Longevity, food consumption, and foraging performance of *Apis cerana* and *Apis mellifera* in mixed colonies

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Abstract – *Apis cerana* is an endemic species of honey bee in Asia. *A. cerana* is believed to have better adaptation to scattered nectar sources than *Apis mellifera*, which implies that honey can be harvested from *A. cerana* colonies, but *A. mellifera* will starve at the same location. We hypothesize that there are differences in foraging performance, worker longevity, and daily sugar consumption between *A. cerana* and *A. mellifera* workers. These parameters in both species were determined. *A. cerana* had longer longevity than *A. mellifera* if longevity was measured in caged bees without pollen or in mixed species colonies with *A. mellifera* queens, but *A. mellifera* had much longer longevity when measured inside cages provided with pollen. *A. cerana* also had more foraging trips and higher proportion of foragers than *A. mellifera* in mixed colonies. The daily sugar consumption of *A. cerana* workers was 32% of that of *A. mellifera*, perhaps mainly due to the smaller biomass of *A. cerana* workers. In addition, *A. cerana* workers showed significantly lower variance in daily sugar consumption. In conclusion, *A. cerana* has more foraging trips, higher forager proportion, less sugar consumption, and longer survival than those of *A. mellifera*, when measured inside the same colonies. These differences might explain why during a dearth or in scattered resource areas, *A. cerana* can store or produce more honey than *A. mellifera*.

Apis cerana / *Apis mellifera* / sugar consumption / foraging / survival

1. INTRODUCTION

Apis cerana (Ac) and *Apis mellifera* (Am) are two main species of honey bees cultured in China. Both of them play important roles on pollination for many crops (Liu et al. 2016). Ac is distributed across temperate and tropical Asia (Hepburn and Radloff, 2011). In China, there are about six

million colonies of Am and three million colonies of Ac (FAO 2016; Ma and Huang 1993).

Ac is believed to have better adaptation to scattered nectar sources than Am (Liu 1964; Yang 2005), although this is mostly based on anecdotal observations. Ac colonies produced 10–15 kg of honey during the winter of 1963/64, but during the same time, each Am colony had to be fed with 5 kg sugar (Liu 1964). These differences could be due to Ac's ability to forage at lower temperatures (Tan et al. 2012a). Ac in China routinely forages on *Eurya* spp. (Theaceae) and produces honey from these plants, but Am rarely produces honey from them (Yang 2005). Comparative honey production data is lacking between the two species at the same location.

Ac could produce more honey in resource scarce areas, perhaps due to the following traits.

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Besides foraging at lower temperatures, in summer, Ac workers also start foraging earlier in the morning and stop foraging later in the evening, which results in about 1 h more foraging duration than Am (Gupta et al. 1984; Partap et al. 2000; Chandel et al. 2000). Ac also has a better learning and memory performance when presented with color and grating patterns (Qin et al. 2012).

However, there are also foraging traits that would allow Am to outperform Ac. Am has better learning ability than Ac during odor acquisition phase (Wang and Tan 2014). Am has a longer maximum foraging distance (over 10 km) (Beekman and Ratnieks 2000), compared to Ac's 1.5 km to 2.5 km (Koetz 2013). Am foragers are more sensitive to sucrose than Ac, allowing them to forage on a larger set of plant sources due to their lower threshold (Yang et al. 2013). However, the same study determined that sugar concentrations of nectar foraged by them are not significantly different, when nectar resources are scarce.

We are interested to determine if there are other factors that would allow Ac to outperform Am when resources are scarce. For example, whether Ac workers consume less sugar or have longer longevity. In this study, we determined survival of both species under different laboratory conditions and also measured their daily sugar consumption. Furthermore, we also measured worker survival and foraging traits of both species in mixed species colonies.

2. MATERIALS AND METHODS

2.1. Honey bee colonies and newly emerged workers

Three healthy colonies from each species (Am and Ac) were selected from the apiary of Apitherapy Institute, Fujian Agriculture and Forestry University, Fuzhou, China (26° 5' 16" N, 119° 14' 6" E) from April 2016 to June 2016. The ambient temperatures ranged from 13.3 (night) to 38.9 °C (day).

