offspring) and mature (post-emergence) nests. Instead of a neatly graded series of differentially aggressive interacting females like that described by PARDI (1948) and other authors (above) colonies were dominated by a territorial queen who chased other females from the regions of the nest containing new or vacant cells. There was little evidence of the distinctive displays characterizing dominance-subordination interactions in some other species of *Polistes* (WEST-EBERHARD, 1982). Thinking that these colonies might represent a novel type of *Polistes* social organization of interest for comparative study, I analysed social dominance in *P. canadensis* by means of the observations and experiments reported here. The results help to illuminate the circumstances in which a hierarchical social organization can occur, as well as certain individual traits affecting dominance behavior and social role.

I thank the D. STROUD family and Dr L. ARANGO for generous hospitality at Hacienda Mozambique during the course of this study. JAMES and JOYCE SPAIN helped with arrangements for work in the Colombian llanos. Fieldwork was supported by the Scholarly Studies Program of the Smithsonian Institution. M. SPIVAK provided valuable assistance and discussion while the manuscript was being written. W.G. EBERHARD, G. GAMBOA, J. STRASSMANN, and SÔICHI YAMANE kindly reviewed the manuscript.

II. MATERIALS AND METHODS

The study was conducted during the period 1 July-20 September 1978 at Hacienda Mozambique, 15 km SW of Puerto Lopez, Meta, Colombia (4°N latitude, 73°W longitude) in a grassy plains characterized by cattle pastures, swamps, and

Table 1.
Colonies observed.

Colony	Stage *	Hours observed	Condition at end of study
A	Post-emergence Late post-emergence	7	abandoned
B	Late post-emergence	3	abandoned
C	Pre-emergence	17	collected: 61 - cell nest 15 females eggs and larvae
D	Newly initiated Pre-emergence	12	collected: 65 - cell nest 3 females - (7 removed) eggs, larvae, pupae
E	Post-emergence	2	collected: 749 - cell nest 71 females eggs, larvae, pupae
Others	(various stages)	8	
Total		49	

* «Newly initiated» means from the time of first oviposition; «pre-emergence» is prior to emergence of first adult offspring; «post-emergence» is following emergence of first adult offspring; «late post-emergence» colonies have produced adults and contain an increasing number of empty cells.

riparian forest. Many colonies of *Polistes canadensis* (Hymenoptera Vespidae) were found on farm buildings and on vegetation, where the oblong, vertical nests were suspended by a single pedicel from branches at between 1 and 2 m above the ground. Voucher specimens, identified by O.W. Richards as *Polistes (Aphanilopterus) canadensis canadensis* (L.) in 1981, are deposited in the British Museum of Natural History, London.

A total of 49 hr of behavioral observations were made, primarily of five colonies (Table 1). Ten other colonies were observed for shorter periods. Wasps were marked for individual identification using quick-drying paint. Dissections were performed immediately after capture and killing with CCl₄. Spermathecae were examined to detect the presence or absence of sperm. Ovarian development was assessed by counting the number of «mature» oocytes (greater than 2.0 mm long; the size exceeded by all of 20 measured freshly laid eggs from nest E: mean = 2.19 mm, range = 2.0-2.4 mm) and the number of swellings (oocytes and nurse-cell clusters) per ovariole. Relative age was estimated using the degree of pigmentation of the abdominal apodemes, according to the method of RICHARDS (1971; see WEST-EBERHARD, 1975b) with the following categories distinguished: (1) uric acid in body cavity; (2) uric acid concentrated in gut; (3) no line at apodeme margin, uric acid absent; (4) thin brown

line at apodeme margin; (5) thin black line at apodeme margin; (6) thick black line at apodeme margin; (7) thick black line bordered by some (cloudy) darkening. Most observations were of colonies *in situ* that were unmanipulated except for marking of individuals, which at most sometimes caused only a momentary disturbance of the individual marked. In addition, three kinds of experimental manipulation were performed:

1. Removal of single eggs or larvae in colonies C, D, and E. This provided empty cells which provoked oviposition (GERVET, 1964), facilitating identification of egg-layers.

2. Removal of a series of known egg-layers (nest D).

3. Tethering of the queen (nest C). A queen's movement was restricted to the upper (older) area of the nest by tying a loose loop of fine nylon fishing line around her thin wasp waist (between thorax and gaster) and fixing the other end of the line to a pin embedded in a branch near the nest pedicel. Tethered in this way the queen could walk, groom, solicit food, build, and oviposit, but could not reach the lower (newer) region of the nest.

Behavioral profiles were conducted during 7 hr of observation (6-12 July) for all of the 29 foundress females marked on nest C prior to tethering of the queen. All aggressive interactions, egg-laying and lateral abdominal vibrations were recorded for each individual; and resting positions (upper comb, lower comb, nest top, off the nest) of all females were censused a total of 13 times, at irregular intervals. Similar observations were made during 10 hr of observation while the queen was tethered (12-16 July). All females present were then collected and dissected (16 July) along with marked females returning to the nest the following morning (17 July).

III. RESULTS

A. *Aggressive behaviors associated with social dominance*

«Aggressive» behavior is defined as a movement or posture that results in fighting or submission (crouching, immobility, or retreat) on the part of others.

