Insectes Sociaux, Paris
1989, Volume 36, n° 3, pp. 219-234

DOMINANCE OF OVARIECTOMIZED FOUNDRESSES OF THE PAPER WASP, *POLISTES GALLICUS* (1)

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Reçu le 11 avril 1988 Accepté le 22 janvier 1989

SUMMARY

By means of ovariectomy it was possible to separate social and reproductive dominance in foundresses of *P. gallicus*. Ovariectomized foundresses could achieve and maintain the dominant position. Characteristics of social dominance (time on nest, low contribution to food collecting, dominance behaviour) were found not to be connected to the presence of ovaries. Reproductive dominance, however, did not occur in ovariectomized foundresses. Ovariectomized dominant females did not inhibit egg-formation in subordinates to the same degree as intact dominant females did and they did not show differential oophagy. For both characteristics the presence of active ovaries is necessary.

RESUME

Prédominance des fondatrices ovariectomisées chez « la guêpe cartonnière »
Polistes gallicus

L'ovariectomie des fondatrices de *P. gallicus* permet de distinguer une dominance sociale d'une dominance de reproduction. Les fondatrices ovariectomisées peuvent acquérir un rang dominant et le conserver. Les caractéristiques de la dominance sociale (temps passé au nid, faible récolte de nourriture, comportement de dominance) ne sont pas liées à la présence des ovaires. Par contre, les ovariectomisées ne manifestent pas de dominance de reproduction. Elles n'inhibent pas la formation des œufs des subordonnées avec la même intensité que les dominantes intactes ; elles ne pratiquent pas d'oophagie différentielle. Ces deux caractères impliquent la présence d'ovaires actifs.

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1. In 1979 it was proposed that the name *gallicus* should be changed to *dominulus* and *gallicus* should be transferred to *foederatus*. However, the switch of a well known name to another species only leads to confusion. Therefore, in the present paper the traditional name *P. gallicus* is used.

INTRODUCTION

In spring, foundresses of *Polistes gallicus* often cooperate in starting a nest (HELDMANN, 1936; PARDI, 1942, 1948; GERVET, 1964a, 1964b ; TURILLAZZI *et al.*, 1982; RöSELER, 1985). They form small associations which rarely contain more than 4 females. A linear dominance hierarchy is established among them. One of the foundresses achieves the dominant α position, or social dominance: she subordinates the other foundresses of the group by a specific behaviour and she solicits them for food. The dominant female α remains on the comb most of the time and seldom participates in foraging for food. The socially dominant foundress also achieves the reproductive dominance. She becomes the principal or even the sole egg-layer of the group. Eggs occasionally laid by subordinates are regularly eaten by the dominant female (differential oophagy, GERVET, 1964a).

Previous studies have shown that dominance is connected to high endocrine activity (RöSELER *et al.*, 1980, 1984; TURILLAZZI *et al.*, 1982). As a rule, the female with the highest endocrine activity is the most dominant female. By injection of juvenile hormone I or 20-hydroxyecdysone dominance behaviour (social dominance) could be induced (RöSELER *et al.*, 1984). However, the precise contribution of both hormones to social dominance is not yet clear. In a previous paper we have shown that ovariectomized foundresses with a low ecdysteroid titre in the haemolymph are also able to achieve the dominant position (RöSELER *et al.*, 1985). They even initiate a nest, though cell construction ceases after some time. In order to test which behaviours characteristic of dominance are connected to the presence of ovaries, we have studied two - and three - foundress associations with ovariectomized α females. The observations were carried out from the construction of the first cell until about three weeks after the emergence of the first adults.

MATERIAL AND METHODS

Wasps

Wasps were collected from their overwintering sites near Marseille (France) in January and kept in small plastic boxes (10 × 10 × 10 cm) filled with soft paper and a water source in a refrigerator at 10-15° C in dim daylight until used.