Frames containing brood near emergence were selected from each colony. Those brood frames were kept in plastic cages separately and incubated at 34.5 °C and 75% RH for 24 h. These bees

that emerged during the last 0–24 h (designated as day 0) were used for experiments.

2.2. Lab study: worker longevity with sugar only and sugar consumption

Sucrose syrup was prepared by mixing sucrose (Sinopharm, China) with water purified by reverse osmosis (RO) in the ratio of 2:1 then evenly heated to 100 °C to evaporate water and obtain a high concentration syrup. Then, the sucrose syrup was cooled to room temperature to become solidified.

Day 0 bees (50 bees/colony) from each colony were selected separately and put in cages (90 × 80 × 110 mm) maintained at 34.5 °C and 50% RH. These cages were constructed with wood and a movable Plexiglas door, which had small holes drilled for ventilation. Additionally, each cage was equipped with two feeding holes on the top to insert feeders. RO water was provided in inverted 15 mL glass bottles with plastic cap (with three holes drilled). Solidified sucrose was provided in a plastic cap 10 mm × 30 mm (height × inner diameter), which was hung with a wire in the cage. Both water and solidified sucrose were replaced daily. A paper towel was kept on the bottom of the cage to facilitate removal of dead bees and was changed daily. The mortality of bees in each cage was checked and recorded daily until experiments were terminated.

The amount of sucrose consumed by workers of both species was determined daily. Solidified sucrose was weighted with a precision electronic balance (Ohaus, C114) daily, accurate to 0.1 mg. The amount of sucrose consumption was recorded as the difference in weight of sucrose between two consecutive days, this was then divided by the number of workers still alive that day to obtain daily consumption per bee. Loss of moisture in sugar, if any, was corrected by measuring the moisture content in the sugar measured sugar content with solid sugar solution with an Abbe refractometer (WYA-2W, INESA Scientific Instrument Co., Ltd., China) at 40 °C each day in a sugar ball not reachable by bees.

The experiment was replicated three times, each time with a different colony from each

species of honey bees (three cages per species and colony).

2.3. Lab study: worker longevity with sugar and pollen

Powdered bee pollen from lotus (*Nelumbo nucifera*) was mixed with 50% sucrose syrup in the ratio of 2:1 (*w:w*) and soaked for 24 h. Caged bees were prepared the same as the last experiment. Water and 50% (*w:w*) sucrose syrup, filled in two 15 mL glass feeding bottles, were provided via two holes on the top of each cage. Bee pollen was supplied with a cap 10 mm × 30 mm (height × inner diameter). All water, sucrose syrup, and bee pollen were replaced daily. Dead workers were recorded and removed from each cage daily.

The experiment was replicated three times, each time with a different colony from each species of honey bees (three cages per species and colony).

2.4. Field study: survival, biomass, and foraging performance of *Ac* and *Am* workers in mixed species colonies

Mixed species colonies were each established by keeping one frame of mature brood from each species and an *Am* queen in the incubator at 34.5 °C and 75% RH for 5 days. The workers were transferred into an observation hive (47 cm length, 5 cm width, and 51 cm height). An empty frame and one frame with half honey and one third pollen were maintained in the observation hive. The mixed species colony contained equal number (~3000) of *Ac* and *Am* workers counted via photos. In addition, the mixture of pollen and sucrose syrup in the ratio of 2:1 (*w:w*, 50 g) was provided on the top of frame via a hole in cover (diameter 2 cm). Sucrose syrup was also supplied with a feeder (15 mL glass bottles with plastic cap) inserted into another feeding holes on the top cover. The mixed species colony was managed for 20–25 days to reach a normal age demography before marked focal bees were introduced. Occasional fighting between *Ac* and *Am* workers was controlled by spraying sucrose syrup (sucrose/olive oil/water = 5:1:4 (*w:w:w*) (Extra virgin grade, Terra Creta S.A.)) in colony.

