APICULTURE AND SOCIAL INSECTS

Temporal Variation in Honey Production by the Stingless Bee *Melipona subnitida* (Hymenoptera: Apidae): Long-Term Management Reveals its Potential as a Commercial Species in Northeastern Brazil

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ABSTRACT Even though stingless beekeeping has a great potential as a sustainable development tool, the activity remains essentially informal, technical knowledge is scarce, and management practices lack the sophistication and standardization found in apiculture. Here, we contributed to the further development of stingless beekeeping by investigating the long-term impact of management and climate on honey production and colony survival in the stingless bee *Melipona subnitida* Ducke (1910). We analyzed a 10-yr record of 155 *M. subnitida* colonies kept by a commercial honey producer of northeastern Brazil. This constitutes the longest and most accurate record available for a stingless bee. We modeled honey production in relation to time (years), age, management practices (colony division and food supplementation), and climatic factors (temperature and precipitation), and used a model selection approach to identify which factors best explained honey production. We also modeled colony mortality in relation to climatic factors. Although the amount of honey produced by each colony decreased over time, we found that the probability of producing honey increased over the years. Colony divisions decreased honey production, but did not affect honey presence, while supplementary feeding positively affected honey production. In warmer years, the probability of producing honey decreased and the amount of honey produced was lower. In years with lower precipitation, fewer colonies produced honey. In contrast, colony mortality was not affected by climatic factors, and some colonies lived up to nine years, enduring extreme climatic conditions. Our findings provide useful guidelines to improve management and honey production in stingless bees.

RESUMO Embora a criação de abelhas sem ferrão apresente um grande potencial como ferramenta para o desenvolvimento sustentável, a atividade ainda é baseada principalmente em técnicas tradicionais e as práticas de manejo não possuem a sofisticação e a padronização encontradas na apicultura. Nesse estudo, contribuímos para o futuro desenvolvimento da meliponicultura investigando o impacto a longo prazo do manejo e do clima sobre a produção de mel e a sobrevivência em colônias da abelha sem ferrão *Melipona subnitida* Ducke (1910), popularmente conhecida como Jandaíra. Analisamos uma série temporal de dez anos de 155 colônias de *M. subnitida* mantidas por um produtor de mel do Nordeste Brasileiro. Esse é o registro mais longo e mais preciso disponível para uma abelha sem ferrão. Modelamos a produção de mel em relação ao tempo (anos), manejo (divisão de colônia e alimentação suplementar) e fatores climáticos (temperatura e precipitação) e, por meio de seleção de modelos, identificamos quais fatores melhor explicaram a produção de mel. Também modelamos a mortalidade das colônias em relação aos fatores climáticos. Embora a quantidade de mel produzido por cada colônia tenha diminuído ao longo do tempo, observamos que a probabilidade de produzir mel aumentou ao longo dos anos. A divisão de colônias afetou negativamente a produção de mel, mas não sua presença, enquanto a alimentação das colônias a afetou positivamente a produção de mel. Em anos mais quentes, a probabilidade de produzir mel diminuiu e a produção de mel foi menor. Em anos com menor precipitação, menos colônias produziram mel. Já a mortalidade não foi afetada por fatores climáticos, e algumas colônias sobreviveram até nove anos, suportando condições extremas de clima. Nossos resultados fornecem diretrizes para o aperfeiçoamento do manejo e da produção de mel de abelhas sem ferrão.

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Although the commercial use of honeybees has become a major global business, the profitable use of stingless bees (designated meliponiculture after the bees from the Meliponini tribe) has received much less attention (Cortopassi-Laurino et al. 2006, Contrera et al. 2011). Currently, meliponiculture can be found in Central and South America, Asia, Africa, and Australia (Quezada-Euán et al. 2001, Cortopassi-Laurino et al. 2006, Alves 2013, Halcroft et al. 2013). In developing nations, meliponiculture remains an essentially informal activity (Villanueva-G et al. 2005, Cortopassi-Laurino et al. 2006). Besides preserving the cultural heritage, stingless beekeeping has an important role in the conservation of native bees, which are increasingly threatened by habitat loss and fragmentation (Brown and Albrecht 2001, Kennedy et al. 2013). Furthermore, stingless beekeeping assures the provision of pollination services, as stingless bees are important pollinators for both native plants and commercial crops (Heard 1999, Cortopassi-Laurino et al. 2006, Giannini et al. 2014).

