Department of Agriculture, Fisheries and Forestry

Asian honey bee Transition to Management Program

Ecology and behaviour of Asian honey bees (*Apis cerana*) in Cairns, Australia

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Summary

The 2007 Cairns' incursion of Asian honey bees (*Apis cerana* Java genotype) generated immense concern amongst Australian beekeepers, government and the community due to fears that *A. cerana* would (i) introduce exotic bee pests and diseases (especially the *Varroa destructor* mite) that could infest Australia's native bee fauna and/or the introduced European honey bee (*Apis mellifera*); (ii) outcompete and/or displace *A. mellifera* upon which the Australian apiary industry is centred; (iii) become an environmental pest with detrimental effects on native flora and fauna, including disrupting pollination and/or facilitating the spread of weeds; and (iv) become a nuisance around human settlements.

The Asian honey bee Transition to Management (AHB T2M) Program was implemented in July 2011 to identify and address gaps in current knowledge required to develop effective *A. cerana* control measures. These measures are intended to enable industry, the community and other stakeholders to safely and effectively mitigate any potential adverse economic, environmental and/or social amenity impacts of *A. cerana*. In this report, we investigate aspects of *A. cerana*'s ecology and behaviour in the Cairns region.

An array of field trials were undertaken in the Cairns region (Queensland, Australia) to establish this species' nesting and swarming characteristics, floral visitation, foraging times, drone flight times and competition with *A. mellifera* in the Cairns region. The key results of the AHB T2M Program's research into the behaviour and ecology of *A. cerana* in the Cairns region were:

- *A. cerana* nests and swarms in the Cairns region were smaller than those in their natural distribution throughout Asia.
- *A. cerana* nests stored approximately equivalent proportions of honey and pollen in Australia.
- *A. cerana* colony size did not vary throughout the year in the Cairns region.
- *A. cerana* were less abundant in the Cairns area when *A. mellifera* were present than when *A. mellifera* were absent.
- *A. cerana* visited a more narrow range of native and introduced floral species than *A. mellifera* in the Cairns region.
- *A. cerana* drones performed their mating flights between 1258 and 1528 hours, with a clear peak at 1413 hours. *A. mellifera* drones commenced drone flights earlier and finished later with a much less defined peak.

Our results suggest that competition between *A. cerana* and *A. mellifera* in the Cairns region has not reached the threshold at which populations of either species are constrained by the other. Together with evidence from the scientific literature, our results imply that *A. mellifera* would likely outcompete *A. cerana* in the Australian context, if competition for resources reaches this threshold.

AHB T2M research outcomes have identified two principal opportunities to develop novel measures to either control *A. cerana* or mitigate the potential adverse effects of exotic bee pests and diseases on *A. mellifera*. The first is the ability to use mating interference between *A. mellifera* and *A. cerana* to reduce the successful production of viable *A. cerana* offspring, thereby suppressing the expansion of *A. cerana* within Australia and reducing the likelihood of close interactions between *A. cerana* and *A. mellifera*. The second is the capacity to

exploit selective breeding of *A. mellifera* strains for increased resistance to *N. ceranae* fungus that is already present in Australia, and for *V. jacobsoni* and *V. destructor* mites that may accompany future introductions of *A. cerana* or *A. mellifera* to Australia.

Introduction

The Cairns region's third incursion of Asian honey bees (*Apis cerana*) was detected in May 2007 in Portsmith (4870, Queensland; Shield, 2007). Unlike the August 2000 and May 2004 Cairns' incursions and others previously found in Australia, this one resulted in the discovery of 7 live *A. cerana* colonies (Shield, 2007). Consequently, Biosecurity Queensland promptly launched an eradication and surveillance program, with the aim of containing the incursion within a 50 kilometre radius of Cairns (Department of Agriculture, Fisheries and Forestry - Australian Government, 2011). Since then, over 800 *A. cerana* Java nests and swarms have been detected and destroyed by Biosecurity Queensland (Koetz, 2013a) and the known infested area (KIA) has expanded to 490 685 hectares (October 2012; Koetz, 2013c).

The Cairns *A. cerana* incursion created considerable concern amongst stakeholders including state and federal Governments, the Australian apiary industry and community. Four main threats were identified, specifically:

i. the risk of *A. cerana* introducing exotic bee pests and diseases to Australia which could infest the nation's endemic bee fauna and the introduced European honey bee, *Apis mellifera* (Shield, 2007). Of particular concern was the potential for introducing the parasitic *Varroa* mite, *Varroa destructor,* a pest that transmits several diseases and whose feeding and reproductive strategies lead to weakened and malformed adult bees (Shield, 2007; Plant Health Australia, 2012),

ii. that *A. cerana* may compete with and/or displace *A. mellifera*, an introduced but economically-valuable species that is central to Australia's $90 million honey bee industry and the provision of paid pollination services estimated to be worth $1.7 billion per annum to agriculture and the Australian economy (Rural Industries Research and Development Corporation, 2012),

iii. the possibility of *A. cerana* becoming an environmental pest that may outcompete native fauna, disrupt pollination in native flora and/or facilitate the spread of weeds (Shield, 2007; Koetz, 2013a), and

iv. the opportunity for *A. cerana* to become a nuisance around human settlements (Koetz, 2013a).

In January 2011, the Australian Government's Australian Asian Honeybee National Management Group deemed that *A. cerana* were no longer eradicable in the Cairns region and would naturally become more widely established in Australia (Koetz, 2013a). Consequently, the Asian honey bee Eradication Program was replaced by the Asian honey bee Transition to Management Program (AHB T2M) in July 2011 (Department of Agriculture, Fisheries & Forestry - Australian Government 2011). The AHB T2M Program aims to address gaps in current knowledge that are required to inform the development of strategies intended to support the community and apiary industry to safely and effectively mitigate any negative economic, environmental and/or social amenity impacts of *A. cerana*.

Critical to our ability to develop effective control measures that exploit aspects of the species' biology is an accurate understanding of *A. cerana*'s ecology and behaviour in Australia. Published literature on the ecology and behaviour of *A. cerana* Java is scarce (Koetz, 2013a). Of the available information for *A. cerana*, most pertains to *A. cerana indica*, an endemic Indian subspecies that is distributed across a wide range of environmental conditions (Ruttner, 1988; Radloff *et al.*, 2010).

This study advances current scientific knowledge of this species' nesting and swarming characteristics, floral visitation, foraging times, drone flight times and competition with *A.*

mellifera in the Cairns region. In addition, this information provides a scientific basis for conclusions about the likely impact of *A. cerana* on the introduced European honey bee (*A. mellifera*) in the Cairns region (4870, Queensland; Koetz, 2013a).

This report systematically discusses two broad topics, namely the (i) ecology, and (ii) behaviour of *A. cerana* Java in the Cairns region. Within the ecology section, we address nest site selection, nest characteristics, nest seasonality, swarm site selection, swarm characteristics, swarm seasonality, and floral resource visitation. In the behaviour section, we focus on foraging times, drone flight times, and interspecific competition between *A. cerana* Java and *A. mellifera* in the Cairns region.

Methods

Ecology of *Apis cerana* in the Cairns region

Nesting

Nest site selection

Data collection

Nest height, habitat (land use) and the structure the nest was located in were recorded by Biosecurity Queensland staff for nests routinely collected from the KIA between 4 May 2007 and 11 February 2013. Staff visually estimated nest height (m). Habitats (land uses) where nests originated were documented by field staff as residential, rural, industrial, commercial, rainforest, cropping, bushland, gardens and semi-natural, mangrove and intertidal, grazing paddocks and grazing land with natural vegetation. Nest location descriptions were recorded in the field and later categorised into six general structure type subgroups for ease of analysis. These structure types included permanent buildings and their fixtures; residential backyard structures; miscellaneous objects and structures; land transport vehicles, parts or machinery; marine transport vehicles; and marine structures. Additionally, structure types were classified as either natural or non-natural.

Analyses

Nest habitat and location structure were summarised by calculating the percentage of nests for each observation category, and number of observations (*n*) using *Microsoft® Office Excel* (2003). Medians, number of observations (*n*), and minimum and maximum values for nest height were calculated in *Microsoft® Office Excel* (2003). Medians were reported as they provided a better measure of central tendency than the mean or mode for nest height since the data were skewed.

