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Original article

Assessment of flight activity and homing ability in Asian and European honey bee species, *Apis cerana* and *Apis mellifera*, measured with radio frequency tags

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Abstract – The Asian honey bee *Apis cerana* and the European honey bee *Apis mellifera* are closely related and morphologically very similar. Where these species coexist, they appear to compete, but the outcomes of competition vary enormously between locations. Here, we report comparative behavioural data for *A. cerana* and *A. mellifera* in China gathered by tracking bees using radio frequency identification. Both species organise their division of labour by temporal polyethism and have remarkably similar demographic structure. Analyses of the homing capacities of both species following large-scale displacement suggest that *A. mellifera* colonies have a larger range than *A. cerana*. We observed that relocation of *A. mellifera* to a new environment disrupted colony function for 3 weeks. Our data show that *A. mellifera* and. *A cerana* occupy extremely similar behavioural niches, and therefore, the potential for competition between these species is very high.

***Apis cerana* / *Apis mellifera* / RFID / behavioural development / homing / navigation**

1. INTRODUCTION

Apis mellifera (the European honey bee) and *Apis cerana* (the Asian honey bee) are closely related cavity nesting honey bee species. It is likely that the two species diverged from a common ancestor around three million years ago, possibly as a result of geographic isolation caused by desertification of the Middle East (Oldroyd and Wongsiri 2006). *A. mellifera* then expanded its range across Europe, Scandinavia and Africa, while the Asian population radiated and diversified across Asia and India, forming five extant recognised species of which *A. cerana* is one (Oldroyd and Wongsiri 2006; Lo et al. 2010).

Until comparatively recently, *A. mellifera* and *A. cerana* were geographically separated (Ruttner 1988), but since the early twentieth century, human action has introduced *A. mellifera* to much of the range of *A. cerana* (Ruttner 1988). While both *A. mellifera* and *A. cerana* have long associations with humans for apiculture (Oldroyd and Wongsiri 2006), *A. mellifera* is more productive (Verma 1991). Thus, *A. mellifera* has been introduced into areas previously occupied by *A. cerana*. Professional

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beekeepers in China, India, Korea, the Philippines, Nepal and Thailand now show a strong preference for *A. mellifera* (Oldroyd and Wongsiri 2006). Human action has also expanded the geographic ranges of both species. *A. mellifera* was introduced to the Americas and Australia alongside European settlement, and *A. cerana* has become established across much of Indonesia and Papua New Guinea and recently arrived in Australia (Somerville 2011).

Both species are important for apiculture and pollination of many food crops, but where these species coexist, there is concern about the extent of competition between them. The two species are morphologically extremely similar [while *A. cerana* is generally considered slightly smaller than *A. mellifera*, when considering the tropical *A. mellifera* races, the two species overlap in size range (Ruttner 1988)]. They overlap in forage plant ranges (Ruttner 1988; Oldroyd and Wongsiri 2006), but *A. mellifera* is behaviourally dominant over *A. cerana* at artificial sucrose feeders (Ruttner 1988). The two species do not seem to easily coexist over much of their joint range. There is a concern that *A. mellifera* is ousting *A. cerana* from areas of China, some of which have seen an 80 % decline in *A. cerana* colony numbers (Zeng 2009). Competitive exclusion of *A. cerana* does not seem to be occurring in tropical regions, however, where biotic interactions with bee predators and parasites may have prevented establishment of wild colonies of *A. mellifera* (Oldroyd and Wongsiri (2006) and perhaps limited any impact of *A. mellifera* on *A. cerana* (Ruttner 1988; Oldroyd and Wongsiri 2006).

In some environments to which *A. cerana* has been introduced, it has become an invasive species that has ousted *A. mellifera*. Recently, *A. cerana* was introduced to Irian Jaya (1977), Papua New Guinea (1987) and The Solomon Islands (2003) (Somerville 2011). In these new environments, *A. cerana* has proved a highly invasive species and effectively outcompeted *A. mellifera* in The Solomon Islands (Somerville 2011). There is concern regarding the possible impact of *A. cerana* on Australian *A. mellifera* populations (Ryan 2010; Somerville 2011).

Knowledge of the foraging behaviour and range of *A. cerana* would help determine the degree of behavioural niche overlap between these two species in a given environment, but (certainly compared to *A. mellifera*) very little is known of the behavioural ecology of the Asian honey bee (Ruttner 1988; Oldroyd and Wongsiri 2006). To address this deficiency, here, we used the technique of radio frequency identification (RFID) tagging to gather comparative data on the, flight range and foraging activity, the age at which bees commenced foraging and the total worker lifespan of *A. cerana* and *A. mellifera* in the same environment in China. RFID tags are small (1 mg) transponders that can be attached to the dorsal thorax of individual bees. The tag has a unique digital ID that is read when the bee passes over a scanner. This technology allows for round-the-clock automatic monitoring of large numbers of bees (Pahl et al. 2010) and has proved to be an extremely useful technique for assessing aspects of bee foraging behaviour, navigation and survival (Pahl et al. 2010; Decourtye et al. 2011; Henry et al. 2012).

