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EFFECTS OF REMOVAL OF ALPHA INDIVIDUALS FROM A *Polistes dominulus* Christ. WASP SOCIETY : CHANGES IN BEHAVIORAL PATTERNS RESULTING FROM HIERARCHICAL CHANGES

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Summary :

Time-activity budgets and interaction rates of several individually identified members of *Polistes dominulus* (Christ.) wasp societies were constructed with the aim of studying changes in behavioral patterns resulting from hierarchical changes following removal of the alpha-individual. Analysis of these data by multivariate statistical techniques demonstrated the existence of an opposition between a high degree of involvement in social interactions, and a weak involvement in the work of the colony. Occupancy of the alpha rank was accompanied by a significant investment in social interaction behavior and an increase in the general level of activity on the nest. We show that the stability of the social set-up ensures permanence of the hierarchical relationships, but the updating of social relationships is established on the basis of the immediate behavioral state of the wasp, when the normal conditions are upset.

Key words : Polistes dominulus, hierarchical structure, behavioral pattern, social regulation, social organisation.

Résumé : Effet de l'enlèvement répété de l'individu alpha dans la société de *Polistes dominulus* (Christ) : conséquences sur le profil comportemental des changements hiérarchiques.

L'action répétée de l'enlèvement de l'individu en position alpha dans des colonies de *Polistes dominulus* (Christ.) dont l'effectif est maintenu constant permet d'étudier les effets de l'accession au rang alpha sur le profil comportemental des individus. L'acquisition du rang alpha se traduit essentiellement par une brusque poussée d'items manifestant la dominance; on note une augmentation importante des taux de dominance, d'ouverture et d'attaque envers les autres membres de la colonie, et de wagging. Alors que dans le même temps, l'individu s'il était impliqué dans des activités de fourragement, a tendance à se maintenir au nid et ne participe qu'accessoirement aux tâches d'alimentation et de construction au sein de la colonie. Si la structure hiérarchique qui s'établie initiallement entre paires d'individus a tendance à se maintenir si la situation sociale reste stable, un bouleversement de cette situation, que peut représenter par exemple l'enlèvement de l'individu alpha peut servir de prétexte à une réactualisation des rapports sociaux; l'examen des cas d'inversion du rang, montre que la nouvelle hiérarchie s'établie alors sur la base de l'état réactionel immédiat des diverses gûepes considérées. Ce dernier s'actualise en particulier à travers une participation importante aux interactions entre individus.

Mots-clés : Polistes dominulus, structure hiérarchique, profil comportemental, régulation sociale, organisation sociale.

Introduction

It has been clearly established for 40 years that Polistes wasp societies are organized in a social hierarchy, which PARDI (PARDI 1946 , 1948) called a scale of dominance. The structuring role of this kind of hierarchy has often been mentioned and its consequences upon egg laying, division of labour and more generally upon the mode of integration of individuals in a society have been described . (DELEURANCE 1946 , GERVET 1962).

Our general aim was to investigate how these various aspects link up together and particularly how the type of relationship each individual establishes with the others affects the general mode of functioning, the organization and the development of the society.

The present paper describes experiments which consisted of repeatedly removing the alpha-individual from a colony. Special emphasis was placed on observing the effects upon social interactions in general and upon other forms of activity such as foraging.

Material and Methods

In this study, parallel experiments were carried out upon 4 monogynous colonies of *Polistes dominulus* (Christ.), all at a comparable developmental stage, which had been reared in glass cages with a capacity of 7 liters. To prevent any variations in the total number of imagos in a society from acting as a supplementary factor in the establishment and maintenance of social interactions, the number of adults present in each society was standardized and maintained at 13.

At the beginning of the experiments, each colony comprised a foundress queen and the first 12 females to emerge; the subsequent females were removed as they emerged. Moreover, each wasp removed during the experiment (as well as any which died) was replaced by a newly emerged wasp.

Two nests were used as controls, and were observed without any manipulation apart from the replacement of dead wasps.

