

Fig. 4. Mean (+SEM) captures of *C. sordidus*, in pitfall traps [4] December 4–10, 1995. Traps were placed 20–30 m apart, contained detergent-laced water as killing agent, and were baited with 250–300 g of fresh-cut pseudostem, pheromone (1a–1d) lures, or both. Means followed by a different letter are significantly different ($P < 0.05$), Tukey-Kramer HSD ($F = 11.69$, $df = 2, 29$, $n = 32$, $P < 0.0002$; ANOVA of ranked data)

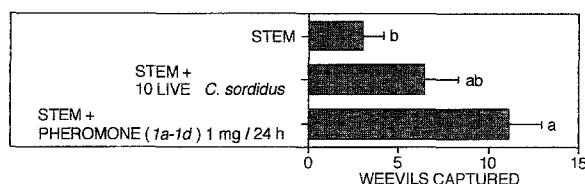


Fig. 5. Mean (+SEM) captures of *C. sordidus*, in pitfall traps [4], December 10–17, 1995. Traps were placed 20–30 m apart and baited with 250–300 g of fresh-cut pseudostem alone, or combined with ten live *C. sordidus* (mixed sex) or pheromone (1a–1d) lures. ANOVA on $\log(X+0.5)$ -transformed data gave $F = 8.60$, $df = 2, 29$; $p < 0.001$, $n = 10$. Means are presented untransformed. Means followed by a different letter are significantly different by Bonferroni test ($P < 0.05$). More than 90% of insect initially placed in traps were alive at the end of the experiment

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1. Ostmark, H.E.: Annu. Rev. Entomol. 19, 161 (1974)
2. Budenberg, W.J., et al.: J. Chem. Ecol. 19, 1905 (1993)
3. Beauhaire, J., et al.: Tetrahedron Lett. 36, 1043 (1995)
4. Weissling, T.J., et al.: J. Chem. Ecol. 19, 1195 (1993)
5. Corey, E.J., et al.: J. Am. Chem. Soc. 94, 6190 (1972)
6. Perez, A.L., et al.: J. Chem. Ecol. (submitted)
7. Oehlschlager, A.C., et al.: Naturwissenschaften 79, 134 (1992)

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On the Relationship Between Gamergate Number and Reproductive Output in the Queenless Ponerine Ant *Pachycondyla* (= *Ophthalmopone*) *berthoudi*

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In several species of ponerine ants, mated egg-laying workers (gamergates) have replaced queens as the functional reproductives, with either monogyny (single gamergate) or polygyny (multiple gamergates) having been described (see [1] for review). The role of physical aggression in regulating reproductive activity has been demonstrated in some of these ants. Dominance orders based on an array of aggressive interactions, such as biting or ritualized antennation, have been described in monogynous species (e.g., *Diacamma* [2] and *Pachycondyla* (= *Bothroponera*) sp.

[3]), and polygynous species (e.g., *Amblyopone* sp. (*reclinata* group) [4] and *Pachycondyla tridentata* [5]). In contrast, no obvious antagonistic interactions take place between gamergates and virgin workers in *Pachycondyla* (= *Ophthalmopone*) *berthoudi*, and oophagy has never been observed ([6], in prep.). Proportion of gamergates varies between nests, and there is no association between this proportion and nest size. Workers of *P. berthoudi* show a correlation between insemination and ovarian activity, and it was postulated that insemination triggers reproductive

differentiation [6, 7]. Subsequent experimental manipulations have shown that virgin workers of *P. berthoudi* are capable of laying eggs [8], but these eggs never hatch (in prep.). Despite the absence of aggressive interactions between gamergates, we demonstrate that their ovarian activity is related to gamergate number: individuals are more fecund in nests with low gamergate numbers. Since aggression between workers is absent, we suggest that this regulation is based on pheromones.

