

Self-organization of Hierarchies in Animal Societies: The Case of the Primitively Eusocial Wasp *Polistes dominulus* Christ

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Possible self-organizing processes leading to the formation of hierarchies in animal societies are studied. Biological data collected on the eusocial wasp *Polistes dominulus* Christ are first presented and used as a basis for building simple models. The models rely on a basic positive feedback mechanism, and assume that individuals do not recognize each other. Models were tested with Monte Carlo simulations, and, depending on parameters such as the functional forms used to describe the probabilities that an individual starts and subsequently wins a fight, we found an ensemble of different profiles whose functional implications are discussed.

1. Introduction

Hierarchical behavior is a widespread phenomenon in animal groups and societies. Since the pioneering studies of Schjelderup-Ebbe (Schjelderup-Ebbe, 1913, 1922), it has been described in chickens (Allee, 1942, 1952; Guhl, 1953), cows (Schein & Fohrman, 1955), ponies (Tyler, 1972) and social insects, especially in wasps (Heldmann, 1936; Pardi, 1942, 1946, 1948; Gervet, 1962, 1964; Theraulaz *et al.*, 1992) and ants (Cole, 1981; Franks & Scovell, 1983; Bourke 1988; Oliveira & Hölldobler, 1990; Heinze, 1990). This behavior occurs through dominance/subordination interactions taking place between pairs of individuals of the same species. Such interactions generally result in differentiation of attitudes adopted by both individuals after the fight, even if only the early stages of the fight have actually taken place. Such a behavior is of central importance in organizing group activities, especially food access of individuals belonging to the group, determination of each individual's reproductive ability, or division of labour by defining

priority orders associated with particular tasks or functions.

Dominance relationships between pairs of individuals in a colony are globally stable. In this way, the set of pair-relationships within a colony typically forms a linear hierarchy, although one can sometimes observe loops or intransitive triads. In a linear hierarchy, all possible groups of three individuals form a transitive triad. In contrast, when the hierarchy is not linear it can contain intransitive triads (or higher-order loops) where for example individual A dominates individual B, B dominates C and C dominates individual A. In a linear hierarchy, each animal can be characterized by a uniquely defined hierarchical rank depending on the number of individuals it dominates, or equivalently on the number of individuals it is subordinated to.

Since the important studies of Landau (1951), and more recently of Chase (1974), little theoretical work has been done to uncover and explain the mechanisms which give rise to and allow to maintain a hierarchy in a group of animals. In this paper we analyze the

potential behavioral processes by which a hierarchy emerges in a primitive wasp society, and we give a model based on these processes. The model relies on a simple "reinforcement algorithm" in which success in a hierarchical interaction reinforces for a given individual its probability to dominate in the next fight. We show that such processes not only enable the genesis of different types of stable hierarchical structures but also allow for the re-establishment of this structure when the dominant (alpha) individual has been destroyed. We then discuss the functional and adaptive values of the underlying mechanisms.

2. Biological Background and Experimental Data

2.1. HIERARCHICAL BEHAVIOR IN *POLISTES DOMINULUS* WASP SOCIETIES

Ethological studies were carried out on a primitively eusocial species of wasp, *Polistes dominulus* (Christ). These wasps, which are found in temperate, northerly regions, build a gymnodome nest (with no external envelope), and their colonies contain a small number of individuals (≈ 20). In this species are observed little individual differentiation, no morphological differences between castes, and no predetermined control of individuals' activities depending on age or on any other known physiological predetermination (Pardi, 1942, 1946, 1948; Theraulaz *et al.*, 1990, 1991a, 1992). The integration and coordination of individual activities is based on the interactions which take place among the members of these societies and on the immediate relationships between the society and its environment.

Among the interactions that control individual behavior, hierarchical interactions are of particular importance. In *Polistes*, hierarchical behavior leads to more or less ritualized fights between pairs of individuals. This interaction results in complementary postures being adopted within any pair of individuals which come into contact: one of the individuals performs an act of dominance, and the other an act of submission. The frequency and intensity of the behavior displayed during dominance/subordination scenes can differ from one hierarchical rank to another. In particular, as was established by the pioneering studies of Pardi (1942, 1946, 1948), the highest ranking members of a hierarchy engage in these scenes most frequently.

The aim of the current experimental study was to determine very precisely the behavioral processes involved in the genesis of the hierarchy. In order to do so, the experiments began with a whole set of newly emerged individuals put together. We then observed the genesis of hierarchy. After stabilization, the

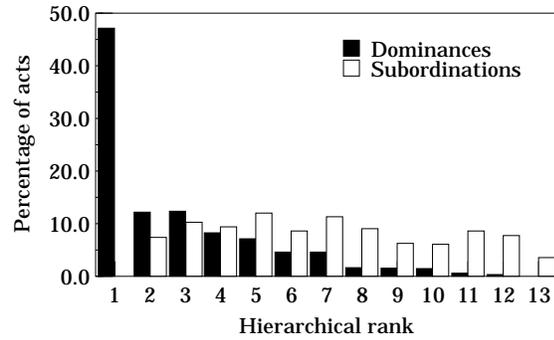


FIG. 1. Proportions of dominances and subordinations as a function of hierarchical rank in colonies of *Polistes dominulus* Christ.

number of wasps in each experimental colony was maintained constant and equal to 13, and successive alpha individuals were removed. Any wasp which was removed during the experiment was then replaced by a newly emerged individual. Each wasp was individually marked and the behavior exhibited by the whole colony was coded and recorded.