Two other nests were used for experiments in which the population was systematically modified according to the following procedure :

after 5 days of observation, the queen was removed. Every 8 days, we then removed the individual which occupied the alpha position. We assumed this time-interval to be sufficent to allow the new hierarchical pattern to become stabilized.

To collect the data, we employed computer observation posts including:

- a micro-computer on which individuals and items were coded. We characterized 31 items. Table 1 gives a comprehensive list of counted items.
- a monitor which was used to correct any errors in the data .
- a tape-recorder where the data were stored for future use.

Two types of observation were carried out with a view to drawing a parallel between a social interaction structure and a set of behavioral patterns.

a. - In the first type, which was frequency-based, we payed particular attention to behavioral interactions which occurred between pairs of individuals, as well as to short items where the number of occurrences seemed to be the most relevant feature. We focused on the dominance-subordination relationships, trophallaxy, transfers and exchanges of prey and solid material, departures and arrivals, and wagging behavior.

DURATION-BASED TYPE ITEMS

ON THE NEST

ALN : Feeding larvae inside the nest
BAN : Building on the nest
NEN : Grooming
IPL : In cells, inspecting the contents or transferring liquid to larvae
MCN : Walking on the nest
AG : Alert position in response to external disturbance with raised antennae
OG : Sitting quietly without doing anything on the face of the nest
OD : Inactivity on the back of the nest

OUTSIDE THE NEST

ALE : Foraging for food
BAE : Foraging for pulp and building material
SUC : Foraging for sugar and sweet solution

MCE : Walking and flying outside
EXT : Inactivity and grooming outside

FREQUENCY-BASED TYPE ITEMS

RELATIONS BETWEEN PAIRS OF INDIVIDUALS

DOM : Dominant interaction
SUB : Submissive interaction
DEC : Giving food to another wasp
REC : Receiving food from another wasp
DTR : Donor in trophallaxis
RTR : Receiver in trophallaxis
DAK : Attacking another wasp
RAK : Receiving attack from another wasp
DOF : Offering food to another wasp
ROF : Receiving food

INDIVIDUAL BEHAVIORS

WAG : Wagging, lateral body vibration
CHA : Foraging for food
SOL : Feeding larvae
PC : Foraging for pulp and bulding material
CCP : Building on the nest
H20 : Foraging for water
AQ : Arrival and Departure from the nest

Table 1 : Behavioral repertoire
Tableau 1 : Definition du répertoire comportemental

b. - Alternately , we carried out observations of the second, duration-based type, where we recorded the total time a wasp spent on the various items chosen for observation.

These items served to characterize :

- The animal's location (within the nest versus outside) ;

- The type of activity performed (prey searching or pulp foraging outside the nest, feeding and building inside the nest, or egg- laying) ;

- The general activity level of the wasp , when it was not engaged in any particular type of work, such as walking, flying, alert behavior,or idleness.

On the basis of this kind of observation, we established the activity range of all the individuals in the society during two-minute periods. We thus gathered for each wasp, 30 accounts per hour of observation, from which it was possible to establish its behavioral pattern.

Daily 4 hour sessions were carried out, with each experimental colony, alternating duration-based and frequency-based observation. Control colonies were observed for 2 hours a day. The total observation time was 37 days with each of the 2 experimental colonies, starting from the 16th day after emergence , whereas each of the 2 control colonies was observed for 63 days.

Results

The first series of results gives a picture of the relationships within the society. We subdivided the development of the colonies into 5 main periods , punctuated by the removal of the alpha-individual. Figure 1 shows the 4 colonies studied : experimental nests (colonies 5 and 8) and control nests (colonies 1 and 12).

For each colony the mean number of dominant-subordinate interactions is given per individual per hour during each of these periods. The queen's or the alpha individual's removal times are marked by arrows.

An increase in the number of these interactions can be seen to have occurred under the experimental conditions, during the periods which began with the removal of the alpha individual in comparison with what occurred in control nests during equivalent periods.

