

Bruno Gobin · Fuminori Ito

Sumo wrestling in ants: major workers fight over male production in *Acanthomyrmex ferox*

Received: 12 September 2002 / Accepted: 29 April 2003 / Published online: 29 May 2003
© Springer-Verlag 2003

Abstract In the myrmicine ant *Acanthomyrmex ferox*, major workers have the same number of ovarioles as queens, thrice that of minor workers, making them well suited for egg-laying. In the queen's presence, infrequent aggression allows ranking of majors but they lay only unviable trophic eggs. Major workers engage each other, but not the minors, in antennal boxing and spectacular shaking contests, a novel interaction in ants. The absence of reversals allows a clear ranking of major workers. After queen removal, aggression becomes very frequent, but previous ranking is maintained. All majors start laying reproductive eggs although they show a skew in ovary development according to ranking. The dominant major, however, actively patrols the egg-pile and cannibalises eggs laid by subordinates.

Electronic Supplementary Material Supplementary material is available for this article if you access the article at <http://dx.doi.org/10.1007/s00114-003-0430-7>. A link in the frame on the left on that page takes you directly to the supplementary material.

Introduction

In many social animals, behavioural mechanisms regulate the number of breeders (Vehrencamp 1983; Keller and Reeve 1994; Clarke and Faulkes 2001). Ritualised or overtly aggressive interactions result in one or a few high ranking individuals getting preferential access to mates or breeding opportunities. This is especially likely when group size is limited, so that dominant individuals can

patrol all members to enforce dominance (Heinze et al. 1994). A straightforward regulation of the reproductive division of labour is particularly important when offspring maturation depends on care by helpers (Monnin and Ratnieks 1999). Many social Hymenoptera evolved morphologically distinct queens and workers so that reproduction is allocated according to caste membership. Workers of most species, however, are not completely sterile and can lay unfertilised eggs that develop into males (Bourke 1988), while workers in species lacking overt caste differences can mate and lay offspring of both sexes (Ross and Matthews 1991; Peeters 1993). The resulting conflict over reproductive rights between queens and workers is often regulated by aggression or, alternatively, is only expressed after queen demise during last-resort worker male production. In ants, aggressive regulation of reproduction is known to be common in two major groups: the subfamily Ponerinae and the myrmicine tribe Formicoxenini. Outside these groups, aggression was discovered in just one ant species lacking morphological castes (Heinze et al. 1999b).

We studied the occurrence of dominance interactions regulating worker reproduction in the myrmicine ant *Acanthomyrmex ferox*. This species has small colony sizes, but three distinct allometric female castes: queens, major workers and minor workers (Gobin and Ito 2000). Major workers have a role in colony defence and seed cracking (Moffett 1985). *A. ferox* is unique because majors have the same number of ovarioles (six) as queens, with minors having only two (Gobin and Ito 2000). In queenright colonies, workers lay only unviable trophic eggs, serving as food for larvae and nestmates, though majors lay eight times as many trophic eggs than minors do (Gobin and Ito 2000). The specialised ovarian morphology and high egg-laying rate led us to expect an important role for majors in male production once the queen dies. We specifically investigated whether aggression is involved in regulating reproduction in orphaned colonies of *A. ferox* and which nestmates can dominate egg-laying.

B. Gobin (✉)

Laboratory of Entomology, KU Leuven,
Naamsestraat 59, 3000 Leuven, Belgium
e-mail: bruno.gobin@bio.kuleuven.ac.be
Tel.: +32-16-323964
Fax: +32-16-324575

B. Gobin · F. Ito

Faculty of Agriculture, Kagawa University,
761-0795 Ikenobe, Miki, Japan

Material and methods

Complete colonies of *Acanthomyrmex ferox*, containing 24.8 ± 10.8 minor workers and 2.6 ± 1.5 majors ($n=49$), were collected at Ulu Gombak, Malaysia, and housed in glass-covered plaster nests connected to a 10×7 cm arena. Majors were individually paint-marked, and the behaviour of all nestmates was randomly observed.

To investigate aggression in queenright colonies, we observed four queenright colonies with 5–6 days of 24 h time-lapse video recording and two others by random observation. We orphaned these and checked the increase in aggression by immediate 24 h videotaping followed by further random observation.

