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Seasonal and diurnal patterns of activity in honeybees (*Apis* spp.) on the northern edge of the Asian tropics; their implications for the climate-change resilience of pollination

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Abstract

Apis honeybees are very important pollinators in tropical Asia but their diversity declines rapidly north of the tropics. This suggests that climate is a major control on their distributions and that climate change may influence the services they provide. Four *Apis* honeybees coexist in a flower-rich botanical garden in Yunnan, China, on the northern margin of the tropics (21°41′N): *A. florea* and *A. andreniformis* (small, open-nesting), *A. cerana* (medium, cavity-nesting), and *A. dorsata* (large, open-nesting). We made standardized observations of their diurnal and seasonal activity patterns and recorded temperature, humidity, and solar radiation at flowers being visited. *A. dorsata* comprised two-thirds of honeybee individuals observed, although this species was largely absent from July to November. *A. cerana* was active on each day that observations were made and tolerated temperatures of 7°C–41.5°C (including observations from two other sites in Yunnan). The other species had higher minimum temperature thresholds for activity, but *A. florea* had a higher maximum temperature tolerance (46.5°C) and *A. dorsata* was sometimes active at night. Generalized linear models showed abundances of *A. cerana* and *A. dorsata* had positive relationships with numbers of flowers and negative ones with temperature. *A. florea* abundance had a positive relationship with temperature, while the presence of *A. andreniformis* was positively related to temperature and humidity. *Apis* bees visited 48.6% of the flower species observed. Impacts of projected warming over coming decades are expected to vary among species, but overall pollination services by honeybees at this site seem likely to be resilient.

Keywords

Apidae, flower visitors, Hymenoptera, insects, phenology, thermal tolerance

Introduction

Honeybees (*Apis* spp., Apidae) are the most important insects to humans, accounting for a large proportion of total global pollination services for pollinator-dependent crops (c. 39%; Rader et al., 2016), as well as providing the bulk of the 1.7 million tonnes of honey a year produced globally in 2013 (http://faostat3.fao.org/download/Q/QL/E). As native species, they are largely confined to Asia, except for one species, *A. mellifera*, the western honeybee, which occurs naturally across most of Africa and parts of Europe, and has been transported worldwide as domesticated colonies that have subsequently often become feral.

Within Asia, 11-12 species are currently recognized (Lo, Gloag, Anderson, & Oldroyd, 2010), all largely confined to the tropics, except for the rock bee, *A. laboriosa,* which occurs along the foothills of the Himalayas from northern India to northern Laos, and the eastern honeybee, *A. cerana*, which occurs from the equator to 45°N in eastern Asia. Within the Asian tropics, 3-5 species can coexist, including 1-2 small, open-nesting species, 1-2 medium-sized, cavity-nesting species, and 1 large, open-nesting species. Co-existing species differ not only in body size and nest sites, but also in colony sizes, habitat

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preferences, daily and seasonal activity patterns, use of floral resources, and, presumably, effectiveness as pollinators (Corlett, 2011; Hepburn & Radloff, 2011). Phylogenetic studies suggest that the small, medium, and large species form separate, monophyletic groups, with the small species basal (Abrol, 2011), and that the honeybees (Apini), in turn, are sister to the stingless bees (Meliponini) and bumblebees (Bombini) (Arias & Sheppard, 2005).

As with *A. mellifera*, most of the research on Asian honeybees has been conducted in crop monocultures. In these systems, bee behavior is partly constrained by plant traits, including the spatial and temporal patterns of nectar and pollen availability (Partap, 2011; Romiguer et al., 2016). The behavior of honeybees in natural and semi-natural vegetation has received much less research attention. A recent review of the role of Asian honeybee species in natural ecosystems concluded that, although they were less important as pollinators in undisturbed natural ecosystems than in deforested areas and agricultural systems, they dominated on some resources at all sites (Corlett, 2011).

The projected changes in climate over the next few decades (IPCC, 2013) will impact the geographical distributions and activity patterns of Asian honeybees, particularly near the margins of the tropics, where low temperatures currently limit bee activity for part of the year (Corlett, 2011). Bees will respond to climate change more rapidly than most plants (Corlett & Westcott, 2013), and potentially use different climate variables as phenological cues, creating opportunities for mismatches in future bee and plant phenologies and distributions (Burkle, Martin, & Knight, 2013). On the other hand, it is expected that the co-existence of multiple honeybee species in the Asian tropics, as well as other social and solitary bees, will buffer the pollinator community against functional changes.

