Ins. Soc. *42:* 303–308 (1995)

1015–1621/95/030303–06 $ 1.50 + 0.20/0

Trophic eggs laid by fertile *Myrmica* queens (Hymenoptera: Formicidae)

J. C. Wardlaw and G. W. Elmes

Furzebrook Research Station, Institute of Terrestrial Ecology, Wareham, Dorset, BH20 5AS, UK

Key words: Myrmica, oviposition, queen, trophic egg.

Summary

Most mature *Myrmica rubra, M. ruginodis, M. schencki* and *M. sulcinodis* queens lay some trophic eggs in addition to reproductive eggs whether reared alone or attended by workers, and regardless of season. Queen trophic eggs resemble those laid by workers. They are oval, slightly flaccid, opalescent and contain no embryo, and in *M. rubra* and *M. schencki* they are significantly smaller than reproductive eggs. Generally, queens lay their first trophic eggs later in the season than their first reproductive eggs.

Introduction

Workers of *Myrmica* ants can lay a mixture of non-viable trophic and fertile male-potential reproductive eggs; the ratio of the 2 types of egg being determined by a complex balance between social and nutritional factors (Brian, 1983). Originally it was assumed that all trophic eggs were laid by workers and all reproductive eggs by queens in *Myrmica* queenright colonies (e.g. Brian and Rigby, 1978). Contact with a queen causes *M. rubra* workers to switch from producing reproductive eggs to trophic eggs (eg. Brian, Jones and Wardlaw, 1981, Smeeton, 1981).

No record exists for trophic egg production by *Myrmica* queens, either mated or virgin, although this has been reported for other genera (Passera, 1978; Taki, 1987; Vargo and Ross, 1989; Hölldobler and Wilson, 1990; Crespi, 1992). Despite rearing hundreds of virgin *Myrmica* queens in captivity we have never observed any eggs laid by them. Their ovaries do not develop fully until they have mated and hibernated; if they remain unmated in the nest they are killed by workers.

Methods

We investigated mature queen oviposition in 4 species – *Myrmica rubra* L., *M. schencki* Emery, *M. sulcinodis* Nyl. and *M. ruginodis* Nyl. Queens were kept at

21 °C ± 3 °C in "Brian" nests with ample food as described by Wardlaw (1991). Eggs were removed and counted weekly; 10 reproductive and 10 trophic eggs were weighed individually. Some of each type of eggs from each trial were kept on moist filter paper in sterile petri dishes for 2 weeks and the others were given to nestmate workers to nurse (any worker reproductive eggs laid subsequently by these nurses could be discriminated and removed from queen trophic egg cultures but not from queen reproductive egg cultures).

Fifty seven queens were reared solitarily. Of these, 9 *M. rubra* were collected in autumn and overwintered with some workers in a refrigerator, and 9 others were taken from the same nests postwinter (1 died soon after collection); 12 *M. schencki* were taken from 4 nests which had been overwintered in the refrigerator and 28 *M. sulcinodis* were collected in early summer from a single nest.

Seventeen queens were reared with workers. Two *M. rubra* queens and 20 workers were collected from 3 separate colonies in spring and divided into groups of 1 queen and 10 workers. The groups from each colony were dyed with either Coccinel Red or Sudan Black B-powdered, lipid-soluble vital dyes (Smeeton, 1981). After 3 weeks, the black queens were transferred to clean nests with their red nestmate workers and the red queens were reunited with black workers giving 3 paired replicates of a dyed queen with 10 contrasting workers. One red queen died a week later. In another experiment, 12 queens of *M. ruginodis* (6 each of var. *macrogyna* and of var. *microgyna*) which had been collected in autumn and overwintered in the refrigerator, were dyed with Coccinel Red before being transferred individually to groups of 20 or 100 undyed nestmate workers.