By monitoring the activity of RFID tagged bees (Streit et al. 2003) as they entered and exited the hive, we here present new estimates of worker flight activity and temporal polyethism in *A. cerana* and *A. mellifera*, and we compared the capacity of *A. cerana* and *A. mellifera* to return to the hive following displacement at different distances from the hive. Our findings suggest that, in China, *A. cerana* and *A. mellifera* occupy extremely similar behavioural niches.

2. MATERIALS AND METHODS

2.1. Experimental bee colonies

Experimental bee colonies of *Apis mellifera ligustica* (*Aml*) and *Apis cerana cerana* (*Acc*) contained approximately 4,500 worker bees and one naturally mated queen. They were housed in three-frame nucleus hive boxes located within a small

building and connected to the outside via a perspex tunnel.

2.2. RFID system

The RIFD system was developed and manufactured by the Honeybee Research Institute of Jiangxi Agricultural University in collaboration with the Guangzhou Invengo Information Technology Co., Ltd. The tags were round disks of 3 mm diameter, 0.08–0.21 mm thickness and weighed 1 mg (Figure 1). Tags emitted at a frequency of 900 MHzs. The specific digital ID of each tag was composed of 24 numbers and letters. Tags were glued to bees' thoraces with shellac glue. Two RFID antennae were connected to the hive entrance tunnel to scan and record the time and digital ID of bees as they entered and exited the colony. The antennae were connected to the entrance tunnel in series such that tagged bees entering the colony passed antenna 1 before antenna 2, and bees exiting the colony did the opposite. By observing the time at which a bee was first detected by an antennae and the order at which the bee registered with antennae s1 and 2, we could determine when tagged bees entered and exited the colony.

2.3. Experiment 1: homing of *Aml* in a new environment

The principle aim of this study was to compare data obtained using these new RFID tags with established bee marking methods and also to investigate how quickly a colony of *Aml* could navigate in a new environment following colony relocation. An *Aml* colony was transported from Meilin (Jiangxi Province, China, Figure 2) to an apiary in Xiangtang (Figure 3), on the 26th June (a distance of 60 km). The following day 80, pollen foragers were captured at the hive entrance, briefly anaesthetised on ice and marked with either colour paint on the thorax, or an RFID tag attached to the thorax with shellac glue (40 of each marking type). Bees were then kept in dark cages with ad libitum access to 40 % sucrose solution for 40 min to recover. All 80 bees were then released from one of four sites: at 1.5 and 3 km to the southeast and southwest of the colony. The time at release was noted. For the RFID tagged bees, their ID number and time of return were recorded by the RFID scanner at the hive entrance when they re-entered the hive; therefore, the RFID system gave us a measure of homing times for these individuals. For the painted bees, at sunset, the colonies were opened and all marked bees were removed and counted. From this, we were able to calculate the proportion of bees able to return from each release site, but not an accurate homing time. The painted bees were included in the experiment because these particular RFID tags had not been used previously on honey bees, whereas paint marking is an established marking method. Comparing homing performance across the marking groups allowed an assessment of the extent to which the tags might impede honey bee flight and/or survival.

Figure 1. *Aml* worker marked with RFID tag.

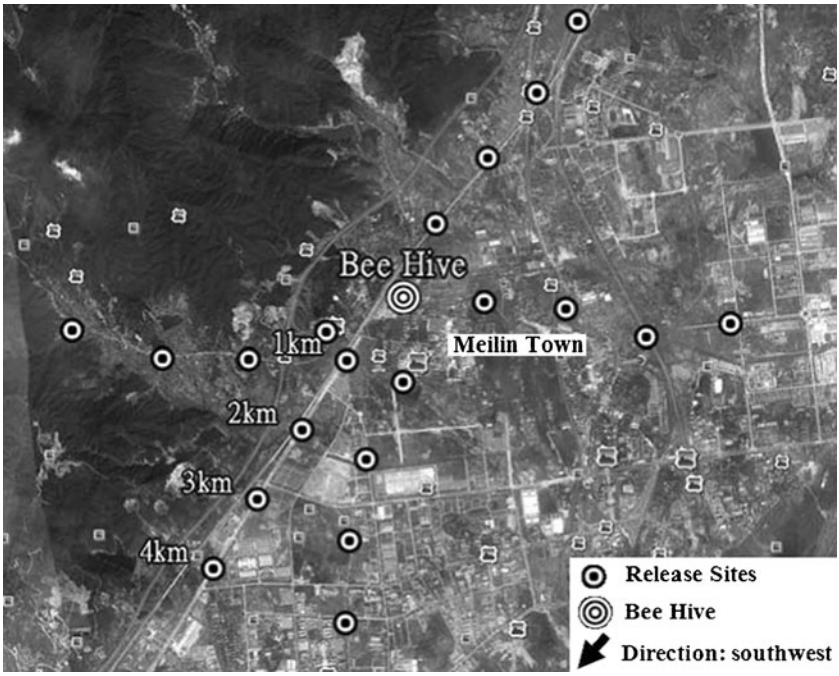

Figure 2. Satellite image of Meilin (obtained from Google Maps) showing location of the hive and bee release sites for experiment 2.

This protocol was repeated every 3 days, over 36 days between June 27 and July 31, 2010 to allow an analysis of how quickly bees were able to adjust to colony relocation.