In order to predict the distribution and activity of honeybees in a warmer world, we need to know how temperature and other weather variables currently influence activity. Studies of diurnal and seasonal activity patterns show that the foraging activities of bees are controlled by both weather and floral resource (nectar and pollen) availability (Muniz, Pereira, Valim, & Campos, 2013; Reddy, Rashmi, & Verghese, 2015; Romiguer et al., 2016). Flowering and nectar production are also influenced by weather, so it is difficult to separate direct and indirect impacts on activity patterns. In this study we minimized the impact of resource availability by making observations in a large, highly diverse, botanical garden, including both semi-natural areas where bees can nest, and planted areas designed to produce flowers year-round. Moreover, most flowers were at eye-level in the garden, which made close observations of numerous individual flower visitors practical without the expense and challenges of accessing canopy layers that observations in the native tropical forests in the same region would entail.

The study site, on the northern edge of the Asian tropics, supports four honeybee species, although one is rare. As part of a larger study of flower visitors, we asked two questions: 1. How does the activity of each honeybee species vary diurnally and seasonally? 2. How does weather affect these activity patterns? We then discuss how projected anthropogenic climate change may influence the distributions, activity patterns, and pollination services of honeybees in Yunnan.

Methods

Study sites

Most field observations were made in the Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences (XTBG), in Yunnan, China (21°41′N, 101°25′E, 570 m above sea-level). This Garden comprises 10.5 km^2 of horticultural displays, living plant collections, secondary regrowth, and disturbed forest patches. Pesticide use is very low. It is on the northern margins of the Asian tropics and has a monsoon climate with hot, wet summers and cool, dry winters. Mean monthly temperature ranges from 16.0°C (January) to 25.7°C (June) and mean annual precipitation is 1500 mm, >80% of which occurs between May and the end of October. Morning fog occurs most days between November and February.

In order to extend the range of temperatures over which honeybee activity could be observed, additional observations were made at two other sites in Yunnan: Kunming Botanical Garden (KBG; 25°N, 1990 m), a smaller, more intensively managed botanical garden, which experiences lower winter temperatures than XTBG, and the Yuanjiang Savanna Ecological Station (YSES; 23°41′N, 770 m), located in a rain-shadow valley with savanna vegetation, which experiences higher summer temperatures.

Data collection

All field data was collected by the first author (QC) to ensure consistency. A standard 4 km walking route through the managed section of the Garden was used to investigate the seasonal activity pattern of flower visitors. It was chosen to maximize the year-round number, diversity, and accessibility of flowering plants present, and passed through an irregular patchwork of tree collections, flower beds, mown grass, and other plants. An area of approximately 6000 m^2 with many types of flowers, adjacent to this route, was used to investigate daily activity patterns over the year, with adjacent areas added when there were insufficient flowers to attract bees.

The standard route was walked once a week from October 2014 to October 2015, starting 3 hours after sunrise (which usually approximated to the time of maximum bee activity) and taking around 3 hours to complete. The walk was postponed for an hour in winter if it was foggy at the usual start time, because fog delayed the start of flower visitor activity, and for a day if there was heavy rain. All plants with open flowers within 2.5 m either side of the observer were recorded and flower numbers were estimated as: 5 (1-10 flowers), 30 (10-50 flowers), 125 (50-200 flowers), 600 (200-1000 flowers) and 1500 (>1000 flowers). Large flower numbers were estimated either by counting a known fraction and multiplying up, or by visual comparison with previous counts of similar numbers. Over the year 387 species of flowering plants in 90 families were observed, including trees (22%), shrubs (34%), herbs (24%), and vines (20%). All flower visitors were identified and counted during approximately 2 minute observation periods, which were extended when necessary, at each flowering plant or group of plants along the route. Once a month, the standard 6000 m^2 area was observed for 90 minutes at 2 hour intervals from sunrise to sunset and similar observations made. Binoculars were used for trees up to a maximum height of 5 m. Unknown species of flowers and flower visitors were photographed and, if necessary, collected. Only observations of honeybees (*Apis* spp.) have been used for the purpose of this paper.