The general conclusions drawn from these experiments were presented in previous papers (Theraulaz *et al.*, 1989, 1992). The main points were as follows:

- Removal of the resident alpha individuals induced a considerable increase in the mean number of dominance scenes initiated per hour in the experimental colonies and differed significantly from the control colonies. It is worth noting that in the experimental colonies, the new alpha individual accounted for 45% of all the dominance scenes recorded, and the immediate subordinate individuals newly promoted to ranks 2 to 4 accounted for 35% of these scenes (see Fig. 1).

- We showed that the probability that an individual will dominate during a hierarchical interaction decreases according to the individual's hierarchical rank. This probability is also called the dominance index (Pardi, 1946). It corresponds to the ratio of the number of dominances (DOM) over the total number

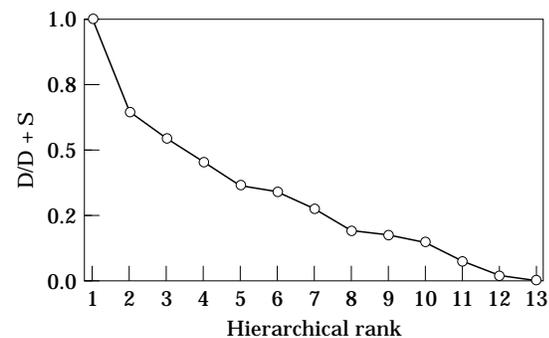


FIG. 2. Dominance index as a function of rank in colonies of *Polistes dominulus* Christ.

of hierarchical interactions (DOM+SUB) which the individual participated in (see Fig. 2). Moreover, we have shown that this dominance index gives a very reliable image of the animal's hierarchical rank (Theraulaz *et al.*, 1992).

• Finally, the higher the probability that an individual will dominate in a hierarchical interaction, the greater its tendency to frequently dominate its subordinates. Conversely, the more subordinate the individual is, the less likely it is to be willing to interact.

2.2. BASIC PROCESSES INVOLVED IN HIERARCHICAL INTERACTIONS

We postulated that one possible mechanism that could be involved in the hierarchical differentiation process was a kind of learning or positive feedback enhancing or decreasing an individual's ability to dominate depending on its previous successes or failures. As wasps move around the nest, the encounters between pairs of individuals occur more or less randomly, and each animal reinforces its probability of dominating through the number of times it is successful in hierarchical interactions; each subordination has the opposite effect. Besides, we wanted to include the observation that the stronger an individual, the more likely it is to engage in a hierarchical interaction.

Here, we first study the establishment of hierarchies in systems whose individuals follow such a simple rule, and the different kinds of collective organizations which can be produced. One crucial point is then to compare the forms of hierarchies with real natural ones and to build hypotheses about the functional value of the mechanisms which generate them. In the next section we examine the forms and the stability of hierarchies towards which the system converges and look at how the hierarchy is re-established when the top-ranking individual is removed from the system.

3. Description of the Model

If the formation of the hierarchy relies, as we hypothesized, on individual learning, the corresponding reinforcement processes can take place at two levels: they can (i) influence the probability of an individual to dominate in a hierarchical interaction, and (ii) also influence the tendency of an individual to engage hierarchical interactions. We chose to consider these two levels separately, and studied their impacts on the hierarchical profiles obtained.

3.1. PROBABILITY OF DOMINATING AN INTERACTION

In this model, we assume that a hidden variable—force—determines an individual's ability to win

during a hierarchical interaction. Such a force could be related to the physiological state of the wasp such as the activity of the corpora allata (CA) or the level of juvenile hormone (JH) in the hemolymph. In fact, high CA activity and JH level have been found to increase the probability for a wasp to become dominant (Röseler *et al.*, 1984).

If two individuals *i* and *j* engage a hierarchical interaction (note that they can meet without having such an interaction), the outcome is assumed to be probabilistic: the *i*-th individual wins with a probability given by a Fermi function

$$Q_{ij}^+ = \frac{1}{1 + e^{-\eta\Delta_{ij}}} \tag{1}$$

(the probability for *i* to lose being equal to the probability for *j* to win:

$$Q_{ij}^- = Q_{ji}^+ = 1 / (1 + e^{-\eta\Delta_{ji}}) = 1 - Q_{ij}^+,$$

where $\Delta_{ij} = F_i - F_j$ if one chooses to resort to an absolute force *F*, which is increased by a constant value in case of victory and decreased by a constant value in case of defeat. Although from a biological point of view the choice of the Fermi function was relatively arbitrary, we used it because it is a classic example of a function with a parameter which easily allows for the modulation of the deterministic/ stochastic aspect (through the inverse temperature-like coefficient η : $\eta \rightarrow \infty$ implies deterministic outcome) together with a saturation at large values.

A more directly observable quantity can be selected to be included in Q_{ij}^\pm , such as $X_i = D_i / (D_i + S_i)$ where *D_i* is the integrated number of acts of dominance since hierarchical interactions have started and *S_i* the integrated number of acts of subordination. *X* thus represents the percentage of acts of dominance with respect to the total number of interactions: this is the dominance index that was used to interpret experimental data in (Theraulaz *et al.*, 1992). The simplest associated Q_{ij}^\pm takes the form

$$Q_{ij}^+ = X_i / (X_i + X_j). \tag{2}$$

However, we chose to use once again the Fermi function given above with $\Delta_{ij} = X_i - X_j$, so that the temperature-like parameter could be modulated. Of course, it must be set to rather large values in order for individual differences not to be smoothed out (since *X_i* varies in [0, 1]). We checked that the results were in that case qualitatively similar to those obtained using eqn (2).

