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MATHEMATICAL MODEL OF SELF-ORGANIZING HIERARCHIES IN ANIMAL SOCIETIES

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We propose a mathematical approach to the modelling of self-organizing hierarchies in animal societies. This approach relies on a basic positive feedback mechanism that reinforces the ability of a given individual to win or to lose in a hierarchical interaction, depending on how many times it won or lost in previous interactions. Motivated by experiments carried out on primitively eusocial wasps *Polistes*, the model, is based on coupled differential equations supplemented with a small stochastic term. Numerical integrations allow many different hierarchical profiles to be obtained depending on the model parameters: (1) the particular form of the probability for an individual to win or lose a fight given its history, (2) the probability of interaction between two individuals, (3) the forgetting strength, which determines the rate at which events in the past are forgotten and no longer influence the force of an individual and (4) two individual recognition parameters, which set the contribution of individual recognition in the process of hierarchical genesis. We compare the results, expressed in terms of a hierarchical index or of the Landau number that describes the degree of linearity of the hierarchy, with various experimental results.

1. Introduction. The emergence of hierarchies in animal groups, colonies and societies is a phenomenon that has attracted a lot of attention for a long time. Hierarchical behaviour has been described, for example, in chickens (Shjelderup-Ebbe, 1913, 1922; Allee, 1942, 1952; Guhl, 1968), cows (Schein and Fohrman, 1955), ponies (Tyler, 1972), fish (Lowe, 1956; Bovbjerg, 1956; Bovbjerg and Stephen, 1971; Wilson, 1971) or frogs when crowded together (Haubrich, 1961; Boice and Witter, 1969), in primates (see e.g. Baldwin, 1971) or social insects, especially in wasps (Gervet, 1962, 1964; Pardi, 1946, 1948; Evans and Eberhard, 1970; Wilson, 1971; Theraulaz *et al.*, 1992) and ants (Cole, 1981; Franks and Scovell, 1983; Heinze, 1990; Heinze *et al.*, 1992; Bourke, 1988; Oliveira and Hölldobler, 1990; Medeiros *et al.*, 1992). This list is far from complete: the literature on dominance orders—a widespread alternative name for hierarchies—contains hundreds of references dating back to the systematic investigations of Shjelderup-Ebbe (1913, 1922) on the domestic fowl *Gallus domesticus*. The present paper was originally stimulated by studies on primitively eusocial wasps *Polistes*, hence a natural emphasis on social insects. However, the mathematical model of self-organizing hierarchies we shall introduce and develop is not intrinsically restricted to these animal societies: we believe in its wider applicability if sufficient care is taken to include all the relevant factors.

The hierarchical level of an individual and its function within the society are often tightly coupled: in some primitive insect colonies, for instance, such as bumblebees *Bombus* and paper wasps *Polistes*, the queen, by physically dominating her daughters and the other females in the nest, regulates most of the colony's activities (e.g. forcing other females into nonreproductive activities (Eberhard, 1969)) and, more generally, hierarchical interactions organize to a large extent the division of labor (Eberhard, 1969; Theraulaz *et al.*, 1991a). In many species of social insects, such interactions lead to reproductive hierarchies, where rank and reproductive success are strongly correlated (the egg-laying rate is often not sufficient to characterize reproductive success because eggs can be eaten by other nestmates, fed to the larvae or develop into nonreproductive workers (Heinze *et al.*, 1994)).

It is worth mentioning here the definition of a social hierarchy given by Allee (1952). According to him, the term hierarchy refers to "any social rank order established through direct combat, threat, passive submission, or some combination of these behaviour patterns." One then knows that an individual A is at a higher level in the hierarchy than another individual B if A dominates (or is most likely to dominate) B when A and B encounter. Such a dominance behaviour can be seen clearly in the attitudes of both individuals during and after the fight or can be limited to a threatening attitude on the part of the dominant. In fact, in social insects, well-defined hierarchies that follow this definition exist mostly in somewhat primitive species: in more evolved species, social control and organization tend to be performed (by the queen and other individuals) through an ensemble of pheromonal substances and not through direct aggressive interactions (Wilson, 1971). Even in primitive species, the expression of the hierarchical structure of the colony in terms of such interactions is limited to a certain amount of time following the formation of the group: there is a decrease of observable hierarchical activity with time, which may correspond to some habituation (or *social inertia* (Guhl, 1968)) or to the fact that individuals fit into their respective roles. This feature also is observed in many other examples of hierarchies outside the realm of social insects. Aggressive interactions usually exhibit a burst after the death or the artificial removal of the dominant individual as individuals of nearly equal ranks compete for the dominant position: then a new stable hierarchy is formed again.

Despite the large amount of experimental and theoretical work on this topic in a variety of ethological examples, only a few authors have dealt with the *genesis* of the hierarchical structure. The first clear and systematic study of plausible mechanisms underlying the formation of hierarchy was proposed by Chase (1974, 1980, 1982a, b) and was built upon the seminal work of Landau (1951). Chase (1974) introduced two types of models whose distinction (although somewhat artificial because reality can be a mixture of both) is insightful: The tournament model (hereafter TM) and the correlational model (hereafter CM).

- In the TM, each individual compares itself with all other animals and the *probabilistic* outcome of an *initial* interaction between A and B (say A dominates B) is "quenched" so that any subsequent encounter of A and B results in the same pattern of dominance (that is, in A dominating B). Obviously, the TM requires or is based on individual recognition: any member of the group must be able to recognize and to remember any other member on an individual basis. As emphasized by Gervet *et al.* (1993), this model can explain the existence of stable pair relationships, but does not account satisfactorily for the *strong linearity* of most hierarchical structures across the animal kingdom, owing to the "quenching" hypothesis.
- In contrast, the CM does not require individual recognition (but does not exclude it); rather it assumes the existence of a high degree of statistical correlation between an individual's rank in the hierarchy and a trait or a set of characteristic features (plausible candidates are, for example, size, strength, mobility, endocrine levels, ovarian development,...) that can be assigned a value. By definition, if the correlation

> is high enough, this value plays the role of a dominance index, because it is expected to predict the dominance rank accurately. After a careful analysis of available experimental data, Chase (1974) concluded that the CM is not a good explanation because strong linearity requires that correlations reach a high level not compatible with experimental data. For example, in observations on hens reported by Guhl (1968), there seemed to be only small correlations between individual positions in hierarchies formed in the same group in two successive experiments separated by a period of isolation.

In the original CM, the set of characteristics was assumed to be pinned at fixed values. According to Wilson (1975), Chase found a solution to this problem by assuming a CM with variable dominance index: in effect, the set of characteristics defining the index can be subject to a positive (respectively, negative) feedback in case of victory (respectively, of defeat). The probability of wining a contest therefore increases (respectively, decreases) with the number of victories (respectively, defeats). Such "loser and winner effects" (Chase 1982a, b, 1985; Chase and Rohwer, 1987) seem to be confirmed experimentally (Chase, 1986) in chickens (McBride, 1958; Chase, 1980, 1982a, b, 1985), crickets (Alexander, 1961; Burk, 1979), fish (Francis, 1983; Beaugrand and Zayan, 1984), mice (Ginsburg and Allee, 1975), rats (Van de Poll *et al.*, 1982), rhesus monkeys (Mendoza and Barchas, 1983; Barchas and Mendoza, 1984), bumblebees (Van Honk and Hogeweg, 1981) and wasps (Theraulaz *et al.*, 1989, 1992).

In this "magnification" mechanism, randomness—luck or lack of luck—combined with the intrinsic abilities of individuals to win fights are the underlying mechanisms of a dynamical process whereby some individuals tend to be shifted upward and others downward through amplifications of individual differences. This reinforcement process leads to the development of a stable close-to-linear hierarchy. This model emphasizes the importance of initial encounters, whose *fluctuations* may be amplified. The appropriate theoretical framework for understanding Chase's model originates from non-linear thermodynamics where it is known as "dissipative structures" (Nicolis and Prigogine, 1977, 1989; Deneubourg, 1977; Deneubourg *et al.*, 1987; Pasteels *et al.*, 1987): an initially undifferentiated state, that is, without any hierarchical structure, may evolve into a differentiated state through the amplification of fluctuations. In a related work, Hogeweg and Hesper (1983) proposed a model based on experimental observations of bumblebees *Bombus terrestris* (Van Honk and Hogeweg, 1981), assuming that a simple positive feedback mechanism applied to a single variable could explain the formation of a hierarchy: the more an individual wins, the more likely it is to win in future fights. They showed with a "socioinformatic" model (that is, a model in which colony-level properties are not explicitly coded but emerge from individual behaviors interacting with one another and with their environment (Hogeweg and Hesper, 1985)) that this type of simple rule, based on the reinforcement of a *single* variable according to the victories and defeats of each individual, can generate a differentiation among initially identical individuals. For this differentiation to take place, however, they found that additional factors arising from the structuring of the environment might be necessary. However, as we shall discuss at the end of this paper, this is due to the highly probabilistic nature of their dominance process: even an individual with a top rank can be defeated with some finite probability. The win–loss function we shall resort to here will be more like "dominance almost always wins" (Jäger and Segel, 1992), which allows us to get differentiation without further assuming a particular structuring of the environment.

Because individuals are rated in terms of a variable representing the dominance index which is allowed to vary according to the "feedback rules" just mentioned, this modified CM can account for the linearity of hierarchies as well as for the problematic experimental results of Guhl (1968), as we shall discuss later on. Finally, and importantly, mixtures of CM (with variable index) and TM (individual recognition) are most likely to occur in nature, because stable intransitive loops *may or may not* be observed in simple animals such as wasps *Polistes* (Gervet *et al.*, 1993, versus Theraulaz *et al.*, 1992), depending on the number of animals that comprise the group. The exact nature of individual recognition processes is still unclear in many animal species (Zayan, 1994). We shall explore a simple model of individual recognition, which seems to apply well to simple animals, but with more difficulty to higher animals, where many additional factors, such as bystander effect, come into play. Indeed, results on chickens and wasps seem to be exactly opposite: loops (of a rather stable kind) may be observed only in small groups of *Polistes* (Theraulaz *et al.*, 1989, 1992; Gervet *et al.*, 1993) whereas they can be observed, under an unstable form, only in large groups of hens (Shjelderup-Ebbe, 1913, 1922).

The mathematical model presented in this paper is based on a very similar feedback or reinforcement hypothesis. The rest of the paper is organized around this hypothesis, which we extend in several directions. The first approach one might think of to model the formation of a hierarchy in simple social animals is a master equation describing the evolution of the population density in each hierarchical class, a class being defined by the range of "forces" of its individuals. This approach, which we describe in more detail in section 5 together with results we obtained from numerical simulations, would be very similar in spirit to the one studied in Jäger and Segel (1992). However, this modelling tool is not accurate enough because it gives no detail about the fluxes between classes: in particular, it is impossible with this description to know which individuals have increasing or decreasing hierarchical ranks, because the studied quantity—the density of individuals per class—is an average. Moreover, forgetting and individual recognition, which we study in this paper, cannot be dealt with satisfactorily within such a description.

The alternative choice that we made consists of recording the evolution of each individual's dominance index, modelled by coupled differential equations with a small random component. This approach allows us to get more refined results about the composition of the population and completes Monte Carlo simulations reported in Theraulaz *et al.* (1995). In the next section, we give some results of ethological studies performed on primitively eusocial wasps *Polistes dominulus* so as to illustrate with a simple example the biological grounding of our approach. In section 3, we introduce the basic ingredients of our model. In section 4, we introduce the coupled equations and study their behaviours in various conditions, including forgetting and individual recognition. In section 5, we review some existing work on this topic and extend the model of Jäger and Segel (1992). Finally, in section 6, we clearly define our contribution to the domain. Following the vocabulary of Chase (1986) and Chase and Rohwer (1987), our aim is to describe the consequences on the hierarchical structure of particular hypotheses about the behavioural dynamics of dominance hierarchy formation. Such hypotheses then serve both as descriptions and as explanations, at the level of proximate causes, of hierarchical genesis. We use a single variable to rank individuals in a well-defined hierarchy. This is the simplest situation: obviously, many more variables would be required to reflect the full complexity of the social functioning of animal groups and colonies. Dominance is not a simple concept: for example, several kinds of orders can coexist within a colony besides agonistic encounters, such as orders related to the access to females (in baboons, Kummer, 1968; in cattle, Barton *et al.*, 1974) or leadership in group movements. However, there exist correlations between the various rank orders in many species. Our model can then be seen either as (1) a model of simple societies such as those encountered in some primitive insect species or (2) as being embedded within a larger model whose additional variables are integrated into working hypotheses, under the form, for example, of a particular probability of interaction between individuals. In this latter case, our model describes just a part of the social relationships between members of the society, and its relevance certainly decreases as this part becomes small.

Because this paper is long enough without further considerations, we made the choice to discuss neither the functional consequences of particular hierarchical (or, more generally, social) structures (that is, what is the exact function of a given organization?) nor the related question of the emergence of hierarchical organizations on evolutionary scales (that is, how did such and such organization appear and persist?). Let us simple mention one important fact that is certainly connected with evolutionary considerations: hierarchical aggressive interactions generally correspond to a very small fraction of the time spent by individuals in social activities; fights take place under specific conditions, for example when individuals are put together for the first time or when they compete for a resource or possibly for mating. Aside from these specific conditions, threat displays replace fights most of the time: from the evolutionary viewpoint, this may result from the fact that fights can be energetically expensive, damaging or even lethal. Ritualized fights, in which individuals assess their opponents' abilities in order to decide whether to escalate the fight or retreat, rather than real fights, belong to the class of evolutionary stable strategies (Maynard-Smith and Price, 1973; Maynard-Smith, 1974).

2. Biological Data: The Example of the Primitively Eusocial Wasp *Polistes dominulus*. *Polistes dominulus* colonies contain a small number of individuals (max ≈ 20). In this species we observe 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). Among the interactions that control individual behaviour, hierarchical interactions are of particular importance. Hierarchical behaviour leads to more or less ritualized fights between pairs of individuals, during which an individual physically dominates another individual. The frequency and the intensity of these fights vary with hierarchical rank. In particular, as was established by Pardi (1946, 1948) and confirmed in experiments reported in Theraulaz *et al.* (1989, 1992), the stronger individuals of a hierarchy tend to interact more frequently than others. To take into account the observation that strong individuals interact more often, we shall use various forms for the probability of interaction between individuals and study how these forms influence the final hierarchical profiles. In the experiments described in Theraulaz *et al.* (1989, 1992), the behaviour of a set of newly emerged individuals put together was recorded. Figure 1 shows the dominance index $X_i = D_i/(D_i + S_i)$ for each individual i (X_i is the proportion of successful interactions D_i with respect to the total number of interactions $D_i + S_i$, where S_i is the number of subordinations) found in these experiments (averaged over 10 colonies). X_i defines the hierarchical rank, which means that the probability integrated over history that an individual has dominated during a hierarchical interaction de-

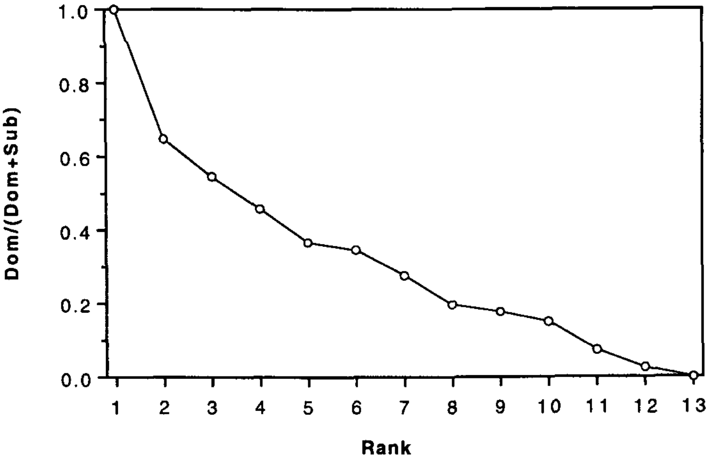

Figure 1. Variation of the dominance index as a function of rank in *Polistes dominulus* (after Theraulaz *et al.*, 1991a). Error bars correspond to the standard deviation over 10 experimental colonies of 13 individuals.

creases with rank. We shall use the dominance index X_i to interpret the results of our model.

We postulate, in the spirit of Van Honk and Hogeweg (1981) and Hogeweg and Hesper (1983), that one possible mechanism that could be involved in the hierarchical differentiation process is a kind of positive feedback. As wasps move around the nest, encounters between pairs of individuals occur more or less randomly, and each animal reinforces its probability of dominating (respectively, of being dominated) every time it dominates (respectively, is dominated). We have reported in previous papers (Theraulaz *et al.*, 1989, 1992) that the tendency of an individual to dominate (respectively, be dominated) in fights increases with the proportion of all previous fights in which it was dominant (respectively, dominated). This means that the dominance index X_i not only describes the past history of interactions of individual i, but also its probability to win in an arbitrary fight to come. One then understands the interest of studying X_i, an experimentally measurable quantity with a powerful meaning. The other noticeable result of these experiments (Theraulaz *et al.*, 1989, 1992) concerns the response of the colony to removal of the resident α individual: it induced a considerable increase in the mean number of dominance scenes per unit time in the experimental colonies and differed significantly from the control colonies. The new α individual accounted for 45% of all the dominance scenes recorded in these bursts of hierarchical activity, whereas the immediate subordinate individuals newly promoted to ranks 2–4 accounted for approximately 35% of these scenes. These last results on the removal of the α individual will not be studied with the model we shall introduce, which cannot account completely for temporal variations in the number of acts: the vanishing observable hierarchical activity accompanying the stabilization of the hierarchy and the bursts of activity following some particular perturbations may certainly be the result of a complex interplay between various factors, such as pheromonal regulation (e.g. the presence of the queen inhibits the development of ovaries of nestmates), that are not taken into account in the model.