We then addressed the question of how male production is regulated in queenless colonies of *A. ferox* through experimental removal of the queen in five more colonies. We observed agonistic interactions for a total of 10–20 h in the second and third weeks after orphaning. Typical observation bouts lasted 10–30 min, repeated 3–4 times per day between 1000 and 1900 hours, with additional random observations. In the fourth week after orphaning we videotaped the colonies for 48 h to check egg-laying, egg-pile attendance and possible cannibalism.

We dissected all individuals after 5–12 weeks to assess ovariole length, the presence of yellow bodies and the presence of distinct trophic and reproductive oocytes (Gobin and Ito 2000).

Results

In all queenright colonies of *Acanthomyrmex ferox*, major workers show sporadic aggression towards each other, either antennal boxing or shaking. During antennal boxing, one individual repeatedly hits its antenna against the body of the adversary. Shaking is initiated when a major worker approaches and puts its forelegs on the head of another major (Fig. 1). Next, the agonist vigorously pushes its own head backward with its forelegs while simultaneously throwing the abdomen forward. The momentum of this movement, transmitted through the forelegs, will shake the body of the opponent. This is rapidly repeated 3–10 times in a single shaking event, ending when the agonist removes its forelegs from the opponent. The opponent submits to shaking by remaining immobile, with the antenna pulled backward (Electronic Supplementary Material shows a short videoclip of this behaviour).

In 552 h, we recorded just 79 interactions in four queenright colonies, or 0.06 ± 0.03 ($X \pm SD$) interactions per major per hour, more often boxing ($66 \pm 14\%$) than shaking ($34 \pm 14\%$). Majors can be clearly ranked, as reversals of aggression do not occur, and this ranking is maintained after queen removal. Agonistic interactions involving minors are scarce in queenright colonies; only twice did we observe a major boxing a bystanding minor worker during aggression towards another major.

Within 10 min following orphaning, the frequency of aggression among majors visibly increased, averaging 3.39 ± 0.66 times per major per hour in the next 30 h (two-tailed $t=10.08$, $P<0.01$, $n=4$), of which $95 \pm 2\%$ were shaking. In the second week after orphaning, agonistic interactions diminished significantly (1.55 ± 0.55 , $t=4.36$, $P<0.01$, $n=4$), and about $71 \pm 23\%$ were shaking. In contrast, minor workers rarely box in orphaned colonies (only observed twice towards other minors), and only

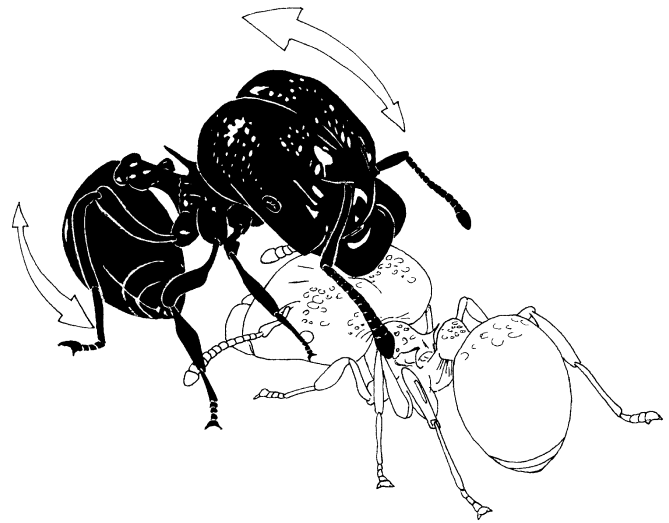


Fig. 1 Drawing (based on a photograph) of two major workers in a shaking contest. The dominant major (*black*) puts his forelegs on the head of the subordinate (*white*), and repetitively throws his abdomen forward and his head backward. The momentum of this movement is transmitted through the forelegs, vigorously shaking the subordinate

once did a major box a minor in the middle of two bouts of boxing towards another major.