This finding was confirmed in the course of the last period of the control situation with nest 12, where the death of the queen led to a change of alpha and a correlated increase in the number of interactions.

Analysis of the degree of involvement in dominance-subordination interactions in terms of the social rank (see figure 2) , showed that alpha individuals, i.e. those belonging to rank 1, exhibited the highest rate of involvement in social interactions. This rate was significantly higher than that of the nearest subordinate, in this case the individuals belonging to ranks 2 ,3 and 4. This result is similar to those obtained on *Polistes fuscatus* (REEVES and GAMBOA , 1983).

Few differences were observed among the latter individuals. On the other hand, among individuals occupying a low position in the hierarchy, i.e. those with ranks 12 and 13 , a weaker interaction rate was observed.

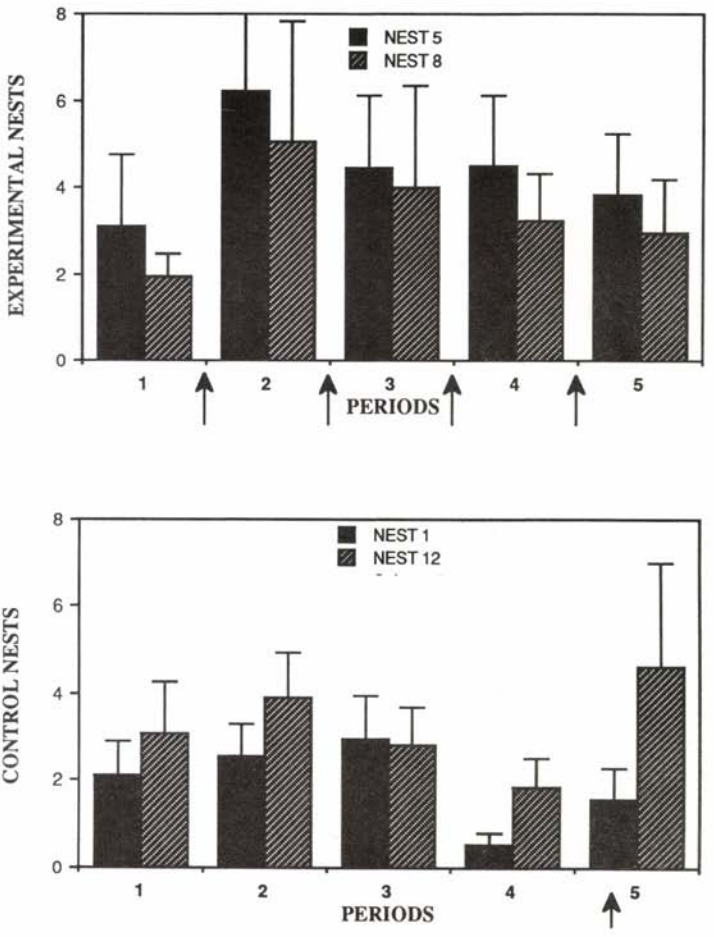

Figure 1 : Mean number of interactions per individual per hour

Figure 1 : Nombre moyen d'interactions par individu et par heure

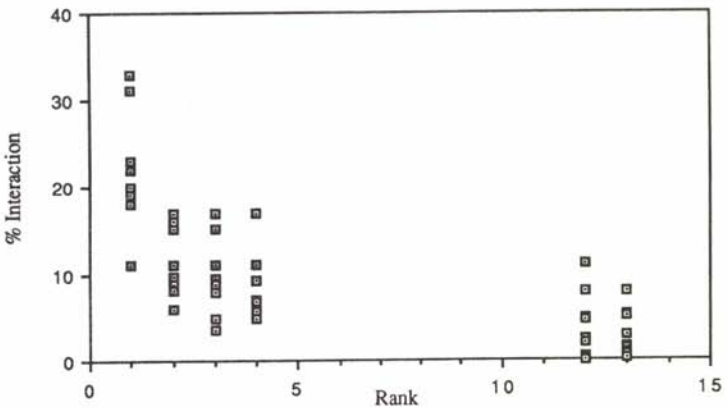

Figure 2 : Frequency of involvement in dominance-subordination interactions versus the wasps' social rank

