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Worker longevity in an Amazonian *Melipona* (Apidae, Meliponini) species: effects of season and age at foraging onset

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Abstract – We studied the relationship between worker longevity and the age of foraging onset in the bee *Melipona fasciculata*, as well as the longevity oscillation in the rainy and dry seasons. Workers that emerged in the rainy season started to forage later and lived at least 50 % longer than foragers from the dry season. In both periods, a higher longevity was observed in workers that started to forage earlier in life but did not forage all days of their careers. We also showed, by using a Weibull model, that workers experienced higher mortalities at older ages in the rainy season, but the same model did not fit with the data from the dry season. This lack of fit in the dry season can be explained by the high mortality of workers that did not start to forage in this season and to other intrinsic factors of the colonies. Thus, the age of foraging onset and internal colonial factors must be considered in studies examining worker longevity in free-foraging colonies in this diverse group of eusocial bees.

Melipona fasciculata / stingless bees / mortality / survival curves / weibull model

1. INTRODUCTION

Longevity is a key evolutionary force affecting adaptations in the different life histories of insects, and solitary and social species contrast in several aspects, such as in their life expectancy (Keller and Genoud 1997) and in the different longevity patterns among castes (Carey 2001). In bees, the main factors used to infer

differences in longevity between queens and workers are behavioral costs, as well as genetic, morphological, and physiological issues (e.g. Biesmeijer and Tóth 1998; Amdam and Omholt 2002).

Regarding the honeybee, studies on their life expectancy in temperate regions have shown differences in the longevity of summer and winter bees. *Apis mellifera* Linnaeus, 1758 workers may live about 1 month in summer, whereas they may survive up to 8 months in winter (Amdam and Omholt 2002). However, in tropical and subtropical environments honeybee longevity does not present these strong seasonal differences. Rather, they present differences related to the age structure of the colonies, with higher mortality associated with high mean

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worker age and low proportion of young workers and a slight increase in longevity is seen in the tropical rainy season (Terada et al. 1975; Winston 1979, 1980).

The energetic effort that workers expend during their life also plays a role in survival patterns, when we take into account the effort to search for resources and predation risks met outside the nest (Page and Peng 2001). This was observed in *A. mellifera* by Wolf and Schmid-Hempel (1989), who showed that workers to which extra work effort was imposed had a reduced life span and diminished foraging activity compared to workers subjected to normal foraging efforts.

In stingless bees (Tribe Meliponini; Michener 2013), most studies on longevity (revision in Halcroft et al. 2013) have been conducted on subtropical species (e.g. Terada et al. 1975; Simões and Bego 1991; Halcroft et al. 2013). In the French Guyana, Roubik (1982), studying *Melipona fulva* Lepeletier, 1836 and *M. favosa* (Fabricius, 1798), found that workers had a longer life-span in the rainy season compared to the dry season, probably due to the greater resource availability and higher foraging effort by workers.

Since most stingless bees feed from pollen and nectar harvested by workers, the foraging effort may be a relevant factor in longevity regulation. The time spent searching and collecting these resources may be considered an equivalent of foraging effort, because the greater the time spent, the greater the energy expenditure in flight and handling the resource. Thus, time and effort spent on foraging probably influences bee longevity, as well as the age at which foragers start their career, as shown in the honeybee (Wolf and Schmid-Hempel 1989; Becerra-Guzmán et al. 2005).

In this study, we looked at the longevity patterns of workers from a meliponine species from the Amazonian Region, *M. fasciculata* Smith, 1854. *Melipona fasciculata* is a medium to large-sized species, whose colonies are relatively small (about 300–400 bees; Kerr et al. 2001). We focused on two main questions: (a) whether workers from this species present

different longevity patterns in the main climatological periods of the region (rainy and dry), and (b) whether there is a relationship between longevity and the age of foraging onset. We hypothesized that foragers would have an extended life expectancy in the rainy season, since they would spend more time inside the nest, and that mortality rate would substantially increase after workers shifted from internal work to external activities.