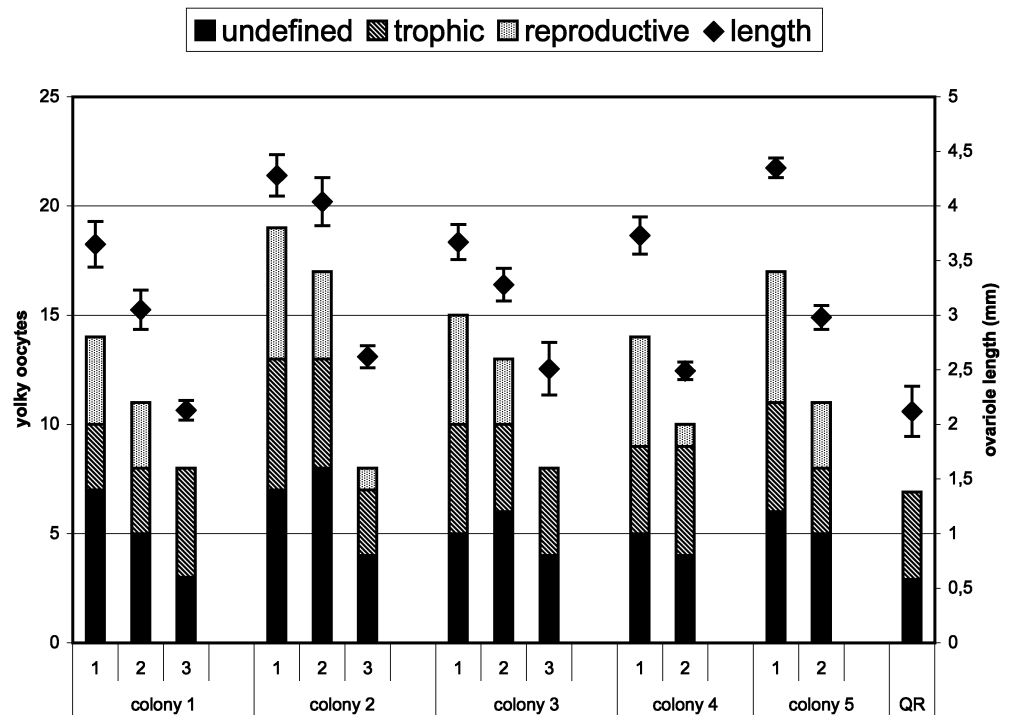
In all orphaned groups, reproductive egg-laying starts after 3 weeks, and males are reared from these eggs. Majors alternate laying single reproductive eggs and single or multiple trophic eggs per oviposition. Rank 1 majors lay 2.25 ± 0.5 eggs per day ($n=4$, in 48 h) of which $63 \pm 14\%$ are reproductive, while rank 2 majors lay 1.38 ± 0.85 eggs per day ($n=4$, 48 h, $t=3.66$, $P<0.05$), of which $48 \pm 42\%$ are reproductive. Two rank 3 majors laid a single reproductive egg outside formal observations. Majors extruded reproductive eggs in $6:46 \pm 1:01$ min and trophic eggs in $2:39 \pm 0:36$ min. Minors take trophic eggs from the major's abdomen and feed them to larvae and adults ($n=12$). Majors drop reproductive eggs on the ground after which minors put them on the egg-pile ($n=8$). The dominant major is the sole major to regularly touch the egg-pile with its antennae (egg-pile patrolling, see Table 1). In three colonies, four out of six reproductive eggs laid by subordinates were quickly eaten by the dominant major. Two eggs could not be followed individually, but the dominant major was eating at the egg-pile within a few minutes.

Majors in orphaned colonies have increased ovary development. Each ovariole contains large yellow bodies, an indication of active egg-laying. A slight skew in ovary development agrees with a major's ranking (Fig. 2). Ovaries contain both developing trophic and reproductive oocytes, which matches alternate egg-laying. In contrast, minor workers had no increased ovary development, their ovariole length (1.02 ± 0.18 mm, $n=33$) did not differ from minors in queenright groups (1.01 ± 0.18 mm, $n=20$; $t=0.24$, $P<0.80$).

Table 1 Dominance interactions and egg-pile patrolling per hour in five orphaned colonies of *Acanthomyrmex ferox*, with an indication of their ranking. A total of antennal boxing plus shaking is given for each major (identified by a double capital letter code) and summarized for all minors (Mn). Egg-pile patrolling frequency was only monitored for majors