2.4. Experiment 2: comparing the homing abilities of *Acc* and *Aml* in a familiar environment

To compare the navigational ability and flight range of these two species, we assessed the capacity of *Acc* and *Aml* to return to their colony when released from various points up to 4 km away. As in experiment 1, we included several different marking methods in this experiment to allow assessment of the RFID method for *Acc* and further assessment of the value of the method for *Aml*.

Colonies of *Acc* and *Aml* were kept in an apiary close to Meilin (Figure 2) for more than 30 days in order that the bees could be considered to be familiar with the environment. For both *Aml* and *Acc*, bees were caught at the hive entrance and marked with either colour paint on the thorax, or an RFID tag or a coloured numbered disk glued to the thorax with shellac. After 40 min recovery, bees were released from one of 20 release sites located in five directions from the colony (easterly, westerly, northeasterly, southerly and southwesterly, Figure 2), with four distances for each direction (1, 2, 3 and 4 km). The time at release was noted. As in experiment 1, for the RFID-tagged bees, we recorded both homing time and the proportion of bees homing for these individuals. For the painted and number-tagged bees, at sunset, we counted the proportion of bees to successfully return home from each marking group. The addition of the disk-marked group to this study allowed further validation of the RFID marking method, since the disks are an established method of marking bees and were of a similar size to the RFID tags.

Sixty bees were released at each site (ten of each marking group for both *Aml and Acc*). On a given experimental day, bees were released at five sites. Given accidental losses of tagged bees, the total number of bees involved in this experiment was 572 *Acc* and 643 *Aml*.

Figure 3. Satellite image of Xiangtang (obtained from Google Maps) showing location of hive and bee release sites for experiment 1.

2.5. Experiment 3: assessing behavioural development and activity in *Aml* and *Acc* with RFID

Frames of emerging brood were removed from *Aml* and *Acc* colonies and held overnight in an incubator at 34.4 °C and 80 % RH. Newly emerged adult bees were marked with an RFID tag as in experiment 1 (*Acc* workers, n=33; *Aml* workers, n=49). Tagged bees were returned to their colonies. The RFID scanner recorded each time a tagged bee entered and exited the colony continuously for 36 days. *Aml* was studied in Meilin Town between March 10 until April 14 2011, and *Acc* was studied in the same apiary between May 21 and June 25, 2010. Since these experiments did not occur simultaneously, we do not quantitatively compare behaviour in the two species; however, these are the first measures of behavioural development and foraging activity patterns in *Acc* measured using RFID and provide some useful behavioural information for this species.

For each RFID tagged bee, we recorded the age at which bees left the hive for the first time. We also recorded the number of trips each bee made outside the hive each day and the duration of each trip. Bee loss was the last date a bee was detected by the RFID scanner. This may have been the point at which the bee died, or it may have been the point at which the tag became dislodged from the bee. If we can assume that rates of tag loss are similar in both species, then analysis of the rates of bee loss in the two species gave an indication of bee lifespan.

2.6. Data analysis

For the homing experiments (experiments 1 and 2) for each release site, the proportion of released bees successfully returning to the hive in each marking group was calculated. For RFID-tagged bees, the time between take-off at the release site and the first scan of each individual at the hive provided a measure of homing time. We compared the effects of different marking methods, species and different release sites on the proportions of bees returning and homing time using generalised linear regression implemented in R (R Development Core Team 2011).

For experiment 3, we estimated the duration of bees' foraging trips by sorting the recorded RFID scans to identify times at which each individual bee entered and exited the hive. We assumed that bees spent period between an exit from the colony and their next entry to the colony outside. Bee loss was the last time an individual tag was detected by an antenna. Time to bee loss was estimated using survival analysis implemented with Graphpad.

3. RESULTS

3.1. Experiment 1: investigating the homing of *Aml* in a new environment

The likelihood of a bee successfully returning to the hive increased significantly with time since the hive was relocated to a new environment when bees were displaced to a location 1,500 m from the hive (Figure 4 and Table I), but when bees were displaced 3 km from the hive, very few bees returned successfully, and homing performance did not improve over time (Figure 4). The likelihood of homing after displacement differed depending on whether bees were displaced to the southeast (SE) or southwest (SW) of the hive: Bees were more likely to home successfully following displacement to the east (Table I). There was no difference in homing success between bees marked with paint or RFID tags.

Homing time also improved with time since the colony was relocated to a new environment (Figure 5 and Table II). Initial homing times from release sites 1,500 m from the colony often exceeded 100 min and therefore could not have reflected direct or even continuous flights, but later on, homing times decreased to <10 min. Bees were faster to home from release sites to the east than following release to the west.

