biology letters

Biol. Lett.
doi:10.1098/rsbl.2009.0849
Published online

Animal behaviour

The police are not the army: context-dependent aggressiveness in a clonal ant

M. Benjamin Barth*,†, Katrin Kellner and Jürgen Heinze

Biologie I, Universität Regensburg, 93040 Regensburg, Germany
**Author for correspondence (benjamin.barth@zoologie.uni-halle.de).*
†Present address: Department of Biology, Martin-Luther-Universität Halle-Wittenberg, Hoher Weg 4, 06099 Halle (Saale), Germany.

Animals often exhibit particular 'personalities', i.e. their behaviour is correlated across different situations. Recent studies suggest that this limitation of behavioural plasticity may be adaptive, since continuous adjustment of one's behaviour may be time-consuming and costly. In social insects, particularly aggressive workers might efficiently take over fighting in the contexts of both nest defence and 'policing', i.e. the regulation of kin conflict in the society. Here, we examine whether workers who engage in aggressive policing in the ant *Platythyrea punctata* play a prominent role also in nest defence against intruders. The participation of individuals in policing and nest defence was highly skewed and a minority of workers exhibited most of the aggression. Workers who attacked reproductives after experimental colony fusion were less active during nest defence and vice versa. This suggests that workers show situation-dependent behavioural plasticity rather than consistently aggressive personalities.

Keywords: *Platythyrea punctata*; colony fusion; worker policing; animal personalities; behavioural syndromes

1. INTRODUCTION

Animals often differ consistently in their behaviour across a wide range of situations. Certain individuals may be always more or less aggressive than others, regardless of whether confronted by a conspecific rival or a predator. However, limiting behavioural plasticity, such 'behavioural syndromes' or 'animal personalities' may be adaptive rather than the results of physiological or neuroanatomical constraints (Sih *et al.* 2004; Réale *et al.* 2007; Wolf *et al.* 2007).

The efficiency of the division of labour in animal societies might be greatly increased through group members exhibiting different 'personalities' (Rueppell *et al.* 2006). For example, particularly aggressive individuals might equally engage in 'policing', i.e. the suppression of reproductive conflict within the group (Ratnieks *et al.* 2006), and defence against rivals and competitors from outside (Clutton-Brock & Parker 1995; Frank 1996; Kitchen & Beehner 2007).

We investigated whether group members with a particularly aggressive 'personality' take over both nest defence and policing in the ant *Platythyrea punctata*. All workers of this species are potentially capable of producing female offspring from unfertilized eggs by thelytokous parthenogenesis (Heinze & Hölldobler 1995), and most colonies are clones (Schilder *et al.* 1999; Hartmann *et al.* 2005*a*). Though kin conflict is thus not expected from relatedness, a reproductive division of labour with one, rarely a few laying workers is maintained by dominance and policing (Heinze & Hölldobler 1995; Hartmann *et al.* 2003, 2005*b*), presumably because egg-laying by too many reproductives would lower colony efficiency (Hartmann *et al.* 2003; see also Pirk *et al.* 2003 for Cape honeybees, *Apis mellifera capensis*).

Population genetic data suggest that unrelated colonies may merge in nature when nest sites are limited (Hartmann *et al.* 2005*a*). Indeed, in a recent study (Kellner *et al.* in press) colonies readily fused in laboratory experiments. However, beginning within 30 min after merging, aggression among reproductives and attacks by non-reproductive workers against reproductives reduce the number of reproductives to one within days. Attacks by non-reproductives are not preferentially directed against the unrelated reproductive but closely resemble attacks against new reproductives in standard policing experiments (Hartmann *et al.* 2003). We thus consider aggression of non-reproductives towards reproductives after fusion as 'worker policing'.

Policing is often taken over by an 'elite' of particularly strong or dominant individuals (Frank 1996; Stroeymeyt *et al.* 2007). If 'behavioural syndromes' existed in *P. punctata*, 'police' workers would also engage more in colony defence against intruders. To test this hypothesis we compared the aggressiveness of individual workers during policing after colony fusion and during defence against introduced alien ants.