1. *Approach*. The simple presence or approach of the principal egg-layer seemed to constitute an aggressive signal (threat) in colonies having an established queen (unmanipulated colonies A, B, C, and E). Two females doing aggressive lateral vibrations (see below) on the egg region of nest B moved upward on the nest when the queen approached. On nest C a co-foundress suspended cell inspections and remained still for more than 3 min following the approach of the queen who rested about 1 cm from her. On other occasions the queen vigorously chased other females from the nest, running toward them from another part of the nest, or turning toward them with a quick dart or lunge, with or without body contact. This approach behavior was not accompanied by any discernible distinctive complex or ritualized threat display like those associated with aggressive approach in some other species of *Polistes* (WEST-EBERHARD, 1982).

The prolonged mouthing («chewing over») of body and wings of subordinates, frequently observed in a related species (*P. erythrocephalus* Latreille: field notes, 1964-65) was observed only once (nest A), and I once saw a hyperaggressive female on nest D bend the abdomen sharply to the side, a posture that has become a ritualized threat in some other species of wasps (WEST-EBERHARD, 1978, 1982). A stereotyped, rapid shaking while in contact with the dorsum of subordinates did not occur, although it was common in a foundress association of a Panamanian population presumably of the same species (unpubl. observation, 1983); nor did these wasps adopt the dominance posture described by Itô (1985). The effective approach-threat distance of the experimentally tethered queen extended to only about two cells from the queen (less than 1 cm); at that distance other females did not lay eggs in empty cells. Experimentally removed eggs and larvae further from the tethered queen were replaced within 30 hr by other females that previously had not oviposited.

2. *Lateral vibrations.* Aggressive females sometimes performed a brisk, audible, side-to-side vibration of the body against the nest called «lateral vibrations» by GAMBOA & DEW (1981). All of 12 females involved in dominance interactions prior to tethering of the queen on nest C performed lateral vibrations during that period, whereas none of six females that were usually present but which were not involved in these interactions did so. Two kinds of observations indicate that lateral vibrations serve as an aggressive signal in this species. On one occasion violent vibration by the queen of nest C was immediately followed by some females moving off the face of the nest; and on six occasions lateral vibrations provoked attack of the performer by nearby nestmates (including non-queens), or preceded attack behavior by the performer.

Stroking — a rubbing of the nest surface with slow, sinuous movements of the gaster — was also observed, though less frequently than lateral vibrations, and sometimes alternating with them. The solitary foundress of a newly initiated, (4-cell) egg-containing nest stroked the nest and (once) the pedicel upon landing. She did not stroke the surface of the nearby parental nest (nest A, Table 1) in repeated visits there; and she did not perform lateral vibrations on either nest. Stroking was also performed by females immediately after antennating empty cells, and by the tethered queen on the lower part of the nest immediately upon her release. It provoked no visible reaction on the part of nestmates.

3. *Territorial guarding of empty cells and newly laid eggs.* Established queens on mature nests B and E usually stayed on the lower «shelf» region of the nests containing new cells, a region of frequent egg-laying (see WEST-EBERHARD, 1969, for an explanation of the «shelf» of new cells in nests containing replacement queens). On a smaller pre-emergence nest

(nest C) the queen always rested on the nest, whereas other females spent nearly half (48.5% of 775 observations) their resting time off the nest, on the branch to which it was attached. Queens chased other females from shelf areas.

The presence of empty cells may increase aggressiveness in queens. This was suggested by experimental egg removal on nest C: prior to egg removal the queen was passive toward two females performing mild lateral vibrations nearby. As soon as she discovered (antennated) the empty cell, she suddenly became aggressive toward them. Similarly, aggressive lateral vibrations and nest stroking were performed immediately after antennation of an empty cell on nest D by females ranking first and second in a hierarchy of seven females.

Oviposition was observed a total of 32 times, and in colonies of all stages of development. There was never a prolonged post-oviposition vigil with the egg-layer's head held directly over the cell containing a newly laid egg as in *P. fuscatus* (Fabr.) (WEST-EBERHARD, 1969) and other social wasps (reviewed in WEST-EBERHARD, 1981). However, aggressive queens rapidly approached and attacked females that came near newly laid eggs, sometimes running to do so from resting positions on other parts of the nest. Differential oophagy, which is sometimes a behavioral concomitant of egg guarding, was likewise never observed. The length of time eggs are recognized as new (the amount of time they would have to be protected against oophagy by nestmates, see WEST-EBERHARD, 1969) is unknown. However, upon tethering of the nest C queen three females made prolonged antennations of an egg laid 65 min before, indicating that it was distinguished from other (older) eggs.

4. *Physical attack.* Fierce fighting occurred on nest D where several females with slightly developed ovaries contested empty cells and no female was persistently dominant. On one occasion a female was disabled (unable to walk normally, trembling) following a ferocious fight in which both females fell from the nest while attempting to bite and sting. Prior to the first queen removals on this nest two females were found dead on the ground beneath the nest. Physical grappling and falling fights of this kind did not occur in observation colonies containing despotic queens (below).

