

Research article

The effect of food reserves on the production of sexual offspring in the stingless bee *Melipona beecheii* (Apidae, Meliponini)

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Received 29 November 2000; revised 18 June 2001; accepted 20 August 2001.

Summary. A long-term study on the production of sexual offspring in relation to food stores was conducted in the stingless bee *Melipona beecheii*. Firstly, the production of sexuals was followed during one year in 10 colonies kept under natural conditions. Of the brood produced, 22.9% were males, and of all female brood, 14.6% were queens. Secondly, we measured the effect of experimentally manipulating the amount of food stores. One set of colonies started with 1.5 kg of food reserves and were regularly fed with pollen and nectar while another set were subjected to reduced food reserves of 0.5 kg, and were not given any extra food. Throughout the study, colonies with no treatment had brood and adults of both sexes all year round with no evidence of their presence being linked to swarming. Colonies with reduced food stores produced fewer males (0.7%) and queens (10.5%) than untreated colonies or colonies with enlarged food stores. The production of sexuals in colonies with enlarged food stores (23.4% males, 13.5% queens) did not differ significantly from that under natural conditions.

We conclude that in *Melipona* only colonies that have accumulated large food stores produce sexuals that contribute to the reproductive population. This may lead to marked differences in the amount of sexuals produced by different colonies, although at the population level sexuals may be present all year round.

Key words: Food stores, *Melipona*, drones, gynes, seasonal reproduction, stingless bees.

Introduction

The Meliponinae are the only highly advanced social bees aside from honeybees (*Apis*), their supposed sister taxon (Michener, 2000, but see Lockhart and Cameron, 2001). Despite a number of similarities, such as reproduction by swarming, their reproductive biology also shows a number of interesting contrasts (Peters et al., 1999). In *Apis*, for example, the mother queen is multiply mated (Tilley and Oldroyd, 1997; Fuchs and Moritz, 1998; Palmer and Oldroyd, 2000). This favours workers to lay eggs, but eat eggs laid by other workers (“worker policing”), as is indeed observed in nature (Ratnieks and Visscher, 1989; Ratnieks, 1993; Visscher, 1996). The result is that nearly all adult males are the mother queen’s offspring. Drones and queens are produced at the end of a seasonal cycle of population increase (Free, 1987; Fuchs and Moritz, 1998).

Within the Meliponinae, on the other hand, queens are typically singly mated (Paxton et al., 1999; Strassmann, 2001) and worker reproduction is frequent, although variable across species (da Silva, 1977; Contel and Kerr, 1976; Koedam et al., 1999; Sommeijer et al., 1999). In some species, reproductives are produced all year round (Sommeijer, pers. comm.) whilst in others there is a defined cycle of gyne and drone production (Engels and Imperatriz-Fonseca, 1990; van Benthem et al., 1995). What factors trigger the production of the different sexes remains unclear (Sommeijer, pers. comm.). For instance, the population size of a colony has not been invariably shown to correlate with sexual production. Males were produced in colonies of *M. beecheii* in Costa Rica during the flowering season provided they were strong and densely populated (van Veen et al., 1992), but in Brazil colonies of *S. postica* produced males all year round independent of their size (Engels and Engels, 1984; van Benthem et al., 1995). Thus, it is not clear if large resource

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availability together with a large forager population result in high investment in sexual offspring, at least not for all species.

The population dynamics of *Melipona* was first studied in Panama and total brood production was found to be related to floral resource availability in this area (Roubik, 1982). Subsequently, the population dynamics of *M. beecheii* has been studied in the southern limits of its geographical distribution in Costa Rica (Van Veen et al., 1992; 1999; Sommeijer, pers. comm.). The results from this area suggest that in *M. beecheii* the production of males may be related to pollen availability (van Veen et al., 1999). Nevertheless, the effect of food stores on the production of sexual offspring has not been directly tested.