Formation of foundress groups

Females were taken out of the refrigerator in the morning, individually marked and separated into small cages (10 × 10 × 10 cm) supplied with honey and water. The cages were kept at room temperature. After 24 hr the cages were heated up to about 30° C by a lamp. After one hour two-foundress groups and three-foundress groups were formed and their dominance rank was tested (RöSELER et al., 1984). During the first encounter the wasps fight for dominance. After a short time one foundress becomes the dominant: she climbs upon the other, antennates her and chews on her body. The subordinated wasp behaves passively. On the following day some dominant foundresses were ovariectomized as described previously (RÖSELER *et al.*, 1985). The groups were then transferred into plastic cages (20 x 25 x 16 cm) supplied with water, honey and small crickets; one wall was covered with soft paper for cell construction. We observed 4 two-foundress groups with intact females and 4 two-foundress groups with ovariectomized α females, 2 three-foundress groups with intact females and 5 three-foundress groups with ovariectomized α females. The dominance hierarchy did not change after the operation. During the observation periods some foundresses died (3 intact females, 1 ovariectomized female) and 3 ovariectomized females were dissected. These colonies were not observed further.

Observation

On 5 days of the week the cages were heated up to about 30° C by a lamp for 7 hr each day (warm days). The rest of the day and during the night the wasps were kept at 15° C. During the following 2 days the lamps were not switched on and the cages were also kept at 15° C (cold days). On warm days, all activities of the wasps were observed for at least one hour. Observation started one hour or two hours after switch-on of the lamps alternately from day to day (9 a.m. resp. 10 a.m.). Most of the eggs are laid in the first hours after switch-on of the light. Egg-laying and egg-eating were additionally recorded throughout the day, whenever we observed them. One person was always present in the room and kept his eye on the colonies, so that especially during the egg-period both events were carefully recorded. In this way, approximately 30% of egg-laying and egg-eating were recorded outside of the observation hours.

Development of colonies we have divided into 3 periods:

1. *Egg-period:* from the first oviposition until hatching of the first larva. The duration is 15 days (11 warm days, 4 cold days).
2. *Larval/pupal-period:* from the appearance of the first larva until emergence of the first worker. This period lasts 48 days (34 warm days, 14 cold days).
3. *Postemergence-period:* after eclosion of the first adult. The colonies were observed on the following 18 warm days.

Statistics

Data were analyzed using χ^2-test and the non-parametric Wilcoxon-U-test (WEBER, 1986). The number of observations was compared for statistical significance.

RESULTS

Presence on nest

Multiple-foundress nests have the advantage that the comb is rarely left unattented. It has been shown for several *Polistes* species that the dominant foundress spends most of the time on the comb, whereas subordinates perform the majority of foraging tasks (*P. gallicus:* PARDI, 1942; *P. canadensis, P. fuscatus:* WEST EBERHARD, 1969; *P. metricus:* GAMBOA *et al.*, 1978).

Table I. — Time spent on nest (percentage of time, mean values and SD) of different ranked foundresses of *P. gallicus* in associations with intact foundresses and with ovariectomized α foundresses.
+ = intact females; — = ovariectomized females; N = number of colonies; n = hours of observation.

Tableau I. — Temps passé au nid (en pourcentage, valeurs moyennes et dispersions) par les fondatrices de rangs α, β, γ des colonies di ou trigynes dans lesquelles la dominante (α) est intacte ou ovariectomisée (*P. gallicus*).
+ = femelle intacte ; — = femelle ovariectomisée ; N = nombre de colonies ; n = heures d'observations.

			Egg-period			Larval/pupal-period			Postermergence period		
	Rank	ovaries	N	n	%	N	n	%	N	n	%
Two-foundress associations	α	+	4	45	81 ± 19	3	84	89 ± 10	3	51	81 ± 17
	β	+			40 ± 33			60 ± 27			48 ± 29
	α	—	4	27	76 ± 20	3	75	87 ± 16	2	46	92 ± 13
	β	+			33 ± 30			65 ± 22			61 ± 15
Three-foundress associations	α	+	2	20	89 ± 10	2	57	92 ± 7	2	38	85 ± 9
	β	+			70 ± 19			79 ± 14			78 ± 11
	γ	+			58 ± 42			74 ± 21			80 ± 10
	α	—	5	30	72 ± 26	3	70	85 ± 22	1	33	94 ± 6
	β	+			46 ± 29			78-± 18			89 ± 13
	γ	+			27 ± 24			51 ± 29			61 ± 16

In this way, the dominant is able to protect her eggs and to prevent non-associates from usurping the nest.