3.2. PROBABILITY OF INTERACTION P_{ij} THAT TWO INDIVIDUALS INTERACT WHEN THEY ENCOUNTER EACH OTHER

This probability is of utmost importance since, as we shall see, it determines most of the properties of the society's hierarchical profile. Different functional forms for P_{ij} have been tested, either based on a simplicity hypothesis or on more biological grounds. To simplify formulas, let us define $Y_i = 1/(1 + e^{-\eta_2 F_i})$.

3.2.1. $P_{ij} = 1$

This is the simplest possible form that can be used. Setting P_{ij} to a constant p means that two individuals which encounter will interact with probability p . Since no other factor enters our simulations (such as forgetting), the actual value of p influences only the speed of the process: thus, one can as well set $p = 1$. This particular form does not take into account the experimental observation.

3.2.2. $P_{ij} = \text{simple product of individual tendencies}$

One way to include the observation that stronger individuals tend to be more willing to fight than weaker ones, made in the previous section, is to use the following form for P_{ij} :

$$P_{ij} = Y_i Y_j \tag{3a}$$

or

$$P_{ij} = X_i X_j, \tag{3b}$$

depending on whether one chooses to resort to the abstract force F or to $D/D + S$ as the meaningful quantity involved in the probabilities. P_{ij} is a symmetric function of i and j , with a value which is maximum when both individuals in the pair are strong, and minimum when both individuals are weak. The middle value taken when a strong individual meets a much weaker one reflects the fact that the strong individual will try to engage a fight while the weak one will tend to escape.

The variations in the frequency of hierarchical interactions observed in experiments may have various origins. It may be due to an increase of mobility on the nest resulting from a better rank in the hierarchy, so that the "newly promoted" individual has much more chance to meet other individuals. But it may as well be due to the spatial distribution of individuals on the nest. In effect, most interactions take place on the main part of the nest: therefore, the number of potential interactions to which a given individual is subject depends on its spatial location. We have shown that middle ranked individuals tend to remain in contact with the larvae, and that they perform most of the

foraging and brood care (Theraulaz *et al.*, 1992). Our aim here was to study whether frequent absences from the nest or intermediate individuals could influence the final form of the hierarchy. To do so, we artificially imposed the probability of interaction for such individuals to be lower than for other individuals.

3.2.3. *Exponential P_{ij}*

A subtle way of taking the above-mentioned phenomenon into account together with other observations consists in taking the following form for P_{ij} :

$$P_{ij} = e^{-|Y_i - Y_j|/\delta Y_c} \tag{4a}$$

or

$$P_{ij} = e^{-|X_i - X_j|/\delta X_c}, \tag{4b}$$

depending once again on whether one chooses to resort to F or to $D/D + S$. δY_c and δX_c set the scales over which interactions can actually take place. We found that these quantities had no strong influence on the general shapes of the hierarchical profiles for a wide range of values. The forms (4a) and (4b) imply that the probability of interaction between i and j decreases exponentially with the difference between the respective forces of i and j . This implicitly means that middle-ranking individuals will have fewer interactions than others because they have a force which is far from both ends of the hierarchy and will thus most probably interact among themselves, making the middle part of the hierarchy relatively stable after a short period of time, as if it had been withdrawn from the game.

3.2.4. *Polynomial function form of P_{ij}*

In order to account for the fact middle-ranking individuals show a tendency to withdraw from the "fighting game" because they leave the nest to forage, we chose a probability of interaction that explicitly includes this observation:

$$P_{ij} = f(Y_i)f(Y_j) \tag{5a}$$

or

$$P_{ij} = f(X_i)f(X_j), \tag{5b}$$

where $f(x) = x^5 - x^2/2 + 1/2$. Note that f is an entirely empirical function designed to take experimental observations into account explicitly. The terms Y_i or X_i more or less represent the probability x of an individual to win in a random fight. Hence they represent biologically meaningful variables ranged between 0 and 1 and used to describe the ranks in the hierarchy. Figure 3 shows how the function $f(x)$ looks like.

We see that strong individuals interact with a high probability, very weak individuals interact more

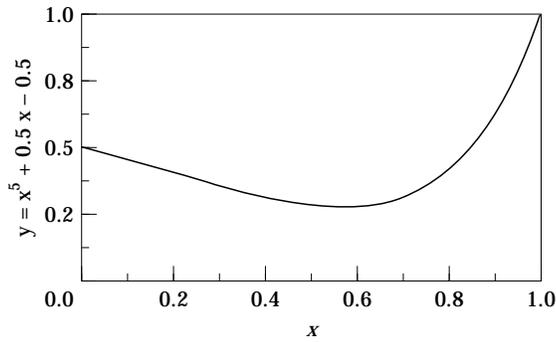


FIG. 3. The function $y = x^5 - 0.5x + 0.5$ is used to describe the fact that middle-ranking individuals frequently leave the nest to forage.

than middle-ranked individuals which have very few interactions. Once again, one expects that this type of probability of interaction should lead to a profile with a plateau in the middle.

4. Simulation of the Genesis of the Hierarchy

4.1. SOME DETAILS ABOUT THE SIMULATIONS

If it is true that in natural colonies initial differences necessarily exist between individuals before hierarchical differentiation has taken place (Röseler, 1991), these differences do not influence the final shape of the hierarchical structure finally obtained. At most, initially stronger individuals will occupy higher levels of the hierarchy. Therefore, we choose to impose equal initial forces to all individuals. We began our simulations with all individuals having the same state (namely, $D = 1$, $S = 1$, $F = 0$, $D/D + S = 0.5$, so that a given individual has an equal probability to win or to be defeated).

