Sex-Ratio Regulation: The Economics of Fratricide in Ants

Michel Chapuisat, Liselotte Sundstrom, Laurent Keller

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Sex-ratio regulation: the economics of fratricide in ants

MICHEL CHAPUISAT[1,2*], LISELOTTE SUNDSTRÖM[2,3]
AND LAURENT KELLER[2]

[1] *Museum of Zoology, CP 448, CH-1000 Lausanne 17, Switzerland* (`michel.chapuisat@izea.unil.ch`)
[2] *Institute of Zoology and Animal Ecology, University of Lausanne, CH-1015 Lausanne, Switzerland*
[3] *Department of Ecology and Systematics, Helsinki University, P.O. box 17, FIN-00014, Finland*

SUMMARY

In many insect societies, workers can manipulate the reproductive output of their colony by killing kin of lesser value to them. For instance, workers of the mound-building *Formica exsecta* eliminate male brood in colonies headed by a single-mated queen. By combining an inclusive fitness model and empirical data, we investigated the selective causes underlying these fratricides. Our model examines until which threshold stage in male brood development do the workers benefit from eliminating males to rear extra females instead. We then determined the minimal developmental stage reached by male larvae before elimination in *F. exsecta* field colonies. Surprisingly, many male larvae were kept until they were close to pupation, and only then eliminated. According to our model, part of the eliminated males were so large that workers would not benefit from replacing them with new females. Moreover, males were eliminated late in the season, so that new females could no longer be initiated, because matings take place synchronously during a short period. Together, these results indicate that workers did not replace male brood with new females, but rather reduced total brood size during late larval development. Male destruction was probably triggered by resource limitation, and the timing of brood elimination suggests that males may have been fed to females when these start to grow exponentially during the final larval stage. Hence, the evolution of fratricides in ants is best explained by a combination of ecological, demographic and genetic parameters.

1. INTRODUCTION

Most animal societies are composed of genetically diverse individuals, which generates potential conflicts over reproduction. In social Hymenoptera (ants, bees and wasps), non-reproductive workers can maximize the transmission of copies of their own genes by raising preferentially reproductive individuals of greater kin-value to them (Trivers & Hare 1976; Bourke & Franks 1995; Crozier & Pamilo 1996). We have previously shown that workers of the mound-building *Formica exsecta* increased their inclusive fitness by killing male brood in colonies headed by a single-mated queen, and sparing them in colonies headed by a multiple-mated queen (Sundström *et al.* 1996). This is because, compared to the population average, female reproductives have a relatively greater kin-value to the workers than male reproductives in colonies headed by a single-mated queen (Boomsma & Grafen 1990, 1991).

However, reproductive manipulation through male elimination must entail costs, because the resources invested in rearing males until the moment of elimination are partly or completely lost. The earlier and more accurately males can be identified the lower are the costs of elimination. For example, honey bee workers eliminate male eggs laid by other workers (Ratnieks & Visscher 1989). However, once males have passed a certain threshold developmental stage, workers benefit more from rearing them to adulthood than from replacing them with individuals having higher kin-value (Nonacs & Carlin 1990).

A better understanding of the modalities of reproductive manipulation in animal societies can be obtained from detailed studies on sex-ratio changes during brood development in social insect colonies. Significant changes in sex ratio between eggs and adults have been demonstrated in several ant species (Aron *et al.* 1994, 1995; Keller *et al.* 1996; Passera & Aron 1996; Sundström *et al.* 1996), but only one of these studies determined the developmental stage at which males were eliminated. In the Argentine ant *Linepithema humile*, about half the male larvae were eliminated immediately after hatching, whereas the remaining males were eliminated shortly before pupation (Passera & Aron 1996). However, the relative costs and benefits of male brood destruction could not be estimated in this laboratory study.

The aim of this study was to characterize the process and selective causes of male elimination in field colonies of the ant *F. exsecta*. We developed an inclusive fitness model to determine the threshold stage in male development below which workers benefit

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[*] Author for correspondence.