In our studies, the intact α females of two and three - foundress groups spent between 80% and 90% of the time on the comb during the three periods (*table I*). The β females were less time on the comb. In two-foundress groups the difference between α and β females is highly significant in all periods ($P < 0.001$). In three-foundress associations, however, the β females spent much more time on the comb than β females of two-foundress groups ($P < 0.001$). Thus, the difference in the mean percentage of time on nest between α and β females in three-foundress groups is highly significant only in the larval/pupal-period, but in other periods $P < 0.005$. There was no significant difference between β and γ females, though β females tended to stay more time on the comb.

Ovariectomized α females spent nearly the same percentage of time on the nest as unmutilated α females did. In two-foundress groups the difference between α and β females is highly significant in all periods, whereas the difference in three-foundress groups is significant at the $P < 0.025$ level in the larval/pupal-period and in the postemergence-period. In contrast to three-foundress groups with intact females, the β females of associations with ovariectomized α females spent significantly more time on the nest than γ females in all periods ($P < 0.005$).

Foraging

In multiple-foundress associations a division of labour is established: subordinates forage for food, the dominant remains on the comb. When the dominant female leaves the nest, she mainly collects pulp for cell construction. *Table II* shows the contribution of foundresses to collecting pulp or food. We have only counted the number of foraging trips, since it was not possible to estimate the amount of pulp or food brought back to nest per trip.

Pulp

Egg-laying dominants contribute to pulp-collecting for the most part. In subordinates, however, a strong positive correlation also exists between egg-laying and pulp-collecting ($r = 0.67$; $df = 20$; $P < 0.001$). Though the mean value indicates a nearly similar contribution of α and β females during the first period, the foundresses contributed to this task according to reproduction. The contribution of non-egg-laying subordinates is zero, whereas that of egg-laying subordinates is sometimes up to 90%. In the larval/pupal-period and in the postemergence-period the mean contribution of α females increases, because egg-laying by subordinates more and more ceases. The contribution of γ females we found to be fairly low in all periods.

The connection between egg-laying and pulp-collecting is clearly seen in ovariectomized foundresses. In three-foundress groups, we never observed ovariectomized females collecting pulp, whereas in two-foundress groups their contribution is significantly lower than that of β foundresses ($P < 0.001$). The difference between ovariectomized α foundresses and egg-laying α foundresses is also highly significant ($P < 0.001$).

Food

In the egg-period, exclusively honey was collected by the wasps; crickets were eaten outside the nest. When larvae were present, wasps also brought pieces of crickets to the nest. Intact α females foraged significantly less for food than β females during the egg - and larval/pupal-period ($P < 0.001$). Dominant females of two-foundress groups participated more often in collecting food than dominant females of three-foundress groups during the first two periods, but the difference is not significant. In the post-emergence period, α females of both associations contributed to food collecting to a similar degree of up to 30%.

Ovariectomized α females of both two - and three-foundress groups foraged for food only during the first and second period. They foraged significantly less than β females ($P < 0.001$). The proportion of foraging was similar to that of unmutilated α females in two - foundress associations. There is no significant difference between ovariectomized females

Table II. — Contribution (percentage, median values and ranges) of different ranked foundresses of *P. gallicus* to total foraging in associations with intact foundresses and with ovariectomized α foundresses,
+ = intact female; — = ovariectomized female; N = number of colonies; n = number of observations.

				Egg-period				Larval/pupal-period		
				pulp		honey				pulp
	Rank	Ovaries	N	n	%	n	%	N	n	%
Two-foundress associations	α	+	4	192	54 (5-100)	6	50 (0-67)	3	276	71 (43-93)
	β	+			46 (0-92)		50 (33-100)			29 (7-57)
	φ				—		—			—
	α	—	4	95	0 (0-31)	27	10 (0-23)	3	221	10 (3-41)
	β	+			100 (69-100)		90 (77-100)			90 (59-97)
	☿				—		—			—
Three-foundress associations	α	+	2	90	48 (17-79)	9	0 (0-0)	2	308	48 (40-56)
	β	+			52 (21-83)		57 (14-100)			34 (17-51)
	γ	+			0 (0-0)		43 (0-86)			18 (10-27)
	☿				—		—			—
	α	—	5	196	0 (0-0)	61	0 (0-11)	3	241	0 (0-0)
	β	+			67 (4-100)		63 (20-100)			56 (44-100)
	γ	+			33 (0-96)		37 (0-80)			44 (0-56)
	☿				—		—			—

and controls. However, in the postemergence-period the contribution of α females decreased to nearly zero.