Four weather variables were recorded as close as possible to the flowers that were visited at each site. Air temperature and relative air humidity were recorded with an iButton Hygrochron Temperature/Humidity data logger (DS1923#5) and total solar radiation was measured with a portable photo-radiometer (LP PYRA 04 pyranometer). Rain was subjectively assessed in three categories (0: no rain, 1: little rain, 2: heavy rain), but since no bees were active in heavy rain and most observations were made in dry weather, this variable was not used in the modeling. We also made use of data for hourly total solar radiation recorded from a meteorological station near the start of the walking route (Xishuangbanna Station for Tropical Rain Forest Ecosystem Studies). Although wind speed is another potentially significant variable for honeybees, the wind is consistently light at XTBG and was never strong enough to limit activity during the observations made for this study.

KBG was visited once a month from December 2014 to November 2015 and observations were made on two consecutive days at each visit. YSES was visited once only, from 7-9 May, 2015, at the hottest time of the year. The same weather variables as at XTBG were recorded during observations. Data from these sites have only been used here to assess the temperature extremes at which the *Apis* species present were active.

Data analysis

The relationship between the estimated total numbers of each bee taxon visiting flowers along the standard route each week and environmental parameters was tested using generalized linear models (GLMs) in R 3.2.3 (R Core Team, 2015). The weather parameters tested were mean air temperature and humidity (from measurements made along the route), and solar radiation (from the weather station, because measurements along the route were incomplete). We also included a quadratic term, the square of air temperature, since the relationship between temperature and activity was expected to be non-linear, and the interaction between solar radiation and temperature, since bees can potentially use exposure to direct sunlight to compensate for low air temperature. Rainfall was not included in the model because all bees were inactive then and formal observations were halted during heavy rain. Other parameters included in the maximal model were total flower numbers, to represent resource availability, and the total numbers of bees recorded in the previous week, the previous two weeks, three weeks, and four weeks, to account for the dependence of bee activity in a given week on the activity in previous weeks, since individual bees forage for several weeks.

The bee count data were over-dispersed so counts of *Apis cerana*, *A. dorsata* (giant honeybee) and *A. florea* (red dwarf honeybee) were modelled as quasi-Poisson. Backward selection was used to choose the most parsimonious model for each species (i.e., the simplest model that could not be significantly improved by adding additional parameters), using t-probability >0.1 to remove terms stepwise, starting with higher order terms and the most non-significant parameters. *A. andreniformis* (black dwarf honeybee) was recorded on only 16 days so we used a binomial model for presence and absence only. To assess the contribution of each variable to the final selected models we compared likelihood ratios generated when that variable was dropped from the model.

Results

Four *Apis* species were recorded visiting flowers at XTBG during this study: *Apis dorsata* Fabricius (body length 17.1 mm), *A. cerana* Fabricius (11.0 mm), *A. florea* Fabricius (8.8 mm), and *A. andreniformis* F. Smith (8.1 mm). Only *A. cerana* was seen at KBG while both *A. cerana* and *A. florea* were seen at YSES. A total of 23,762 individual *Apis* bees were recorded at XTBG, including *A. dorsata* (65%), *A. cerana* (28%), *A. florea* (5%), and *A. andreniformis* (2%). These *Apis* species accounted for 66% of all the Hymenoptera individuals recorded and 46% of all flower visitors. A total of 4,046 *A. cerana* were seen at KBG, accounting for 87% of all Hymenoptera and 59% of all flower visitors. On the single visit to YSES in early May, 269 *Apis* bees were recorded, of which 86% were *A. florea* and 14% *A. cerana*.

A. cerana was resident year-round at both XTBG and KBG, whereas *A. dorsata* was resident at XTBG from December to June, with only a few individuals at other times (Figure 1). The conspicuous comb nests of *A. dorsata* were absent at XTBG from July to November, but temporary bivouacs (combless clusters of bees) of migrating colonies were sometimes seen. Both larger species had peak abundances in the first half of the year. *A. florea* was probably present throughout the year at XTBG, although it was not recorded in March and August, while the numbers of *A. andreniformis* were too low to discern any clear pattern. Both small species showed peak abundances during the flowering times of *Cissus verticillata* and *Cissus* sp. (Vitaceae), on which they dominated.

