Male Production: Predictions & Tests

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Whose Sons To Rear?

Queen Honey Bee Laying an Egg

Honey Bee: Female Reproductive Systems

Queen

Worker

has ovaries but cannot mate

Workers With Ovaries but Cannot Mate

Queens

Workers

Bombus terrestris

Apis mellifera

Vespula vulgaris

Lasius niger

Queenless Honey bee Colony with Worker-Laid Eggs
Male Production by Workers is Rare

Queenright honey bee colonies

Only 0.1% males are workers’ sons

Visscher 1989 Behav Ecol Sociobiol

By using a body colour marker caused by the cordovan recessive gene, Visscher was able to visually screen thousands of males reared in queenright honey bee colonies. The results showed that approximately one male per thousand was a worker’s son.

He set up colonies that were cc (queen) x C,C,C,C,C,C….C (males). The workers were all Cc, meaning that half the workers’ sons were c (cordovan: pale colour) and half C (normal). Queens’ sons were all c (cordovan: pale colour).

Why Don’t Workers Produce Males?

More related to sons than brothers

1.0 v 0.5 regression relatedness

0.5 v 0.25 life for life relatedness

Ratnieks 1988 Am Nat

The fact that only 0.1% of the males are workers’ sons seems to go against what we would expect from inclusive fitness theory, because (due to haplodiploidy) a worker bee is more related to sons than to brothers.

Intracolony Conflict Over Male Rearing

Regression Relatedness of

<table>
<thead>
<tr>
<th>To sons of</th>
<th>Queen</th>
<th>Worker 1</th>
<th>Worker 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Queen</td>
<td>1.0</td>
<td>0.5</td>
<td>0.5</td>
</tr>
<tr>
<td>Worker 1</td>
<td>0.5</td>
<td>1.0</td>
<td>0.25-0.75</td>
</tr>
<tr>
<td>Worker 2</td>
<td>0.5</td>
<td>0.25-0.75</td>
<td>1.0</td>
</tr>
</tbody>
</table>

Each female in the colony is more related to her own sons (1) than to the sons of other females. Workers are related to the sons of half sisters by 0.25 and sons of full sisters by 0.75. (Life for life relatedness values are just half the above values.)

Why So Few Workers’ Sons in Honey Bees?

Hypothesis

Workers prevent each other from reproducing

Ratnieks 1988 Am Nat

Could Worker Policing be Effective?

Worker Policing

many against many

Queen Policing

one against many

Ratnieks 1988 Am Nat
In many species with small colonies, such as bumble bees or Polistes or wasps, the queen tries to stop workers from reproducing by killing worker-laid eggs or by aggression. A single queen can be quite effective if the nest is small and with few workers. But it would not be possible for such “queen policing” to be effective in large colonies, such as that of the honey bee, *Apis mellifera*, with up to 50,000 workers.

However, worker policing could be effective in a large colony. Worker policing is a mutual inhibition. The more workers there are, the more there are to stop each other reproducing.

**Could Worker Policing be Effective?**

**Discovery of Worker Policing in the Honey Bee**

**Policing Bioassay with Discriminator Colony**

1. **Obtain Eggs**
   Egg source colonies
   Queenright (queen-laid eggs)
   Queenless (worker-laid eggs)

2. **Transfer Eggs**
   Harvest eggs and place on slide. Transfer eggs with forceps into adjacent drone cells.

3. **Compare Egg Acceptance**
   Place comb into “discriminator” hive between two frames of brood above the queen excluder. Check at intervals.

**Moving Eggs with Forceps**

**Eggs Placed into Drone Cells by Hand**

**Discriminator Colony**

queen excluder
One Hour Later Many Eggs Have Gone

Worker-laid eggs removed
Queen-laid eggs remain

Ratnieks & Visscher 1989 Nature

All study colonies (n = 15) discriminated against worker-laid eggs

Worker Bee Inspecting Worker-Laid Egg

Worker Bee Killing Worker-Laid Egg

How Widespread is Worker Policing?

How Widespread in Worker Policing By Egg Eating?

Apis mellifera
Ratnieks & Visscher (1989, Nature)…and many others

Apis cerana
Oldroyd et al. (2001, Behav Ecol Sociobiol)

Apis florea
Halling et al. (2001, Behav Ecol Sociobiol)
How Widespread is Worker Policing?

**Wasps**

*Polistes chinensis*

*Vespa crabro*
Foster, Gulliver, Ratnieks (2002, Insectes Sociaux)

*Dolichovespula saxonica*
Foster & Ratnieks (2000, Nature)

*D. sylvestris*
Wenseleers, Tofilski, Ratnieks et al. (Behav Ecol 2005)

*D. norwegica*
Wenseleers, Tofilski, Ratnieks et al. (in preparation)

*Vespula vulgaris*

*V. rufa*
Wenseleers, Tofilski, Ratnieks et al. (Evolution, 2005)

How Widespread is Worker Policing?