Newly merged bees (99/colony/species) were tagged with numbered and colored tags (Bee Research Institute at Dol, Czech Republic) and then introduced into the mixed species colony. In addition, newly emerged workers of *Ac* were also introduced periodically (about 500 bees, once in every 2 weeks) to balance with the *Am* workers produced by the *Am* queen. Sampling grids, 1 to 32 on one side, and 33 to 64 on the other side, were constructed on the window wall of observation hive. The census was done starting from first grid on the top left, and toward right and lower grids sequentially in a black room at 21:00 (Time Zone + 8). The numbers of bees for each species still alive in the colony were censused every 3 to 5 days at the same time. If a tagged bee was absent in all dates after one certain date, this date was assumed to be its last day alive. The experiment was also replicated three times, each time with a different mixed species colonies (three mixed species colonies).

The biomass of departing exiting workers was measured with a precision electronic balance (Ohaus, C114). Exiting workers were caught with a pair of soft forceps (Bioquip, USA) and individually put into Eppendorf tubes (1.5 mL). The weight difference between an Eppendorf tube only and the tube with a labeled worker was measured and considered to be the weight of a labeled worker. The weight of a labeled worker minus their tag weight is the biomass of a worker. The biomass of different aged (days 15 to 31) *Ac* and *Am* workers was determined. Weight of workers of each age ($N = 10$) were determined in three different mixed species colonies.

Similarly, the foraging frequency and forager number of *Am* and *Ac* workers were compared when the tagged bees were 14 to 25 days old. A special entrance (S Figure 1) was designed to separate incoming and outgoing bees, so that the time and direction of their trip could be recorded. The outgoing and incoming bees were recorded 7 to 10 am in the morning and 1 to 4 pm in the afternoon (UTC+08:00). To remove a possible effect of time of observation, the time of observation was rotated evenly among the three colonies (e.g., starting at 7, 8, and 9 for colonies A, B, and C for day 1, then 9, 10, and 8 for day 2, and 10, 8, and 9 for day 3, etc.). The number of foragers was

Figure 1 Survival of *A. cerana* and *A. mellifera* workers fed with only sucrose in laboratory (34.5 °C, 50% RH) ($N = 50$ per group, bees caged by species, replicated over three colonies). The difference in survival was highly significant (log rank test, $P < 0.0001$) between the two species.

normalized to the number of alive bees. Workers were regarded as foragers when their duration of trip was longer than 5.5 min (Capaldi et al. 2000).

2.5. Data analysis

The results are reported as means $\pm$ standard errors ($\pm$ SE). Normality test was performed using StatView Version 5.0.1 for Windows (SAS Institute Inc. 1992–1998, NC, USA) with the K-S Normality Test, and all data conformed to normal distribution. Biomasses of different aged foragers were compared by ANOVA. Sugar consumption and foraging frequency during different ages were treated as repeated measures ANOVA using StatView software. Survival analysis of both species of honey bees was carried out using SPSS version 19.0. with log rank tests.

3. RESULTS

3.1. Lab study: worker longevity with sugar only and sugar consumption

Survival of Ac workers fed with sucrose only was significantly higher than that of Am workers (Figure 1; log rank $X^2 = 11.5$, $df = 1$; $P < 0.0001$).

The daily sucrose consumption was higher for Am workers than that of Ac workers throughout

the lifespan (1-day-old to 30-day-old) (Figure 2; repeated measures ANOVA, $F_{1, 59} = 601.02$, $P < 0.0001$). There were significant changes in sugar consumption among different ages ($F_{29, 87} = 1.78$, $P = 0.03$) for either species. The average daily sucrose consumption of Am workers (11.73 ± 0.45 mg) was almost three times that for Ac workers (3.76 ± 0.20 mg). In addition, the variance of sugar consumption was also much higher for Am workers (16.61) than that of Ac workers (2.95); the difference between the two variances was highly significant ($F_{90, 90} = 5.64$, $P < 0.001$).