3. Parameters of the Model. In this section, we describe how the probabilistic outcome of a hierarchical fight is computed and introduce the probability of interaction between two individuals, of which we give some candidate functional forms.

3.1. *Probabilistic outcome of a fight.* If two individuals i and j start a hierarchical interaction, the outcome of the fight is assumed to be probabilistic: individual i wins with a probability given by $Q_{ij}^{+} = 1/(1 + \exp(-\eta\Delta_{ij}))$, with $\Delta_{ij} = F_i - F_j$, where F_i is a quantity that we call force, increased by a constant value (δ^{+}) in case of victory and decreased by a constant value (δ^{-}) in case of defeat. One can interpret this force, within the framework of a modified correlational model (CM) (Chase, 1974; Gervet *et al.*, 1993), as an indicator of the physiological state of the animal. This state includes e.g. in wasps, the activity of the corpora allata (CA) or the level of juvenile hormone (JH) in the hemolymph: CA activity and JH level have been found to increase with rank (Röseler *et al.*, 1984; Röseler, 1991). Of course, the observation of correlations between some hormones in wasps or in other animals (e.g., adrenal hormones in squirrel monkeys (Candland and Leshner, 1971)) is no proof of a causal relationship from hormone level to rank or the other way round. It is therefore part of our assumptions to start from the existence of an aggregate quantity, denoted by F, which directly determines the ability of an individual to dominate in a hierarchical interaction and which is subject to a feedback mechanism whose sign depends on how well an individual with force F is performing given the current hierarchical state of the colony. When $\delta^{+} = \delta^{-}$, F_i is simply proportional to the number of times the individual has been successful minus the number of times it has been dominated. The probability for i to lose is equal to the probability for j to win: $Q_{ij}^{-} = Q_{ji}^{+} = 1/(1 + \exp(-\eta\Delta_{ji})) = 1 - Q_{ij}^{+}$. Although from a biological point of view the choice of the sigmoid function was relatively arbitrary, we chose to resort to it because it is a classic example of a function that combines easy modulation of the deterministic/stochastic aspect thanks to η together with a saturation at large values. Once again, dominance is a complicated notion that can involve several interdependent "forces," but to make the study tractable, we make the simplifying assumption that all these forces can be described by one single variable, which is certainly relevant at least in primitive animals.

We have to justify the fact that we assume the outcome of a fight to be probabilistic and not deterministic. If it is rare to see a less dominant individual win a fight in a well-established hierarchy, reversals of "instantaneous" ranks are not at all rare in the initial stage of hierarchy formation, that is, when unacquainted individuals are placed together for the first time to form a group. Because the respective hierarchical positions of individuals are not clearly defined, the results of successive encounters between A and B appear to be stochastic. After the stabilization of the hierarchy, it is quite unusual to see a less dominant individual win, except in very specific conditions (for example within the less dominant's territory). However, the convergence of F toward a stationary value cannot ensure asymptotic determinism, especially in large colonies, where many individuals may have very similar F: occasional loops should be expected, most probably in the middle of the hierarchy, but are rarely observed. We can infer from this that outcomes are close to deterministic (large η or "dominance always wins" (Jäger and Segel, 1992)) or that the dynamics undergoes a progressive "quenching" whereby $\eta(t)$ diverges as time t increases. We shall assume for simplicity throughout this paper that η is constant in time. In addition, there are cases, such as large groups of hens (Shjelderup-Ebbe, 1913, 1922), where unstable loops are observed: this might be caused by the probabilistic nature of fights' outcomes, with potentially small values of η. In doves and pigeons (Allee, 1951), hierarchies exist only on a statistical basis, that is, the α individual delivers more pecks to others than he receives, down to the bottom of the hierarchy.

3.2. *Probability of interaction.* Let us now turn to the probability P_{ij} of interaction between two individuals i and j when they meet. The probability P_{ij} is of utmost importance because, as we shall see, it determines a lot of the properties of the society's hierarchical profile. We shall study different functional forms for P_{ij}. Let us first introduce the variable $Y_i = 1/(1+\exp(-\eta_2 F_i))$, which will simplify formulas. Here η_2 is an additional parameter proper to the probability of interaction. Unless otherwise stated, we set $\eta_2 = 1$.

Let us briefly discuss the fact that F plays a role in the probability of interaction. As we have introduced it, F is a quantity that describes the aggregate effect of an ensemble of *intrinsic or internal* characteristic features, such as hormonal levels, associated with each individual's "power."

As a consequence of its force F, an individual with, say, a larger value of F, may be intrinsically more aggressive and seek fights or simply move more quickly on the nest and thus naturally interact with more individuals than a slower animal. However, F may be more than just an internal variable: it can also serve as a "label" signaling in various ways the individual's "confidence" or ability to dominate (Gervet *et al.*, 1993); this is an additional way for F to exert an influence on the probability of interaction. In effect, the dominant may e.g. enforce its superiority by inhibiting other individuals' hierarchical "ambitions" through the emission of special substances. The dominant may also have a distinctive behaviour that makes its subordinates "aware" of its status; the subordinates then try to avoid contacts with the dominant. In the words of Etkin (1965), "the way [the dominant] carries itself betrays its status." Etkin (1965) gives the example of the "posturing advertisement" of the Indian antelope and other large mammals: stiff, strutting walk, with head high on stiffly bent neck, folded ears, etc. Many other examples of cues that show the confidence of an individual are known. In summary, F can play a role in the probability of interaction in two (not unrelated) ways: (1) by influencing the intrinsic willingness of an individual i to interact with other individuals (speed, aggressiveness, etc.) and (2) by influencing the willingness of other individuals to interact with i. In role (1), F is an internal variable; in (2), F is an external label or mechanism. Note that the definition of Q_{ij}^{+} alone also can include attitudes that impress (or fail to impress) other individuals and prevent them from winning or even attacking (or on the contrary enhance their winning abilities or their tendencies to attack).

$P_{ij} = p \leq 1$ (called hereafter case $C = 1$) is the simplest possible choice. Setting P_{ij} to a constant p implies that two individuals that encounter each other interact with probability p. If there is no other factor in the model, the actual value of p influences only the speed of the process: thus, one can as well set p to be equal to 1. Yet, if one includes forgetting, the ratio between forgetting and p can be very important, because if p is too small, an individual will forget its last fight before the next one, so that one should expect a uniform population with no hierarchical differentiation. The choice $C = 1$ does not take into account the experimental fact that stronger individuals are more willing to fight than weaker ones (Theraulaz *et al.*, 1989, 1992). One way to include this observation is to use the following form for P_{ij} (case $C = 2$):

$$P_{ij} = Y_i Y_j. \tag{1}$$

P_{ij} is a symmetric function of i and j, with a value that 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 stronger individual will try to start a fight whereas the weaker one will be more willing to escape. Note that case $C = 2$ need not involve any kind of individual recognition, because the probability $P_{ij} = Y_i Y_j$ is simply the product of individual tendencies to engage an interaction, independently of any information about the hierarchical rank of other individuals in the colony. Another possibility, which includes, as we shall discuss, some kind of class recognition, is to choose the following form for P_{ij} (case $C = 3$):

$$P_{ij} = \exp\left(-|Y_i - Y_j|/P_c\right), \tag{2}$$

where P_c is a characteristic distance in the space of forces over which there may be interactions taking place. This form implies 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 rank individuals will have fewer interactions than others because they have a force that is far from both extremes of the hierarchy and they will thus interact most probably 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. As we shall see, the result we obtained when simulating such a probability of interaction matches this expectation. Expression (2) also involves a particular type of recognition: class recognition, in which an individual is able to evaluate the approximate hierarchical rank or ability to dominate of another individual. The mechanisms that allow such a recognition can be of various types, relying, for instance, on chemical or visual information: a particular individual, given the information available, can then assess its willingness to engage a fight by comparing its "force" with the apparent force of the other individual. The biological relevance of expression (2) stems from the observation that in wasps (but also in other animals), individuals of nearly equal ranks interact much more often and usually with more violence (Eberhard, 1969; Theraulaz *et al.*, 1989, 1992). A related observation also has been reported, for example, in cattle (Schein and Fohrman, 1955) and in pigs (see Broom, 1981). One additional refinement that could be included to describe the violence of fights would be to make the net gain δ^+ or loss δ^- in force depend on $\Delta_{ij} = F_i - F_j$. To keep things simple, we shall ignore this possibility, which has been studied by Hogeweg and Hesper (1983) in a related context.

In order to incorporate the field observation that middle-ranked individuals show a tendency to withdraw from the "fighting game" because they leave the nest to forage, we may finally choose a probability of interaction that explicitly includes this observation (case $C = 4$):

$$P_{ij} = \left[Y_i^5 - Y_i/2 + 1/2\right]\left[Y_j^5 - Y_j/2 + 1/2\right]. \tag{3}$$

The term Y_i more or less represents the mean-field probability for an individual i to win in a random fight (it is an increasing function of force). Hence it represents a biologically meaningful variable ranged between 0 and 1 that can be used to describe the ranks in the hierarchy. The function $f(x) = x^5 - 0.5x + 0.5$ was chosen so that strong individuals interact with a high probability and very weak individuals interact more than middle-ranked individuals, which have very few interactions. The fact that f is a fifth-order polynomial should not be taken literally. Only the global shape of f on the interval $[0, 1]$ is important: f integrates all the spatiotemporal effects not explicitly taken into account in the model (as opposed e.g. to the model of Hogeweg and Hesper (1983), where space is an explicit component of the model—which turns out to be crucial). Once again, one expects that this type of probability of interaction should lead to a profile where there is a plateau in the middle of the hierarchy. Because (3)—like (1)—is the product of individual tendencies, we need not invoke any process of class or individual recognition.

Finally, let us discuss briefly the evolution with time of the interaction process. We have already mentioned the notion of social inertia (Guhl, 1968), which manifests itself in the drastic decrease in the number of aggressive interactions with time, unless the system is perturbed. A quick quench of the hierarchy, combined with the use of threat attitudes, resulting in only very few real fights, can be argued to be an evolutionary stable strategy (Maynard-Smith, 1974). It is clear that the present model can neither fully account for the decrease of visible hierarchical activity with time nor for the burst of activity following a perturbation. Such observations could, in principle, be included in the model by supplementing P_{ij} by a time-dependent term, that is, by replacing P_{ij} by $g(t)P_{ij}$, where $g(t)$ is a function that converges toward a small positive value in the absence of perturbation, as t tends to infinity. If the system is perturbed, $g(t)$ can be suddenly "reset" to a value close to 1 and decrease again. This resetting mechanism might correspond to a sudden release of (hormonal) constraints or inhibitions previously exerted by the removed α individual on the rest of the population. Because, according to all our simulations (without forgetting), all stationary hierarchical profiles are reached quite rapidly, we shall ignore the time dependence of g and assume $g = 1$: in effect, g no longer influences the particular shape of the profile after its establishment. Moreover, we have shown in Monte Carlo simulations (Theraulaz *et al.*, 1995) that the profile is reestablished after the removal of the α individual (a strong perturbation) with a constant g: this is consistent with experimental results (Theraulaz *et al.*, 1989, 1992), despite the fact that the relative number of interactions in simulations and experiments were different.

4. Mathematical Model and Results.

4.1. *Basic model.*

4.1.1. *Equations.* In order to study the establishment of hierarchical profiles, we model the temporal evolution of quantities of interest with a set of (weakly stochastic) differential equations that describe the behaviours of D (dominances), S (subordinations) and F(abstract force) $= D - S$:

$$\frac{\mathrm{d}D_i}{\mathrm{d}t} = \frac{1}{N} \sum_{\substack{j=0 \text{ to } N \\ j \neq i}} \frac{P_{ij}}{1 + \exp\left(-\eta(F_i - F_j)\right)},$$

$$\frac{\mathrm{d}S_i}{\mathrm{d}t} = \frac{1}{N} \sum_{\substack{j=0 \text{ to } N \\ j \neq i}} \frac{P_{ij}}{1 + \exp\left(+\eta(F_i - F_j)\right)},$$

$$\frac{\mathrm{d}F_i}{\mathrm{d}t} = \delta^{+} \frac{\mathrm{d}D_i}{\mathrm{d}t} - \delta^{-} \frac{\mathrm{d}S_i}{\mathrm{d}t} + \xi(i,t), \tag{4}$$

where the noise term added is taken to be gaussian. Its first two moments suffice to characterize it: we choose it centered of variance θ^2 and uncorrelated in space and time:

$$\forall i,j,t,t' \quad \langle \xi(i,t) \rangle = 0 \quad \text{and} \quad \langle \xi(i,t)\xi(j,t') \rangle = \theta^2 \delta(i-j)\delta(t-t'), \tag{5}$$

where δ is a Dirac function. The preceding equations express the fact that each individual, labeled by i, evolves in the mean field of the other individuals. In the numerical integration of (4), unless otherwise stated, we used uniform initial conditions: $\forall i$, $D_i = S_i = 1$ and $F_i = 0$. This state being a (sometimes unstable) fixed point of the dynamics, we have supplemented the last equation with a small noise term, which integrates the effects of random encounters and imperfect assimilation of subordinations and dominances. Any finite amount of noise then allows us to destabilize (accidental) unstable equilibria. We kept noise to a low enough level in order not to destroy stable asymptotic profiles by too large fluctuations. This addition of noise is simply a convenient alternative to starting from random initial conditions, and it does not change the averaged numerical results significantly. The theoretical discussions of Appendixes A and B are made on the deterministic system. In conclusion, our (mean-field) approach is essentially deterministic.

It is important to remark that the force is allowed here to take arbitrarily large values. Given the forms used for the probabilities of winning and losing, these large values allow for a stabilization of the hierarchical profile. As we mentioned in section 2, $X_i = D_i/(D_i + S_i)$ will be used here as a characterization of the hierarchical profile.

We have integrated the Langevin equations numerically for 13 individuals, because it is a typical number for experimental colonies of *Polistes*. Other animal societies that are comprised of a larger number of individuals exhibit non-trivial hierarchical structures: this is the case, for instance, of bumblebees, whose colonies may contain about 75 individuals or more (Hogeweg and Hesper, 1983; Van Honk and Hogeweg, 1981). Numerical tests carried out on such larger populations show that the same hierarchical profiles are obtained, yet on a larger scale. We choose, unless otherwise specified, $\delta^+ = \delta^- = 1$. Finally, although the present study was motivated by our experiments on *Polistes*, we believe that the applicability of our results can be extended beyond *Polistes*, and even beyond social wasps to include potentially most social insects and possibly higher-level social animals, although certainly with restrictions.

4.1.2. *Results*. Figure 2 represents the results for the Langevin-like equations in the absence of forgetting or individual recognition, with different probabilities of interaction. We obtain some profiles similar to those found in Monte Carlo simulations (Theraulaz *et al.*, 1995), such as a linear profile or two profiles with a middle plateau whose exact shapes can be modulated by varying the parameters. We find, however, another more specific exponentially decreasing profile saturated at about $D/D + S = 0.4$, whereas the saturation value observed in Monte Carlo simulations is about 0.05: the mean-field description embodied in equations (4) and (5) should in this particular case be supplemented by a more careful treatment of fluctuations. The value of η_2 is of great importance in the determination of the profile obtained for $C = 2$. For high values of η_2, one observes a wide plateau at middle and lower ranks, and a small plateau in higher classes, whose width is amplified as η_2 decreases. As η_2 is further decreased, this plateau shrinks and eventually disappears. In all cases, a saturation at about 0.35–0.4 is observed (see Fig. 3). The parameter P_c does not have an influence on the general shape of the profile in the case $C = 3$, but different values for P_c yield different widths for the observed plateaus in the middle of the hierarchy (see Fig. 4).

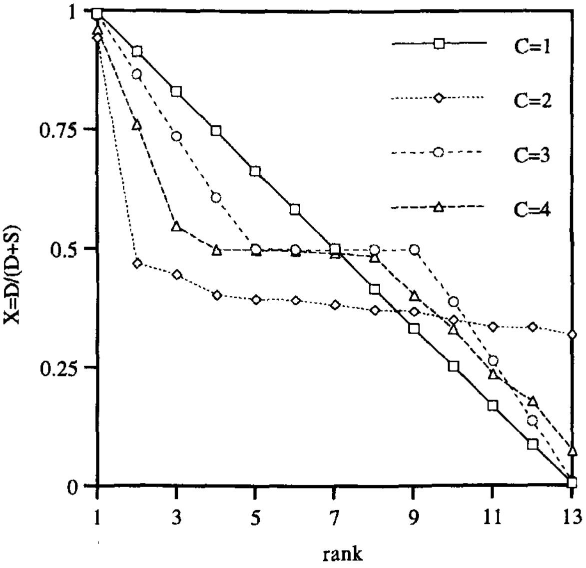

Figure 2. Hierarchical profiles obtained for various choices of P_{ij}; $\eta_2 = 1$ in cases $C = 2, 3, 4$. (a) $C = 1$: The profile is linearly varying with rank, as can be shown analytically (see Appendix A). (b) $C = 2$: The profile exhibits an exponential decay with decreasing ranks, and is saturated at about 0.3. (c) and (d) $C = 3$ and $C = 4$: The profiles exhibit a plateau in the middle classes, as expected due to the particular forms of P_{ij}. The width of the plateau depends on the parameter P_c (see Fig. 4).