Important efforts have been directed to train beekeepers and standardize management practices (Nogueira-Neto 1997, González-Acereto et al. 2006, Venturieri 2008, Villas-Bôas 2012, Frazão 2013), quantify investment costs and profit perspectives (Lobato and Venturieri 2010), and assess honey properties, quality and commercialization routes (Vit et al. 2013). However, there is still a large knowledge gap in terms of the appropriate techniques needed to maintain healthy colonies and ensure the consistent production of honey over time (but see Jaffé et al. 2015). Research devoted to this end could thus contribute toward transforming the activity into a powerful tool for sustainable rural development (Venturieri et al. 2003, Cortopassi-Laurino et al. 2006).

The main products commercialized by stingless beekeepers are colonies and honey. Stingless bee honey is quite distinct from *Apis mellifera* L. honey. It has higher water content (20–42% of water) and its flavor is sour and slightly sweet, varying among bee species and flowers visited by the bees (Nogueira-Neto 1997, Souza et al. 2006, Deliza and Vit 2013). Stingless bee honey consumption is deeply rooted in some communities, who believe it has medicinal properties (Zamora et al. 2013), and its price is much higher than the price of honeybee honey (Alves, 2013).

Generally, larger stingless bee species produce more honey and, hence, are more likely to be exploited for honey production (Alves 2013). One such species is *Melipona subnitida* Ducke (1910), which is among the main cultivated species across northeastern Brazil. Colonies produce relatively large amounts of honey as compared with other stingless bee species, can be artificially reared in wooden boxes, and support management practices such as honey extraction and colony divisions (Cortopassi-Laurino et al. 2006). A central figure in the commercial use and conservation of *M. subnitida* was Father Huberto Bruening (1914–1995). A priest in the city of Mossoró, Rio Grande do Norte, he improved informal beekeeping practices, established links with national and international researchers, and motivated the local population to engage in stingless beekeeping (Bruening 2006). Mr. Paulo Menezes, one of his disciples, inherited Bruening's colonies and has continued his work as a teacher and promoter of meliponiculture. Currently, Mr. Menezes is a major stingless bee honey producer and well-known beekeeper across northeastern Brazil, having received the first license for stingless bee honey commercialization in the country. Mr. Menezes (co-author of this study) meticulously recorded honey production and management practices in 155 of his colonies over a period of 10 yr. Here, we analyze his dataset, which, to our knowledge, is the longest and most accurate yet available for any stingless bee. By assessing the long-term impact of management and climate on honey production and survival in *M. subnitida*, we provide an important contribution to the development of commercial stingless beekeeping.

Materials and Methods

The Data Set. We analyzed a temporal record of 155 *M. subnitida* colonies, closely monitored for a period of 10 yr (Supp Tables 1 and 2 [online only]). The colonies were kept at the "Meliponário Monsenhor Huberto Bruening," in Mossoró, Rio Grande do Norte, Brazil (Fig. 1). This state is dominated by the Caatinga biome, a semi-arid region with extreme climate (high temperatures and low and irregular precipitation) and defined seasonality (Prado 2003). Between 1999 and 2008, Mr. Menezes followed his colonies (identifying each one with a different code), and recorded the total amount of honey produced by each colony each year, the management provided to each colony, and whether the colony died (the variables recorded are described in Supp Table 3 [online only]). Whenever a colony was reported dead, a new colony was established in the same wooden box and a new identification code was given to it.

To replace dead colonies and increase the size of the beekeeping operation, colonies were periodically divided. To this end, 50 to 70% of the brood discs containing bee pupae near emergence were removed from selected colonies (those with more brood and workers) and placed in an empty wooden box to create a new daughter colony. In the *Melipona* genus, many queens are produced per brood comb [14–20%, Wenseleers and Ratnieks (2004)] and, hence, a queen will normally hatch from the transplanted combs. Upon emergence, the new queen will mate (presumably with a single male), return to the colony and begin laying eggs. Colony divisions were performed between January and July, overlapping with the rainy season

Fig. 1. Colonies of *M. subnitida* held in the "Meliponário Monsenhor Huberto Bruening", Mossoró (Rio Grande do Norte, Northeastern Brazil). Photo by Paulo Menezes.

(which comprehends November to April) (Prado 2003), when more floral resources are available (Zanella and Martins 2003; Supp Table 4 [online only]). The colonies were divided once per year, except in one case in 2004 when a colony was divided twice in the same year. Honey was harvested from the divided colonies, but only 1 to 5 mo after the procedure. When new colonies were purchased from other beekeepers (either inside tree branches or in boxes), the entire colony was transferred to a new wooden box and assigned a new identification code.