Twelve nests of *P. berthoudi* were collected over a 2-year period from Hoedspruit (30° 50' E, 25° 25' S) in South Africa. Ovaries and spermathecae of all gamergates and some virgin workers were dissected to determine reproductive status. Ovarian activity was assessed by recording the following features (except in nests 1 and 2): length of ovarioles, number of mature oocytes, number of yolk-containing immature oocytes, and presence and color of yellow bodies (corpora lutea) at the base of individual ovarioles. Intensity of yellow bodies can be used to infer the past occurrence of regular egg-laying, although this method is not quantitative. The longest ovariole in each individual

was measured, as there was little difference in the lengths of all six ovarioles. The composition of the nests at time of collection and the dissection results are presented in Table 1. A total of 619 workers were dissected. Gamergate number per nest ranged from 1 to 36. All inseminated workers were found to have developed ovaries. Gamergates in nests with one to six gamergates had dark, well-defined yellow bodies, while those gamergates in nests with higher numbers (13 to 36) generally had less well-defined yellow bodies, or none at all (indicating lower levels of egg-laying). The ovarioles of gamergates were significantly longer than those of virgin workers, both within nests (Nest K two sample t-test, $t_{47} = 8.347$, $p < 0.001$; for other nests Mann-Whitney U-tests, $p < 0.02$) and when nest data were pooled (Mann-Whitney U-test = 39378.5, $p < 0.001$). Ovariole lengths of virgin workers were not significantly different between nests (Kruskal-Wallis statistic = 1.081, $p = 0.999$). Within nests, the distribution of gamergate ovariole lengths was not significantly different from normal (Lilliefors test for normality, all nests $p > 0.05$), suggesting that there is no skew in fecundity. Mean ovariole length was correlated with both mean mature oocyte number ($r = 0.902$, $p = 0.014$) and mean immature oocyte number ($r = 0.944$, $p = 0.005$). This suggests that ovariole length is a good measure of ovarian activity. This is important because assessing fecundity on the basis of number of mature oocytes found is biased if dissections of ovaries are conducted immediately after an oviposition event (especially in species with a maximum of three mature oocytes per ant). Regression analysis revealed a significant relationship between ovariole length and gamergate number (Fig. 1). Significant relationships were also found when mean number of mature oocytes ($y = 1.74 - 0.49 \log_e x$; $R^2 = 0.849$; $p = 0.009$) and mean number of immature oocytes ($y = 2.99 - 0.49 \log_e x$; $R^2 = 0.867$; $p = 0.007$) were regressed against gamergate number. As oophagy is absent in *P. berthoudi*, these measures are direct indications of reproductive output. There was no relationship between gamergate ovariole length and

Table 1. Demographic data and dissection results from 12 nests of *Pachycondyla* (= *Ophthalmopone*) *berthoudi*. Numbers in parentheses indicate percentage of gamergates

| Nest code | Date of collection | Number of workers | Brood | | | Gamergate number (%) |
|-----------|--------------------|-------------------|-------|--------|------|----------------------|
| | | | Pupae | Larvae | Eggs | |
| 1 | 12/10/93 | 41 | * | * | * | 1 (2.4) |
| 2 | 12/10/93 | 81 | * | * | * | 2 (2.4) |
| A | 19/03/94 | 35 | 0 | 0 | 6 | 6 (17) |
| B | 17/03/94 | 51 | 23 | 0 | 0 | 13 (25) |
| C | 23/11/94 | 127 | 69 | 32 | 18 | 2 (1.6) |
| D | 23/11/94 | 65 | 18 | 9 | 7 | 6 (9.2) |
| E | 24/11/94 | 79 | 21 | 16 | 9 | 6 (7.5) |
| G | 02/03/95 | 86 | 42 | 28 | 15 | 2 (2.3) |
| H | 03/03/95 | 112 | 71 | 22 | 7 | 2 (1.8) |
| K | 22/04/95 | 101 | 0 | 0 | 3 | 36 (35) |
| L | 22/04/95 | 135 | 107 | 52 | 29 | 23 (21) |
| M | 21/04/95 | 68 | 4 | 1 | 3 | 5 (7.4) |

* Brood present but not counted.

