Experimentally induced circular dominance relationships in a polygynous Polistes (*Polistes dominulus* Christ) wasp colony

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Abstract. Circular dominance relationships were set up in polygynous Polistes wasp colonies at the pre-emergence phase, by making use of the effects of priority of residence. The results are discussed in relation to various models which have been proposed to explain social dominance.

Key words. Circularity; dominance; model; polygyny; wasp.

Since the pioneer studies by Schjelderup-Ebbe[1] and later studies by Allee[2], the term social dominance has been applied to any stable hierarchy which is set up within a group of animals as the result of fighting, even when the fighting is restricted to ritualized preludes. This definition indicates that we are dealing with an ethological mechanism subserving social organization. Dominance can be said to involve the following two basic features: 1) the existence of a gradable property (hierarchy) which can be detected by means of visible cues: the amount of aggression displayed by different individuals, for example, or the order of priority in which the individuals have access to food sources; 2) the establishment of this hierarchy by fighting, or sometimes by the mere suggestion of a fight, showing that some form of competition is at work.

In any group where dominance prevails, each member has a specific position in relation to each of the other members, and the whole set of binary relationships has a linear overall pattern of organization. Dominance can therefore be said to be transitive, since if individual I dominates individual J, and if J dominates K, I will predictably dominate K. The triad I J K is therefore said to be transitive.

In addition to this linear hierarchical model, there exists another hierarchical model in which the relations are not transitive but circular. According to this type of model, individual I dominates individual J, which dominates individual K, but K dominates I. This pattern of organization is to be found less frequently in nature. In particular, it seems unlikely that in a group organized on the basis of dominance alone, the leader will be involved in circular relationships. Although few circular triads have been found to exist in hierarchical groups, it seemed likely that they would be more numerous if dominance relations were distributed separately within pairs of individuals[3].

Two families of models have been developed[4] to account for the origin of social hierarchies. The first, which has been called the Tournament Model, focuses on the relationships between any two subjects: each encounter between two animals results in one of them becoming superior to the other, and the same pattern is therefore repeated at each subsequent encounter. This model involves the assumption that each member of a group is capable of recognizing the other members individually. It accounts very satisfactorily for stable relationships between two individuals, but does not deal so efficiently with transitive relationships within a whole group. It explains quite clearly why particularly aggressive and unaggressive animals end up at the top and bottom of the hierarchy, but not why so few of the middle-ranking animals belong to circular triads.

The models of the second type, which have been called Correlational Models, are based on the assumption that there exists a high degree of statistical correlation between some inherent characteristic or group of characteristics (which might serve as a dominance index) and the actual positions of the animals within a hierarchy. The salient characteristic in question might be, for instance, the animals' size, strength, combativity, fecundity, or endocrine levels, and the fact that these factors are gradable is in line with the transitivity of dominance relations. In models of this kind, individual recognition need not necessarily be assumed to take place; what is assumed, however, is the existence of a strong correlation between an animal's hierarchical rank and its rating in terms of the gradable characteristic. A fine discriminatory ability is therefore presumably necessary in order to ensure that the parameter values are properly assessed and arranged; indeed, the differences between two neighbouring animals in the hierarchy must be very slight, especially in the middle of the hierarchy, whenever the group contains more than seven or eight individuals. One might therefore expect to encounter some *ex aequo* relationships, instabilities, or even, perhaps, some circular triads among the middle ranks.

Since situations of the latter type are very scarce, it was subsequently proposed (references 5–7) that some more specifically social factors should be taken into account, in addition to the inherent salient characteristics. Here the basic assumption was that an animal's social experience can have feedback effects on the strength of its inherent characteristics which enhance the link between these characteristics and the animal's social rank. This helped to side-step some of the difficulties previously encountered, and the resulting model was a combination between some of the characteristics of both Tournament and Correlational models.