3.2. Experiment 2: comparing the homing abilities of *Acc* and *Aml* in a familiar environment

Table III summarises the output of a generalised linear model testing the effects of direction, distance and marking type on the likelihood of successful homing by *Acc* and *Aml*. Homing was significantly affected by distance as successful homing rates declined sharply when bees were displaced more than 1 km from the colony (Figure 6). Homing rates also differed between species, with more *Aml* returning home than *Acc*. This difference was most pronounced for distances <2 km. At greater distances, the performance of both species was equally poor (Table III and Figure 6). Homing rates varied with release points at different directions around the hive. As in experiment 1, marking technique did not significantly affect homing rate (Table III), providing further evidence that these

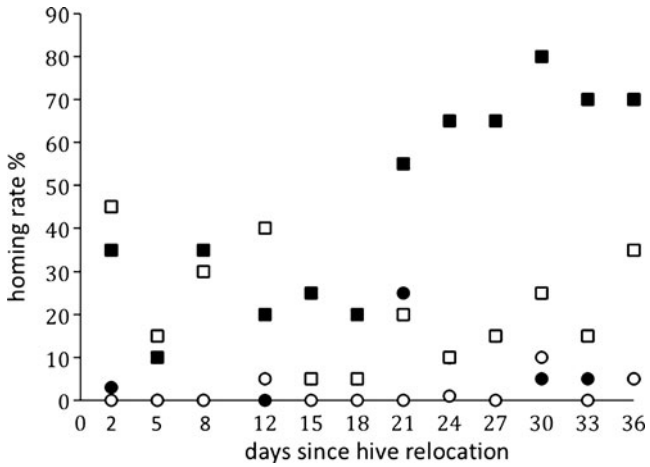

Figure 4. Scatterplot of percentages of *Aml* successfully returning to the hive following displacement. Data from experiment 1. Each point represents return rate as the percentage of bees from a group of 20 that returned to the hive from 4 different release points (*filled symbols* south east, *open symbols* south west; *squares* 1,500 m; *circles* 3,000 m). The experiment was repeated with different bees from the same colony on a series of days following relocation of the colony to Xiangtang. Analysis summary in Table I.

Table I. ANODEV summary table of GLM testing the null hypothesis that the likelihood of *Aml* bees returning home after displacement did not differ with direction (displaced SE or SW from the colony), distance (displaced 1.5 or 3 km from the colony), marking method (RFID tag or paint marks) or with time since relocation to a new environment, or any possible interaction of these terms.

	df	Δ Deviance	Residual *df*	Residual deviance	*P* value
Null			953	938.46	
Direction	1	35.64	952	902.82	0.031
Distance	1	148.46	951	754.36	<0.001
Day	1	18.16	950	736.19	0.567
Direction/distance	1	0.10	949	736.08	0.045
Direction/day	1	17.015	948	719.07	<0.001
Direction/distance/day	1	6.411	947	712.66	0.010

Marking method and direction were modelled as multi-level factors. Distance and day was modelled as continuous variables. The model assumed binomial error structure and a logit link. Only the minimum adequate model (determined by a process of iterative factor addition) is shown. Data from experiment 1

RFID tags did not impede bee flight any more than a paint mark or number disk might.

When comparing the homing times of *Aml* and *Acc*, *Aml* was also faster than *Acc* to return home, especially when released 1 km from the colony. This difference was far less pronounced at the 2 km distance (Table IV and Figure 7). Because so few homing times were recorded for the 3 and 4 km distances in either species (only one record for 4 km for *Aml* and three records at 3 km and one at 4 km for *Acc*), these distances were not included in this analysis.

3.3. Experiment 3: assessing behavioural development and activity in *Aml* and *Acc* with RFID

Tracking individual bees with RFID allowed us to assess patterns of behavioural development and flight activity in both *Aml* and *Acc*. For *Aml*, RFID data revealed the typical pattern of behavioural development that is well known for this species. Bees did not begin to leave the hive until they were >14 days old as adults (Figure 8a), and bees spent most time outside

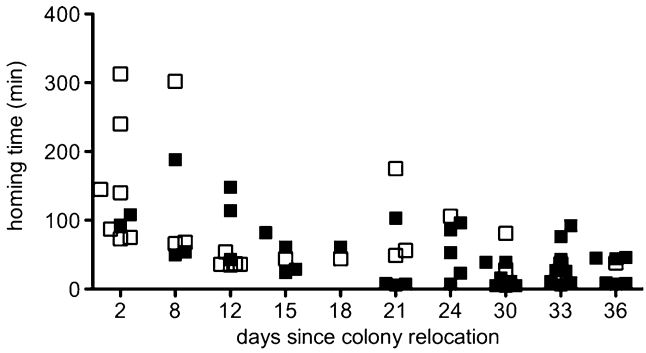

Figure 5. Scatterplot of homing time of RFID-tagged *Aml* bees measured as the time from release at sites 1,500 m southeast (*filled symbols*) or southwest (*open symbols*) of the colony until detection at the hive entrance. Each point represents a single bee that homed successfully. The experiment was repeated with different bees from the same colony on a series of days following relocation of the colony. Data from experiment 1. Analysis summary in Table II.