Given uneven sample sizes for habitat type, a parametric restricted maximum likelihood (REML) test was conducted in *GenStat® for Windows™ 14.0* (VSN International, 2011) to evaluate whether *A. cerana* nest heights varied according to habitat type. A transformation was used to normalise the residuals for nest height, specifically by adding 1 to each nest height value before applying a $\log_{10}$ transformation. This was done to avoid those nests located at ground height from being inappropriately discarded as missing values. The transformed values for predicted mean nest height were directly back-transformed for reporting herein. These back-transformed means approximate the median and are consequently a more reliable measure of central tendency than the predicted means. Predicted means represent the data inaccurately as high raw data values disproportionately inflate the overall mean relative to other raw data values.

Nest characteristics

Data collection

A. cerana nests detected via field operations or public reports in the KIA between 28 February 2012 and 13 November 2012 were chemically destroyed and, where possible, manually extracted from the nest cavity or comb attachment surface. Nests were destroyed using the methods described in the *Destruction Techniques – Nests* section of the *Asian honey bee manual: Techniques for the identification, detection and destruction of Apis cerana* (Foley, 2013). The contents of each nest, including comb and dead bees, were enclosed in a plastic bag and transported to Biosecurity Queensland's laboratory in Portsmith (Queensland, Australia), where they were frozen for a minimum of 24 hours before having a series of characteristics measured using either digital callipers or precision balance scales, as appropriate.

Nest characteristics included comb length, width and thickness (mm); comb mass (g); comb area (mm^2); number of cells containing honey; number of cells containing pollen; number of queen cells/cups, drone cells and worker cells; number of empty drone cells; number of empty worker cells; diameter of queen cells/cups, drone cells and worker cells (mm); mass of 100 bees ($mass_{100\ bees}$; g); and mass of all bees collected for the nest ($mass_{all\ bees}$; g). Comb area was measured by tracing around the outside edge of the comb on graph paper and counting the number of grid squares that were at least half filled.

Laboratory staff calculated the total number of bees as ($mass_{all\ bees}/mass_{100\ bees}$) x 100. The number of drones and queens were counted and recorded, while the number of workers was assumed to be equivalent to the estimated total number of bees.

Analyses

The data for nest and comb dimensions (comb length, width, thickness, mass, area), comb caste composition (number of queen cells/cups, drone cells and worker cells), cell sizes (diameter of queen cells/cups, drone cells and worker cells), resource storage (number of cells containing honey, number of cells containing pollen) and colony size (total number of bees per nest) were divided into: (i) newly-established nests and (ii) established nests. Established nests were considered to be those with a minimum of 3 combs in accordance with Koetz (2013a), while newly established nests were deemed to have 1 to 2 combs. Only the established nest results are reported here.

Nest characteristics were summarised by calculating means, standard deviations, numbers of observations (*n*), and minimum and maximum values using *Microsoft® Office Excel* (2003).

Nest seasonality

Data collection

A. cerana nests and swarms attended by Biosecurity Queensland staff between 1 August 2008 and 29 August 2012 were collected from their host location after being destroyed in accordance with the relevant *Nests* or *Swarms* section described in the *Destruction Techniques* procedures of the *Asian honey bee manual: Techniques for the identification, detection and destruction of Apis cerana* (Foley, 2013). Data was available for the periods 1 August 2008 to 28 August 2012 and 9 January 2012 to 29 August 2012 for nests and swarms respectively. Dead bees were collected in the field and returned to Biosecurity Queensland's laboratory (Portsmith, Queensland, Australia) for estimation of bee numbers. This data is referred to as *Swarm and nest counts* throughout this report.

Analyses

The date of nest collection and total number of bees in each nest were extracted from the data described for the *Nest characteristics* section above. A non-parametric Kruskal-Wallis test was then applied to determine if nest size (that is, total number of bees) varied according to month of the year.

For the nests and swarms described in *Nest seasonality: Data collection*, laboratory staff calculated the total number of bees as ($mass_{all\ bees}/mass_{100\ bees}$) x 100. The number of drones and queens were counted and recorded, while the number of workers was assumed to be equivalent to the estimated total number of bees.

As the AHB T2M Program spanned two years in total, insufficient data meant that it was not feasible to ascertain whether nest size varied by year, or to calculate relevant descriptive statistics (that is mean ± standard deviation (s), median, or minimum and maximum values for each year). This was because the data sets described for *Nest characteristics* and *Swarm and nest counts* both contained data from a single year only (2012), thus inhibiting comparisons of nest sizes across multiple years.

Swarming

Swarm site selection

Data collection

Swarm heights were visually estimated by Biosecurity Queensland field staff for swarms attended between 1 August 2008 and 8 November 2012. Swarm habitat data, specifically land uses, swarm location descriptions, swarm location structure types, and the naturalness of structures were treated in the same manner described for *Nest habitat*.

Analyses

Since sample sizes for habitat type were unbalanced (varying from $n = 1$ to $n = 122$), a non-parametric restricted maximum likelihood (REML) test was conducted in *GenStat® for Windows™ 14.0* (VSN International, 2011) to ascertain if *A. cerana* swarm height varied according to habitat type. A $\log_{10}$ transformation was used to normalise the residuals for swarm height, and a value of 1 added to each nest height value before applying the $\log_{10}$ transformation to prevent those swarms located on the ground being disregarded as missing values. The transformed values for mean swarm height were directly back-transformed for reporting here. These back-transformed means approximate the median and are accordingly a more stable measure of central tendency than the non back-transformed mean values for this data.

Swarm characteristics

Data collection

Swarms detected between 1 August 2008 and 28 August 2012 were allowed to settle on a surface to facilitate encapsulation of bees within a plastic bag. If a portion of the swarm could not be collected on the initial bagging attempt, the process was repeated until as many bees as possible had been gathered. The swarm was then chemically destroyed as per the *Destruction Techniques – Swarms* section of the *Asian honey bee manual: Techniques for the identification, detection and destruction of Apis cerana* (Foley, 2013). Dead bees were relocated to Biosecurity Queensland's laboratory (Portsmith, Queensland, Australia), frozen

for at least 24 hours, and the number of bees in each caste determined, as detailed for *Nest characteristics*.

Analyses

Microsoft® Office Excel (2003) was used to establish means, standard deviations, numbers of observations (*n*), and minimum and maximum values for the number of workers, drones, and queens and total swarm size.

Swarm seasonality

Data collection

The *Swarm and nest counts* data described in the preceding *Nest seasonality* section were used to investigate swarm seasonality.

Analyses

Using swarm size data collected between 1 August 2008 and 28 August 2012, non-parametric Kruskal-Wallis tests were performed in *GenStat® for Windows™ 14.0* (VSN International, 2011) to examine whether (i) *A. cerana* exhibit differences in swarm size by month, and (ii) whether *A. cerana* swarm size varies according to year. Where significant differences were detected, pairwise Mann-Whitney U tests were completed to establish if any homogeneous subsets existed. Median, minimum and maximum swarm sizes were ascertained using *GenStat® for Windows™ 14.0* (VSN International, 2011).

Floral resources

Data collection

The exact methods used to collect *A. cerana* and *A. mellifera* floral resource visitation data have been detailed in the *Field Trials* methods section of *Detection efficacy of Asian honey bees (Apis cerana) in Cairns, Australia* (Koetz, 2013b). In summary, standardised transect walks and timed floral observations were concurrently undertaken between September 2012 and March 2013 at a total of eight study sites in Kuranda, a rainforest location, Cairns city and Gordonvale. During standardised transect walks, two staff walked slowly along the perimeter of a 500 m x 500 m transect study site, one person on each side of the road, scanning for *A. cerana* and *A. mellifera* on any flowering plant. For timed floral observations, staff walked the transect until they came across a plant listed in the *Field guide to plant hosts of Apis cerana including declared plants pests within the AHB restricted area as potential hosts* (Durkan, 2010). Once such a plant was located, the observer searched the flowers of the plant for 10 minutes. For both surveillance techniques, the number of *A. cerana* and *A. mellifera* encountered on a single flowering plant, plant species and GPS coordinates were recorded, with the observation period start time also being documented during the timed floral observations.