In this paper we experimentally manipulate the amount of food stores inside colonies and follow the annual production of sexuals in colonies of *M. beecheii* with no treatment, with restricted food stores and enlarged food stores. This allows us to gain insight into what factors trigger the production of sexuals in this species.

Materials and methods

1. Colony rearing and measurement of sexual production under natural conditions

This study was conducted in Xmatkuil, Yucatán, México. In the first part of the study, 10 colonies of *M. beecheii* were randomly selected from a population of 45. Colonies had been hived in wooden boxes for at least one year before the experiment. The dimensions of the wooden hives were 44 cm × 14 cm × 24 cm. We used these colonies because they were already adapted to hives and an abnormal production of individuals was unlikely to occur as a result of severe manipulation (Sommeijer, pers. comm.). In this way, we expected to gather data that closely resembled the normal patterns of production of reproductives.

In each of these colonies cells were marked soon after they were sealed and the development of the combs was followed by means of video cameras. Forty five days later, combs containing pupae ready to emerge were removed from the nests, taken to the lab and placed in wooden boxes in an incubator at 32°C to allow individuals to emerge. This procedure was repeated every fortnight during one year. In the lab, the combs were inspected on a 24 h basis using video camera recorders and the numbers of individuals of each caste and sex were registered. At the end of each day individuals were reintegrated to their mother colonies in order to avoid a reduction in colony size.

A regression analysis was performed to investigate the relationship between the amount of drones and gynes produced. This allowed us to test whether sexual production was linked to a specific swarming season, since drone and gyne production should then occur synchronously. A generalized linear model was used to test for significant differences in sexual production across different colonies and seasons. The independent factors entered into the analysis were “colony” and “month”; the dependent variable was either the sex (male or female) or caste (gyne or worker) of each individual measured. Because in both cases the dependent variable could only take on two values, a binomial error structure and a logit link function was specified. All statistical analyses were performed using Statsoft Statistica v. 5.5.

2. Production of sexuals after experimental manipulation of food stores

To investigate the effect of food availability on sexual production, we randomly chose 6 colonies, and subjected 3 of these to a low-food

regime (group A) and the 3 others to a high-food regime (group B). Sexual production was subsequently measured over a full year. The colonies were housed in wooden hives measuring 34 cm × 12 cm × 19 cm and were provided with an adult population of ca. 450 workers and 200 cells of brood at different stages of development. The three group A colonies were given 0.5 kg of food pots (ca 50% pollen and 50% honey) without any additional food; the 3 group B colonies were given ca. 1.5 kg of food pots (same proportion of pollen and honey) plus an additional 100 g of pollen and honey every 15 days. The numbers and weight of pollen and honey pots were calculated in accordance to van Veen et al. (1999). Colonies were left to forage for resources that were available. One month after the colonies were transferred to hives, the procedure for detecting brood cells and counting and sexing the individuals was initiated (same procedure as in section 1).

As in section 1, a generalized linear model with binomial error structure was used to test for the significance of the effect of the experimental treatment, as well as to test for significant differences in sexuals produced by different colonies in various seasons. The categorical independent factors were “treatment”, “colony” and “month”, with “colony” nested within “treatment” and “month” nested within “colony” (so that intercolony differences were compared only for a given treatment, and seasonal differences were compared only for a given colony). The total amount of brood and food storage (both in grams) present at any given time were included as covariates.