B. *Foraging by subordinate females*

Thirteen of the 19 non-queens seen on nest C were observed to forage, but their foraging rate was low (0.24 loads per female per hour, compared to 0.95 per female per hour for *P. fuscatus*), (WEST-EBERHARD, 1969). There was no significant correlation between individual foraging rate and age or ovarian development. However, the most developed female (the queen) did not forage.

C. Results of tethering a despotic queen

On four of the five primary observation nests (A, B, C, E) the dominant queen was «despotic» in that she appeared to exercise absolute dominance over all other females and suppressed aggressive behavior by others, even when not directed at her. Despotic queens responded aggressively toward aggression among nestmates. On nests dominated by such queens no hierarchy was apparent because dominance interactions among non-queens were rare. For example, in 7 hr observation of 17 foundress females on nest C prior to tethering of the (despotic) queen, only 20 aggressive interactions occurred (mean = 0.17/female/hour), and nearly half of these (nine) were dominations by the queen. By contrast, in colony D, a pre-emergence nest of about the same size and age (Table 1) lacking a despotic queen, aggressive interactions were 70 times more frequent (mean = 12/female/hour) and only 28% of 42 interactions recorded in 30 min involved the queen.

Prior to tethering the despotic queen of nest C, I removed five eggs in the lower part of the nest. One hour later, after the queen had oviposited twice, she was tethered out of reach of the two newly laid eggs and three remaining empty cells. At first she strained toward the bottom of the nest, chewed at cells and groomed where touched by the restraining nylon thread. However, for most of the 10 hr of observation during the 4 days the queen was tethered (see II. Materials and methods) her aggressive, feeding, grooming, and oviposition behavior were normal.

In the 1st hr after the queen was tethered (12 July) several marked changes occurred in the behavior of other females: four females seldom (female C11) or never (females C6, C10, C15) recorded present on the lower part of the comb during the pre-tethering period suddenly appeared there and repeatedly inspected the newly laid eggs. C15 briefly performed strong lateral vibrations, 1 of only 2 times this usually passive female was seen to do so in 10 hr of post-tethering observation. Ten post-tethering assessments of resting position showed that five females (C1, C9, C10, C15, C16) that were never recorded on the lower comb during pre-tethering censuses appeared there during the post-tethering period. While the queen was tethered the non-queens were significantly more often present on the nest, and on the lower portion of the comb (Table 2).

When the nest was briefly observed at 17.00 hr, 30 hr after tethering of the queen, eggs were present in the three remaining empty cells, and C16 was stationed on the lower part of the nest behaving aggressively. Prior to tethering, C16 was the female among those usually present that least came onto the nest, being seen there only 9% of the 11 times she was censused (3 times the standard deviation from the mean of 57% for all non-queens, Table 2). Dissection showed that this female had the most

Table 2.
Resting positions of foundresses before and after queen tethered (nest C).

	Position			N
	On nest	Off nest	Lower comb	
Queen before tethered	1.00	0.00	0.38	13
Non-queens before queen tethered	0.57	0.43	0.07	117
after queen tethered	0.92 (a)	0.08	0.22 (b)	74

N = total records of females present in 13 pre-tethering censuses and 11 post-tethering censuses. Decimal values give proportion of N a given category of female was found at the indicated location. Difference (a) significant at $P < 0.001$; (b) significant at $P < 0.025$ (Mann-Whitney U-test).

developed ovaries (11 swellings per ovariole, three mature oocytes) among the mated non-queens dissected (figure 1, Table 3). She was also one of the four females (C1, C10, C16, C17) that although present more than half the times censused were never recorded to perform lateral vibrations or interact aggressively with others prior to tethering of the queen. Thus, in the presence of the despotic queen the queen's greatest potential aggressive challenger adopted a pattern of non-aggressive waiting off the nest.

It is of interest to compare the reaction of this female (C16) to that of C15 upon tethering of the queen. Both had approximately equally developed ovaries (three mature oocytes each; 11, 12 ovariole swellings, respectively). Prior to tethering C15 frequently came onto the nest in contrast to C16; and she added pulp to cells 3 times, whereas C16 never did so. With the exception of brief lateral vibrations immediately after tethering, she never behaved aggressively toward others as did C16. Dissection showed that the spermatheca of aggressive female C16 contained sperm, whereas that of C15 did not. All of the six unmated foundresses were never recorded to show aggressive behavior following tethering of the queen, even though three of them (C9, C10, C15) thereafter came onto the lower part of the nest for the first time and one of them (C15) oviposited twice (both times without the lateral vibration or aggressiveness toward others frequently associated with oviposition). By contrast, five of the six mated females were observed to exhibit aggressive behavior at least once after tethering (difference between unmated and mated females significant at $P = 0.008$, Fisher's Exact Test). These mated females were not consistently younger than unmated

Table 3.
Age and ovarian development of captured foundresses (nest C).