2. MATERIAL AND METHODS

We studied the behaviour of individually paint-marked workers in eight colonies, each resulting from the experimental fusion of two formerly separate thelytokous colonies (colonies sizes directly after fusion: 11 to 27; fusion details given in Kellner *et al.* (in press) and the electronic supplementary material). Ten to 60 days after fusion, the fused colonies (colony sizes in this experiment: 5–21) were successively confronted with single workers of four sympatric ant species ('enemies', *Odontomachus* sp., *Pachycondyla stigma*, *Solenopsis invicta*, *Camponotus* sp.). We recorded the frequency of attacks by non-reproductive *P. punctata* workers towards reproductives after colony fusion and against introduced enemies. For both situations, the frequency distributions of attacks per worker were tested for goodness of fit to a Poisson distribution (assuming a similar likelihood of attacking for all individuals, i.e. random sharing of aggression) separately per colony and pooled over all colonies to determine whether some individuals were more aggressive than others (χ^2-tests).

In four of eight fused colonies, some highly aggressive workers died during the experiments. In each of the remaining four colonies (colony sizes: 15–21), we determined the four most aggressive non-reproductives after fusion ('police') and the four most aggressive non-reproductives against intruders ('army'). In order to test whether workers were equally aggressive across the situations, we compared the proportional aggression of these workers in one situation with their proportional aggression in the other situation over all four colonies using Wilcoxon matched-pairs tests. Statistical analyses were performed with Statistica 6.0 (StatSoft Inc. 2001). For details see the electronic supplementary material.

Electronic supplementary material is available at http://dx.doi.org/10.1098/rsbl.2009.0849 or via http://rsbl.royalsocietypublishing.org.

