

THE KILLING OF NESTMATE QUEENS IN ANT COLONIES

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ABSTRACT

I review the literature on the killing of queens by conspecific nestmates in ant colonies, with special emphasis on the red imported fire ant, *Solenopsis invicta* Buren (Hymenoptera: Formicidae.) Killings in pleometrotic associations and incipient colonies are distinguished from those occurring in secondarily formed polygynous colonies. In the former, queen mortality follows a typical pattern where all queens except one are killed or abandoned following worker emergence. In the latter, queen eliminations serve partly to counterbalance increases in queen abundance that may result from adoptions of related or unrelated queens. Pheromones produced by queens apparently trigger workers to execute queens, but the compounds have never been identified. Characterization of the "execution" pheromone of *S. invicta* has been a major objective of my research over the past several years, and I comment on progress towards this goal.

INTRODUCTION

Within colonies of social insects, queens are often killed, and I here review the literature and comment on recent research on such killings in ants (Hymenoptera: Formicidae). The discussion is restricted to executions by workers or other queens of the same species. Emphasis is placed on the red imported fire ant, *Solenopsis invicta* Buren, the myrmecine featured in this supplemental issue.

The number of wingless queens harbored by an ant colony ranges widely, from zero to over a hundred (Hölldobler and Wilson 1990, Elmes and Keller 1993). A single queen (monogyny) is typical of most species, but multiple queens (polygyny) can be common especially in social parasites, and in species specializing on short-lived nest sites or long-lived patchily distributed habitats (Hölldobler and Wilson 1977). Polygyny is either primary or secondary. In the former, foundresses form a group to start a new nest (pleometrosis), and they and their workers continue to tolerate each other through colony maturation (Hölldobler and Carlin 1985, Mintzer 1987, Rising and Pollock 1988, Rissing et al. 1989, Trunzer et al. 1998). In the latter, colonies fuse or they adopt young queens. The adopted queens are either foreign individuals or queens returning to their own natal nest following their nuptial flight (Stuart et al. 1993, Goodisman and Ross 1997, Sundström 1997).

Queens are commonly killed in both pleometrotic associations and in secondarily formed polygynous colonies (Rissing and Pollock 1987, Keller et al. 1989). Their

elimination may occur when direct conflict between queens escalates and culminates in death (Heinze 1993), or when workers attack and execute them (Bartz and Hölldobler 1982, Fig. 1). Such killing of queens by nestmates has garnered modest attention by researchers from both basic and practical perspectives. Rationales for studies have included clarifying proximate and ultimate causes of the behavior, and uncovering traits linked to greater risk of mortality. My own efforts over the past several years have involved exploring the pheromonal basis of worker execution of queens in *S. invicta*, with the ultimate goal of exploiting the behavior to induce self-destruction of colonies.



FIG. 1. Workers (*S. invicta*) attacking and dismembering one of their queens. An executed queen often ends up with her head, limbs and gaster severed from the thorax.

PLEOMETROSIS AND QUEEN ELIMINATION

Pleometrosis is one of several successful strategies employed by ants to navigate the challenging founding stage, and foundresses partaking in it experience various advantages over those initiating colonies independently. Pleometrotic queens, for instance, tend to have reduced mortality, raise more brood, produce larger minors, and raise both workers and sexuals sooner (Stumper 1962, Taki 1976, Mintzer 1979, 1987, 1990, Hölldobler and Carlin 1985, Rissing and Pollock 1987, Vargo 1988, Peeters and Andersen 1989, Sommer and Hölldobler 1995, Cahan and Julian 1999, Kenne et al. 2000). In *S. invicta*, pleometrosis during the claustral phase of nest founding increases total offspring output (Tschinkel and Howard 1983, Tschinkel 1993), but does not improve mortality rates of foundresses like in *Lasius flavus* Fabricius (Waloff 1957). Maximum initial production of workers is achieved by queens in groups of intermediate size (Tschinkel and Howard 1983), as is the case with *Myrmecocystus mimicus* Wheeler (Bartz and Hölldobler 1982) and *Formica podzolica* Francoeur (Deslippe and Savolainen 1995).

Queens in pleometrotic associations often die from both natural causes like starvation and aggressive social interactions during colony development. Their death rates tend to increase dramatically once workers begin eclosing, for fighting among queen escalates as in *Azteca xanthacroa* Roger (Choe and Perman 1997) or workers harass some queens but not others as in *M. mimicus* (Bartz and Hölldobler 1982). Normally, the killings continue until only a single queen remains alive. In *Messor pergandei* Mayr, for instance, foundresses contribute equally to nest excavation, oviposition and brood care, and they only begin to fight and die regularly six days after workers first emerge (Rissing and Pollock 1986, 1987). Likewise in *L. niger* Linnaeus, queens are amicable, but they fight for hours and to the death once workers first appear (Sommer and Hölldobler 1992). Experimental removal and addition of workers confirmed that worker presence indeed triggered fighting, as removal prolonged cooperation and addition generated premature fighting (Sommer and Hölldobler 1995).