Analyses

Microsoft® Office Excel (2003) pivot tables were employed to summarise a variety of data obtained during standardised transect walks and timed floral observation surveillance, including the (i) floral host species upon which *A. cerana* and/or *A. mellifera* were observed, (ii) number of each of these bee species located on each floral species, (iii) number of plant species visited by either *A. cerana* or *A. mellifera* at each of the eight study sites, (iv) number of each of these bee species at each study site, and (v) number of floral host species visited by at least *A. cerana* for each overall site. Percentages of all observations and numbers of

observations (n) were calculated in *Microsoft® Office Excel* (2003) for the number of floral host species for *A. cerana* and *A. mellifera*, and the number of *A. cerana* and *A. mellifera* detected at each of the eight individual sites and four overall sites.

Non-parametric Mann-Whitney U tests were used to ascertain whether there was a significant difference in the number of *A. cerana* and *A. mellifera* observed at (i) the two Cairns city sites, (ii) the two Gordonvale sites, (iii) the two Kuranda sites, or (iv) the two rainforest sites. A non-parametric Kruskal-Wallis analysis was undertaken to determine if the bee-visited floral diversity of the four locations differed significantly as the samples were not normally distributed and had unequal variances. Data gained through standardised transect walks and timed floral observation surveillance were pooled for these analyses.

Non-parametric Spearman's rank correlations were employed to establish whether a relationship existed between the number of floral host species surveyed across all four overall locations and (i) the number of *A. cerana*, or (ii) the number of *A. mellifera.* A linear regression was undertaken to establish whether the number of vegetation species bees were observed on (i.e. bee-visited floral diversity) could predict the number of *A. mellifera* present, but not to characterise a relationship between bee-visited floral diversity and *A. cerana* presence since the latter variables were not correlated. Pooled standardised transect walk and timed floral observation surveillance data underpinned this analysis.

Behaviour of *Apis cerana* in the Cairns region

Foraging times

Data collection

Between 10 September 2012 and 18 January 2013, Biosecurity Queensland staff monitored *A. cerana* workers returning to hive and nest entrances in the morning (commencing between 0900 and 0920 hours), at noon (commencing any time between 1200 and 1230 hours) and in the afternoon (commencing any time between 1400 and 1650 hours). The exact time that observations commenced varied due to operational constraints. Each of these time categories was divided into three 10-minute intervals, and the number of workers returning with (i) pollen or (ii) nectar recorded for each interval. Staff sat close to the nest or hive of interest, observing and counting workers by naked eye. Temperature (^{o}C), relative humidity (%) and light (lux) were measured and noted at the commencement of the first 10-minute interval for each overall time category. Nests were observed for as many weeks as possible before the colony absconded. Replicates (that is, observation dates) varied from 6 to 8 for nests (n = 2) and from 1 to 3 for hives (n = 5).

Analyses

Peak foraging times

Non-parametric Kruskal-Wallis tests were applied to the nest observation data to determine whether the number of *A. cerana* returning to the nest (i) with pollen or (ii) nectar differed significantly between the morning, noon and afternoon time categories. Mann-Whitney U tests facilitated analysis of whether the number of *A. cerana* presenting at the nest with pollen differed between the morning and noon, morning and afternoon, and noon and afternoon time categories respectively. From this, peak pollen foraging times could be identified.

A Kruskal-Wallis analysis was also undertaken to determine if the tally of *A. cerana* attending the nest with nectar varied between the morning, noon and afternoon time categories.

Foraging seasonality

Given unbalanced data for the number of *A. cerana* returning to the nest with pollen, a non-parametric restricted maximum likelihood (REML) test was conducted in *GenStat® for Windows™ 14.0* (VSN International, 2011) to evaluate whether the number of *A. cerana* returning to the nest with pollen varied according to month. A transformation was used to normalise the residuals for the number of *A. cerana* returning to the nest with pollen. Specifically, a value of 0.5 was added to the number of *A. cerana* returning to nest with pollen before applying a $\log_{10}$ transformation. The transformed values for predicted mean number of *A. cerana* returning to the nest with pollen were directly back-transformed for reporting here. These back-transformed means approximate the median and are accordingly a more stable measure of central tendency than the non back-transformed mean values for this data.

The same process and analysis was followed to ascertain whether the number of *A. cerana* attending the nest with nectar varied by month.

Mating and reproduction: Drone flight times of *Apis* species in the Cairns region

Drone flight times were determined for two colonies of *A. cerana* and two colonies of *A. mellifera* by observing the times at which drones emerge and leave the colony between December 2012 and February 2013. The methods closely followed those presented in Jordan *et al*. (Jordan *et al*., 2007).

Data collection

Drone flight times were determined by simultaneously video-taping the nest entrances of two colonies each of *A. cerana* and *A. mellifera*. In a preliminary study, nest entrances of one *A. cerana* and one *A. mellifera* colony were filmed simultaneously from sunrise until sunset over two days, to determine approximate drone flight times for both species. The target colonies (two *A. cerana* colonies and two *A. mellifera* colonies) were then filmed simultaneously from 120 minutes prior to, and following, the first and last drone emerging, respectively, as established in the preliminary study. Filming was repeated such that each colony was filmed for a total of three days in January and February 2013. Videos were then downloaded onto a computer.

Analyses

The number of drones leaving each colony was counted on-screen in 15-minute intervals. Numbers of drones leaving during each 15-minute interval were then averaged across all colonies and graphed. The difference in the frequency distributions of drones leaving across the 15-minute time intervals was determined using a non-parametric Kolmogorov-Smirnov test using *GenStat® for Windows™ 14.0* (VSN International, 2011).

Drones were also given a score according to the time in which they departed equal to the number of minutes after 1028hrs (solar time). For example, a bee leaving at 1128hrs was given a score of 60 minutes. Solar time was calculated by subtracting 17 minutes from the local time (4 minutes for each 1˚ of longitude west of the centre of the time zone; Otis *et al*., 2000). Differences between *A. cerana* and *A. mellifera* arrival scores were tested using a non-parametric Mann-Whitney U test due to non-normality of data.

Interspecific competition between *Apis cerana* and *Apis mellifera* in the Cairns region

Data collection

Data collected via standardised transect walks and timed floral observations (as described in the previous *Floral resources – Data collection* methods section were pooled to facilitate analysis of whether there was any interspecific competition between *A. cerana* and *A. mellifera*.

Analyses

A Spearman's rank correlation was applied to determine if a relationship existed between the number of *A. cerana* present when *A. mellifera* were present and the number of *A. mellifera* present. The nature of the predictive relationship between the number of *A. cerana* present when *A. mellifera* are present and the number of *A. mellifera* present was defined using a linear regression.

Results

Ecology of *Apis cerana* in the Cairns region

Nesting

Nest site selection

Nest habitat

Land Use: *Apis cerana* nests attended between 4 May 2007 and 11 February 2013 were located in a broad spectrum of habitats including residential (n = 276), and rural areas (n = 79), industrial land (n = 45), commercial (n = 40), rainforest (n = 35), cropping (n = 15), bushland (n = 13), gardens and semi-natural land uses (n = 10), mangrove and intertidal land (n = 8), grazing paddocks (n = 4) and grazing land with natural vegetation (n = 3). Land use was not recorded for an additional 11 nests.

Structure Type: 353 of the 547 nests (64.53%) were established within non-natural structures. Of these, 39.85% (n = 218) inhabited permanent buildings and their fixtures (residential, rural and commercial buildings, sheds, roller doors, guttering, and stairwell posts); 11.33% (n = 62) were on residential backyard structures (fences, barbecues, barrels, bird boxes, garbage bins, compost bins, letter boxes, fake rocks, water fountains, retainer walls, spa baths, garden pots, statues and water tanks); 7.13% (n = 39) were located in or on miscellaneous objects and structures (wooden pallets, besser blocks, cable reels, caravan roofs, power poles, horse troughs, rolls of veneer, rolls of carpet, washing machines, traffic lights, eskies, electricity boxes and metal pipes); 4.21% (n = 23) were on land transport vehicles, parts or machinery (cement mixers, trucks, railway containers, cranes, tyres, farm machinery, incinerator, engines, irrigation drum and trailer); 1.83% (n = 10) were on marine transport vehicles (boats, shipping containers, boat masts, and shipping pallets); and 0.18% (n = 1) were on marine structures (jetties).

Natural structures formed the foundation for the residual 194 nests (35.47%), specifically trees, tree stumps, pot plants, logs, and fallen palm fronds.

