SHORT COMMUNICATION

Opportunities for mate choice in the fission-performing ant *Cataglyphis cursor*

ADAM L. CRONIN,[1] THIBAUD MONNIN,[1] CLAUDY HAUSSY[1] and CLAUDIE DOUMS[1,2]   [1]Laboratoire Écologie & Évolution UMR 7625, Université Pierre et Marie Curie, Paris, France and [2]École Pratique des Hautes Études, Paris, France

Abstract. 1. Sexual selection has been little studied in social insects. Nonetheless, because mating is generally for life, opportunities for selecting among mating partners should be exploited.

2. In some ants, males aggregate at nest entrances to mate with emerging gynes. Both males and females thus have access to multiple mates over a relatively protracted period, giving rise to opportunities for mate choice and multiple mating.

3. We provide data from field observations of the male mating biology of the ant, *Cataglyphis cursor* Fonscolombe. In this species, females mate with, on average, six males each at the nest entrance and found colonies with the help of workers.

4. Males were present at the field site for approximately 1 month in spring, with up to 40 males at a single nest entrance for, on average, 4.7 days. Individual males were observed to survive up to 3 days, and mate up to eight times.

5. Thus both males and females of this species have the ability to mate multiply and have a window permitting mate choice to occur. Workers actively attacked males and may take part in the mate choice process, making *C. cursor* an interesting model to study questions relating to sexual selection and male mating strategies.

Key words. Ant, fission, mate choice, mating strategy.

Introduction

Sexual selection has been little studied in social insects and opportunities to exercise mate choice may be limited, because mating usually takes place in highly ephemeral aggregations characterised by scramble competition ('male aggregation syndrome'; Bartz & Hölldobler, 1982; Baer *et al.*, 2003; Boomsma *et al.*, 2005). Nonetheless, sexual partners in social insects are committed for life (Boomsma & Ratnieks, 1996; Boomsma *et al.*, 2005), and thus being 'choosy' makes good sense.

Many species employ an alternative form of mating, 'female calling syndrome', whereby females attract mates via the release of pheromones, either after dispersing or at the natal nest (Boomsma *et al.*, 2005; Peeters & Molet, 2010). Females in the latter group are protected by the sanctity of the nest and there is no urgency to found a new colony to escape predation. This mode of mating may also be correlated with male longevity and extended and asynchronous reproductive activity (Kaspari *et al.*, 2001; Shik & Kaspari, 2009), and

may yield greater options for mate choice to occur, because the window of opportunity for one or both sexes becomes protracted. In addition, mating at the nest means that males must 'run the gauntlet of the workers' (Franks & Hölldobler, 1987), which can be aggressive toward and may kill males, forming a second potential mechanism of mate choice (e.g. Jaffé *et al.*, 2009; Thurin & Aron, 2009).

Here, we provide data on the presence and mating activity of males at colonies of the ant *Cataglyphis cursor* Fonscolombe. This species reproduces via colony fission, whereby the queen founds a new nest with the help of workers. Gynes are produced in spring (4–24 per colony), are short-winged and cannot fly, and mate at the nest entrance with on average six males over several days (Lenoir *et al.*, 1988; Pearcy *et al.*, 2004; Pearcy & Aron, 2006; Chéron *et al.*, 2011b). Males aggregate at nest entrances, giving rise to opportunities for both female and male mate choice.

Materials and methods

We monitored 268 (in 2009) and 225 (in 2010) colonies of *C. cursor* for male activity near Argelès-sur-mer in southern

Correspondence: Adam L. Cronin, Laboratoire Écologie & Évolution UMR 7625, Université Pierre et Marie Curie, Paris VI, 7 quai St Bernard, 75252 Paris, France. E-mail: adamcronin@gmail.com

France, for 24 days spread over a total period of 38 days in 2009 (15 May to 22 June) and 12 days over a period of 27 days in 2010 (24 May to 19 June). We observed each colony once daily from 15 to 28 May, and once every other day from 29 May to 22 June in 2009. Monitoring in 2010 was more limited, and in the following account we rely primarily on 2009 data for seasonal trends. Single observations of males were regarded as transient and not recorded. See also Chéron *et al.* (2011a) for further details on methods and colonies monitored.