In short, there exist two mechanisms which can possibly be used to account for stable dominance relations. They are not mutually exclusive, and involve: 1) the ability to recognize the other members of the group individually, which stabilizes the hierarchical relations between each pair of individuals. This mechanism, which is assumed to exist in the Tournament model, does not however account for the transitivity of dominance relations. In addition, when the size of the population increases in a hierarchical group, it requires cognitive capacities with which mammals and birds are sometimes endowed, but which seem hardly likely to exist among insects; 2) the existence of a sufficiently effective behavioural property on the basis of which the outcome of any encounter between two individuals can be settled. This decisive property can either be adopted once and for all prior to the first encounter (Correlational Model) or be modulated by the first social contacts. The main point is that it does not depend in the latter case only on the animals' individual characteristics, but operates rather like a label signalling each subject's rank. By convention, we have therefore adopted the term 'Labelling Model' for hypotheses of this kind, which include the Correlational Model but also take various social processes into account. Labelling models account for the existence of groups of individuals with approximately equal rank; but like Correlational models, they do not account for the existence of non-transitive triads within a linear overall hierarchy.

The Polistes are eusocial wasps which have an annual colony cycle. In the spring, a foundress emerging from hibernation sets up a new nest and rears the first larvae on her own. In some Polistes species, however, particularly in *P. dominulus* Christ, several foundresses can form an association and set up a colony together, which is then known as a polygynous colony. One of the foundresses then becomes the main egg-layer, and the others (the auxiliaries) carry out practically no reproductive activities but are responsible for rearing the brood.

It has been established[8] that this differentiation among the foundresses may reflect the linear dominance hierarchy in which the entire social group is involved. Several authors[9-12] have studied the corresponding forms of specialization which are to be found either in a polygynous colony or in a colony at the post-emergence stage, including workers. Various physiological factors, such as the egg-laying rate[13] and the juvenile hormone levels[14], have been found to influence the wasps' social relations and to be affected in turn by the social hierarchy once it has been set up. A wasp's chances of acquiring the dominant position at the outcome of an encounter are enhanced if it is the prior resident, and it has been assumed that some individual recognition ability does exist since the trace of previous social experience seems to influence the outcome of the dominance relations which are set up when two females which previously entertained dominance relations are reunited after a period of separation[15].

In a model of a more formal type[16], the dominance scene itself was taken to be the main factor determining the setting up and the maintenance of a hierarchy. Here each member of the group is rated in terms of a parameter known as 'force', which determines the outcome of any encounter. The difference between the forces of two individuals which meet is proportional to the probability that the more 'forceful' of the two will become the dominant member of the pair. On the other hand, the outcome of the encounter will modify the forces of the two protagonists: that of the dominant member increases by the value df, and that of the subordinate member decreases by the same amount. A simulation involving several subsidiary parameters has shown that this model can lead to some differentiation within the group, which mimicks that which takes place in the corresponding natural situation even when the initial group consists of identical individuals. This model is obviously of the Labelling type, and the 'force' of the individuals stands for the whole set of processes constituting the label signalling a difference between the individuals' ranks. Here again, since the difference in force is a transitive property, difficulties arise with models of this type when it comes to explaining the presence of circular triads.

The force parameter therefore has the status of a hidden quantitative variable, and it is not necessary at the present stage to specify the physiological counterparts involved, i.e. the wasp's physiological state, fecundity, etc.

Statement of the problem and principles underlying the experiments

From what has been said above about the various models developed so far, two main points remain to be elucidated as regards the dominance mechanisms at work in Polistes wasps. The first question is whether or not individual recognition is possible (some possible clues to the answer have been mentioned above). The second point is how to explain the existence of circular triads, which does not fit the transitive nature of the hierarchical scheme as a whole. Both categories of models fail in one way or another. Tournament models fail to satisfactorily explain the overall transitivity, whereas Labelling models, which are based on the existence of a gradable quantity, fail to explain the possible existence of stably established circular triads.

It was therefore decided to make use of those factors which have been said to influence the setting up of hierarchical relationships to design an experimental situation in which the relationships amoung the members of a colony are no longer transient. More specifically, it was proposed to experimentally set up circular dominance relations among three female wasps such that Wasp I dominates Wasp J, Wasp J dominates Wasp K, and Wasp K dominates Wasp I. If this hierarchy, which never occurs under natural conditions, can be set up without any difficulty and turns out to be stable, we will be able to say that the basic regulatory mechanism involved is not of the labelling type, or at least that if this mechanism is present, it is not essential. Incidentally, the results obtained in this case will demonstrate the efficiency of the factors we have manipulated. If on the contrary we fail to achieve a stable circular triad, it will be likely that a gradable underlying factor is at work, the effects of which override all the more immediate factors we have brought into play.