Figure 5 shows the effects of asymmetric rewards $\delta^+ \neq \delta^-$ when $C = 1$. We can assume that $\delta^+ + \delta^- = 2$ without loss of generality. When the difference between δ^+ and δ^- is small, there is a small distortion of the linear profile, but as this difference increases, the profile progressively shifts toward a low level of differentiation: for instance, the hierarchical structure becomes despotic when $\delta^+ = 0.25$ and $\delta^- = 1.75$, with one individual having a dominance index of 1 and all others a dominance index of 0. The (somewhat counterintuitive) reverse situation is observed when the values of δ^+ and δ^- are reversed. Mathematical details about the asymptotic profiles in various cases are given in Appendix A.

4.2. *Forgetting.*

4.2.1. *Introduction.* The role of memory and hence of forgetting is certainly a highly relevant biological factor in hierarchy formation and maintenance. Individuals may have not only to establish but also to maintain their ranks among the society by repeated aggressive encounters (Wilson, 1971): the need to *maintain* the rank can be understood as a clue

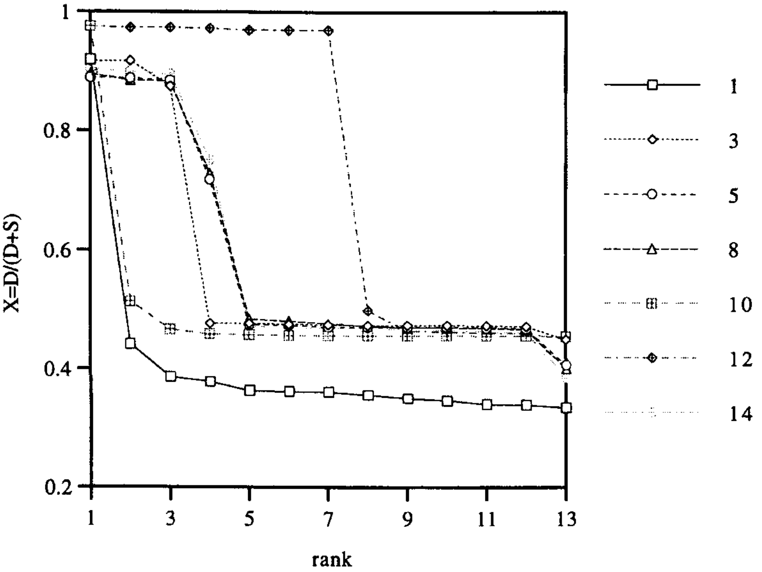

Figure 3. Hierarchical profiles obtained in the case $C = 2$, for various values of η_2 $(1, 3, 5, 8, 12, 14)$ and $\eta = 1$.

in favor of forgetting. An interesting experimental setup to determine the contribution of forgetting is to withdraw an individual from the fighting game during variable amounts of time and to see whether or not it keeps its rank in the colony once put in the game again (Röseler *et al.*, 1984). Another setup is to measure how replicable a hierarchy is when, after a stable hierarchy among a group of individuals has been disbanded, the same individuals are put together again some time after (Dugatkin *et al.*, 1994). Röseler *et al.* (1984) showed that in *P. dominulus* wasp colonies, when the α foundresses were removed for up to 24 hours, these individuals invariably became dominant again upon their return (Röseler *et al.*, 1984). The α foundress of one colony even regained the top rank after she had been absent for up to seven days. One important fact was that the longer the foundress was absent, the more severe and the more frequent were her interactions with subordinates when she returned. Finally, early experiments carried out on chickens (Shjelderup-Ebbe, 1913, 1922) showed that they can maintain their precise hierarchical structure for a limited amount of time, up to three weeks: shorter periods of separation do not influence the hierarchy, but longer periods lead to the emergence of new hierarchies. It is nevertheless difficult to clearly establish the respective roles of individual memory and the capacity for individual recognition in the whole process because both factors are closely intertwined. This latter factor and its

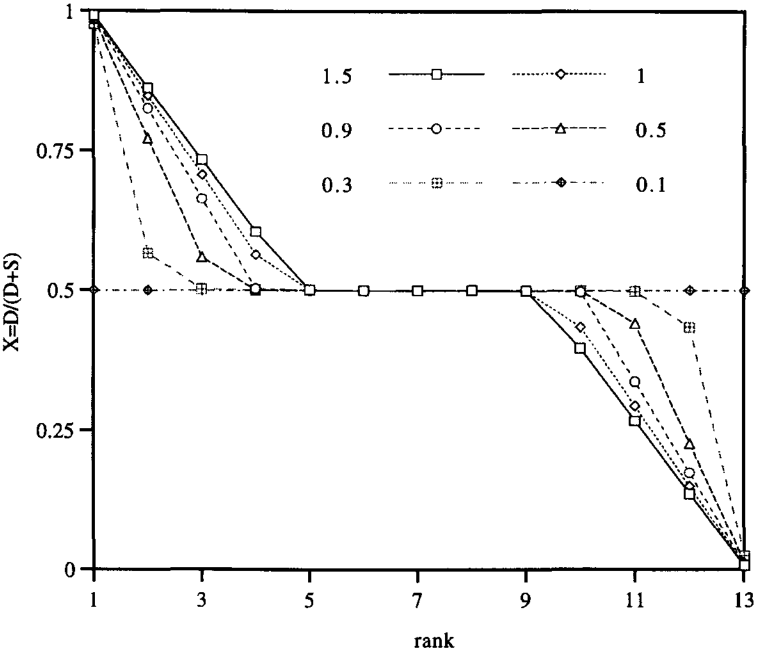

Figure 4. Hierarchical profiles obtained in the case $C = 3$, for various values of the parameter P_c. The width of the plateau clearly depends on P_c: the smaller P_c, the wider the plateau. $\eta_2 = 1$ and $\eta = 1$.

influence in the hierarchical formation process will be examined in the next section.

4.2.2. *Equations.* Forgetting can be included easily by supplementing the evolution equation of F in equations (4) by a term that accounts for the relaxation of the force F toward the neutral value 0. Only the case where all individuals interact with equal probability ($C = 1$) is studied; all other choices yield qualitatively similar results. We also slightly modify the basic equations so as to introduce the density ρ of individuals:

$$\frac{\mathrm{d}D_i}{\mathrm{d}t} = \frac{\rho}{N} \sum_{\substack{j=0 \text{ to } N \\ j \neq i}} \frac{1}{1 + \exp\left(-\eta(F_i - F_j)\right)},$$

$$\frac{\mathrm{d}S_i}{\mathrm{d}t} = \frac{\rho}{N} \sum_{\substack{j=0 \text{ to } N \\ j \neq i}} \frac{1}{1 + \exp\left(+\eta(F_i - F_j)\right)},$$

$$\frac{\mathrm{d}F_i}{\mathrm{d}t} = \frac{\mathrm{d}D_i}{\mathrm{d}t} - \frac{\mathrm{d}S_i}{\mathrm{d}t} - \mu g(F_i) + \xi(i,t). \tag{6}$$

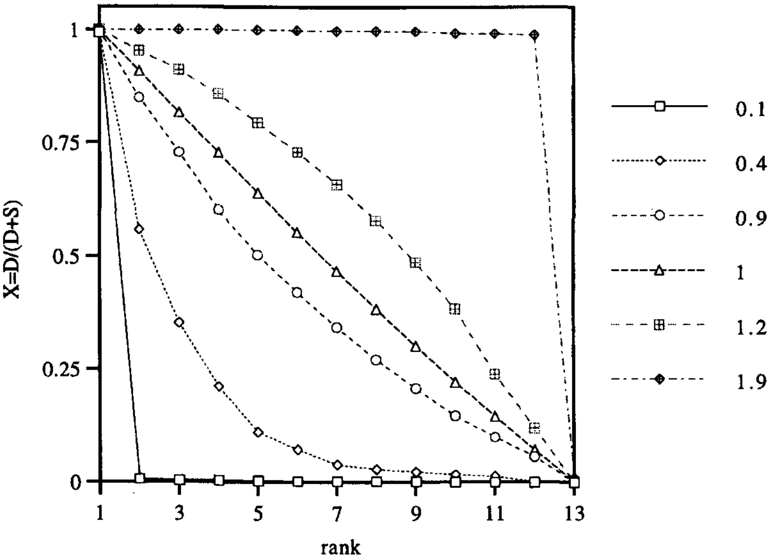

Figure 5. Simulations of the case $C = 1$, with different values of δ^+ and δ^- after 20,000 time units. The close-to-linear profiles are obtained when δ^+ and δ^- are close. The other profiles correspond to more or less pronounced biases in favour of upper or lower forces, leading to a poor differentiation in terms of the dominance index X. The value indicated on the figure is δ^+ (in all cases, $\delta^+ + \delta^- = 2$). $\eta = 1$.

In (6), μ is the (constant) decay rate (set to 0.1 in the subsequent numerical integrations) and g is a function that describes the effect of forgetting. We took $g(F_i) = \tanh(F_i)$. g seemed to us to represent a plausible candidate for a decay function, because it is bounded for large values of F and linearly decreasing as F approaches 0. However, this choice is certainly arbitrary to a large extent: the aim of this section is to explore "formally" the consequences of the inclusion of a forgetting term without paying too much attention to the detailed implementation of the forgetting mechanisms. We expect forgetting to be a crucial parameter: a small value of ρ/μ certainly prevents the hierarchy from appearing because dominance and subordination events are forgotten between two successive interactions. As we already mentioned, it is the ratio between the probability of interaction and the forgetting coefficient that is the relevant parameter. For instance, a densely populated region should correspond to a higher probability of interaction than sparsely distributed individuals: therefore, there is a connection between the formation of hierarchies and the density of population—or the number of individuals.

4.2.3. *Results.* The inclusion of forgetting leads to important new phenomena that are qualitatively different depending on the value of η. To summarize, a bifurcation is always observed as the population density ρ is increased from 0 to 1. The bifurcation takes place at $\rho = 2\mu/(\eta(1 + 1/N))$, where the number of individuals in the population is $N + 1$. As easily can be shown (see Appendix B1), $2\mu/(\eta(1 + 1/N))$ is in fact the value at which the flat profile becomes linearly unstable. For $\rho < 2\mu/(\eta(1 + 1/N))$, there is no hierarchical differentiation, that is, the profile is flat, whereas for $\rho > 2\mu/(\eta(1 + 1/N))$ the asymptotic profile corresponds to a developed hierarchy.

To understand the meaning of that bifurcation, see Figs. 6, 7 and 8, which present results from Monte Carlo simulations of $(N + 1) = 50{,}000$ individuals performing random walks on a 2D lattice, with $\eta = 2$. When two individuals encounter, they have a hierarchical interaction, but when an individual is alone, its force is relaxed toward 0. Equations (6) are precisely the mean-field equations associated with these Monte Carlo simulations. We have run Monte Carlo simulations of N individuals performing a random walk on a 2D square lattice: at each discrete time step, all individuals arrive at a site where there may be another individual (there are 0, 1 or 2 individuals at any particular site). Then a fight takes place and the probabilistic outcome is given by the function Q_{ij}^{+} and the forces of both individuals are incremented (the winner) or decremented (the loser) by 1. The forces of all individuals relax toward 0 at each time step as follows: $F \rightarrow F - \mu \tanh(F)$, where μ is a small parameter that determines the

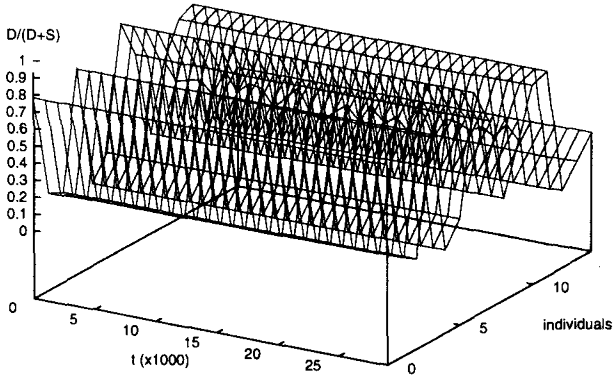

Figure 6. Time evolution of $\langle P_i \rangle$ for 15 individuals randomly extracted from 50,000 individuals simulated on a 2D lattice whose size is 400 × 400 ($\rho = N/L \times L$), for $\eta = 5$ and $\mu = 0.1$. The x axis corresponds to the individuals (numbered from 0 to 14); the y axis corresponds to time (1 unit = 10^3 time steps: $\langle P_i \rangle$ is recorded every 10^3 time steps, so that time ranges here from 0 to 30×10^3 steps; the first 10^6 steps of the simulation have been discarded); the z axis represents $\langle P_i \rangle$ (ranges from 0 to 1). Here, $\rho \gg \rho_c \approx 0.1$; individuals rapidly reach their asymptotic $\langle P_i \rangle$; fluctuations are rare.

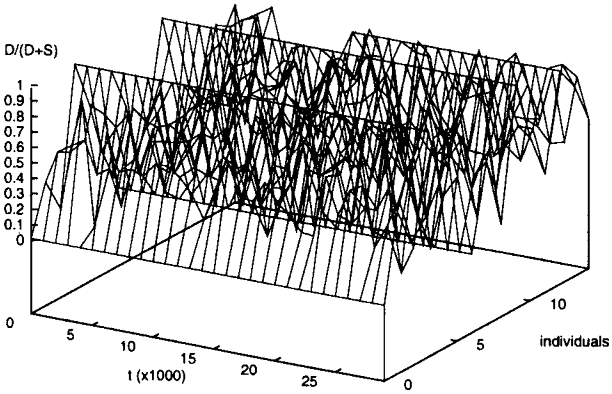

Figure 7. Same as previous figure for a lattice of size 55 × 55. The $\langle P_i \rangle$'s begin to undergo important temporal fluctuations, precursor of the supercritical bifurcation.

forgetting rate. Both the winner and the loser continue their random walks after the fight. The instantaneous dynamics of the hierarchical profile can be characterized by the set $\{\langle P_i \rangle\}$, where

$$\langle P_i \rangle = \frac{1}{N-1} \sum_{\substack{j=1 \\ j \neq i}}^{N} \frac{1}{1 + \exp\left(-\eta(F_i - F_j)\right)}$$

denotes the instantaneous probability that individual i wins in a random fight. The "statics" is well described by $X_i = D_i/(D_i + S_i)$, where D_i (resp. S_i) is the number of fights won (resp. lost) by individual i: X gives a good

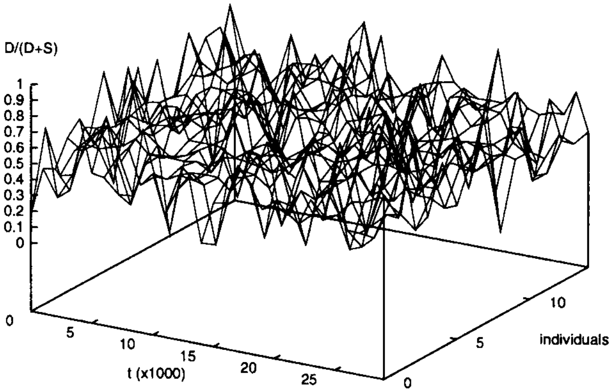

Figure 8. Same as Figs. 1, 2 and 3, for a lattice size 100 × 100. Here, ρ is less than ρ_c. The evolution of the $\langle P_i \rangle$'s is erratic.

image of the overall probability integrated over time of an individual to win against another randomly selected individual, but X does not vary if no interaction takes place. Therefore, when an individual moves for a long time without interacting, its force relaxes to 0, but its dominance index X remains at the value set after the last encounter: $\langle P_i \rangle$ then gives a better dynamic picture of the real instantaneous dominance index, but both are asymptotically equivalent. Moreover, it is, as we shall see, more convenient to use X in the mean-field approach presented next, and X then gives the same information as $\langle P_i \rangle$ because in the mean-field theory interactions take place *at every time step*. Another advantage of X_i is that it is experimentally accessible, contrary to $\langle P_i \rangle$, and thus our results in terms of X can be confronted with biological data.