Table II. ANOVA summary table of linear model testing the null hypothesis that homing time of *Aml* bees did not differ with direction or with days since location to a new environment.

	df	Sum of squares	Mean square	*F*	*P* value
Direction	1	3,369	3,369	1.132	0.2926
Day	9	55,089	6,121	2.057	0.0528
Direction/day	9	21,507	2,390	0.8032	0.6153
Residual	48	142,811	2,975		

Data from experiment 1. Details as in Table I, but since only 7 values were recorded from the 3 km distances this model considered the 1.5 km data only. Marking type had no effect on homing time and was dropped from the model; only the minimum adequate model is shown

the hive when they were more than 3 weeks old as adults (Figure 8a). Figure 8a shows the average time tagged bees spent outside the hive on each day. This gives an impression that bees gradually increased their time outside the hive. However, studying data for each individual bee suggests that each individual quite rapidly switched from spending very little time outside the hive to spending the majority of the daylight hours outside the hive, but different individuals varied at the age in which they make this transition. To illustrate this, we have plotted the data from all individual bees that survived to 36 days old (Figure 8b). Mean time to bee loss was estimated at 26 days (Figure 8c).

RFID data indicated an almost identical pattern of behavioural development in *Acc*. Here, bees also did not leave the hive until they were >14 days old, and individuals showed a similarly rapid transition from time spent inside the hive to spending a majority of time outside the hive (Figure 9a, b). This suggests a qualitatively similar pattern of temporal polyethism organising division of labour in these two species. In this study, mean time to bee loss of *Acc* was estimated at 22 days (Figure 9b), very similar to the estimate for *Aml*.

4. DISCUSSION

Here, we used a new RFID system to compare aspects of foraging behaviour in *Aml* and *Acc* in the same environment in China. Our data suggest that both species begin foraging at very similar ages and have similar overall

Table III. ANODEV summary table of GLM testing the null hypothesis that the likelihood of a bee returning home after displacement did not differ between species (*Aml* and *Acc*), with direction (displaced in five different directions from the colony), distance (displaced 1, 2, 3 or 4 km from the colony) and marking method (RFID tag, colour paint marks or numbered disks), or any possible interaction of these terms.

	df	Δ Deviance	Residual *df*	Residual deviance	*P* value
Null			1,214	1,284.68	
Distance	1	432.43	1,213	852.24	<0.001
Species	1	16.35	1,212	835.89	<0.001
Direction	4	27.81	1,208	808.08	<0.001
Distance/species	1	5.91	1,207	802.17	0.0148

Marking method, direction and species were modelled as multi-level factors. Distance was modelled as a continuous variable. The model assumed binomial error structure and a logit link. Only the minimum adequate model (determined by a process of iterative factor addition/elimination) is shown. Because marking method did not explain a significant amount of deviance in the data it does not feature in the minimum adequate model. Data from experiment 2

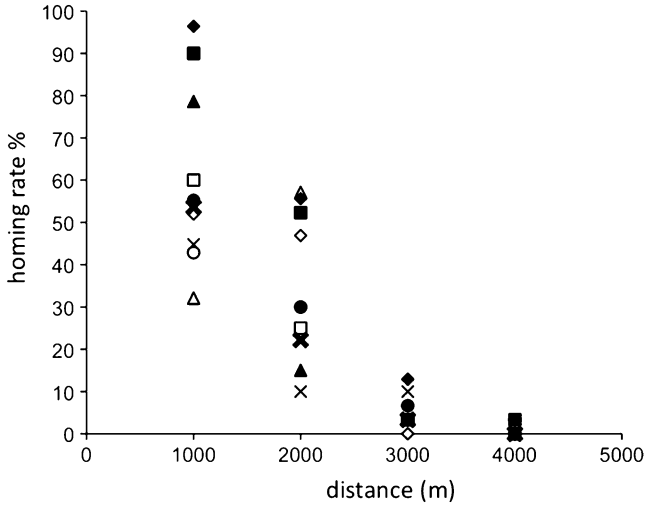

Figure 6. Scatterplot showing the percentage of bees successfully returning to the colony after release at sites located at four different distances (1,000–4,000 m) and five different directions from the hive. Each point represents homing rate as a proportion of bees that returned to the hive from approximately 30 that were released at a given site. Data from experiment 2. *Black symbols*, *Aml*; *open symbols*, *Acc. Triangles* Northeast, *squares* south, *crosses* east, *circles* west, *diamonds* south west. Summary of statistical analysis in Table III.

lifespans. However, *Aml* has a larger effective foraging range than *Acc.*

RFID tags (Streit et al. 2003) are proving an extremely effective tool for efficiently gathering large behavioural datasets for honey bees. Previous studies have used the Microsensys RFID system (Pahl et al. 2010; Streit et al. 2003; Decourtye et al. 2011; Henry et al. 2012). In this study, we used a new form of RFID tag from Invengo for the first time with honey bees. While both systems rely on similar basic technology (excitation of a transponder tag to emit a specific coded digital signature), the Invengo tags are smaller and lighter than those of Microsensys, and the detection range is larger (up to 9 mm form the antenna). The Invengo tags weigh <1 mg and can be easily fixed to the dorsal thorax with shellac glue. The homing performance of RFID-tagged bees did not differ from that of paint marked or number tagged bees (experiments 1 and 2), showing that the tags do not impede bee flight any more than

Table IV. ANOVA summary table of linear model testing the null hypothesis that homing time (measured as the time from release after displacement to a bee being detected by the RFID scanner at the hive entrance) did not differ between species, with direction or with distance.