Results

1. Production of sexuals under natural conditions

A total of 10,193 individuals were collected from the 10 study colonies over a 12 month period. Of these, 2,346 were drones, 1,139 were gynes and 6,708 were workers. The year-round average production of gynes and drones, as a percentage of total and female production, was 14.6% (95% confidence interval: [13.8–15.3%]) and 22.9% (95% confidence interval: [22.1–23.7%]) (Table 1). For both sexes, however, there was also significant seasonal variation (*GLZ*, gynes: $p < 0.0001$, drones: $p < 0.05$, Figs. 1 and 2 and Table 2), with the magnitude of the seasonal effect depending upon colony factors (*GLZ*, month × colony interaction effect, Table 2). For drones, the lowest proportion in the colonies was recorded in September (11.36%) whilst the highest was recorded in June (25.04%) (Fig. 1). For gynes, the lowest proportion was recorded in September (8.9%) and the highest in May (20.8%) (Fig. 2). The production of both gynes and drones also varied significantly between individual colonies (*GLZ*, gynes: $p < 0.0001$, drones: $p < 0.0001$; Table 2). Gyne production was lowest in colony 5 (6.34%) and highest in colony 10 (16.14%). The production of drones was lowest in colony 8 (8.6%) and highest in colony 1 (37.5%).

For seasonally swarming social insects, one would expect drone and gyne production to be synchronised at the population level. A regression analysis, however, showed that there was no significant relationship between the percentage of drones and gynes produced at any given moment ($p = 0.4$; Fig. 3). Sexual production, therefore, does not seem to be causally linked to swarming. It should be noted, however, that although colonies produced sexuals all year-round there was no evidence of swarming during the experimental period.

Table 1. Drone and gyne production (as percentage of total and female production) in 10 colonies of *M. beecheii* under natural conditions, 3 colonies with restricted food supplies and 3 colonies with surplus amount of food

Month	Natural N = 10		High Food N = 3		Low Food N = 3	
	Drones Mean ± s.d.	Gynes Mean ± s.d.	Drones Mean ± s.d.	Gynes Mean ± s.d.	Drones Mean ± s.d.	Gynes Mean ± s.d.
Jan	20.77 ± 11.65	15.87 ± 3.84	16.44 ± 11.61	13.30 ± 5.70	0	10.00 ± 3.35
Feb	21.63 ± 11.60	12.22 ± 7.75	0	11.64 ± 5.08	0	11.12 ± 1.10
Mar	21.96 ± 15.46	17.27 ± 8.93	3.40 ± 5.89	15.99 ± 4.15	0	10.87 ± 0.95
Apr	23.71 ± 11.44	13.83 ± 10.14	4.73 ± 4.31	8.33 ± 5.04	0	6.83 ± 1.90
May	24.32 ± 10.14	20.80 ± 5.00	26.06 ± 7.73	20.30 ± 1.77	0.78 ± 0.68	13.65 ± 7.64
Jun	25.04 ± 14.49	15.35 ± 7.36	37.05 ± 7.10	21.69 ± 14.04	0	11.16 ± 6.53
Jul	21.88 ± 18.01	10.64 ± 3.84	25.29 ± 6.02	12.68 ± 11.38	1.93 ± 1.79	8.16 ± 3.53
Aug	17.92 ± 10.59	12.86 ± 4.69	32.86 ± 3.46	11.05 ± 3.30	0	10.00 ± 5.20
Sep	11.36 ± 12.18	11.65 ± 6.24	35.58 ± 3.48	9.55 ± 6.65	0	6.32 ± 4.32
Oct	18.22 ± 11.31	13.14 ± 6.85	11.98 ± 12.56	14.94 ± 10.00	3.67 ± 2.1	9.34 ± 4.46
Nov	19.21 ± 10.80	15.60 ± 10.99	19.14 ± 6.12	14.20 ± 3.70	0	13.28 ± 7.67
Dec	18.44 ± 15.85	16.22 ± 5.53	26.58 ± 19.44	13.64 ± 5.03	0	9.03 ± 5.84
Mean	22.9%	14.6%	23.4%	13.5%	0.7%	10.5%
[95% C.I.]	[22.1–23.7%]	[13.8–15.3%]	[22.0–24.7%]	[12.3–14.8%]	[0.4–1.0%]	[9.4–11.6%]

Table 2. Significance of factors affecting gyne (a) and male (b) production under natural conditions tested using a GLZ model