We observe that no non-uniform hierarchical profile gets established if the population density ρ is too low: $\forall i$, $X_i = \frac{1}{2}$, even after a long time. This result simply stems from the fact that the force of every individual has time to relax to 0 between two successive encounters. See Figs. 6–8, where the time evolutions of 15 randomly chosen $\langle P_i \rangle$'s are represented for different values of ρ (the number N of individuals is 50,000 in all cases; the linear size L of the lattice is varied from 300 to 1000: $\rho = N/L \times L$). The values used in these figures are $\eta = 5$ and $\mu = 0.1$. When ρ lies below a value ρ_c (≈ 0.1 in the present case), no stable asymptotic profile can be reached: the evolution of $\langle P_i \rangle$ (see Fig. 6) is erratic and the temporal average of X_i is equal to 0.5, i.e. a flat profile. Above ρ_c, a non-uniform asymptotic profile ($\exists i \, \langle\langle P_i \rangle\rangle \neq 0.5$) emerges and all $\langle P_i \rangle$'s become stable after a very short time and rapidly reach their asymptotic values, which are all different: this corresponds to the "ordered" or "laminar" phase (see Fig. 1). Figure 7 represents an intermediate situation, where ρ is close to but above ρ_c: as ρ approaches ρ_c, fluctuations of the $\langle P_i \rangle$'s increase, but all $\langle P_i \rangle$'s reach a stable state after a variable amount of time.

The case represented in Figs. 6–8 corresponds to a situation in which the "turbulent" phase in entered smoothly: the system exhibits "critical fluctuations" as ρ gets closer to ρ_c. By contrast, for other values of η, fluctuations remain small and the transition from the laminar to the turbulent phase takes place abruptly. One other interesting observation is that the amount of time taken to reach the asymptotic state *may or may not diverge* as ρ_c is approached, depending on the value of η. This strongly suggests that there is a crossover from a critical (or super-critical) bifurcation exhibiting critical slowing down to a sub-critical bifurcation characterized by a discontinuous jump from a flat to a differentiated hierarchical profile. These observations can be clarified with the mean-field equations, which yield similar properties (see for example Fig. 9, which represents X_i as a

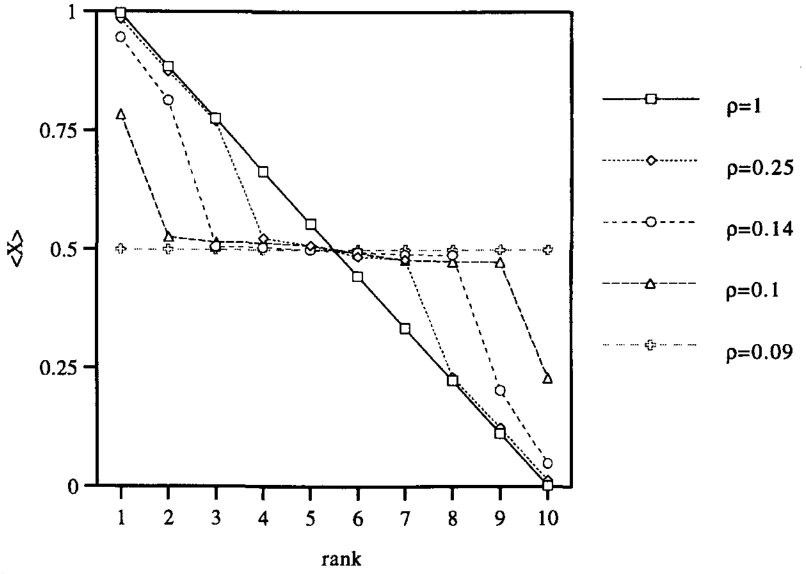

Figure 9. Asymptotic profile for various values of ρ: $\rho = 0.2$, where the profile is linear; $\rho = 0.13$ and 0.11, where the profile is piecewise linear, that is, still differentiated; $\rho = 0.09$, where the profile is flat.

function of rank for $\eta = 2$ and different values of ρ around $2\mu/(\eta(1 + 1/N)))$.

Let us return to the analytically tractable mean-field model embodied in the set of equations (6). Some mathematical details are given in Appendix B and deeper physical implications of this forgetting model are studied in Bonabeau *et al.* (1995). When $\eta < 2/((1 + 1/N))$, the bifurcation is sub-critical (or discontinuous; see Figs. 10 and 11, where the "order parameter" is simply the variance of the profile $\sigma^2 = \Sigma_{i=0}^{N}(X_i - 0.5)^2)$ provided initial conditions are not too disordered, and when $\eta \geq 2/((1 + 1/N))$, the bifurcation is critical (or continuous; see Fig. 11), exhibits critical slowing down and can be characterized by critical exponents. In fact, in the case $\eta < 2/((1 + 1/N))$, it is easy to show that there are many coexisting stable states, but the undifferentiated state (flat profile) is linearly stable and has a wide basin of attraction. Linear stability does not imply stability under macroscopic perturbations, so that strong enough fluctuations or perturbations can make the hierarchy appear, even for $\rho < 2\mu/(\eta(1 + 1/N))$. Yet, simulations show that such perturbations must indeed be very strong to destabilize the non-hierarchical behaviour (Fig. 12). If the system starts with initial conditions close enough to the flat profile, the bifurcation therefore gives the impression of being sub-critical: at the bifurcation point,

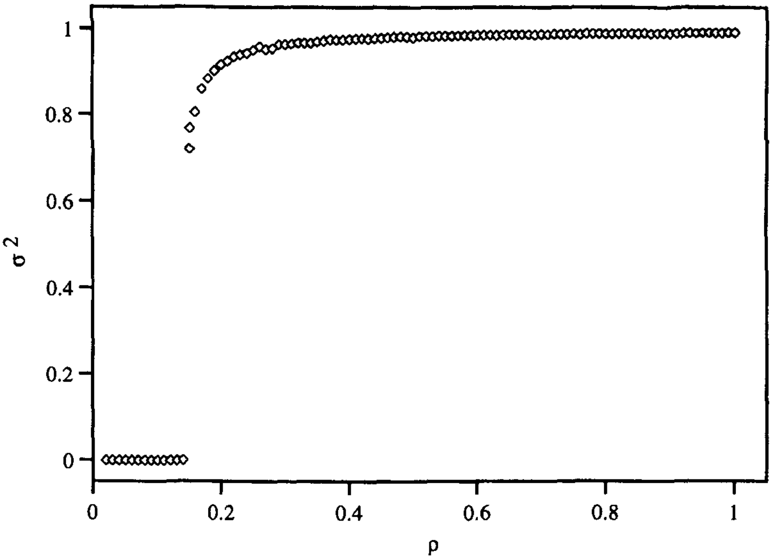

Figure 10. Order parameter as a function of ρ for $\eta = 1.5$.

there is an abrupt change in the profile due to the coexistence of other stable states. In contrast, when $\eta \geq 2/((1 + 1/N))$, the transition is smooth because there is only one single stable state in the low density region: this stable state becomes unstable at the transition point that also corresponds to the appearance of new stable states (which did not exist below the

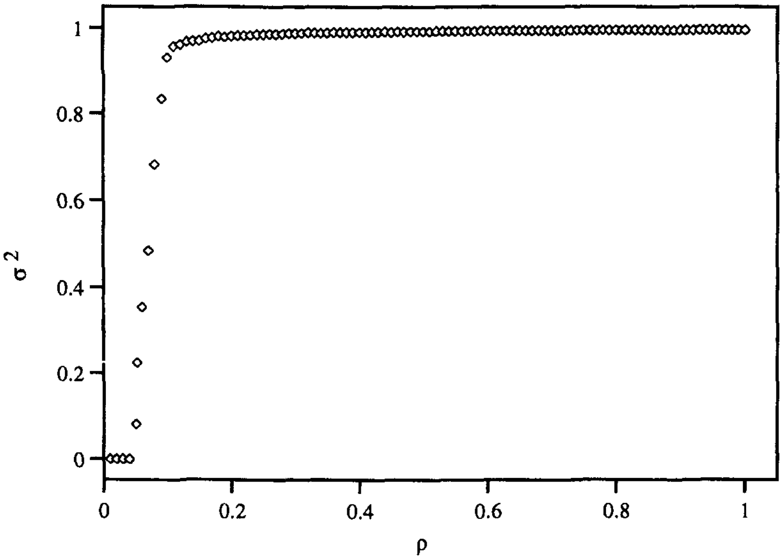

Figure 11. Order parameter as a function of ρ for $\eta = 4$.

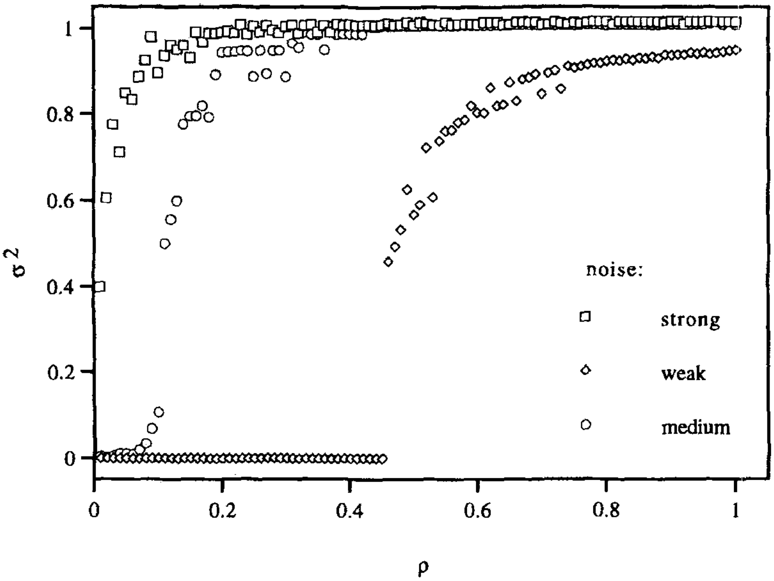

Figure 12. Effects of the strength of perturbations on the bifurcation and the stable states for $\eta = 0.5$, $\mu = 0.1$, $N = 10$. Strong noise means that initial conditions for F were chosen to be uniformly distributed in $[-500, +500]$, in $[-50, +50]$ for medium noise and in $[-5, +5]$ for weak noise. The effects would be similar with different levels of noise in the dynamics itself (instead of initial conditions).

critical density). Such a destabilizing process is typical of critical phase transitions in physics.

Although the critical bifurcation indicates a continuous transition from non-hierarchical to hierarchical behaviour, the sub-critical case is more interesting for biologists, owing to its subtle consequences. In effect, it can be interpreted in two different—but related—ways:

(1) Two populations of the same species, but with different individuals, can lead to a hierarchical society as well as to a non-hierarchical one. In particular, it seems that, in the appropriate range of parameters, a population comprised of individuals that emerged together (close-to-uniform initial conditions) is more likely to be undifferentiated. On the other hand, if individuals with different histories are put together, they may in some cases, in the same range of parameters as before, form a hierarchy (this situation corresponds to strongly disordered or non-uniform initial conditions). A related phenomenon has been observed in groups of cockroaches. In fact, one of the simplest predictions that can be made by our model is that when a group has a stable hierarchy, there is a high probability that if the group is taken

apart and then re-formed, a different hierarchical order will emerge among the same individuals. Indeed, experiments reported in Dugatkin *et al.* (1994) for the cockroach *Nauphoeta cinerea* showed that only about half of the hierarchies examined were replicable. Such a variability emphasizes the important role of stochastic factors in hierarchy formation and maintenance. In particular, the foregoing experiments point out the fact that ranks were more clear-cut in groups in which the previous hierarchy was replicable than in the groups in which the previous hierarchy was not replicable.

(2) A stable non-differentiated population can suddenly become hierarchically organized in response to a sufficiently strong perturbation. Consider, for instance, the case where a single individual dominates a population of hierarchically identical individuals: the population as a whole possesses a hierarchical organization, but the remaining sub-population as the dominant individual is removed has no such hierarchical structure. The removal of the dominant individual can then be considered as strong perturbation, triggering the emergence of a hierarchical structure within this previously structureless sub-population. Forgetting could as well be invoked in experiments where a wasp in the β position does not reach the α rank when the α individual is removed. We have reported such examples of reversals of dominance ranks between a wasp and the one ranking immediately below it in a previous study (Theraulaz *et al.*, 1989). Another well-known phenomenon that is observed in vertebrates could be interpreted in the framework of our model: this is the transition from territorial to hierarchical behaviour that is observed when territorial animals are forced into close proximity in laboratory conditions or when unusual environmental conditions arise. In fact, certain crayfish (*Cambarellus*, *Procambarus*) and anurans such as the frogs *Rana pipiens* and *Xenopus laevis* that are ordinarily territorial, form stable linear dominance hierarchies when they are forced together (Lowe, 1956; Bovbjerg, 1956; Bovbjerg and Stephen, 1971; Haubrich, 1961; Boice and Witter, 1969). Many kinds of fish show a similarly easy transition between territorial defense and dominance orders (Wilson, 1975). Two other known examples cited by Wilson (1975) are iguanid lizards (Evans, 1951, 1953) and some rodents, who normally live as solitary or territorial individuals, but become involved in dominance orders when forced together. However, there are puzzling exceptions to this "general" rule: for instance, Black-Cleworth (1970) reports that the banded knife fish is territorial at high density and exhibits dominance order at low density.

4.3. *Individual recognition.*

4.3.1. *Introduction.* Individual recognition is known to play an important role in social animals, especially in higher-level animals, where it shapes much of the social structure (for a recent review on individual recognition, see Zayan (1994)). Some recent experiments (Gervet *et al.*, 1993) have shown that individual recognition may take place in social wasps, at least in very small groups consisting of three individuals, and that this process might play a role in the genesis of circular hierarchies. Circular hierarchies rarely occur in natural colonies of wasps whose number of individuals is large ($n \gg 3$) (Theraulaz *et al.*, 1989, 1991a,b, 1992). These observations must be contrasted with most experiments performed on higher-level animals (summaries can be found in Wilson, 1975, and Chase, 1986), where loops are almost never observed in small groups, but sometimes in large groups. Our model, owing to its simplicity, is more likely to be applicable to wasps than to, say, hens or monkeys. The definitions of the probabilities for an individual to win and for two individuals to interact already contained some kind of "individual" recognition. As argued by Barnard and Burk (1979), there is a continuum between the recognition of cues that either indicate the confidence or the status of an individual and the recognition of the individual itself. Now, cue recognition can be deceived: the possibility of cheating, which we did not consider at all—this would require, for instance, the addition of another "hidden" force together with the "official" force—has evolutionary consequences, because a strategy that consists of systematically avoiding fights against individuals bearing "dominant" cues can be replaced with high benefit in the presence of cheating by a strategy that consists of probing the reality of the cues. Our aim here is now to study individual recognition explicitly.

Individual recognition can be dealt with through the introduction of two parameters ε_1 and ε_2, where ε_1 is the portion of the whole population that one particular member of the colony can recognize on an individual basis (this proportion is expected to decrease when the size of the colony increases, that is, the individual recognition capacity is limited to a maximum number) and ε_2 quantifies the effect of individual recognition on the force of an individual with respect to any other individual.