	N	No. having mature oocytes	Swellings per ovariole *		Relative age	
			Mean	Range	Mean	Range
Queen	1	1	16.0	—	5.0	—
Non-queens unmated	6	1 (16.6%)	7.2 s = 2.8	4-12	4.0	3-6
mated	8	2 (25.0%)	9.4 s = 3.7	5-12	5.1	4-6

* Eggs plus nutritive cell clusters. Difference between mean swellings per ovariole of mated and unmated non-queens not statistically significant (Mann-Whitney U-test, $P < 0.10$).

females; nor did they have less developed ovaries (Table 3). Non-aggressive, unmated females also oviposited on nests D and E. Thus, independent of age and ovarian development, being mated contributed significantly to female aggressive potential. However, this potential was only realized when mated females were not inhibited by the activities of a markedly more dominant rival.

On the final day of the tethered-queen experiment, 5 hr and 20 min of observation (9.40-15.00 hr) revealed that C11 and C16 were at the time the principal aggressive females on the lower nest, with C16 dominant to C11. The only other mated female with comparable ovarian development (female C6, with one mature oocyte and 12 swellings per ovariole) usually stayed either off the nest (20% of times censused) or on the nest top (80% of times censused), where she twice performed lateral vibrations (once leading to attack by the tethered queen), and once attacked female C15. Females C11 and C16 engaged in frequent lateral vibrations, jerked abruptly toward others, and once fought with each other. Occasionally the activities of these two females extended to the upper part of the nest. At the same time C15 was active on the surface of the nest, but her behavior continued to be passive and unaggressive. At 10.15 hr female C15 laid an egg in a peripheral cell of the upper comb. She exhibited quasi-worker behavior and other procedures commonly performed by surreptitiously ovipositing females in this species: while the queen was facing in the opposite direction on the other side of the nest she approached the queen's vicinity carrying pulp (building material) in her mouth. While inspecting the nest surface she made pre-oviposition

movements with her abdomen in a shallow empty cell. After adding a small amount of pulp to the cell she oviposited in it. She was passive when briefly inspected and gently chewed by the queen. At 11.35 hr I created five empty cells by removing two larvae in the upper part of the nest patrolled by the tethered queen, and three eggs in the lower part of the nest dominated by C16. At 12.05 hr passive female C15 laid an egg in one of the lower empty cells, without performing any aggressive abdominal movements or other aggressive behavior. Soon afterward she walked slowly to the upper region of the nest following a series of aggressive threats by C16 toward her and C11.

At about 13.00 hr the queen's tether broke, leaving her free to walk to the bottom of the nest. However, she did not do so until more than 1 hr later. The queen first antennated the hitherto undiscovered upper empty cells at 12.50 hr. By 13.40 hr she had laid eggs in both upper cells. When the released queen first visited the lower part of the nest (14.04 hr) C11 responded to her approach by doing aggressive jerking movements but promptly moved away. C15 slowly went off the nest. The queen extensively stroked the surface of the cells that she had been unable to reach for the previous 4 days. This energetic stroking stopped as soon as she laid an egg (14.15 hr). At 14.58 hr she oviposited in the final remaining empty cell. She did not find and eat the egg laid by C15, 2 hr before. Two hours after the queen's liberation the situation existing prior to tethering had been restored, with the queen dominating the entire nest and her aggressive challengers back in their former positions on the supporting branch.

In spite of having laid four eggs on the day of her release, the despotic queen C18 still had a mature oocyte when dissected the same day, and her ovary, with 16 swellings per ovariole, was $1/3$ larger than those of the other females containing mature oocytes (Table 2). Thus, the markedly greater ovarian development of the despotic queen coincided with her markedly greater dominance relative to nestmates. The despotic queen of mature colony E also had far greater ovarian development than that of her next most developed nestmates: dissections showed that only two of the 70 subordinate females present on nest E contained mature oocytes, and of these the largest ovary contained only three mature oocytes and nine swellings per ovariole. Both of the two slightly ovary-developed females were young (relative age 4 and 5) and unmated. The queen's ovary, on the other hand, contained six mature oocytes and 42 swellings per ovariole.

The tethered-queen experiment suggests that queen control in this species requires ability of a territorial female to physically reach subordinates. The radius of her dominance effectiveness was only slightly greater than the topological limits of her movements.

Table 4.
Characteristics of successive egg-layers removed from nest D.

Suc- cessive queens	Date*	Egg replacement time**	Mated (+) Unmated (-)	Mature oocytes	Swellings per ovariole	Rel. age
1	8 Sept.	12 min	+	2	—	5
2	10 Sept.	15 min	+	2	5-6	5
3	12 Sept.	15 min	—	1	6-8	5
4	15 Sept.	> 20 hr	+	3	9-10	5
5	17 Sept.	18 hr 35 min	+	2	12	6
6	19 Sept.	> 30 hr < 34 hr	+	2	10-11	6
Females remaining when nest collected						
	20 Sept.	—	+	0	9***	6
	20 Sept.	—	—	0	5	5
	20 Sept.	—	+	0	6	4

* Date collected after being observed to replace experimentally removed egg; ** time elapsed between egg removal and replacement; *** ovary with some yellow bodies (degenerate oocytes).