	Degrees of freedom	Wald Statistic	<i>p</i>
<i>(a) Effects on gyne production</i>			
Intercept	1	0.0056	0.94
Colony	9	62.61	<0.0001
Month	11	55.71	<0.0001
Colony × Month	99	154.59	0.0003
<i>(b) Effects on drone production</i>			
Intercept	1	0.00066	0.98
Colony	9	235.25	<0.0001
Month	11	23.19	0.017
Colony × Month	99	331.66	<0.0001

2. Production of sexuals after experimental manipulation of food stores

A total of 1,525 brood cells were sampled from the three group A colonies, yielding 152 gynes, 15 drones and 1,358 workers. In group B, a total of 3,503 brood cells containing 379 gynes, 792 drones and 2,332 workers were collected. This amounts to 0.7% (95% C.I.: [0.4–1.0%]) and 23.4% (95% C.I.: [22.0–24.7%]) drones and 10.5% (95% C.I.: [9.4–11.6%]) and 13.5% (95% C.I.: [12.3–14.8%]) gynes for groups A and B respectively (Table 1). This shows that both drone and gyne production are lower in food deprived (group A) colonies than in well fed (group B) or natural colonies (Fig. 1 and 2). A GLZ analysis shows that both trends are highly significant (drone production: *p* < 0.0001, gyne production: *p* < 0.001; Table 3). Sexual production by the well-fed B type colonies, however, was not significantly different from the colonies kept under natural conditions (GLZ, *p* > 0.05 for both gynes and drones; Figs. 1 and 2).

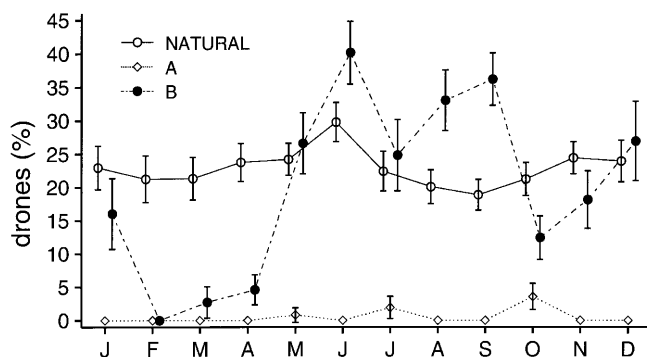


Fig. 1. The monthly percentage of drones (% of total brood) produced in *M. beecheii* colonies under natural conditions and with experimentally reduced (A) or enlarged (B) food reserves. The whiskers denote 95% confidence intervals.

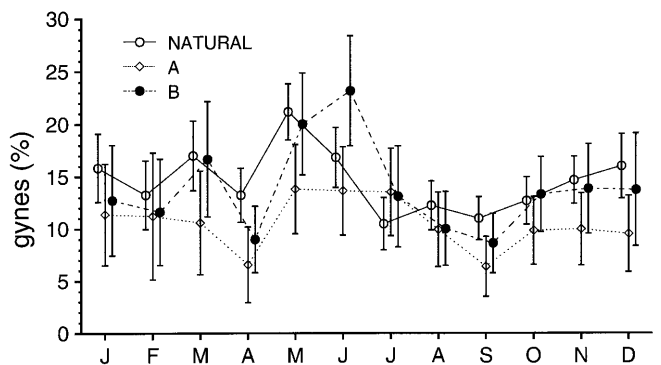


Fig. 2. The monthly percentage of gynes (% of female brood) produced in *M. beecheii* colonies under natural conditions and with experimentally reduced (A) or enlarged (B) food reserves. The whiskers denote 95% confidence intervals.

