

Tragedy of the commons in *Melipona* bees

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In human society selfish use of common resources can lead to disaster, a situation known as the ‘tragedy of the commons’ (TOC). Although a TOC is usually prevented by coercion, theory predicts that close kinship ties can also favour reduced exploitation. We test this prediction using data on a TOC occurring in *Melipona* bee societies.

Keywords: caste conflict; tragedy of the commons; stingless bees; *Melipona*

1. INTRODUCTION

Since Hardin’s (1968) influential analysis of the ‘tragedy of the commons’ (TOC), the consensus has been that coercive management is necessary to prevent overexploitation of common resources such as fish stocks or grazing land (Hardin 1998; Ostrom 1999). Hardin (1968) argued that rational individuals benefit from increasing their share, even if this depletes the resource on which they depend. In his view, the only way to curb individual selfishness and prevent a TOC was by ‘mutual coercion mutually agreed upon’ (Hardin 1968). Models developed by evolutionary theorists (Hamilton 1964; Frank 1995, 1998), however, show an additional mechanism. If the level of exploitation is heritable and groups are composed of kin, a rational or ‘evolutionary stable’ exploitation rate will evolve that is inversely related to genetic relatedness (Frank 1995, 1998). However, this prediction has never been tested because in most societies or family groups kinship benefits co-occur with coercion (Mock & Parker 1998), making it impossible to determine their relative contributions. We test the effects of kinship on the outcome of a TOC that, uniquely, cannot be prevented by coercion. It concerns the exploitation of a common resource—the workforce—in *Melipona* stingless bee societies.

In highly eusocial bees, such as honeybees and stingless bees, all work is carried out by morphologically specialized worker individuals that, like queens, are female (Wilson 1971). The workforce is necessary for colony reproduction, whether by rearing males or by establishing new colonies via colony fission, in which a queen and a swarm of workers establish a new nest. Becoming a queen, however, is potentially more rewarding than becoming a worker since queens have greater reproductive potential than workers and only queens can ever head daughter colonies (Bourke & Ratnieks 1999; Wenseleers *et al.* 2003). So why do more females not attempt to develop as queens rather than workers? In TOC terms, what prevents the

common resource—the workforce—from being exploited by larvae selfishly choosing to develop into queens? As in Hardin’s ‘mutual coercion mutually agreed upon’, a TOC is usually prevented by enforcement (Bourke & Ratnieks 1999). In honeybees (*Apis*) and most stingless bees (Trigonini), queens are larger than workers (Wilson 1971). As a result, the adult workers can prevent larval females from developing into queens by controlling their access to food (‘nutritional caste determination’; figure 1). As expected from theory, colonies in these taxa rear few queens, just enough to permit seasonal swarming or superseding of a failing mother queen (Wenseleers *et al.* 2003). For example, in the honeybee *Apis mellifera* and in the trigonine bee *Tetragonisca angustula*, only ca. 0.02% of all females develop into queens over a single season (Winston 1987; van Veen & Sommeijer 2000).

Melipona stingless bees are a unique exception to this pattern (Ratnieks 2001; Wenseleers *et al.* 2003). In *Melipona*, the adult workers have little power to control the caste fate of developing females because queens and workers are the same size, and are reared in identical sealed cells (Engels & Imperatriz-Fonseca 1990; figure 1). This gives individual female larvae the power to determine their own fate (Bourke & Ratnieks 1999; Ratnieks 2001; Wenseleers *et al.* 2003; figure 1). Theory shows that in the pursuit of their individual interests, self-determination should result in a TOC in which many more immature females develop into queens than are needed for swarming (Bourke & Ratnieks 1999; Ratnieks 2001; Wenseleers *et al.* 2003). This general prediction is supported because *Melipona* colonies greatly overproduce queens (Wilson 1971; Engels & Imperatriz-Fonseca 1990) (5–16% of all females develop into queens; figure 2). This is costly to the colony as a whole since the excess queens serve no useful purpose and are swiftly executed by the workers after they emerge from their cells (Koedam *et al.* 1995; figure 1). However, inclusive fitness theory also makes more detailed predictions; in particular, that fewer females should selfishly develop into queens when the cost of queen overproduction falls on closer kin (Wenseleers *et al.* 2003). One major factor that affects kinship is the extent of worker reproduction. Workers can lay male eggs. When more of the colony’s males are workers’ sons, the cost of excess queen production is borne by more highly related individuals, namely workers’ sons (nephews, $r = 0.375$) rather than queen’s sons (brothers, $r = 0.25$). Theory predicts that queen overproduction should be reduced when more males are workers’ sons (Ratnieks 2001; Wenseleers *et al.* 2003). We present the first test, to our knowledge, of this prediction using data on queen production in *Melipona* species with different degrees of worker reproduction (figure 2; see electronic Appendix A).