D. Reproductive potential of subordinate foundresses

Probably most of the subordinate foundress females of nests C and D were «potential queens». All were relatively young females with some ovarian development (Tables 2, 3). Only one relatively old foundress female (Table 4) showed signs of ovarian regression like that characterizing 24 subordinate females of intermediate relative age (categories 5-6) in a mature queenright colony (nest E). And none were as old (category 7) as the queen and four presumed workers (0 swellings per ovariole) of nest E. In the absence of an aggressive female preventing their oviposition most subordinate foundresses are probably capable of laying eggs, if not immediately within a few days of access to empty cells. This was indicated by removal of a series of egg-layers from nest D. During the period 8-19 September six «queens» (females observed to be the first to replace experimentally removed eggs following removal of the previous observed egg-layer) were removed and dissected. All six had ovary development (Table 4) comparable to that of the non-queens of nest C (Table 3). Five of the six were mated. Three females (one of them unmated) that had not yet oviposited when the experiment was terminated had somewhat developed ovaries but differed from the «queens» in lacking mature oocytes (Table 4). Such females may eventually oviposit if allowed access to an empty cell: the last three succeeding queens showed greatly increased egg-

Table 5.
Dominance hierarchy on nest D, September 9.

Dominant female	Subordinate							Total aggressive interactions
	D1	D2	D3	D4	D5	D6	D7	
D1	X	5	—	2	2	2	1	12
D2	0	X	2	1	—	—	—	10
D3	—	2	X	—	—	—	—	4
D4	0	0	—	X	2	—	1	6
D5	0	—	—	—	X	1	—	5
D6	0	—	0	—	0	X	—	3
D7	0	—	—	0	—	—	X	2

replacement intervals (Table 4), suggesting that they did not possess a mature oocyte at the time of queen removal and experimental creation of an empty cell. Late-succeeding queens also took a long time to oviposit (3 min 30 sec in the case of replacement queen # 5, Table 4) (see IV. Discussion).

E. Hierarchy in a newly founded colony lacking a despotic queen

As already mentioned, the foundress association of nest D lacked a despotic queen, and was characterized by frequent and violent physical combat in which some contestants were injured and some apparently killed. Aggressive interactions were so frequent that in just 1 hr 30 min of observation on 9 September, 42 aggressive interactions occurred, revealing a linear dominance hierarchy (Table 5). As in the classic *Polistes* hierarchy described by PARDI (1946, 1948) most (12/21 or 57%) of all interactions, and 7/9, or 77.7% of those not involving the queen were with closest competitors. Except for female D3, the higher ranking the female, the greater her frequency of involvement in aggressive interactions (Table 5).

F. Dominance in mature colonies

Although I did not attempt a systematic study of dominance relations in mature colonies, two observations are noteworthy: in nest E (the largest active nest seen during this study, see Table 1) oviposition occurred in vacated cells located in the upper third of the nest, as well as in the shallow new cells at the bottom (growing edge) of the comb. The well-developed queen (above) patrolled both areas. However a young unmated

female having ovarian development (nine swellings per ovariole) comparable to that of the foundresses of nests C and D (Tables 3, 4) oviposited in cells of the upper region while the queen was patrolling the lower periphery. This suggests that even in colonies containing a well-developed aggressive queen, queen control of oviposition by nestmates apparently requires physical proximity of the queen. The decline in dominance of the aged (wing-worn) queen of colony A, indicated by oviposition by many young females and their occasional behavioral dominance of the queen in aggressive encounters, was associated with gradual abandonment of nest A, and formation of new colonies by nest A females. Thus, as in other *Polistes* species (WEST-EBERHARD, 1969), the reproductive and dominance of the queen affects the termination of the colony cycle and can lead to colony multiplication.

IV. DISCUSSION

Dominance and queen control in the observed (Ilanos) population of *P. canadensis* resembled that of *P. erythrocephalus* near Cali (WEST-EBERHARD, 1969), and of *P. canadensis* in Panama (ITÔ, 1985). Dominance was by overt physical interaction, with approach of a dominant individual constituting a threat. Such dominance interaction represents an extreme of what might be called «confrontational» dominance, to distinguish it from the kind observed in some *Polistes* species (e.g., *P. gallicus*, *P. fuscatus* and *P. metricus* Say) in which queen control involves more «non-confrontational» behavior, such as differential oophagy, and allows temporary «standing aside» permitting worker task performance on the nest by closely ranked competitors while the queen moves off the nest and refrains from attack (see PARDI, 1948; WEST-EBERHARD, 1969; and GAMBOA & DROPKIN, 1979). The highly ritualized aggressive threat displays seen in many *Polistes* species (see WEST-EBERHARD, 1982) represent an intermediate category in which confrontation occurs but only occasionally escalates into physical battle, and very rarely into mortal fights. Such displays were not observed during this study.

Confrontational dominance must be particularly ineffective on large nests, where the queen cannot maintain a vigil of the entire comb at once. As pointed out by SÔICHI YAMANE (pers. communication) vertical combs enlarged only at the bottom might permit more efficient queen control than horizontal combs enlarged on the entire circular perimeter, providing egg-laying occurs only in newly constructed cells. However, in *P. canadensis* nest E vacated cells were reused, while the nest was still being enlarged, creating two egg-laying regions at opposite ends of a very large nest. This permitted egg-laying by young females distant from the queen

(as YAMANE's suggestion would predict). Multiple egg-layers are common in very large nests of usually monogynous species of social wasps (WEST-EBERHARD, 1977).