Nest height

Overall average nest heights differed significantly amongst the twelve habitat types (REML: $F_{11, 523} = 5.70$, $p < 0.001$). Median nest height was 3.00 m ($n = 554$). Across all habitat types, nests were found at heights ranging from ground height (0 m, $n = 37$) to 40 m ($n = 1$). Back-transformed mean nest heights for the ten habitat types with observations varied from 1.83 m in industrial land uses ($n = 44$) to 6.35 m in gardens and semi-natural areas ($n = 10$; Table 1). A single 200 m nest height recorded from residential land was discarded from this analysis as it was deemed to be unrealistic.

Table 1: Back-transformed mean *A. cerana* nest heights for the 10 habitat types with observations.

	Average (m)	***n***
Industrial	1.83	44
Residential	2.33	270
Commercial	2.98	40
Bushland	3.05	13
Parkland	3.08	14
Rural	3.23	79
Cropping	3.90	15
Rainforest	5.35	35
Grazing (paddock)	5.56	4
Gardens and semi-natural	6.35	10

Nest characteristics

Nest and comb dimensions

Of the *A. cerana* nests collected and analysed by Biosecurity Queensland between 28 February 2012 to 13 November 2012, the number of combs ranged from 1 to 11, with a mean of 3.76 combs per nest ($n = 37$; SD = 2.53). Amongst these nests, 13 (35.14%) were newly established (1-2 combs) and 24 (64.86%) were established (3 or more combs). Only established nest results are presented here. Overall nest and newly established nest results are included in Appendix 1.

On average *A. cerana* combs within established nests were longer than they were wide, and wider than they were thick (Table 2). Large variation was observed for all comb dimensions measured (Table 2).

Table 2: Average comb dimensions for established *A. cerana* nests collected in the Cairns region between 28 February 2012 and 13 November 2012.

	Average	SD	Min-Max	*n*
Comb length (mm)	101.37	50.01	11.38-244.31	108
Comb width (mm)	69.72	31.53	11.20-150.27	108
Comb thickness (mm)	18.52	3.16	8.02-32.28	107
Comb mass (g)	40.09	41.76	0.75-274.00	115
Comb area (mm^2)	13 455.53	10 967.68	1 650.00-40 550.00	108

Comb caste composition

Queen cells or cups Six (19.35%) of the 31 nests examined had queen cells or cups. Of these nests with queen cells or cups, only one nest (16.67%) had queen cells or cups on multiple combs. This nest was an established nest. Established nests had a mean 0.14 queen cells or cups per comb (n =115, SD = 0.71), ranging from no cells for this caste (n = 88) to 6 queen cells or cups per comb (n = 1).

Drone cells The average number of drone cells per side of comb was 19.73 (n = 220, SD = 46.17), varying from a minimum of no drone cells per side of comb (n = 88) to 288 drone cells per side of comb (n = 1).

Worker cells Established *A. cerana* nests had 179.53 worker cells on average (n = 220, SD = 210.23), with a minimum of no worker cells (n = 27) to a maximum of 878 worker cells per comb face (n = 1).

Empty cells The number of empty cells per whole *A. cerana* established nest ranged from 600 (n = 1) to 9934 (n = 1), with 24.4% of cells being void of contents. Data was available for 13 established nests for this criterion. These results must be treated with caution due to the large amount of variability present.

Cell sizes

Queen cells or cups The average queen cell or cup diameter was 5.51 mm (n = 25, SD = 1.80 mm), ranging between 3.35 mm and 8.79 mm.

Drone cells Drone cell diameters averaged 4.61 mm (n = 80, SD = 0.40 mm) for established nests, with minimum cell diameters of 3.60 mm and a maximum cell diameters of 5.64 mm.

Worker cells Ranging from 3.03 mm to 5.47 mm, average worker cell diameters were 3.97 mm (n = 209, SD = 0.44 mm) for nests with 3 or more combs.

Resource storage

Honey For each side of comb, established *A. cerana* nests had an average of 11.01 honey cells (n = 215, SD = 24.35), with 54% of these combs having no honey (n = 116). A maximum of 136 cells contained honey on a single side of comb in an established nest.

Pollen On average, 9.82 pollen cells were present in established *A. cerana* nests (n = 214, SD = 19.80), with a maximum of 135 pollen cells per side. 35% of cells had no pollen present in established nests (n = 76).

Colony size

Total nest/colony size The average established *A. cerana* colony comprised 0.41 queens (0.02%), 12.16 drones (0.67%) and 1 812.63 workers (99.31%), giving a mean colony size of 1 825.20 *A. cerana* per nest.

Queens On average, each established *A. cerana* nest had 0.41 queens (n = 32, SD = 0.50), ranging between nil (n = 19) and one queen (n = 13) per nest. Where nests were recorded as having no queen, it is likely that the queen was not captured.

Drones Established *A. cerana* nests had a mean of 12.16 drones (n = 32, SD = 19.89), with the lowest drone count being nil (n = 16) and the highest count being 67 drones (n = 1) per nest.

Workers The average number of workers per established *A. cerana* nest was 1 812.63 (n = 34, SD = 2 088.18), with the smallest worker total being 8 (n = 1) and the largest total being 9 765 (n = 1).

Nest seasonality

There was insufficient data to determine whether *A. cerana* nest size varied by year. *Apis cerana* nest size did not differ significantly by month (Kruskal-Wallis: $\chi^2(8) = 9.317$, n = 43, p = 0.316) for 43 nests collected between 28 February 2012 and 13 November 2012 (Figure 1). There were no cases recorded for nest size for January or March 2012 (Figure 1).

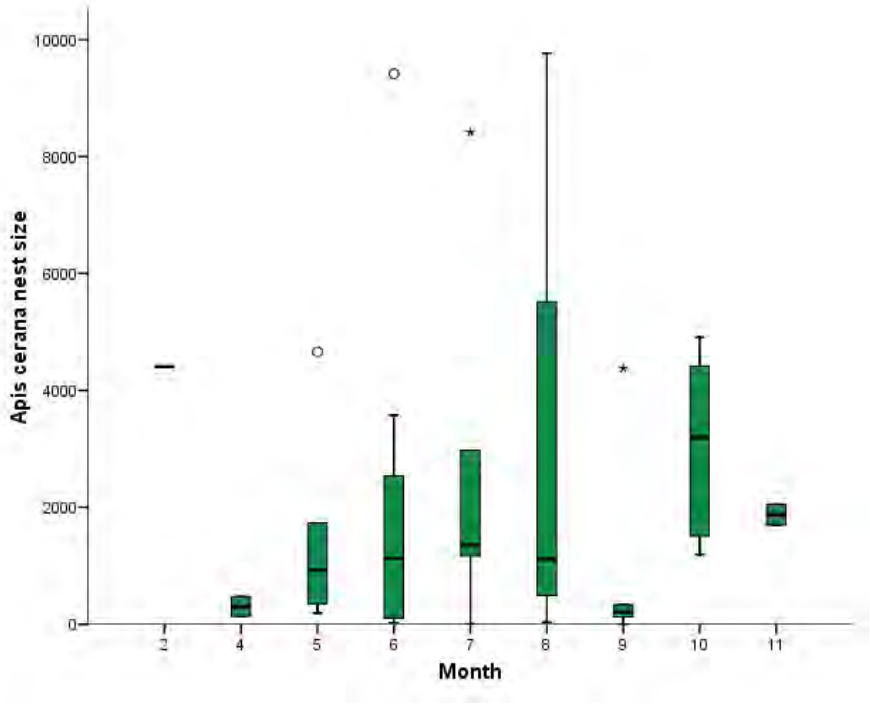

Figure 1 Nest size variation by month for *A. cerana* nests collected in the Cairns region between February 2012 and November 2012. *Apis cerana* nest size did not vary significantly by month (Kruskal-Wallis: $\chi^2(8) = 9.317$, n = 43, p = 0.316). There were no nest sizes documented for January (1) or March (3).

Swarming

Swarm site selection

Land Use: *Apis cerana* swarms located between 1 August 2008 and 8 November 2012 occupied a wide variety of habitats in the Cairns region (Table 3). Although the majority of swarms were situated in residential areas, a substantial proportion were discovered in commercial, industrial or rural locations (Table 3). A minor proportion of swarms were located in cropping areas, parkland, gardens and semi-natural land, rainforest, bushland and grazing paddocks (Table 3).

Table 3: Land uses in which *A. cerana* swarms were located between 1 August 2008 and 8 November 2012.