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from replacing males with extra females. We then determined changes in colony sex ratios between egg, larval and pupal stages in colonies which produced female-biased adult sex ratios. These empirical data were used to infer the developmental stage at which male larvae were eliminated and to determine the selective causes underlying fratricide.

2. MATERIAL AND METHODS

The study population comprised 59 colonies of *F. exsecta* located on three islands in the archipelago near Tvärminne, southern Finland. The number of queens per colony, the number of queens' mates, egg and pupal sex ratios had been assessed previously (Sundström *et al.* 1996). For the current study, we selected eight colonies that satisfied four criteria: (1) colonies were headed by a single queen; (2) they contained both male and female eggs; (3) at least 96% of the pupae were females; and (4) haploid males could be unambiguously discriminated from diploid females on the basis of their genotypes, because 20 workers which had been analysed previously were all heterozygous at least at one microsatellite locus. In seven of the selected colonies the queen was single-mated, and in one colony (J31) the queen was double-mated.

Brood was searched for in different parts of the nest mound, and sampled randomly, to avoid a potential bias if males and females were spatially segregated. Eggs were collected between 11 and 18 May 1995, and sexed by counting the number of chromosomes (Sundström *et al.* 1996). Larvae were collected from all colonies on 8 June. Additional larvae were also collected from one colony (J5) on 12 and 24 May. We measured the length of all larvae to the nearest millimetre and dried a subsample at 50 °C for 24 h to determine dry weight. Larvae were sexed on the basis of their genotype at two microsatellite loci, FL21 and FL20 (Chapuisat 1996). Most of the brood laid early in the season develops into sexuals, and only a minor fraction of the diploid eggs and larvae sampled may have developed into workers (Sundström *et al.* 1996). Pupae were collected between 5 and 9 July and sexed by morphology. The dry weights of pupae and adults of both sexes were measured from samples taken from the experimental colonies and from additional nests in the same population.

One colony was excluded from the analysis, because it provided results which strongly suggested an error during data collection. In this colony, the proportion of females was 61% at the egg stage ($n = 28$) and 98% at the pupal stage ($n = 50$), yet all the larvae collected were males ($n = 41$).

3. RESULTS

(*a*) *The model*

This model determines the threshold in male development below which workers benefit from eliminating males and rearing extra females instead. Specifically, workers should destroy male brood as long as the fitness return per unit of resources still to be invested in the brood is smaller if they rear the existing male brood to adulthood than if they rear new female brood. For workers, the inclusive fitness pay-off provided by a male or a female equals the regression relatedness of this male or female to workers (b_{m} or b_{f}) multiplied by it's sex-specific reproductive value (the contribution of this sex to the genetic constitution of the next generation, V_{m} or V_{f}) and by the relative mating success of each sex (Grafen 1986; Pamilo 1991). If F is the population-wide numerical sex ratio expressed as the proportion of females, the relative mating success of a female is $1/F$ and that of a male is $1/(1-F)$. The amount of resources needed to raise a female is C times that needed to rear a male. Let x denote the fraction of the total resources needed to rear an adult male that has already been invested in a developing male at the time of its potential elimination. If we first assume that resources invested into a male are completely lost when eliminated, workers would benefit from replacing a male at stage x with a new female when

$$\frac{b_{\mathrm{m}}V_{\mathrm{m}}}{(1-x)(1-F)} < \frac{b_{\mathrm{f}}V_{\mathrm{f}}}{CF}; \tag{1}$$

that is, when the fitness return from a male $(b_{\mathrm{m}}V_{\mathrm{m}}/(1-F))$ divided by the relative amount of resources still needed to rear this male to adulthood $(1-x)$ is smaller than the fitness return from a female $(b_{\mathrm{f}}V_{\mathrm{f}}/F)$ divided by the relative amount of resources required to rear a new female (C).

