



**Intracolony nepotism
during colony fissioning
in honey bees?**

Juliana Rangel

Co-authors: Heather Mattila, Thomas Seeley
Department of Neurobiology and Behavior
Cornell University

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Polyandry in social insects



Yellow jackets



Leaf-cutter ants



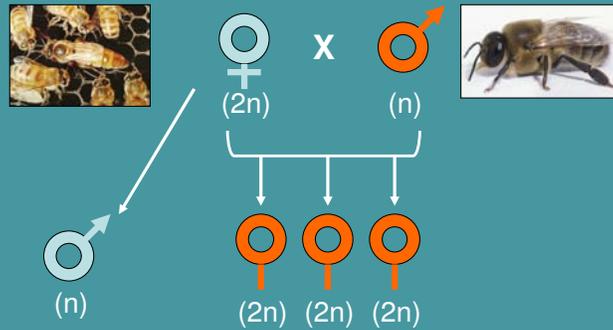
Army ants



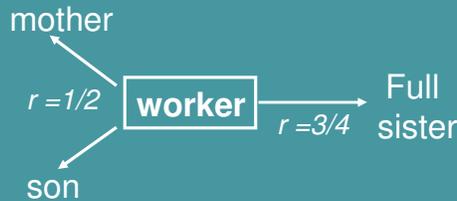
Honey bees

Although queens in most social insect species do not mate with multiple males), polyandry is prominent in certain taxa including yellow jacket wasps, leaf-cutter, army ants, and honey. One consequence of this polyandry is that the females in a colony (queens and workers) are not all full sisters. Instead, they constitute several patrilineal groups, with females in the same patriline related as full sisters ($r=0.75$) and those in different patrilines related as half sisters ($r = 0.25$).

Relatedness ratios under monoandry

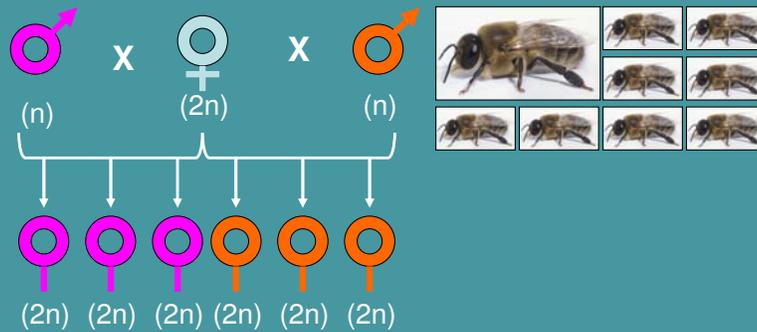


Monoandry produces **one** subfamily in a colony:

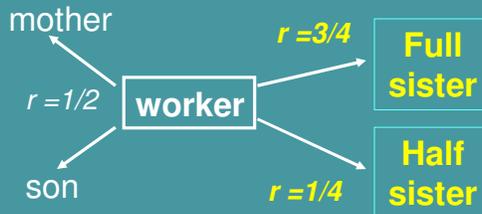


In diploid organisms (most plants and animals), each homologous chromosome is inherited from a different parent. A haplodiploid species is one in which one of the sexes has haploid cells and the other has diploid cells. Most commonly, the male is haploid and the female is diploid. In such species, the male develops from unfertilized eggs, a process called arrhenotokous parthenogenesis or simply arrhenotoky, while the female develops from fertilized eggs: the sperm provides a second set of chromosomes when it fertilizes the egg. One consequence of haplodiploidy is that the relatedness of sisters to each other is higher than in diploids; this has been advanced as an explanation for the eusociality common in this order of insects as it increases the power of kin selection.

Relatedness ratios under polyandry



Polyandry produces **several** subfamilies in a colony:



In diploid organisms (most plants and animals), each homologous chromosome is inherited from a different parent. A haplodiploid species is one in which one of the sexes has haploid cells and the other has diploid cells. Most commonly, the male is haploid and the female is diploid. In such species, the male develops from unfertilized eggs, a process called arrhenotokous parthenogenesis or simply arrhenotoky, while the female develops from fertilized eggs: the sperm provides a second set of chromosomes when it fertilizes the egg. One consequence of haplodiploidy is that the relatedness of sisters to each other is higher than in diploids; this has been advanced as an explanation for the eusociality common in this order of insects as it increases the power of kin selection.