The data presented here, offer the first evidence of a behavioral difference between mated and unmated females (independent of ovary development) known in social wasps. Unmated females were unaggressive, and engaged in surreptitious oviposition accompanied by workerlike behavior possibly facilitating access to brood cells without inviting attack.

Unmated foundresses are surprisingly common in *Polistes* both in the tropics (WEST-EBERHARD, 1969) and in the temperate zone, where they are reported in *P. metricus* (22% of 58 dissected foundresses; DROPKIN & GAMBOA, 1981), *P. annularis* (L.) (53% of 43 dissected foundresses; KRISPYN, 1979), and *P. commanchus navajoe* Cresson (4.4% of 68 dissected overwintered females in Cochise Co., Arizona; WEST-EBERHARD, unpublished). However, GERVET (1964) could see no behavioral difference between mated and unmated females in *P. gallicus*; and PARDI & MARINO PICCIOLI (1970) reported that unmated egg-layers in *Belonogaster griseus* (Fab.) are aggressive. The uncoupling of aggressiveness from degree of ovarian development found in the unmated females of the present study provides a striking contrast to the well known pattern of correlation between rank and reproductive condition discovered by PARDI (1946) and confirmed by both behavioral and physiological studies (see RÖSELER et al., 1984) in many *Polistes* species.

It is common in social wasps for young, or relatively undeveloped queens to remain an unusually long time in the egg-laying position (abdomen thrust deeply into a cell) before an egg is deposited. This was documented by PARDI (1942), who noted that dominant queens had mean egg-deposition times of 2 min 52 sec ($n = 85$) whereas the mean for subordinates was 3 min 48 sec ($n = 35$), (similar to the 3 min 30 sec oviposition time noted for queen # 5 of nest D). In addition, late-succeeding (presumably, more subordinate) queens on nest D had very long egg-replacement times, suggesting that they (like the females remaining at the end of the queen-removal experiment) did not possess a mature oocyte at the time of queen removal and experimental creation of an empty cell. It would be of interest to know whether contact with an empty cell promotes oocyte maturation. If so, the mechanism by which dominant females inhibit ovary development in subordinates may include territorial defense of empty cells; and aggressive guarding of the egg-laying region of nests may have a dual function, both preventing stimulation of oviposition (GERVET, 1964) and preventing ovary maturation in competitors.

While dominance and aggressiveness appear to be universal in the *Polistes* species that have been studied, a linear hierarchy is not. As

illustrated by this study of *P. canadensis*, linear hierarchy formation requires repeated interaction by aggressive individuals, and this was prevented on a nest with a despotic queen that suppressed the aggressive behavior of nestmates. The existence of pheromonally maintained hierarchies, perceived by wasps, but invisible to the human observer, remains an intriguing possibility. Aggressive females of *P. fuscatus* have unusually well developed Dufour's glands whose function is unknown (DOWNING & JEANNE, 1983); and DOWNING & JEANNE (1983) recently found that the sternal gland cells of the penultimate (fifth gastral) abdominal segment, in contrast to those of the sixth sternite (which are known to produce an ant-repellent substance), are much larger in dominant females than in subordinates, «suggesting a possible role in the communication of dominance». However, if such signals exist in *P. canadensis* they must be backed up by physical dominance to be effective, as suggested by the tethered queen experiment (and by the theoretical conclusion that aggressive signals must indicate true ability to fight; see WEST-EBERHARD, 1979). Secretions of these (and perhaps other) glands may conceivably be involved in non-confrontational dominance communication in *P. canadensis*.

In *P. canadensis*, as in other social wasps, different behavior patterns are associated with different reproductive states (especially, degree of ovarian development relative to nestmates). It is clearly relative (not absolute) rank and reproductive state that affects behavior (e.g., oviposition rate, degree of aggressiveness, and position on the nest), as shown by queen tethering and queen removal experiments. The fact that «switch points» between behavior patterns are determined by *relative* conditions or cues results in remarkable flexibility in the adaptive responses of individual wasps. Hierarchy itself is probably not «adaptive» but is an artifact of the repeated interaction of differentially aggressive individuals (WILLIAMS, 1966). Thus normally haplometrotic foundress of *P. foederatus* (Kohl), artificially placed on the same nest, formed hierarchies; but rank did not lead to a division of labor, as it does in group-living foundresses of many species (PERNA et al., 1978). In group-forming populations of foundresses, the fact that degree of aggressiveness and dominance rank is related to reproductive (ovarian) state (evidently by a hormonal mechanism; see RÖSELER et al., 1984) enables relative aggressiveness to function (after generations of selection) as a cue for switching among different reproductively advantageous behavior patterns (WEST, 1967). In *P. canadensis* relative reproductive state appeared to affect degree of involvement in aggressive interactions, and position on the nest, and (hence) oviposition rate. Except for the complete absence of foraging by the nest C queen, worker (foraging) behavior showed no clear relation to ovarian state, in contrast to the situation in *P. gallicus* (PARDI, 1948). This may be brought about through the failure of *P. canadensis* foundresses to interact

aggressively; in *P. gallicus* the more frequent foraging of subordinate foundresses was a direct result of aggressive interaction with more dominant females (PARDI, 1948). In any case, dominance-difference thresholds for worker behavior and other activities (such as group joining vs solitary nesting) are expected to be different in different species, in accord with such variables as degree of relatedness of group members, likelihood of future egg-laying on the nest, and probability of survival of lone nest initiators (NOONAN, 1981).