2. METHODS

(a) Male parentage and caste ratios

To test the effect of kinship on queen production we collated all available data on male parentage and female caste ratio in *Melipona*. A total of 32 studies and four reviews across 13 species were found. However, we only used studies where male parentage and caste ratio were known for the same population or geographical region, and were measured in either their natural environment or laboratory conditions where conditions approached natural ones as closely as possible. This produced 12 studies on four species: *Melipona beecheii* (three studies, all from Yucatan, Mexico), *M. favosa* (Tobago, West Indies), *M. quadrifasciata* (various sites, Brazil) and *M. subnitida* (Rio Grande do Norte, Brazil) (see tables 1, 2 in electronic Appendix A). Male production by workers and female caste ratios in these four species are

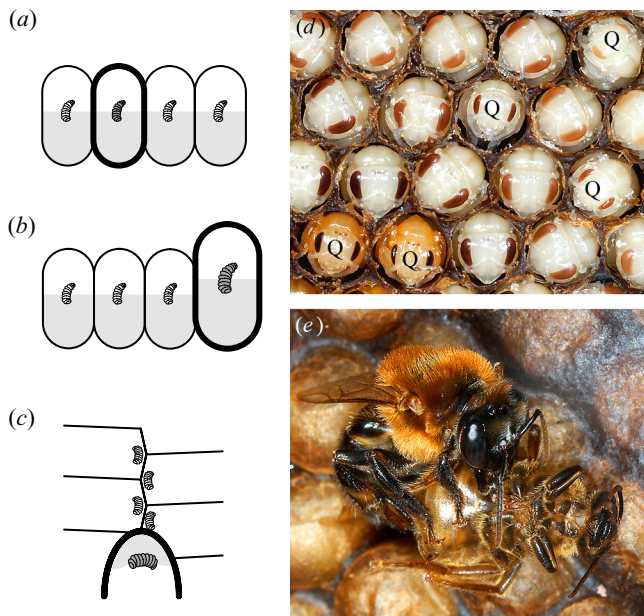


Figure 1. In *Melipona* bees queens are the same size as workers and develop individually in a sealed cell (bold) on a provision mass (a). This gives female larvae sufficient resources to develop into either caste. In other highly eusocial bees, Trigonini stingless bees (b) and honey bees (c), the larger queens develop in special cells and their rearing is under the control of the adult workers who build and provision the cells. In *Melipona*, individual control of caste development results in a TOC in which many more queens are reared than are needed ((d) Q, queen pupae in cells from which cappings have been removed). Excess queens are killed by workers (left) soon after emergence (e).

summarized in figure 2. Detailed statistics and a complete list of the original studies are available in electronic Appendix A.