The experiment involved two stages:

In the first stage, we attempted to set up a 'virtual' circular triad, i.e. one where the animals involved met only two by two: first Wasp I was expected to submit to Wasp J, then Wasp J was expected to submit to Wasp K and, in the last place, Wasp K was expected to submit to Wasp I. We repeated this procedure every day for a week to make sure that such relationships are stable. If we were to succeed, this would mean that a Correlation model could not fully account for this situation. Success would also show the efficiency of those factors that we used to control the outcome of the dominance encounters.

In the second stage, we attempted to transform this virtual circular triad into an actual one by placing all three individuals together in the same nest. Here, if the trace of previous encounters is a decisive factor, as assumed by the Tournament Model approach, the triad should turn out to be actually circular. Any gaps in the circularity of the dominance relationships would suggest on the other hand that the simultaneous coexistence of the three wasps in the same nest, and the subsequent possibility of frequent encounters have short-term back-effects on the social hierarchy. These might be responsible for establishing a linear hierarchy in accordance with the predictions of the Labelling Model.

In fact, we decided to make very gradual shifts from the first stage to the second one; in this way, we hoped both to facilitate the making of fine distinctions between the various factors liable to intervene and to avoid disturbing the wasps by making drastic changes in their social surroundings.

Material and methods

The female wasps used in the present study all originated from the same colony and were therefore presumably sisters or at least close relatives. They had previously been hibernating under outdoor conditions. On 15/2/92, 140 gynes were placed in nesting cages under the customary experimental conditions (12-h day, 12-h night, honey and prey provided *ad libitum*).

Ten wasps were placed in each cage. As soon as the first nest foundations occurred, only the two most active foundresses (in terms of nest building, egg-laying and presence at the nest) were kept in the cages. These digynous societies then developed without any further handling until some of the larvae reached the large-sized instar stage. From then on, the larval brood (consisting of 4 or 5 large sized larvae) in each nest was maintained at a constant level by destroying any excess larvae. This meant that no workers could possibly emerge, since the colonies were artificically maintained throughout these experiments at the pre-emergence stage.

The wasps were successively exposed to several conditions, each of which (unless otherwise stated) was maintained during a six-day observation period:

In the preparatory step, we attempted to set up virtually circular dominance relations by making use of the effects of prior residence. Here three digynous colonies were used in each experimental set (fig. 1). The alpha 3 (the dominant individual in colony 3) was introduced into digynous colony 1, where it was expected to be subordinated by the alpha 1 individual (also denoted the Dominant resident: Dr). One hour later, alpha 3 was returned to nest 3 (its 'usual nest'); alpha 1 was then placed on nest 2, where it was expected to be subordinated by alpha 2 (the Dr at that nest), before being returned one hour later to its usual nest; lastly, alpha 2 was introduced into nest 3. If it was subordinated by alpha 2 (the Dr at nest 2), virtual circularity was taken to have been established. All that was then required was therefore to repeat the experiment in order to test the stability of the resulting dominance relations. When circular dominance relations failed to be established, other combinations of wasps were tested until a sufficiently large number of virtually circular hierarchies was obtained. In fact, three sets of three digynous colonies containing virtually circular triads were obtained in this way for the purpose of our experiments.

Stage 1 included three successive steps. In step 1.1, the stability of the virtual circularity thus obtained was tested. A system of rotation was organized within each set of three digynous colonies, whereby each dominant resident spent one hour per day as a 'subordinate visitor' (Sv) at another digynous nest, (that on which it had become subordinate during the preparatory step). It spent the remaining 23 hours at its usual nest as the 'Dominant resident' (Dr). The scheme of rotation was varied from day to day, to ensure that no two

