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ORIGINAL ARTICLE

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Social regulation of ovary activation in 'anarchistic' honey-bees (*Apis mellifera*)

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Abstract Honey-bee (*Apis mellifera*) colonies exhibit extreme reproductive division of labour. Workers almost always have inactive ovaries and the queen monopolises egg laying. Although extremely rare, 'anarchistic' colonies exist in which workers produce male offspring despite the presence of the queen. By comparing the rates of ovary activation in anarchistic and wild-type bees fostered to host colonies of different genotype (i.e. anarchist and non-anarchist) and queen status (i.e. queenless and queenright), we investigated the factors involved in inhibiting ovary activation. Fostered anarchist workers always had a higher level of ovary development than fostered wild-type bees in both anarchist and non-anarchist host colonies. Fostered workers of both genotypes had more active ovaries in anarchistic than in wild-type hosts. Fostered workers of both strains also had more active ovaries in queenless than in queenright hosts. The results suggest that selection for worker reproduction in the anarchistic line has both reduced the effects of brood and queen pheromones on worker ovary inhibition and increased the likelihood that workers of the anarchistic line will develop ovaries compared to wild-type workers.

Keywords *Apis mellifera* · Worker egg laying · Anarchy · Worker sterility

Introduction

Reproductive division of labour is a characterising feature of social insects. In honey-bee (*Apis mellifera*) colonies, the queen is usually the sole female reproductive, but should a colony lose its queen, workers are able to change their reproductive status. In queenless colonies, some workers undergo ovary activation and after 5–46 days worker-laid eggs are observed (Ruttner and Hesse 1981; Page and Erickson 1988; Robinson et al. 1990). As a consequence of arrhenotoky, these unmated workers can produce fully viable male offspring because males arise from unfertilised eggs.

In the honey-bee, workers are related to their own male offspring by 0.5, to the male offspring of their supersisters by 0.375, to sons of half sisters by 0.125 and to sons of the queen by 0.25 (Ratnieks 1988). Thus the hierarchy of worker preferences for the maternity of a colony's males is own son >son of supersister >son of queen >son of a half sister, while the queen always favours her own eggs. This sets the stage for potential conflicts among workers and their half sisters over the maternity of males. However Ratnieks (1988) showed that intra-colonial conflicts over male production can be resolved via worker restraint of personal reproduction in favour of greater reproduction by the queen. 'Policing' alleles that cause workers to enforce effective sterility of their sisters can spread in populations where queens are polyandrous (Ratnieks 1988).

There is strong evidence for effective worker policing in *A. mellifera* (Ratnieks and Visscher 1989; Visscher 1996; Oldroyd and Ratnieks 2000). Honey-bee workers can distinguish worker-laid and queen-laid eggs, and remove the former. Given that worker policing is highly efficient, queenright workers can maximise their inclusive fitness by refraining from personal reproduction and working to maximise colony-level reproduction of drones and swarms. This sets the scene for the evolution of a signal communicating the queen's presence to the workers (Keller and Nonacs 1993). Two pheromonal signals appear to serve this function, one produced by the queen and one produced by larvae (Jay 1970; Jay and Nelson 1973; Free 1987; Winston and Slessor 1998).

Larvae produce a pheromone (Arnold et al. 1994; Mohammedi et al. 1998), which is the principle cue inhibiting worker ovary activation (Winston and Slessor 1998). Queens also inhibit worker reproduction via 'queen substance' (Free 1987). The nature and mode of

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action of this signal are not fully understood, but the signal may inhibit vitellogenin production in workers (Winston and Slessor 1998).

In 1995, we identified a queenright colony of bees in which there was extensive worker reproduction (Montague and Oldroyd 1998). We have line bred this colony to produce a strain of bees in which workers reproduce at high frequency. Typically 5–10% of workers have fully activated ovaries, even in the presence of the queen (Oldroyd and Osborne 1999; Oldroyd et al. 1999) whereas almost no workers have activated ovaries in normal colonies (Ratnieks 1993). Furthermore, the vast majority of male offspring of these colonies are workers' sons (Montague and Oldroyd 1998), indicating that workers not only activate their ovaries, but that levels of policing are lower in anarchistic than in wild-type colonies (Oldroyd and Ratnieks 2000).