3. RESULTS

As predicted, in species where many males are workers' sons (*M. favosa*, Sommeijer *et al.* 1999; *M. quadrifasciata*, da Silva 1977; Tóth *et al.* 2002; *M. subnitida*, Contel & Kerr 1976; Koedam *et al.* 1999), fewer females selfishly become queens (5.1–8.6%; Kerr 1950; Koedam *et al.* 1999; Sommeijer *et al.* 2003) than in *M. beecheii* (15.8%; Darchen & Delage-Darchen 1975; Moo-Valle *et al.* 2001), where all males are queens' sons (Paxton *et al.* 2001) (see tables 1 and 2 in electronic Appendix A). In addition, queen production is lower in *M. favosa* (5.1%), a species in which nearly all males are workers' sons (Sommeijer *et al.* 1999), than in *M. subnitida* (7.1%; Koedam *et al.* 1999) and *M. quadrifasciata* (8.6%; Kerr 1950), where 36–51% of the males are workers' sons (see tables 1 and 2 in electronic Appendix A). The negative relationship between queen overproduction and worker reproduction is significant ($\gamma = 1$, $Z = 2.04$, $p = 0.04$) and supports the role of kinship in influencing a tragedy of the commons. The observed caste ratios, 5–16%, are slightly lower than those predicted by theoretical models (14–20%; Wenseleers *et al.* 2003). However, these models assume that excess queen production causes a linear reduction in total colony productivity (male and swarm production; Wenseleers *et al.* 2003). If the cost function were concave, a closer match between theoretical and empirical figures occurs

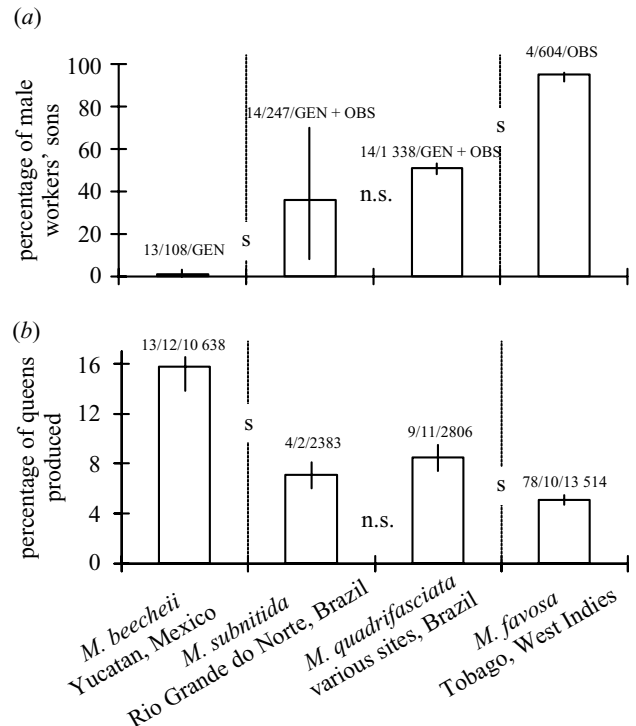


Figure 2. The effect of the colony kin structure on queen production in *Melipona*. Theory predicts that fewer females should selfishly develop as queens when many males are workers' sons because the cost of excess queen production is then borne by closer relatives, nephews ($r = 0.375$) rather than brothers ($r = 0.25$). This prediction is supported by levels of queen production in *Melipona* species with variable degrees of worker reproduction. In *Melipona favosa*, where (a) nearly all males are workers' sons, and (b) fewer females selfishly become queens (5.1%) than in *M. beecheii* (15.8%), where all males are queens' sons. In *M. subnitida* and *M. quadrifasciata*, where (a) the queen and the workers share male parentage, and (b) queen production is intermediate (7.1 and 8.6%). The negative relationship between queen overproduction and worker reproduction is significant ($\gamma = 1$, $Z = 2.04$, $p = 0.04$). For each data point the mean, 95% binomial confidence limit and sample size are shown (number of colonies/months/individuals for queen production data and number of colonies/males for male parentage data). For the male parentage data, it is also shown whether the data come from genetic (GEN) or observational studies (OBS), or both combined (GEN + OBS). Significant ($p < 0.05$) and non-significant ($p > 0.05$) differences between data points, as indicated with a non-overlap of the confidence limits, are indicated with 's' and 'n.s.'. A detailed list of the source studies on which the comparison is based is given in electronic Appendix A.

(Wenseleers *et al.* 2003). Importantly, however, a negative relationship between queen production and worker reproduction is predicted by the theory irrespective of the exact shape of the cost function. Hence, relative predictions are robust and independent of detailed assumptions.