Contexts of potential nepotism

- Polyandry in honey bees creates a potential for intracolony nepotism in various contexts including:



The genetic structure of multi-patriline colonies creates a potential for intracolony nepotism in various contexts, including food-sharing and brood-rearing, though there is no convincing evidence that workers behave nepotistically in these two particular contexts (Breed *et al.* 1994, Tapy *et al.* 2004, and Châline *et al.* 2005). A third context with great potential for intracolony nepotism arises in species, such as honey bees and army ants, whose colonies reproduce by fissioning (Wilson 1971). During this process of colony multiplication, the workers rear several young queens, all of whom are the workers' sisters. Eventually, once the original colony divides itself, one of these young (sister) queens will head one of the derivative colonies and typically the old (mother) queen heads the other derivative colony. Thus the workers in a colony that is fissioning might choose between serving a young queen or the old queen. And in making this choice, a worker might act nepotistically, preferring to serve a young queen if she is likely to be a full sister ($r = 0.75$) or preferring to serve the old queen ($r = 0.50$) if all the young queens are half sisters ($r = 0.25$).

Intracolony nepotism during swarming

Main question

Does the presence of a full-sister among the virgin queens being reared in the parental nest encourage workers to stay at home rather leave with the swarm?

Set up of observation colonies

- May - June 2008
- Liddell Biological Station, Ithaca, NY
- 3 observation colonies
- ~ 6,000 bees / colony



To set up observation colonies, we went to apiary and chose frames from one healthy colony. We used the queen, and three frames that were covered with workers, and had about $\frac{1}{2}$ food, and $\frac{1}{2}$ middle-aged brood. We took the observation hives to the Liddell Biological Station in Ithaca, and placed them in a light-proof room, each connected to the outside through a hole in the wall. Two weeks after the colonies had been set up the workers were foraging normally and the colonies had begun the queen-rearing process, which is one of the conditions needed in a colony that is preparing to swarm

Data collection

- Waited until the swarm clustered
- Combed surface of the swarm bottom-top
- Opened observation hive and sampled from both sides



~ 150 swarm
bees



~ 150 remnant
bees



All immature
queens

DNA analysis

- Used 7 microsatellite loci to genotype every bee:
{ Ap033, Ap068, A079, A113, Ap226, Ap256, and Ap289 }



- Inferred paternity of all the workers and all the immature queens



- Segregated workers into subfamilies for each group of “stayers” and “leavers”

DNA Analysis

•Microsatellites

For each colony, the queen's genotype for each locus was inferred by comparing the genotypes of immature queens and workers.

- Genotyped workers were assumed to belong to the same patriline if their profile of drone-derived alleles was the same.

A worker's decision during swarming



← stay?



→ leave?



Decision

If VQ is

Relatedness

Stay

Full sister

($r_{VQ} = 3/4$)

Leave

Half sister

($r_{VQ} = 1/4$)

Remember: ($r_{MQ} = 1/2$)

Results: Proportion of “stayers” vs. relatedness

Null hypothesis (H_0): No preference for staying

H_0 : Proportion of stayers in subfamilies *with* sister queens = Proportion of stayers in subfamilies *without* sister queens

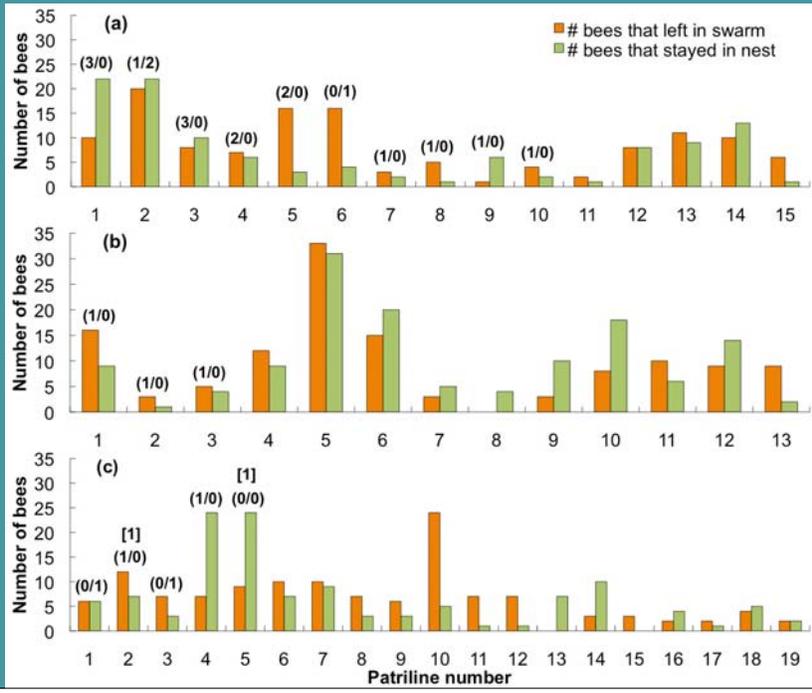
Alternative hypothesis (H_a): Preference for staying