Honey harvesting was performed between April and September, after the rainy season, when the honey storages are full (Supp Table 4 [online only]). Honey was normally collected once per year, but in atypical years, two honey batches were harvested from each colony. In these cases (12% of all honey-producing colonies), honey production was still quantified as the total volume of honey produced per colony per year. In stingless bee colonies, honey and pollen are stored in egg-shaped pots, apart from the brood area (Nogueira-Neto 1997, Supp Fig. 1 [online only]). During honey collection, the pots were opened and honey was either harvested by flipping the boxes and leaving the honey to drain into a collection container, or in the later years, by suction with a plastic hose attached to an electric pump. Although the total honey reserves were harvested, some honey always remained in honey pots and was left for the colonies. The volume of honey harvested was recorded and honey production <100 ml was considered essentially nil, and was registered as zero production (Supp Table 3 [online only]). This happened when virtually no or very little honey was found in the colonies, either because they were too weak (and thus consumed more than what they could store) or when floral resources were scarce. In 2008, colonies received supplementary feeding consisting of sugar syrup (1:1 sugar, water; 250 ml) every fortnight. Syrup was provided in feeders placed inside the colonies and the total amount was consumed by the bees in 2–5 d. Supplementary feeding was only provided during the dry season months, between May and October, and it ceased at the onset of the rainy season.

Climate Data. Climate data were obtained for the nearest meteorological station with available historic data, which is located in the city of Apodi, 73 km from

Mossoró (Instituto Nacional de Metereologia [INMET] 2014). We gathered all available climatic data for the years 1999–2008, including: 1) number of days with precipitation, 2) total precipitation (mm), 3) mean maximum temperature (°C), (4) mean weighted temperature (°C), 5) mean minimum temperature (°C), and 6) mean relative humidity (%) (Supp Table 5 [online only]).

Statistical Analyses. We modeled honey production across time using generalized linear mixed models (R package glmmADMB; Skaug et al. 2013). Because some colonies did not produce any honey in many years (all honey produced was consumed by the bees or the production was <100 ml and considered nil), we jointly modeled the amount of honey that the colony produces and the probability that a given colony will produce honey in a given year. To do so, we used a hurdle model, which consists of two submodels: 1) a zero-truncated count model (henceforth count model) for which the response variable is honey production (using only those data for which honey production is greater than zero) and follows a negative binomial distribution, and 2) a logistic regression for which the response is binary (honey presence, using all data) and follows a Bernoulli distribution (henceforth zero model). The hurdle model implicitly assumes that the zero-generating process is distinct from the count-generating process. In the context of our study, we consider that an overall greater honey production per colony does not necessarily imply more frequent honey production, and that different causative factors may mediate these two processes.

Both the count- and zero-processes reflect the response of individual colonies over time. To account for these dependencies, we included a random intercept for each colony (e.g., the mean honey production or probability of producing honey varies randomly with colony), and a random slope (e.g., the change in honey production across time varies randomly with colony). In the zero model (honey presence), the interaction between colony and time was not included as year showed zero variance in a random slope model. For both submodels, we fitted a full model with time (year), colony division (brood comb removal for new colony foundation), supplementary feeding, and climate variables as fixed effects. Yearly mean minimum temperature (henceforth referred to as temperature) and yearly total precipitation (henceforth referred to as precipitation) were chosen as the climatic predictors because they were found to minimize multicollinearity. Supplementary feeding was not included in the zero model for honey presence, as there was a complete separation (all fed colonies produced honey) and thus feeding was not an informative predictor (Supp Table 6 [online only]). All continuous predictor variables were centered and scaled to aid model convergence. For each submodel, we used marginal likelihood ratio tests to choose the best model and assess the explanatory power of predictors. We used likelihood ratio test to compare reduced models without each predictor variable, with full models containing them. Because our aim was to assess how management practices, time, and climatic variations influenced honey production, we decided to analyze only established colonies that had enough time to respond to such predictors. Thus, for this analysis, we excluded shortly established colonies (recently bought or created) and colonies that died right after being created (see Table 1 for final sample sizes).

To assess the sensitivity of these results to the inclusion of data from 2008 (the only year supplementary feeding was provided), we fitted an additional model without the data from this year. The effect of supplementary feeding in 2008 was also assessed in a separate analysis, comparing honey production in 2008 against all previous years. We modeled honey production using a negative truncated binomial analysis of variance, with a custom set of orthogonal contrasts, in which a given year was compared to all previous years. As in the previous models, a random intercept was included for each colony (the production of honey between years varies randomly with colony). The years 1999 and 2001 were not included because 1999 had only one observation on honey production, and in 2001, no colony produced honey.