To investigate male mating frequency and longevity, we also marked and observed all males seen at the entrance of seven colonies between 25 and 29 May 2010. Each colony was observed 5–11 times, with each observation session lasting 5–40 min according to the level of activity. During each session any unmarked males were marked, marked males were censused and the number of matings recorded. We marked a total of 114 males (7–32 per colony) and performed a total of 743 min of observation. Marked males were each present for 28.4 min of observations on average. In most cases marking did not disturb behaviour, and males attempted to copulate a few seconds after being released. A mating was noted only when a male and gyne remained in copula for at least a few seconds, with the males in a characteristic position with the anterior legs spread. We did not record unsuccessful mating attempts as they were at times too numerous to track.

Results and discussion

We observed male activity at 27% (73 of 268) colonies in 2009, and 40% (91 of 225) colonies in 2010. Between 1 and 40 males were observed at any one time at a single entrance. The number of males censused daily at nest entrances is shown in Fig. 1, which indicates that male presence increased from the end of

May into early June and subsequently declined, with a total duration of approximately 1 month for the site in both 2009 and 2010 (see also Lenoir *et al.*, 1988). This coincided with the occurrence of colony fission (Chéron *et al.*, 2011a), which began on average 3.5 ± 2.8 days (SD) after the first males were observed at a given nest (range 1–11 days; $n = 19$ colonies from 2009). The duration of male presence at each nest varied from 1 to 19 days in 2009 (mean = 4.69 days, $n = 73$; Fig. 1, inset), though the longest uninterrupted presence was 5 days ($n = 4$). Our data on male activity indirectly demonstrate that emergence of females can be asynchronous over a wide area, such that sampling at any given time may not accurately reflect the pattern of sexual production in this species.

Male aggregations lasting several days at the nest entrance gives rise to two possible mechanisms for female mate choice in *C. cursor*: worker vetting of males and queen selection of males. Males harassed gynes as soon as they ventured outside of the nest, and queens attempted to avoid most mating attempts (see also Lenoir *et al.*, 1988). Gynes darted in and out of the nest among excited workers and frenzied males. Gynes apparent reluctance to mate likely reflects mate choice rather than unwillingness to mate, as gynes remained outside the nest when males were removed (for marking) or were absent. Workers often attacked all males present, such that to access elusive gynes males had to remain in the vicinity of the nest and constantly avoid attacks from workers. This implies that workers may take part in the mate choice process while gynes may to some degree be able to control with whom they mate. The aggressiveness of workers varied between colonies and in some colonies some males succeeded entering the nest for a few minutes, but we observed no clear difference in the behaviour of workers toward any given male.

Competition among males should be high in *C. cursor* as the sex ratio is male biased (1 : 4; Pearcy & Aron, 2006)
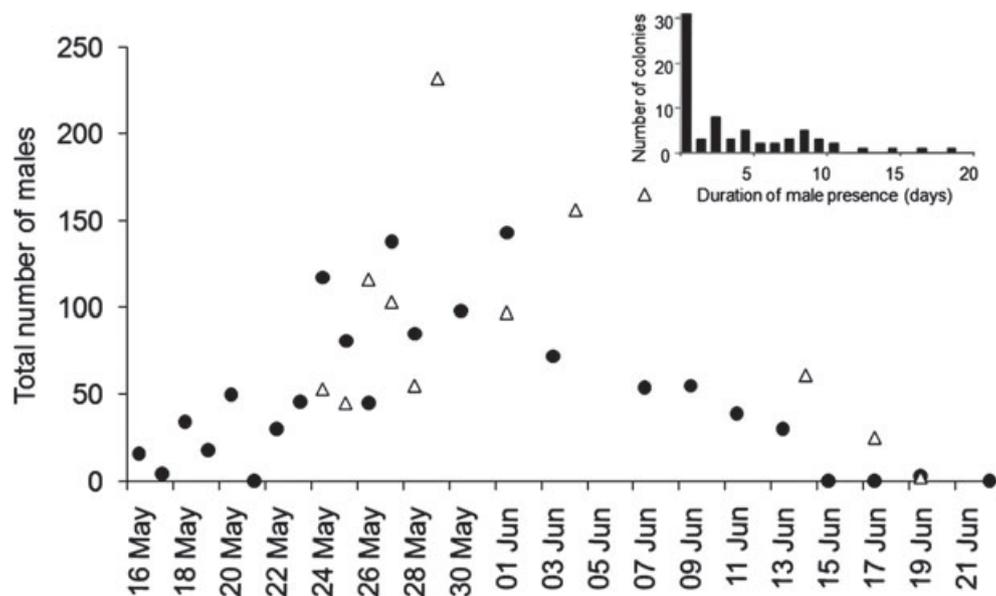
Fig. 1. Number of males present at the site in 2009 (black circles, $n = 268$ colonies) and 2010 (white triangles, $n = 225$ colonies) over the observation period. Inset: Histogram of the duration of male presence at 73 colonies in 2009.