Solving (1) for x gives

$$x < 1 - \frac{FCb_{\mathrm{m}}V_{\mathrm{m}}}{(1-F)b_{\mathrm{f}}V_{\mathrm{f}}}. \tag{2}$$

However, if a proportion, E, of the resources invested in male brood can be recycled into female brood, the amount of resources needed to raise a female is reduced by Ex. Thus, inequality (1) becomes

$$\frac{b_{\mathrm{m}}V_{\mathrm{m}}}{(1-x)(1-F)} < \frac{b_{\mathrm{f}}V_{\mathrm{f}}}{F(C-Ex)}. \tag{3}$$

Solving (3) for x gives

$$x < \frac{(1-F)b_{\mathrm{f}}V_{\mathrm{f}} - FCb_{\mathrm{m}}V_{\mathrm{m}}}{(1-F)b_{\mathrm{f}}V_{\mathrm{f}} - EFb_{\mathrm{m}}V_{\mathrm{m}}}. \tag{4}$$

(*b*) *Empirical estimation of the model's variables*

In a colony headed by a single-mated outbred queen, $b_{\mathrm{f}}V_{\mathrm{f}}$ equals 0.75 and $b_{\mathrm{m}}V_{\mathrm{m}}$ equals 0.25, if all males are produced by the queens, which is largely the case in our study population (Sundström *et al.* 1996). The observed population-wide numerical sex ratio, F, was 0.65 females (Sundström *et al.* 1996). If we assume that energy is the limiting resource, then an estimate of the energetic cost ratio, C, can be obtained from the dry weights of adult females and males. In the study population, the dry weight of adult females was 4.9 ± 0.4 mg and that of males was 3.9 ± 1.0 mg (mean over colonies ± s.d., $n = 20$ (Sundström *et al.* 1996)). Hence, the female-to-male energetic cost ratio was 1.17, as estimated from dry weight ratio with a 0.7 power conversion (Boomsma 1989; Boomsma *et al.* 1995). Replacing all parameters in the right-hand term of inequality (2) by the above empirical estimates, one can calculate that, when the energy invested into males cannot be recycled, workers benefit from replacing males by females only if less than 27% of the total energy needed to raise an adult male has already been invested into males.

However, part of the energy invested into males can be recycled into females through cannibalism. The energy transfer efficiency can be estimated by multiplying the assimilation efficiency (the proportion of ingested energy that is assimilated across the gut wall) by the production efficiency (the proportion of assimilated energy that is incorporated into new biomass) (Begon *et al.* 1990). For carnivorous insects, the assimilation efficiency is typically around 0.8, and the production efficiency around 0.56, which is the highest value reported for animals (Begon *et al.* 1990). Hence, E may be as high as 0.45 for ants that cannibalize larvae. If 45% of the energy invested into males is converted into new females, inequality (4) shows that workers enhance their inclusive fitness if they replace males by new females before the males have reached 38% of their total development in terms of energy.

In order to determine the larval weight that corresponds to the above thresholds, a weight reflecting the total energy needed to produce adult males should be estimated. The dry weight of male larvae at the time of pupation provides such an estimate, because little energy is invested in males after pupation (figure 1) (Boomsma & Isaaks 1985; Passera & Keller 1987). Two lines of evidence suggest that the largest larvae found in our sample had reached their maximal size and were ready for pupation. First, at pupation, larvae build a silk cocoon around themselves, and therefore cocoon length should reflect the maximal larval size. Male cocoons measured 7.3 ± 0.6 mm (mean over individuals ± s.d., $n = 72$), a length close to that of the largest male larvae found in our sample, which measured between 6.5 and 7.5 mm ($n = 13$ individuals). Second, larvae between 6.5 and 7.5 mm had a mean dry weight of 6.3 ± 0.6 mg (mean over individuals ± s.d., $n = 10$, figure 1), which is about 30% heavier than the pupae, and clearly indicates that these larvae were close to pupation (figure 1) (Horstmann 1982; Boomsma & Isaaks 1985; Passera & Keller 1987). If we assume that the mean dry weight of male larvae just before pupation is 6.5 mg, then 27 and 38% of the final investment in a male correspond to larval weights of 1.8 and 2.5 mg, respectively.