To discriminate between the effect of time from the effect of colony age on honey production and honey presence, we fitted similar hurdle models to a subset of the data containing only colonies with known age (born from divided colonies, $n = 47$). Colony age was included as an additional fixed factor in the best zero and count models previously found using the whole data set. As described above, marginal likelihood ratio tests were used for model selection and assess the explanatory power of predictors.

To assess the influence of climate on colony mortality, we analyzed the number of lost colonies per year with a generalized linear model with an overdispersed binomial distribution. We treated the number of lost colonies each year (out of the total number of colonies) as the response variable, and included temperature and precipitation as predictor variables (Supp Table 6 [online only]). Marginal likelihood ratio tests were also used to assess the explanatory power of predictor variables. We excluded data for the year 2008 in this analysis, as supplementary feeding is known to affect colony performance (Nogueira-Neto 1997). In addition, we excluded mortality cases related to queen removal ($n = 3$), colony transportation or ant attacks ($n = 3$).

Results

The total number of colonies monitored each year varied from 9 to 108 (Table 1). Honey production per colony varied from 0 to 1.8 liters, with a mean (±SD) yearly production of 0.43 (±0.4) liters. Considering only colonies that did produce some honey, mean yearly production was 0.67 (±0.3) liters. Total joint honey production ranged from 0 to 60.9 liters per year, with a mean joint production of 23.1 (±21.4) liters per year. Overall, we analyzed data from 155 different colonies through the 10 yr.

The best count model (honey production) included all predictors except annual precipitation. The best

Table 1. Ten-year record for 155 *M. subnitida* colonies

Record of *M. subnitida* Colonies							
Year	No. colonies (mortality analysis/honey production analysis)	No. (proportion) of lost colonies	No. of colony divisions	Honey production per colony (mean ± SD) (milliliters)	Honey production per colony: colonies producing honey (mean ± SD) (milliliters)	Min.–Max honey production per colony (milliliters)	Honey production per year (milliliters)
1999	9/1	1 (0.11)	0	800	800	800	800
2000	17/10	6 (0.35)	3	160 ± 267	400 ± 294	0–800	1,600
2001	50/25	22 (0.44)	1	0	–	0–0	0
2002	63/42	5 (0.08)	0	486 ± 464	817 ± 293	0–1,380	20,430
2003	65/58	5 (0.08)	16	726 ± 605	1002 ± 474	0–1,800	42,100
2004	84/63	12 (0.14)	32	522 ± 372	710 ± 254	0–1,250	34,800
2005	90/75	8 (0.09)	0	51 ± 188	633 ± 280	0–1,000	3,800
2006	108/82	17 (0.16)	2	501 ± 309	586 ± 247	0–1.300	41,050
2007	92/92	0 (0)	0	276 ± 261	454 ± 175	0–900	25,400
2008	92/92	0 (0)	0	662 ± 135	662 ± 135	400–1,000	60,900
Mean ± SD	67 ± 34	7.6 ± 7.38 (0.16 ± 0.14)	5.4 ± 10.5	421 ± 284	674 ± 186	120 ± 270–1,023 ± 474	23,088 ± 21,414

The table shows the number of colonies (used in the mortality and honey production analyses, respectively), the number (proportion) of lost colonies, the number of colony divisions, honey production per colony (for all colonies and only for colonies that produced honey), minimum and maximum honey production, and the total honey production per year. Honey production is reported in milliliters.

Table 2. Parameter estimates and hypothesis tests for the best models describing honey production (honey amount and honey presence models)

Generalized Linear Mixed Effects Model for Honey Production								
			Fixed effects					
Model	Data sets	No. observation/ colony number	Predictor	Estimate	SE	χ^2	Degrees of freedom	*P*-value
Honey amount (count model)	Established colonies 1999–2008	345/109	Year	−0.1143	0.0155	46.54	1	<0.0001
			Colony division	−0.2073	0.0702	8.44	1	0.0037
			Supplementary feeding	0.3142	0.0675	20.70	1	<0.0001
			Temperature	−0.4670	0.0964	20.78	1	<0.0001
Honey amount (count model)	Established colonies 1999–2007	253/97	Year	−0.1138	0.0176	31.34	1	<0.0001
			Colony division	−0.2142	0.0799	6.94	1	0.0084
			Temperature	−0.4733	0.1120	16.64	1	<0.0001
Honey amount (count model)	Established colonies of known age 1999–2008	123/42	Year	−0.1414	0.0221	34.12	1	<0.0001
			Supplementary feeding	0.4501	0.0965	19.62	1	<0.0001
Honey presence (zero model)	Established colonies 1999–2007	540/124	Year	0.2307	0.0519	20.69	1	<0.0001
			Temperature	−0.8169	0.3193	73.70	1	0.0095
			Precipitation	0.0048	0.0006	6.73	1	<0.0001
Honey presence (zero model)	Established colonies of known age 1999–2007	236/65	Colony age	0.6033	0.0982	52.05	1	<0.0001
			Temperature	−1.7832	0.7109	9.67	1	0.0019