Trophic and reproductive eggs laid by queens were easily discriminated: trophic eggs were oval in shape, slightly flaccid and uniformly opalescent; reproductive eggs were kidney-shaped, firm when touched and translucent with zones of embryonic development visible after a few days (Fig. 1). When kept unattended by workers in

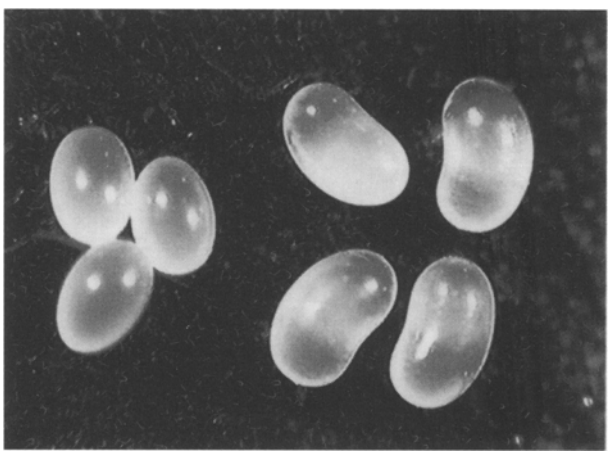

Figure 1. Eggs laid by a solitary *Myrmica schencki* queen in one week, comprising four kidney-shaped reproductive eggs and three smaller oval trophic eggs with thin chorions

Table 1. The number and type of eggs laid by queens of *Myrmica schencki*, *M. sulcinodis* and *M. rubra* in isolation and by single queens and workers of *M. rubra* and *M. ruginodis* when kept together. Eggs were either trophic = T or reproductive = R. All queens which laid trophic eggs also laid reproductive eggs = (T + R) Q; queens which laid only reproductive eggs = (R)Q. Means for individual queens or attendant workers were obtained by averaging their values over the study period. Mean values ± standard deviations for species were calculated from these means of individual queens or their workers.

Myrmica species	Solitary queens			Queens with workers		
	schencki	*sulcinodis*	*rubra*	*rubra*	*ruginodis var.*	
					macrogyne	*microgyne*
Queens	12	28[1]	17	5	6[1]	6
(R) Q	2	6	6	1	0	0
(T+R) Q	10	21	11	4	5	6
Mean wt (mg) of (R) Q	4.99 ± 0.88	5.36 ± 0.21	5.14 ± 0.71	5.73	*	*
Mean wt (mg) of (T+R) Q	5.09 ± 0.44	5.81 ± 0.36	5.81 ± 0.44	5.97 ± 0.41	*	*
Mean eggs/ R Q/day by	0.26 ± 0.04	0.83 ± 0.32	0.69 ± 0.31	1.10 ± 0.21	3.01 ± 3.59	3.99 ± 1.65
(T+R) Q T	0.14 ± 0.13	0.22 ± 0.14	0.21 ± 0.19	0.46 ± 0.23	1.04 ± 0.94	0.85 ± 0.39
Mean R/Q/day by (R) Q	0.28 ± 0.03	0.53 ± 0.29	0.40 ± 0.22	0.52	*	*
Mean R egg wt (µg) by (T + R) Q	70.7 ± 2.0	57.5 ± 5.5	48.3 ± 3.5	50.0 ± 1.6	44.6 ± 5.8	42.4 ± 3.9
Mean T egg wt (µg) by (T + R) Q	57.9 ± 7.5	62.0 ± 8.9	38.5 ± 7.5	41.5 ± 2.7	48.5 ± 6.4	42.8 ± 4.1
Mean R egg wt (µg) by (R) Q	73.5 ± 2.1	60.2 ± 6.0	46.2 ± 8.7	55.7 ± 4.4	*	*
Mean worker R/worker/day	*	*	*	0.003	0.12 ± 0.11	0.02 ± 0.03
Mean worker T/worker/day	*	*	*	0.05 ± 0.03	0.06 ± 0.06	0.07 ± 0.06
Mean worker R egg wt (µg)	*	*	*	42	54.16 ± 5.55	47.87 ± 5.57
Mean worker T egg wt (µg)	*	*	*	39.78 ± 3.63	49.93 ± 5.01	45.63 ± 7.05

[1] includes 1 non-laying queen, * no data available

petri dishes, no queen trophic eggs developed and most shrivelled and became mouldy during the second week, whereas almost all queen reproductive eggs showed signs of development after a week, and many hatched into first instar larvae. When reared by nurse workers, the queen reproductive egg cultures produced young workers and males (males possibly originated from reproductive eggs laid by the nurse workers) but the queen trophic eggs were inviable.