Figure 2 : Degré de participation aux interactions de dominance-subordination selon le rang de naissance

			SOCIAL	RANK		
NEST	PERIOD	1	2	3	4	TOTAL
5	1	41,79	8,96	13,93	12,93	76,61
	2	47,43	16,63	11,9	3,9	79,86
	3	37,17	21,61	14,98	6,34	80,1
	4	22,22	16,29	24,81	17,03	80,35
	5	33,77	24,41	9,7	14,71	82,59
8	1	40,94	11,02	16,53	8,66	77,15
	2	67,84	15,94	3,54	3,54	90,86
	3	69,94	6,94	5,49	3,47	85,84
	4	47,39	6,64	10,42	6,64	71,09
	5	43,33	8,14	9,62	16,66	77,75
MEAN		45,18	13,76	11,99	9,39	80,22

Table 2 : Dominance behavioral items by individuals of rank 1 to 4

Tableau 2 : Dominances réalisées par les individus de rang 1 à 4

In spite of the considerable dispersion, a tendency was observed for the lowest individuals, to have a weak social interaction rate, whereas individuals at the top of the hierarchy had the monopoly of social interactions. In fact, if we combine all the observation periods, the individuals with ranks 1 to 4 accounted on average for 80 % of the total dominance behavioural items recorded (table 2).

These experiments show that an individual which was previously subordinate could achieve alpha rank. It was therefore possible by studying an animal's behaviour to distinguish between what features were acquired with the rank, and what features were its own.

Let us take nest 8 to illustrate this point. For each period, Figure 4 gives the value of the mean number of dominance-subordination interactions in which each individual was engaged per hour .

The number marked on the abcissa gives the rank of birth, and the arrow the wasp which occupied the alpha rank during each period. We would mention that this example was chosen because it includes a singular case, that of a rank 2 wasp, hence one in the beta-position, which did not reach alpha-rank when the alpha was removed. In this case, a reversal of dominance occurred between this wasp and the one ranking immediately below it. This kind of reversal was again observed during period 4.

This example shows the existence of two phenomena :

- In a given individual, the acquisition of alpha rank is accompanied by an increase in the number of interactions, that is to say dominance overtures which are made towards the other members of the group.

- Examination of the cases of reversal shows the existence of a difference between the wasp with rank 2 and that with rank 3: the number of interactions was higher in the rank 3 wasp which was about to attain alpha rank.

These differences presumably reflect differences in the individuals' behavioral state which may contribute to the reversal of these individuals' ranks.

The acquisition of alpha rank also affected individuals' participation level in the social work of the colony (see figure 5). The types of work which were examined here were building (pulp foraging, cell initiation and cell raising) and feeding (chasing, foraging and prey sharing inside the nest). Figure 5 shows the distribution of the social work in the same nest as previously, in minutes per hour : the various wasps are arranged according to their rank of birth, and for each of the periods considered the mean time devoted to feeding and building by the whole colony is indicated. The arrow designates the alpha-individual during a given period.

Acquiring alpha rank was accompanied by a sharp fall in social activity,evaluated in terms of larva feeding and building activity .

On the other hand, although the participation of theses wasps in larva feeding seems to have been generally higher than participation in building activity, no real individual specialization can be seen to be maintained from one period to another.

If we now attempt to define as accurately as possible the main behavioral tendencies revealed by the multifactorial analysis of the diverse items collected with our 2 types of observation, we are brought back to the opposition which we found to exist in these wasps' interactions and social work, between a high degree of participation in social interactions and a weak involvement in the work of the colony.