2. MATERIAL AND METHODS

2.1. Study site

This study was conducted in the meliponary of the Botany Laboratory of Embrapa Amazônia Oriental (1°26'11.52" S, 48°26'35.50" W), located in Belém, Pará State, Brazil, from February–April and August–November 2012, which corresponded to the rainy and dry seasons in the region, respectively (Moraes et al. 2005). For the categorization of rainy and dry seasons we used the rainfall data generated in the São Brás weather station (Climurb Project (IG/UFPA/CNPq).

2.2. Colonies

Three colonies of *M. fasciculata* of similar population sizes and food stores (all strong colonies with large populations and large food stores reserves) were used in this study. They were kept in hives designed for their breeding (model in Cortopassi-Laurino et al. 2006) and a glass plate was placed between the lid and the upper-nest, to allow the observation of internal structures and of bee behavior. A 15-cm plastic tube was placed in the entrance (3-cm diameter), to ease the visualization of forager departure and entrance. The glass plate and tube were placed in the nests at least a month before the experiments, to allow the bees to habituate to them and thus not alter their normal behavior.

2.3. Bee marking

In each colony, the older brood combs from which bees were ready to emerge were removed and placed in an incubator box to allow the capture of newly emerged individuals. After their emergence, the

workers used in the experiment (rainy season, $n=91$; dry season, $n=109$) were weighed with a digital precision balance ($d=0.001$ g) and received an individual tag with unique colors and numbering to differentiate workers and colonies (tag weight, 0.01 g; Queen Marking Kit, E.H. Thorne beehives Ltd.). The tags were placed with non-toxic and unscented glue on the thorax, so as to not hinder bee movement and flight, and workers were returned to their hives a few minutes after marking.

2.4. Data collection

After the marked workers were returned to the nest, they were observed daily at least four times a day, in the afternoon, to verify their survival. The interval between each observation was at least 60 min. Observations lasted up to 10 days after the last registry of a living worker, and to determine the life-span of each worker, we counted both external and internal (in-nest) observations. Thus, the longevity of workers was defined as the number of days between emergence and the last day it was observed inside the nest or performing foraging activities.

For all colonies, we recorded the age at which bees began to forage, the resource that they collected, and the amount of time they spent foraging (time between nest departure and return). We measured foraging time and foraging activity during two separate consecutive intervals, alternating the data collected on different days, to avoid bias. For example, in 1 day we measured foraging time from 0600 to 0659 h and again from 0800 to 0859 h. In the same day, we measured foraging activity from 0700 to 0759 h and from 0900 to 0959. On the next day, we started by measuring foraging activity.

Foraging activity was registered through direct observation in the nest entrance during a 5-min period/colony in each hour interval, to identify which marked workers returned with pollen or nectar. According to the type of resource collected, workers were classified as pollen, nectar or mixed foragers. To be considered a single resource specialist, at least 80 % of the recorded foraging trips of the individual had to be from this resource, and mixed foragers were those who collected pollen or nectar in proportions lower than 80 % (following Biesmeijer and Tóth 1998). Resin or mud collection by marked workers were not observed and thus not considered in this study. We also calculated, for each forager, the *potential days of foraging*, using the

time interval (in days) when the bee was observed foraging for the first time until its death.

2.5. Data analysis

To verify possible seasonal differences on the survival curves of *M. fasciculata* colonies, we used Kaplan-Meier curves and later comparisons through the log-rank test (StatSoft, Inc 2013). To test the relation between worker longevity and weight, and between longevity and foraging onset age in the two periods, we employed a Spearman correlation test.

We performed a Kruskal-Wallis variance analysis (data were not normal nor had variance homogeneity) to compare longevity and the foraging onset age among the resource specialists and mixed foragers, during the rainy season. We used the Mann-Whitney test to compare the days of potential foraging between seasons and the time of pollen and nectar harvesting during the rainy season. For this analysis, we only considered the total amount of time of harvesting on different days, to ensure the maximum sample independence. Because of the low number of samples, in the dry season, these analyses could not be performed.

We also performed a Weibull analysis to fit the theoretical longevity patterns with the survival data observed (Carroll 2003). The analysis is based on a density probability function, and corresponds to mortality rates that increase as a power function of time. The parameters represent the characteristics of a theoretical survival curve in which the risk of death can be constant (weight 1), increasing (weight 2), or decreasing (weight 3) over the chosen parameter (in this study, age). We also calculated the hazard function based on the Weibull distribution, which describes the probability of death happening across time (StatSoft, Inc 2013), using the same weights described above. All analyses were performed in STATISTICA® 7.0, using a <0.05 significance level.