At each time step, a pair of individuals (i, j) is randomly selected, and is first tested to see if there will be an interaction: this is done according to the probability P_{ij} . If the answer is positive, one of the individuals wins and the other one loses, with probabilities defined above. D or S are updated according to the fight's outcome. Since $F = D - S$, this means that F can theoretically take arbitrarily large values. Though forgetting could lead to interesting results, we did not take it into account in these simulations (this will be examined in detail in a future paper). We observed the profile of the hierarchy which is most meaningfully represented by the quantity $D/(D + S)$ as a function of the rank. When the profile has become somewhat stable (low temporal variance), we remove the alpha individual to study the response of the colony to this important perturbation. In particular, we focus on the following points: (i) does

the colony recover a similar profile as before the removal, and (ii) have there been changes in the relative ranks of the individuals (or in other words, have some individuals switched ranks)?

Let us use the following shorthand notation to describe the simulations: each type of simulation is associated a pair of numbers ($C1, C2$), where $C1$ (choice_1) is 0 if one uses F and 1 if one uses $D/D + S$, and $C2$ (choice_2) is 0, 1, 2 or 3 with clear correspondence with the different probabilities of interaction presented in the previous section. It can be seen that we get eight different situations for different values of $C2$ and $C1$. We present below the results of simulations run on 20 colonies of 13 individuals.

4.2. PROPORTION OF DOMINANCES AND SUBORDINATIONS AS A FUNCTION OF INDIVIDUAL RANKS

When studying the proportion of dominances with respect to the number of acts of subordination as a function of individual ranks, three types of profiles appear (see Fig. 4):

- The first group comprises situations $C1 = 0$ and $C2 = 0$; $C1 = 1$ and $C2 = 0$; $C1 = 1$ and $C2 = 2$; $C1 = 1$ and $C2 = 3$, where the number of dominances (respectively, subordinations) decreases (respectively increases) linearly as one goes down the hierarchy. The middle individual of rank 7 has approximately the same number of dominances and subordinations.

- The second group comprises situations $C1 = 0$ and $C2 = 2$; $C1 = 0$ and $C2 = 3$, and can be characterized by the presence of a plateau in the dominance index as a function of rank. This plateau is due to the fact that the probability of interaction between two individuals decreases exponentially with the difference between the forces of the two individuals ($C1 = 0$ and $C2 = 2$), or to the fact that middle-ranked individuals have a low probability to interact ($C1 = 0$ and $C2 = 3$). The plateau disappears when the probability of winning an interaction depends on the integrated number of dominances and subordinations (situations $C1 = 1$ and $C2 = 2$; $C1 = 1$ and $C2 = 3$).

These first two types of profiles are very different from those observed in real colonies of *Polistes* (see Fig. 1), and would apply more satisfactorily to larger colonies of, for example, bumblebees (van Honk & Hogeweg, 1981). When the colony becomes very large, a linear hierarchy implies only a weak differentiation of individuals. A more functionally relevant hierarchical form would be to have a series of plateaus of individuals having a similar dominance index.

- Profiles of the third type ($C1 = 0$ and $C2 = 1$; $C1 = 1$ and $C2 = 1$) exhibit an exponential decrease of the proportion of dominances with rank. In $C1 = 0$

and $C2=1$, there is an exponential increase of the number of subordinations starting from rank 2. In $C1=1$ and $C2=1$, the evolution of this quantity presents a maximum for middle individuals. These two profiles are close to the one observed in real colonies (Fig. 2): the global number of acts of dominance exerted by the first four individuals is

of 85.8% and 67.9% respectively for situations $C1=0$ and $C2=1$ and $C1=1$ and $C2=1$, and of 80% in real colonies. The number of dominances exerted by the alpha individual is of 52% and 25%, respectively, for situations $C1=0$ and $C2=1$ and $C1=1$ and $C2=1$, while the number found in experiments is 47%.