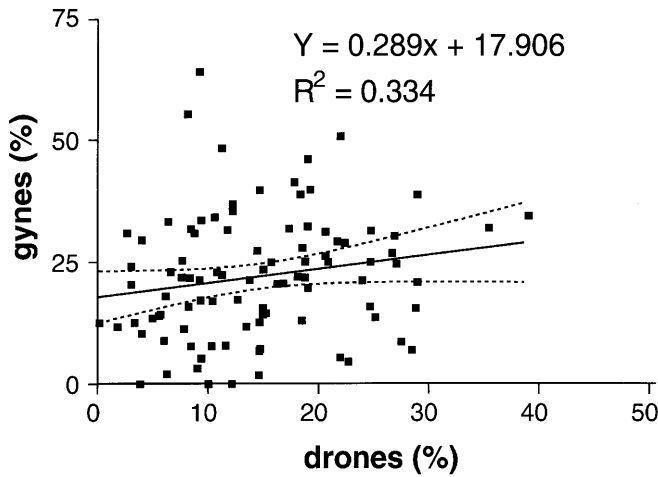


Fig. 3. A regression line of the proportion of drone brood against the proportion of gyne brood present in 10 colonies of *M. beecheii* kept under natural conditions

Table 3. Results of a GLZ model that shows that levels of gyne and male production are significantly lower in colonies with experimentally reduced food stores ('Treatment'). 'Brood' is the amount of brood present in any given month (in g), 'Food' is the total weight of all food stores (in g)

	Degrees of freedom	Log-Likelihood	Chi-square	p
<i>(a) Effects on gyne production</i>				
Intercept	1	-2106.87		
Treatment	1	-2100.62	12.51	0.0004
Colony (Treatment)	4	-2075.13	50.97	<0.0001
Month (Colony)	33	-2029.43	91.40	<0.0001
Brood	1	-2029.42	0.019	0.89
Food	1	-2029.40	0.048	0.83
<i>(b) Effects on drone production</i>				
Intercept	1	-2656.67		
Treatment	1	-2190.95	931.43	<0.0001
Colony (Treatment)	4	-2187.04	7.82	0.098
Month (Colony)	33	-1924.74	524.60	<0.0001
Brood	1	-1924.31	0.86	0.35
Food	1	-1924.20	0.22	0.64

As for the colonies kept under natural conditions, there were also significant seasonal and, in terms of gyne production, intercolony effects (Table 3). In group A colonies, gyne production was lowest in September (6.32%) and highest in May (13.65%) (Fig. 2, Table 1). Drones were produced in very small numbers, in May (0.8%), July (2.49%) and October (2.96%) (Fig. 1, Table 1). In group B colonies, drones and gynes were produced almost all the year. Gyne production was lowest in April (8.33%) and highest in June (21.69%) (Fig. 2); drone production was lowest in February (0%) and highest in June (41.08%) (Fig. 1, Table 1).

The total amount of brood and food stores present at any given time did not explain any additional variation in the production of gynes or drones, beyond that already explain-

ed by the treatment itself (Table 3). Nevertheless, both factors were obviously correlated with the treatment effect: 1874.5 ± 463.6 g total amount of food stores were present in well-fed colonies vs. just 541.2 ± 182.4 g in poorly fed colonies and 151.7 ± 24.2 g total amount of brood was present in well-fed colonies vs. just 52.0 ± 15.3 g in poorly fed colonies.

Discussion

The production of sexual offspring in social insects is an event that is thought to be triggered by a complex interaction between intra- and extra-colony factors (van Veen et al., 1999). In this study we investigated the effect of colony-wide nutrition on the production of sexual offspring in the stingless bee *Melipona beecheii*. In colonies kept under natural conditions, sexuals were constantly produced but in varying quantities by different colonies. Food manipulation experiments were performed to assess whether the size of the food stores could explain such intercolony variation. A major conclusion was that the size of a colony's food reserves had a strong influence on sexual production, since food deprived colonies produced a reduced proportion of drones, and a smaller proportion of gynes, than well-fed colonies. Drone production was affected most, and dropped from 23.4% in well-fed colonies to 0.7% in food restricted colonies. This means that weak colonies (such as those that recently swarmed) are impaired to contribute to the effectively reproducing population until they build up their food reserves. This makes sense, given that colonies are expected to first use up their food resources to produce workers before directing the excess to produce drones because the former carry out a wide variety of tasks ultimately related to colony survival (Oster and Wilson, 1978). Interestingly, such a strategy implies that colonies have the ability to modulate the production of drones in relation to the amount of accumulated food stores. That is, there must exist an information link between a colony's state of food reserves and the behavioural and/or physiological state of the individuals producing the drones. Such a link may provide either an excitatory feedback when the food reserves are large or an inhibitory feedback when the food reserves are small.