Table 1. Summary of mating observations for seven colonies.

	Colony number						
	712	747	760	800	821	874	900
Number of days	3	3	3	3	4	4	3
Duration of observations (min)	41	118	88	141	157	145	53
Mean male presence (min)	34	41	25	25	26	28	20
Total sessions	5	5	9	7	11	11	9
Session with observations	3	5	7	6	7	7	6
Marked males	7	24	14	14	17	32	6
Matings	4	20	6	25	16	6	0
Males that mated at least once	3	9	5	7	6	6	0
Males that mated at least twice	1	4	1	5	4	0	0

Shown are number of days over which observations were taken, total duration of observations, mean time for which males were present during observations, total number of sessions, number of sessions where observations of mating behaviour were taken (i.e. those with activity, otherwise only censuses were taken), number of males observed and marked, number of matings observed, number of males that mated at least once and twice.

as in other species employing colony fission, and may be associated with a strong variance in male success. Thirty-six of the 114 marked males (31.6%) were observed mating, of which 15 (42% of those observed mating) mated multiply (Table 1). The maximum number of matings observed by a single male was eight, with seven of these occurring in one 20 min observation session during which a total of nine matings were observed. In many sessions, one or a few males clearly sought mating opportunities more actively than others and monopolised mating activity.

Multiple mating by males is thought to be rare in ants, although male mating strategies in social insects have suffered from a lack of attention to date (Boomsma *et al.*, 2005). Whereas selection may favour multiple mating in taxa where sperm is not limiting, spermatogenesis is discontinued in adult life in most ants (Hölldobler & Wilson, 1990), and thus there should be strong selection to optimise sperm usage. In most species the chance of repeated mating is so low that males are selected to invest all their sperm in a single queen. Males in *C. cursor* may benefit from mating multiply to maximise the chance of mating with a successful queen, as only very few will survive to head new nests produced by fission (Chéron *et al.*, 2011a). Recent work, however, demonstrates that males investing too little sperm when mating are unlikely to father future young queens (Chéron *et al.*, 2011b). Our data showed that multiple mating by males may be common in *C. cursor*, but how males allocate sperm to different partners deserves further study.

In *C. cursor*, young queens mate with, on average, six different males, presumably to increase genetic diversity among workers (Pearcy *et al.*, 2004). If this is true, queens should avoid mating with the same partner and, similarly, if multiple mating by males is an optimal strategy for gene transmission,

males should also avoid mating with the same queens. Males and queens would then have a common interest in avoiding re-mating with the same partner. Testing the potential for mate recognition would help clarify the underlying selective pressure driving the evolution of multiple mating in *C. cursor*.

Our preliminary data indicate that *C. cursor* could be a very interesting model to study questions relating to sexual selection and male mating strategies. The use of parthenogenetic reproduction by queens for producing gynes in this species markedly decreases the transmission of male genes, which may exacerbate competition among males and lead to evolution of elaborate counter measures (e.g. Fournier *et al.*, 2005). Male mating strategy can also affect female mating strategy indirectly if, for example, females are obliged to mate multiply to obtain sufficient numbers of sperm (Kraus *et al.*, 2004; Baer, 2005). Finally, although known to occur in other ants and bees (den Boer *et al.*, 2010), the potential for sperm competition and cryptic female choice in this species remains to be investigated.