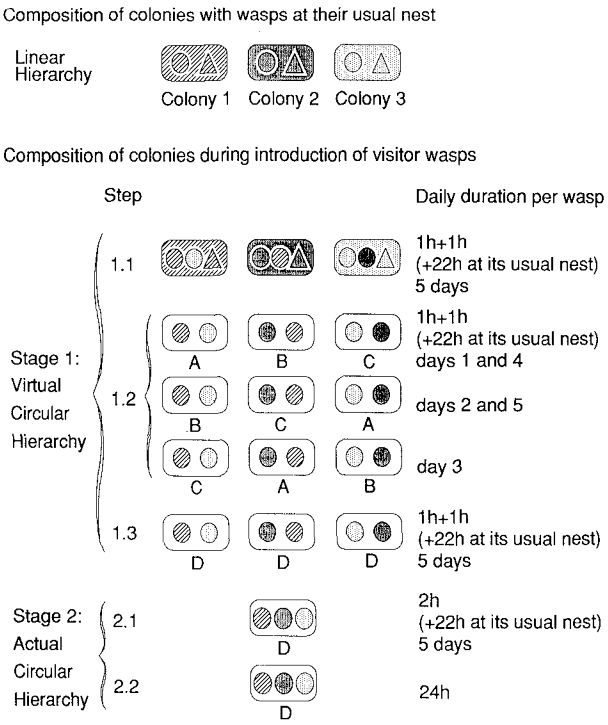

Figure 1. Experimental procedure. The progressive steps leading to the setting up of circular hierarchies are described in rows. For stages 1 and 2, the columns give the situation during successive daily periods. Two values in the 'daily duration' column (i.e. 1 h + 1 h) means that each of the Alpha wasps was in two successive situations during the duration indicated. Circles and triangles symbolize Alpha and Beta wasps, respectively. Rectangles symbolize nests: each one is identified by a letter in the case of nests from another set, or by a filling pattern in the case of a nest in the set under investigation. Nests A, B, C, and D were therefore from colonies other than colonies 1, 2 and 3. A wasp and a nest symbol filled with the same pattern therefore indicate that this wasp was one of the foundresses of this nest.

wasps could meet at the same time of day on consecutive days.

Steps 1.2 and 1.3 differed from step 1.1 in that the daily 1-hour encounters between two alpha wasps took place here on neutral ground, at a nest other than their usual ones, with no other wasps and in particular no subordinate residents present. Contrary to the situation in the preparatory step and in step 1.1, none of the wasps was therefore a prior resident in this case. If the dominance relations established in step 1.0, were maintained here, this would mean that the wasps were able to memorize some individual characteristic of previously encountered conspecifics. The difference between the subsequent steps 1.2 and 1.3 concerned the neutral nests where this encounter took place. During step 1.2, the wasps met every day at a different nest from that where they met on the previous day. The only stable component in this situation was therefore the identity of the wasp with which each wasp was confronted. In practice, the neutral nests (denotes A, B, C and D in fig. 1) in each set of three colonies were those from one of the other two sets. For example, the virtual hierarchy established between the foundresses from set 1 was tested on nests from sets 2 and 3. All the nests in any set had a similar brood composition. The original foundresses of the nests from sets 2 and 3 were removed from their colonies just for the experiments and then reinforced after each experiment. The same procedure was carried out to test virtual circularity between the wasps in set 2 (on nests from sets 1 and 3) and between the wasps from set 3 (on nests from sets 1 and 2).

Each alpha wasp therefore spent 22 hours per day as the alpha at its usual nest, one hour per day at a previously unknown nest (possibly as a Dominant visitor: Dv) together with the wasp that it had formerly encountered (on its own usual nest) as a Subordinate visitor (Sv), and one hour per day at another previously unknown nest together with the formerly Dominant resident (Dr) of the colony into which it had been introduced at step 1.1. During step 1.3, with each experimental step, the encounters between wasps transferred from their usual colonies took place consistently at the same nest, which was scheduled to become their common abode at stage 2. At this nest, each wasp therefore spent one hour a day with a female it had previously dominated, and one hour with a female to which it had previously submitted. The remaining 22 hours per day were spent at its usual nest in the company of its subordinate resident.

Lastly, during stage 2, all three Alpha wasps in each experimental set were brought together at the same time, at the nest previously frequented during step 1.3. Stage 2, which was intended to improve the actual circularity among the wasps, consisted however of the two following steps.