At XTBG, *A. cerana* was seen visiting flowers at temperatures of 11.5°C – 41.0°C and relative humidities of 20.7% – 96.8%, which was almost the entire range of conditions recorded during the observation periods (Table 1). The other sites extended the temperature range down to 7°C (KBG; on a still, sunny day) and up to 41.5°C (YSES). The other three *Apis* species had higher minimum temperature thresholds for activity (*A. dorsata*, 14°C; *A. florea*, 16°C; *A. andreniformis*, 25°C, but from only a few observations) and similar upper thresholds, except for *A. florea*, which was still active at 46.5°C in YSES. All species except *A. andreniformis* were sometimes active in light rain, but heavy rain prevented all activity.

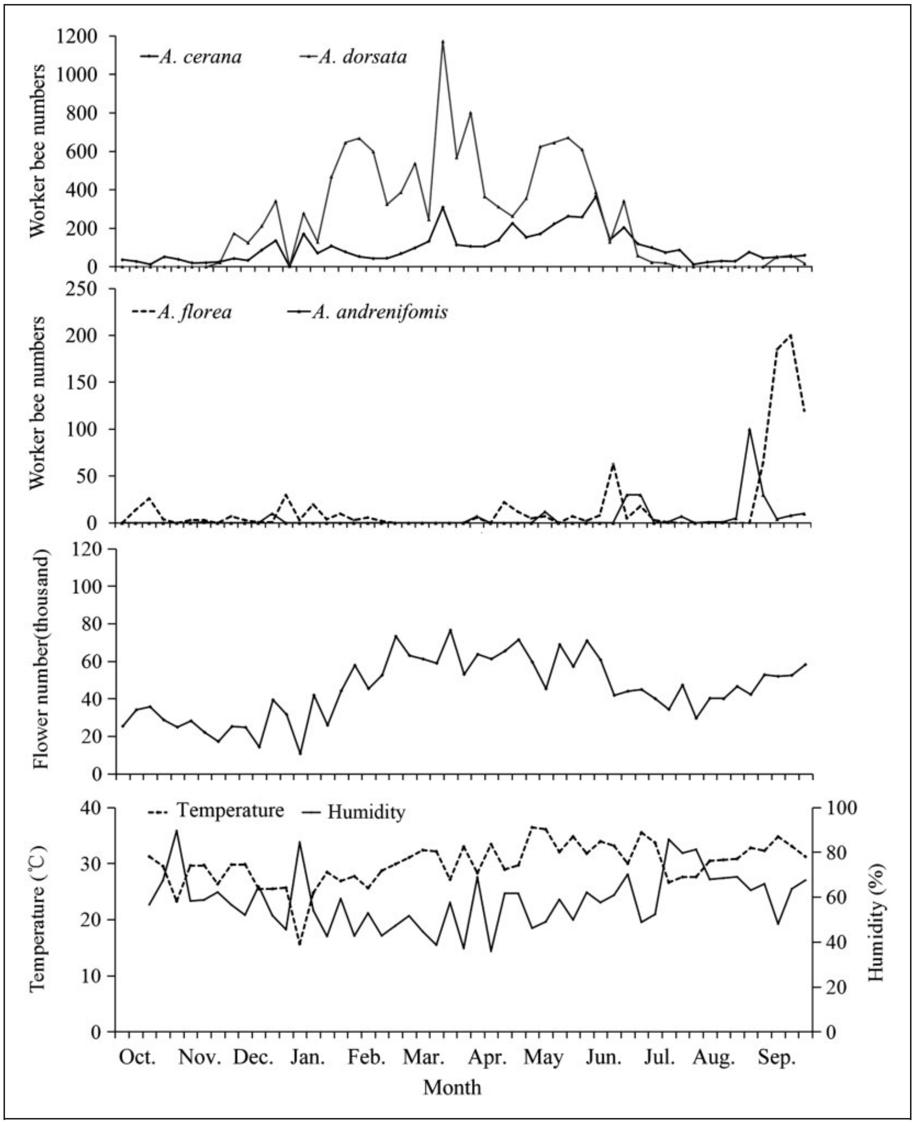

Figure 1. Seasonal variation in abundance of four species of *Apis* and estimated flower abundance.

Table 1. Ranges of three environmental factors during the observation periods and during the activity periods of each honeybee species at the three sites.