Alternatively, the influence of food reserves on male production could be explained by the fact that well-fed colonies potentially could support more reproductive workers. In fact, in other stingless bees, egg-laying workers have been shown to have better access to pollen stores than non-reproductive workers, and workers handling pollen for larval food-provisioning more frequently have developed ovaries (Sommeijer et al., 1984, 1985; pers. comm.). Unfortunately, in *M. beecheii*, it is not currently known whether workers contribute to drone production, although worker reproduction has been shown in several other species (da Silva, 1977; Contel and Kerr, 1976; Sommeijer and van Buren, 1992; Koedam et al., 1999; Sommeijer et al., 1999).

In contrast with drone production, gyne production in *M. beecheii* was found to be less dependent on food reserves. In

our study ca. 10 and 14% of the female larvae developed into gynes under plentiful and reduced food conditions. By comparison, food limited colonies almost ceased to produce any drones. The greater constancy of gyne production might be explained by the fact that in *Melipona* caste determination is thought to be under partial genetic control (Kerr, 1950, 1969). Even so, the drop in gyne production of 4% under poor food conditions was statistically significant, and is hard to explain if caste determination were purely genetic (Kerr, 1950, 1969). In an extension of Kerr's hypothesis, Velthuis and Sommeijer (1991) argued that a genetically set maximum of 25% gyne production is reached only under ideal food conditions. They hypothesized that in colonies with large pollen stores, the female larvae may receive larger quantities of better quality food causing them to develop into gynes. Unfortunately, it is hard to see what could prevent females to develop as gynes under poor food conditions, given that in *Melipona* gynes are no larger than workers (Kerr, 1969; van Veen, 1999). In fact, even in trigonine stingless bees, where gynes are larger than workers, some percentage of the female larvae may develop as dwarf gynes (Imperatriz-Fonseca et al., 1997). This means that in stingless bees, food conditions as such are not as restrictive for the development of gynes as envisaged by Velthuis and Sommeijer (1991).

Adaptionist reasons might provide better explanations for why food deprived colonies produce fewer gynes. For example, if females develop into gynes according to some evolutionary set optimum, then females might not develop as gynes, or with lower probability, when the prospects for swarming are low. Indeed, since we found food deprived colonies produce little brood, they might not be fit enough to swarm. Unless the mother queen were replaced, a gyne produced under such circumstances would represent a dead end.

Ultimately, it appears that the production of sexuals in the Meliponini may not be seasonal as in *Apis* but rather related to the amount of food reserves that the colony has stored over time. This strategy makes sense in tropical ecosystems where food availability is constant year-round. The consequent non-synchronized production of drones and gynes may cause sexuals to be present all-year round. Colonies with adequate food supplies also produced both drones and gynes, which contrasts with findings in Costa Rica where colonies produced either drones or gynes but not both (van Veen et al., 1999).

In sum, we conclude that in Yucatán, there is evidence that the production of sexuals in *M. beecheii* occurs continuously at the population level but that there are quantitative differences at the individual colony level. Differences in sexual productivity among colonies were most strongly affected by differences in accumulated food stores. This causes sexuals to be present fairly continuously across the year.

Acknowledgements

We are grateful to Robert Paxton, Francis Ratnieks, Marinus Sommeijer and an anonymous reviewer for discussion and suggestions on our manuscript. We also thank CONACyT and the IFS for supporting this study.

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