The seemingly endless variety of competitive behavior and social structure observed in *Polistes*, makes the study of dominance relations in this genus consistently rewarding, even 40 years after PARDI first focussed attention on these phenomena and their potential general significance (PARDI, 1950). In *Polistes* it is feasible to study social dominance at several levels from its physiological basis to its role in affecting social structure, and its relationship to population parameters (relatedness, group size, length of breeding season, longevity, etc.). As a result *Polistes* promises to continue to be a key genus in understanding the evolution of social behavior, especially in relation to the behavioral and ontogenetic flexibility of individuals.

SUMMARY

Most established colonies of *Polistes canadensis canadensis* (L.) (Hymenoptera Vespidae) observed in eastern Colombia (Meta) were dominated by despotic, territorial queens that actively suppressed aggressive behavior of nestmates via physical approach and attack. Dominance hierarchies, which require repeated interaction on the part of aggressive subordinates, were not observed in such colonies; however, a classic (PARDI, 1946) hierarchy formed on a nest lacking a despotic queen. Restricting the movements of a despotic queen to a limited region on the nest showed that physical contact or very near approach is necessary for queen control in this species: females that had remained off the nest prior to queen tethering began to frequent the egg-laying region of the nest out of reach of the tethered queen, and one established a territory there. Unmated females were unaggressive even when possessing developed ovaries and ovipositing on queenright nests; they exhibited surreptitious oviposition and workerlike behavior that may have facilitated egg-laying in the presence of aggressive queens. All aggressive foundresses observed were mated. Simple approach of an aggressive female constituted an effective threat; elaborate ritualized aggressive behavior was not observed. Physical attack sometimes escalated into mortal battle. Aggressive females performed stereotyped abdominal movements (lateral vibrations, and stroking). Lateral vibrations, while they may spread a pheromone, are

«confrontational» in nature since they provoke an aggressive response by nestmates. Abdominal stroking (or slow «wagging») may function in non-confrontational pheromonal dominance communication and queen control.

RIASSUNTO

La maggior parte delle colonie di *Polistes canadensis canadensis* (L.) (Hymenoptera Vespidae) osservate nella parte orientale della Colombia (Meta) sono dominate da regine dispotiche e territoriali che sopprimono attivamente il comportamento aggressivo delle compagne di nido assalendole e perseguitandole. In tali colonie non sono state osservate gerarchie di dominazione, che richiedono ripetute interazioni da parte di subordinate aggressive; tuttavia una gerarchia «classica» (PARDI, 1946) si stabilì in una colonia dove mancava una regina dispotica. Vincolando i movimenti di una regina dispotica ad una regione limitata del nido si osservò che il contatto fisico o una vicinanza molto stretta sono necessari in questa specie perché la regina imponga il suo controllo. Femmine che erano fuori dal nido prima dell'intervento sulla regina cominciarono a frequentare la parte del nido adatta alla ovideposizione che rimaneva fuori portata della regina vincolata e una di esse stabilì qui il suo territorio. Le femmine non fecondate non sono aggressive anche quando possiedono ovari sviluppati e depongono in nidi forniti di regina; esse depongono furtivamente e presentano un comportamento di tipo operaio; ciò può facilitare la deposizione in presenza di regine aggressive. Tutte le femmine aggressive osservate erano fecondate. Il semplice avvicinamento di una femmina aggressiva costituisce una minaccia effettiva; non è stato mai osservato un elaborato comportamento aggressivo ritualizzato. Le aggressioni, talvolta, si risolvono in scontri mortali. Le femmine aggressive manifestano movimenti addominali stereotipati (vibrazioni laterali e ondeggiamenti). Le vibrazioni laterali, durante le quali potrebbe essere emesso un feromone, sono di tipo «provocatorio» in quanto sollecitano una risposta aggressiva nelle compagne di nido. L'ondeggiamento addominale (o «scodinzolamento» lento) può avere una funzione nella comunicazione feromonale di dominanza e nel controllo regale.

REFERENCES

- AKRE, R.D. 1982. Social wasps, pp. 1-105. In: H.R. Hermann, Edit. Social insects. Vol. IV. New York; Academic Press Inc., XIII + 385 pp.
- DOWNING, H.A. & R.L. JEANNE 1983. Correlation of season and dominance status with activity of exocrine glands in *Polistes fuscatus* (Hymenoptera: Vespidae). J. Kans. ent. Soc. 56: 387-397.