Number of observation is the number of observations of each model and colony number refers to the total number of colonies included. For each predictor, estimates and SEs from the model are given. The *P*-values and degrees of freedom refer to the marginal likelihood ratio tests (using a χ^2 test statistic), in which the full model was compared with a reduced model without each of the predictor variables. For more details on the different data sets used see Supp Table 6 (online only).

zero-model (honey presence) included time and climatic factors (temperature and precipitation) (Table 2). The quantity of honey harvested decreased over the years (Fig. 2). This reduction was not related to colony aging, as in a complementary analysis, age was not included in the best model, while honey production still showed a significant decrease with time (Table 2). Colony division decreased the amount of honey produced in a given year (reduction of 19% on average; Fig. 3), while food supplementation increased honey production (increment of 37% on average; Fig. 4). Years with higher temperatures were associated with decreased honey production (Table 2). The results remained unaltered when we excluded data for 2008 (the only year supplementary feeding was provided, Table 2). In addition, the mean difference between honey production in 2008 and all previous years was positive and significant (0.1165 ± 0.0255, *P*-value < 0.001), revealing that honey production was significantly higher in the year when supplementary feeding was provided.

The probability of a given colony producing any quantity of honey (honey presence) increased over time (Table 2; Fig. 5a). However, this temporal pattern was best predicted by age, as including colony age in place of time resulted in a substantial increase in the model's likelihood (Table 2). Hence, older colonies had a higher probability of producing honey. Higher temperatures were associated with the absence of honey, and higher levels of precipitation were associated with

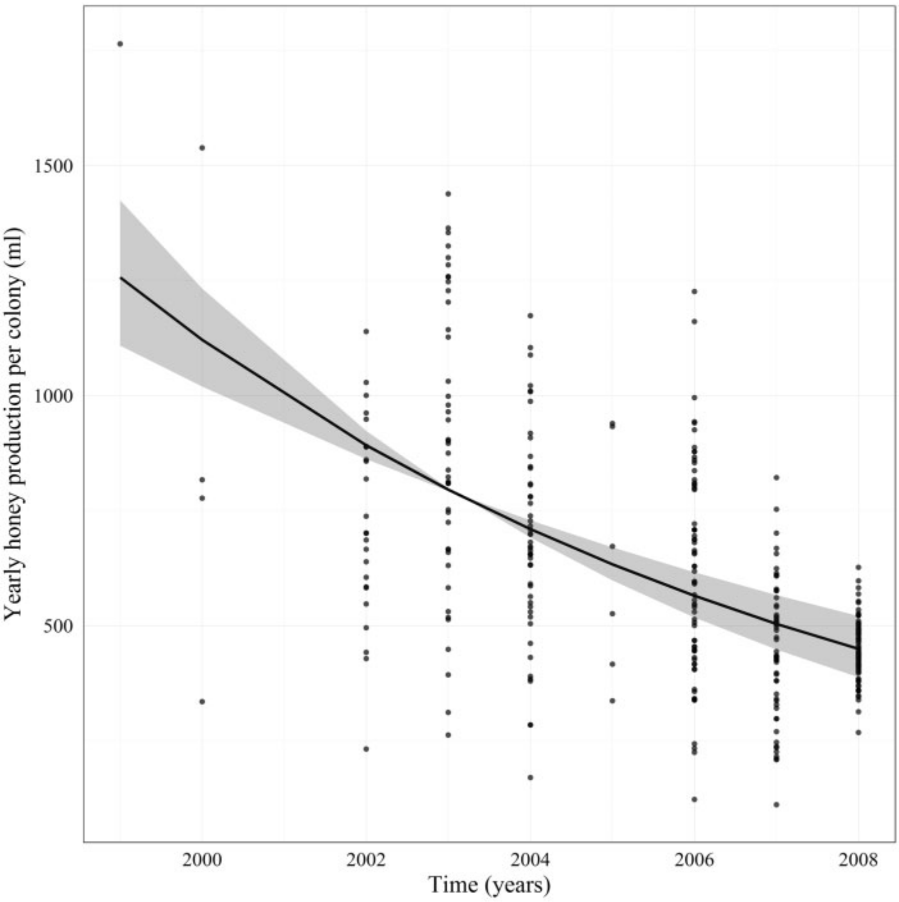

Fig. 2. Honey production (ml) over 10 yr in *M. subnitida* colonies. While each point represents a record, the line represents the fitted curve and the grey area shows the 95% CI. The figure reveals a decrease in the amount of honey produced by each colony over time. Yearly honey production per colony is detrended to show the correct relationship between honey production and time (the effect of the other predictor variables has been subtracted out).

the presence of honey (Fig. 5b–c). Colony mortality was variable over the years, ranging from 0 to 44% (Table 1). Temperature and precipitation did not influence the number of colonies lost in a year (Table 3). Even though many colonies died after few years of observation, some colonies survived up to 9 yr.