3.2. Lab study: worker longevity with sugar and pollen

Survival of Am workers with sucrose and bee pollen in the laboratory was significantly higher than that of Ac workers (Figure 3; $X^2 = 159$, $df = 1$; $P < 0.0001$).

3.3. Field study: survival, biomass, and foraging performance of Ac and Am workers in mixed species colonies

In mixed species colonies, survival of Ac workers was significantly better than that of Am workers (Figure 4; $X^2 = 10.9$, $df = 1$; $P < 0.0001$).

Figure 2 Daily mean ($\pm$ SE) sucrose consumption of different aged *A. cerana* and *A. mellifera* workers in laboratory (34.5 °C, 50% RH) ($N = 50$ per cage, three colonies). This was calculated from total sugar consumed divided by the number of live workers in each cage on each day. The difference in daily sucrose consumption was highly significant (ANOVA with repeated measures, $P < 0.0001$) between the two species. In addition, the variance of *A. mellifera* was significantly higher than that of *A. cerana* (F test, $P < 0.001$).

Biomasses between Ac and Am were significantly different (Figure 5; $F_{1, 270} = 67.69$, $P < 0.0001$). The body masses of Ac and Am changed significantly with age ($F_{4, 270} = 73.91$, $P < 0.0001$). There were no significant differences in worker biomass for both species among the three different mixed species colonies ($F_{2, 270} = 0.29$, $P = 0.75$). There were no significant

interactions between species and colonies ($F_{2, 270} = 0.47$, $P = 0.62$), age and colonies ($F_{8, 270} = 0.21$, $P = 0.99$), and species, age, and colonies ($F_{8, 270} = 0.43$, $P = 0.90$) with an exception of species and age ($F_{4, 270} = 15.36$; $P < 0.0001$) in worker biomass.

Number of foraging trips (all foragers together) per 2 h was significantly higher for Ac than Am

Figure 3 Survival of *A. cerana* and *A. mellifera* workers fed with sucrose and bee pollen in laboratory (34.5 °C, 50% RH) ($N = 50$ per group, bees caged by species, three colonies). The difference in survival was highly significant (log rank test, $P < 0.0001$) between the two species.

Figure 4 Survival of *A. cerana* and *A. mellifera* workers in the mixed species colony ($N = 99$ bees in the same colony per species, averaged over three colonies). The difference in survival was highly significant (log rank test, $P < 0.0001$) between the two species.

(Figure 6a; repeated measures ANOVA, $F_{1, 24} = 30.22$, $P < 0.0001$). There was also a significant age effect on number of foraging trips ($F_{11, 24} = 21.23$, $P < 0.0001$) in both species. There were significant interactions between species and worker age for the number of foraging trips ($F_{11, 34} = 2.7$, $P = 0.02$).

Number of foragers were significantly higher for Ac workers than that of Am

(Figure 6b; $F_{1, 24} = 17.87$, $P = 0.0003$). Forager numbers changed significantly as age changed ($F_{11, 24} = 23.59$, $P < 0.0001$). There were also significant interactions between species and worker age for forager number ($F_{11, 34} = 2.66$, $P = 0.022$). The average number of foraging trips per forager per time period of Ac was also significantly higher than Am ($F_{11, 24} = 3.186$, $P = 0.0085$).

Figure 5 Mean ($\pm$ SE) weight of exiting workers of *A. cerana* and *A. mellifera* ($N = 10$ bees per day per species). The difference in biomass was highly significant (ANOVA with repeated measures, $P < 0.0001$) between the two species. There were also significant age-related changes ($P < 0.0001$) in both species.

Figure 6 Foraging performance of *A. cerana* and *A. mellifera* workers in mixed species colony ($N = 99$ per species, averaged over three colonies). The differences were highly significant between the two species, for the number of foraging trips per 2 h (ANOVA with repeated measures, $P < 0.0001$) and number of foragers ($P = 0.0004$). The number of foraging trips (duration longer than 5.5 min) of tagged workers (**a**) was based on observation in 2 h. Forager numbers (**b**) were also determined in the same period.