Over the study period, the mean weight, mean egg number and mean egg weights were calculated for each individual queen. For any group (e.g. *M. sulcinodis* queens producing only reproductive eggs, sample size n = 6, Table 1) these values were averaged to give an overall mean and standard deviation. Each queen therefore contributed a maximum 1 degree of freedom to statistical comparisons. These were made using "Student's" t test with variances assumed to be unequal. Correction for small sample sizes were made by calculating the degrees of freedom (df) for t using the method in Bailey (1959 p. 173). Each species was tested separately. Separate tests were also performed for *M. rubra* and *M. ruginodis* queens with workers; these included tests for the effects of worker presence in *M. rubra*, numbers of workers and queen variety in *M. ruginodis*.

Results

Only 2 queens laid no eggs at all (1 solitary *M. sulcinodis* and 1 *M. ruginodis var. macrogyna* with workers). All 72 others laid reproductive eggs and 57 laid some additional trophic eggs (Table 1). Queens which laid trophic eggs did not differ significantly (probability level $p > 0.05$) in weight from conspecifics which laid only reproductive eggs.

With the exception of *M. ruginodis var. macrogyna*, individual queens of all species produced significantly fewer trophic eggs than reproductive eggs (all $p < 0.02$). There was no evidence that queens produced significantly fewer reproductive eggs if they also laid trophic eggs. Weights of trophic eggs were more variable than reproductive eggs laid by the same queen and on average they were significantly lighter than reproductive eggs in *M. rubra* ($df = 20.9$, $p < 0.001$) and *M. schencki* ($df = 13.7$, $p < 0.001$) but not significantly different in *M. sulcinodis* and *M. ruginodis* (Table 1). On average, trophic eggs appeared 15 days later than reproductive eggs in cultures when queens had been overwintered in the laboratory and 7 days later in *M. sulcinodis* collected in summer. Some queens laid trophic eggs regularly over consecutive weeks, while others produced them sporadically. Both forms of egg were often laid by an individual queen within a week.

Queen and worker castes both contributed reproductive and trophic eggs when cultured together; queen eggs were indistinguishable from worker eggs other than by artificial coloration. In *M. rubra*, significantly more reproductive eggs were laid by queens with workers than by solitary queens ($df = 12.6$, $p < 0.02$) but their weight was similar. In *M. ruginodis*, the number of attendant workers did not affect the quantity or quality of queen oviposition. Unlike *M. rubra*, there was no evidence that *M. ruginodis* queens significantly suppress the production of reproductive eggs by workers.

Discussion

A queen which produces trophic eggs may improve the survival of her own offspring especially when founding a colony haplometrotically (Crespi, 1992). If workers are sterile, then even in large colonies a queen might enhance survival of

first instar larvae by providing them with an egg meal (Weir, 1959). The advantage of trophic egg production by *Myrmica* queens is less clear because workers are fertile and colony foundation by solitary queens is rare, most colonies being formed either by groups of queens or by colony budding. However, if newly mated *Myrmica* queens found haplometrotically sometimes, then it might be advantageous for them to lay trophic eggs, at least during their first season.

We did not know the age of our queens, but the high turnover of queens in *Myrmica* colonies makes it probable that a proportion (perhaps 50%) were first-year queens (Elmes and Petal, 1990). However 77% of queens laid trophic eggs so this trait is not confined to young queens. In spring, a proportion of fecund queens are often ejected from or desert established colonies (Elmes, 1982); these are not always first-year queens. The retention of the ability to lay trophic eggs beyond the first season might have evolved if these mature queens (>1 year old) attempt to found colonies solitarily or pleometrotically.