Received 16 October 2009
Accepted 10 December 2009

FirstCite e-publishing

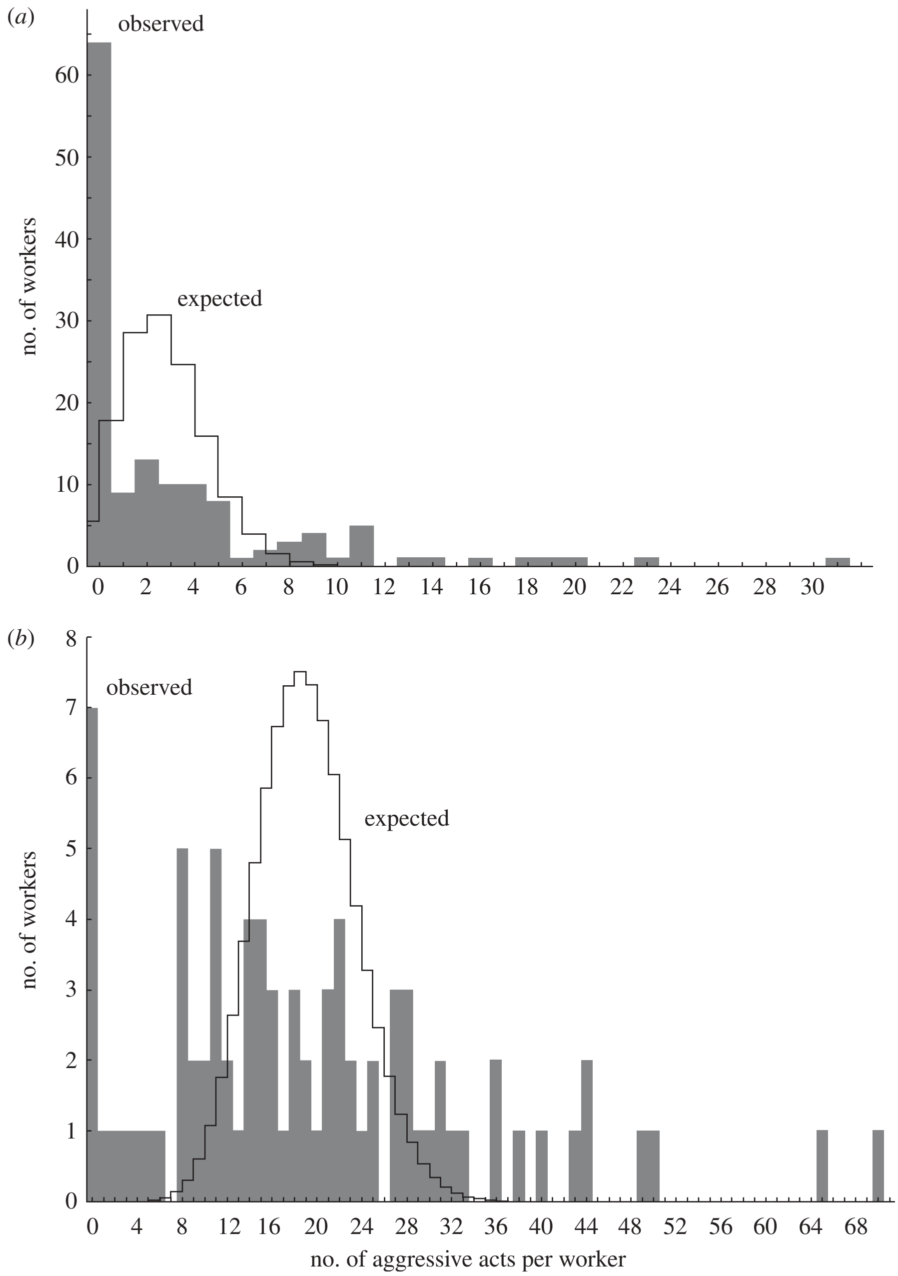

Figure 1. Frequency distribution of aggression among non-reproductive *P. punctata* workers over all colonies ($n = 8$) during (*a*) colony fusion and (*b*) enemy introduction. Observed distributions were significantly more skewed than expected from random sharing of aggression (χ^2-test, assuming a Poisson distribution, λ = average number of aggressive acts per worker: (*a*) $\chi^2 = 707.81$; $\lambda = 3.2$; (*b*) $\chi^2 = 89.94$; $\lambda = 19.53$; $p < 0.001$ in both cases).

3. RESULTS

In experimentally fused colonies, after fusion, remarkable aggression was directed against surplus reproductives. Furthermore, attacks against introduced *Odontomachus*, *Solenopsis* and *Camponotus* resulted in their elimination within 30 min. Only *P. stigma* workers successfully defended themselves, even killing some *P. punctata* workers.

In both experiments, a minority of non-reproductive workers engaged in a disproportionally large part of aggression. Other individuals avoided fighting, even though all had a similar likelihood of encountering surplus reproductives or alien ants because of small nest sizes (8 × 5.5 × 0.5 cm, see the electronic supplementary material) and the rapid movements of the attacked ants. The frequency distribution of attacks per worker significantly deviated from random (χ^2-tests, $p < 0.05$ for each colony and both situations, see figure 1 for pooled data). Reproductives were aggressive towards each other after colony fusion but rarely attacked alien ants.

Each of the four most aggressive police workers per colony initiated on average 11 per cent of the attacks after fusion ($n = 16$, median, quartiles 8%, 15%), but had a considerably lower share in aggression against enemies (median 5%, quartiles 2%, 6%, Wilcoxon matched-pairs test, $Z = 3.46$; $p < 0.001$, figure 2). Similarly, most of the four most aggressive army workers per colony ($n = 16$, median 12%, quartiles 1%, 14% of attacks against introduced ants), had engaged much less in aggression after fusion (median 3%, quartiles 0%, 7%, $Z = 3.52$; $p < 0.001$,