Colony	Rank	From	Toward				Total	Egg-pile
			GG	PP	YY	Mn		
1	1	GG		3.6	2.1		5.7	3.4
	2	PP			0.5		0.5	0.2
	3	YY Mn					0 0	0.1 –
2			BB	GG	RR			
	1	BB		2.8	1.6		4.3	5.9
	2	GG			1.6		1.6	0
	3	RR Mn		0.05			0.05 0	0.1 –
3			RR	YY	GG			
	1	RR		2.8	1.2	0.1	4.1	4.1
	2	YY			0.8		0.8	0.1
	3	GG Mn					0 0.1	0.1 –
						0.1	0.1	–
4			WW	BB				
	1	WW		1.8			1.8	3.7
	2	BB Mn					0 0	0.2 –
5			WW	RR				
	1	WW		2.2			2.2	4.7
	2	RR Mn					0 0	0.1 –

Fig. 2 The ovary development of the majors in five orphaned colonies according to their rank (1–3), compared to the average of ten majors from six queenright colonies (QR). Colony identity and ranking of majors as in Table 1. *Diamonds* indicate the mean length (and standard deviation, mm) of each major's ovarioles. *Bars* represent the number of yolky oocytes in the ovaries of a given soldier, discriminating between clearly recognisable reproductive and trophic oocytes, and small undefined yolky oocytes



Discussion

After orphaning, colonies of *Acanthomyrmex ferox* produce haploid male brood. Although worker reproduction in queenless colonies is common in ants (Bourke 1988), *A. ferox* is exceptional in that it is the major workers that produce male eggs. Majors risking their life for colony defence – therefore often referred to as soldiers (Oster and Wilson 1978; Moffett 1985) – are unlikely reproducers.

Indeed, some authors have suggested that self-sacrificial major behaviour is more likely to evolve if workers have lost their potential to reproduce (Oster and Wilson 1978; Bourke 1999). In *A. ferox*, however, major workers have identical ovaries to queens, and are actively laying unviable trophic eggs under queenright conditions (Gobin and Ito 2000), making them morphologically and physiologically well-suited for an important role as male producers. This is similar to *Crematogaster smithi*, in

which large workers with ovariole numbers intermediate between queens and workers, produce most eggs (Heinze et al. 1999a). Majors of *A. ferox* do not entirely relinquish trophic egg production after the start of male egg-laying. Trophic eggs are indeed essential for colony survival, as even the queen of mature *A. ferox* colonies lays trophic eggs, investing only half of her oocytes in reproduction (Gobin and Ito 2000). Dual egg production is possible as trophic and reproductive oocytes differentiate only in the last developmental stage (see Gobin et al. 1998).

Unlike the non-aggressive *C. smithi* workers (Heinze et al. 1999a), orphaned major workers of *A. ferox* compete with each other through spectacular shaking contests. These contests resemble a Sumo wrestling contest, as the dominant major uses its full body mass to exert force on the head of the subordinate, which submits to being shaken. The sharp increase in frequency immediately after orphaning underlines the importance of shaking in becoming dominant. Shaking is a novel type of interaction in ants. Like antennal boxing, a common interaction that also occurs in *A. ferox*, it is a form of ritualised dominance fighting which results in differential status rather than physical harm (Ito 1993; Peeters and Tsuji 1993; Gobin et al. 2001). In some species dominants will bite and pull, jerk or lift subordinates (Medeiros et al. 1992; Liebig et al. 2000), but even these interactions rarely result in injury.

Dominance interactions among majors leads to a skew in ovary development, but does not prevent lower ranking majors from laying reproductive eggs. Aggression thus seems inefficient, considering that even ritualised aggression is costly (Gobin et al. 2003). However, aggression is restricted to the few major workers only, limiting costs to the colony, as the non-aggressive minors can raise the brood (Monnin and Ratnieks 1999). Aggressive dominance guarantees access to the egg-pile, so the highest ranked major can cannibalise eggs laid by other majors. Egg-eating is an efficient way to monopolise reproduction in ants (Bourke 1991; Monnin and Peeters 1997; van Walsum et al. 1998), although molecular markers for *Acanthomyrmex* would be needed to check whether egg-pile patrolling allows the dominant major to destroy all eggs.

Acknowledgements We thank R. Hashim of the University of Malaya for permitting fieldwork at the Ulu Gombak field station. JSPS (T98.167) and Monbusho (08041136, 11691130) grants supported this work. B.G. is a postdoctoral fellow of the Fund for Scientific Research, Flanders.