	Study site		*A. cerana*		*A. dorsata*		*A. florea*		*A. andreniformis*	
	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max
XTBG										
Temperature (°C)	11.0	41.5	11.5	41.0	14.0	41.0	16.0	41.0	25.0	37.5
Humidity (%)	19.3	100.0	20.7	96.8	20.0	94.4	27.6	89.7	36.0	86.3
Solar Radiation (W/m^2)	0.0	1126.4	0.0	1125.2	0.0	1125.2	32.1	1042.5	38.4	931.0
Rain	0	2	0	1	0	1	0	1	0	0
KBG										
Temperature (°C)	0.0	34.5	7.0	34.5	——	——	——	——	——	——
Humidity (%)	13.9	100.0	13.9	99.6	——	——	——	——	——	——
Solar Radiation (W/m^2)	0.0	1185.0	0.0	1185.0	——	——	——	——	——	——
Rain	0	2	0	1	——	——	——	——	——	——
YSES										
Temperature (°C)	25.0	47.5	25.0	41.5	——	——	25.0	46.5	——	——
Humidity (%)	8.8	60.6	11.8	60.6	——	——	8.8	60.0	——	——
Solar Radiation (W/m^2)	0.0	948.6	5.8	684.1	——	——	5.0	948.6	——	——
Rain	——	——	——	——	——	——	——	——	——	——

Daily patterns of activity differed between species. *A. cerana* was active the longest, almost from sunrise to sunset (Figure 2). However, it was not active in the afternoon in May, which was the longest and hottest whole day studied. Peak activity in the cooler months, from October to February, when mornings were often foggy, was in the afternoons (4-8 hours after sunrise). However, in other months, apart from June and August, it was in the mornings (2-4 hours after sunrise). When present at XTBG, *A. dorsata* was also active most of the day, except in January and September, when activity started later. From December to February, its peak activity time was the same as *A. cerana*, while in other months in which it was present its peak activity (4-10 hours after sunrise) was later than that of *A. cerana*. Outside the formal observation periods, *A. dorsata* was sometimes seen foraging in low light after sunset, when *A. cerana* was absent, and it was once seen visiting flowers near midnight on a moonlit night in June. This species is sometimes attracted to street lights at night, suggesting that nocturnal activity may have been under-recorded in this study. In contrast to the larger species, the activity period of *Apis florea* was very short: only 2-4 hours in the afternoon, with a maximum of 6 hours from April to July (2-10 hours after sunrise). Peak activity for this species was always in the afternoon. *A. andreniformis* had very few records but their timings were similar to *A. florea*.

The most parsimonious GLMs for the abundance of *A. cerana* and *A. dorsata* included strong positive relationships with the numbers of bees recorded in the previous week, positive relationships with the numbers of flowers, and negative relationships with air temperature (Table 2). For *A. cerana* only, there was also a significant relationship with T^2, although this causes little curvature in the temperature-abundance relationship over the range of temperatures experienced at XTBG, and also with humidity. For *A. florea* the model showed a strong positive relationship with the numbers of bees recorded in the previous week and a positive relationship with air temperature. The presence of *A. andreniformis* was positively related to temperature and humidity.

Over the whole year, *Apis* species at XTBG were recorded visiting 188 flower species: 48.6% of all the plant species that flowered along the standard route. *A. cerana* visited 133 flower species, *A. dorsata* visited 128, *A. florea* visited 36, and *A. andreniformis* visited 11. During the period when *A. dorsata* was nesting in XTBG, it visited 66.4% of the 110 flower species visited by *A. cerana*, while *A. cerana* visited 57.5% of the 127 species visited by *A. dorsata* (Figure 3). The smaller bee species overlapped mostly with *A. cerana* and neither were exclusive visitors to any flower species during this period.

Discussion

This study shows that four *Apis* species coexist in a botanical garden on the northern margin of the Asian tropics: *A. florea* and *A. andreniformis* (open-nesting, dwarf bees), *A. cerana* (cavity-nesting bee, medium-size bee),