Solenopsis invicta Buren, whose workers do not lay viable or trophic eggs, provide the only published record of mature queens producing trophic eggs (Vargo and Ross, 1989). They recorded trophic eggs from inseminated queens taken directly from large polygynous field colonies. When such queens were kept individually with a group of nestmate workers and brood in the laboratory, equivalent to monogynous colony founding groups, they laid almost 100% embryonated eggs. Inseminated *S. invicta* queens laid fewer trophic eggs than uninseminated ones. *Myrmica* queens differ from *S. invicta* as virgin queens never lay eggs and mature queens usually lay a mixture of eggs, even in the presence of workers.

Queens with the most active ovaries attract most attention from workers (Cammaerts and Scanu, 1985). In highly polygynous colonies, the ability to produce additional trophic eggs might increase the attraction and thereby retention of surplus queens.

Acknowledgements

We wish to thank Ralph Clarke for his statistical advice and Laurent Keller for his helpful comments on the manuscript.

References

Bailey, N.T.J., 1959. *Statistical Methods in Biology.* The English Universities Press, London. 200 pp.

Brian, M.V., 1983. *Social Insects, Ecology and Behavioural Biology.* Chapman and Hall, London. 377 pp.

Brian, M.V., R.M. Jones and J.C. Wardlaw, 1981. Quantitative aspects of queen control over reproduction in the ant *Myrmica. Ins. Soc. 28*:191–207.

Brian, M.V. and C. Rigby, 1978. The trophic eggs of *Myrmica rubra* L. *Ins. Soc. 25*:89–110.

Cammaerts, M.-C. and M. Scanu, 1985. Étude des facteurs expliquant la variabilité des groupements d'ouvrières de *Myrmica rubra* L. (Hymenoptera: Formicidae) autours de leurs reines. *Annls. Soc. r. zool. Belg. 115*:13–28.

Crespi, B.J., 1992. Cannibalism and trophic eggs in subsocial and eusocial insects. In: *Cannibalism: ecology and evolution among diverse taxa* (M.A. Elgar and B.J. Crespi Eds.), Oxford University Press. pp. 176–213.

Elmes, G. W., 1982. The phenology of five species of *Myrmica* (Hym. Formicidae) from South Dorset, England. *Ins. Soc. 29*:548–559.
Elmes, G. W. and J. Petal, 1990. Queen number as an adaptable trait: Evidence from wild populations of two ant species (Genus *Myrmica*). *J. Anim. Ecol. 59*:675–690.
Hölldobler, B. and E. O. Wilson, 1990. *The Ants.* The Belknap Press of Harvard University Press, Cambridge, Mass., 732 pp.
Passera, L., 1978. Une nouvelle catégorie d'oeufs alimentaires émis par les reines vièrges de *Pheidole pallidula* (Nyl.) (Formicidae, Myrmicinae). *Ins. Soc. 25*:117–126.
Smeeton, L., 1981. The source of males in *Myrmica rubra* L. (Hym. Formicidae). *Ins. Soc. 28*: 263–278.
Taki, A., 1987. The trophic eggs of colony founding ant queens. In: *Chemistry and Biology of Social Insects* (J. Eder and H. Rembold Eds.), Verlag J. Peperny, München. p. 268.
Vargo, E. L. and K. G. Ross, 1989. Differential viability of eggs laid by queens in polygyne colonies of the fire ant, *Solenopsis invicta. J. Insect Physiol. 35*:587–278.
Wardlaw, J. C., 1991. Techniques for rearing *Myrmica* ants (Hym.) and *Maculinea rebeli* Hir. caterpillars (Lep., Lycaenidae). *Ent. Mon. Mag. 127*:233–241.
Weir, J. S., 1959. Egg masses and early larval growth in *Myrmica. Ins. Soc. 6*:187–201.

Received 19 December 1994;
revised 17 February 1995;
accepted 20 February 1995.