Dominance behaviour

After a dominance hierarchy has been established in *P. gallicus*, no severe fights occur among foundresses. Dominance behaviour becomes more and more ritualized. In encounters, the dominant female shortly antennates the subordinate, which immediately adopts a submissive posture, i.e. the body is pressed to the ground, head and antennae are lowered. Mostly, the subordinate offers regurgitated food. Other behaviours such

Tableau II. — Contribution (en pourcentage, valeurs médianes et rangs) aux récoltes de papier ou de nourritures (miel, grillon) des fondatrices de rangs α, β, γ des colonies di ou trigynes dans lesquelles la dominante (α) est intacte ou ovariectomisée (*P. gallicus*).
\+ = femelle intacte ; — = femelle ovariectomisée ; N = nombre de colonies ; n = nombre d'observations.

					Postemergence-period					
honey		crickets			pulp		honey		crickets	
n	%	n	%	N	n	%	n	%	n	%
63	19 (13-21) 81 (79-87) —	121	14 (2-17) 86 (83-98) —	3	163	63 (48-78) 5 (0-37) 15 (0-17)	101	31 (23-31) 33 (3-34) 36 (35-74)	160	17 (4-27) 55 (35-66) 18 (17-61)
37	20 (0-36) 80 (64-100) —	75	16 (0-20) 84 (80-100) —	2	143	12 (0-24) 74 (50-98) 14 (2-26)	95	0 (0-0) 28 (25-31) 72 (69-75)	135	1 (0-2) 66 (63-69) 33 (31-35)
53	0 (0-0) 46 (36-56) 54 (44-64) —	87	2 (0-4) 49 (47-52) 49 (44-53) —	2	145	61 (59-62) 30 (22-38) 10 (3-16) 0 (0-0)	123	48 (34-62) 27 (22-32) 23 (16-29) 3 (0-5)	106	34 (33-34) 41 (40-42) 20 (15-24) 6 (2-11)
47	9 (0-27) 73 (29-82) 18 (0-66) —	123	5 (0-13) 55 (26-75) 41 (13-69) —	1	304	0 3 34 63	84	0 0 5 95	80	0 3 46 51

as "abdominal wagging" and "rubbing behaviour" are so closely related to dominance that they are regarded as components of dominance behaviour.

Domination

There are great differences in the frequencies of domination between the associations, probably depending on the difference in dominance level between foundresses (Pardi, 1948). Foundresses of similar dominance level interact more often than foundresses more distant in dominance level. The results on frequencies of domination listed in *table III* indicate therefore only tendencies, the differences are not significant.

Table III. — Frequency of dominations per hour (mean values and SD) of intact α females and of ovariectomized α females in multiple foundress associations of *P. gallicus*.

+ = intact female; — = ovariectomized female; N = Number of colonies; n = hours of observation.

Tableau III. — Fréquence de domination par heure (valeurs moyennes et dispersions) par des femelles α intactes et ovariectomisées de colonies di ou trigynes chez *P. gallicus*.

+ = femelle α intacte ; — = femelle α ovariectomisée ; N = nombre de colonies ; n = heures d'observation.

				Egg-period				Larval/pupal-period				Postemergence-period	
				α female dominates				α female dominates				α female dominates	
	Ovaries of female	N	n	β female (x/hour)	γ female (x/hour)	N	n	β female (x/hour)	γ female (x/hour)	N	n	β female (x/hour)	γ female (x/hour)
Two-foundress associations	+	4	45	0.6 ± 0.2	—	3	84	2.2 ± 1.5	—	3	51	1.7 ± 1.1	—
	—	4	27	1.5 ± 1.2	—	3	75	1.0 ± 0.2	—	2	46	1.0 ± 0.1	—
Three-foundress associations	+	2	20	1.4 ± 0.6	0.3 ± 0.1	2	57	6.0 ± 3.0	4.4 ± 1.8	2	38	2.9 ± 3.2	2.0 ± 0.1
	—	5	30	0.9 ± 0.4	0.9 ± 0.8	3	70	1.7 ± 1.1	0.7 ± 0.7	1	33	8.7	0.4

In two-foundress groups, some ovariectomized α females subordinated β females more often than intact α females did during the egg-period. The frequency increased in intact foundresses during the larval/pupal-period, whereas ovariectomized α females dominated the β females as frequently as during the egg-period. Unmutilated α females in three-foundress associations subordinated β females more often than α females in two-foundress groups did. The frequency also increased during the larval/pupal-period. Ovariectomized dominant foundresses in three-foundress associations dominated the subordinates less frequently than unmutilated α females did. The γ females received less attention from the dominant than the β females in all periods. Since γ females, however, were additionally subordinated by β females, both subordinates experienced a similar amount of domination.