	df	Sum of squares	Mean square	*F*	*P* value
Distance	1	781,972	781,972	235.41	<0.001
Species	1	17,321	17,321	5.21	0.025
Distance/species	1	46,754	46,754	14.07	<0.001
Residual	81	269,051	3,322		

Details as in Table I, but since so few values were recorded from the 3 and 4 km distances for either species this model considered the 1 and 2 km data only. Direction had no effect on homing time and was dropped from the model; only the minimum adequate model is shown. Data from experiment 2

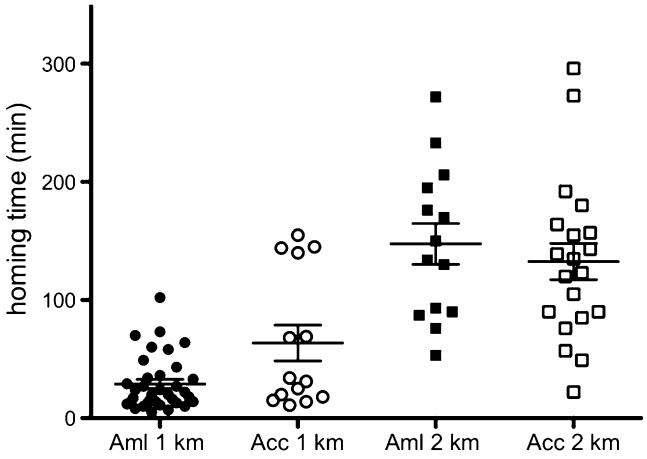

Figure 7. Scatterplot of homing time of RFID tagged bees (measured as the time from release after displacement until detection at the hive entrance) for *Aml* and *Acc* released at 1 and 2 km from the hive. Data from experiment 2. *Bars* show mean, *whiskers* extend to ±1 SEM. Data from different release sites pooled for this figure. Analysis summary in Table IV.

other marking methods routinely used in bee research.

Experiment 1 showed *Aml* worker behaviour was negatively affected for three weeks following colony relocation (Figure 5), which cautions against repeated movements of colonies. Homing ability varied depending on the direction of displacement, an effect also reported by Pahl et al. (2010), and perhaps reflecting the reliance of large-scale homing on large-scale landmarks, which may be more obvious from some directions than others (Pahl et al. 2010). Colony relocation is an essential aspect of commercial migratory beekeeping where colonies are rotated among flowering crop plants to provide a pollination resource. It is usually assumed that while the move may disorient the established foraging force, the colony should be able to rapidly adjust for the move. Instead, our data show that individual bees show evidence of disorientation for up to 3 weeks after colony relocation. This would be expected to impact colony growth and pollination performance. It suggests that the effects of colony relocation are not limited to the loss of the generation of established foragers but are also seen in far younger bees that may not have commenced foraging fully at the old location. Our data caution against frequent repeated movements of a bee hive.

The flight activity data collected by the RFID system clearly showed the pattern of temporal polyethism that has been well documented for *A. mellifera* (Figure 8a, b) (Winston 1987; Seeley 1995). Data for *Acc* were collected at a different time, which precludes quantitative comparisons between the species, but qualitatively *Acc* shows a very similar pattern of behavioural organisation. Individual bees began life restricted to the hive and showed a quite rapid transition to spending the majority of their time outside the hive (Figure 9a, b).

A limitation of the RFID system is that bee death can only be estimated from the point at which an individual was last detected by the scanner (the point of bee loss). Bees retaining their tags throughout their lives must have gone on to die at some point after their last detection. More seriously, this method could not distinguish whether bees had died, or never returned to the hive, or simply lost their RFID tag. For these two reasons, measures of bee loss have to underestimate bee longevity to a degree, but even so, for *Aml*, our estimate of bee loss (Figure 8b) agreed well with other estimates of bee survival for this species (Sakagami 1968).