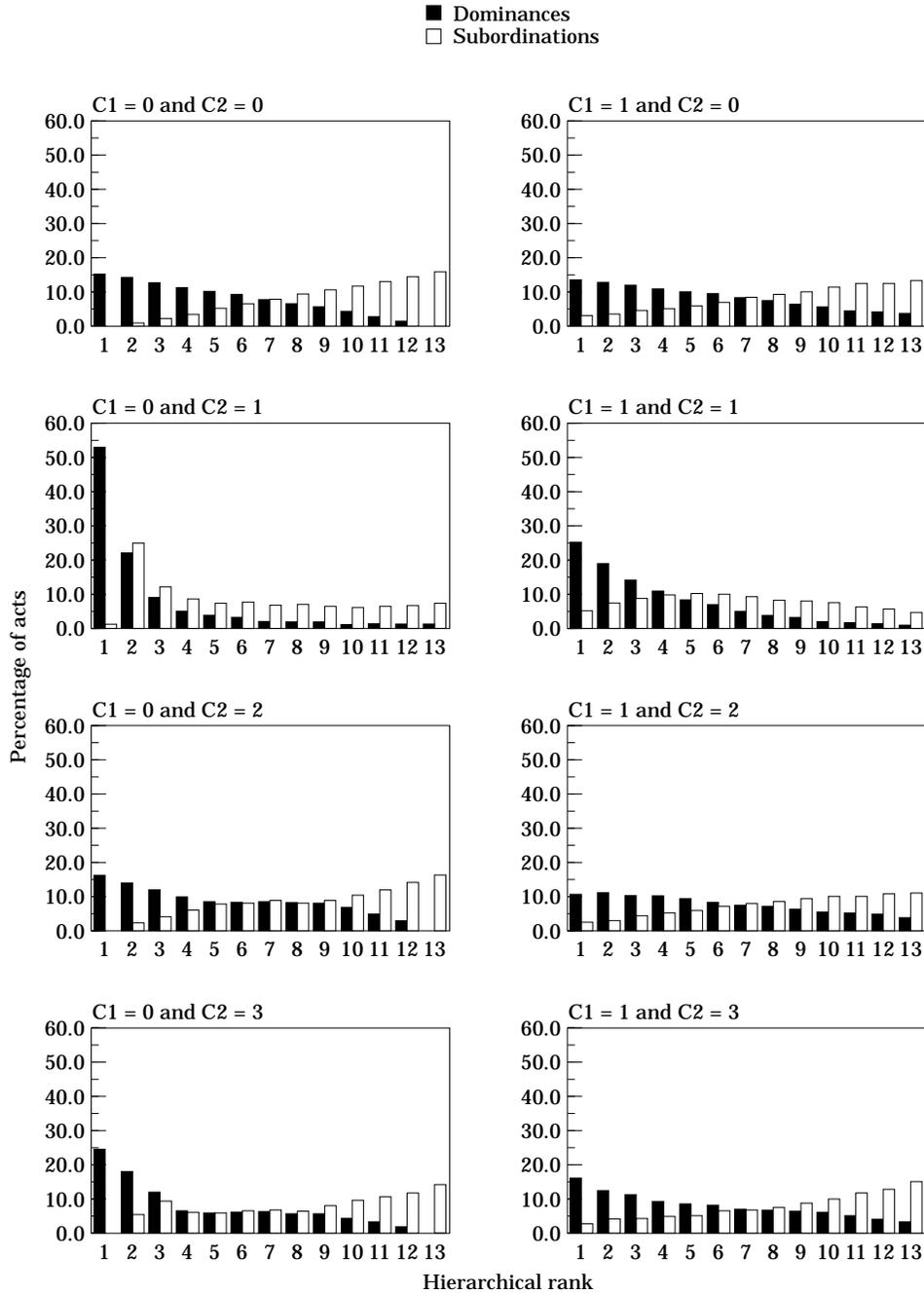


FIG. 4. Distribution of dominances and subordinations (percentage of the total acts) as a function of hierarchical rank. Twenty colonies of 13 individuals were simulated for each situation, $\eta_1 = 5$ and $\eta_2 = 1$. No substantial modification has been observed in the results when varying the parameters η_1 and η_2 (for both $C1=0$ and $C1=1$). The same statement holds for δX_c and δY_c (modifying these parameters results only in changes in the widths of the observed plateaus), which have both been set to 1. Steps/colony = 100000.