Figure 6 is a diagram of spatial axes 1 and 2 of the items collected , in a principal

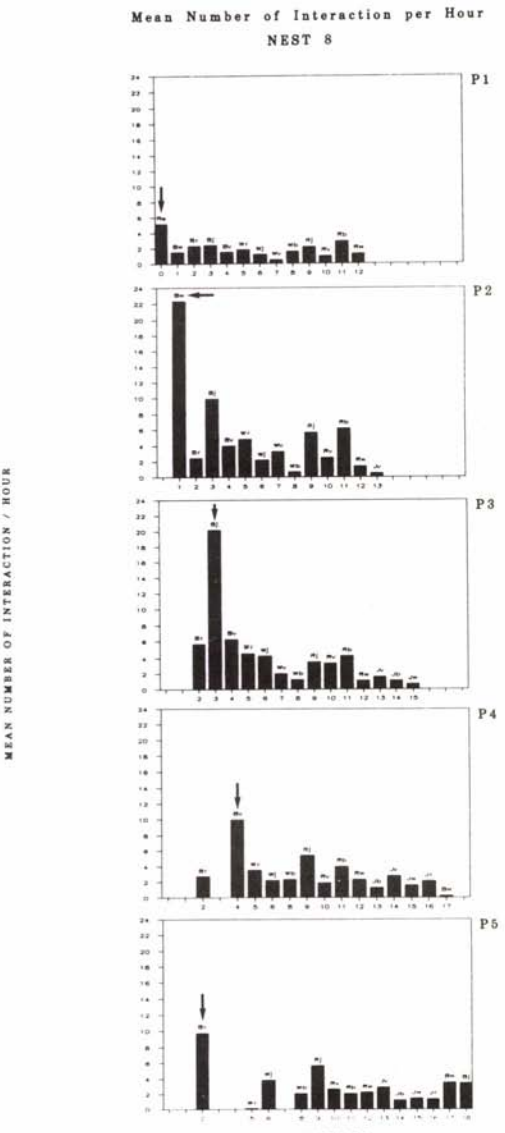

Figure 4 : Mean number of dominance-subordination interactions per individual per hour

Figure 4 : Nombre moyen d'interaction de dominance-subordination par heure pour chacun des individus

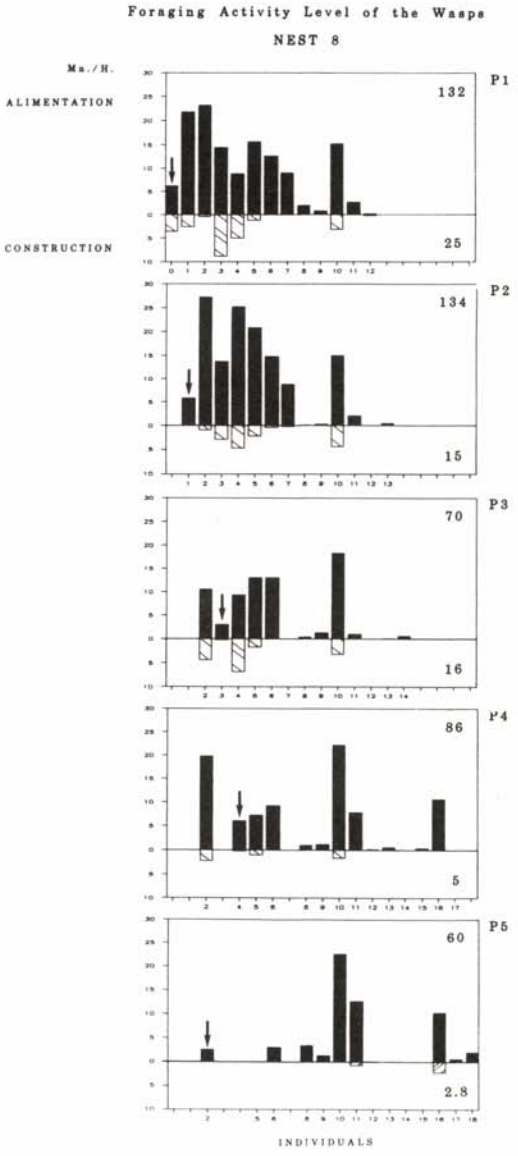

Figure 5 : Foraging activity level of the wasps during each period
Figure 5 : Participation au travail social alimentation et construction des individus du nid 8 au cours des diverses périodes

component analysis conducted with experimental nests .