the ratio of gamergates/virgins in a nest ($r = 0.774$, $p = 0.071$). Nest size was not dependent on number of gamergates in a nest ($R^2 = 0.191$, $p = 0.718$). Our results demonstrate that the ovarian activity of individual gamergates is strongly influenced by gamergate number in nests of *P. berthoudi*. In some queenless polygynous species, aggression regulates reproductive activity among mated workers. Ritualized antennation among mated workers in *Pachycondyla* (= *Bothroponera*) sp. leads to functional monogyny [3], while in *Harpegnathos saltator*, dominance interactions among mated workers result in some of them being sterile [1]. In *Amblyopone* sp., stereotyped antennation among gamergates regulates their degree of ovarian activity [4]. Top-ranked gamergates have well-developed ovaries, while lower-ranked gamergates show reduced ovarian activity. In *Rhy-*

tidoponera confusa and *R. chalybeae*, ovarian activity of gamergates (measured by number of oocytes present in the ovarioles), is negatively correlated with gamergate number [9]. An inverse relationship between queen number and queen fecundity has been shown to occur in many social insects (reviewed in [10]), and this has been claimed to result from the production of inhibitory pheromones by queens ([11], although [12] failed to find this). Recently, it was proposed that these pheromones are honest signals, rather than having a direct physiological effect [13]. Circumstantial evidence for the use of pheromones in regulating ovarian activity has been reported in several ponerine ants. Physical interactions between workers have never been observed in *Pachycondyla krugeri* [14], *Platythyrea lamellosa* [15], and *Streblognathus aethiopicus* [16]. Similarly, in *Amblyopone* sp., gamergates never act aggressively towards virgin workers [4]. In *P. berthoudi*, manipulation experiments revealed that gamergates do not participate in dominance interactions with either gamergates or virgin workers ([6], in prep.). This suggests that the production of chemical cues by gamergates may be important in regulating oogenesis in virgin workers (in prep.). Thus, the decrease in gamergate ovarian activity described here may be another consequence of this regulation. In the absence of information about the effects of such signals, it cannot be established whether they are honest or inhibitory signals.

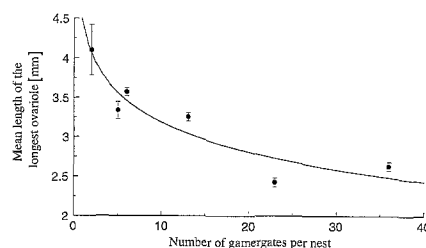


Fig. 1. Regression of the relationship between number of gamergates present in a nest and longest ovariole length. The curve is described by $y = 4.43 - 0.54 \log_e x$ ($R^2 = 0.882$; $p = 0.005$)

Gamergates in *P. berthoudi* do not forage [6], therefore nests with very high proportions of gamergates (more than 50% in some cases [6]) will have a diminished percentage of foragers, and less energy will be available per individual gamergate to be converted into egg production. Ito [4] found this to be important in *Amblyopone*. Our results suggest that this has little effect in *P. berthoudi*, as the relationship between gamergate ovariole length and the ratio of gamergates/virgins in a nest was not significant. Furthermore, a feature of the life history of this species may counter effects of extreme polygyny. *P. berthoudi* is polydomous with two to seven distinct nests (30 cm to 75 m apart) occurring in each colony [17]. Each nest in a colony can contain different numbers of gamergates (partly related to the success of nest location by males during the mating period). Polydomy is important because it allows for the internest transfer of brood and workers [17]. Virgin workers are carried from their "home nests" to a recruiter's nest after an extended period of vigorous antennation. Not all instances of recruitment are successful, and workers often refuse to be carried. Peeters [17] first noted that workers seem to behave selfishly by trying to enlarge the population of their own nest, apparently at the expense of other nests in the same colony. This apparent selfishness may be adaptive at the colony level when certain nests contain large proportions of gamergates, resulting in a reduced number of sterile workers (especially after the mating period). The recruitment of workers and/or brood then has the effect of increasing the la-

