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A Linear Dominance Hierarchy Regulating Reproduction and Polyethism of the Queenless Ant *Pachycondyla sublaevis*

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In the vast majority of ants, females are divided into two morphologically distinct castes: queens which principally perform reproduction and workers which are engaged in other tasks. However, some species of the primitive subfamily Ponerinae have no morphologically distinct queens. In the queenless colonies of such species as *Rhytidoponera metallica* [1], *Rhytidoponera* sp. 12 [2], and *Ophthalmopone berthoudi* [3], reproduction is performed by several workers that have fortuitously succeeded in mating. In the queenless species *Diacamma australe* [4] and *D. rugosum* [5], however, colonies have only one mated egg-layer, called a gamergate. Their reproductive dominance is controlled by a unique mechanism, in which retention of a pair of thoracic appendages determines mating and reproduction. A single gamergate with vestigial wings controls reproduction by inhibiting the mating and oviposition of other nestmates whose vestigial wings have been removed by the gamergate soon after their emergence. The colonies of *Pachycondyla krugeri* also have only one gamergate [6]; however, the mechanism controlling the reproductive dominance is as yet unknown. In the queenless ant *Pachycondyla (= Bothroponera) sublaevis* we discovered an almost linear dominance hierarchy in which (1) the dominance display was well ritualized with no occurrence of fighting, (2) only a top-ranked worker was inseminated and laid eggs, (3) all colony members other than bottom-ranked workers could develop their ovaries when higher-ranked workers were removed, and (4) higher-ranked workers conducted the care of eggs and larvae and lower-ranked workers were engaged in foraging. In ants, this is the first discovery of dominance hierarchy in which most members of a colony are potential successors of the reproductive female.

P. sublaevis belongs to the *rufipes* group, and occurs in the dry *Eucalyptus* woodland of nothern Australia. Its colonies are possibly among the smallest of all ants, comprising an average of 9 (± 2.5 s.d.) workers. In most colonies, only one of these is inseminated and bears a reproductive ovary [7]. The behavior of workers was observed in the laboratory in colonies collected at Mt. Garnet, North Queensland, Australia, in October to December of 1987 and 1989. In colony A, comprising 11 workers, antagonistic interactions between individuals were observed 85 times during a total of 42 h of observation (Table 1). In the typical sequence, the dominant worker rapidly lunged her vibrating antennae and aggressively pummeled the head of a subordinate (Fig. 1). She repeated this behavior one to eight times in each display. The subordinate crouched with her antennae drawn backward until the dominant ceased her coercive behavior. This dominance display was well ritualized with no occurrence of fighting. Between a given pair of workers, the dominance was unilateral except between No. 10 and No. 30 in which the former was dominant three times and subordinate two times. Although it was difficult to determine the order among low-ranked workers, who were usually ignored by other nestmates, the dominance hierarchy appeared almost linear with few tripartite deadlocks. The position in the hierarchy was apt to determine the function of the worker concerned. Only the top worker possessed a sperm-filled spermatheca and a well-developed ovary and actually laid eggs. This gamergate and other high-ranked workers preferred care of eggs and larvae to foraging, which was mostly performed by low-ranked workers (Fig. 2). Cocoons were most frequently tended by middle-ranked workers.

Fig. 1. A ritualized display between a dominant (right) and a subordinate (left)

Table 1. Dominance hierarchy in colony A. Each number shows the frequency of display during a total of 42 h

Dominant No.	Subordinate No. 40	20	10	50	33	30	4	2	3	1	22	Total
40	+	26	–	–	–	23	–	1	1	–	–	51
20		+	2	2	–	12	–	–	2	–	–	18
10			+	2	–	3	–	–	1	–	–	6
50				+	1	1	–	–	2	–	–	4
33					+	1	–	2	–	–	–	3
30			2			+	–	–	–	1	–	3
4							+	–	–	–	–	0
2								+	–	–	–	0
3									+	–	–	0
1										+	–	0
22											+	0
Total		26	4	4	1	40	0	3	6	1	0	85