4. DISCUSSION

What general lessons can be learned from the way that bees resolve tragedies of the commons? The *Melipona* case shows that in a situation where a common resource is free to be used by all, selfish exploitation is inevitable (Hardin 1968, 1998). In this respect, Hardin's conclusion that

'freedom in a commons brings ruin to all' remains (Hardin 1968, 1998). Not considered by Hardin (1968, 1998), however, were the effects of kinship. Our results provide the first tentative evidence, to our knowledge, that kinship can also partly reduce a TOC. This may be relevant to human society, such as in cases where common resources are shared by an extended family. However, coercion is more effective than kinship in resolving a TOC. Consider the honeybee *A. mellifera*. Because of multiple mating by queens, relatedness among offspring females is low (*ca.* 0.30), and the optimum proportion of female larvae that should develop into queens, given the ability to do so, is very high (56%; Wenseleers *et al.* 2003). However, excess queen production in honeybees is effectively prevented because the adult workers can enforce the caste fate of larvae by rearing them in distinct cells and on different foods (Winston 1987; Beekman *et al.* 2003; figure 1). This shows that nutritional caste determination, found in most social Hymenoptera with morphologically distinct queen and worker castes (Wilson 1971), is actually a form of social suppression that forces individuals to work for the benefit of society, even when this is against the individuals' own selfish interests. In other words, social insect workers may usually be oppressed rather than genuinely altruistic (cf. Michener & Brothers 1974; Alonso & Schuck-Paim 2002). In human society, social suppression is also widespread, but fortunately never reaches the point found in bees where individuals are fated, by their morphology, to work.

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ELECTRONIC APPENDIX A

Description of the data set

To test the effect of kinship on queen production we collated all available data on male parentage and female caste ratio in *Melipona*. A total of 32 studies and 4 reviews across 13 species were found. However, we only used studies where male parentage and caste ratio were known for the same population or geographical region, and were measured in either their natural environment or laboratory conditions where conditions approached natural ones as closely as possible. This left 12 studies on four species: *Melipona beecheii* (3 studies, all from Yucatan, Mexico), *M. favosa* (3 studies, all from Trinidad), *M. quadrifasciata* (3 studies, various sites, Brazil) and *M. subnitida* (3 studies, all from Rio Grande do Norte, Brazil) (Tables 1, 2).

Worker reproduction, as inferred from either genetic or observational studies, ranges from high to low. In *M. favosa*, 95% of males are workers' sons, in *M. subnitida* and *M. quadrifasciata* the workers and queen share in male production, and in *M. beecheii* all of the males are queen's sons (Table 1). These differences are statistically very highly significant (Table 1). In all four species colonies are headed by a single singly-mated queen (Kerr et al. 1962; da Silva et al. 1972; Kerr 1975; Contel & Kerr 1976; Peters et al. 1999; Paxton et al. 2001), so that sister-sister relatedness equals 0.75. (Double mating by queens was erroneously reported for *M. beecheii* due to the accidental inclusion of workers that drifted between colonies, Paxton et al. 1999).

Table 2 summarizes caste ratios in the same four species. Caste ratios, too, vary considerably. *M. beecheii* produces most queens (16%), *M. subnitida* and *M. quadrifasciata* produce an intermediate amount (7-9%) and *M. favosa* produces the least (5%). The differences between species with high, intermediate and low queen production are highly significant (Table 2). To determine whether queen production correlated with male production by workers we used the gamma statistic (Siegel & Castellan 1988) to test predicted rankings. *M. favosa* and *M. beecheii* were coded as having high and low predicted and observed queen production (the two studies on *Melipona beecheii*, Darchen & Delage-Darchen 1975 and Moo-Valle et al. 2001, were averaged into one data point). The predicted and observed ranks of *M. subnitida* and *M. quadrifasciata* were intermediate and considered to be tied, as both had nonsignificantly different caste ratios and levels of worker reproduction (Tables 1, 2).