(*c*) *Developmental stage of males when eliminated*

In the study colonies, between 20 and 78% of the eggs were males (table 1). In four colonies, no males were found among the larvae sampled on 8 June, and the proportion of males decreased significantly between egg and larval samples. By contrast, the proportion of males among larvae was still high (21–87%) in the remaining three colonies, with no significant change compared to the egg stage. In these three colonies, the proportion of males significantly decreased between larval and pupal samples. The proportion of males at the pupal stage was very low in all colonies (0–4%).

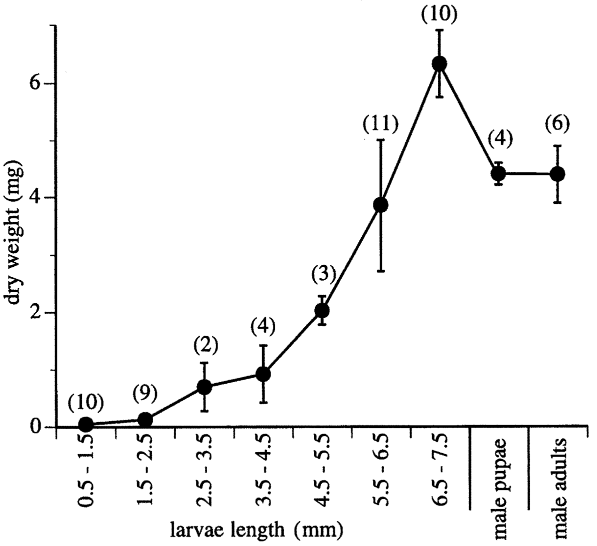

Figure 1. Dry weight (mean ± s.d.) of larvae, pupae and adults. Sample sizes are given in parentheses (number of individuals for larvae, number of colonies for pupae and adults).

Table 1. *Proportion of males among eggs, larvae and pupae in field colonies of* Formica exsecta

(Sample sizes are given in parentheses. Superscript lowercase letters indicate the date of sampling: a, 11.5.95; b, 12.5.95; c, 13.5.95; d, 18.5.95; e, 12 and 24.5.95; f, 8.6.95; g, 5.7.95; h, 6.7.95; i, 9.7.95. Significance of sex-ratio changes between eggs and larvae (1) and between larvae and pupae (2): ns = $p > 0.05$, $* = p < 0.05$, $** = p < 0.01$, $*** = p < 0.001$ (Fisher's exact test).)

colony	eggs	(1)	larvae	(2)	pupae
J31	0.33 (27)^a	ns	0.63 (27)^f	***	0.02 (50)^g
J27	0.21 (24)^a	ns	0.21 (29)^f	**	0.02 (50)^g
Kh7	0.78 (27)^c	ns	0.87 (23)^f	***	0.00 (50)^i
J5	0.20 (25)^b	ns	0.36 (14)^e	***	0.02 (50)^h
		*	0.00 (31)^f	ns	
J10	0.23 (31)^d	*	0.00 (27)^f	ns	0.02 (50)^h
J26	0.33 (24)^a	**	0.00 (20)^f	ns	0.04 (50)^g
J30	0.54 (28)^a	***	0.00 (28)^f	ns	0.00 (50)^g

The minimum weight reached by male larvae before elimination can be estimated for the three colonies in which most males were eliminated after larval sampling on 8 June (table 1). This is simply the weight of male larvae at the time of sampling. In these three nests, male larvae weighed on average 2.0, 2.3 and 4.7 mg (table 2). Hence, the weight of male larvae averaged over colonies was 3.0 ± 1.5 mg (mean ± s.d., $n = 3$). This is slightly, but not significantly, higher than the 2.5 mg developmental threshold at which male replacement by extra females ceases to be beneficial, under the assumption that energy is recycled with high efficiency ($E = 0.45$). Overall, 47% of the male larvae were above this threshold, and in one colony (Kh7), the mean weight of male

Table 2. *Mean length and weight of male and female larvae found in each colony*

(95% confidence intervals are given in parentheses. Data from additional samplings in colony J5 on 12 and 24 May were pooled, due to small sample size.)