References

- Bourke AFG (1988) Worker reproduction in the higher eusocial Hymenoptera. *Q Rev Biol* 63:291–311
- Bourke AFG (1991) Queen behaviour, reproduction and egg cannibalism in multiple-queen colonies of the ant *Leptothorax acervorum*. *Anim Behav* 42:295–310
- Bourke AFG (1999) Colony size, social complexity and reproductive conflict in social insects. *J Evol Biol* 12:245–247
- Clarke FM, Faulkes CG (2001) Intracolony aggression in the eusocial naked mole-rat *Heterocephalus glaber*. *Anim Behav* 61:311–324
- Gobin B, Ito F (2000) Queens and major workers of *Acanthomyrmex ferox* redistribute nutrients with trophic eggs. *Naturwissenschaften* 87:323–326
- Gobin B, Peeters C, Billen J (1998) Production of trophic eggs by virgin workers in the ponerine ant *Gnamptogenys menadensis*. *Physiol Entomol* 23:329–336
- Gobin B, Billen J, Peeters C (2001) Dominance interactions regulate mating in *Gnamptogenys menadensis*. *Ethology* 107:495–508
- Gobin B, Heinze J, Strätz M, Roces F (2003) The energetic cost of reproductive conflicts in the ant *Pachycondyla obscuricornis*. *J Insect Physiol* 49: DOI 10.1016/s0022-1910(03)00111-2
- Heinze J, Hölldobler B, Peeters C (1994) Conflict and cooperation in ant societies. *Naturwissenschaften* 81:489–497
- Heinze J, Foitzik S, Oberstadt B, Ruppell O, Hölldobler B (1999a) A female caste specialized for the production of unfertilized eggs in the ant *Crematogaster smithi*. *Naturwissenschaften* 86:93–95
- Heinze J, Hölldobler B, Alpert GD (1999b) Reproductive conflict and division of labor in *Eutetramorium mocquersyi*, a myrmicine ant without morphologically distinct female reproductives. *Ethology* 105:701–717
- Ito F (1993) Social organization in a primitive ponerine ant: queenless reproduction, dominance hierarchy and functional polygyny in *Amblyopone* sp. (reclinata group) (Hymenoptera: Formicidae: Ponerinae). *J Nat Hist* 27:1315–1324
- Keller L, Reeve HK (1994) Partitioning of reproduction in animal societies. *Trends Ecol Evol* 9:98–102
- Liebig J, Peeters C, Oldham NJ, Markstädter C, Hölldobler B (2000) Are variations in cuticular hydrocarbons a reliable signal of fertility in the ant *Harpegnathos saltator*. *Proc Natl Acad Sci USA* 96:15013–15016
- Medeiros FNS, Lopes LE, Moutinho PRS, Oliveira PS, Hölldobler B (1992) Functional polygyny, agonistic interactions and reproductive dominance in the neotropical ant *Odontomachus chelifer* (Hymenoptera, Formicidae, Ponerinae). *Ethology* 91:134–146
- Moffett MW (1985) Behavioral notes on the Asiatic harvesting ants *Acanthomyrmex notabilis* and *A. ferox*. *Psyche* 92:165–179
- Monnin T, Peeters C (1997) Cannibalism of subordinates' eggs in the monogynous queenless ant *Dinoponera quadriceps*. *Naturwissenschaften* 84:499–502
- Monnin T, Ratnieks FLW (1999) Reproduction versus work in queenless ants: when to join a hierarchy of hopeful reproductives? *Behav Ecol Sociobiol* 46:413–422
- Oster GF, Wilson EO (1978) Caste and ecology in the social insects. Princeton University Press, Princeton, N.J.
- Peeters C (1993) Monogyny and polygyny in ponerine ants with or without queens. In: Keller L (ed) Queen number and sociality in insects. Oxford University Press, Oxford, pp 234–261
- Peeters C, Tsuji K (1993) Reproductive conflict among ant workers in *Diacamma* sp. from Japan: dominance and oviposition in the absence of the gamergate. *Insectes Soc* 40:119–136
- Ross K, Matthews R (1991) The social biology of wasps. Comstock (Cornell University Press), Ithaca, N.Y.
- Vehrencamp SL (1983) A model for the evolution of despotic versus egalitarian societies. *Anim Behav* 31:667–689
- Walsum E van, Gobin B, Ito F, Billen J (1998) Worker reproduction in the ponerine ant *Odontomachus similimus* (Hymenoptera: Formicidae). *Sociobiology* 32:427–440