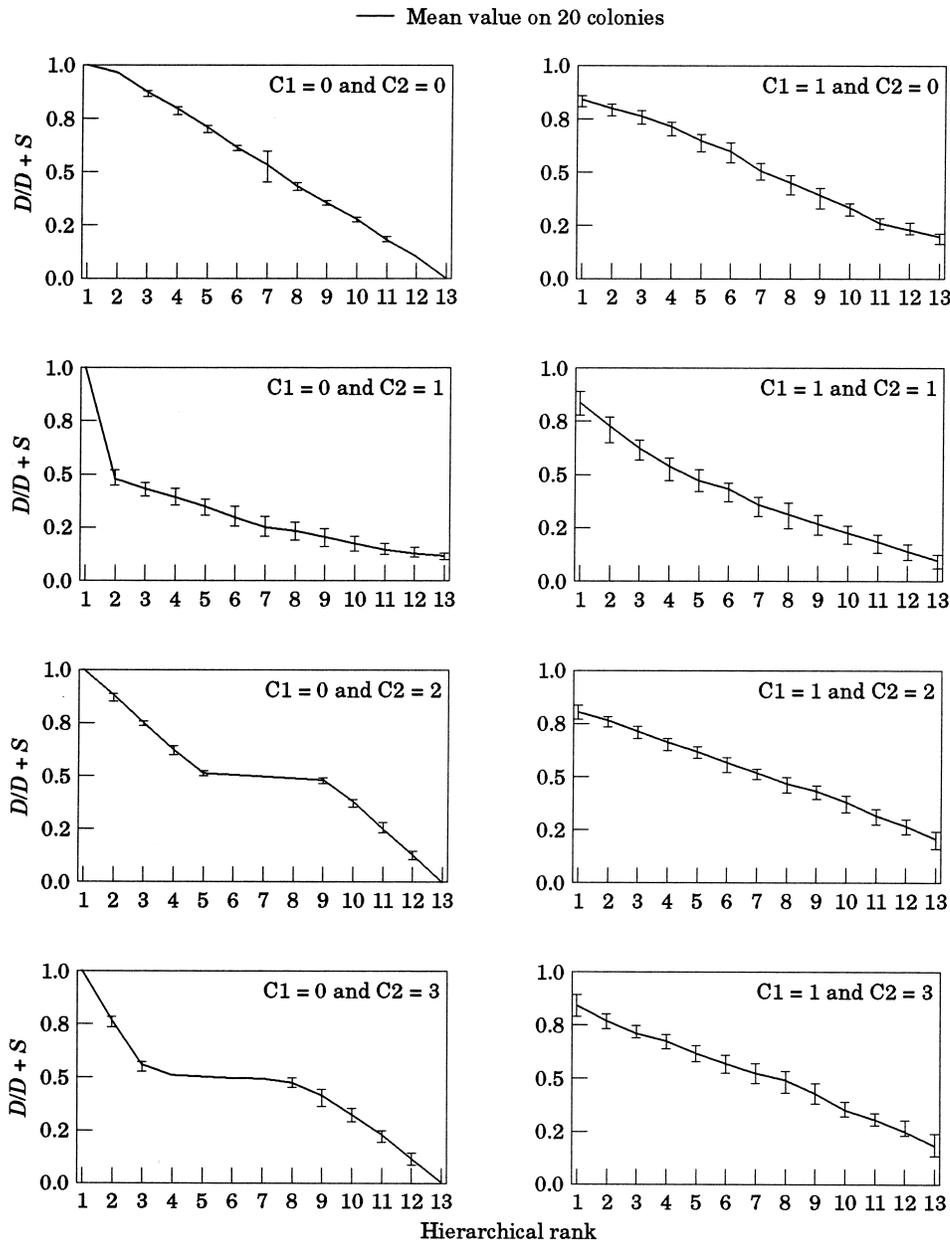


FIG. 5. Dominance index as a function of hierarchical rank. Twenty colonies of 13 individuals were simulated for each situation. Same remarks (and same parameters values) as for Fig. 4. Steps/colony = 100000.

4.3. DOMINANCE INDEX AND HIERARCHICAL STRUCTURE

Figure 5 represents the profile averaged over 20 simulations with the associated standard deviation. A study of the dominance allows three different types of structures to be distinguished:

- In the first group (situations C1=0 and C2=0; C1=1 and C2=0; C1=1 and C2=2; C1=1 and C2=3) we find linear structures whose slopes are more or less pronounced.

- In the second group, we find plateaus in the dominance index as a function of rank

(situation C1=0 and C2=2; C1=0 and C2=3).

- Finally, in the third group (C1=0 and C2=1; C1=1 and C2=1) we find an exponentially decreasing dominance index as a function of rank, where the first ranked individual is singularly stronger than the others, particularly in situation C1=0 and C2=1. This latter profile is relatively close to the one observed in experiments.

We have a rather linear profile when C2=0, an “exponential” profile which best matches the

experimental profile when $C2=1$ (the reinforcement process is amplified due to the particular form of the probability of interaction), and two profiles with a more or less pronounced plateau when using $C2=2$ and $C2=3$. When $C1=1$, there is not much variation in the close-to-linear profile, as the probability of interaction is varied. Note that the small number of simulations (20 colonies per parameter value) is justified by the very low standard deviation. The results are extremely robust with respect to variations in the temperature-like parameters, so that we present only simulations with these quantities arbitrarily set to 5 and 1, respectively.

4.4. REMOVING THE ALPHA INDIVIDUAL

The removal of the alpha individual (rank 1) results in all situations in the re-establishment of the initial hierarchical structure before removal (see Fig. 6).

The shape of the social structure towards which the society converges is therefore not determined by the initial intrinsic forces of individuals, but rather by the processes which influence the outcome of an interaction between two individuals. A careful study of how ranks evolve after the removal of the alpha individual shows that individuals do not swap ranks in the restructuring process provided initial force differences were sufficiently high. For instance, in the situation $C1=0$ and $C2=0$, there is a simple translation in the hierarchy. It must be emphasized that in experiments, individuals swapping ranks are not rare in the bottom of the hierarchy only, where there is not too much hierarchical differentiation, which is compatible with the results obtained in simulations.

5. Introduction of Individual Recognition in the Process

We have made no assumption so far concerning the ability of an individual to recognize the other members of its society on an individual basis. All members are anonymous individuals and their past experience contains no information about the precise identity of the individual(s) with which they engaged hierarchical fights. Previous experiments have shown that individual recognition might take place at least in very small groups and that this process might play a role in the genesis of circular hierarchies (Gervet *et al.*, 1993). Such a process may in turn stabilize the hierarchical interactions between pairs of individuals. However, circular hierarchies rarely occur in natural colonies of wasps in which the number of individuals is important ($n \gg 3$). This could be explained by the low cognitive capacities of a wasp to recognize a large number of individuals.

Since a model based on anonymous encounters and reinforcement processes will face difficulties in explaining the presence of circular triads, it is interesting to examine to what extent the effects of individual recognition may alter the profile of the resulting hierarchical structure. Hence, for individual i , the corresponding *effective force* F_{ij}^{eff} used in computing the probability of individual i to win when interacting with individual j will have the following form

$$F_{ij}^{\text{eff}} = \epsilon F_{ij} + \frac{1-\epsilon}{N} \sum_{\substack{k=1 \\ k \neq i}}^N F_{ik}, \quad (6a)$$

where F_{ij} is the relative force of individual i with respect to individual j , and ϵ is a parameter characterizing the weight of individual recognition in the outcome of the interaction. Depending on the value of ϵ , different profiles can be obtained. The most natural form for F_{ij} is to take $F_{ij} = \text{Dom}_{ij} - \text{Sub}_{ij}$ where Dom_{ij} (respectively, Sub_{ij}) is the number of interactions in which i has defeated j (respectively, has been defeated by j). An alternative way of evaluating Q_{ij}^+ is by taking

$$Q_{ij}^+ = \epsilon \frac{\text{Dom}_{ij}}{\text{Dom}_{ij} + \text{Sub}_{ij}} + \frac{1-\epsilon}{N} \frac{\sum_{k \neq i} \text{Dom}_{ik}}{\sum_{k \neq i} \text{Dom}_{ik} + \text{Sub}_{ik}}. \quad (6b)$$

When $\epsilon=0$, we find the model presented in this paper using abstract forces where there is no individual recognition, while when $\epsilon=1$, only individual recognition is involved in the hierarchical process, so that the hierarchical graph of dominance is basically random. Figure 7 shows results of (very time consuming) simulations aimed at studying the crossover from $\epsilon=0$ to $\epsilon=1$ for groups of three individuals when varying the parameter ϵ : there is a “phase transition” in the number of observed circular hierarchies about $\epsilon=0.6$.