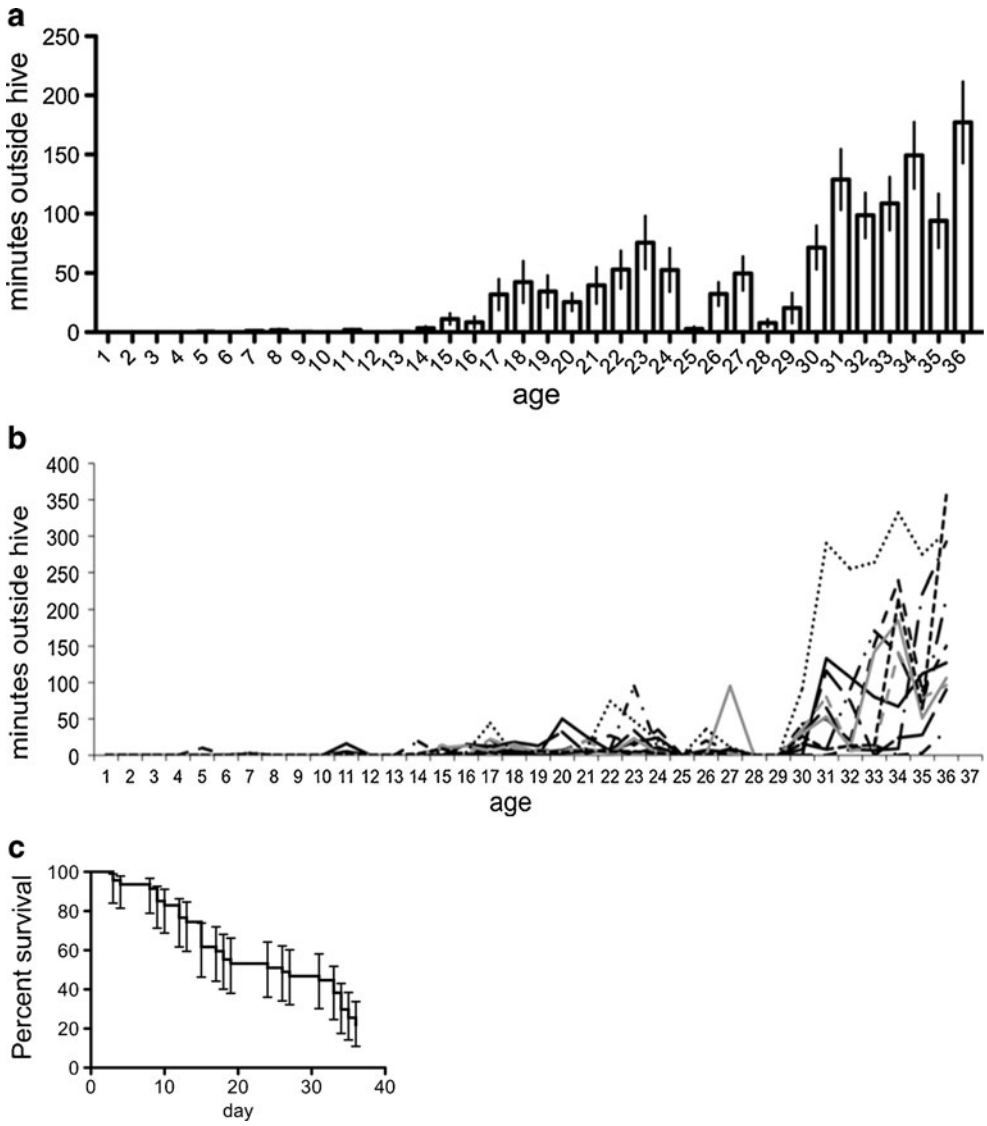

Figure 8. Behavioural development and time to loss of *Aml* estimated by RFID. **a** Mean±SEM duration bees spent outside the hive plotted against age for a cohort of 47 bees tracked for 36 days by RFID. **b** Plots of time spent outside hive against age for each individual bee that survived to 36 days old. Each line represents one individual. For the data plotted in **a** and **b**, rain occurred on days 13, 25, 28 and 29; hence, low activity recorded on those days. **c** Time to loss of bees (for these data 'loss' is considered the last day at which a bee was detected by the RFID scanner). Standard error estimated from the Kaplan–Meier estimator of the survivor function. Median survival estimated at 26 days.

Both the age at onset of foraging and rates of bee loss were qualitatively similar for the two species (Figures 8 and 9). Given that embryonic and larval development times are also similar between tropical races of *A. mellifera* and *Acc* (Ruttner, 1988), it would seem that both species in China have very similar demographic structures to their colonies,