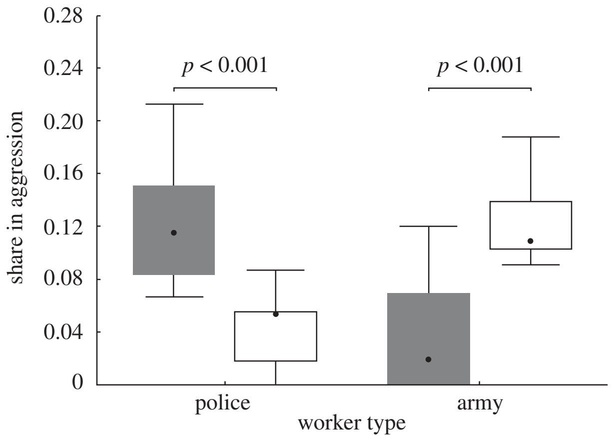

Figure 2. Share in aggression (medians, percentile, range without outliers) of the four most aggressive non-reproductive *P. punctata* workers in each of four colonies after fusion ('police') and against enemies ('army') in two situations: colony fusion (grey bars) and enemy introduction (white bars). Aggressiveness is situation-dependent: police workers are less aggressive against enemies and army workers are less aggressive during fusion (Wilcoxon matched-pairs tests, $n = 16$ in both comparisons).

figure 2). Only one individual was among the four most aggressive workers in both situations.

4. DISCUSSION

Our experimental setup reveals patterns of potential disposition to aggression among workers in *P. punctata* colonies. Only a few individuals initiated a disproportionally large part of worker policing in colony fusion experiments, and likewise only few workers engaged disproportionally in attacks against introduced alien ants. Different workers took over aggression in the different situations. Police workers less frequently attacked enemies, while nest defenders were less active in policing. This suggests that aggressiveness is context-specific, though similar types of behaviour are involved. Aggressiveness is often governed by single physiological and endocrine pathways (Kravitz & Huber 2003) and therefore is correlated across situations (Sih *et al.* 2004; Rueppell *et al.* 2006). In contrast, the physiological mechanisms underlying aggression in *P. punctata* appear to be more flexible.

This behavioural plasticity refutes the hypothesis of an 'aggression syndrome' in *P. punctata*. Age polyethism, with individuals switching with age from safe indoor tasks to more risky tasks, such as nest defence, cannot explain our results, because the time interval between the experiments was short relative to the life expectancy of *P. punctata* workers (Hartmann & Heinze 2003). Furthermore, from age polyethism we would expect that workers who had been aggressive after fusion exhibit similar aggression several weeks later against enemies.

Instead, our data match the hypothesis that individuals in insect societies who engage in policing are often 'hopeful reproductives', who begin laying eggs themselves once the old reproductives are removed (e.g. Wenseleers *et al.* 2005; Stroeymeyt *et al.* 2007). Individuals with greater expected future fitness often invest less in helping and refrain from dangerous tasks, thus saving their resources for future reproduction (Cant & Field 2005; Field *et al.* 2006; Field & Cant 2009). Ant queens and female sexuals hide when the nest is attacked and leave nest defence to workers (Wilson 1971), and dominant workers in the ant *Harpagoxenus sublaevis* or in Cape honeybees engage less in helping than low-ranking individuals (Bourke 1988; Neumann *et al.* 2003). In analogy, *P. punctata* workers with a high reproductive potential may cede dangerous nest defence to lower ranking, perhaps older workers with low reproductive potential. Dominant, younger workers might directly or indirectly benefit from aggressively excluding rivals from egg-laying. As documented by Brunner *et al.* (2009), those *P. punctata* workers who most actively engage in policing usually also take over reproduction when the old egg-layer is removed.

Division of aggression between policing and nest defence therefore differs strikingly between highly eusocial insects and naked mole-rats (*Heterocephalus glaber*; Bennett & Faulkes 2000), and social animals with totipotent individuals, such as primates, 'primitively' eusocial paper wasps, and Damaraland mole rats (*Cryptomys damarensis*). In the latter taxa, high-ranking individuals attack both predators and potential usurpers from within and outside the group (Judd 2000; Cooney 2002; Kitchen & Beehner 2007). They have the most to lose, while low rankers may have a reasonable chance of reproducing away from the nest or would suffer higher costs from aggression (Heinsohn & Legge 1999; Cant & Field 2005). This difference might reflect the distinction between indirect fitness-driven sociality with sterile helpers and cooperative breeding, in which helpers may gain both indirect and direct fitness (Korb & Heinze 2008). Although colonies of *P. punctata* consist of totipotent individuals, the species has evolved from highly eusocial ancestors (Hartmann *et al.* 2005*a*) and thus belongs to the first class of social animals. Dominance and policing may have been retained in spite of regular clonality due to occasional colony fusion in the field and sporadic sexual reproduction because they may maintain colony efficiency.