3. RESULTS

3.1. General patterns of survival and foraging

During the rainy season, the maximum longevity reached by workers ($n=90$; one

marked worker was never observed) was 80 days, while the minimum was 17 days. In this season, the first forager was observed leaving the nest at 41 days of age, while the oldest registry of a forager was a 75-day-old worker. Emergence weight had no correlation with worker longevity (Spearman $R=0.09$; $P=0.07$).

Longevity ($H=1.65$; $d.f.=2$; $n=78$; $p=0.44$) and the foraging onset age ($H=1.89$; $g.l.=2$; $n=78$; $P=0.39$) did not differ significantly among the different foraging categories (Online Resource 1). The three types of foragers presented different work agendas; mixed foragers worked an average of 18 days, while the nectar and pollen specialists foraged 12 and 8 days, respectively. The time spent on nectar collection was significantly higher (average of 24 min) than pollen (average of 13 min; $U=74.000$; $P=0.029$; nectar $n=25$; pollen $n=11$).

During the dry season, the maximum worker longevity ($n=109$) was of 56 days while the minimum was of 3 days. The first registers of foraging were on 32-d-y old workers, while the last register of a first foraging was a 51-day-old worker. Heavier bees lived significantly longer in this season (Spearman $R=0.17$; $P<0.001$). Only 62 workers were observed in foraging activities, and longevity and the foraging onset age were similar in the three types of foragers (Online Resource 1).

Mixed foragers worked an average of 5.25 days ($n=4$), while nectar ($n=56$) and pollen ($n=2$) specialists foraged 5.76 and 3.5 days, respectively. It was not possible to test whether these differences were statistically significant due to the low number of pollen foragers in this season (also applied to the time spent in resource harvesting).

Figure 1. Kaplan-Meier survival curves of three *Melipona fasciculata* colonies compared by a log-rank test during the rainy season.

3.2. Survival curves

3.2.1. Rainy season

During the rainy season there were no significant differences between the survival curves of the three *M. fasciculata* colonies (log-rank test; $P=0.272$; Fig. 1), as well as in the average longevity and in the age of foraging onset (Online Resource 2). Thus, the data of the three colonies were pooled into a single analysis.

In the rainy season, the first death records started in 18-day-old individuals. After 40 days of emergence, 10 % of the labeled workers had died; after this period they started to forage and the proportion of survivors declined daily (Fig. 1 and Online Resource 3). Worker longevity was positively correlated with the age of foraging onset (Spearman $R=0.23$; $P=0.036$; Fig. 2).

3.2.2. Dry season

During the dry season there were significant differences between the survival curves of the

three studied colonies (log-rank test; $P<0.001$), and colony 3 (in this season it became more populated than other colonies) had a different survival pattern compared to colonies 1 and 2 (Fig. 3). Thus, we did not include colony 3 in the general analysis of survival patterns in the dry season. Colony 3 showed the lowest worker longevity compared to the other two colonies; however the age of foraging onset was similar to those of the other nests (Online Resource 2).

From emergence and up to 31 days, about 20 % of *M. fasciculata* workers (from colonies 1 and 2) had died. After the foraging onset, mortality increased, and consequently, an accentuated decline of survivors occurred (Online Resource 3). Worker longevity during the dry season was positively correlated with the age of foraging onset (Spearman $R=0.17$; $P<0.001$; Fig. 4).

3.2.3. Comparisons between seasons

The longevity of workers in the rainy season was significantly higher than in the dry season (log-rank test, $P<0.001$), and workers started to

Figure 2. Correlation between longevity and the age of foraging onset in *Melipona fasciculata* workers, during the rainy season. Group A: workers that started to forage earlier and presented higher longevity. Group B: Workers that started to forage later and had a lower longevity.

Figure 3. Kaplan-Meier survival curves of three *Melipona fasciculata* colonies compared by a log-rank test during the dry season. Colony 3 had a different pattern survival compared to colonies 1 and 2.

forage earlier in the dry season ($U=552$; $P<0.001$; $n_{\text{rainy\_season}} = 78$; $n_{\text{dry\_season}} = 62$).