Discussion

By meticulously following 155 colonies over a period of 10 yr, Mr. Paulo Menezes provided the longest and most accurate record of honey production and mortality available for a stingless bee. Analyses of these records reveal that honey production by *M. subnitida* is influenced by time, colony age, management techniques (colony division and supplementary feeding) and climatic factors.

Along the years, the amount of honey produced by each colony decreased and this reduction was not related to colony age. The increase in colony number during the 10 yr of record could have resulted in competition for floral resources, leading to a lower honey production per colony. However, our results do not suggest an effect of colony density on honey production because the total number of colonies was not found to have an effect on honey production (results not shown). Nevertheless, we caution that our study could not fully quantify the effect of the total number of colonies on honey production per colony because there were more colonies located in the vicinity of the study colonies that were not accounted for. In addition, feral and managed *A. mellifera* colonies from the region, probably compete with native bees for limited food resources (Bruening 2006). Another possible cause for the observed decrease in honey production over time is that larger colonies were usually selected for division. By so doing, colonies were not allowed to grow indefinitely, thus constraining honey production (which is usually proportional to colony size (Chinh and Sommeijer 2005). Furthermore, colony division itself has a negative impact on honey production (see below). Although this effect was probably stronger in 2003 and 2004, when more colonies were divided, this practice could have had a long-term impact on honey

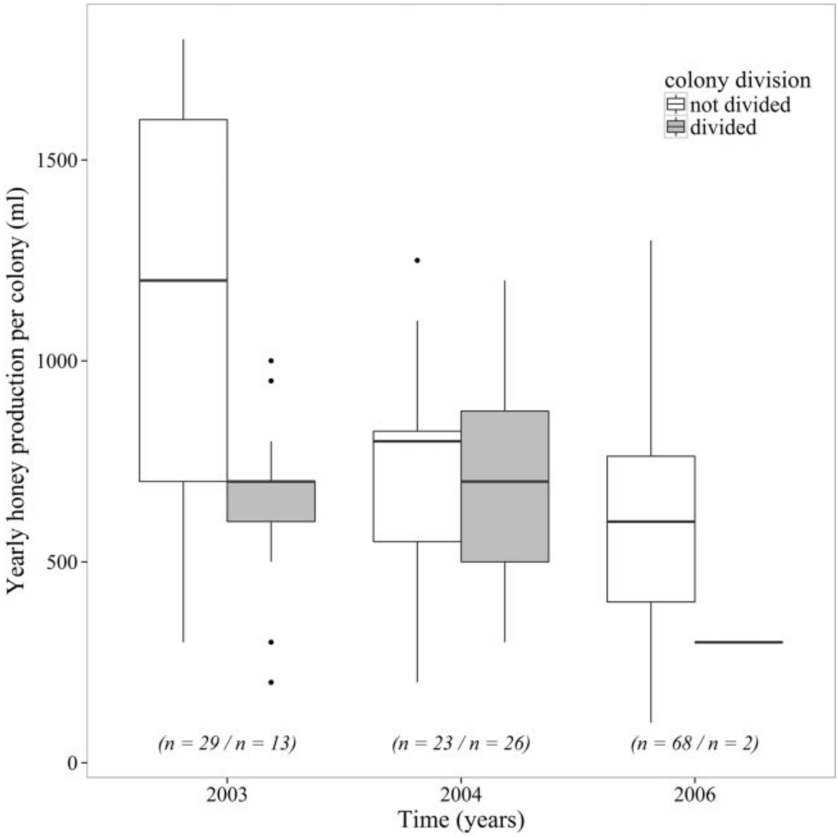

Fig. 3. Honey production per colony (ml) in years in which colony divisions were performed, showing that colonies that underwent division produced less honey than colonies that were not divided. Only colonies that produced honey are shown (n = 161; all colonies are shown in Fig. S2).