Abdominal wagging

Dominant foundresses often show abdominal wagging, i.e. rapid horizontal oscillations of the gaster. In *P. metricus*, three types of gaster oscillations have ben described by GAMBOA and DEW (1981). It is thought that this behaviour is a vibration signal involved in adult-larva and in adult-adult communication, though it is not exactly analyzed. In *P. gallicus*, only one type of gaster oscillation occurs, which resembles the "abdominal wagging" of *P. metricus;* however, in *P. gallicus* the oscillations last not longer than 2-3 seconds. This behaviour is exhibited in different contexts. It is frequently performed during larvae feeding. In the present study we have not observed a significant difference between ovariectomized and unmutilated α females in exhibiting this behaviour. Both types of foundresses equally participated in larvae feeding and both performed this vibration signal. Abdominal wagging connected to dominance is sometimes shown by the dominant foundress when she antennates a subordinate. The latter retreats and then often leaves the comb for foraging. Moreover, foundresses sometimes perform abdominal wagging when they inspect cells containing eggs, or after they have brought pulp to the comb.

In associations with unmutilated foundresses, abdominal wagging was shown by α females as well as by β females during the egg-period, when they inspect cells containing eggs or, occasionally, prior to oviposition (*table IV*). We have never observed this behaviour in γ females. During the larval/pupal-period the frequency of abdominal wagging increased. In that phase, this behaviour was also shown in encounters with subordinates during antennation as well as without any direct body contact. Abdominal wagging was also exhibited by foundresses when they had landed with pulp on the comb. In the postemergence-period, foundresses only seldom showed abdominal wagging when they inspected cells with eggs, but frequently in encounters with subordinates and after return with pulp. In general, we have observed abdominal wagging more often in three-foundress groups than in two-foundress groups throughout the observation periods ($P < 0.001$).

Table IV. — Frequency of abdominal wagging (number of observations) of different ranked foundresses of *P. gallicus* in associations with intact foundresses and with ovariectomized α foundresses.

+ = intact female; — = ovariectomized female; N = number of colonies; n = hours of observation. Abdominal wagging (except during feeding) was shown: a = during inspecting eggs; b = shortly prior to oviposition; c = during antennating a subordinate; d = during encounters without contact; e = after return with pulp.

Tableau IV. — Fréquence de frétillements de l'abdomen (nombre d'observations chez les fondatrices de rangs α, β, γ des colonies di ou trigynes dans lesquelles la dominante (α) est intacte ou ovariectomisée (*P. gallicus*).

+ = femelle intacte ; — = femelle ovariectomisée ; N = nombre de colonies ; n = heures d'observation. Le frétillement de l'abdomen a été observé, en dehors des scènes de trophallaxie : a = pendant l'inspection des œufs ; b = peu avant la ponte ; c = pendant le frappement d'une subordonnée par les antennes ; d = lors de rencontres sans contact ; e = lors du retour au nid avec une boulette de papier.

			Egg-period							Larval/pupal-period							Postemergence-period						
	Rank	Ovaries	N	n	a	b	c	d	e	N	n	a	b	c	d	e	N	n	a	b	c	d	e
Two-foundress associations	α	+	4	45	1	2	—	—	—	3	84	15	5	—	1	3	3	51	—	—	3	—	6
	β	+			4	—	—	—	—			—	—	—	—	1			1	—	—	—	—
	α	—	4	27	1	—	1	1	—	3	75	—	—	1	2	2	2	46	2	—	2	5	1
	β	+			—	—	—	—	1			—	1	—	—	1			—	—	—	—	—
Three-foundress associations	α	+	2	20	2	—	—	—	—	2	57	11	8	31	25	15	2	38	1	1	39	25	11
	β	+			18	5	—	—	—			24	1	—	—	1			—	—	—	1	2
	γ	+			—	—	—	—	—			—	—	—	—	—			—	—	—	—	—
	α	—	5	30	—	—	18	18	—	3	70	1	—	11	7	—	1	33	1	—	20	2	—
	β	+			—	1	4	1	1			1	—	3	—	2			—	—	—	—	—
	γ	+			—	—	—	—	—			—	—	—	—	—			—	—	—	—	—