A switch from a closed to an open energy system explains the pulse of killings following worker eclosion in cases where foundresses are claustral and unrelated (Rissing and Pollock 1986). In claustral species, queens remain in their sealed founding chambers and rear their first brood entirely on stored reserves and the metabolic breakdown of the body (Keller and Passera 1989, Wheeler and Buck 1995, 1996). As the system is closed to food input, foundresses, in theory, should avoid escalated contests to preserve energy. Conversely, once the system opens to food input, the cost to benefit ratio of extra foundresses increases, and their elimination serves both to reduce food competition and to supply nutrients via cannibalism (Rissing and Pollock 1986, Reeve and Ratnieks 1993, Tschinkel 1993). As pleometrotic queens are normally unrelated (Hagen et al. 1988, Rissing et al. 1989, Sasaki et al. 1996), benefits associated with inclusive fitness do not apply (Hamilton 1964).

Although queen mortality follows a typical pattern, there are exceptions to and much variation within the pattern. For example, queens of both *Pachycondyla villosa* Fabricius (Trunzer et al. 1998) and the non-claustral *Acromyrmex versicolor* Pergande (Cahan and Julian 1999) live together in harmony, and they continue to do so even in the presence of workers, enabling the unusual transition to primary polygyny. Fighting, in sharp contrast, is common throughout the founding period among co-foundresses of *Camponotus ferrugineus* Emery (Fowler and Roberts 1983) and *F. podzolica* (Deslippe and Savolainen 1995). In the latter, this aggression frequently culminates in dismemberment, and accounts for the majority of deaths. In *S. invicta*, as in most pleometrotic species, foundress associations usually develop into monogyne colonies after eclosion of the first workers (Taber 2000). On one hand, however, queens occasionally die before worker eclosion and at least sometimes from overt aggression (Adams and Tschinkel 1995, Bernasconi and Keller 1996, 1998, 1999). On the other hand, they may continue to coexist for weeks and even months after worker eclosion (Balas and Adams 1996a, Bernasconi and Keller 1998).

Do winning queens prevail over others because they possess particular characteristics? Occasionally, yes, but trends are weak at best. Sometimes the largest or heaviest queen tends to win (Bartz and Hölldobler 1982, Nonacs 1990, Balas and Adams 1996a, Bernasconi and Keller 1996, 1998, 1999). Other times the most productive egg-layer or queen closest to the brood tends to win (Balas and Adams 1996a; Bernasconi et al. 1997). The lack of strong trends is not especially surprising, for if winning were always associated with a trait like larger body size, inferior competitors would have no chance of surviving or producing reproductive offspring. Faced with only zero fitness, we should never observe them forming pleometrotic associations with non-relatives (Strassman 1989).

Who becomes victorious is also likely influenced by whether it is the queens themselves or the workers who do the killing. When the former are involved, selection should favor improved fighting ability of queens. Investigators typically assume such ability is associated with larger size or weight (Nonacs 1992, Balas and Adams 1996a; Bernasconi and Keller 1999), but the link may be weaker than presumed. For instance, sometimes queens are heaviest because they become physogastric sooner, and their cumbersome gasters then inhibit rather than promote fighting ability (personal observations on *F. podzolica*). Likewise, smaller queens can be superior fighters and readily kill larger ones, as illustrated in dynamics between parasitic and larger host queens during usurpation of colonies (Hölldobler and Wilson 1990). When workers eliminate the supernumerary queens, they may do so on the basis of pheromone production by queens. If such production is linked to ovarian development as in *S. invicta* (Vargo 1992, 1999), then selection should favor greater brood production. Greater production should also be favored when workers can distinguish their mothers from other queens, because a queen should have a better chance of surviving when most of the offspring are her own.

Survivorship of incipient colonies depends critically upon the initial investment in workers, as a larger or more able force can better withstand threats to the colony (Tschinkel and Howard 1983, Jerome et al. 1998). One such threat is intraspecific brood raiding resulting from intense competition among young colonies (Bartz and Hölldobler 1982, Rissing and Pollock 1987, 1991, Nonacs 1993, Adams and Tschinkel 1995). During raids, workers transport eggs, larvae and pupae between nests until they accumulate in the winning colonies. Workers from the losing colonies then join the victors, leaving behind their queens. Generally, neither raiding nor raided workers attempt to recruit the raided queen, but sometimes the abandoned queens try to join the strengthened colonies and successfully displace the original queens (Stamps and Vinson 1991, Tschinkel 1992a,b, Balas and Adams 1997).