6. Discussion

The observations of hierarchical interactions not only in wasp societies (Pardi, 1946; Theraulaz *et al.*, 1992), but also in ant colonies (Heinze, 1990; Meideiros *et al.*, 1992), reveals a highly inhomogeneous participation of individuals in these interactions. Moreover, the dominance index, associated with the hierarchical rank of each individual, is not a *linearly* decreasing function of the rank. It is the variation of the probability of interaction according to the rank which results in this heterogeneity: the probability of interaction decreases exponentially with rank. The simulations we performed, and in particular

the situation $C1 = 0$ and $C2 = 1$, show that a combined reinforcing process involving both the probabilities of dominating—and of interacting, in the case of success—can reproduce a hierarchical profile which compares very favorably to the one observed in real colonies. The weak standard deviation that we report

for any of the studied situations shows that simulations converge to highly stable profiles. The reinforcing process amplifies small individual differences and generates a stable, unique profile.

Study of situations $C1 = 0$ and $C2 = 2$ and $C1 = 0$ and $C2 = 3$ shows that the fact that individuals

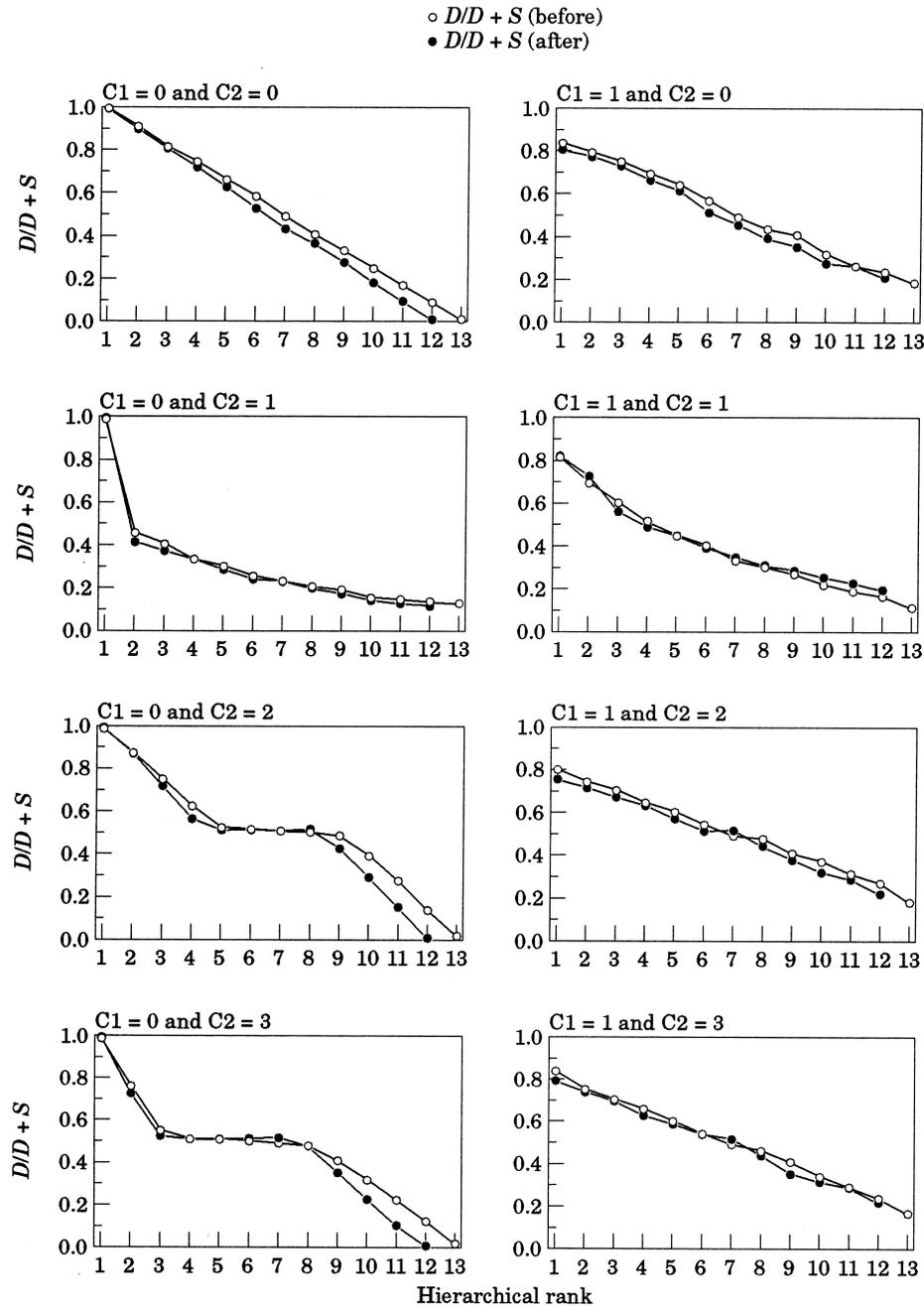


FIG. 6. Effect of the removal of alpha individual on the hierarchical profile of the colony. For each situation, the proportion of individuals who change their rank after the alpha individual has been removed is indicated. $C1 = 0$ and $C2 = 0$: no changes are observed; $C1 = 0$ and $C2 = 1$: 50% (18.33% of which are upranking); $C1 = 0$ and $C2 = 2$: 28.33% (14.58% of which are upranking); $C1 = 0$ and $C2 = 3$: 35.42% (18.33% of which are upranking); $C1 = 1$ and $C2 = 0$: 16.25% (8.33% of which are upranking); $C1 = 1$ and $C2 = 1$: 36.25% (15.83% of which are upranking); $C1 = 1$ and $C2 = 2$: 16.25% (7.92% of which are upranking); $C1 = 1$ and $C2 = 3$: 50.08% (25.42% of which are upranking).