Ovariectomized α foundresses rarely performed abdominal wagging in context with egg inspection. This behaviour, however, was elicited in encounters with subordinates even in the egg-period during which we have not observed it in associations with intact foundresses. Ovariectomized foundresses returing with pulp also showed this behaviour. In ovariectomized females of three-foundress groups we have not observed abdominal wagging more often than in ovariectomized females of two-foundress groups.

Rubbing behaviour

Foundresses sometimes rub the gaster on the pedicel of the comb, whereby the surface is presumably coated with an ant repellent (TURILLAZZI and UGOLINI, 1979). Since dominant foundresses more often show this behaviour, a dominance pheromone might be applied.

In control groups, the intact α foundresses rubbed the gaster against the pedicel significantly more often than β females (α: 41x; β: 11x during the whole observation period; $P < 0.001$). Ovariectomized α females rubbed the gaster on the pedicel to the same degree (42x) as intact α females did, but the subordinates showed this behaviour even more frequently (52x). In three-foundress groups with ovariectomized dominants, the γ females also exhibited this behaviour.

Reproduction

The reproductive output of multiple-foundress nests is greater than that of single-foundress nests (RÖSELER, 1985), though egg-laying is more or less restricted to the α foundress. By the division of labour, however, the dominant foundress is able to invest more energy in egg-formation than a lone foundress, which must also perform the energetically expensive foraging tasks. In multiple-foundress associations, the α females attempt to monopolize reproduction by preventing other females from reproducing in several ways: Egg-formation in subordinates is reduced or even completely inhibited in presence of a dominant. The mechanisms involved (behaviour? pheromones?) are unknown. When eggs are laid by subordinates, they are mostly eaten by the dominant (differential oophagy, GERVET, 1964a).

Egg-laying and oophagy

The first sign of egg-laying is an attempt to oviposit (*essai de ponte*, GERVET, 1964b). Previously we have found that ovariectomized foundresses did not show this behaviour (RÖSELER *et al.*, 1985). In the present study we have observed five ovariectomized foundresses attempting to lay eggs. We have dissected three females: one of them was not completely ovariectomized the remains of the ovaries containing a ripe egg; another had a swelling tumor at the rectum; the third one had a swollen rectum and was not able to defaecate. Thus, a mechanical stimulus might have released laying behaviour in these females.

We have egg-laying and oophagy recorded not only during the observation hour, but whenever we have seen them. All the data given below are, therefore, the total amount we have observed in the different periods. Egg-eating could be clearly judged to be differential oophagy only in the egg-period. When larvae are present, egg-eating regularly occurs. Then even a lone foundress often eats her own eggs and feeds larvae.

In two of the two-foundress groups with intact foundresses the β females also laid eggs. In both colonies we have observed a total of 37 ovipositions of α females and 22 ovipositions of β females in the egg-period. Sixteen β eggs were seen to be eaten by the dominant foundresses within 30 min. In nests in which the α females were the sole egg-layers, we have not observed oophagy during that period. In the subsequent larval/pupal-period, both β females continued egg-laying but they oviposited less than α females. We have seen 66 ovipositions by α females and 19 ovipositions by β females in both nests. Fourteen β eggs were eaten by the dominants. However, in all colonies we have observed that α females ate their own eggs as well (2 eggs) and that β females ate their own eggs (5 eggs) and even one α egg. In the postemergence-period we noticed only one β female still laying 7 eggs, of which three were observed to be eaten by the dominant. In general, egg-eating decreased in that period, and we have not observed an egg-eating β female.