Acknowledgements

References

Baer, B. (2005) Sexual selection in *Apis* bees. *Apidologie*, **36**, 187–200.

Baer, B., Schmid-Hempel, P., Hoeg, J.T. & Boomsma, J.J. (2003) Sperm length, sperm storage and mating system characteristics in bumblebees. *Insectes Sociaux*, **50**, 101–108.

Bartz, S.H. & Hölldobler, B. (1982) Colony founding in *Myrmecocystus mimicus* wheeler (Hymenoptera: Formicidae) and the evolution of foundress associations. *Behavioral Ecology and Sociobiology*, **10**, 137–147.

den Boer, S.P.A., Baer, B. & Boomsma, J.J. (2010) Seminal fluid mediates ejaculate competition in social insects. *Science*, **327**, 1506–1509.

Boomsma, J. & Ratnieks, F.L.W. (1996) Paternity in social Hymenoptera. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences*, **351**, 947–975.

Boomsma, J.J., Baer, B. & Heinze, J. (2005) The evolution of male traits in social insects. *Annual Review of Entomology*, **50**, 395–420.

Chéron, B., Cronin, A., Doums, C., Fédérici, P., Haussy, C., Tirard, C. *et al.* (2011a) Unequal resource allocation among colonies produced by fission in the ant *Cataglyphis cursor*. *Ecology*, DOI: 10.1890/10-2347.1.

Chéron, B., Monnin, T., Fédérici, P. & Doums, C. (2011b) Variation in patriline reproductive success during queen production in orphaned colonies of the thelytokous ant *Cataglyphis cursor*. *Molecular Ecology*, **20**, 2011–2022.

Fournier, D., Estoup, A., Orivel, J., Foucaud, J., Jourdan, H., Breton, J.L. *et al.* (2005) Clonal reproduction by males and females in the little fire ant. *Nature*, **435**, 1230–1234.

Franks, N.R. & Hölldobler, B. (1987) Sexual competition during colony reproduction in army ants. *Biological Journal of the Linnean Society*, **30**, 229–243.

Hölldobler, B. & Wilson, E.O. (1990) *The Ants.* Springer, Berlin, Germany.

Jaffé, R., Moritz, R.F.A. & Kraus, F.B. (2009) Gene flow is maintained by polyandry and male dispersal in the army ant *Eciton burchellii*. *Population Ecology*, **51**, 227–236.

Kaspari, M., Pickering, J., Longino, J.T. & Windsor, D. (2001) The phenology of a Neotropical ant assemblage: evidence for continuous and overlapping reproduction. *Behavioral Ecology and Sociobiology*, **50**, 382–390.

Kraus, F.B., Neumann, P., Praagh, J.V. & Moritz, R.F.A. (2004) Sperm limitation and the evolution of extreme polyandry in honeybees (*Apis mellifera* L.). *Behavioral Ecology and Sociobiology*, **55**, 494–501.

Lenoir, A., Quérard, L., Pondicq, N. & Berton, F. (1988) Reproduction and dispersal in the ant *Cataglyphis cursor* (Hymenoptera, Formicidae). *Psyche*, **95**, 21–44.

Pearcy, M. & Aron, S. (2006) Local resource competition and sex ratio in the ant *Cataglyphis cursor*. *Behavioral Ecology*, **17**, 569–574.

Pearcy, M., Aron, S., Doums, C. & Keller, L. (2004) Conditional use of sex and parthenogenesis for worker and queen production in ants. *Science*, **306**, 1780–1783.

Peeters, C. & Molet, M. (2010) Colonial reproduction and life histories. *Ant Ecology* (ed. by L. Lach, C. Parr and K. Abbott), pp. 159–176. Oxford University Press, Oxford, U.K.

Shik, J.Z. & Kaspari, M. (2009) Lifespan in male ants linked to mating syndrome. *Insectes Sociaux*, **56**, 131–134.

Thurin, N. & Aron, S. (2009) Sib-mating in the ant *Plagiolepis pygmaea*: adaptative inbreeding? *Journal of Evolutionary Biology*, **22**, 2481–2487.