4.3.2. *Equations.* Because a model based on anonymous encounters and reinforcement processes will face difficulties to explain 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. To do so, we introduce pair forces F_{ij}, which describe the force of i when facing j. The corresponding *effective force* F_{ij}^{eff} used in to compute the probability of individual i to win when interacting with individual j will have the form

$$F_{ij}^{\mathrm{eff}} = \varepsilon_2 F_{ij} + \frac{1-\varepsilon_2}{N} \sum_{\substack{k=1 \\ k \neq i}}^{N} F_{ik}, \tag{7}$$

where F_{ij} is the relative force of individual i with respect to individual j and ε_2 is the parameter that characterizes the *weight* of individual recognition in the force of individual i with respect to individual j. The most natural form for F_{ij} is to take $F_{ij} = \mathrm{Dom}_{ij} - \mathrm{Sub}_{ij}$, where Dom_{ij} (respectively, Sub_{ij}) is the number of interactions in which i has defeated j (respectively, has been defeated by j). The proportion of individual recognition involved in the determination of the probabilistic outcome of the fight is precisely given by ε_1:

$$\begin{aligned}
\frac{\mathrm{d}D_{ij}}{\mathrm{d}t} &= P_{ij}\left\{\frac{\varepsilon_1}{1+\exp\left(-\eta\left(F_{ij}^{\mathrm{eff}}-F_{ji}^{\mathrm{eff}}\right)\right)} + \frac{(1-\varepsilon_1)}{1+\exp\left(-\eta\left(F_{ij}^{\mathrm{int}}-F_{ji}^{\mathrm{int}}\right)\right)}\right\}, \\
\frac{\mathrm{d}S_{ij}}{\mathrm{d}t} &= P_{ij}\left\{\frac{\varepsilon_1}{1+\exp\left(+\eta\left(F_{ij}^{\mathrm{eff}}-F_{ji}^{\mathrm{eff}}\right)\right)} + \frac{(1-\varepsilon_1)}{1+\exp\left(+\eta\left(F_{ij}^{\mathrm{int}}-F_{ji}^{\mathrm{int}}\right)\right)}\right\}, \\
\frac{\mathrm{d}F_{ij}^{\mathrm{eff}}}{\mathrm{d}t} &= \varepsilon_2\left(\frac{\mathrm{d}D_{ij}}{\mathrm{d}t} - \frac{\mathrm{d}S_{ij}}{\mathrm{d}t}\right) + \frac{1-\varepsilon_2}{N}\sum_{\substack{k=0 \\ k\neq i}}^{N}\left(\frac{\mathrm{d}D_{ik}}{\mathrm{d}t} - \frac{\mathrm{d}S_{ik}}{\mathrm{d}t}\right) + \xi(i,j,t) \\
&= \varepsilon_2\frac{\mathrm{d}F_{ij}}{\mathrm{d}t} + (1-\varepsilon_2)\frac{\mathrm{d}F_i^{\mathrm{int}}}{\mathrm{d}t} + \xi(i,j,t), \\
\frac{\mathrm{d}F_i^{\mathrm{int}}}{\mathrm{d}t} &= \frac{1}{N}\sum_{\substack{k=0 \\ k\neq i}}^{N}\left(\frac{\mathrm{d}D_{ik}}{\mathrm{d}t} - \frac{\mathrm{d}S_{ik}}{\mathrm{d}t}\right),
\end{aligned} \tag{8}$$

where D_{ij} is the number of victories of i in fights against j, S_{ij} is the number of defeats of i in fights against j, F_i^{int} is the “intrinsic force” of i (that is, the aggregate result of all the interactions of i with all other individuals), F_{ij} is the (i,j) force resulting from the historical record of interactions between i and j (that is, $F_{ij} = D_{ij} - S_{ij}$), F_{ij}^{eff} is the effective force used to compute the probability of victory or defeat of i and j in a (i,j) encounter with a weight ε_1 (F_{ij}^{eff} is a mixture of F_i^{int} and F_{ij} with weights $(1-\varepsilon_2)$ and ε_2) and

$$\forall i,j,k,l,t,t' \qquad \langle \xi(i,j,t)\rangle = 0 \quad \text{and}$$
$$\langle \xi(i,j,t)\xi(k,l,t')\rangle = \theta^2\delta(i-k)\delta(j-l)\delta(t-t'). \tag{9}$$

Let us summarize the respective roles of ε_1 and ε_2:

- The meaning of ε_1 is quite clear: it is the average percentage of the whole population that a given animal can recognize *on an individual basis*. Individual recognition must be distinguished from kin recognition or social recognition (Zayan, 1994). ε_1 is related to a particular set of intrinsic cognitive capabilities of the animal: the nature of the cognitive processes involved in individual recognition is to a large extent an unresolved matter. In principle, an animal may be able to know individually a limited number of other animals, and perhaps only the last few encountered. We deal with this question with the simplifying assumption that a given animal can recognize a fraction ε_1 of *each* of all other individuals or, equivalently, can recognize any other individual with a probability ε_1. We understand that this choice is not perfect, but it has the merit of being simple.
- ε_2 is somewhat more complicated to understand. To see how ε_2 works, let us consider two tennis players—A and B. We can assume with confidence that $\varepsilon_1 = 1$ in this case. A and B both have a (global) rank in the world hierarchy, which is the aggregate result of all the matches they have played within a year (there is also a forgetting mechanism in the rating of tennis players, that we omit here for simplicity). In the present model, this global rank corresponds to the rank given by F_A^{int} or F_B^{int}. However, the pair (A, B) also has a more personalized historical record: for instance, A may be rated no. 1 and B no. 200, but A may have been defeated five times out of seven times by B, because B plays in a way that A has difficulty coping with. If one wants to bet about the outcome of a match between A and B, one has to evaluate the respective chances of A and B. To do so, one resorts to a mixture of the intrinsic forces of A and B (their rank) and of the historical record of the pair (A, B). The respective weights given to these two factors are precisely $(1-\varepsilon_2)$ and ε_2. ε_2 may as well reflect the psychological state of A in front of B due to their common history. In any case, ε_2 quantifies the influence (or the expected influence) of the history of the pair (A, B) on the outcome of a fight or match between them.

As in the previous section, only the case where all individuals interact with equal probability ($C = 1$) is studied; all other choices yield qualitatively similar results. In the rest of this section, we therefore assume that $P_{ij} = 1/N$.

4.3.3. *Results.* As we have just mentioned,

$$F_i^{int} = (1/N) \sum_{k=0, k \neq i}^{N} (D_{ik} - S_{ik})$$

can be considered as the "intrinsic force" of individual i: this intrinsic force determines its rank. In particular, in the case $C = 1$ that we have studied, $F_i/t = 2X_i - 1$ (Appendix A), where F_i is defined in the set of equations (4). This relation can be generalized to $F^{\text{int}}/t \equiv 2X_i^{\text{int}} - 1$, so that is is possible to evaluate the effects of individual recognition on the hierarchical profile, characterized by X_i^{int}.

One of the most important results of this section is that when $\varepsilon_1 \neq 1$ or when ε_1 is not relatively close to 1 ($\varepsilon_1 = 1$ means that the whole population can be recognized on an individual basis by any member of the colony), no modification in the hierarchical profile is observed. Moreover, when $\varepsilon_1 = 1$, ε_2 must be large enough for modifications to be observable.

When $\varepsilon_1 = 1$, the results are as follows: when $\varepsilon_2 = 0$, we recover the model with no individual recognition; when $\varepsilon_2 = 1$, individual recognition is the only process involved in the formation of the hierarchy, so that the hierarchical graph of dominance is basically random. For values of ε_2 between 0 and 0.40, we obtain the linear profile already discussed. For ε_2 greater than 0.40, new profiles appear, characterized by one or several plateaus located throughout the profile; for low values of ε_2, these plateaus occur in the lower ranks (Fig. 13). For higher values of ε_2 (where the contribution of individual recognition is stronger), the plateaus occur at all levels in the hierarchy. Moreover, the highest ranking individual has a value of X that decreases with increasing ε_2 (Fig. 14). For an intermediate value of ε_2 (0.66), we obtain a fully developed profile (extending from $X = 0.04$ to $X = 0.96$) with three plateaus in the middle and lower ranks, whereas the two top ranking individuals clearly dominate the others (Fig. 15). This last figure is reminiscent of profiles that one would obtain in bumblebees, yet with larger populations. Similar profiles are obtained for values of ε_1 close to 1.

An important quantity is the Landau number, which is aimed at characterizing the degree of linearity of the hierarchy or conversely the number of intransitive loops. It is possible within the present framework to calculate a Landau number (Landau, 1951; Chase, 1974) if it is considered that an individual dominates another individual on the basis of the force F_{ij}: if

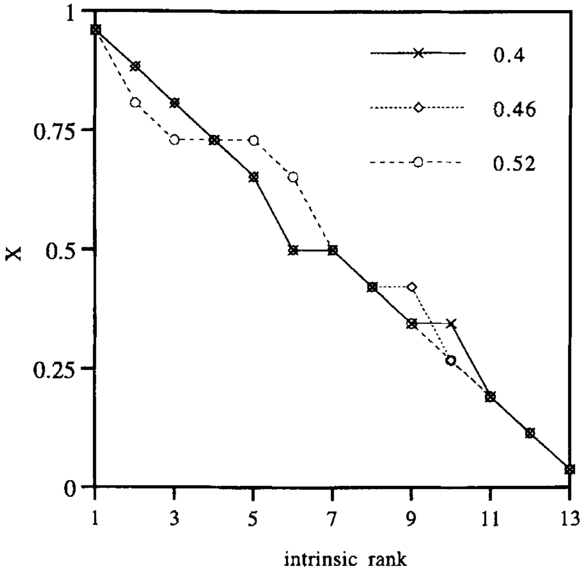

Figure 13. Profiles obtained for $\varepsilon_1 = 1$ and various (low) values of ε_2 (0.40, 0.46, 0.52), $C = 1$, $\delta^+ = \delta^-$ and $\eta = 1$. For $\varepsilon_2 < 0.40$, we obtain the usual profile where X is a linear function of rank, but as individual recognition is increased, plateaus start to appear, especially in lower classes.

$F_{ij} > F_{ji}$, this means that i dominates j and if $F_{ij} < F_{ji}$, j dominates i. Let us denote by n_i^+ the number of individuals dominated by individual i according to this criterion. The Landau number of the hierarchy is defined by

$$h = \frac{12}{N^3 - N} \sum_{i=1}^{N} \left(n_i^+ - \frac{N-1}{2} \right)^2, \tag{10}$$

where h ranges from 0, for a colony where all individuals dominate the same number of other individuals, to 1, for a perfectly linear hierarchy, that is, containing no loop. Now, this constitutes a crude approximation, because the outcome of a fight is not deterministic but probabilistic: i dominates j with a probability $Q_{ij}^+ = 1/(1 + \exp(-\eta(F_{ij}^{\text{eff}} - F_{ji}^{\text{eff}})))$. Landau has extended his index (Landau, 1951; Chase, 1974) to probabilistic cases to calculate the expectation of h,

$$\begin{aligned} \langle h \rangle &= \frac{12}{N^3 - N} \sum_{i=1}^{N} \left\langle \left(n_i^+ - \frac{N-1}{2} \right)^2 \right\rangle \\ &= \frac{12}{N^3 - N} \sum_{i=1}^{N} \sum_{\substack{j=1 \\ j \neq i}}^{N} \sum_{\substack{k=1 \\ k \neq i \\ k \neq j}}^{N} Q_{ij}^+ Q_{ik}^+ - \frac{3(N-3)}{N+1}, \end{aligned} \tag{11}$$

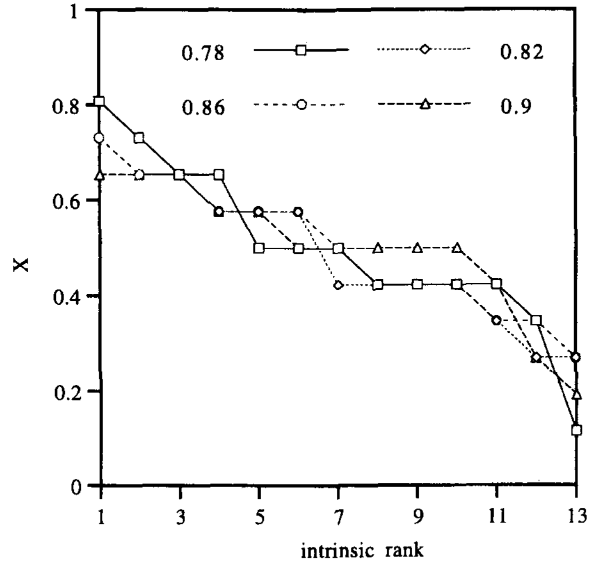

Figure 14. Profiles obtained for $\varepsilon_1 = 1$ and various (high) values of ε_2 $(0.78, 0.82, 0.86, 0.90)$, $C = 1$, $\delta^+ = \delta^-$ and $\eta = 1$. We see that these profiles exhibit plateaus at all levels and that the top ranking individual has lower and lower values of X as ε_2 is increased.

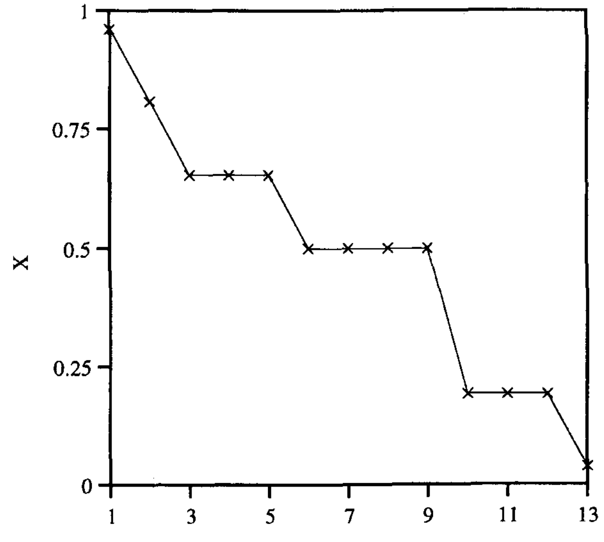

Figure 15. Profile comprising three plateaus obtained for $\varepsilon_1 = 1$ and $\varepsilon_2 = 0.66$, $C = 1$, $\delta^+ = \delta^-$ and $\eta = 1$.

so that $\langle h \rangle = 3/(N+1)$ if all individuals have a probability 0.5 to win irrespective of the other fighting individual and $\langle h \rangle = 1$, once again, in a perfectly linear hierarchy. We shall use $\langle h \rangle$ as an indicator of the linearity of the hierarchy. Figure 16 shows the variations of $\langle h \rangle$ as a function of the individual recognition parameters ε_1 and ε_2. For a fixed value of ε_1 sufficiently close to 1, there appears to be a crossover in the behaviour of $\langle h \rangle$ as a function of ε_2. For instance, for $\varepsilon_1 = 1$, we observe a departure from pure linearity at $\varepsilon_2 \approx 0.4$, a value already encountered in the interpretation of the profiles. We also observe a saturation at $\langle h \rangle \approx 0.21$ on Fig. 16 (which represents both h and $\langle h \rangle$) as ε_2 becomes close to 1: this corresponds exactly to $\langle h \rangle = 3/(N+1)$, with $N = 13$, the number we used in the simulations, so that for ε_2 close to 1, all individuals have a probability 0.5 to win or lose an arbitrary fight; the hierarchy is then maximally random. Note also that the departure of the hierarchical profile from pure linearity corresponds to the appearance of plateaus, and therefore associated local loops, in Figs. 13, 14 and 15.

Let us now observe how the extended Landau number $\langle h \rangle$ varies as a function of both ε_1 and ε_2. The same observations as for the hierarchical profiles hold, but $\langle h \rangle$ allows for a different viewpoint. We observe in particular that ε_1 must be in all cases close to 1 in order for loops to appear (for sufficiently large values of ε_2) (Fig. 17). η has a small influence:

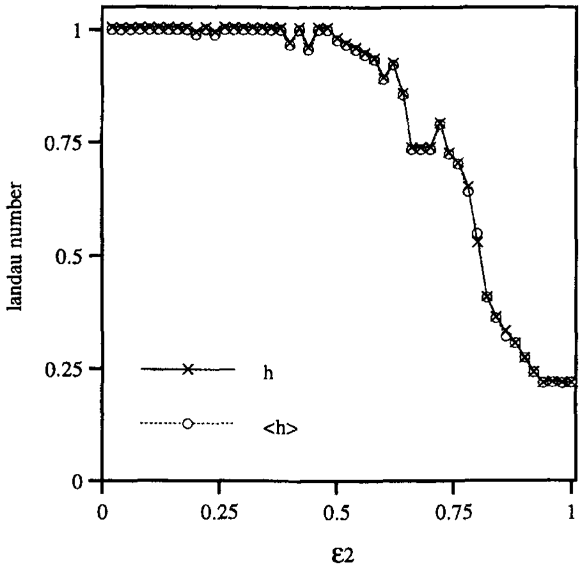

Figure 16. h and $\langle h \rangle$ as a function of ε_2, with $\epsilon_1 = 1$, $C = 1$, $\delta^+ = \delta^-$ and $\eta = 1$, $N = 13$, one simulation.

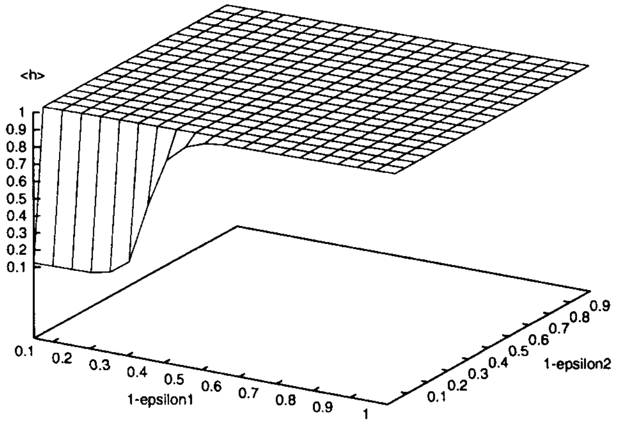

Figure 17. $\langle h \rangle$ as a function of both ε_1 and ε_2, for $N = 20$, $\eta = 0.1$. The x axis represents $1 - \varepsilon_1$ and the y axis represents $1 - \varepsilon_2$.

the more deterministic the outcome of a fight, the more loops there may be, but this effect saturates as η increases (no more effect above $\eta = 5$) (see Figs. 17, 18 and 19). On Fig. 20, strongly disordered initial conditions have been used, with the F_{ij}'s at $t = 0$ being random variables uniformly distributed in the interval $[-100, +100]$ instead of being set to 0: non-linearity in the profile persists over a larger portion of, but is still limited to a fixed zone of, the $(\varepsilon_1, \varepsilon_2)$ plane. We have studied the variations of $\langle h \rangle$ when the number of individuals N is varied and ε_1 is taken to be a simple "plausible" function of N: assuming that each individual has a fixed memory capacity, the maximum that it can recognize on an individual basis

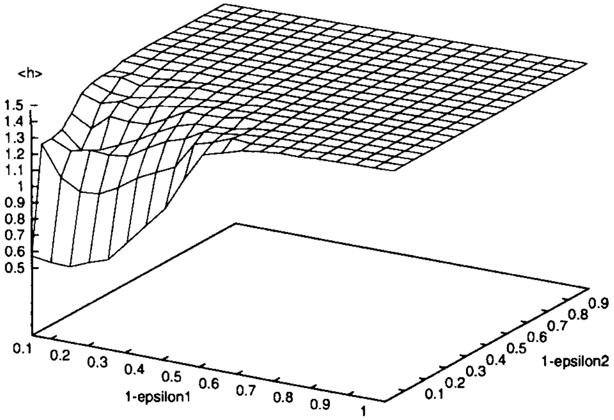

Figure 18. $\langle h \rangle$ as a function of both ε_1 and ε_2, for $N = 20$, $\eta = 1$. The x axis represents $1 - \varepsilon_1$ and the y axis represents $1 - \varepsilon_2$.