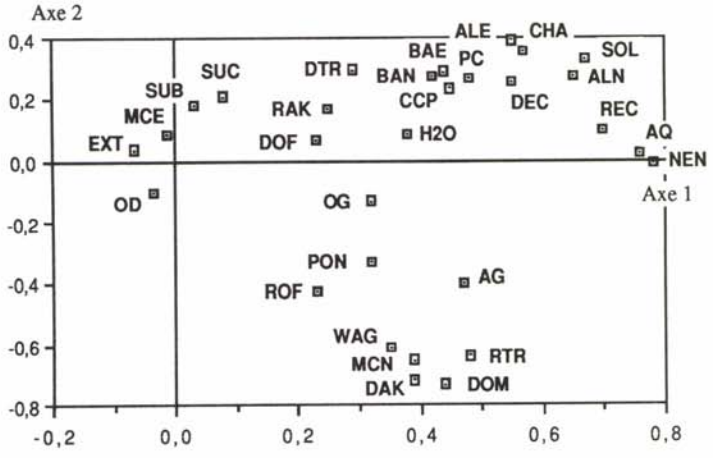

Figure 6 : Item space of the first two principal components
Figure 6 : Espace des items sur le plan des axes 1 et 2 de l'analyse en composantes principales

- axis 1 shows the greatest variance (22%), and basically reflects the degree of social integration, setting inactivity on the outside (EXT) against all forms of activity linked to integration and social work (ALN, ALE, IPL, NEN, DEC, SOL, CHA, AQ).

- axis 2, which is of particular interest to us here, and accounts for 13% of the total variance, basically sets those forms of activity which are linked to dominance (DOM), such as opening (DAK), wagging (WAG), walking on the nest (MCN), alarm behavior (AG), and egg laying (PON), against a set of actions linked to a strong involvement in prey and pulp foraging (CHA, PC, ALE, BAE), and in their distribution and exploitation at the nest (SOL, CCP, ALN, BAN, DEC).

Discussion

A balance seems to exist between the two forms of activity investigated here, indicating that a given subject can show opposite reactional state tendencies .

The wasp engages in various ways in these two forms of activity :
- Occupancy of the alpha rank is accompanied by a significant investment in social interaction behaviours, which are primarily characterized by the emergence of a high degree of dominance and overture toward the other members of the colony, by the emergence of wagging and by an increase in the general level of activity on the nest;

- whereas in subordinates, investment in social tasks is more pronounced when it is accompained by integration into the nest.

The functioning of the social hierarchy in Polistes suggests the existence of a two-fold process :

- The hierarchical relationships which are initiated between pairs of individuals, on the joint basis of prior residence (GERVET, 1964) and differences in endocrinal state (ROSELER and coll.,1984), tend to remain unchanged when the social conditions are stable.

- But the dominance then established has repercussions on the behavioral state of each member of the colony :

- the alpha-individual engages strongly in a few behaviors linked to egg-laying and the expression of its dominance;
- the subordinate individuals, which are less strongly oriented toward these activities, may either abandon all forms of social activity (leaving the nest or settling at the back of the nest) or turn towards foraging tasks. Individuals' orientation towards one or the other of these patterns may be modulated by several social factors such as its relationships with the alpha, or the amount of larval stimulations received.

It can be said that inside a hierarchically organized group, the behavioral state of an individual can change depending on several factors, such as ageing or humoral state, whereas the permanence of the hierarchical relationships depends on the stability of the social set-up.

On the other hand, when the normal conditions are upset (for instance, by the removal of the alpha individual or an unusually high emergence of females), the updating of social relationships can ensue and a new hierarchy can be established on the basis of the immediate behavioral state of the wasps present at that particular moment.

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