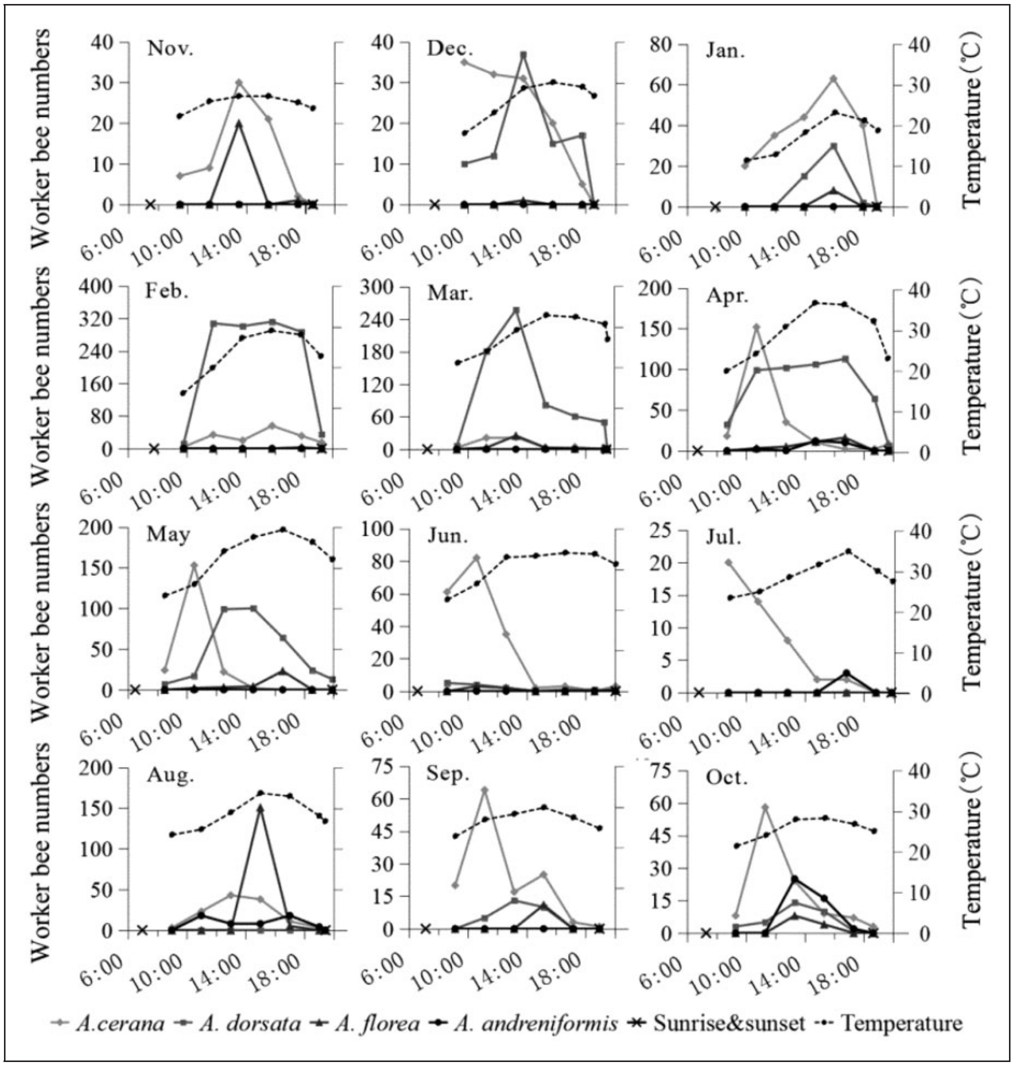

Figure 2. Diurnal activity patterns of four species of *Apis*.

and *A. dorsata* (open-nesting, giant bee). Only *A. cerana* was present during one year's observations at KBG, which has considerably colder winters than XTBG, and only *A. cerana* and *A. florea* were seen on the single visit to YSES, which has hotter summers. At XTBG, *A. cerana* was active for at least part of the day on every day that observations were made, whereas *A. dorsata* was absent from July to November. The two small species may have been present year-round but our records are insufficient to confirm this. When all species were present, *A. cerana* was generally active for longer than the others, reflecting its tolerance of lower temperatures, although only *A. dorsata* is capable of nocturnal activity. At YSES, *A. florea* showed an exceptional tolerance of high temperatures. In general, these differences among the three most abundant species match descriptions of their activity patterns at other sites in the seasonal Asian tropics, although minimum temperatures for activity were generally lower at XTBG than those reported elsewhere (Corlett, 2004; Romiguer et al., 2016). This may reflect the frequent occurrence of still, sunny weather conditions during winter in Yunnan, which favors bee activity at low air temperatures.

Cavity-nesting bees are expected to have an advantage in seasonal climates, since the enclosed nest allows efficient thermoregulation (at 33°C–34°C in *A. cerana*), with the result that foraging bees are pre-warmed before take-off (Tan, Yang, Wang, Radloff, & Oldroyd, 2012). This, as well as its lower threshold temperature for flight at XTBG, is consistent with the extensive north-temperate distribution of *A. cerana*. The other species are largely confined to the tropics. It is striking, however, that the open-nesting *A. dorsata*, which is near the northern limits of its range, accounted for nearly two-thirds of the individual bees recorded during this study, despite being absent, or almost absent, for much of the year.

