

it is reasonable to conclude that highly fertile *Diacamma* workers or gamergates have distinct CHC profiles, and these are physiologically coupled with the endocrine processes that regulate fertility.

STREBLOGNATHUS: DOMINANCE AND FERTILITY UNCOUPLED

Studies of the African ponerine *Streblognathus peetersi* by Virginie Cuvillier-Hot and her coworkers have documented the physiological mechanisms of dominance and fertility in queenless ponerine ants in even greater depth.^{64, 65} The same negative correlation exists in this species between degree of fertility and juvenile hormone titer as in *Diacamma*, but dominance and fertility are uncoupled. When the dominant ant is treated with Pyriproxyfen, a juvenile hormone analog, the fertility of the alpha individual is markedly decreased. Although such treated alpha ants remain aggressive, they are attacked and immobilized by low-ranking workers. Interestingly, the treated individual is not challenged by the next highest ranking ants in the dominance hierarchy, but policed by low-ranking subordinates. While the alpha individual is immobilized, one of the high-ranking workers begins to exhibit dominance behavior—and it subsequently assumes the alpha position. During this process, the CHC profile of the treated ant undergoes modifications that are opposite to those of the high-ranking challenger ant. Such CHC profiles most likely signal fertility status, and although the treated alpha still exhibits the full repertoire of aggressive dominance, the police workers perceive the decline in fertility and react by immobilizing the alpha. These findings have impressively demonstrated the crucial role of sterile helpers in regulating reproduction. They underscore yet again the distinction between dominance interactions and policing as discrete agonistic behavioral mechanisms.^{66, 67}

64 | V. Cuvillier-Hot, A. Lenoir, and C. Peeters, "Reproductive monopoly enforced by sterile police workers in a queenless ant," *Behavioral Ecology* 15(6): 970–975 (2004).

65 | V. Cuvillier-Hot, A. Lenoir, R. Crewe, C. Malosse, and C. Peeters, "Fertility signalling and reproductive skew in queenless ants," *Animal Behaviour* 68(5): 1209–1219 (2004).

66 | V. Cuvillier-Hot, A. Lenoir, and C. Peeters, "Reproductive monopoly enforced by sterile police workers in a queenless ant," *Behavioral Ecology* 15(6): 970–975 (2004).

67 | C. Brent, C. Peeters, V. Dietemann, R. Crewe, and E. Vargo, "Hormonal correlates of reproductive status in the queenless ponerine ant, *Streblognathus peetersi*," *Journal of Comparative Physiology A* 192(3): 315–320 (2006).

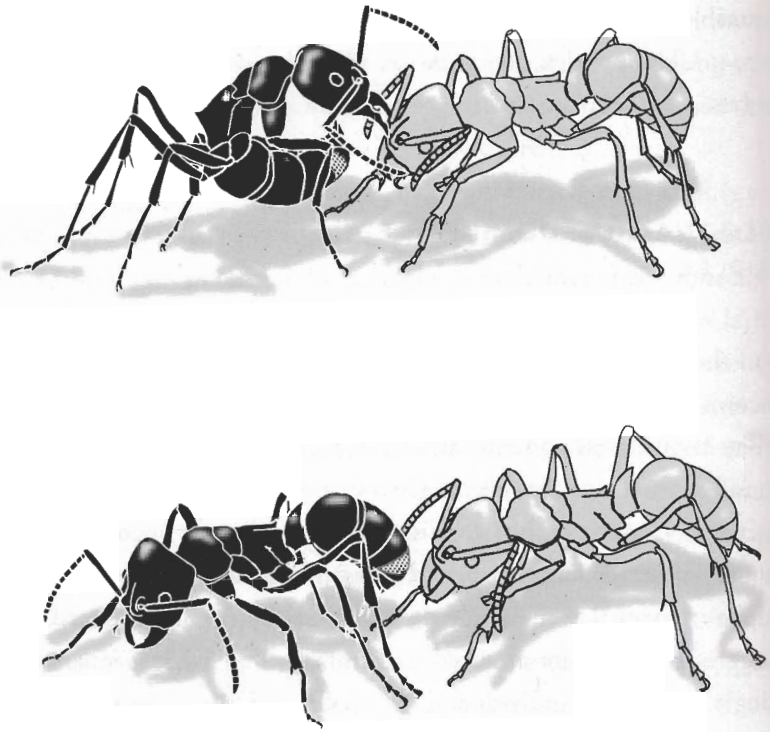


FIGURE 8-14. Dominance behavior in *Streblognathus peetersi*. Two agonistic acts are especially conspicuous. *Above:* In gaster curling, the dominant (black) worker bends her gaster forward and exposes the intersegmental membrane close to the gastral tip. During this confrontation, the dominant individual grabs the mandible at the base of the subordinate's (gray) antennae. *Below:* In the gaster rise posture, the dominant arches her gaster, again exposing the intersegmental membrane, and turns around and places her gaster in front of the subordinate. Based on V. Cuvillier-Hot, A. Lenoir, and C. Peeters, "Reproductive monopoly enforced by sterile police workers in a queenless ant," *Behavioral Ecology* 15(6): 970–975 (2004).

Each colony of *Streblognathus peetersi* comprises 30 to 130 workers, with only one individual occupying the alpha position in the hierarchy. This individual has mated and assumed the gamergate role. The dominance hierarchy is formed, as in other ponerine ants described earlier, by aggression. Among the several agonistic acts, two are especially conspicuous. In *gaster curling*, the dominant worker bends her gaster forward and exposes the intersegmental membrane close to the gastral tip. This has the look of uncapping an intersegmental gland of some kind, perhaps the pygidial gland itself, but no evidence has yet been found that true glandular secretions are involved. More likely, the dominant ant exposes intersegmental tissue loaded with a special blend of hydrocarbons. During the *confrontation*, the dominant ant grabs the mandibles or the base of the subordinate's antennae (Figure 8-14). In the *gaster*

rise movement, the dominant arches her gaster, again with the intersegmental membranes at the distal region of the gaster exposed. She then turns around and places her gaster in front of the subordinate individual (see Figure 8-14).