The abandonment of nestmate queens can be adaptive when colony takeover is possible. In essence, workers make the best of a bad situation by hoping their queen can usurp the colony to which they have relocated (i.e., the "hopeful co-emigration" hypothesis) (Pollock and Rissing 1989). Support for this notion comes from the most studied of the brood raiding species, *S. invicta*. In this ant, attempts at usurpation succeed more often when the migrating queen penetrates a colony with familiar workers (Adams and Tschinkel 1995, Balas and Adams 1996b, 1997). They are also more successful when abandonees enter a colony within a few hours following conclusion of brood raiding (Balas and Adams 1997). Presumably, the challenger is desperate, for failure to takeover a colony ensures her imminent death.

SECONDARY POLYGYNY AND QUEEN EXECUTIONS

Following a queenright (i.e., one queen per nest) period, queen abundance can increase because workers sometimes adopt either related or unrelated queens into their nests, or because alate queens shed their wings despite not being fertilized. Although workers of monogyne forms normally adopt only when their colonies are queenless (Fletcher and Blum 1983, Sorensen and Fletcher 1985), workers of polygyne forms adopt more readily even when their colonies house fertilized queens (Fletcher and Blum 1983, Brian 1988, Glancey and Lofgren 1988, Fortelius et al. 1993, Sundström 1997). The resulting increase in nestmate queens can be substantial, and may be counterbalanced by their executions. This combination of adoptions and executions enables the critical ability to regulate queen abundance.

When queens are killed in polygynous colonies, workers usually perform the deeds rather than other queens, especially when populous colonies are formed and queens

are poorly equipped for fighting as in *S. invicta* (Wilson 1966, Fletcher and Blum 1983, Lipski et al. 1992, Heinze 1993). In such colonies, workers are larger, and are more numerous and aggressive than those in incipient colonies. These traits facilitate the process of workers overcoming their nestmate queens, which are normally larger and, understandably, resistant to their own execution. Further, at least some of the dealated queens in polygynous colonies are older than those in incipient colonies, thus probably making them better pheromone producers. Elevated pheromone production may enable queens to control worker behavior better, including control over worker execution of other queens (Fletcher and Blum 1983, Fletcher and Ross 1985, Fletcher 1986). In this way, queens can indirectly kill other nestmate queens.

A remarkable pulse of queen executions occurs at the beginning of the reproductive season in the Argentine ant, *Linepithema humile* Mayr. Every spring, about 90% of nestmate queens are killed by workers, resulting in a loss of about 8% of the total biomass of the colony (Markin 1970, Keller et al. 1989). Markin (1970) noted that workers attacked queens as they would large prey, and described an event where many queens joined workers on the foraging trails. Workers attacked about 10% of these queens and eventually severed the gasters and heads of their victims. Further study of the phenomenon revealed that the age, weight and fecundity of queens played no substantial role in which individuals that workers selected for execution (Keller et al. 1989). The drastic reduction in queens enables female larvae to develop as new queens, apparently a result of being released from the inhibitory effect of a queen primer pheromone (Vargo 1998).

INVOLVEMENT OF PHEROMONES

The fertility of a queen is positively associated with her pheromonal influence (Fletcher and Blum 1983, Willer and Fletcher 1986, Cariou-Etienne and Passera 1993). In *S. invicta*, the shedding of wings corresponds to rapid changes in the endocrine system of queens, and these changes stimulate pheromone production and ovary development (Vargo 1999). As a result, wingless queens are superior over winged ones in controlling nestmates via pheromones (Vargo and Fletcher 1986, 1987). Less than 50% of wingless queens may be fertilized in *S. invicta* colonies, and although they tend to be more fecund than their unfertilized nestmates (Vargo and Fletcher 1989), dealate queens, regardless of reproductive status, are more effective than alate queens at pheromonal control. The rate of worker execution of sexual larvae, for example, was significantly greater in queenright than in queenless colonies, but did not differ between queenright colonies containing either a fertilized or unfertilized queen (Klobuchar and Deslippe unpublished).

With respect to the regulation of queen numbers, it is thought pheromone concentration in colonies plays a key role. Fletcher and Blum (1983) proposed that deviations from an optimal range in the amount of queen pheromones circulating in a colony stimulates workers to restore the concentration within the optimal range by either adopting new queens or executing supernumerary queens, as appropriate. Working with the monogyne form of *S. invicta*, they introduced pairs of foreign queens into 12 queenless colonies and monitored their acceptance by workers. Workers killed at least one queen in every colony, as predicted. More recently, Deslippe and Guo (unpublished) monitored worker execution rates of queens in the polygyne form of *S. invicta*. They established 66 subset colonies with 1, 3, 5, 10 or 15 queens, and found that mortality rate of queens was positively correlated with initial density of queens. Interestingly, the nature of the density-dependent response was under-compensating, a result consistent with the idea of mutual inhibition of pheromone production among queens.