H_a : Proportion of stayers in subfamilies *with* sister queens > Proportion of stayers in subfamilies *without* sister queens

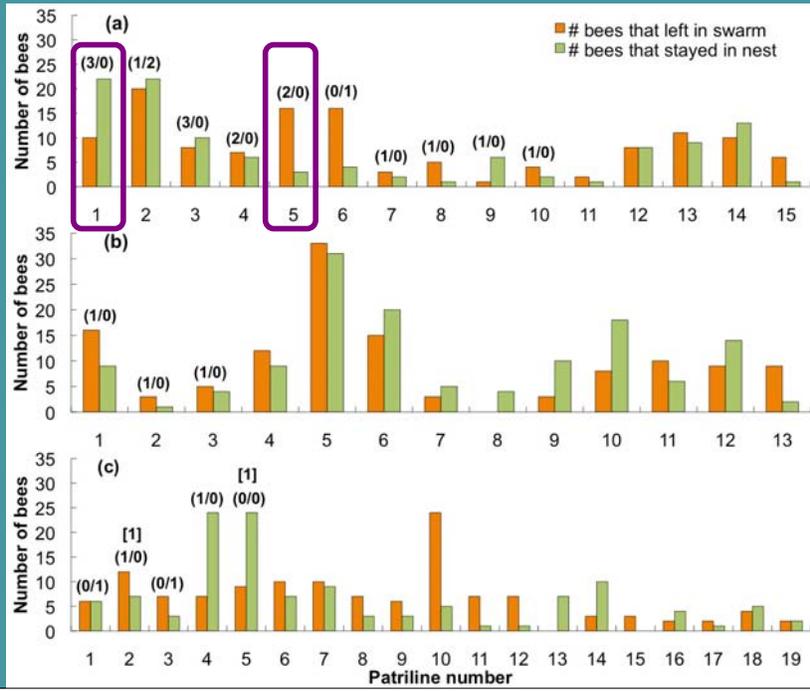
| Colony of immature queens | Number of immature queens | Patriline w/ immature queens | | Patriline w/o immature queens | | t | d.f. | p-value |
|---------------------------|---------------------------|------------------------------|-----------------------|-------------------------------|-----------------------|-------|------|---------|
| | | Number of patrilines | Proportion of stayers | Number of patrilines | Proportion of stayers | | | |
| 1 | 18 | 10 | 0.46 ± 0.21 | 5 | 0.40 ± 0.17 | 0.61 | 13 | 0.28 |
| 2 | 3 | 3 | 0.35 ± 0.10 | 10 | 0.62 ± 0.23 | -1.63 | 11 | 0.87 |
| 3 | 6 | 5 | 0.57 ± 0.17 | 14 | 0.43 ± 0.25 | 1.16 | 17 | 0.13 |