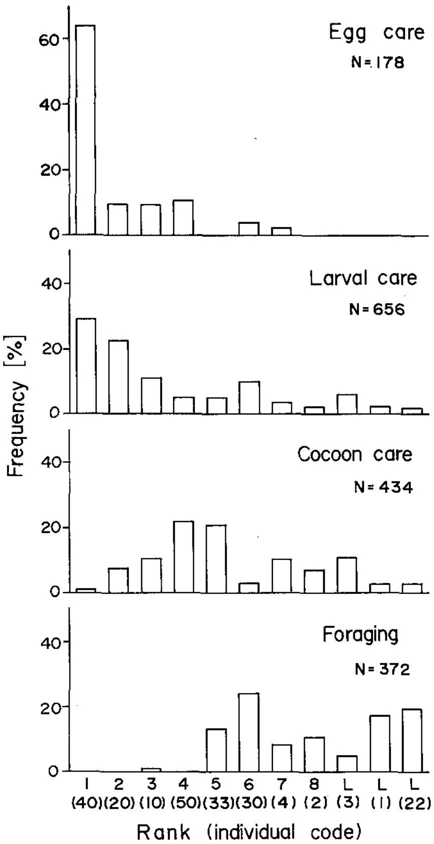

Fig. 2. Polyethism with reference to dominance hierarchy in colony A observed for 42 h. For ranking the low-ranked workers, the data shown in Table 2 were adopted, too; *L* impossible to determine exact rank but doubtlessly low-ranked

Table 2. Dominance hierarchy in colony A during a total of 28 h after the removal of gamergate (No. 40). Nos. 30 and 22 shown in Table 1 died before the removal experiment

Dominant No.	Subordinate No. 20	10	50	33	4	2	3	1	Total
20	+	34	17	18	4	2	20	2	97
10		+	2	4	–	–	1	–	7
50			+	4	–	2	3	1	10
33				+	–	1	1	–	2
4					+	1	–	–	1
2						+	1	–	1
3							+	–	0
1								+	0
Total		34	19	26	4	6	26	3	118

In colony A, the gamergate was removed and the behavior of the remaining workers was observed for 28 h. They were activated and the mean frequency of dominance display per hour increased from 2.0 (± 2.1 s.d.) times in preremoval to 4.2 (± 3.4) times in post removal, the difference being significant statistically ($p < 0.005$ in *t*-test). Especially during the first hour after removal, dominance display occurred as frequently as 18 times; thereafter, the dominance hierarchy was reestablished with few changes in order with the worker previously ranked second becoming the new top-ranked worker (Table 2).

In colony B, consisting of six workers, the gamergate was imprisoned in a small vial, the opening of which was covered with steel mesh to isolate her from other workers without interrupting air flow. In this experiment, the frequency of the dominance display significantly increased from 5 times per hour in preisolation (5 h of observation) to 42 times per hour in postisolation (2 h of observation). This suggests that the supremacy of the gamergate is maintained mostly by the frequent physical contact rather than exclusively by pheromonal or visual signals.

In colony C, composed of seven workers, the top worker was removed and dissected every seventh day. The first six top workers removed bore developed oocytes in their ovarioles, indicating that most workers of a colony are potential egg-layers when the dominant workers are removed. However, the bottom-ranked worker did not develop any oocytes after she became solitary in the nest. To determine whether this was due to the bottom-ranking or due to the solitude, all members of colony D comprising six workers were isolated from each other for 7 days. Dissection of these workers demonstrated that the top four workers developed oocytes but the last two workers did not, suggesting that a few of the low-ranked workers cannot become gamergates even if they are released from the control by dominant nestmates.

One male emerged in colony E. He was indifferent to his nestmates; however, when introduced into another colony, he was remarkably excited and frequently tried to copulate with the top-ranked worker only. He was not interested in other workers. This indicates that the top workers can exclusively produce some sexual attractants.

Peeters et al. [7] discoverd two *P. sublaevis* colonies, in which a single worker bore developed ovaries but was still virgin. These colonies seemed very young because the nest was simple with a shallow shaft and a single chamber and the colony was composed of only seven or eight workers with no immatures. This suggests that new colonies are founded by budding where several non-top workers leave a mother colony and a newly top-ranked worker develops her ovary prior to mating with males from other colonies.