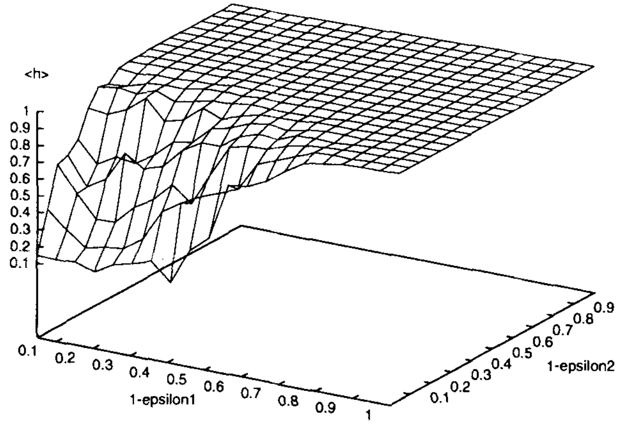

Figure 19. $\langle h \rangle$ as a function of both ε_1 and ε_2, for $N = 20$, $\eta = 10$. The x axis represents $1 - \varepsilon_1$ and the y axis represents $1 - \varepsilon_2$.

is fixed and equal to some number k. ε_1 should then be equal to k/N. We tested $k = 3$ to $k = 10$ and obtained similar results in all cases: the probability of obtaining loops in the hierarchy vanishes *very* rapidly upon increasing the population size (see Fig. 21, $k = 3$ and $\eta = 1$; Fig. 22, $k = 10$ and $\eta = 1$; or Fig. 23, $k = 10$ and $\eta = 10$), which shows that ε_1 must be equal or quite close to 1 for loops to exist (provided our basic reinforcement model is relevant). Finally, Fig. 24 shows how the Landau number reaches its stable value in the present model. All curves start from a maximally random state, where the probability of each individual to domi-

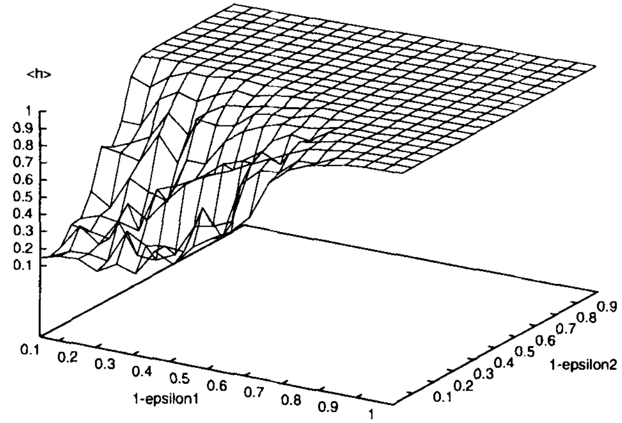

Figure 20. $\langle h \rangle$ as a function of both ε_1 and ε_2, for $N = 20$, $\eta = 5$, with strongly disordered initial conditions. The x axis represents $1 - \varepsilon_1$ and the y axis represents $1 - \varepsilon_2$.

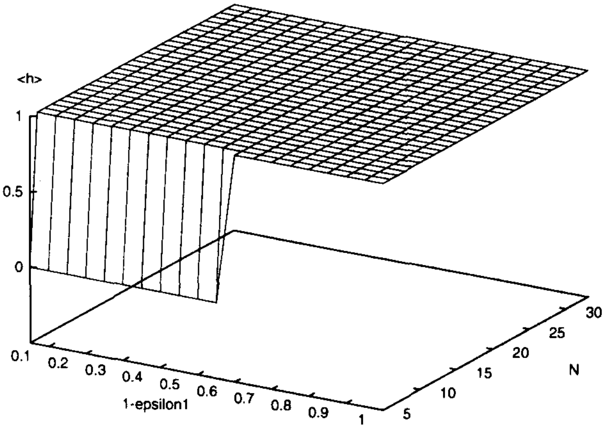

Figure 21. $\langle h \rangle$ (z axis) as a function of ε_1 and N, $\varepsilon_2 = 3/N$, $N = 5$ to 30, $\eta = 1$. The x axis represents $1 - \varepsilon_1$ and the y axis represents N.

nate another one is 0.5 and converge quite rapidly to a stable value of $\langle h \rangle$. Note that this stable value of $\langle h \rangle$ corresponds to *stable* loops. Although convergence is quick, a snapshot taken before stationarity may reveal the existence of loops, whereas the stationary profile may not contain any.

This finding does not seem to be in agreement at all with some early experimental observations performed on hens (Shjelderup-Ebbe, 1913, 1922), which showed that loops are more frequent in large populations:

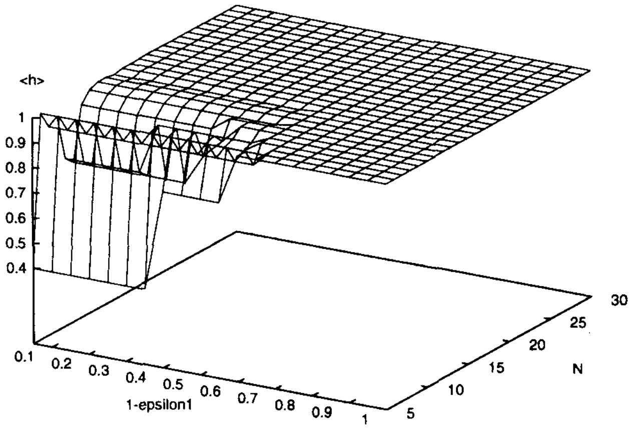

Figure 22. $\langle h \rangle$ as a function of ε_1 and N, $\varepsilon_2 = 10/N$, $N = 5$ to 30, $\eta = 1$. The x axis represents $1 - \varepsilon_1$ and the y axis represents N.

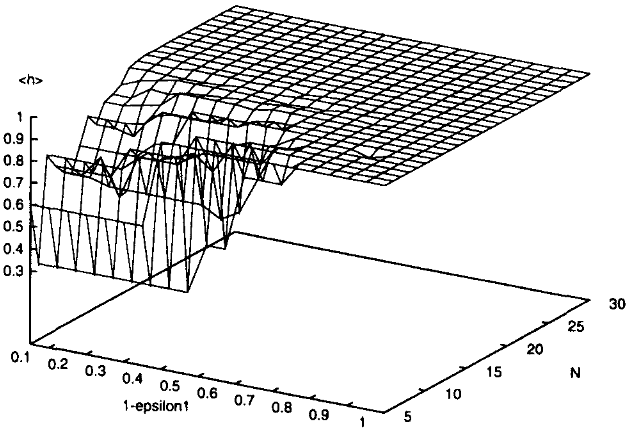

Figure 23. $\langle h \rangle$ as a function of ε_1 and N, $\varepsilon_2 = 10/N$, $N = 5$ to 30, $\eta = 10$. The x axis represents $1 - \varepsilon_1$ and the y axis represents N.

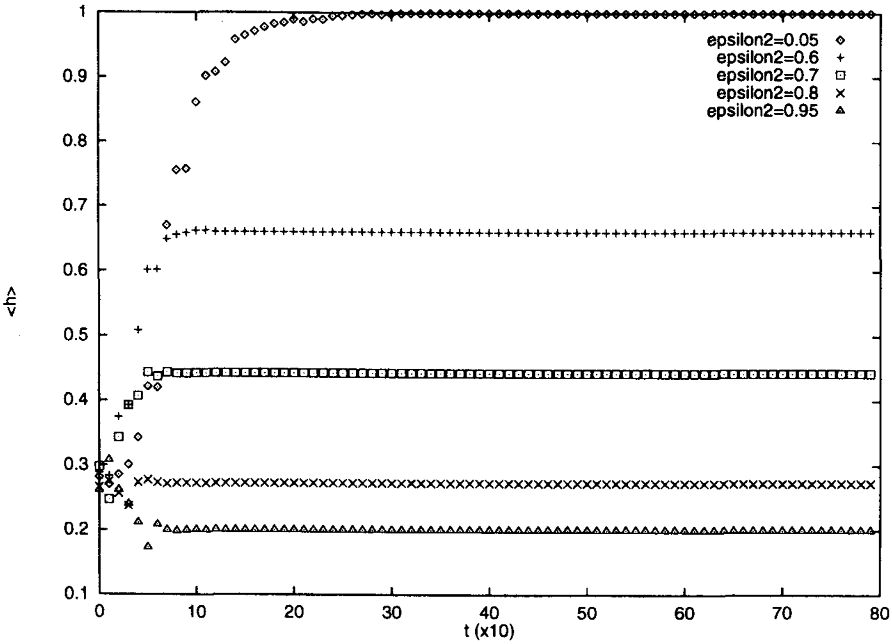

Figure 24. $\langle h \rangle$ as a function of t for various values of ε_2 (0.05, 0.6, 0.7, 0.8, 0.95), $\varepsilon_1 = 1$, $\eta = 1$.

when the population is below approximately 10, loops are unstable and rapidly disappear after the formation of the group, so that the hierarchical form the group converges to is a stable linear one; when the group's size exceeds this experimental threshold, loops still exist after a long time. This apparent contradiction between our model and these experimental observations can be traced back to the stability of loops: in effect, in flocks of hens of sizes greater than 10, loops exist under an *unstable* form, that is, the hierarchy exhibits loops but changes over relatively small time scales, preventing a linear type from appearing. In conclusion, loops are never stable in these experiments: in the low population case, all loops simply disappear, whereas in the large population case, loops transform into other loops. Our results are then in some sense complementary: they show that loops *can be stable* if the degree of individual recognition is sufficiently high and strongly influences the result of a given flight. The experiments on hens are concerned with *snapshots* of the hierarchical structure; we deal with asymptotic profiles. Such asymptotic profiles are well defined, owing to their stability: in order to reconcile the experimental instability of loops and the numerical results that we reported, it may be necessary to include a forgetting term applied to *every* F_{ij}, in the same way as it was applied in section 3 to F_i. This would easily explain the presence of unstable loops transforming into one another when the population is large: in effect, the amount of time separating two successive encounters of individuals i and j increases with the number of individuals in the population if the average number of interactions per unit time is maintained constant, so that the force F_{ij} can then have time to relax to 0 between two such interactions between i and j. Moreover, the experimental observation that loops quickly disappear in small populations shows that individual recognition may have only a rather small—but finite—influence on the process. Therefore, there is no profound contradiction between our model and those experiments.

On the other hand, our result that loops may be stable under some particular conditions of individual recognition is entirely new and might turn out to apply to real cases, e.g. when loops are artificially induced (Gervet *et al.*, 1993). Indeed, Gervet *et al.* (1993) have observed stable triads, but other experiments performed in the same laboratory on exactly the same species (*Polistes*) have never detected the existence of intransitive loops in (larger) colonies comprised of around 10–15 animals (Theraulaz *et al.*, 1989, 1991a, b, 1992). Finally, the exciting paper of Gervet *et al.* (1993) also reports some difficulties in setting up the triads: one possible explanation would be that three individuals involved in a loop must have *comparable* forces; the difficulty of forming a loop would then reduce to that of finding three individuals with nearly equal forces. Such an explanation would imply a *weak contribution of individual recognition* (small ε_2), a contribution clearly seen only with animals of comparable forces; in all other cases, the intrinsic force of an individual would be the essential component determining the result of a fight. Once again, the comparison with tennis players seems appropriate: for two players A and B of similar ranks, the record of the pair (A, B) may turn out to predict much of the result of the match.

5. Related Work.

5.1. *The jigsaw puzzle approach* (*Chase*, 1982a, b, 1985). It is worth mentioning Chase's "jigsaw puzzle" approach, because the present paper is in some sense a continuation of this work that attempts to understand the self-organized genesis of hierarchies. Chase introduced this notion because pairwise competitive ability models failed to explain linear hierarchical structures, which are by far the most widespread ones in nature. The jigsaw puzzle (JP) approach is based on a triadic representation of the hierarchy (triads are the pieces of the JP): (1) any complete hierarchy (that is, a hierarchy in which all individuals can be compared) can be defined by the patterns of interactions within all possible triads and (2) a complete hierarchy is linear if and only if all triads are transitive, hence linearity can be reduced to transitivity in triads. Because there are by definition three possible relationships in a triad $[A, B, C]$, the knowledge of two should not suffice to infer anything about the linearity of the hierarchy. There are, however, two among the four possible configurations of double relationships among three individuals that always lead to a transitive triad, irrespective of the third outcome (A beats B and A beats C, or A beats B, and C beats B); the other two configurations (A beats B and B beats C, or A beats B and C beats A) may either lead to a transitive or intransitive triad, depending on the third outcome. Chase observed that in chickens, who are known to form linear hierarchies, configurations that ensure linearity occur much more often than others. This result, although it indicates that finding why hierarchies are linear amounts to finding why the two favourable configurations are most often selected, does not explain in itself the mechanisms that lead to these two particular configurations. That was to some extent the aim of the present paper. Let us end with the JP approach by remarking that the most probable configuration is "double-dominance" (A beats B and A beats C: 60%) (Chase, 1982b), which suggests (1) that being dominant in the first fight helps in subsequent fights and also (2) that being dominant means being more aggressive, two facts that we have used extensively throughout this paper.

5.2. *Hierarchy and self-organization.* We have already described in detail the contributions of Landau (1951), Chase (1973, 1974, 1980, 1982a, b, 1985,

1986) and Chase and Rohwer (1987) on the topic of hierarchy formation. These works constitute the basis upon which the model presented in this paper has been built. In addition, the simulations of hive behaviour by Hogeweg and Hesper (1983), based on previous ethological studies on bumblebees *Bombus terrestris* by Van Honk and Hogeweg (1981), have been crucial to the understanding that hierarchical structure may result from a self-organizing process in which interacting behaviours "specified" at the individual level give rise to a differentiation. There is today a clear recognition of self-organization as a widespread and powerful structuring mechanism in many important activities (foraging, division of labour or simply aggregation) of social insects, for example (Deneubourg, 1977; Deneubourg *et al.*, 1987; Franks and Sendova-Franks, 1992; Pasteels, 1987; Sendova-Franks and Franks, 1992; Theraulaz *et al.*, 1991a, b).

5.3. *Simulations of hive behaviour in bumblebees.* The simulations of Hogeweg and Hesper (1983) are more complex than the model studied in this paper, because they include in particular a lot of features of a real hive of bumblebees *Bombus terrestris*: space (individuals interact with other members of the colony in the particular region where they are), various tasks (feeding, foraging, building cells, ovipositing), ontogeny (adults develop from eggs); all these features are part of a large interconnected network. Hogeweg and Hesper also introduced rewards, which depend on the difference of forces between two individuals interacting in a fight: the more surprising the result of the fight (that is, the less dominant individual wins despite the larger force of the other individual), the more rewarding. To justify this feature of their model, they invoke observations that those workers that were more frequently in contact with the queen showed an increased tendency to lay eggs in the late stages of the nest. They infer from these observations that frequent interactions with a more dominant, with a small chance to win, is the best way to be lifted upward in the hierarchy. However, many other explanations could be given to account for the aforementioned observations. Therefore, the variable reward hypothesis seems fragile (but cannot be ruled out), at least in the context of simple animals, and we did not keep it. It may be very relevant in higher level organisms, including human beings.

Hogeweg and Hesper found that their model generates a stable elite, but the division of space into two separated regions turned out to be crucial in the differentiation of the colony: in the absence of spatial differentiation, no hierarchical differentiation occurs. This result can be understood with the mathematical approach of Jäger and Segel (1992), who found that given the win–loss function used by Hogeweg and Hesper (1983), no splitting of the population was to be expected in the absence of additional factors such as the division of space. In a related work, Theraulaz *et al.* (1991b) studied a model, including a division of space (nest, periphery and rest of the world), in which dominance and task allocation were mutually defined. In this somewhat more complicated model, they showed that both division of labour and hierarchical differentiation could emerge with a "dominance almost wins" win–loss function.

5.4. *Boltzmann–Master equations.*

5.4.1. *Jäger and Segel's model.* Jäger and Segel (1992) studied a Boltzmann-like equation with an ensemble of classes characterized by the probabilities of their members winning and being defeated of to describe the evolution of dominance in a population of anonymous organisms. Their work was initially inspired by the observations of Van Honk and Hogeweg (1981), and the simulations of Hogeweg and Hesper (1983, 1985). They were interested in the question of whether the population would split into two groups: one characterized by a low dominance index, and the other by a high dominance index. They have studied the cases of a continuum of classes and of a discrete set of classes. They have tested several win–loss functions and found that the population splits in cases where "dominance always wins," whereas the splitting is not assured when a less dominant individual has a non-negligible probability to dominate a more dominant individual. The "dominance always wins" mechanism enables the population to be "convected" toward the two ends of the hierarchy. To make contact with our model, the choice of the Fermi function clearly corresponds to a case where dominance almost always wins, except when the parameter η becomes close to 0 ("high temperature phase"). When $\eta > 0$, we have found a weak dependence of the qualitative results on the precise value of η. A noticeable exception is forgetting, where η determines the nature of the transition to hierarchical behaviour. In summary, the Fermi win–loss function falls within the "dominance almost always wins" regime. The model of Hogeweg and Hesper (1983, 1985) was based on a win–loss function that does not fall within this regime: this may explain why the appearance of a stable hierarchy was strongly dependent upon space differentiation.