We thank Tina Wanke and Jon N. Seal for assistance in fieldwork, the Ministry of Agriculture & Rural Development of Barbados and La Dirección General de Vida Silvestre y Biodiversidad of the Dominican Republic for providing permits, and DFG (He 1623/20) for financial support.

Bennett, N. C. & Faulkes, C. G. 2000 *African mole-rats ecology and eusociality.* Cambridge, UK: Cambridge University Press.

Bourke, A. F. G. 1988 Dominance orders, worker reproduction, and queen-worker conflict in the slave-making ant *Harpagoxenus sublaevis*. *Behav. Ecol. Sociobiol.* **23**, 323–333. (doi:10.1007/BF00300579)

Brunner, E., Kellner, K. & Heinze, J. 2009 Policing and dominance behaviour in the parthenogenetic ant *Platythyrea punctata*. *Anim. Behav.* **78**, 1427–1431. (doi:10.1016/j.anbehav.2009.09.022)

Cant, M. A. & Field, J. 2005 Helping effort in a dominance hierarchy. *Behav. Ecol.* **16**, 708–715. (doi:10.1093/beheco/ari051)

Cooney, R. 2002 Colony defense in Damaraland mole-rats, *Cryptomys damarensis*. *Behav. Ecol.* **18**, 160–162. (doi:10.1093/beheco/13.2.160)

Clutton-Brock, T. H. & Parker, G. A. 1995 Punishment in animal societies. *Nature* **373**, 209–216. (doi:10.1038/373209a0)

Field, J. & Cant, M. A. 2009 Social stability and helping in small animal societies. *Phil. Trans. R. Soc. B* **64**, 3181–3189. (doi:10.1098/rstb.2009.0110)

Field, J., Cronin, A. & Bridge, C. 2006 Future fitness and helping in social queues. *Nature* **441**, 214–217. (doi:10.1038/nature04560)

Frank, S. A. 1996 Policing and group cohesion when resources vary. *Anim. Behav.* **52**, 1163–1169. (doi:10.1006/anbe.1996.0263)

Hartmann, A. & Heinze, J. 2003 Lay eggs, live longer: division of labor and life span in a clonal ant species. *Evolution* **57**, 2424–2429.

Hartmann, A., Wantia, J., Torres, J. A. & Heinze, J. 2003 Worker policing without genetic conflicts in a clonal ant. *Proc. Natl Acad. Sci. USA* **100**, 12 836–12 840. (doi:10.1073/pnas.2132993100)

Hartmann, A., Wantia, J. & Heinze, J. 2005*a* Facultative sexual reproduction in the parthenogenetic ant *Platythyrea punctata*. *Insectes Soc.* **52**, 155–162. (doi:10.1007/s00040-004-0786-5)

Hartmann, A., D'Ettorre, P., Jones, G. R. & Heinze, J. 2005*b* Fertility signaling—the proximate mechanism of worker policing in a clonal ant. *Naturwissenschaften* **92**, 282–286. (doi:10.1007/s00114-005-0625-1)

Heinsohn, R. & Legge, S. 1999 The cost of helping. *Trends Ecol. Evol.* **14**, 53–57. (doi:10.1016/S0169-5347(98)01545-6)

Heinze, J. & Hölldobler, B. 1995 Thelytokous parthenogenesis and dominance hierarchies in the ponerine ant, *Platythyrea punctata*. *Naturwissenschaften* **82**, 40–41. (doi:10.1007/BF01167871)