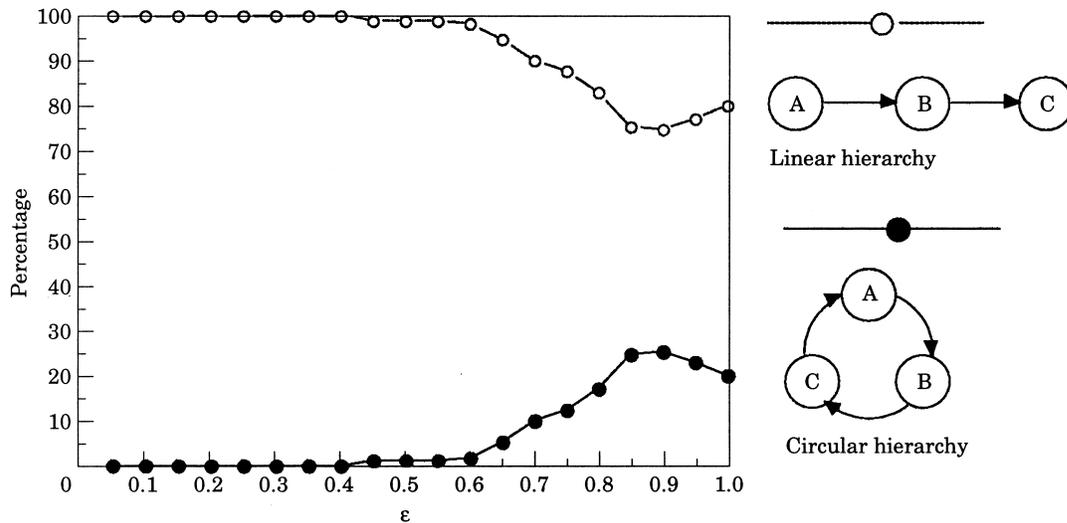


FIG. 7. Proportions of linear and circular hierarchies as a function of ϵ . One hundred colonies of three wasps with 500 steps/colony were simulated.

frequently leave the nest strongly affects the shape of the social structure, mostly by decreasing the number of subordinations for individuals in ranks 2, 3 and 4 (see Fig. 4).

The functional role of hierarchies is two-fold. First, it allows the emergence of a single reproducing individual, with differential reproduction. The most dominant individual must consequently be clearly stronger than the others: this is indeed the case since the dominance index does not decrease linearly but rather exponentially with rank. Second, it enables the progressive exclusion of non-reproducing individuals from the nest space, therefore inducing a process similar to that of territoriality in non-social species, yet in a more restricted space. Dominated individuals escape to the back of the nest, or simply leave it, while the strongest ones stay on the main part of the nest. The individual that becomes the alpha individual undergoes a physiological modification to acquire the reproducing ability, and rarely leaves the nest. The other individuals living in the neighbourhood of larvae due to their intermediate positions in the hierarchy are the ones that leave the nest the most frequently for foraging and are the most exposed to predators.

According to these simple observations, one may consider hierarchy as a basic differentiating process from which more focused differentiating refinements such as task-allocation processes, can take place: such processes can develop on the basis of the hierarchical structure in place (Theraulaz *et al.*, 1992). For instance, indirect interactions between individuals via the level of satisfaction of larvae certainly leads to

a specialization of individuals into, for example, foraging tasks or brood care, as has been shown in wasps (Theraulaz *et al.*, 1991b) and in ants (Franks & Sendova-Franks, 1992; Sendova-Franks & Franks, 1992).

This model relies on a reinforcement mechanism that can be negative as well as positive. Such a reinforcement is not necessarily a classical kind of learning process, but may very well be the result of a combination of physiological processes, as we already mentioned. One may consider hierarchical structuration as a particular case of social differentiation. In this way, the model is very similar in its underlying principles to the models of dynamical division of labour in ants where individual randomness and amplification mechanisms through learning generate the specialization of workers (Deneubourg *et al.*, 1987). In both cases simple learning rules at the individual level and direct or indirect interactions are able to shape social structures (e.g. hierarchy and division of labour) which are endowed with a high level of flexibility, adaptability and reliability. Other models of hierarchical differentiation belong to the same approach (Hogeweg & Hesper, 1983). In particular, the model introduced in Hogeweg & Hesper (1983) applies to colonies of bumblebees where hierarchical plateaus with groups of individuals having the same hierarchical level have been noticed. However, these societies comprise a much larger number of individuals ($n \approx 100$). An interesting mathematical analysis of this approach based on Boltzmann equations has been carried out in Jäger & Segel (1990), but it seems to be too "mean-field" to be conclusive.

Finally, we did not include forgetting in the present model. The inclusion of this feature would certainly lead to the appearance of a whole new set of phenomena, owing to the competition between speeds of learning and forgetting. For instance, it must be possible to prevent the hierarchy from appearing when the colony's size reaches a critical number. This should be reminiscent of results on self-organization where structures appear and can be maintained for certain values of parameters and do not exist for other values—for example, the emergence of turmites pillars (Deneubourg, 1977) or the collective mass recruitment in ants (Pasteels *et al.*, 1987) depending on a critical size of the colony.

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