colony	date	sex	length (mm)	weight (mg)	n
J31	8.6	F	3.2 (2.5–3.9)	0.9 (0.4–1.3)	10
		M	4.6 (4.0–5.2)	2.0 (1.3–2.6)	17
J27	8.6	F	3.8 (3.4–4.3)	1.2 (0.9–1.5)	23
		M	5.2 (4.7–5.6)	2.3 (1.6–3.1)	6
Kh7	8.6	F	2.0 (2.0–2.0)	0.1 (0.1–0.1)	3
		M	5.9 (5.0–6.8)	4.7 (3.5–5.9)	20
J10	8.6	F	5.3 (4.7–5.8)	3.1 (2.4–3.9)	27
J26	8.6	F	5.1 (4.4–5.7)	2.7 (2.1–3.4)	20
J30	8.6	F	5.6 (4.9–6.3)	4.1 (3.1–5.0)	28
J5	8.6	F	5.6 (5.0–6.2)	3.9 (3.1–4.8)	31
J5	12, 24.5	F	1.0 (1.0–1.0)	0.05 (0.05–0.05)	9
		M	1.0 (1.0–1.0)	0.05 (0.05–0.05)	5

larvae was significantly higher (table 2; $t_{19} = 3.9$, $p < 0.001$). Hence, these results suggest that a considerable proportion of males were eliminated at such an advanced developmental stage that it would not pay the workers to replace them with extra females.

The developmental stage of male larvae at elimination cannot be determined precisely for the four colonies in which only female larvae were found. However, our data suggest that males in these four colonies might also have reached an advanced developmental stage before being eliminated. This is because brood from these colonies were in a more advanced developmental stage than brood from other colonies: female larvae in these colonies were significantly heavier than female larvae in colonies containing male larvae (table 2; $t_5 = 6.0$, $p = 0.002$). Moreover, in the colonies where larvae of both sexes were found, male larvae were significantly heavier, and thus in a significantly more advanced developmental stage, than female larvae (table 2; two-way ANOVA: $F_{1,73} = 28.7$, $p < 0.0001$). There was no significant effect of colony ($F_{2,73} = 1.7$, $p = 0.18$), but a significant interaction ($F_{2,73} = 5.8$, $p = 0.005$) between sex and colony, indicating that the weight difference between males and females varied among colonies. Thus, colonies where only female larvae were found might have been sampled after males had reached an advanced developmental stage, and been eliminated. Data from colony J5, where samples of larvae were collected at different dates, also support this view. On 12 and 24 May, this colony contained very small larvae of both sexes, and the sex ratio equalled that of the eggs (table 1 and 2). However, on 8 June this colony contained only female larvae that were close to pupation (table 2).

4. DISCUSSION

A surprising finding of this study is that workers of the ant *F. exsecta* eliminated a significant proportion of their brothers, and possibly all of them, at a late developmental stage, when they were close to pupation. Our model shows that workers destroyed males that had grown beyond the threshold size before which workers should replace males with extra female to increase their inclusive fitness. Moreover, at least part of the males were eliminated when they were more than three weeks old. This late elimination suggests that these males were not replaced by a new batch of female sexuals, because in *F. exsecta* sexuals are produced synchronously and mate during nuptial flights that start shortly after the first sexuals mature, and last for at most three weeks, usually less (L. Sundström, personal observation).

Hence, the question arises: why was male brood eliminated at such a late developmental stage? One cause may be the necessity to eliminate part of the brood due to resource limitation. In this case, workers would still maximize there inclusive fitness by selectively eliminating the sex to which they are less related compared to the population average; that is, males in colonies headed by single-mated queens. This accounts for both the fact that workers eliminated brood late in development, and the fact that workers selectively eliminated males.

Late brood reduction is common in many insect, amphibian, fish, bird and plant species (Mock & Forbes 1995), in which supernumerary offspring are initiated and culled if resources become limiting (Lack 1947). In *F. exsecta*, colonies cannot react to an unusual excess of resources during late brood development by initiating a new batch of sexual brood, because all matings occur over a short period. Therefore, the best strategy for all colony members might be to initiate more brood than can usually be reared, and to eliminate part of the brood unless resources turn out to be particularly abundant.