—step 2.1, which can be called the alternation step, during which the three wasps spent only 2 hours a day together and the rest of the time back at their usual nests;

—step 2.2 which can be called the permanence step, during which the wasps remained together all the time and were therefore no longer exposed to any of the influences exerted upon them at their previous usual nests.

The full procedure involved 54 days of observation, i.e. 170 hours in all, in addition to the brief checks which were caried out on the social situation. The observation data on the wasps' dominance patterns and the use they made of the available space were recorded on a microcomputer.

The wasps were rated on the following behavioural items: resting on the back of the nest (RSB) – any period during which a wasp remained motionless on the back of the comb; checking cells (CHK) all cell inspections for whatever reason, whether the cell was empty or contained an egg or a larva; total time at the nest (TTN), which was the total time spent at the nest during the whole observation period, whatever the type of behaviour involved. Lastly, to give an idea of each wasp's activity, the ratio between the total time spent by each wasp on each of these two behavioural items and the total time spent at the nest by that individual was calculated (CHK/TTN and RSB/TTN).

Results

The most noteworthy general finding made in this study was that it turned out to be possible to set up virtually circular dominance relations between three gynes and then to transform these relations into actually circular ones without giving rise to any unusually strong social tensions. Although great care was taken in applying the procedure, circular dominance was not, however, consistently generated under the conditions described above. Since the preparatory step involved a simple procedure intended just to set up virtually circular triads, we did not take particular care to balance the samples; any wasps which did not react as expected were reutilized in other combinations until the required result was obtained. Fourteen different resident wasps (and twelve introduced wasps) were necessary to obtain the intended population of nine digynous nests.

The results of the experimental confrontations show that prior residence was a factor which significantly favoured an individual's likelihood of becoming the dominant individual (Fisher, $p < 0.01$). In numerous cases, however, the introduced wasps were nevertheless capable of dominating and the resident wasps became subordinate. This finding indicates that there were decisive differences among the individuals: setting up circular triads involved making a selection, presumably resulting in only individuals with similar characteristics being selected. The data recorded in step 1.1 show that a stable situation had been created; the nine wasps alternately adopted the role of Dr and Sv, thus showing an ability to adapt to quite different social situations. They did not overreact to the changes by abandoning a nest when they were Sv, or by showing excessively agressive behaviour when they were Dr.

The wasps' behaviour varied, however, from one situation to another. When they acceded to the rank of Dr, both the total time they spent at the nest (TTN: Wilcoxon, $p < 0.03$) and the proportion of this time they spent inspecting cells (CHK/TTN: Wilcoxon, $p = 0.03$) increased, whereas wasps which became Sv spent more time idling on the nest (RSB/TTN: Wilcoxon, $p = 0.03$). It is worth recalling here that the two situations Dr and Sv did not differ only as regards the wasps' social ranks, but also in that a wasp which became Dr in these experiments was always at its own usual nest.

Steps 1.2 and 2.3 differed fundamentally from phase 1 since the possibility facilitatory effects of presence at the usual nest were abolished in the case of the previous Dr. Here the encounter between two wasps took place on ground which was unknown to both wasps. The only possible means whereby they could reconstitute their previously established hierarchical ranks was therefore by memorizing each other's individual identities.

It was in fact at this stage that the only case of rank inversion occurred during all these experiments: in one of the nine encounters which took place during step 1.2, the ranks of the protagonists were reversed as soon as they met at the unknown nest, and the newly established relations were durably maintained throughout the experiment. In the eight other cases, the dominance relations were the same as those previously established: this overall stability (Fisher, $p < 0.01$) shows that a stable hierarchy can be maintained purely on the basis of the mnesic trace of the identity of another wasp. The persistence of circular dominance relations means of course that no gradable underlying characteristic or 'label' can have been responsible for these relationships. With the data collected in step 1.2 on the six diads involved, it was possible to discriminate between the effects of social rank (i.e. whether a wasp was Dr or Sv) and those depending on whether a dominant wasp was at its usual nest. Although both wasps were placed at this phase on an unknown nest, the dominant visitor spent more time on CHK (Mann and Whitney, $p = 0.04$) and the subordinate visitor more time on RSB (Mann and Whitney, $p = 0.04$). The effect of a dominant wasp's being at its usual territory was determined by comparing its behaviour at step 1.1 (when it was on its usual nest) with that observed during step 1.2. Here the behavioural scores recorded on TTN (Wilcoxon, $p = 0.03$) and CHK (Wilcoxon, $p = 0.02$) and the CHK/TTN ratio (Wilcoxon, $p = 0.03$) were both found to be higher in step 1.1 which indicates that the dominant wasp tended to have a higher level of activity at a nest which was its own usual nest.