All data were considered phylogenetically independent. This can be defended given that both the level of worker reproduction and caste ratios are evolutionary labile. For example, cytochrome oxidase I sequencing has shown that *M. favosa* and *M. beecheii* are phylogenetically very closely related (J.C. Nieh, unpublished data), yet they are at the two extremes in terms of both caste ratio and male parentage. Conversely, *M. subnitida* and *M. quadrifasciata* produce similar caste ratios and have similar levels of worker reproduction, but are not closely related phylogenetically, since they belong to different subgenera, *Melipona sensu strictu* and *Michmelia* Moure, 1975 (Moure 1992).

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Table 1. Data on male parentage in 4 *Melipona* species with sample sizes and 95% confidence limits. Levels of worker reproduction are significantly different ($p < 0.05$) when the 95% confidence intervals do not overlap; significant differences are indicated by distinct letters in column 8. The difference between *M. beecheii* and *M. favosa* is significantly different at the $p < 10^{-17}$ level (GLZ).

Species	Type of study (# of loci)	# Colonies	# Males	% males workers' sons	Overall estimate ^a	95% confidence limits ^a	Significant differences	References
<i>M. beecheii</i>	genetic (6)	13	108	0%	0%	0-3%	a	Paxton et al. 2001
<i>M. subnitida</i>	genetic (1) ^b	13	224	33%	36%	8-70%	b	Contel & Kerr 1976
	observational	1	23	65%				Koedam et al. 1999
<i>M. quadrifasciata</i>	genetic (4)	2	47	64%	51%	48-53%	b	Tóth et al. 2002
	observational	2	1,291 ^c	50%				da Silva 1977
<i>M. favosa</i>	observational	4	604	95%	95%	92-96%	c	Chinh et al. 2003; Sommeijer et al. 1999
total		35	2,297					

^aWeighted averages and confidence limits calculated by fitting a generalized linear (GLZ) model (McCullagh & Nelder 1989) with binomial error structure on the assigned parentage of the males ('COLONY' was nested within 'SPECIES'; for the genetic studies the maximum likelihood estimate of the proportion of workers' sons, calculated following Tóth et al. (2002), was used as the expected value). ^bSince only a single diagnostic locus was used, individual parentage of males could not be inferred very accurately. Hence, confidence limits were calculated from per colony estimates of the percentage of males that were workers' sons rather than from individual male parentage.

^cTwo colonies were given equal weight by subsampling to $N=518$ for both colonies.

Table 2. Caste ratio data in the same 4 *Melipona* species with sample sizes and 95% confidence limits. Fewer females selfishly become queens in *M. favosa*, where nearly all males are worker's sons, than in *M. subnitida* and *M. quadrifasciata*, where only 35-51% are workers' sons (Table 1). *M. subnitida* and *M. subnitida* in turn produce fewer queens than in *M. beecheii* where all males are queen's sons (Table 1). These differences are very highly significant (column 7, GLZ, $p < 10^{-17}$). The negative relationship between queen overproduction and the level of worker reproduction is also significant overall ($\chi^2 = 1$, $Z = 2.04$, $p = 0.04$). This supports the prediction that there should be less exploitation within groups when the cost is borne by close relatives (nephews, $r = 0.375$, rather than brothers, $r = 0.25$).

Species	# Colonies	# Individuals	# Months	Caste ratio (% of queens) ^a	95% confidence limits ^a	Significant differences	References
<i>M. beecheii</i>	13	10,638	12	15.8%	15.1-16.5%	a	Darchen & Delage-Darchen 1975; Moo-Valle et al. 2001
<i>M. subnitida</i>	4	2,383	2	7.1%	6.0-8.1%	b	Koedam et al. 1999
<i>M. quadrifasciata</i>	9	2,806	11	8.5%	7.4-9.5%	b	Kerr 1950
<i>M. favosa</i>	78	13,514	10	5.1%	4.7-5.5%	c	Sommeijer et al. 2003
total	104	29,341					

^aWeighted averages and confidence limits calculated from a fitted GLZ model (McCullagh & Nelder 1989) with binomial error structure and 'SPECIES', 'COLONY' and 'SEASON' (month of the year) as hierarchically nested factors.