Anarchistic workers appear to be behaviourally normal (Oldroyd et al. 1999). When day-old anarchistic workers were added to anarchistic hosts, an average of 9% activated their ovaries after 10 days, whereas only 1.3% did so in a wild-type host (Oldroyd et al. 1999). However, the behaviour of anarchistic workers when queenless is unknown. Here we investigate the origin of the signals inhibiting worker reproduction in honey-bees by exploiting differences between our 'anarchistic' strain and wild-type bees. We assume that our selection program has led to disruption of the normal signals between queens and workers. We compare the rate of ovary activation of anarchistic and wild-type workers when these bees are fostered into both queenless and queenright colonies of both anarchistic and wild-type background. We hypothesise that if brood and queen pheromones are totally absent in anarchistic stocks, ovary activation of cross-fostered workers should be similar in queenright and queenless anarchistic colonies. Conversely, if pheromone production from queens and brood are normal in anarchistic colonies, but anarchistic workers do not respond to these signals, then we would expect cross-fostered anarchistic workers to develop their ovaries whatever the genotype and queen status of the host colony. Between these two extremes, a range of conditions might prevail in which brood and queen pheromones are produced, but at a low level, and anarchistic workers respond to queen pheromones, but to a lesser extent than wild-type workers.

Methods

General approach

Our basic experimental protocol was to foster anarchist (A) and wild-type (W) workers into queenless (Q–) and queenright (Q+) colonies with different genetic backgrounds (i.e. A and W). Anarchist workers were obtained from the line maintained at the University of Sydney. Full details of the production of this line can be found in Oldroyd and Osborne (1999).

For each experiment, newly emerged (0–24 h) bees were collected from A and W colonies by placing combs containing mature worker brood in nylon mesh laundry bags (Homemaker, Sydney). Bagged combs were returned to their original hives and left overnight. The following morning, freshly emerged workers were harvested from the bags and these workers were individually marked using combinations of numbered disks (Opalithplättchen; Graze) glued to the thorax, and dots of enamel paint (Humbrol Super Enamel, Hull) on the abdomen.

Between 350 and 500 1-day-old bees of each type (A and W) were added to each host colony. Up to 4 days were required to mark all the bees for each host colony. Approximately equal numbers of A and W bees were marked each day.

To establish a control, a colony of the appropriate genotype (A or W) was divided into two, one containing the original queen, and one queenless. These colonies were then set up in observation hives comprising three standard Langstroth combs (Seeley 1995). Each half contained about 4,000 bees, brood of varying ages, some honey and some drone comb. The Q– hives were checked every other day for queen cells, which were destroyed if present. The marked bees were added 2 days after the colonies were divided.

Experiments were conducted in observation hives (rather than normal hives) so that we could monitor food reserves and note the first signs of oviposition and thus know when to terminate each experiment.

Between 12–14 days after introducing the last marked bees, the first eggs or workers with their abdomens inserted into drone cells (presumably laying eggs) were seen in the queenless part of the hive. The next day, the hives were sealed and the bees killed by fumigation with 2 ml ethyl acetate.

All marked bees were recovered from the host colonies, sorted according to age, and genotype and stored at –20°C until they could be dissected. Bee abdomens were dissected according to Dade (1977) and assigned as being activated (clearly defined ova present in ovaries) or unactivated (ovaries thin and lacking defined ova) (Oldroyd et al. 1999).

The experiments were conducted between October 1999 and February 2000 during spring and early summer. Nectar availability was variable, but conditions were always good for bees and colony populations were expanding throughout the experimental period. When nectar availability was low, we fed sugar syrup. Queenless and queenright sections of colonies were studied simultaneously. Anarchist and wild-type colonies were studied arbitrarily throughout the season to reduce a season-based bias in the data.

Experiment 1: effect of queenlessness on ovary development of cross-fostered workers in a wild-type host

Two W colonies (1 and 2; Table 1, Fig. 1) were each split into two (Q+ and Q–) halves and moved to a new site. To reduce drifting, the divided colonies were placed 5 m apart and the entrances were conspicuously marked.