Land Use	%	*n*
Residential	51.19	129
Commercial	16.67	42
Industrial	13.49	34
Rural	10.71	27
Cropping	4.37	11
Parkland	1.59	4
Gardens and semi-natural	0.79	2
Rainforest	0.04	1
Bushland	0.04	1
Grazing paddocks	0.04	1

Structure Type: The majority of swarms occupied non-natural structures (55.82%, $n = 139$), including permanent buildings and their fixtures (residential and commercial buildings, sheds, guttering, downpipes, whirly bird on roof, internal light fixtures, electrical boxes, stairwells and spa baths); residential backyard structures (fences, gates, letterboxes, garbage bins, compost bins, clothes lines, barbecues, bird feeders, pool pumps and tents); miscellaneous objects and structures (generators, scaffolding, ladders, rolls of carpet, sign posts, umbrellas, power poles, commercial hive and the ground); land transport vehicles, parts or machinery (cars, machinery, railway cargo containers, car and tractor tyres and sugar cane bins); marine transport vehicles (boats, shipping containers and yacht masts); and marine structures (wharves, boat ramps and mooring piles; Table 4). The remaining swarms (44.18%, $n = 110$) were located on natural structures, namely vegetation (trees, shrubs, fallen palm fronds and sugar cane paddocks; Table 4).

Table 4: Structures in which *A. cerana* swarms were located in the Cairns region between 1 August 2008 and 8 November 2012.

Naturalness	Structure	%	*n*
Non-natural	Permanent buildings and fixtures	20.48	51
	Residential backyard structures	12.05	30
	Miscellaneous objects and structures	11.24	28
	Land transport vehicles, parts or machinery	8.84	22
	Marine transport vehicles	2.01	5
	Marine structures	1.20	3
Natural	Vegetation	44.18	110

Swarm height

Apis cerana swarms attended to by Biosecurity Queensland between 1 August 2008 and 8 November 2012 were found at a back-transformed predicted mean height of 0.00 m for bushland ($n = 1$), 0.49 m for commercial ($n = 42$), 0.46 m for cropping ($n = 11$), 0.45 m for gardens and semi-natural ($n = 2$), 0.60 m for grazing (paddock; $n = 1$), 0.49 m for industrial ($n = 34$), 0.65 m for parkland ($n = 4$), 1.32 m for rainforest ($n = 1$), 0.44 m for residential ($n = 130$) and 0.52 m for rural habitats ($n = 27$). Overall, mean swarm height was 2.56 m ($n = 253$, SD = 3.00m), with the lowest swarms detected at ground level (0 m, $n = 26$) and the highest swarm at 25 m ($n = 1$). With the exception of the rainforest, all habitats had a median swarm height between 0 m and 3 m (Figure 2).

Swarm heights differed significantly amongst the twelve habitat types (REML: $F_{9,234} = 2.42$, $p = 0.012$) and could be grouped into three homogeneous subsets (Figure 2). However, no biologically meaningful pattern could be found.

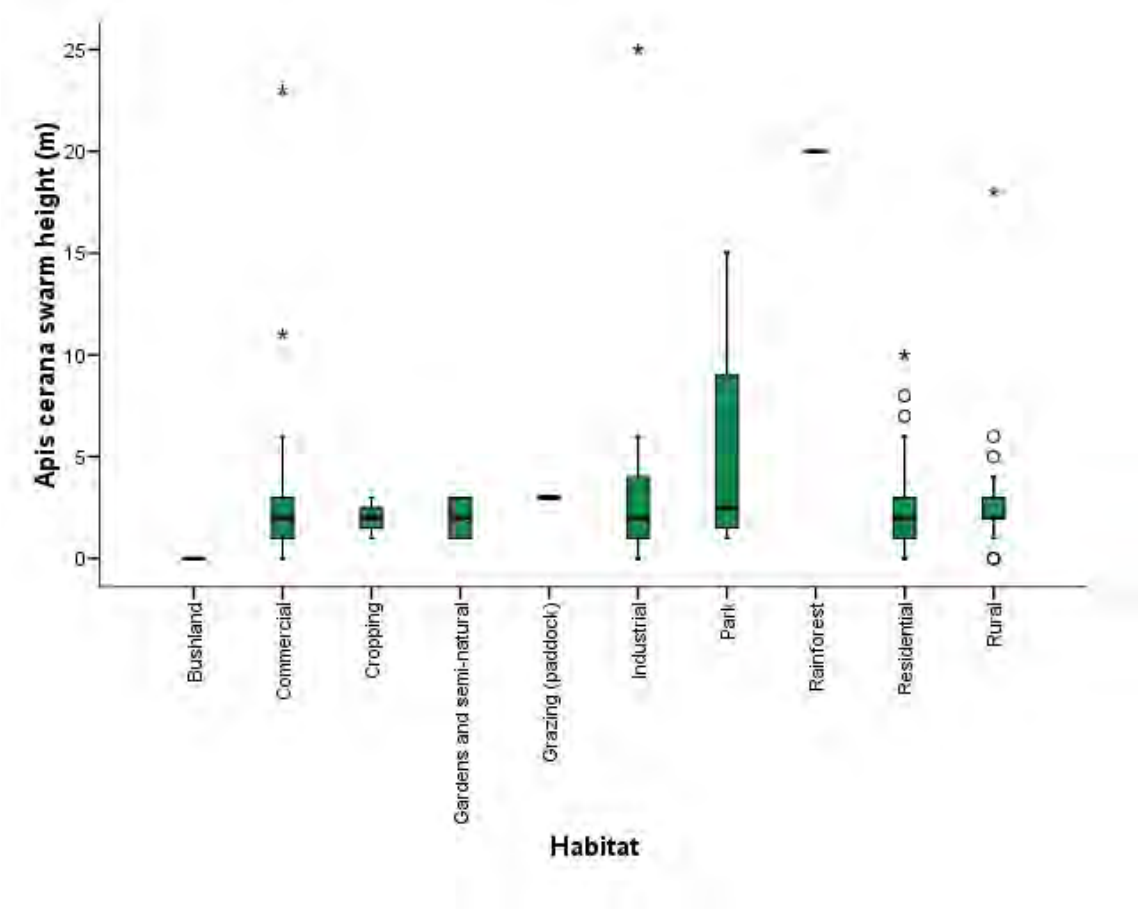

Figure 2 *Apis cerana* swarm height (m) varied significantly by habitat type (REML: $F_{9,234} = 2.42$, $p = 0.012$). Habitats sharing a common label (that is, A or B) did not have significantly different swarm heights from each other. There were no swarms recorded in grazing (natural vegetation) or mangrove/intertidal habitats.

The greatest variation in swarm height was observed in parkland, with heights ranging from 1 m to 15 m ($n = 4$). Both bushland and rainforest habitats had a single swarm height observation each, specifically at ground height (0 m) and 20 m respectively (Figure 2). Outliers for commercial (11 m and 23 m), industrial (25 m), residential (10 m) and rural habitats (18 m) were much higher than the mean swarm heights described above and more similar to the only rainforest observation.

Swarm characteristics

Swarm size

For 141 *A. cerana* swarms collected between 1 August 2008 and 28 August 2012, the median swarm size was 1750 bees ($n = 2$), with a minimum swarm size of 45 bees ($n = 1$) and a maximum swarm size of 12 225 bees ($n = 1$). Among these nests, median worker numbers were 1 740 per nest (range = 41 to 12 224), median drone numbers were 24.5 per nest (range = 0 to 220), and median queen number was 1 per nest (range = 0 to 1).

Swarm seasonality

Apis cerana swarm size varied temporally throughout the year (Kruskal-Wallis: $\chi^2 = 208.7$, $n = 141$, $p < 0.001$) and between years (Kruskal-Wallis: $\chi^2 = 5.615$, $n = 141$, $p = 0.018$). Two homogeneous subsets were present for months, with subset A consisting of all months except July, while subset B encompassed July only (Figure 3). The median swarm size in July (median = 3 036) was higher than all of the months in subset A, except February which showed large variability (Figure 3). There were two homogeneous subsets for years, specifically subset A which comprised 2008, 2009, 2010 and 2012 and subset B which included 2011 only (Figure 4). With the exception of 2009, *A. cerana* median swarm size was lowest in 2011 (median = 1 550) relative to all other years examined. Swarm size was more variable in 2009 ($n = 14$), 2010 ($n = 37$) and 2012 ($n = 28$) than 2011 ($n = 57$), but not in 2008 ($n = 2$).