Although the Boltzmann equation idea is very "mean field" and does not provide any detail about many important features, two major aspects of the present paper—the probability of interaction between individuals and forgetting—can be cast more or less satisfactorily in terms of Jäger and Segel's model, with the Fermi function of section 2 as outcome probability (that is, with a model close to "dominance always wins," a sufficient condition for differentiation to take place within the master equation framework (Jäger and Segel, 1992)).

5.4.2. *Extensions of Jäger and Segel's model.* Consider a population of m individuals subdivided into $N+1$ different hierarchical levels or classes. Each class is characterized by a force F_n, that without loss of generality (because varying the parameter η allows us to modulate this choice), we set to $F_n = n - (N/2)$ (symmetric around 0). This choice means that hierarchical rank decreases with increasing n. One can study the repartition of the population among the different classes through the density of individuals per class, ρ_n. The time evolution of ρ_n is given by the following master equation, in which one assumes that each class evolves in the mean-field force of the other classes (for $\delta^+ = \delta^-$),

$$\frac{\mathrm{d}\rho_n}{\mathrm{d}t} = \rho_{n-1}\overline{Q^+_{n-1}} + \rho_{n+1}\overline{Q^-_{n+1}} - \rho_n\left(\overline{Q^+_n} + \overline{Q^-_n}\right) \qquad \forall n, 0 < n < N, \tag{12}$$

and the following boundary conditions:

$$\frac{\mathrm{d}\rho_N}{\mathrm{d}t} = \rho_{N-1}\overline{Q^+_{N-1}} - \rho_N\overline{Q^-_N},$$

$$\frac{\mathrm{d}\rho_0}{\mathrm{d}t} = \rho_1\overline{Q^-_1} - \rho_0\overline{Q^+_0}. \tag{13}$$

Equations (13) express the fact that there are a maximum force and a minimum force (or equivalently minimum and maximum classes in our formulation, because each class is assigned a given force), and that a successful (respectively, unsuccessful) individual in class N (resp., 0) remains in class N (resp., 0). Here, $\overline{Q^+_n}$ (resp. $\overline{Q^-_n}$) represents the mean-field probability that an individual chosen at random in class n at time t will be in class $n+1$ (resp. $n-1$) at $t + \mathrm{d}t$: it includes both the probability for this individual to interact and the probability to win (respectively, to lose) the fight if it does interact: $\overline{Q_n^{+(-)}} = \sum_{j=0}^{N} \rho_j P_{nj} Q_{nj}^{+(-)}$. It is possible to use whatever form presented in section 2 for P_{nj}. We assume that an individual in class n at time t will be in class $n-1$ or in class $n+1$ at time $t+1$ *if it did interact*, but it can as well remain in class n if it did not interact. This is manifested in the fact that $\overline{Q^+_n} + \overline{Q^-_n} \neq 1$ in general.

Numerical integration shows that whatever the initial distribution of the population, the asymptotic state is always the same, depending only on the choice of P_{ij}. The final state is generally reached with a time scale which depends on the initial distribution (Fig. 25). We simulated only 15 classes because the computation of the transition probabilities is very time consuming and must be performed at every integration time step. However, we

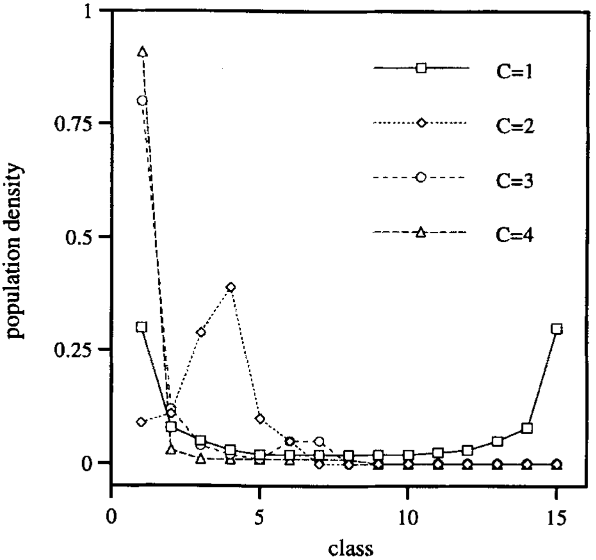

Figure 25. Stable asymptotic distributions for different choices of P_{ij}, irrespective of the initial state. (a) $C = 1$: The population converges toward a bimodal, symmetric distribution, with two peaks at the extremal classes. (b) $C = 2$: The middle-lower classes (3, 4, 5) are densely populated, the higher classes do not contain any individual and classes 1 and 2 have an intermediate density. This curve corresponds to an effective plateau in the middle classes, but the distribution is somewhat shifted to the lower classes compared to the expected result. The differentiation is not marked. (c) and (d) $C = 3$ and $C = 4$ yield the same asymptotic distribution, with the whole population concentrated in classes 1, 2 and 3 for $C = 3$ and in class 1 for $C = 4$. In the latter case, there is therefore apparently no differentiation.

checked on a few examples that the same qualitative results do hold for a much larger number of classes (100). For $C = 1$, the asymptotic state is a "bimodal" state in which both the upper classes and the lower classes are very populated, whereas middle classes have a very low level of population (Fig. 25). Both extreme classes are absorbing states, as can be seen from equations (13). An individual lying in the middle of the hierarchy "diffuses" in the field it is subject to. See Appendix C for more mathematical details.

For $C = 2$, the final distribution comprises a peak at class 4. Classes 1, 2, 3 and 5 are also relatively populated, and classes 6–15 contain virtually no individual. This observation corresponds to the expected result that one should obtain a plateau in the middle classes, but this plateau is shifted to the lower classes compared to the expectations. In this case, hierarchical differentiation exists but is not marked. The existence of plateaus has been reported in bumblebees, but with several plateaus rather than with only one (Van Honk and Hogeweg, 1981). η_2 has a rather large influence on the exact shape of the density profiles obtained (Fig. 26). For large values of η_2 (≥ 2), a profile with a peak at class 1 appears, whereas for lower values of η_2 (between 0 and 2), one obtains a profile that comprises a more and more pronounced peak in the center of the hierarchy as η_2 approaches 0. This is in sharp contrast with the influence of η, which is found to have almost no impact on the obtained profiles in all cases ($C = 1$ to 4), provided $\eta \neq 0$.

For $C = 3$, and $P_c = 1$, class 1 is by far the most populated, with about 80% of the population. Classes 2 and 3 may contain a small number of individuals, whereas classes 4–15 contain virtually no individual. In this case, hierarchical differentiation appears to be limited. However, when the value of P_c is varied from 0 to 2, one gets quite different results, shown in Fig. 27, with a smooth crossover between profiles obtained for low values of P_c and those obtained with higher values.

Finally, for case $C = 4$, we observe only one highly populated class: class 1 contains about 93% of the whole population, whereas the 14 other classes share the remaining 7%. There is therefore no hierarchical differentiation (Fig. 25).

Forgetting can be included in the present model by imposing a bias in the transition probability toward, e.g. the lower part of the hierarchy. Let us introduce a forgetting parameter μ, which can take values between 0 and 1.

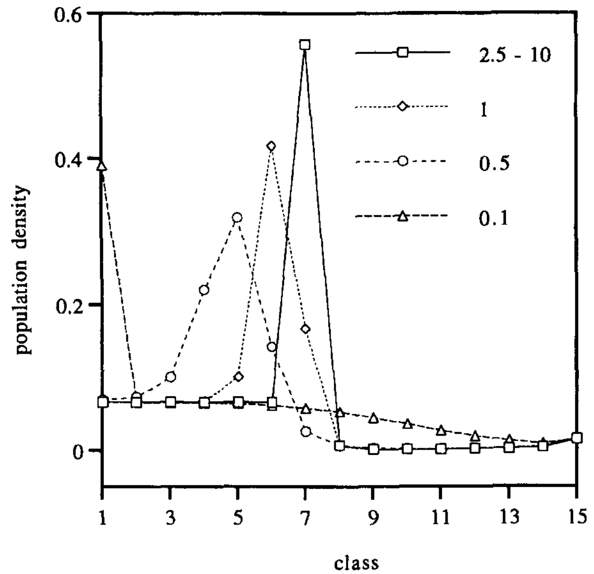

Figure 26. Density profiles obtained in the case $C = 2$ with various values of η_2, with $\eta = 1$.

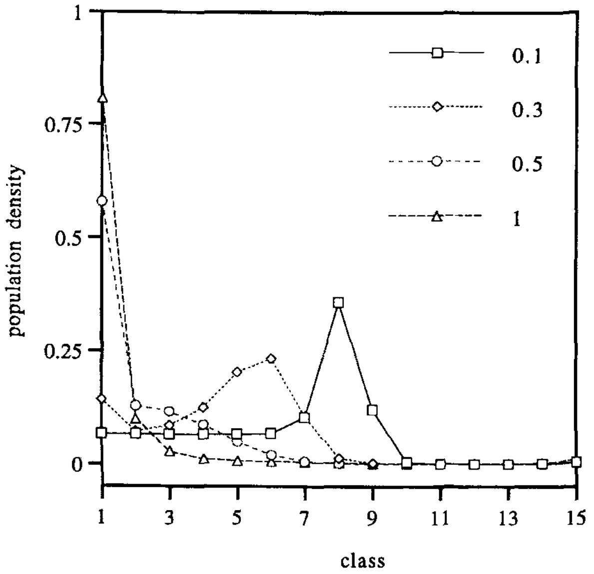

Figure 27. Simulations of $C = 3$ with different values of P_c (0.1, 0.2, 0.3, 0.4, 0.5, 0.7 and 1.0). Low values of P_c yield density profiles where intermediate classes are more populated, whereas profiles obtained with higher values exhibit almost no differentiation.

We then modify the transition probabilities in the following way:

$$\overline{Q_n^-} \to \overline{Q_n^-} + \mu \overline{Q_n^+} \quad \text{and} \quad \overline{Q_n^+} \to (1-\mu)\overline{Q_n^+} \tag{14}$$

so as to ensure that all transition probabilities remain between 0 and 1. We see in equation (14) that the forgetting force is much like an elastic recall force that is greater for classes far away from the lower part. Equation (14) illustrates the intuitive fact that forgetting is generally a hierarchical disadvantage: an individual withdrawn from the game is more likely to have a lower rank than a higher rank when put back into the game. One observes a crossover from the asymptotic distribution reported in the absence of forgetting to a distribution that comprises a peak in the lower class, as the forgetting strength μ is varied. This point is illustrated in Fig. 28 for $C = 1$, but this observation holds whatever the choice of P_{ij}.

In summary, the inclusion of the probability of interaction and forgetting in Jäger and Segel's model, in a case where "dominance almost always wins," drastically modifies the detailed composition of the population by imposing constraints on the various fluxes between classes. This observation

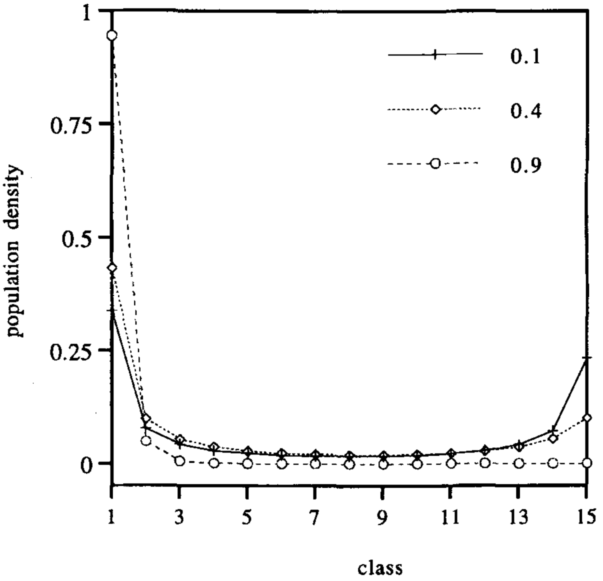

Figure 28. Asymptotic distributions for various values of the forgetting parameter μ, with a bias toward lower level classes. The simulations have been performed in the case $C = 1$ only. There is a smooth crossover from the distribution obtained in the absence of forgetting ($\mu = 0$) to the one reached with maximum forgetting strength ($\mu = 1$).

is a confirmation of the importance of these factors from a different viewpoint.

6. Conclusion and Future Directions. Although there are fundamental similarities between the two previous models and ours (both rely on the idea that the tendency to dominate or to be dominated is amplified by a positive feedback), there are also some important differences. We have explored a mathematical representation in which each individual's behaviour is recorded and we have studied the evolution of the hierarchical profile of the colony in terms of the dominance index X. We used both the dominance index and a more abstract quantity F to study the profile of the population. More importantly, we introduced the probability of interaction between individuals, based on experimental observations (the introduction of this factor turned out to be crucial to the formation of particular hierarchical profiles). We included forgetting (which leads to a phase transition in the observed hierarchical profiles). Finally, we studied how individual recognition could influence the whole process of hierarchy formation and lead to the presence of hierarchical loops. Note that this paper was aimed at exploring the consequences of the self-organization hypothesis (that is, the emergence of a hierarchical structure from local positive and negative feedbacks), but other mechanisms of hierarchy formation cannot and should not be ruled out (see, for example, Chase and Rohwer (1987)): this becomes even more true when it comes to higher level animals, where additional effects (such as the bystander effect) or completely different mechanisms may play an essential role.

Our results are related to the three aspects studied in this paper: (1) the probability of interaction between two individuals, (2) the introduction of memory and forgetting, that is, a relaxation of individual forces to 0 and (3) individual recognition.

(1) The probability of interaction between individuals appeared to be a crucial parameter. Various experimentally observed profiles have been reproduced. One interesting question, which can certainly be answered experimentally, is to know whether the pattern of interactions between individuals (embodied in P_{ij}) actually leads to the formation of the expected profile; that is, does the model predict the correct profile from the knowledge of the pattern of interactions? A positive answer would undoubtedly validate the model to a large extent. In the case of the wasps *Polistes dominulus* that we studied, the answer is positive. We urge new experiments to be carried out or existing data to be reprocessed and reinterpreted along these lines.

(2) We have seen that the inclusion of forgetting led to new results. Forgetting is biologically relevant. As an additional indication of this relevance, let us mention the fact that our model (with or without individual recognition) always leads to a stable asymptotic profile in the absence of forgetting: successive snapshots of the precise hierarchical structure are similar once the asymptotic profile has been reached. The experimental observation of unstable hierarchical forms over long time scales is a strong clue in favour of forgetting, which is the only case where we found unstable hierarchies (the chaotic state when the population density is low). Many more experiments are required to make the nature of forgetting clearer: not only the effects of forgetting should be observed, but also its possible physiological underlying "implementation."

(3) Our model predicts the absence of loops in large populations, which seems to be in contradiction to experimental observations on hens. Our results, on the other hand, seem to be in agreement with the experiments on wasps reported by Gervet *et al.* (1993). We have

already discussed this point, but it should also be emphasized that none of our results, and particularly those on individual recognition, can be easily extended to higher-level animals where processes other than simple reinforcement may come into play. Therefore, the artificially induced loops of Gervet *et al.* (1993) remain the most promising starting point for experimenting with the effects of individual recognition: our model allows us to make clear predictions that can be compared with experiments. One important question is, of course, how to measure the parameters ε_1 and ε_2 that we introduced.

In conclusion, in the following ways we have contributed to the understanding of the self-organization of hierarchical structures in animal societies:

- By extending the basic models of Chase (1974), Hogeweg and Hesper (1983, 1985), and Jäger and Segel (1992) to include several important aspects. We have shown the diversity of the possible hierarchies that can emerge when such aspects are taken into account. Owing to this diversity, the model may appear to be general, whereas it is in fact built upon a very small set of specific hypotheses and parameters: this shows the richness of the model and highlights the creativity potential of positive feedback mechanisms.
- By introducing a clear mathematical model that can in certain cases be solved.
- By suggesting new directions for experiments.

APPENDIX A

Asymptotic Profiles. It can be shown, in the case $C=1$, when $\delta^+ = \delta^-(=1$ without loss of generality) that the linear dependence of X_i with respect to the rank is an asymptotic stationary state (in X_i). In effect, when $C=1$, X_i and F_i can be simply related by $F_i/t = 2X_i - 1$, because $F_i = D_i - S_i$ (there is exactly one interaction per time step for every individual) and $X_i = D_i/D_i + S_i$. Therefore, a time-independent linear variation of X_i as a function of rank should result in $F_i =_{t\to\infty} k_i t$, where k_i is a time-independent quantity. Under very general conditions, assuming that individuals are numbered according to their ranks, the only asymptotically stationary profile is given by $k_0 = -1, \dots, k_i = -1 + 2i/N, \dots, k_N = 1$, that is, a profile linear in the rank i. To see this, let us assume that we have $F_i =_{t\to\infty} k_i t$, and that the k_i's satisfy strict inequalities: $k_0 < k_1 < \cdots < k_i < \cdots < k_N$.