For weeks after the alpha ant has established herself in the top position, she remains aggressive, but on a relatively low level—just enough, it appears, to confirm her top rank. In fact, *Streblognathus* colonies, like colonies of *Harpegnathos* and some other queenless ponerine ant species with dominance systems, go through phases of social stability and instability. During periods of calm, few acts of aggression occur and the alpha ant exhibits high fertility. During periods of instability, which occur soon after a dominance turnover has taken place, the new alpha individual has only slightly developed ovaries and uses aggression to enforce her position. A similar cycle has been observed in colonies of *Dinoponera quadricaps*.

To summarize to this point, aggression is the mechanism by which dominance hierarchies are established in the ponerine ants thus far studied, but the maintenance of reproductive monopoly is due to fertility signaling. Gamergate replacement is a very significant event in the life cycle of colonies, making colonies of queenless ants potentially immortal. It is also an important event in the life history of individual members of the colony, since nestmates compete from time to time to seize the reproductive role. The winners advertise their status. The alpha ant and her high-ranking nestmates in *Streblognathus peetersi* colonies are distinguished by their CHC profiles, “which encode sufficient and graded information to label not only egg layers but also workers with intermediate reproductive potential. . . . Moreover, a new alpha of *Streblognathus peetersi* can be detected by nestmates several days before the onset of her oviposition, which suggests that the CHC-profile reflects the hormonal state of a worker more than its current egg-laying rate.”⁶⁸ Presumably, the ants use variation in CHC profiles to signal or detect reproductive capacity. Once the alpha individual is reproductively active, her chemical signals appear to replace most aggressive interactions as the mechanism for regulating reproduction in the *Streblognathus* colony.

Strong supporting evidence for the hypothesis that CHC profiles function as “honest” signals of social status and fertility has been provided by the measurement

68 | V. Cuvillier-Hot, A. Lenoir, R. Crewe, C. Malosse, and C. Peeters, “Fertility signalling and reproductive skew in queenless ants,” *Animal Behaviour* 68(5): 1209–1219 (2004). Virginie Cuvillier-Hot and Alain Lenoir investigated the neurochemical basis of the behavioral plasticity observed in the queenless *Streblognathus* colonies in V. Cuvillier-Hot and A. Lenoir, “Biogenic amine levels, reproduction and social dominance in the queenless ant *Streblognathus peetersi*,” *Naturwissenschaften* 93(3): 149–153 (2006).

of vitellogenin (Vg) levels in the blood (hemolymph) of different kinds of ants.⁶⁹ Vitellogenin is a yolk precursor that is synthesized in the fat body, secreted into the hemolymph, and incorporated in the oocytes to form vitellins, the major storage proteins in eggs. The relative amount of vitellogenin in the hemolymph is an excellent indicator of the readiness for egg production, regardless of whether the ant is currently in her oviposition phase.⁷⁰ Correlative analysis has demonstrated that the CHC profiles match both the social status and the levels of circulating vitellogenin in the *Streblognathus* workers. Workers with no more than trace levels of vitellogenin, or with none at all, exhibit the cuticular hydrocarbon blends identified in infertile foragers or freshly eclosed callows. Workers with higher vitellogenin level express CHC profiles close to those of egg layers or alpha individuals. Most importantly, “the more vitellogenin a worker had in her hemolymph, the further along the axis of fertility her cuticular profile occurred. The cuticular hydrocarbon signature thus provides reliable information not only about current fertility, but also about the reproductive potential of high rankers.”⁷¹

GAMERGATES VERSUS ERGATOID QUEENS

The term *gamergate* (married worker) is applied to workers who mate and produce fertilized eggs.⁷² William Morton Wheeler and his associate James Chapman were the first, in the early 1920s, to describe worker mating in *Diacamma rugosum*;⁷³ morphologically distinct queens had never before that time or since been found in this genus. Wheeler and Chapman correctly pointed out that reproductive workers are morphologically identical to nonreproductive workers and are different from ergatoid queens, a permanently wingless queen caste found in other kinds of ants. Nevertheless, as Christian Peeters has stressed, “the use of the term ‘ergatoid’ has

69 | V. Cuvillier-Hot, A. Lenoir, R. Crewe, C. Malosse, and C. Peeters, “Fertility signalling and reproductive skew in queenless ants,” *Animal Behaviour* 68(5): 1209–1219 (2004).

70 | T. Martinez and D. E. Wheeler, “Effect of the queen, brood and worker caste on haemolymph vitellogenin titre in *Camponotus festinates* workers,” *Journal of Insect Physiology* 37(5): 347–352 (1991).

71 | V. Cuvillier-Hot, A. Lenoir, R. Crewe, C. Malosse, and C. Peeters, “Fertility signalling and reproductive skew in queenless ants,” *Animal Behaviour* 68(5): 1209–1219 (2004).

72 | C. Peeters and R. Crewe, “Insemination controls the reproductive division of labour in a ponerine ant,” *Naturwissenschaften* 71(1): 50–51 (1984).

73 | W. M. Wheeler and J. Chapman, “The mating of *Diacamma*,” *Psyche* (Cambridge, MA) 29: 203–211 (1922).