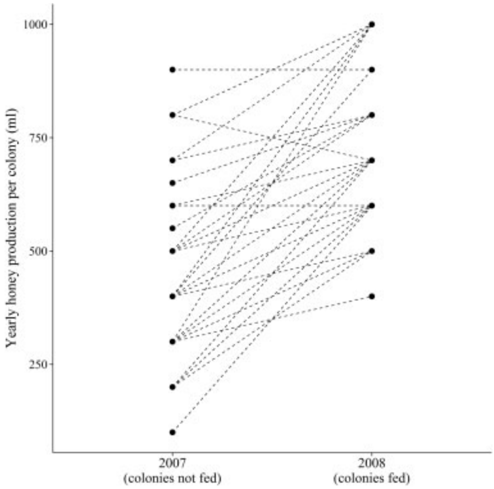

Fig. 4. Honey production per colony (ml) for the year 2007, when no supplementary food was provided, and for 2008, when colonies were fed with sugar syrup every fortnight. Each line represents a colony and only colonies that produced honey are shown (n = 56; all colonies are shown in Fig. S3).

production. In addition to colony division, the extraction of honey itself could also have influenced long-term honey production. However, our dataset did not allow assessing the effect of honey extraction on honey production because the amount of honey produced by each colony was only quantified after being extracted. The different techniques used to collect honey do not seem to have affected the amount of honey harvested, as the method used in later years (syringe coupled with a pump) causes less harm to colonies, but we still observe a decrease in honey production. Future studies aiming to quantify the effect of honey extraction could implement less invasive methods to measure honey production (perhaps returning the honey to colonies).

Despite the decrease on honey amount produced per colony, the proportion of colonies producing honey increased over the course of the study, potentially because of colony aging. In the beginning of the colony life cycle, most resources (nectar and pollen) are expected to be invested in colony growth (Oster and Wilson 1978), and they only begin to be stored after colony establishment. This behavioral pattern would result in an increase in the probability of honey presence over the years, even though not related to an increase in honey amount.

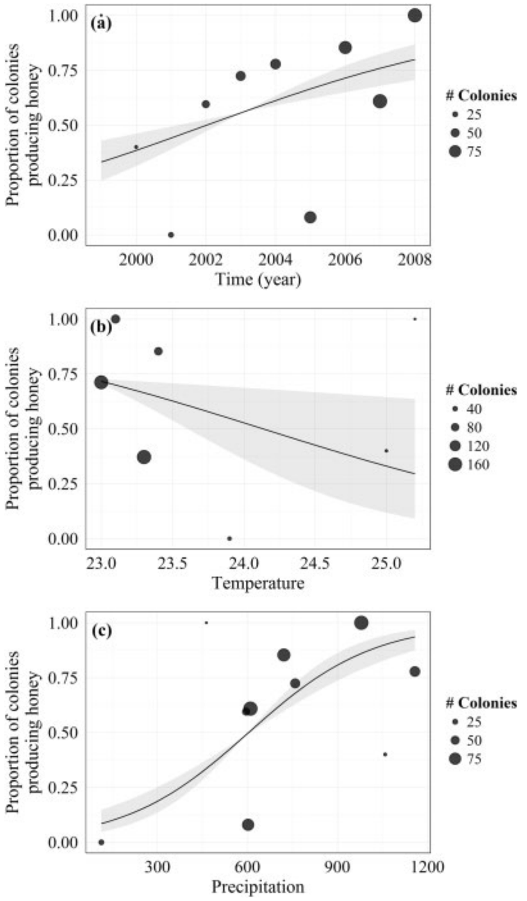

Fig. 5. Proportion of *M. subnitida* colonies producing honey in relation to (a) time, (b) temperature, and (c) precipitation. The line represents the fitted curve and the grey area shows the 95% CI of the model. For each plot the other covariates were held constant at their mean, and the size of the points indicates the number of colonies in each year.

Management techniques also affected colony performance. Colony division decreased the amount of honey produced, which could be related to the decline in the worker population of the colony caused by the removal of some brood combs. As brood combs are constructed sequentially (Nogueira-Neto 1997), removing combs results in a gap of bees of a determined age cohort, which can affect the entire dynamic of the colony and temporarily reduce the number of foragers. However, the probability of honey production was not affected by colony division, revealing that even with a dramatic decrease in colony population, colonies would not cease producing honey. These results indicate that colony division has a short-term negative impact for the beekeeper—an immediate decrease in the amount of honey produced—which may be offset by a long-term increase in the number of honey-producing colonies.