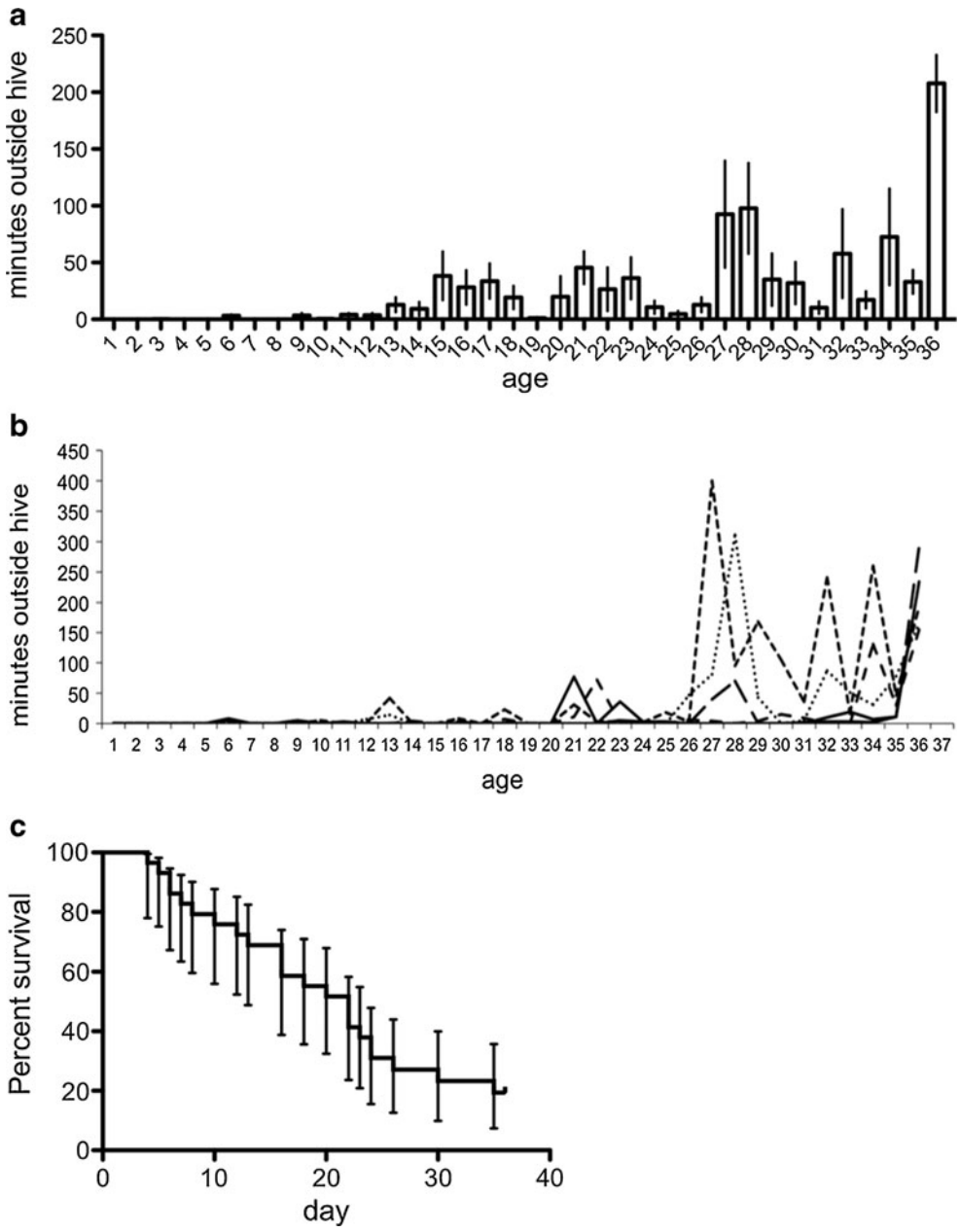

Figure 9. Behavioural development and time to loss of *Acc* estimated by RFID. **a** Mean±SEM duration bees spent outside the hive plotted against age for a cohort of 30 bees. **b** Plots of time spent outside hive against age for each individual bee that survived to 36 days old. Each line represents one individual. **c** Time to loss of bees. Median survival estimated at 22 days. Details as in Figure 8.

In the homing experiment (experiment 2), *Aml* performed better than *Acc* both in terms of the proportion of bees returning home after displacement and also in terms of time taken to

return home, suggesting that *Aml* workers are capable of navigating a larger area around their hive than *Acc* workers. Whether this difference is due to differences in flight ability between the two species or differences in retained landmark information is not clear, but these data are consistent with other earlier studies that have indicated that *Acc* has a smaller foraging range than *Aml*. Evidence gathered from training bees to feeders (Darade et al. 1989; Dyer and Seeley 1991), beelining (Seeley et al. 1982) and analyses of distances indicated through dances (Dyer and Seeley 1991) have all suggested that the majority of *A. cerana* workers forage within 1 km of their colony. Analyses of *A. mellifera* foraging distances inferred from observation of the dance behaviour of returning foragers suggest the median forage range of temperate races of *A. mellifera* to be approximately 1.6 km, but far longer foraging trips (up to 10 km) are not unusual (Seeley 1995; Stefan-Dewenter and Kuhn 2003). Foraging range is influenced by floral quality and distribution: On heather (*Calluna vulgaris* L.) in the UK, mean foraging distances of >5 km have been inferred for *A. mellifera* (Beekman and Ratnieks 2000). However, it should be noted that in a tropical climate, the mean foraging range of the African honey bee *A. mellifera scutellata* is smaller than that of the temperate races (typically <1 km) (Schneider 1989; Schneider and McNally 1993). This would place the foraging ranges of tropical *A. mellifera* subspecies more similar to that of *Acc*.

In summary, these behavioural data reveal extreme behavioural similarities between *A. cerana* and *A. mellifera*, highlighting the potential for competition between these sister species when in sympatry. Sometimes, similar and closely related species show specific behavioural adaptations to reduce competition between them. For example different sympatric species of *Myrmecia* ants each have distinct temporal niches, which will act to reduce foraging competition between them (Narendra et al. 2011). We found no evidence of behavioural specialisations in foraging and life history of *Aml* or *Acc*, which might have acted to reduce competition between these species. Since these species evolved in geographic isolation from a close common ancestor and have only recently been in sympatry, it seems that there has been no selection for their foraging ecology to diverge or time to evolve behavioural buffers to competition now that they are sympatric. As a consequence, given the close morphological and behavioural similarities of these two species, intense resource competition between them seems inevitable.

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Evaluation de l'activité de vol et de la capacité à retourner à la colonie chez les abeilles asiatique et européenne, *Apis cerana* et *Apis mellifera*, mesurée à l'aide de radio-étiquettes.

Apidae / évolution du comportement / navigation / retour à la colonie

Beurteilung der Flugaktivität und des Heimfindevermögens bei den asiatischen und europäischen Honigbienenarten *Apis cerana* und *Apis mellifera* gemessen mithilfe von Radio-Frequenz Chips

***Apis cerana* / *Apis mellifera* / RFID / Entwicklung des Verhaltens / Heimfindevermögen / Navigation**

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