- DROPKIN, J.A. & G.J. GAMBOA 1981. Physical comparisons of foundresses of the paper wasp, *Polistes metricus* (Hymenoptera: Vespidae). Can. Ent. 113: 457-461.
- GAMBOA, G.J. & H.E. DEW 1981. Intracolony communication by body oscillations in the paper wasp, *Polistes metricus*. Insectes soc. 28: 13-26.
- GAMBOA, G.J. & J.A. DROPKIN 1979. Early foundress associations of the paper wasp, *Polistes metricus* (Hymenoptera: Vespidae). Can. Ent. 111: 919-926.
- GERVET, J. 1964. La ponte et sa régulation dans la société polygyne de *Polistes gallicus* L. (Hyménoptère Vespidae). Annls Sci. nat. (Zool.) (12) 6: 601-778.
- ITÔ, Y. 1985. A comparison of frequency of intra-colony aggressive behaviours among five species of polistine wasps (Hymenoptera: Vespidae). Z. Tierpsychol. 68: 152-167.
- KRISPYN, J.W. 1979. Colony productivity and survivorship of the paper wasp *Polistes annularis*. Ph. D. Thesis, Entomology, Univ. Georgia, 30 pp.
- NOONAN, K.M. 1981. Individual strategies of inclusive-fitness maximizing in *Polistes fuscatus* foundresses, pp. 18-44. In: R.D. Alexander & D.W. Tinkle, Eds. Natural selection and social behavior. Recent research and new theory. New York: Chiron Press, XII + 532 pp.
- PARDI, L. 1942. Recherche sui Polistini. V. La poliginia iniziale di *Polistes gallicus* (L.). Boll. Ist. Ent. Univ. Bologna 14: 1-106.
- PARDI, L. 1946. Ricerche sui Polistini. VII. La «dominazione» e il ciclo ovarico annuale in *Polistes gallicus* (L.). Boll. Ist. Ent. Univ. Bologna 15: 25-84.
- PARDI, L. 1948. Dominance order in *Polistes* wasps. Physiol. Zool. 21: 1-13.
- PARDI, L. 1950. Dominazione e gerarchia in alcuni invertebrati. Colloques int. Struct. Physiol. Soc. Anim., Paris: 183-197.
- PARDI, L. & M.T. MARINO PICCIOLI 1970. Studi sulla biologia di *Belonogaster* (Hymenoptera, Vespidae). 2. Differenziamento castale incipiente in *B. griseus* (Fab.). Monitore zool. ital. (N.S.) Suppl. 3: 235-265.
- PERNA, B., M.T. MARINO PICCIOLI & S. TURILLAZZI 1978. Osservazioni sulla poliginia di *Polistes foederatus* (Kohl) (Hymenoptera, Vespidae) indotta in cattività. Boll. Ist. Ent. Univ. Bologna 34: 55-63.
- RICHARDS, O.W. 1971. The biology of the social wasps (Hymenoptera, Vespidae). Biol. Rev. 46: 483-528.
- RÖSELER, P.-F., I. RÖSELER, A. STRAMBI & F. AUGIER 1984. Influence of insect hormones on the establishment of dominance hierarchies among foundresses of the paper wasp, *Polistes gallicus*. Behav. Ecol. & Sociobiol. 15: 133-142.
- WEST, M.J. 1967. Foundress associations in polistine wasps: dominance hierarchies and the evolution of social behavior. Science, N.Y. 157: 1584-1585.
- WEST-EBERHARD, M.J. 1969. The social biology of polistine wasps. Misc. Publs Mus. Zool. Univ. Mich. 140: 1-101.
- WEST-EBERHARD, M.J. 1975a. The evolution of social behavior by kin selection. Q. Rev. Biol. 50: 1-33.
- WEST-EBERHARD, M.J. 1975b. Estudios de las avispa sociales (Hymenoptera, Vespidae) del Valle del Cauca. I. Objetivos, metodos y notas para facilitar la identificación de especies comunes. Cespadesia 4: 245-267.
- WEST-EBERHARD, M.J. 1977. The establishment of reproductive dominance in social wasp colonies. Proc. Congr. Int. Un. Study Soc. Ins. (IUSSI), Wageningen 8: 223-224.
- WEST-EBERHARD, M.J. 1978. Temporary queens in *Metapolybia* wasps: non-reproductive helpers without altruism? Science, Wash. 200: 441-443.
- WEST-EBERHARD, M.J. 1979. Sexual selection, social competition, and evolution. Proc. Am. phil. Soc. 123: 222-234.

- WEST-EBERHARD, M.J. 1981. Intragroup selection and the evolution of insect societies, pp. 3-17. In: R.D. Alexander & D.W. Tinkle, Edits. Natural selection and social behavior. Recent research and new theory. New York: Chiron Press, XII + 532 pp.
- WEST-EBERHARD, M.J. 1982. Communication in social wasps. Predicted and observed patterns, with a note on the significance of behavioral and ontogenetic flexibility for theories of worker «altruism», pp. 13-36. In: A. de Haro, Edit. Communication chez les insectes sociaux (Colloque International U.I.E.I.S., Sect. Française, Sept. 1982). Barcelona: Bellaterra, 257 pp.
- WILLIAMS, G.C. 1966. Adaptation and natural selection. Princeton, N.J.: Princeton University Press, X + 307 pp.
- WILSON, E.O. 1975. Sociobiology. The new synthesis. Cambridge, Massachusetts: The Belknap Press of Harvard University Press, 697 pp.

Address of the author: Dr. MARY JANE WEST-EBERHARD, Escuela de Biología, Universidad de Costa Rica, Ciudad Universitaria, Costa Rica (Centro América).