Supplementary feeding had a positive effect on the amount of honey produced. In the year when colonies were fed with sugar syrup, we observed a sharp increase in posterior honey production. Providing food resources helps the maintenance of the nest, especially in the dry season when floral resources are scarce and the colonies become weaker (Nogueira-Neto 1997, Contrera et al. 2011). During this season, the bees consume the sugar syrup provided and no honey is normally stored. Honey production starts at the onset of the rainy season with the first blooms. At this point, supplementary feeding is ceased and honey is harvested a few months later. An additional strategy to avoid the harvesting of sugar syrup-based honey is discarding any stored honey before the rainy season, a known practice amongst beekeepers. Thus, because only nectar-based honey was harvested, the observed increase in honey production was not due to the transformation of sugar syrup into honey. This result suggests that honey production was constrained, and that it can be boosted through supplementary feeding. Supplementary feeding thus proved a particularly important practice to help strengthen colonies during periods when floral resources are scarce, and later maximize honey production when resources are available. Another strategy for stingless beekeepers to enhance honey production is to place their colonies near areas with abundant floral resources, thus minimizing the need for supplementary feeding.

We found that temperature had a more drastic effect on honey production than precipitation, as both the probability of a colony producing honey and the amount of honey produced were significantly influenced by the annual mean temperature. In warmer years, fewer colonies produced honey, and those that did produce yielded a lower amount. This is a concerning situation as global warming predictions point to an increase in temperature (International Panel on Climate Change [IPCC] 2014) that could compromise honey production. In contrast, annual precipitation only affected the presence of honey in the colonies. In the Brazilian Caatinga, the relationship between climate and plant phenology is well documented, with two distinct seasons: a rainy season during which the majority of plant species flower, and a dry season with less abundant floral resources (Zanella and Martins 2003). Seasonal variations in floral resources are known to affect bee foraging intensity and honey production (Schneider and Blyther 1988, Maia-Silva et al. 2015). For instance, father Huberto Bruening described the bee's ability to predict climate, noticing that *M subnitida* colonies "intensify egg-laying activity 45 d before the first rain" (Bruening 2006). Water availability is also important for colony thermoregulation through evaporative cooling (Nogueira-Neto 1997, Jones and Oldroyd 2006).

In contrast to honey production, colony mortality was not affected by climatic factors. This indicates the resilience of *M. subnitida* colonies to long intervals of drought and warm weather. *M. subnitida* occurs in regions with the highest temperatures and lowest precipitation recorded in Brazil, suggesting that the species is highly adapted to arid regions (Silveira et al. 2002, Giannini et al. 2012, Maia-Silva et al. 2015). Colony failure thus seems to be related to factors other than climate, such as resource availability, management,

Table 3. Parameter estimates and hypothesis tests for the model describing colony mortality

Generalized Linear Model for Colony Mortality							
Response	*N*	Predictor	Estimate	SE	χ^2	Degrees of freedom	*P*-value
Colony mortality	76	Temperature	0.8718	0.5448	2.21	1	0.14
		Precipitation	−0.0007381	0.001122	0.44	1	0.51

N is the number of observations of the model. For each predictor, estimates and SEs from the model are given. The *P*-values and degrees of freedom refer to the marginal likelihood ratio tests (using a χ^2 test statistic), in which the full model was compared with a reduced model without each of the predictor variables.

parasite attacks or disease (Nogueira-Neto 1997, Maia-Silva et al. 2013, Jaffé et al. 2015).

According to our results, two different strategies can be outlined for stingless beekeepers: To maximize honey production in a given year, beekeepers should avoid excessive colony divisions, and only divide colonies to maintain an optimal number of honey-producing colonies. Likewise, by providing colonies with sugar syrup when floral resources are scarce, beekeepers could boost posterior honey production. On the other hand, to maximize the production of new colonies, beekeepers should divide their colonies frequently, at a rate that does not compromise colony survival. Not harvesting honey and providing the colonies with sugar syrup could help increase survival and maximize the colony division rate. For instance, many stingless beekeepers already specialize in colony sells (Jaffé et al. 2015). Both strategies are expected to yield economic returns, as the mean local prices for *M. subnitida* honey and colonies are US$25 per liter and US$50 per colony (Maia, 2013). Future efforts are needed to determine the optimal division rate, which maximizes the total joint honey production.

Overall, our results show that both environmental factors and management can influence honey production in stingless bees. Likewise, our work highlights the benefits of *M. subnitida* as a commercial species for honey production in northeastern Brazil, given that it proved resilient to management and extreme weather conditions. Our study emphasizes the importance of keeping detailed long-term records on honey production and management practices, and illustrates the importance of establishing partnerships between scientists and beekeepers to further develop stingless beekeeping.

Supplementary Data

Supplementary data are available at *Journal of Economic Entomology* online.

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