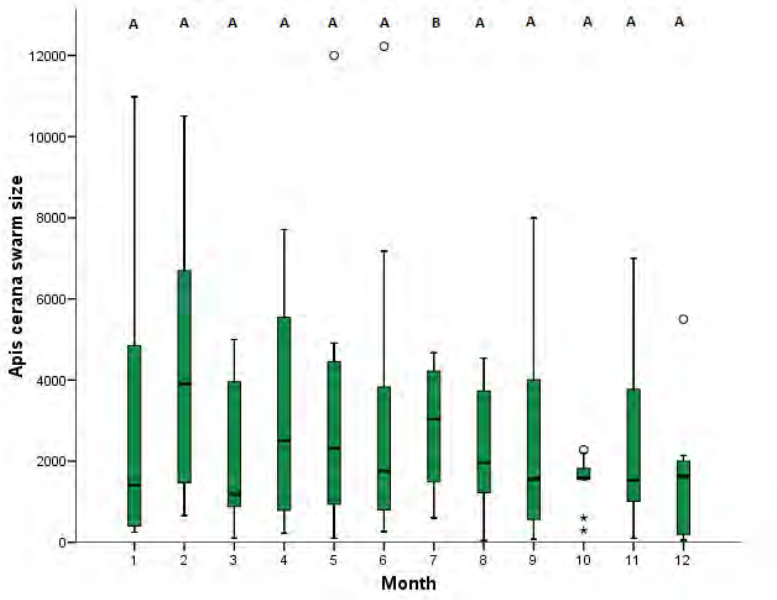

Figure 3 *Apis cerana* swarm size by month for swarms collected between 1 August 2008 and 28 August 2012. *Apis cerana* swarm size did throughout the year (Kruskal-Wallis: $\chi^2 = 208.7$, $n = 141$, $p < 0.001$). Months sharing a common label (that is, A or B) did not have significantly different swarm sizes to each other. Specifically, July swarms differed significantly in size to those of all other months.

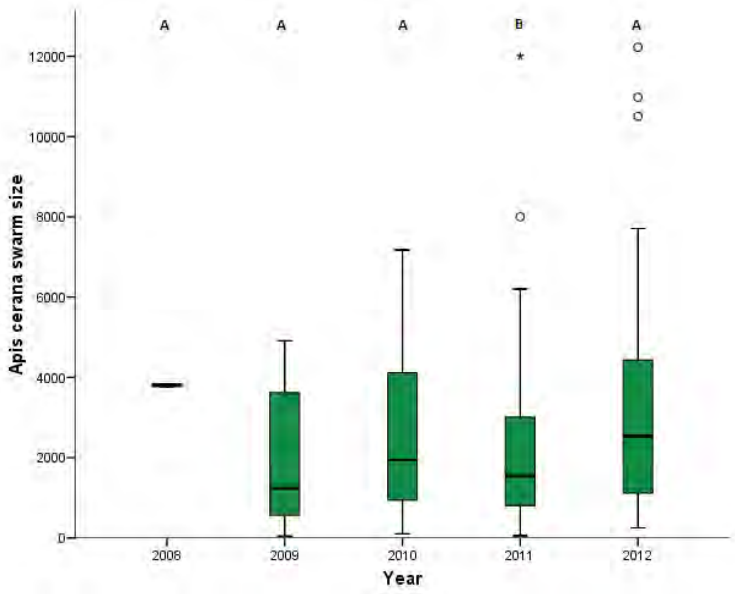

Figure 4 *Apis cerana* swarm size by year for swarms collected between 1 August 2008 and 28 August 2012. *Apis cerana* swarm size did vary significantly between 2008 and 2012 (Kruskal-Wallis: χ^2 =5.615, *n* = 141, p = 0.018), with swarm size in 2011 being significantly different to all other years. Years sharing a common label (that is, A or B) did not have significantly different swarm sizes.

Floral resources

Apis cerana were detected on 27 floral host species (36.49%) out of a total of 74 species surveyed as part of the floral preferences field trials (Table 5). *Apis mellifera* were found on 73 (98.65%) of the 74 floral species. The only species on which *A. cerana* were detected where *A. mellifera* were absent was Koster's Curse (*Clidemia hirta*; Table 5).

Table 5: Host plants that *A. cerana* were detected on during timed floral observations and transect walks, with the total number of *A. cerana* and *A. mellifera* observed for each of these floral species.

Common name	Scientific name	*Number of A. cerana observed*	*Number of A. mellifera observed*
Coral vine	*Antigonon leptopus*	32	69
Mad Hatter	*Cuphea* sp.	27	10
Golden cane	*Dypsis lutescens*	21	101
Bottlebrush	*Callistemon* sp.	16	80
Tridax daisy	*Tridax* sp.	8	74
Geisha girl	*Duranta erecta*	7	133
Weeping tea tree	*Melaleuca fluviatilis*	7	85
Sensitive weed	*Mimosa pudica*	7	22
Coconut palm	*Cocos nucifera*	5	13
Ixora	*Ixora* sp.	4	2
Morning star	*Turnera subulata*	3	24
Singapore daisy	*Sphagneticola trilobata*	2	390
Calliandra	*Calliandra* sp.	2	7
Cassia	*Cassia* sp.	2	7
Croton	*Codiaeum variegatum*	2	1
Tea tree	*Melaleuca* sp.	1	29
Lilly pilly	*Syzgium* sp.	1	15
Fan palm	*Licuala ramsayi*	1	13
Cordyline	*Cordyline* sp.	1	11
Lantana	*Lantana camara*	1	9
Poinciana	*Delonix regia*	1	7
Queen palm	*Syagrus romanzoffiana*	1	3
Pony tail palm	*Nolina recurvata*	1	2
Eucalypt	*Eucalyptus* sp.	1	1
Evodia	*Evodia* sp.	1	1
Umbrella tree	*Schefflera actinophylla*	1	1
Koster's curse	*Clidemia hirta*	1	-

A list of the 47 host plants that only *A. mellifera* were present on during timed floral observations and transect walks in the Cairns region can be found in Appendix 2.

Floral observation along transects revealed 16 flowering plant species that had not been previously identified as host plants for *A. cerana* in the *Field guide to plant hosts of A. cerana including declared plant pests within the AHB restricted area as potential hosts* (Durkan, 2010). Specifically, these were Calliandra (*Calliandra* sp.), Cassia (*Cassia* sp. if the observed species was not *Cassia fistula*), Koster's curse (*Clidemia hirta*), Coconut palm (*Cocos nucifera*), Croton (*Codiaeum variegatum*), Cordyline (*Cordyline* sp.), Poinciana (*Delonix regia*), Eucalypt (*Eucalyptus* sp.), Evodia (*Evodia* sp.), Ixora (*Ixora* sp.), Fan palm (*Licuala ramsayi*), Weeping tea tree (*Melaleuca fluviatilis*), Tea tree (*Melaleuca* sp.), Pony tail palm (*Nolina recurvata*), Umbrella tree (*Schefflera actinophylla*) and Queen palm (*Syagrus romanzoffiana*).

Apis cerana were observed within all of the locations surveyed, including urban (Cairns city), urban/rural (Gordonvale), rural/rainforest (Kuranda) and rainforest areas (Table 6). *A. cerana* counts were highest at Cairns city (n = 132, 62.86%), followed by Gordonvale (n = 71, 33.81%), Kuranda (n = 6, 2.86%) and Rainforest (n = 1, 0.48%; Table 6).

Table 6: Number of *A. cerana* and *A. mellifera* detected via timed floral observations and transect walks

Site	*A. cerana*	*A. mellifera*
Cairns city	132	111
Gordonvale	71	526
Kuranda	6	572
Rainforest	1	268
TOTAL	**210**	**1477**

Apis mellifera were detected at all of the locations surveyed (Table 6), with highest to lowest counts found at Kuranda (n = 572, 38.73%), followed by Gordonvale (n = 526, 35.61%), rainforest habitats (n = 268, 18.14%) and Cairns city sites (n = 111, 7.52%; Table 6).

Numbers of *A. cerana* were lower than numbers of *A. mellifera* at all sites except the Cairns city sites where there were 1.19 times more *A. cerana* than *A. mellifera.* However, this difference in the number of *A. cerana* and *A. mellifera* observed at the two Cairns city sites was not significant (Mann-Whitney: U = 5 795.00, Z = -1.575, n = 230, p = 0.115; Table 6). This habitat type had the highest *A. cerana* density out of all 4 habitats, yet the lowest *A. mellifera* density out the four alternatives.