**Ants**

*Diacamma sp.*
Kikuta & Tsuji (1999, Behav Ecol Sociobiol)

*Formica fusca*

*Pachycondyla inversa*

*Camponotus floridanus*
Endler et al. (2004, PNAS)

Conditions that Favour Worker Policing of Worker-Laid Eggs

Effect of Relatedness

1. sons (1) > workers’ sons (0.75) > queen’s sons (0.5)
2. sons (1) > workers’ sons (0.5) = queen’s sons (0.5)
10. sons (1) > queen’s sons (0.5) > workers’ sons (0.3)

The table above gives the relatedness of a worker to her sons, to the sons of other workers (nephews), and to the sons of the queen (brothers) when the queen is mated to 1, 2, or 10 males (assume equal sperm use).

Note that a worker is always most related to sons. But her number two choice changes. With single mating, nephews are more related than brothers. With multiple mating brothers are more related than nephews. With double mating they are equal.

Multiple mating has this effect because with multiple mating most workers are half sisters not full sisters.

The implication is that worker policing will be favoured by multiple mating. Workers will have an incentive to lay eggs, but also to stop other workers from reproducing.

Male Production in D. saxonica

![Graph showing male production in D. saxonica](image)

Foster & Ratnieks 2000 Nature
In many bees, wasps and ants, workers police each other in order to prevent individual workers from selfishly producing their own male offspring. Although several factors can selectively favour worker policing, genetic relatedness is considered to be of special importance. In particular, kin selection theory predicts that worker policing should be more common in species where the workers are more related to the queen's sons than to other workers' sons. Here we provide strong novel support for this theory based on a comparative analysis of policing and male parentage in 109 species of ants, bees and wasps. First, an analysis of behavioural data confirms that worker policing occurs more frequently in species where workers are more related to the queen's sons (WP present in 7/7 = 100% of the species) than in species where they are more or equally related to other workers' offspring (WP present in 7/34 = 21% of the species). Second, an analysis of male parentage shows that, as predicted, a significantly higher percentage of the males are workers' sons in 75 species where the workers are more related to other workers' sons (avg. 14%) than in 15 species where they are more related to the queen's sons (avg. 0.14%). The correlations between relatedness and male parentage and the incidence of worker policing are also highly significant when phylogenetic non-independence is controlled for. Although our analysis provides strong overall support for the theory that the colony kin structure affects male parentage patterns, there is also significant unexplained variation. Several factors that may cause this residual variation are discussed.

Analysis of Behavioural Data

In species in which workers are:

- More related to queen's sons than workers' sons
- worker policing occurs in 100% species (n = 7/7)
- worker policing occurs in 21% species (n = 7/34)

p worker policing = 0.00015
p queen policing = 0.0009
p negative correlation queen and worker policing = 0.00009
**Analysis of Behavioural Data**

*In species in which workers are:
  * More related to queen's sons than workers’ sons
    * worker policing occurs in 100% species (n = 7/7)
    * queen policing occurs in 0% species (n = 0/4)
  *
  * Not more related to queen's than workers’ sons
    * worker policing occurs in 21% species (n = 7/34)
    * queen policing occurs in 91% species (n = 30/34)

\[ p \text{ worker policing} = 0.00015 \]
\[ p \text{ queen policing} = 0.0009 \]
\[ p \text{ negative correlation queen and worker policing} = 0.00009 \]
Acquiescence

Policing can solve crimes (like Sherlock Holmes). But policing can also deter crime (which is what a patrolling Bobby is supposed to do).

So, if policing is effective, why try to reproduce?

• All honey bee workers have ovaries
• But only 0.1% - 0.01% lay eggs

Does better policing lead to greater altruism?

Comparative Study of Acquiescence

This comparative study of 9 species of wasps and the honey bee shows that when policing is more effective (% of worker-laid eggs killed), fewer workers lay eggs. In other words, policing deters antisocial acts. Wenseleers, T., Ratnieks, F. L. W. 2006. Enforced altruism in insect societies. Nature 444: 50
Comparative Study of Acquiescence

Supplementary Figure S1. Data on the phylogenetic relationships among workers (Table S1), the effectiveness of policing (Tables S2, S5) and queen-worker dimorphism in 5 species of Vespid wasps and the honeybee Apis mellifera. Worker-laid egg can be poisoned by the queen (C), by workers (W) or by both (C+W).

Supplementary Figure S2. Analysis of worker egg laying in a 2 × 2 × 2 factorial design using phylogenetically independent contrasts (A). The percentage of eggs laid by workers as a function of contrasts in the efficiency of egg killing (policing) and the queen-worker dimorphism in 5 species of Vespid wasps and the honeybee Apis mellifera. Worker-laid egg can be poisoned by the queen (C), by workers (W) or by both (C+W).