bor force and maintaining productivity in such nests. Number of gamergates is thus independent of nest size (as our results demonstrate), and measures of ovarian activity are real reflections of mutual regulation because the effects of decreased foraging levels are mitigated by polydomy. Furthermore, as the proportion of gamergates decreases in the nest during the rest of the year, their ovarian activity would increase and maintain rates of worker production. This is confirmed by the fecundity of gamergates in those nests with low gamergate number, collected before the mating period (April in this region; Table 1; e.g., Nest G and Nest H). Polydomous organization thus modulates the regulation of ovarian activity of gamergates. Gamergates are carried above ground only when new nests are established, while virgin workers and brood are transferred routinely between nests [17].

As there are no aggressive interactions among reproducing workers in *P. berthoudi*, the proximate mechanisms leading to and maintaining polygyny are not understood. All workers of a suitable age can mate [6], and thus no regulation occurs at this stage. This study illustrates that even in the absence of aggressive interactions, fecundity of individual gamergates is influenced by other gamergates. Pheromonal involvement in maintaining reproductive division of labor in ponerine ants must now be directly addressed.

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1. Peeters, C., in: Queen Number and Sociality in Insects, p. 234 (L. Keller, ed.). Oxford: Oxford Univ. Press 1993
2. Peeters, C., Higashi, S.: *Naturwissenschaften* 76, 177 (1989); Fukumoto, Y., Abe, T., Taki, A.: *Physiol. Ecol. Japan* 26, 55 (1989); Peeters, C., Billen, J., Hölldobler, B.: *ibid.* 79, 572 (1992)
3. Ito, F.: *Ethology* 95, 126 (1993)
4. Ito, F.: *J. Nat. Hist.* 27, 1315 (1993)
5. Sommer, K., Hölldobler, B.: *Naturwissenschaften* 79, 470 (1992)
6. Peeters, C., Crewe, R.M.: *Behav. Ecol. Sociobiol.* 18, 29 (1985)
7. Peeters, C., Crewe, R.M.: *Naturwissenschaften* 71, 50 (1984)
8. Villet, M.H.: *Ethol. Ecol. Evol.* 4, 389 (1992)
9. Ward, P.S.: *Behav. Ecol. Sociobiol.* 12, 285 (1983)
10. Keller, L., Vargo, E.L., in: Queen Number and Sociality in Insects, p. 16 (L. Keller, ed.). Oxford: Oxford Univ. Press 1993
11. Vargo, E.L., Fletcher, D.J.C.: *Physiol. Entomol.* 14, 223 (1989); Vargo, E.L.: *Behav. Ecol. Sociobiol.* 31, 205 (1992)
12. Bourke, A.F.G.: *Anim. Behav.* 45, 501 (1993); *Ethology* 101, 46 (1995)
13. Keller, L., Nonacs, P.: *Anim. Behav.* 45, 787 (1993)
14. Wildman, M.H., Crewe, R.M.: *Insect. Soc.* 35, 217 (1988)
15. Villet, M., Hart, A., Crewe, R.M.: *S. Afr. J. Zool.* 25, 250 (1990)
16. Ware, A.B., Compton, S.G., Robertson, H.G.: *Insect. Soc.* 37, 189 (1990)
17. Peeters, C.: PhD Thesis, Univ. of the Witwatersrand, Johannesburg 1985

Transection of Intraganglionic Connections Causes Synchrony of Hindleg Stridulation in the Gomphocerine Grasshopper *Stenobothrus lineatus*

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Bilaterally symmetrical animals need to integrate the functions on their two sides; for example, in all forms of loco-

motion the movements of the right and left limbs must be precisely coordinated with one another. As a rule, com-

plicated sensorimotor circuits have been evolved for this purpose [1], but examples of coordination mechanisms comprising largely central nervous elements have also been found [2]. Certain acridid grasshoppers provide a particularly useful example for further studies of this aspect: here, the motor patterns of hindleg stridulation are generated and coordinated exclusively by the central nervous system, with no requirement for acute sensory feedback [3]. Acridid species of the subfamily Gomphocerinae stridulate by moving the