In the three habitat types where *A. mellifera* out-represented *A. cerana*, the magnitude of the differences in relative numbers were far greater than in the Cairns city sites where *A. cerana* outnumbered *A. mellifera*. There were 7.41 times more *A. mellifera* than *A. cerana* at Gordonvale, 95.33 times more at Kuranda and 268 times more at the rainforest sites (Table 6). The number of *A. mellifera* at the two Gordonvale sites was significantly greater than the number of *A. cerana* (Mann-Whitney: U = 13 819.00, Z = -2.255, n = 569, p = 0.024). By contrast, the number of *A. cerana* and *A. mellifera* did not diverge significantly at the Kuranda sites (Mann-Whitney: U = 1 119.50, Z = -1.325, n = 546, p = 0.185) or rainforest sites (Mann-Whitney: U = 81.00, Z = -0.719, n = 268, p = 0.612).

Overall, bee-visited floral diversity was greatest at Kuranda, followed by Gordonvale, Cairns city and rainforest sites (Table 7). The number of plant species visited by either *A. cerana* or

A. mellifera (i.e. bee-visited floral diversity) was greatest at Kuranda (n = 49), then Gordonvale (n = 48), Cairns city (n = 26) and the rainforest (n = 15; Table 7). There was no significant difference in the bee-visited floral diversity at each of these four locations (Kruskal-Wallis: χ^2 = 1.858, d.f. = 3, p = 0.602).

Table 7: Number of host plants that either *A. cerana* and *A. mellifera* were detected on during timed floral observations and transect walks

Site	Bee-visited floral diversity		
	Either *A. cerana* or *A. mellifera*	*A. cerana*	*A. mellifera*
Kuranda	49	4	48
Gordonvale	48	17	46
Cairns city	26	22	19
Rainforest	15	1	14

There was no relationship between the number of *A. cerana* detected and the number of vegetation species surveyed across all sites (Spearman's rank: $r_s(8) = 0.315$, p = 0.453; Figure 5). Visual inspection of Figure 5 indicates that *A. cerana* occur in areas with lower floral diversity than *A. mellifera*.

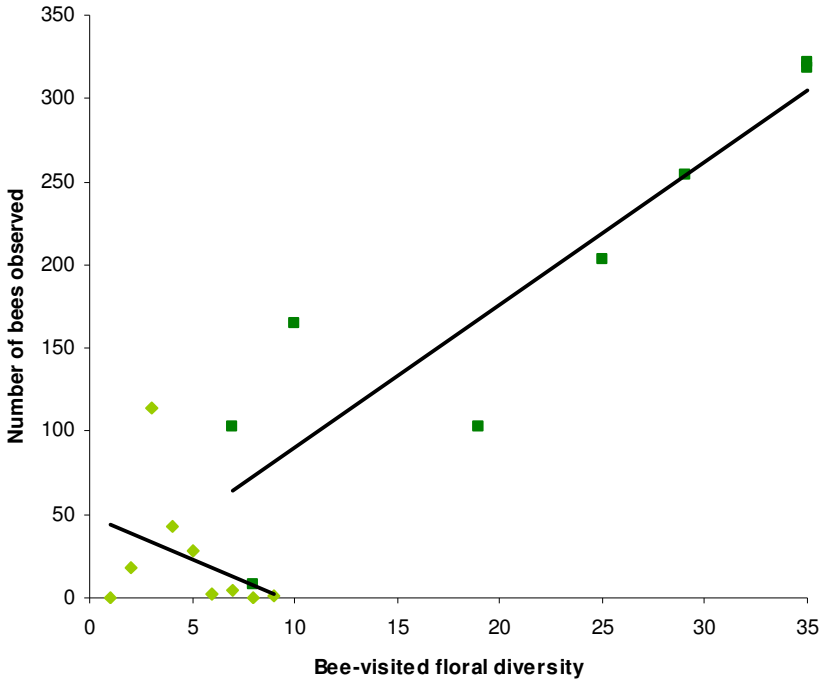

Figure 5 The relationships between bee-visited floral diversity and the number of *A. cerana* (◆) or *A. mellifera* (■) across all sites. There was no significant relationship between the number of vegetation species that bees were observed on and the number of *A. cerana* detected (Spearman's rank: $r_s(8) = 0.315$, p = 0.453) across all sites. The number of *A. mellifera* increased as the bee-visited floral diversity increased across all sites in accordance with the equation: *Number of A. mellifera = 4.7 + (8.56 * Number of vegetation species bees observed on)* (Linear regression: adjusted $r^2_{1,6} = 78.2$, p = 0.002).

A highly significant and positive relationship was established between the number of *A. mellifera* and the bee-visited floral diversity across all sites (Spearman's rank: $r_s(8) = 0.917$, p = 0.001; Figure 5). This relationship can be predicted by the equation *Number of A. mellifera = 4.7 + (8.56 * Number of vegetation species bees observed on)* (Linear regression: adjusted $r^2_{1,6} = 78.2$, p = 0.002).

Behaviour of *Apis cerana* in the Cairns region

Foraging times

Peak foraging times

The number of *A. cerana* returning to the nest with pollen differed significantly between the morning (0900 to 0920 hours; time categories 1 to 3), noon (1200 to 1230 hours; time categories 4 to 6) and afternoon (1400 to 1650 hours; time categories 7 to 9; Kruskal-Wallis: $\chi^2 = 49.85$, d.f. = 2, $p < 0.001$). The number of bees presenting at the nest with pollen in the morning was significantly higher than at noon (Mann-Whitney: $U_{63,63} = 935.5$, $p < 0.001$) and the afternoon (Mann-Whitney: $U_{63,63} = 634.0$, $p < 0.001$). Noon and afternoon did not differ significantly in the number of *A. cerana* returning to the nest with pollen (Mann-Whitney: $U_{63,63} = 1\,675.5$, p = 0.132). Accordingly, there were two homogenous subsets, with the morning solely comprising Subset A, and noon and afternoon belonging to Subset B (Figure 6). Specifically, *A. cerana* in the Cairns region have a peak pollen foraging time in the morning (Subset A; Figure 6).

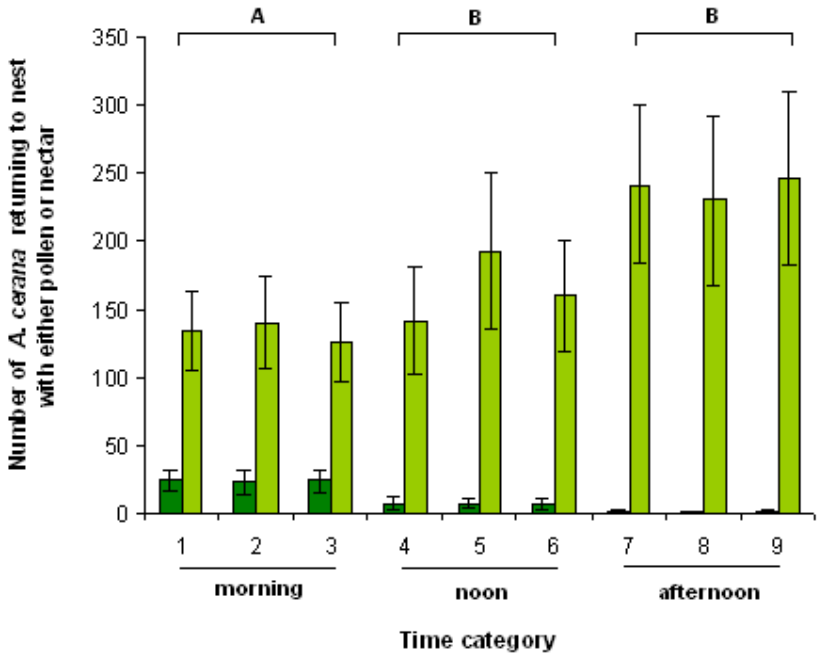

Figure 6 Average (± SE) number of *A. cerana* bees returning to the nest with either pollen (■) or nectar (■) during nine timeslots between 10 September 2012 and 18 January 2013 in the Cairns region. Each time category represents a 10-minute interval, with categories 1 to 3 beginning consecutively any time between 0900 and 0920 hours (local time); categories 4 to 6 starting consecutively any time between 1200 and 1230 hours (local time); and categories 7 to 9 commencing consecutively any time between 1400 and 1650 hours (local time). Time categories sharing a common label (that is, B) did not have significantly different numbers of *A. cerana* returning to the nest with pollen. Time categories 1 to 3, 4 to 6 and 7 to 9 formed the morning, noon and afternoon timeslots respectively.