4. DISCUSSION

The main findings of this study are that Ac workers have longer longevity than Am workers if longevity is measured in caged bees without pollen or in mixed species colonies; Ac workers have lower sugar consumption than Am; and finally Ac workers have higher proportion of foragers and make more foraging trips. These results suggest new mechanisms that Ac can perform better than Am at the colony level, when nectar and/or pollen resources are scarce.

The longevity of Ac and Am differed under different conditions. For example, when provided

with pollen, Am survived much longer than Ac (Figure 3), even though Ac survived longer than Am when no pollen was provided, or measured inside the mixed species colonies. It is possible that *Nelumbo* pollen is highly nutritious for Am but not for Ac, thus accounting for the reversal of our longevity data of the two species when provided with pollen. Our results showing that both species increased their longevity when provided with pollen (Figure 1 and Figure 3) are consistent with previous studies showing that in general pollen increases worker longevity (Schmidt et al. 1987; Schmidt et al. 1995). The survival results of both species in the same mixed species colonies might be most reliable, because there all conditions for both species remained the same; and it has been known both conditions outside and inside colonies can affect honey bee survival (Woyciechowski and Kozłowski 1998). The slightly longer lifespan of Ac workers would help Ac colonies build up faster, when all other conditions are equal.

The second advantage of Ac is lower sugar consumption. Ac consumed 3.76 mg sucrose per worker per day while Am needed 11.73 mg in lab condition (34.5 °C and 50% RH) (Figure 2). This is very close to the 11 mg sugar consumption per day per worker reported by Huang et al. (1998). Obviously, colonies with less sugar consumption should have more honey left when their worker numbers and honey stores started at the same levels. The lower sugar consumption of Ac might be partly due to their smaller sizes. Larger biomass animals have higher resting metabolic rates (Speakman 2005; Chown et al. 2007). This is also true for honey bees, with Am showing higher metabolic rates than Ac both during foraging (1.21 ± 0.06 vs 0.73 ± 0.16 J/bee/day, for Am and Ac, respectively) and during rest (0.027 vs 0.011 J/bee/day) (Abrol 2007). However, the differences in metabolism were only about two times in that study and our data here show a threefold difference in sugar consumption. It is possible that this is due to a combined effect of differences in body sizes and metabolic rates. Am workers also show a much higher variation for their daily sugar consumption. This variation could also cause starvation more frequently if food supply is constant.

There have been a few studies showing that foragers in Am are much lighter than in-hive workers, with foragers weighing about 40% less

compared to younger bees (Harrison 1986). Our data here show that Ac workers have the same pattern: that foragers lose about 20.2% of weight compared to 15-day-old workers (Figure 5). The forager weight of Am was 81.44 ± 1.32 mg and Ac was 73.75 ± 1.21 mg (Figure 5, for bees 23 days or older). These results for Am are similar to those of Harrison and Hall (1993) and Feuerbacher et al. (2003). Our biomass data of Am and Ac foragers are different from another study in China (93.3 ± 1.7 mg for Am and 69.3 ± 1.0 mg for Ac) (Tan et al. 2012a) but show the same trend. The differences of workers' biomass between our data and previous report may due to the genetics (Harrison and Hall 1993) or foragers' age (Figure 5).

Another advantage of Ac is that they have a higher proportion of foragers and their foragers make more foraging trips. Ac had 20% more foragers with the same group size ($n = 99$) (Figure 6a) and foragers made 25% more foraging trips (Figure 6b). The higher numbers of foraging trips of Ac could be due to their shorter foraging distance (Koetz 2013; He et al. 2013) or its better learning and memory for color and grating patterns (Qin et al. 2012), or both. With more foraging trips, Ac will increase the amount of nectar brought into the colonies when all other conditions are equal. However, Am foragers carry heavier nectar loads than Ac (51.0 ± 1.9 vs 31.3 ± 1.2 mg) (Tan et al. 2012a), while the two species of foragers show no different sugar concentrations in collected nectar (Yang et al. 2013). The longer foraging life, more foragers and more foraging trips of Ac will increase the amount of nectar brought into colonies.