We can inject this form for F_i in the equation giving the evolution of F_i (in the absence of noise):

$$\frac{\mathrm{d}F_i}{\mathrm{d}t} = \frac{1}{N} \sum_{\substack{j=0 \text{ to } N \\ j \neq i}} \left(\frac{1}{1+\exp(-\eta t(k_i - k_j))} - \frac{1}{1+\exp(+\eta t(k_i - k_j))} \right). \tag{A1}$$

As $t \to \infty$, $1/(1+\exp(-\eta t(k_i - k_j)) \to_{t\to\infty} 0$ (resp., 1) and $1/(1+\exp(-\eta t(k_i - k_j)) \to_{t\to\infty} 1$ (resp., 0) if $j > i$ (resp. $j < i$). Consequently, there are i terms equal to 1 and $N - i$ terms equal to -1 in the sum, so that finally

$$\frac{1}{N} \sum_{\substack{j=0 \text{ to } N \\ j \neq i}} \left(\frac{1}{1+\exp(-\eta t(k_i - k_j))} - \frac{1}{1+\exp(+\eta t(k_i - k_j))} \right) \underset{t\to\infty}{=} \frac{2i - N}{N}, \tag{A2}$$

which corresponds to the linearly varying profile $k_i = -1 + 2i/N$. Moreover, this result is obviously consistent with the condition $k_0 < k_1 < \cdots < k_i < \cdots < k_N$. Simulations confirm that this state is an effective attractor of the hierarchy formation dynamics. We can also see that $\eta > 0$ does not have any influence on the final profile (only on the time required to reach this profile): expression (A2) remains true. However, for $\eta = 0$, equation (A2) for F_i reduces to $\mathrm{d}E_i/\mathrm{d}t = \xi(i,t)$, so that the F_i's perform independent random walks.

The situation is more complicated when $\delta^+ \neq^- \delta^-$ (we assume that $\delta^+ \geq 0$, $\delta^- \geq 0$ and moreover, we can set $\delta^+ + \delta^- = 2$ without loss of generality, because a simple rescaling of time is sufficient to include other cases). Following the same reasoning as before, (A2) must be changed into

$$\frac{1}{N} \sum_{\substack{j=0 \text{ to } N \\ j \neq i}} \left(\frac{\delta^+}{1+\exp(-\eta t(k_i - k_j))} - \frac{\delta^-}{1+\exp(+\eta t(k_i - k_j))} \right) \underset{t\to\infty}{=} \frac{2i - N\delta^-}{N} \tag{A3}$$

and $F_i \approx \delta^+ D_i - \delta^- S_i$, $X_i = 1/2(\delta^- + F_i/t)$. The result should be the same as before $X_i = i/N$. However, Fig. 5 shows the profiles obtained for different values of δ^+ and δ^- at $t = 20{,}000$. The close-to-linear profiles eventually (slowly) converge to the linear profile; the others remain unchanged. This means that when the bias $\delta^+ - \delta^-$ is too high, we must give up the hypothesis that $k_0 < k_1 < \cdots < k_i < \cdots < k_N$: obviously, some of the k_i's are equal. When $\eta = 0$, the equation for F_i reads $\mathrm{d}F_i/\mathrm{d}t = (\delta^+ - \delta^-)/2 + \xi(i,t)$. This means that the F_i's perform independent biased random walks in the direction of $\delta^+ - \delta^-$.

Still following the same reasoning as before, it is possible to understand to some extent the saturation at 0.4 observed in the case $C = 2$. In effect, (A1) is then transformed into

$$\frac{\mathrm{d}F_i}{\mathrm{d}t} = \frac{1}{N} \frac{1}{1+\exp(-\eta_2 t k_i)} \sum_{\substack{j=0 \text{ to } N \\ j \neq i}} \frac{1}{1+\exp(-\eta_2 t k_j)} \times \left(\frac{1}{1+\exp(-\eta t(k_i - k_j))} - \frac{1}{1+\exp(+\eta t(k_i - k_j))} \right). \tag{A4}$$

Because $1/(1+\exp(-\eta_2 t k_i)) \to_{t\to\infty} 0$, $1/2$ or 1 depending on whether $k_i < 0$, $k_i = 0$ or $k_i > 0$, and because the right-hand side of (A4) is obviously bounded, k_i cannot be strictly negative:

$$\frac{\mathrm{d}F_i}{\mathrm{d}t} \underset{t\to\infty}{=} k_i(<0) = \underbrace{\frac{1}{1+\exp(-\eta_2 t k_i)}}_{\substack{\to 0 \\ t\to\infty}} \underbrace{\frac{1}{N}\sum_{\substack{j=0 \text{ to } N \\ j\neq i}} \frac{1}{1+\exp(-\eta_2 t k_j)}\left(\frac{1}{1+\exp(-\eta t(k_i-k_j))} - \frac{1}{1+\exp(+\eta t(k_i-k_j))}\right)}_{\text{bounded}} \underset{t\to\infty}{=} 0, \qquad \text{(A5)}$$

which is obviously impossible. It can be also shown that $k_i = 0$ is not possible either, unless all k_i's are equal to 0: in effect, $1/(1+\exp(-\eta_2 t k_i)) \to_{t\to\infty} 1/2$, so that the sum should be equal to 0 for consistency, and this cannot be achieved unless all k_i's are 0. The conclusion is therefore $\forall i$, $k_i > 0$, so that the corresponding values of X_i should not be less than 0.5 (0.4 in the simulations). It must be noticed that in the cases $C = 1, 2, 3$, the probabilities of interaction between two individuals depend on the quantity $Y_i = 1/(1+\exp(-\eta_2 t k_i))$, which converges as $t \to \infty$.

APPENDIX B

B1. Linear Stability Analysis. Let us study the last equation of (6):

$$\frac{\mathrm{d}F_i}{\mathrm{d}t} = H_i(\{F_j\}) = \frac{\rho}{N}\left(\sum_{\substack{j=0 \text{ to } N \\ j\neq i}} \frac{1}{1+\exp(-\eta(F_i-F_j))} - \frac{1}{1+\exp(+\eta(F_i-F_j))}\right) - \mu g(F_i). \qquad \text{(B1.1)}$$

The associated Jacobian matrix $[\partial H_i/\partial F_j]$ is defined by

$$\frac{\partial H_i}{\partial F_i} = \frac{\rho}{N}\left(\sum_{\substack{j=0 \text{ to } N \\ j\neq i}} \frac{\eta\exp(-\eta(F_i-F_j))}{(1+\exp(-\eta(F_i-F_j)))^2} + \frac{\eta\exp(-\eta(F_i-F_j))}{(1+\exp(+\eta(F_i-F_j)))^2}\right) - \mu\frac{\mathrm{d}g}{\mathrm{d}F}(F_i),$$

$$\left.\frac{\partial H_i}{\partial F_j}\right|_{i\neq j} = -\frac{\rho}{N}\left(\frac{\eta\exp(-\eta(F_i-F_j))}{(1+\exp(-\eta(F_i-F_j)))^2} + \frac{\eta\exp(-\eta(F_i-F_j))}{(1+\exp(+\eta(F_i-F_j)))^2}\right). \qquad \text{(B1.2)}$$

The stability of a state such that $F_0 = F_2 = \cdots = F_N = F$ is determined by the eigevalues of

$$\left[\frac{\partial H_i}{\partial F_j} \bigg|_{F_0 = F_2 = \,-\, - = F_N = F} \right]$$

$$= \begin{bmatrix} \rho\frac{\eta}{2} - \frac{\mathrm{d}g}{\mathrm{d}F} & -\frac{\rho}{N}\frac{\eta}{2} & \cdots & \cdots & -\frac{\rho}{N}\frac{\eta}{2} \\ -\frac{\rho}{N}\frac{\eta}{2} & \ddots & -\frac{\rho}{N}\frac{\eta}{2} & \ddots & \vdots \\ \vdots & -\frac{\rho}{N}\frac{\eta}{2} & \ddots & -\frac{\rho}{N}\frac{\eta}{2} & \vdots \\ \vdots & \ddots & -\frac{\rho}{N}\frac{\eta}{2} & \ddots & -\frac{\rho}{N}\frac{\eta}{2} \\ -\frac{\rho}{N}\frac{\eta}{2} & \cdots & \cdots & -\frac{\rho}{N}\frac{\eta}{2} & \rho\frac{\eta}{2} - \frac{\mathrm{d}g}{\mathrm{d}F} \end{bmatrix}, \tag{B1.3}$$

which is a circulating matrix. The state $F_0 = F_2 = \cdots = F_N = F$ is therefore stable for

$$\rho < \frac{2\mu\frac{\mathrm{d}g}{\mathrm{d}F}}{\eta\left(1 + \frac{1}{N}\right)}. \tag{B1.4}$$

Since $\mathrm{d}g/\mathrm{d}F \to 0$ as F increases, the most stable state of this kind is when $F = 0$. The stability condition is then given by

$$\rho < \frac{2\mu}{\eta\left(1 + \frac{1}{N}\right)} \tag{B1.5}$$

if $\mathrm{d}g/\mathrm{d}F|_{F=0} = 0$, which is indeed satisfied in the studied case. To summarize, the flat profile is linearly stable for $\rho < 2\mu/(\eta(1 + 1/N))$ and linearly unstable for $\rho > 2\mu/(\eta(1 + 1/N))$.

B2. Allowed Profiles. The stability analysis is not sufficient. In particular, there are constraints imposed on the profiles. If the constraints are not satisfied ($\rho < \mu$), slightly differentiated profiles may appear in the region where the flat profile is linearly unstable, but these profiles are local attractors, and two runs of the process lead to two different profiles. On the contrary, if the constraints are satisfied ($\rho > \mu$), one particular profile is a global attractor, and two runs converge to the same profile. Note that a profile is anonymous: it is a function that associates a dominance index to a rank; therefore two equivalent profiles may correspond to situations where individuals are in different situations (the hierarchical symmetry between individuals is broken). One then understands that the nature of the transition from a flat to a differentiated situation depends on the relative locations of the linear unstability point and the point where the constraints become satisfied, that is, $2\mu/(\eta(1 + 1/N))$ and μ. We follow the same reasoning as in Appendix A, including the forgetting term: the corresponding deterministic equations read

$$\frac{dF_i}{dt} = \rho \frac{d}{dt}[t(2X_i - 1)] - \mu g(F_i). \tag{B2.1}$$

From the discussion of Appendix A, it is reasonable to start by assuming that $dF_i/dt =_{t\to\infty} \rho k_i$. Looking for a stationary solution for X_i, we get the following equations:

$$-1 + \frac{2i}{N} - \mu g(\rho k_i t) = \rho(2X_i - 1). \tag{B2.2}$$

If $g(F_i) = \tanh(F_i)$, (B2.2) can be approximated by $-1 + 2i/N - \mu\,\mathrm{sign}(k_i) = \rho(2X_i - 1)$, that is,

$$X_i = \begin{cases} \dfrac{i}{N} + \dfrac{\mu}{2\rho}, & \text{if } k_i < 0, \\ \dfrac{i}{N} - \dfrac{\mu}{2\rho}, & \text{if } k_i > 0. \end{cases} \tag{B2.3}$$

This set of equations (B2.3) has a solution, with some of the $X_i \neq 0.5$ (that is, a differentiated profile) if and only if the following set of consistency conditions are satisfied: $i/N|_{i=0} + \mu/2\rho < \frac{1}{2}$ and $i/N|_{i=N} - \mu/2\rho > \frac{1}{2}$, which both reduce to

$$\rho > \mu. \tag{B2.4}$$

Therefore the profile should, in principle, be completely flat below $\rho_c = \mu$. To be more accurate, for $\rho > \rho_c$, the profile is expected to be flat between two values of i, symmetric with respect to $i = N/2$, $i_{\mathrm{inf}}(\rho) = N/2 - N\mu/2\rho$ and $i_{\mathrm{sup}}(\rho) = N/2 + N\mu/2\rho$, and to vary linearly from $i = 0$ to i_{inf} and from i_{sup} to N. This is indeed observed for $\eta = 2/(1 + 1/N)$. For other values of η, the situation is different:

(1) If $\rho > \mu$, but the flat profile is still linearly stable (this is the case when $\eta < 2/(1 + 1/N)$), small fluctuations will not suffice to make the hierarchy appear, but as soon as the flat profile is unstable, the hierarchy emerges abruptly, defined by the equations (B2.3).
(2) If $\rho < \mu$ and the flat profile is linearly unstable (this happens when $\eta > 2/(1 + 1/N)$), the hierarchy appears (because the flat profile cannot persist), but not in a structured way: the profiles look more or less random. This is due to the fact that the profile is entirely the effect of fluctuations, because condition (B2.4) is not fulfilled.
(3) When $\eta = 2/(1 + 1/N)$, condition (B2.4) becomes satisfied exactly at the time when the flat profile becomes linearly unstable (that is, at $2\mu/\eta$).

APPENDIX C

Stationary Profile of the Master Equation. Although it is hard to find analytically stationary solutions to the master equation even in the simplest case ($C = 1$ without forgetting) due to the dependence of transition probabilities on the whole distribution of the population, it is nevertheless possible to check that a particular solution satisfies stationarity conditions.

How to find such a solution is yet another matter, but guided by simulations, one can test the following solution for $C = 1$: $\rho_0 \approx p$, $\rho_N \approx 1 - p$ and $\forall n \neq 0, N$, $\rho_n \approx 0$, if one assumes that only fights with members of other classes count, that is, a fight between two members of the same class has no consequence on either individual. The conditions for stationarity are given by (a) $\rho_n = \rho_{n-1} Q_{n-1}^+ + \rho_{n+1} Q_{n+1}^-$, $\forall n$, $0 < n < N$, (b) $\rho_0 Q_0^+ = \rho_1 Q_1^- = 0$ and (c) $\rho_N Q_N^- = \rho_{N-1} Q_{N-1}^+ = 0$. The tentative solution is obviously consistent for all ρ_n, except $\rho_0, \rho_1, \rho_{N-1}$ and ρ_N. (d) Let us for instance consider condition (b): (b) $\Rightarrow Q_0^+ = \rho_N/(1 + e^{\eta N}) = 0$. This relation, though impossible to satisfy strictly, becomes true when the system gets frozen ($\eta \to \infty$) or in the thermodynamic limit ($N \to \infty$: not to be confused with the continuum limit of the master equation, which would imply infinitesimal differences in the forces of neighboring classes and therefore prevent the consistency condition (d) from being satisfied). It is easy to check that the three other consistency conditions are then also satisfied. Any value of p would work. The final result clearly depends on the initial composition of the population.

Taking into account intraclass fights, we can study the three-class case, which can be exactly solved in the low-temperature limit. In effect, the stationary equations read

$$\begin{array}{l} \rho_1 Q_1^- = \rho_0 Q_0^+ \\ \rho_0 Q_0^+ + \rho_2 Q_2^- = \rho_1 \\ \rho_1 Q_1^+ = \rho_2 Q_2^- \\ \rho_0 + \rho_1 + \rho_2 = 1 \end{array} \quad \Rightarrow \quad \left| \begin{array}{l} \dfrac{\rho_0^2}{2} + \dfrac{\rho_0 \rho_2}{1 + e^{2\eta}} = \dfrac{\rho_1^2}{2} + \dfrac{\rho_1 \rho_2}{1 + e^{-\eta}} \\ \dfrac{\rho_2^2}{2} + \dfrac{\rho_0 \rho_2}{1 + e^{2\eta}} = \dfrac{\rho_1^2}{2} + \dfrac{\rho_0 \rho_1}{1 + e^{-\eta}} \\ \rho_0 + \rho_1 + \rho_2 = 1 \end{array} \right. . \tag{C1}$$

In the limit where $\eta \to \infty$ (that is, when the dominance–subordination process is deterministic, or equivalently, when "dominance always wins"),

$$\begin{array}{l} \dfrac{\rho_0^2}{2} = \dfrac{\rho_1^2}{2} + \rho_1 \rho_2 \\ \dfrac{\rho_2^2}{2} = \dfrac{\rho_1^2}{2} + \rho_0 \rho_1 \\ \rho_0 + \rho_1 + \rho_2 = 1 \end{array} \quad \Rightarrow \quad (\rho_2 - \rho_0)\left(\frac{1}{2}(\rho_2 + \rho_0) - 1\right) = 0$$

$$\Rightarrow \quad \left| \begin{array}{l} \rho_2 = \rho_0 = \sqrt{2} - 1 \approx 0.41 \\ \rho_1 = 3 - 2\sqrt{2} \approx 0.17, \end{array} \right. \tag{C2}$$

which is consistent with the findings that the two extreme classes are more populated than the middle class; however, the middle class is still populated, due to a current of individuals. We can reasonably expect this result to hold for more classes, which is indeed confirmed by simulations.

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