In both three-foundress groups with unmutilated females, subordinates also laid eggs. In the first period we observed 34 ovipositions by α females, 21 ovipositions by β females, and 9 ovipositions by one of the γ females. We have seen egg-eating by nearly all egg-laying foundresses: α females: 4 β eggs and 5 γ eggs; one β female. 7 α eggs; one γ female: 3 β eggs. In the subsequent larval/pupal-period egg-laying by subordinates decreased. We have observed 60 ovipositions by both α females, 17 ovipositions by both β females, and 6 ovipositions by both γ females. As in the preceding period, all foundresses participated in oophagy: both α females: 1 α egg, 8 β eggs, 5 γ eggs; both β females: 5 α eggs, 3 β eggs, 1 γ egg; one γ female: 2 α eggs, 2 β eggs, 1 γ egg. In the post-emergence-period, egg-laying, was more restricted to α females We have seen only one β female egg-laying and one α female egg-eating.

In all two-foundress associations with ovariectomized α females all the β females laid eggs. In contrast to control groups, ovipositions by β females did not decrease during the observation periods. We have observed them laying 8 eggs/female in the egg-period, 11 eggs/female in the larval/pupal-period, and 14 eggs/female in the postemergence-period. In the egg-period, oophagy did not occur. The ovariectomized α females often inspected cells with eggs, but they tolerated the eggs laid by β females. In the larval/pupal-period, both foundresses started egg-eating (ovariectomized α females: 12 eggs, β females: 3 eggs). In the postemergence-period, we only once saw an egg-eating ovariectomized α female and once a β female.

In three-foundress groups with ovariectomized α females, all five β females and four of five γ females laid eggs during the first period (10 eggs/β female; 8 eggs/γ female). In the larval/pupal-period we observed 19 ovipositions/β female and 8 ovipositions/γ female. Oophagy occurred in four groups during the first period. We saw β females eating 10 γ eggs and one γ female eating one β egg. Only one ovariectomized α female was once seen eating a β egg. In the larval/pupal-period all foundresses participated in oophagy. We observed in three nests: ovariectomized α females: 12 β eggs, 10 γ eggs; β females: 8 β eggs, 13 γ eggs; γ females: 2 β eggs, 2 γ eggs. In the postemergence-period,

Table V. — Mean size of combs and amount of brood in association of *P. gallicus* with intact foundresses and with ovariectomized α foundresses. + = intact females; — = ovariectomized females; N = Number of colonies; range in brackets.

Tableau V. — Taille des nids (nombre de cellules) et quantité de couvain (œufs, larves, nymphes) des colonies di ou trigynes dont la dominante (α) est intecte ou ovariectomisée (*P. gallicus*).
+ = femelle intacte ; — = femelle ovariectomisée ; N = nombre de colonies. Valeurs médianes et entre parenthèses, rangs.

			End of egg-period			End of larval/pupal-period						End of postemergence period					
	Rank	Ovaries	N	cells	eggs	N	cells	eggs	larvae	pupae	total	N	cells	eggs	larvae	pupae	total
Two-foundress associations	α	+	4	38 (31-45)	29 (22-38)	3	82 (55-112)	30 (16-38)	20 (17-28)	26 (18-40)	76 (51-113)	4	98 (55-138)	32 (15-44)	23 (18-47)	24 (15-36)	89 (48-127)
	β	+															
	α	—	4	18 (14-21)	13 (10-16)	3	47 (28-57)	23 (1-36)	7 (4-9)	12 (11-13)	42 (23-53)	2	64 (57-71)	25 (13-37)	29 (28-30)	7 (3-11)	61 (52-70)
	β	+															
Three-foundress associations	α	+	2	40 (31-48)	32 (25-38)	2	77 (74-80)	23 (22-24)	27 (25-29)	24 (23-25)	74 (73-75)	2	89 (85-93)	27 (22-32)	23 (21-25)	31 (28-34)	81 81
	β	+															
	γ	+															
	α	—	5	29 (21-38)	23 (14-38)	3	56 (37-81)	21 (4-48)	12 (8-17)	12 (11-13)	45 (30-72)	1	114	46	45	9	100
	β	+															
	γ	+															

the β female of the one colony laid the majority of eggs. We have not observed the ovariectomized α female nor the γ female egg-eating, but the β female was seen eating 5 γ eggs.

Reproductive success of nests

The number of cells and the amount of brood were counted every day. *Table V* shows the mean size of nests at the end of each of the three periods. Associations with intact foundresses had larger nests on average and more brood than associations with ovariectomized α foundresses. The difference is significant in two-foundress groups ($P < 0.025$), but not in three-foundress groups.