In both seasons, there were workers that started to forage at early ages (Group A; Figs. 2 and 4), but presented a higher longevity than workers that started to forage later in life. These bees had a high potential foraging life (interval between foraging onset and end), but they were observed in external activities for a reduced number of days. In the rainy season, the potential days of foraging was 24.37 ± 10.31 days ($n=8$), and the actual days in which they were seen foraging was 5.12 ± 3.35 days (Group A, Fig. 2). In the dry season, workers had a potential foraging life of 17.28 ± 1.25 days ($n=8$) but were actually observed foraging only 3.28 ± 0.95 days (Group A, Fig. 4).

3.3. Weibull modeling

The Weibull modeling showed that during the rainy season the worker longevity had the

best fit with the model of increased mortality at older ages, and the hazard function predicted the mortality dynamics in this season (Fig. 5; Weibull: Weight 2; $P=0.08$)

Unlike from the rainy season, in the dry season no parameter of Weibull modeling fit the observed survival patterns or the hazard risk in each age interval (Fig. 6; Weibull $P<0.001$). The probability of death was low during the early stages of life, considerably increasing in the period close to the onset of foraging (from the 24th to the 32nd day of life), and with a peak close to the 40th day (at the 38th day, half of the workers had already started their foraging life).

4. DISCUSSION

Extrinsic factors like predation or death by physiological wear in conjunction with environmental factors may act as a regulator of worker

Figure 4. Correlation between longevity and the age at foraging onset in *Melipona fasciculata* workers, during the dry season. Group A: workers that started to forage earlier and presented higher longevity. Group B: Workers that started to forage later and had a lower longevity.

life expectancy (O'Donnell and Jeanne 1995; Remolina et al. 2007). In our work, we found that during the rainy season, workers had an extended longevity, which can be explained by the reduced external activity of workers and thus, a reduced exposure to extrinsic factors such as predation. In the dry season, the *M. fasciculata* longevity was lower than in the rainy season, a trend that was also observed by Roubik (1982), studying *M. fulva* and *M. favosa*. The author suggests that individual survival as well as the colony growth follow the pattern of seasonal abundance of resources, i.e. workers spend more time inside the nest when the external resources are scarce. Regarding colonial differences, in our work, during the rainy season, the three colonies presented similar worker longevity patterns; they were probably subjected to the same dynamic of low external resources and external activity, and they had similar population sizes. In the dry season, only colony 3 had a different pattern compared with the other colonies,

probably due to its greater population size in this season.

Foraging was also influenced by season; *M. fasciculata* workers began foraging later in the rainy season than in the dry. In the rainy season, while 75-day-old foragers were starting to forage, many others already had died. According to Rueppell et al. (2007), the transition between internal work and foraging in *Apis* is a critical period of their life history, because it probably interferes in the life expectancy of many individuals of the colony due to energetic expenditure (O'Donnell and Jeanne 1995).

Nectar harvesting by *M. fasciculata* was mainly observed in the dry season, while pollen was collected by relatively few foragers. The lower pollen availability during the rainy season of Amazonian tropical forests (Jansen 1967; Cortopassi-Laurino et al. 2002), and the preemptive competition with other pollen consumers (Roubik 1989), may explain the lower pollen harvesting observed in the colonies.

Figure 5. Observed and estimated hazard risk through the Weibull function (weight 1; weight 2 and weight 3) for *Melipona fasciculata* workers during the rainy season.

Regarding the effort to collect resources, during the rainy season, the time spent collecting nectar was significantly higher than for pollen collection, opposite that of *M. beecheii* (Biesmeijer and Tóth 1998), in which the inverse pattern was found. For a worker to fill its crop and return to the nest, normally several visits to different flowers are necessary, whereas for pollen, fewer visits are needed to load the corbiculae (in *A. mellifera*; Michener 1974), although the spatial distribution of these resources in the actual foraging range of the colonies also has an influence on the time and effort foragers experience to collect them.

