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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 influential analysis by Hardin (1968) 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—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 supersEDURE 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. javae (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
queens are reared than are needed (\(\text{caste development results in a TOC in which many more}\) observed caste ratios, 5–16%, are slightly lower than those \(\text{kinship in influencing a tragedy of the commons. The}\) queens are killed by workers (left) soon after emergence (\(\text{cells from which cappings have been removed). Excess}\) \(\text{and provision the cells. In}\) rearing is under the control of the adult workers who build \(\text{(a)}\) \(\text{productivity (male and swarm production; Wenseleers}\) \(\text{et al.}\)) \(\text{predicted by theoretical models (14–20%; Wenseleers}\) \(\text{al.}\)) \(\text{in which nearly all males are workers’ sons (Sommeijer}\) \(\text{1999), than in}\) \(\text{M.beecheii}\) \(\text{selfishly become queens (5.1%) than in}\) \(\text{M. subnitida}\) \(\text{where all males are queen’s sons (Paxton et al. 2001) (see}\) \(\text{tables 1 and 2 in electronic Appendix A). In addition,}\) \(\text{queen production is lower in}\) \(\text{M. favosa (5.1%), a species in which nearly all males are workers’ sons (Sommeijer et al. 1999), than in}\) \(\text{M. subnitida (7.1%; Koedam et al. 1999)}\) and \(\text{M. quadrifasciata (8.6%; Kerr 1950), where 36–51% of the males are workers’ sons (see tables 1 and 2 in electronic}\) \(\text{Appendix A). The negative relationship between queen overproduction and worker reproduction is significant (}\(\gamma = 1, Z = 2.04, p = 0.04)\) \(\text{and supports the role of kinship in influencing a tragedy of the commons. The observed caste ratios, 5–16%, are slightly lower than those predicted by theoretical models (14–20%; Wenseleers et al. 2003). However, these models assume that excess queen production causes a linear reduction in total colony productivity (male and swarm production; Wenseleers et al. 2003). If the cost function were concave, a closer match between theoretical and empirical figures occurs}\)

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

(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 \(\text{Melipona}\) 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
very high (56%; Wenseleers et al. 2003), and the optimum proportion of female larvae that 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.


Ostrom, E. 1999 Governing the commons. Cambridge University Press.


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