Experiment 2: effect of queenlessness on ovary development of cross-fostered workers in an anarchistic host

This experiment was identical to experiment 1 except that it was conducted with A hosts, and the colonies were each divided within an observation hive. Due to a constraint of physical resources, colonies were divided within the same physical hive for experiment 2. Following Visscher and Dukas (1995), a metal grid made from 0.5-mm wire mesh was placed between the top and the lower two combs. The grid prevented bees moving between the two sections and also prevented exchange of contact pheromones, while allowing transfer of airborne odours. The queen was restricted to the lower section of the hive. Each section had a separate entrance, and these were conspicuously marked.

Table 1 Proportions of marked wild-type and anarchist workers recovered from each host colony. Numbers in *parentheses* indicate the number of bees added initially. In cases where the number of bees recovered from the colony showed a bias towards one genotype, that genotype is *italicised*

Host colony type	Hive code	Anarchists recovered	Wild types recovered	χ^2 with Yates correction (df=1)	P
Queenright wild type	1_{Q+}	37.7% (381)	34.9% (381)	0.55	0.458
	2_{Q+}	54.5% (398)	51.9% (402)	0.38	0.537
Queenless wild type	1_{Q-}	42.1% (444)	*57.9%* (404)	21.21	<0.001
	2_{Q-}	56.9% (388)	55.4% (393)	0.11	0.740
Queenright anarchist	3_{Q+}	33.4% (350)	*52.5%* (350)	25.36	<0.001
	4_{Q+}	36.8% (350)	*54.5%* (350)	10.68	0.001
Queenless anarchist	3_{Q-}	22.2% (350)	18.0% (350)	1.54	0.214
	4_{Q-}	36.2% (350)	*44.6%* (350)	4.64	0.031

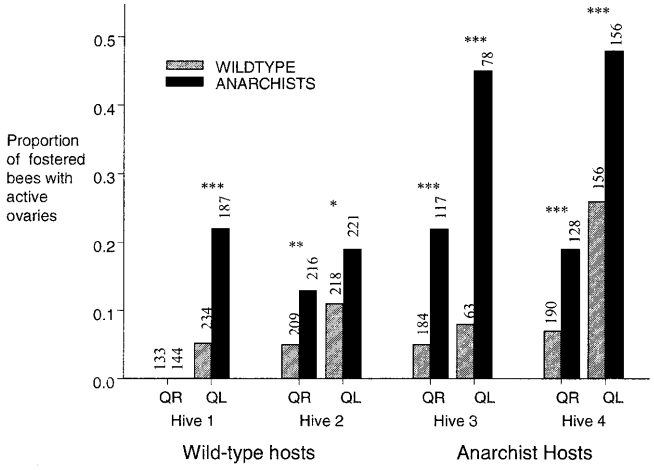

Fig. 1 Proportion of dissected bees with active ovaries. Values above the columns give the sample size from which the proportions were calculated. *Asterisks* represent the *P*-values from χ^2 tests (with Yates correction) comparing the proportions of fostered anarchists and wild-type bees with active ovaries within each colony (*none* $P > 0.05$, $*P < 0.05$, $**P < 0.01$, $***P < 0.01$)

Results

General observations

Both the marked A and W bees added to each host colony appeared to go through normal behavioural development, but the anarchists showed some signs of precocious behavioural ontogeny. Anarchists were often seen foraging earlier than age-matched wild-type bees. Little drifting of marked bees between host colonies was observed, and anarchists were neither more nor less likely to drift than wild-type bees.

Recovery of marked bees

Table 1 summarises the numbers of marked bees recovered from each observation hive for dissection. The null hypothesis that equal proportions of A and W bees were recovered was tested with a χ^2-test for each colony (Table 1). In four of the eight experimental units studied, more W bees were recovered than A bees.