Fletcher and Blum (1983) also proposed that individual differences in pheromone production should lead workers to execute the lower ranking queens in the pheromone hierarchy when pheromone concentrations exceed the optimal range for the colony. They tested this idea by introducing pairs of queens to queenless colonies, and then monitored which was killed. Each pair was composed of a physogastric and a non-physogastric queen, with the former being the more fecund in all likelihood. As predicted, workers almost always killed the non-physogastric female. Likewise, I have even observed some alate queens occasionally killed when kept in laboratory colonies for some time (Fig. 2). These victims may have been among those alate queens that begin ovarian development and pheromone production prematurely, and would be low ranking in the pheromone hierarchy.

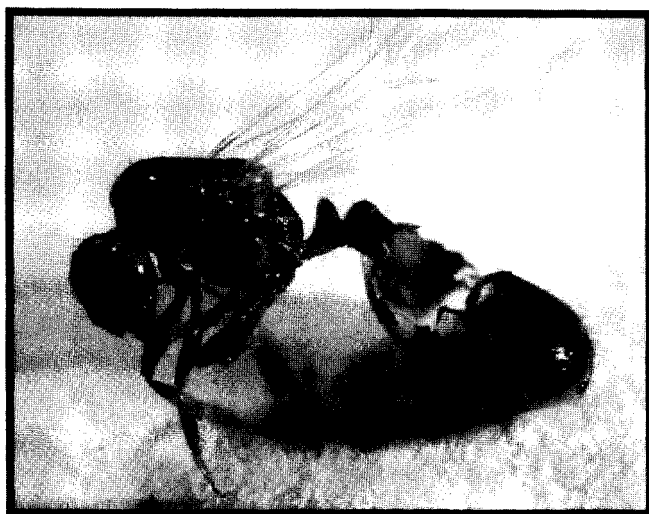


FIG. 2. An alate queen (*S. invicta*) that had been attacked and killed by worker nestmates. Her gaster was ripped open and its contents removed by workers while she was still alive. The queen was several months old, and may have started producing new pheromones prematurely (i.e., before dealation).

Besides the quantity of pheromones circulating through a colony, I propose that pulses or rapid changes in pheromone signals play a key role in worker execution of queens. Vargo and Laurel (1994) determined that virgin queens with their antennae removed dealated both in the presence and absence of a queen, and many of the virgins were killed once they were wingless. The queens may have been executed because workers detected a pulse of pheromones, as pheromone production typically begins shortly after dealation (Vargo 1999). Likewise, in an experiment in which either a winged or wingless queen was paired with a wingless queen, at least one queen was executed in only those colonies containing a winged queen. Of the 13 cases involving an alate queen, seven alates had shed their wings within 40 days. Six of the 7 queens were executed, and in these cases, the time between dealation and execution was 2.8 ± 1.2 days. In all but one case, the executed queen was the original alate queen (Deslippe and Guo unpublished).

Anecdotal evidence also points to a key role of pheromone pulses, as three physogastric queens from an *S. invicta* colony were each executed by their workers, but only after they were separated from each other (S.B. Vinson, personal communication).

ATTEMPTS TO EXTRACT THE "EXECUTION" PHEROMONES

Although queen pheromones apparently trigger executions, the compounds have never been identified. I have tried to extract the "execution" pheromone of *S. invicta* in organic solvents, as part of the process involved in characterizing the chemical or chemicals. Early attempts were only partially successful. For example, application of hexane extracts to colonies produced significantly more queen executions than did applications of hexane (control). This result confirmed the link between queen pheromones and executions, but the extracts were prepared with hundreds of queens, and the increase in execution rate was modest. In other words, the pheromone probably lost most of its activity, and was only effective because extremely high concentrations were prepared (Deslippe and Guo unpublished). Similarly, there was no difference in the percent of sexual larvae and pupae executed by workers exposed to acetone extracts of queens and only acetone (control). However, when extracts were prepared in a buffered salt solution, they induced worker execution of sexual larvae and pupae to the same degree as living queens. The extracts were introduced to colonies once every 12 h for 96 h at concentrations of only single-queen equivalents (Klobuchar and Deslippe unpublished).

CONCLUSION

Because the queen pheromone has been extracted with full activity, and it is stable in the buffered solution (Klobuchar and Deslippe unpublished), identification of the compound can proceed in a straightforward fashion. Whether the pheromone is the same one that induces workers to execute mature queens remains to be seen, but one can readily deduce that it is not the same as those queen pheromones extractable in harsh organic solvents, like the attraction pheromone, venom alkaloids, or the compound inhibiting dealation. The pheromone appears to be proteinaceous, perhaps a small peptide, and its identification should pave the way for a greater understanding of the chemical communication system of ants, and enable exploitation of the communication system.

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