We also show that the type of resource was not related to worker longevity; thus, the age at onset of foraging and the worker's mass are more important for the regulation of forager's life expectancy. These data contrast with those of Biesmeijer and Tóth (1998) for *M. beecheii*, where resource specialization had a strong

relationship with longevity. Probably, differences in the food stores levels, the spatial distribution of resources in the two areas studied, and individual behaviors related to foraging can be indicated to explain the differences between *M. beecheii* and *M. fasciculata*.

In relation to body mass, we only found a significant correlation with worker longevity in the dry season, i.e. the heavier the bee, the greater its longevity. The dry season of the Amazon forest is the period of year when most plants are flowering, and thus is a potential phase for the colonies to replenish their food stores. Thus, higher body masses could allow foragers to live longer in times of high energy expenditure. This was not observed in the rainy season, a natural death period in the Amazon (Jansen 1967; Roubik 1982), when workers spend longer periods inside the nest, mostly relying on the food storage to survive.

Figure 6. Observed and estimated hazard risk through the Weibull function (weight 1; weight 2 and weight 3) for *Melipona fasciculata* workers during the dry season.

Age at onset of foraging in our study was positively correlated with worker longevity, although the death of workers that did not start to forage also stresses the influence of intrinsic colonial factors. Colony 3, the most populated colony in the dry season, showed a high mortality of workers both before and after the onset of foraging. In *A. mellifera*, colonial differences alter the individual value of workers, and mortality increases in the least valuable individuals (i.e. unhealthy individuals; older workers with considerable wing damage), which start to forage earlier than their healthier cohorts (Tofilski 2009; Woyciechowski and Morón 2009). If this concept also applies to *M. fasciculata*, it may account for the differences found in colony 3, although which internal factors could have influenced worker longevity remain to be investigated.

An earlier start of foraging life was observed in the dry season, although a trade-off (Rueppell et al. 2009) between foraging and longevity was observed in both seasons. Some *M. fasciculata* workers began to forage earlier than the others, alternating days of foraging and days inside the nest, and had an extended life expectancy compared to the rest of the workers (Rueppell et al. 2009). This earlier foraging onset combined with a reduced foraging effort (measured as actual days foraging) probably results in increased longevity compared to workers with a short, but intense foraging life (Rueppell et al. 2008).

Using the Weibull model (Carroll 2003), we found that *M. fasciculata* mortality increased in the final stages of life, as also observed in *A. mellifera*, *M. favosa*, *M. fulva*, and *S. postica* (Sekiguchi and Sakagami 1966; Roubik 1982; Simões and Bego 1991). Differently than the

rainy season, during the dry season, the estimated parameters of the Weibull analysis did not fit the observed patterns, which can be related to the high death risk workers experienced in this season. Since we showed that the transition between intranidal work and foraging has a relevant effect on *M. fasciculata* longevity, it seems that in the dry season the Weibull analysis could not incorporate the changes in the mortality patterns of the pre- and post-foraging periods. In *M. fasciculata* the chance of death (hazard rate) was higher in the dry season, and with foraging onset it increased about three times compared with the pre-foraging period. This high chance of death can be justified by the increased chance of predation (Carey 2001), physiological expenditure (O'Donnell and Jeanne 1995) or natural loss of wing area (Higginson et al. 2011) caused by the excessive wing beating during foraging flights.

In summary, we show that *M. fasciculata* workers in tropical environments have two longevity patterns, mainly as a consequence of the foraging behavior of each individual in different seasons. However, the complexity of internal and external factors that affect the colonies made it difficult to fit theoretical patterns to the observed. Therefore, studies of internal colonial influences, especially colony size and internal resource levels, on bee foraging behavior as well as of the behavioral plasticity of workers (see Münch and Amdam 2010), must be performed to help illuminate stingless bee's mortality patterns.

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Longévité des ouvrières chez une espèce amazonienne de *Melipona* (Apidae, Meliponini): effets de la saison et de l'âge au début de l'activité de butinage

***Melipona fasciculata* / abeille sans aiguillon / mortalité / courbe de survie / modèle de Weibull**

Lebensdauer der Arbeiterinnen einer amazonischen *Melipona*-Art (Apidae, Meliponini): Saisonale Effekte und Einfluss des Alter während des Sammelbeginns

***Melipona fasciculata* / Stachellose Bienen / Mortalität / Lebensdauerkurven / Weibul Modell**

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