Since first discovered in the wasp *Polistes gallicus* [8], the dominance hierarchies have been considered as one of the most important mechanisms organizing the societies of some social wasps and bees [9]. In ants, the antagonistic behavior for reproductive supremacy has been observed among queens of such polygynous species as *Iridomyrmex purpureus* [10], *Camponotus ferrugineus* [11], and *Leptothorax* sp. [12], and among workers competing to lay male eggs in the colony of *L. allardycei* [13], *Protomognathus americanus* [14], *Harpagoxenus sublaevis* [15], and *Pachycondyla apicalis* [16]. In these ant species, however, the reproduction is principally monopolized by a morphologically differentiated queen caste and, as in many species of ants, the division of labor is probably based on size and/or age-polyethism. Therefore, the antagonistic behavior has not been regarded as one of the major mechanisms organizing ant societies. In this respect, *P. sublaevis* is unique among ants, since most members of a colony are potential gamergates if released from the inhibition by the present gamergate, and the linear dominance hierarchy strictly regulates not only the reproduction but also the polyethism.

The social organization of *P. sublaevis* is also unique when compared with other queenless species of ant. Unlike polygamergate species in which the development of ovaries is triggered by fortuitous success in mating [1 – 3], the top-ranked *P. sublaevis* worker can develop her ovary prior to the mating. The social organization of *P. sublaevis* is superficially similar to that of *Diacamma australe* [4] and *D. rugosum* [5], in which only one gamergate monopolizes the reproduction and behaviorally inhibits the emergence of another gamergate by mutilating nestmates. However, the determination of a gamergate in *Diacamma* is as fortuitous as in polygamergate species. In this case, a worker can become a gamergate without its vestigial wings being removed only if she happens to be the first new worker eclosed after the previous gamergate has disappeared either due to her natural death or to colonial budding. In contrast, the reproductive worker of *P. sublaevis* is produced by a ritualized display of all members of a colony. Even after the gamergate has been determined, other workers can still have an opportunity to become the gamergate.

The development of a linear dominance hierarchy, in which all members of a colony recognize each other's status, seems greatly dependent on the colony size. This system cannot operate in colonies comprising too many workers to recognize each other. The colony size of *P. sublaevis* is probably the smallest of all ant species hitherto discovered; and the small size of their colonies may have enabled them to recognize all nestmates so that a linear dominance hierarchy could develop.

Unlike wasps and bees, presocial stages have been already lost in ants and it is still unknown how they could have developed eusociality at the beginning of their evolution. However, it is reasonable to assume that the ancestral ants formed very small colonies in which the morphological differentiation between queens and workers was negligible. In this context, further research on the social organization of the relatively primitive ant *P. sublaevis* may provide important information on the evolution of eusociality in ants.

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Extraocular Photoreceptors in the Last Abdominal Ganglion of a Swallowtail Butterfly, *Papilio xuthus*

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A papilionid butterfly (*Papilio xuthus*), both male and female, has two pairs of photoreceptive sites on the genitalia. Each site contains a single photoreceptive neuron (genital photoreceptor, GP). The GP has a soma just beneath the body surface and sends one axon to the last abdominal ganglion (LAG). In the LAG, the GPs and certain abdominal motoneurons are functionally connected to each other, i.e., the light stimulation of the GPs excites or inhibits the activity of the motoneurons [7, 8]. In the course of further study on the input-output relations between the GPs and LAG motoneurons, we found another type of EOP within the LAG. Thus, the butterfly now appears to have two categories of EOP; the peripheral EOP on the genitalia, and the CNS-EOP in the LAG.

Extraocular photoreceptors (EOP) have been found in various phyla of animals (for reviews [1, 2]). The EOP systems are divided into two categories. One is found within the central nervous system (CNS-EOP). The crayfish caudal photoreceptor, a photoreceptive interneuron, is one of the most extensively studied cases of the CNS-EOP [3]. Another category of EOP is found outside the CNS as sensory neurons with the somata located in the periphery of the animals. The existence of the peripheral EOP in arthropods was indicated in certain scorpions [4, 5], but was first conclusively documented as the butterfly genital photoreceptors by Arikawa et al [6].