Mixed species colonies were used to compare different honey bee behaviors in this study. Mixed species colonies with the same numbers of bees in two species, Am and Ac, have been used previously in many studies for different purposes, such as worker reproductive physiology (Tan et al. 2009a), brood recognition (Tan et al. 2009b), comb building (Yang et al. 2010a), retinue behavior (Yang et al. 2010b), thermoregulation (Yang et al. 2010c), defensive behavior against wasps (Tan et al. 2012b), communication using the dance language (Tan et al. 2008), and proboscis extension response to sugar solutions (Yang et al. 2013). In some of these studies, behaviors in mixed species colonies and in their own colonies were compared. The behaviors of

worker reproductive physiology (Tan et al. 2009a), thermoregulation (Yang et al. 2010c), defense against wasp (Tan et al. 2012b), brood recognition ability (Tan et al. 2009b), and proboscis extension response to sugar syrup (Yang et al. 2013) in mixed species colonies were consistent with behaviors in their own colonies. These results suggest that mixed species colonies are useful tools to compare the differences between behaviors of different species of honey bees. But there are differences in comb building (Yang et al. 2010a) and retinue behaviors (Yang et al. 2010b) when studied in mixed species colonies compared to when in their own colonies. Mixed race colonies with European and Africanized bees were also used for foraging performance (Winston and Katz 1982). There are no differences between duration of first flight and total flight duration in conspecific colonies and those in mixed species colonies; but age of first flight, age of first foraging, and flights per hour are different in these two types of colonies. Winston and Katz (1982) conjectured that these differences were due to different stimulus thresholds in the two races of honey bees, and the stimulus levels are also different in the colonies of these two bees. Because of this, Africanized bees foraged earlier than European bees when they are in their own colonies, but Africanized bees foraged later than European bees when they were co-fostered in the same colony. Thus, some behaviors can be complex and might have to be studied under both conditions.

We used three mixed species colonies, all with Am queens but no Ac queen, because mixed species colonies headed by Ac queen are too difficult to obtain. Queen mandibular gland pheromone (QMP) can affect foraging behavior, notably by delaying the foraging age and decreasing the number of returning foragers at a natural dose (Pankiw et al. 1998). In present study, Ac workers receive more QMP in mixed species colonies hosted by Am queen than in Ac's own colonies because of Am queens having 45% more QMP than Ac queen (Yang et al. 2010b). We however believe that the higher foraging frequency and more foragers in Ac than those in Am is not due to the higher amount of QMP experienced by Ac in mixed species colonies. Indeed, in Am colony, higher amount of QMP enhances pollen foraging (Higo et al. 1992) and increases nectar foragers and nectar foraging activity

at the third day after treatment (Pettis et al. 1995) but has no effect on total foragers or foraging activity. These studies however used Am and the data are lacking in how do Ac workers respond to different levels of QMP. Further studies are needed to determine what factors regulate foraging effort and frequency in Ac workers.

5. CONCLUSION

In conclusion, *Apis cerana* workers make more foraging trips, have a higher forager proportion, consume less sugar, and survive longer compared to *Apis mellifera* workers under the same conditions. These features may contribute to the ability of *Apis cerana* to store more honey during winter and/or in resource poor areas such as mountainous areas.

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AUTHOR CONTRIBUTIONS

WY and ZYH designed and conceived this research, analyzed the data, and wrote the manuscript; SP and CZ performed experiments; XM and ZW provided experimental materials and advised on the experiments. All authors read and approved the final manuscript.

COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interest The authors declare that they have no conflict of interest.

Longévité, consommation alimentaire et performance de butinage d' *Apis cerana* et d' *Apis mellifera* dans des colonies mixtes

Apis cerana / *Apis mellifera* / consommation de sucre / butinage / survie

Lebensdauer, Futteraufnahme und Sammelleistung von *Apis cerana* und *Apis mellifera* in gemischten Bienenvölkern

Apis cerana / *Apis mellifera* / Zuckeraufnahme / Sammelaktivität / Überleben

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