In case of starvation, supernumerary brood can be used to feed larvae. Food shortage has been shown to trigger sibling cannibalism in various animals, including ants, beetles, bees, amphibians and predatory birds (Sorensen *et al.* 1983; Mock & Forbes 1995). In *F. exsecta*, resources may initially suffice to feed large numbers of small larvae, but shortage is likely to occur during the final larval instar of the females, when they grow exponentially and in synchrony. At this particular stage, males might be eliminated to feed the females. Hence, workers might use male brood to store resources. It has long been recognized that ant larvae could serve for storage function (Wilson 1971). This role of larvae might be particularly important in predator ants, because insect preys degrade quickly and cannot be stored in raw form.

The hypothesis that males were eliminated to sustain female growth during the final larval instar is consistent with our data. No males were found in colonies with females above 2 mg (figure 2), and in colony Kh7 very large males were found together with exceptionally small females (table 2). This suggests that males might be eliminated regardless of their developmental stage once females have reached a given size. By contrast, if each male had been kept until a certain size and then eliminated, some small

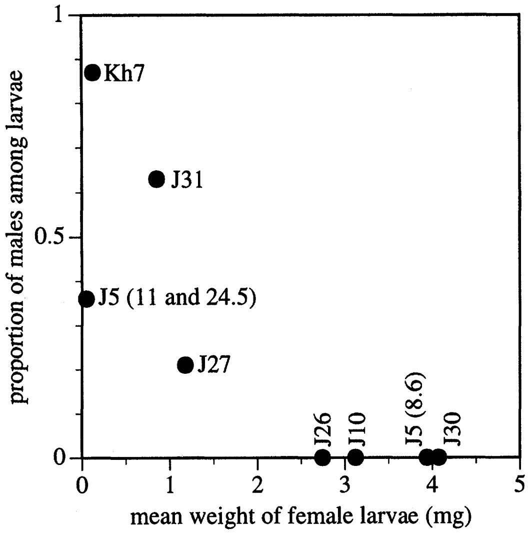

Figure 2. Sex ratios among larvae as a function of dry weight of female larvae.

males should also have been found in colonies containing large female larvae.

The above hypothesis accounts for late male elimination, but does not explain why workers did not replace supernumerary males with extra females earlier on. Two mutually non-exclusive hypotheses may explain this. First, early sex-ratio biasing may entail a high cost if workers make errors when determining the sex of young brood. A high error rate early in development may arise if the mother queen and males conceal the sex of the brood, in order to resist workers' manipulation (Nonacs & Carlin 1990; Nonacs 1993). Workers may thus reduce the costs associated with errors by postponing male elimination until males and females can be reliably distinguished. Second, queens may prevent early sex-ratio biasing by limiting the number of female eggs. If there are not enough extra female eggs to replace young male larvae, workers might be forced to keep supernumerary males.

In conclusion, late elimination of males in *F. exsecta* might be accounted for if ecological, demographic and genetic parameters are considered simultaneously. Our hypothesis that resource limitation triggers selective elimination of males could be experimentally tested by manipulating resources during brood development. The prediction is that colonies with increased resource levels should produce less marked bimodal sex ratios because more food is available to also rear the less preferred sex. In particular, colonies headed by single-mated queens should start producing some males if resources are augmented. By contrast, colonies with reduced resource levels should produce one sex only, and the sex will depend on the relative relatedness asymmetry of the colony, according to split sex-ratio theory (Boomsma & Grafen 1990, 1991). Such predictions are distinct from those based on resource abundance influencing queen–worker caste determination (Nonacs 1986), local mate competition (Frank 1987) and multifaceted parental investment (Rosenheim *et al.* 1996). In general, these three hypotheses predict increased female investment with increasing resources, independently of relatedness asymmetry. However, the four hypotheses mentioned above are not mutually exclusive.

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