Judd, T. M. 2000 Division of labor in colony defence against vertebrate predators by the social wasp *Polistes fuscatus*. *Anim. Behav.* **60**, 55–61. (doi:10.1006/anbe.2000.1449)

Kellner, K., Barth, B. & Heinze, J. In press. Colony fusion causes within-colony variation in a parthenogenetic ant. *Behav. Ecol. Sociobiol.*

Kitchen, D. M. & Beehner, J. C. 2007 Factors affecting individual participation in group-level aggression among non-human primates. *Behaviour* **144**, 1551–1581. (doi:10.1163/156853907782512074)

Korb, J. & Heinze, J. 2008 The ecology of social life: a synthesis. In *Ecology of social evolution* (eds J. Korb & J. Heinze), pp. 245–259. Heidelberg, Germany: Springer.

Kravitz, E. A. & Huber, R. 2003 Aggression in invertebrates. *Curr. Opin. Neurobiol.* **13**, 736–743. (doi:10.1016/j.conb.2003.10.003)

Neumann, P., Radloff, S. E., Pirk, C. W. W. & Hepburn, R. 2003 The behaviour of drifted Cape honeybee workers (*Apis mellifera capensis*): predisposition for social parasitism? *Apidologie* **34**, 585–590. (doi:10.1051/apido:2003048)

Pirk, C. W. W., Neumann, P. & Ratnieks, F. L. W. 2003 Cape honeybees, *Apis mellifera capensis*, police worker-laid eggs despite the absence of relatedness benefits. *Behav. Ecol.* **14**, 347–352.

Ratnieks, F. L. W., Foster, K. R. & Wenseleers, T. 2006 Conflict resolution in insect societies. *Annu. Rev. Entomol.* **51**, 581–608. (doi:10.1146/annurev.ento.51.110104.151003)

Réale, D., Reader, S. M., Sol, D., McDougall, P. T. & Dingemanse, N. J. 2007 Integrating animal temperament within ecology and evolution. *Biol. Rev.* **82**, 291–318. (doi:10.1111/j.1469-185X.2007.00010.x)

Rueppell, O., Chandra, S. B. C., Pankiw, T., Fondrk, M. K., Beye, M., Hunt, G. & Page, R. E. 2006 The genetic architecture of sucrose responsiveness in the honeybee (*Apis mellifera* L.). *Genetics* **172**, 243–251. (doi:10.1534/genetics.105.046490)

Schilder, K., Heinze, J. & Hölldobler, B. 1999 Microsatellites reveal clonal structure of populations of the thelytokous ant *Platythyrea punctata* (F. Smith) (Hymenoptera; Formicidae). *Mol. Ecol.* **8**, 1497–1507. (doi:10.1046/j.1365-294x.1999.00727.x)

Sih, A., Bell, A. & Johnson, J. C. 2004 Behavioral syndromes: an ecological and evolutionary overview. *Trends Ecol. Evol.* **19**, 372–378. (doi:10.1016/j.tree.2004.04.009)

StatSoft Inc. 2001 Statistica (data analysis software system), v. 6. www.statsoft.com.

Stroeymeyt, N., Brunner, E. & Heinze, J. 2007 'Selfish worker policing' controls reproduction in a *Temnothorax* ant. *Behav. Ecol. Sociobiol.* **61**, 1449–1457. (doi:10.1007/s00265-007-0377-3)

Wenseleers, T., Tofilski, A. & Ratnieks, F. L. W. 2005 Queen and worker policing in the tree wasp *Dolichovespula sylvestris*. *Behav. Ecol. Sociobiol.* **58**, 80–86. (doi:10.1007/s00265-004-0892-4)

Wilson, E. O. 1971 *The insect societies*. Cambridge, MA: Harvard University Press.

Wolf, M., van Doorn, G. S., Leimar, O. & Weissing, F. J. 2007 Life-history trade-offs favour the evolution of animal personalities. *Nature* **447**, 581–585. (doi:10.1038/nature05835)