The GLM results are also largely consistent with what is known about the biology of these bees. For *A. cerana*,

Table 2. Results of generalized linear model (GLM) analysis of the relationship between the total numbers of each *Apis* species observed and environmental variables, including the number of flowers. LRChisq is the likelihood ratio chi-square test used to compare the contribution of each variable to the model.

Species	Parameter	Estimate	S.E.	t value	P	LRChisq
A. cerana	Intercept	12.55	4.758	2.637	0.012	
	ln(N(week-1))	0.64	0.098	6.530	<0.001	44.80
	Temperature	−0.82	0.319	−2.557	0.014	6.19
	Humidity	0.01	0.006	1.726	0.092	3.00
	Temperature^2	0.01	0.005	2.450	0.019	5.70
	Flowers	0.03	0.006	4.957	<0.001	26.10
A. dorsata	Intercept	3.78	0.943	4.006	<0.001	
	ln(N(week-1))	0.55	0.106	5.159	<0.001	44.11
	Temperature	−0.07	0.031	−2.294	0.027	5.40
	Flowers	0.021	0.010	2.087	0.043	4.52
A. florea	Intercept	−4.05	2.852	−1.419	0.163	
	ln(N(week-1))	0.68	0.141	4.829	<0.001	24.52
	Temperature	0.17	0.088	1.901	0.064	3.84
A. andreniformis	Intercept	−22.29	7.785	−2.863	0.004	
	Temperature	0.41	0.172	2.390	0.017	7.97
	Humidity	0.15	0.050	3.045	0.002	15.48

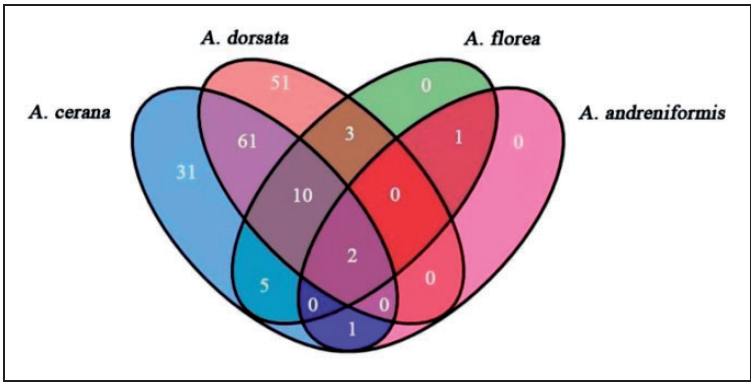

Figure 3. Numbers of flower species used by four species of *Apis* during the December-June period when all species were present at XTBG. The numbers in areas of overlap representing flower species visited by 2-4 of the *Apis* species.

A. dorsata, and *A. florea*, the most important contributions to the selected models were from the abundances of the species the week before, reflecting the fact that the weather variables during the observation times were usually well within the ranges of tolerance for these species. Total flower numbers were next in importance for *A. cerana* and significant for *A. dorsata*, both of which are extreme generalists at XTBG, but not for the two smaller bee species, which were observed visiting only a small subset of the flowers available (Figure 3). The negative relationships between abundance and temperature in *A. cerana* and *A. dorsata* were unexpected, but the temperature in XTBG during the weekly observation periods was always above the range at which low temperature limited activity in *A. cerana* further north at KBG. In Bengaluru, India (13°N), the number of foraging *A. cerana* declined significantly above 30°C (Reddy et al., 2015), supporting the theory that this species is adapted to a lower range of temperatures than the others. In contrast, temperature had a positive influence on the activity of *A. florea*, which is consistent with both its tropical distribution and the tolerance of very high temperatures exhibited at YSES. Warm, humid weather predicted the occurrence of *A. andreniformis*, which is consistent with its reported preference for tropical forests (Hepburn & Radloff, 2011).