Table 2 Effect of the genotype of cross-fostered workers on ovary development in various hosts. For each colony, the null hypothesis that ovary activation was equal in the anarchistic and wild-type workers was evaluated with χ^2-tests. A significant heterogeneity χ^2 indicates that the two genotypes responded differently in queenless and queenright hosts

Status	df	χ^2	P
Colony 1 wild type			
Queenless	1	21.21	<0.001
Queenright	1	0.01	0.926
Total of χ^2s	2	21.22	<0.001
χ^2 of totals	1	10.43	0.001
Heterogeneity	1	10.78	0.001
Colony 2 wild type			
Queenless	1	6.34	0.011
Queenright	1	5.13	0.023
Total of χ^2s	2	11.47	0.003
χ^2 of totals	1	11.78	<0.001
Heterogeneity	1	0.31	0.577
Colony 3 anarchist			
Queenless	1	14.32	<0.001
Queenright	1	13.26	<0.001
Total of χ^2s	2	27.58	<0.001
χ^2 of totals	1	55.13	<0.001
Heterogeneity	1	27.55	<0.001
Colony 4 anarchist			
Queenless	1	14.09	<0.001
Queenright	1	11.77	<0.001
Total of χ^2s	2	25.86	<0.001
χ^2 of totals	1	24.78	<0.001
Heterogeneity	1	1.08	0.298

Experiment 1: the effect of queenlessness on ovary development of cross-fostered workers in wild-type hosts

In colony 1, no workers fostered into the Q+ section had activated ovaries whereas in the Q– section, a few W and many A workers activated their ovaries (Fig. 1, Table 2). In colony 2, 12.9% of A and 5.2% of W fostered workers activated their ovaries in the Q+ host. A much higher proportion of both A and W workers activated their ovaries in the Q– host, but A workers were much more likely to be activated (Fig. 1, Table 2). The Q+ split of colony 2 absconded on the day we were due to kill the colony, but since we were able to collect the swarm we chose to include this colony in the data set.

Experiment 2: effect of queenlessness on ovary development of cross-fostered workers in an anarchist host

In the Q+ A hosts, a mean of 18.7% of A workers had activated ovaries. However, in the queenless units, nearly 50% of A workers showed ovary development. The response of W workers to the absence of the queen and declining brood was variable. In colony 3, the proportion of W workers with activated ovaries was not significantly different in the Q– section compared to the Q+ section (χ^2=0.52, *df*=1, *P*=0.38) whereas in colony 4, the frequency of workers with activated ovaries was much higher in the Q– section for both genotypes (Fig. 1).

Discussion

In Q– W colonies, both A and W cross-fostered workers activated their ovaries, but A workers did so at a higher frequency (Fig. 1). This indicates that A workers are less inhibited than W workers by brood pheromones and more likely to activate their ovaries.

Both W and A fostered workers had higher levels of ovary activation in Q– A hosts than Q+ A hosts (Fig. 1). This suggests that some queen pheromones are produced in anarchistic colonies. If this were not the case, then there would be no differences in ovary activation in the Q– and Q+ sections.

Both A and W workers had higher rates of ovary activation in Q+ A hosts than in Q+ W hosts. This indicates that our selection program has weakened the signals or cues that are normally produced by queens and brood of W colonies that curtail the reproductive development of workers.

In Q+ W colonies, nearly all workers failed to activate their ovaries. Nevertheless, a few A workers were activated in W hosts (Fig. 1; Oldroyd et al. 1999). Workers cross-fostered into the Q+ section of colony 2 of this study showed the highest levels of ovary development that we have seen in a Q+ W colony, probably because the colony absconded late in the experiment. Gravid queens must cease laying before they can swarm, and this may reduce the production of queen pheromones circulating in the colony. Thus these combined results imply that normal W colonies produce sufficient brood and queen pheromones to constrain ovary development in most workers, even anarchistic ones (Oldroyd et al. 1999).

Experiments 1 and 2 were conducted with slightly different experimental protocols. This may have permitted some signals from the queenright section of the colony to affect conditions in the queenlees section. However, this does not effect the interpretation of our results for two reasons. First, the likely means of suppression of ovary activation is brood pheromone. These signals are known to be non-volatile (Arnold et al. 1994). Second, ovary activation was actually greater in the split hives (experiment 2) than the divided hives (experiment 1), suggesting there was no communication of an inhibitory signal from the queenright section.