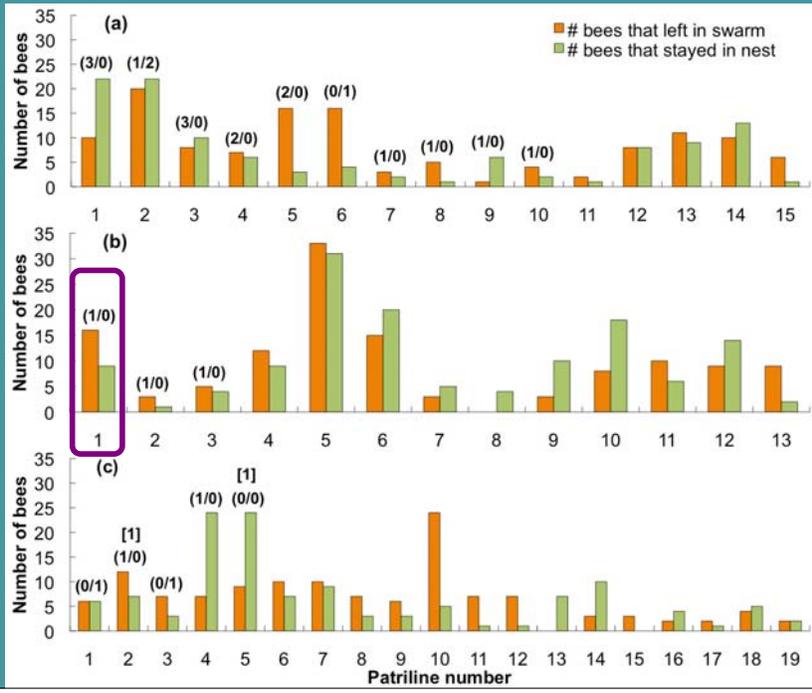
Results: Number of “stayers” vs. “leavers”



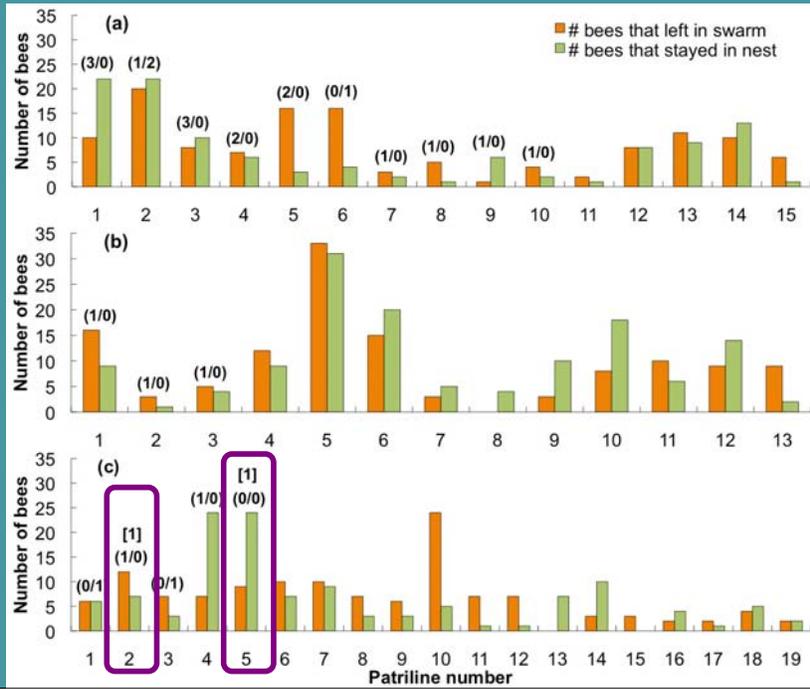
Results: Number of “stayers” vs. “leavers”



Results: Number of “stayers” vs. “leavers”



Results: Number of “stayers” vs. “leavers”



Conclusions

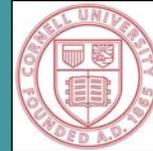
- The presence of a full-sister among the virgin queens being reared in the parental did not encourage workers to stay at home rather than to leave with the swarm
- Workers who had an adult full-sister queen in the nest prior to swarming did not show a higher tendency to stay compared to workers who had an immature full-sister queen or no full-sister queen inside the nest
- **“No intracolony nepotism during colony fissioning in honey bees”** (*Proc. R. Soc. B.* online Aug 2009. doi:10.1098/rspb.2009.1072)

Possible reasons for the lack of nepotism

- Scrambling (muting) of the kin recognition cues by the queens to prevent half-sister workers (the vast majority) from withholding resources (Reeve 1998)
- Weak discrimination between full-sister queens and half-sister queens due to a low allelic diversity of genetic odor cues used in recognition (Ratnieks 1991)
- High colony-level costs of kin discrimination (i.e. reduction in queen production) may outweigh the benefit that a worker gains from her selfish interest to support a full-sister queen (Ratnieks and Reeve 1991)
- Extreme polyandry results in so many patrilineages in a colony that a worker's probability of encountering and detecting a full-sister queen is low

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Juliana Rangel
jr369@cornell.edu