The results suggest no obvious explanation for the migration of *A. dorsata*. It disappears while flowers are still abundant, returns when they are relatively scarce, and spends the coldest months at XTBG. Although this study covered only one year, informal observations over multiple years (by RTC) confirm that this very conspicuous behavior is seasonal rather than irregular. Presumably, the departure of colonies is at least partly determined by resource availability at their currently unknown destination. Note that the other three species studied here are also known to migrate, at least short distances, in some areas (Hepburn, 2011), and it is possible that some of the fluctuations in the abundance of other species reflect colony movements rather than the responses of resident colonies to environmental conditions.

Weather probably also influences honeybee activity in other, indirect, ways that our observations would not detect. Nectar production from individual flowers is affected by temperature, humidity and soil moisture (Muniz et al., 2013), while flower production responds to the physical environment on multiple timescales. Honeybee colony size and colony density presumably integrate the availability of floral resources over longer timescales. It is also possible that the activity patterns reported here were influenced by interspecific interactions, between honeybee species, or with other bees or other flower visitors (Romiguer et al., 2016). Aggressive interactions between honeybee species have sometimes been reported in the literature (Koeniger & Vorwohl, 1979; Romiguer et al., 2016), but were not observed during this study.

Implications for conservation

A. cerana provides year-round pollination services at XTBG on the northern margins of the tropics, although its potential daily activity period is shortened in winter by low temperatures and in summer by heavy rain. Among the major flower visitors at XTBG, only the homeothermic sunbirds were active over a wider range of air temperatures and more tolerant of rain. *A. dorsata* dominates when present and could potentially provide a unique service to night-flowering species. Moreover, it is considerably larger than *A. cerana* and, although it shared 73 species of flowers with this species, it was the only *Apis* species recorded that visited 51 other species during the observation periods. On the whole, the smaller honeybees visited species that were also visited by *A. cerana*.

No *Apis* species has yet been assessed for the IUCN Red List, but all of the species studied at XTBG, except possibly *A. dorsata*, would certainly be rated Least Concern. *A. dorsata* is still widespread and locally abundant, but it has declined massively in many parts of Asia in recent decades as a result of overexploitation of the conspicuous colonies by honey-hunters (Corlett, 2011). This decline, in combination with the unique nocturnal pollination service reported at some sites (Corlett, 2011), suggests that this species is of potential conservation concern. This study, however, focused on the resilience of the pollination service provided for plants, rather than the conservation of individual bee species.

Mean annual air temperature at XTBG has increased by 0.64°C since 1959 (Zhao, Zhang, Song, Xu, & Xiao, 2012), and an additional increase of 1°C to 3°C, depending on the assumptions made, is projected for the remainder of this century (IPCC, 2013; Zomer et al., 2014). Although the negative relationship with temperature in the GLM results suggests that the activity of the two commonest *Apis* species will decline at XTBG during the current peak activity time, this is likely to be at least partly compensated for by earlier start times on cool mornings. The impacts of warmer temperatures on start times are less predictable, however, because the bees also avoid the dense morning fog and the impact of climate change on this is not covered by existing model projections (IPCC, 2013). Predicting climate change impacts on *A. dorsata* is also complicated by its migratory habits, which are not obviously explained by the local climatic conditions. Our results suggest that both of the smaller species are likely to benefit from higher temperatures, but these currently play a much less important role in pollination.

Overall, however, it seems that pollination services by honeybees at XTBG are likely to be resilient to the projected warming, since the ranges of all four species currently include areas that have higher temperatures than those predicted for the garden in the future (Hepburn & Radloff, 2011). Warming should also allow the tropical *Apis* species (i.e. all except *A. cerana*) to extend their distributions further north by several hundred kilometers, although this expansion may be delayed by the expected slower response of plant migration (Corlett & Westcott, 2013). The potential impact on *A. cerana* is less obvious, since the impact of warming on colony fitness is likely to be positive in winter and negative in summer. Moreover, this species already does well in areas well north of our study sites. Large changes in rainfall duration would also impact on foraging by honeybees and thus, potentially, colony viability, but rainfall projections for the region are currently model-dependent, with no consistent predictions (IPCC, 2013; Zomer et al., 2014).

Finally, it is important to remember that these results come from an artificially flower-rich habitat and should be extrapolated to natural habitats — such as seasonal rainforests in this region — with caution. There is no data available for comparison, but the greater seasonality in flowering in native forests that we have observed may lead to differences in the seasonal activity of honeybees. The results from this study demonstrate, however, that honeybees are potentially available as pollinators year-round on the northern margin of the Asian tropics, and suggest that they will probably continue to be available despite the changes in climate projected for the coming decades.

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