DISCUSSION

Dominance in *Polistes* consists of social dominance as well as of reproductive dominance. In the field, both are closely connected: the socially dominant females also achieve reproductive dominance. Experimentally, both components of dominance can be separated by means of ovariectomy. In a previous investigation we have shown that ovariectomized foundresses are able to achieve the dominant position and to initiate a nest (Röseler *et al.*, 1985). The present results show, moreover, that ovariectomized foundresses are also able to maintain their social dominance rank over intact subordinates, at least until the postemergence-period. This confirms the observation of Gervet (1964b), who has remarked in a short notice that ovariectomy of the dominant foundress does not change social hierarchy.

Characteristics of social dominance are not connected to the presence of ovaries. Dominant foundresses without ovaries behave as do dominant foundresses with ovaries. They spend most of their time on the comb, they seldom forage for food, but they solicit for food. They participate in larvae feeding to the same extent as intact foundresses. Ovariectomized dominants exhibit the complete dominance behaviour including abdominal wagging.

Characteristics of reproductive dominance, by contrast, are connected to the presence of active ovaries. Previously we have found that ovariectomized foundresses are able to start a nest and to construct some cells (Röseler *et al.*, 1985). In the present study, ovariectomized foundresses associated with intact subordinates rarely participated in collecting pulp; in three-foundress groups we have never seen them performing this task. This behaviour, therefore, is presumably stimulated by several factors, by the intention to start a nest, by the intention to lay eggs, by the need of the colony.

Differential oophagy is an important factor in the control of reproduction. In contrast to unmutilated α females, the ovariectomized α females accepted the eggs laid by subordinates, in three-foundress groups the eggs of β females as well as of γ females. It is yet unknown by which cues foundresses are able to distinguish the origin of eggs. Since the presence of active ovaries and egg-laying are prerequisites for this behaviour, wasps are thought to learn the smell of their own eggs during oviposition or during subsequent antennation (GERVET, 1964a). On the other hand, wasps were not able to recognize their own eggs after the abdominal nerve cord was severed, and they ate their own eggs as well as eggs derived from other foundresses. GEVRET (1964a) has assumed « que la Guêpe n'étant plus informée de l'acte de ponte considère alors comme étrangers tous les œufs rencontrés ». When larvae are present, all females start egg-eating in order to feed larvae. During that period ovariectomized foundresses also eat eggs.

Unmutilated dominant foundresses are able to inhibit egg-formation in subordinates, which cease egg-laying after a certain time. There exist great differences between foundress associations depending on the distance in dominance among foundresses. Some foundresses with small and apparently inactive corpora allata immediately behave subordinatly in the first encounter and they never oviposit (RÖSELER et al., 1980. 1984). The dominance level is far from that of the α female. Other females with very large, active corpora allata and developed ovaries are subordinated only after severe fights. They may oviposit in the first days of colony establishment, but sometimes they continue egg-laying during the preemergence-period. In general, egg-laying by subordinates decreases with time. Ovariectomized foundresses are not able to prevent subordinates from egg-laying. Since α females without ovaries dominate the subordinates to the same extent or even more frequently than do α females with ovaries, dominance behaviour alone is not sufficient to completely suppress egg-formation. Other behaviours preferentially shown by dominants (abdominal wagging, rubbing behaviour) also do not seem essentially to influence egg-formation in subordinates. However, nests of associations headed by ovariectomized dominants tended to be smaller and to contain less brood than nests headed by intact dominants. This could be a hint that egg-formation in subordinates is inhibited to a certain degree. Probably several factors must act synergistically to sterilize subordinates. It is likely that they are connected to egg-formation or oviposition of the dominant.

Previously it was not possible to distinguish between social dominance and reproductive dominance. PARDI (1948) deduced from the correlation between them a causal connection. This resulted in the severe debate between him and DELEURANCE (DELEURANCE, 1952; PARDI, 1952).

ACKNOWLEDGEMENTS. — This work was supported by Deutsche Forschungsgemeinschaft (Ro 242/8-3). We are very grateful to Alain STRAMBI for many stimulating comments. We thank Mrs. H. FOà for her excellent technical assistance.

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