The only differences between 1.2 and 1.3 was the wasps' degree of habituation to the nest where the encounter occurred: since they showed no detectable reactions upon being shifted from one situation to the other, this difference does not seem to have been significant. The dominance scenes gradually decreased in frequency, moreover, as occurs classically in colonies where the members have been cohabiting for some length of time. The wasps' behaviour at the nest was generally very similar during both of these two experimental phases.

Among the six remaining pairs of gynes, shifting to stage 2 of the experiment resulted in no changes in the social relations. In the two groups in which no reversal of the dominance relations occurred at the shift from step 1.1 to 1.2, circular dominance relationships were actually established at the nest among the three wasps which were previously Dr during step 1.1. Permanent cohabitation was maintained for two weeks without any subsequent changes being observed. The three wasps continued to live together peacefully, and very few dominance scenes took place: the outcome of those which did occur continued to confirm the circularity of the dominance scheme.

Discussion

The existence of stable circular dominance relations in trigynous groups of wasps cannot be explained in terms of a Labelling model of the Force type, which we have adopted elsewhere[16]. When the wasps were in a situation involving permanent cohabitation, the lack of both *ex aequo* and transitive relations rules out the possibility that their hierarchical ranking may have been caused, in this case, by a hidden gradable variable. If the circularity had remained only virtual (stage 1), models of this kind might have been applicable, assuming in addition that the decisive variable may fluctuate depending on the environment; but the existence of a circular dominance scheme among permanent cohabitants renders this explanation null and void. It is nevertheless true that since it was necessary to make a selection when setting up the virtually circular triads, the existence of circular triads might be possible only among females endowed at the outset with roughly the same degree of 'force'.

The overall stability of the hierarchical relationships despite the change of nest (particularly from steps 1.1 to 1.2) shows the efficiency, at least in the short term, of the mnesic trace which must have been used by the wasps to identify partners with which dominance relations had been previously established. Evidence supporting the idea that wasps may make use of traces of this kind has been put forward by other authors[14,15], but the latter have generally admitted that their results do not completely exclude the existence of basic differences between individuals, and they thus fit the framework of the Correlational Model. The circularity of the hierarchies set up here means that this possibility can definitely be ruled out in the present study.

It is actually quite possible to account for the multiple factors liable to contribute to setting up hierarchical relationships by means of a 'state model' involving, for instance, the notion of 'force': all these factors might affect the 'force' of an individual, and the fact that we had some difficulty in setting up virtually circular relations may have been due to differences in the wasps' 'force' levels, possibly reflecting constitutional factors and/or factors having to do with the various individuals' recent history: their hormonal levels, for example, or their past social or territorial experience. On the other hand, once a hierarchy has been established, neither the wasps' force levels nor the frequency of the dominance scenes can be directly responsible for its stability. At this stage, dominance scenes between two hierarchically classified individuals might simply reflect their respective ranks. The gradual reduction in the frequency of these scenes, observed once the social situation has stabilized, is probably due to the fact that each individual has become habituated to the presence of the other one. The existence of a stable hierarchy therefore means that the social situation as a whole has stabilized, and only a change in this situation is liable to increase the social tension sufficiently to trigger a reversal of the individuals' hierarchical ranks.

The above considerations explain why we had to design such a complex procedure to obtain a circular hierarchy. With this procedure, we attempted (successfully) to limit the effects of the other factors liable to influence the setting up of the wasps' hierarchical ranks, and thus to prepare the way for the particular factor we intended to utilize to establish circular social relations within a group of wasps. The selection of individuals (preparatory step) and the precautions taken to ensure that the shifts from one situation to another were very gradual enhanced the efficacity of the mnesic traces of other individuals' characteristics, the effects of which might have been masked if the social changes had been too sudden or if the initial differences between the individuals had been too pronounced.

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