In summary, these results show that our breeding program has strongly influenced the signal system between a laying queen and workers that constrains worker oviposition. This has had two major affects. First, the brood and queen pheromones that normally constrain ovary activation in workers are produced at lower levels in A than in W colonies. However, A queens and brood must still produce some of these inhibitory pheromones, or ovary development would be similar in Q+ and Q– sections. Second, A workers are less influenced than W workers by these pheromones.

What kind of signals may have been disrupted by our selection programme? Heritable variation in the production of inhibitory stimuli could arise from characters expressed by queen or by the collective workers. Worker-derived signals that inhibit ovary activation include a brood pheromone (Arnold et al. 1994; Mohammedi et al. 1998; Winston and Slessor 1998), direct aggression (Visscher and Dukas 1995) and nutritional factors (Jay and Nelson 1973; Korst and Velthuis 1982; Lin et al. 1999).

Queens inhibit worker reproduction through the production of non-volatile queen pheromone (Free 1987). The glandular source and nature of the queen-produced reproduction-inhibiting pheromone is not fully understood (Winston and Slessor 1998). The tergal glands seem to be involved (Wossler and Crewe 1999) and the mandibular glands may be involved, but their role seems to be less pivotal than was once thought (Willis and Winston 1990; Plettner et al. 1993). The composition of the queen pheromone can vary with the race of bee and, to some extent, with individual queens (Crewe 1982; but see Pankiw et al. 1994). Anarchistic queens seem likely to produce either small quantities of queen pheromone, or an ineffective pheromonal blend.

In the Cape honey-bee, *A. m. capensis* from South Africa, worker reproduction in queenright hives is relatively common and worker policing is more permissive in this subspecies (Moritz et al. 1999). The Cape honeybees differ from the anarchistic bees in that Cape honeybee workers can reproduce by thelytoky to produce daughters (which can be reared as workers or queens) as well as arrhenotoky to produce males. Thelytokous reproduction by workers results in a female carrying the full complement of her mother's genes and related to her by unity (Greef and Villet 1993; Greef 1996). Thelytokous reproduction by workers relaxes the selection pressure for worker policing and several studies have reported permissive worker policing in this subspecies (Anderson 1963; Moritz et al. 1999). Thelytoky has never been observed in the anarchist bees.

Workers with either a low sensitivity or a reduced response to ovary-inhibiting stimuli may benefit from increased personal reproduction of drones in queenless colonies. Page and Erickson (1988) found that the majority of drones reared to maturity in a queenless colony were laid within the first few days of worker oviposition, be-

cause social cohesion and brood care diminish rapidly. In every case, a higher proportion of A workers than W workers had activated ovaries in queenless colonies (Fig. 1), but this does not necessarily mean that anarchist workers were producing the majority of the drone brood (Page and Robinson 1994; Montague and Oldroyd 1998).

In four of the eight experimental units studied, more W marked workers than A workers were recovered from the host colonies. This suggests that marked anarchist workers had a lower survival than age-matched W bees. Oldroyd et al. (1999) also reported low recovery of anarchists from observation hives. We observed that A workers commenced foraging earlier than W bees. Since foraging is risky, this could have contributed to their lower survival. Higher levels of ovary development in the anarchists may also have impacted negatively on their survival. This could have been due to the physiological costs associated with ovary activation, or indirectly due to elevated aggression from other workers (Sakagami 1958; Evers and Seeley 1986; Visscher and Dukas 1995). However, Oldroyd et al. (1999) did not observe high levels of aggression towards anarchists in queenright colonies, and neither did we here.

In conclusion, these cross-fostering experiments have shown that selection for worker reproduction has acted on both signals produced by queen and/or brood and the way these signals are perceived by the workers. We hypothesise that this involves both a reduction in inhibitory signals produced by the queen and a reduction in sensitivity or responsiveness of workers to those signals. Whether this involves the same genes, which are expressed differently in queen or worker castes, or different genes is not clear, but more than one major gene seems to be involved (Oldroyd and Osborne 1999). Understanding how the pheromonal signalling systems in anarchist colonies has failed promises to reveal which signals, among the many candidates in a bee hive, are crucial for effective worker ovary inhibition.

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