The count of *A. cerana* attending the nest carrying nectar did not vary significantly between the morning, noon and afternoon time categories (Kruskal-Wallis: $\chi^2 = 3.292$, d.f. = 2, p = 0.193). This means that *A. cerana* in the Cairns region did not exhibit a peak nectar foraging time throughout the day.

During the morning, temperatures ranged from 24.8 °C to 38.0 °C, relative humidity varied from 34% to 84%, and light level extended from 100 lux to 122 200 lux. Around noon, temperatures were between 24.6 °C and 39.2 °C, relative humidity spanned from 27% to 84%, and light level ranged from 100 lux to 125 500 lux. For the afternoon observation period, temperatures extended from 25.4 °C to 38.0 °C, relative humidity was between 35% and 81%, and light level spanned from 100 lux to 119 600 lux.

Foraging seasonality

The quantity of *A. cerana* presenting at the nest with pollen did not change significantly between September 2012 and January 2013 (REML: $F_{4, 202} = 1.21$, p = 0.309). The (direct) back-transformed predicted means for the number of *A. cerana* presenting at the nest with pollen were 1.73 for September ($n = 90$), 2.43 for October ($n = 54$), 2.95 for November ($n = 45$), 0.91 for December ($n = 9$) and 1.00 for January ($n = 9$). This indicates that there were no seasonal differences in *A. cerana's* pollen foraging behaviours in the Cairns region.

The amount of *A. cerana* arriving at the nest with nectar did alter significantly according to month (REML: $F_{4,202} = 2.51$, p = 0.043). The (direct) back-transformed predicted means for the number of *A. cerana* arriving at the nest with nectar were 28.81 for September ($n = 90$), 76.77 for October ($n = 54$), 71.78 for November ($n = 45$), 41.67 for December ($n = 9$) and 52.47 for January ($n = 9$). This shows that there were seasonal differences in *A. cerana's* nectar foraging behaviours in the Cairns region.

Mating and reproduction: Drone flight times of *Apis* species in the Cairns region

Although overlapping, the distribution of *A. cerana* and *A. mellifera* drone flight times in the Cairns region was significantly different (Kolmogorov-Smirnov: $\chi^2_{2,26} = 13.0$, D = 0.5, $n = 26$, p = 0.002; Figure 7), indicating that the start/end times and peak drone flight time differs, with *A. cerana* having a narrow drone flight time distribution while *A. mellifera* have a broad drone flight time distribution. *A. cerana* drone flights in the Cairns region occurred between 1258 hours and 1528 hours, with a defined peak at 1413 hours. *A. mellifera* drones flew between 1228 hours and 1643 hours, with peak flight times occurring at 1528 hours. Mean flight time was also significantly different between the species (1358-1413 hours for *A. cerana* vs. 1458-1513 hours for *A. mellifera*; Mann-Whitney: U = 147 659.5, $n = 4{,}167$, p < 0.001). Drone flight distribution of *A. cerana* was narrower with a clear peak, whereas that of *A. mellifera* was broader with an earlier start and later finish and a less defined peak (Figure 7).

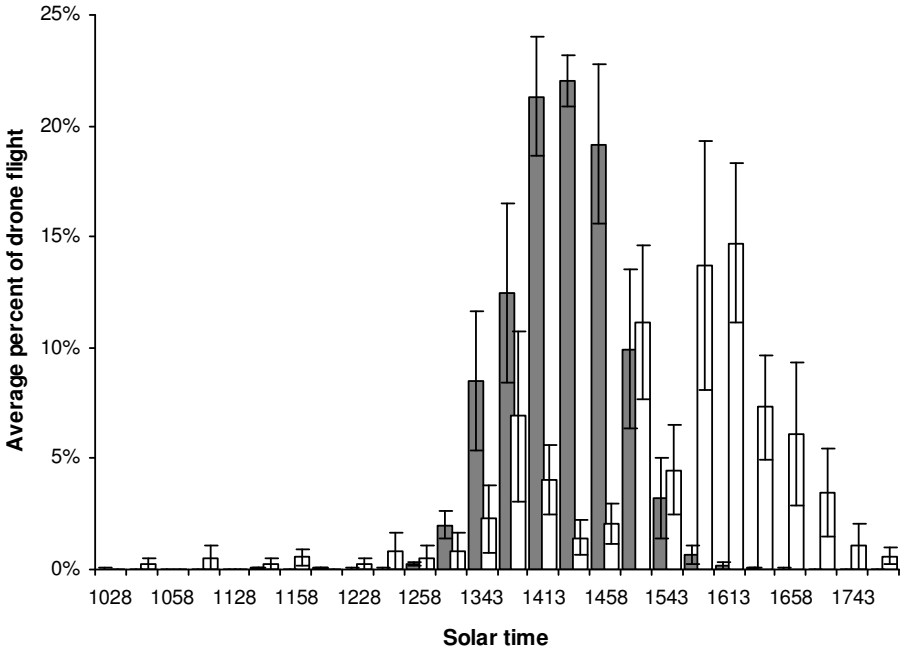

Figure 7 Average (± SE) percentage of total numbers of drones departing *A. cerana* (grey bars) and *A. mellifera* (white bars) colonies per 15-minute time intervals (solar time) in the Cairns region.

Interspecific competition with *Apis mellifera* in the Cairns region

There was a significant association between the number of *A. cerana* present when *A. mellifera* were present and the number of *A. mellifera* present (Spearman's rank: $r_{s\,1,1468}$ = 0.479, $p < 0.001$). The number of *A. mellifera* present was able to predict this relationship as follows: *Number of A. cerana present when A. mellifera are present = 0.1742 + (0.00986 * Number of A. mellifera present)* (Linear regression: adjusted $r^2_{1,1466}$ = 0.3, p = 0.024).

Discussion

Ecology of *Apis cerana* in the Cairns region

Nesting

Nest site selection

As has been reported in other studies, *A. cerana* were found to inhabit highly disturbed areas (rural, cropping, grazing paddocks, grazing land with natural vegetation), human settlements (residential, commercial, industrial, and gardens and semi-natural land) and forests (rainforests, bushland, mangrove and intertidal) in the Cairns region. It is noteworthy that approximately ninety percent of the nests observed occurred in disturbed habitats and agricultural land. This could be due to a preference for disturbed habitat. However, this is highly unlikely as search efforts and the number of public reports were much greater in disturbed areas and may have contributed to this result. Our results are supported by the results of Bakker (1999) who found that *A. cerana* tended to nest in disturbed agricultural areas in Sulawesi when they co-occurred with another cavity-nesting honey bee species, *Apis nigrocincta*. In her study, Bakker (1999) found that *A. nigrocincta* inhabited forested areas when co-occurring with *A. cerana*.

Approximately two thirds of *A. cerana* nests were established in non-natural structures, including permanent buildings and their fixtures; residential backyard structures; miscellaneous objects and structures; land transport vehicles, parts or machinery; marine transport vehicles and marine structures. The remaining nests were built in natural structures including trees, tree stumps, pot plants, logs and fallen palm fronds.

A. cerana nests were constructed at considerably higher locations in the Cairns region than within the species' natural Asian distribution. In the Cairns region, nest heights ranged from 0 m (n = 37) to 40 m (n = 1), with a median height of 3.00 m (n = 554), while, on average, Asian *A. cerana* nests occurred between 0 m and 2.00 m (Inoue *et al.*, 1990). The nest height data reported by Hyatt (2011) has been incorporated into the data used to draw conclusions in this report and consequently have not been used for comparison. Differences in nest heights between geographic locations may be a strategy used to reduce nest accessibility for predators (Seeley *et al.*, 1982).

Nest heights differed significantly amongst the ten habitat types for which there were data, with the lowest mean nest heights being found in industrial areas (1.83 m) and the highest located in gardens and semi-natural land (6.35 m). From our results, it appears that nest heights were not solely constrained by the maximum height of available nesting structures within a habitat. For instance, it would be expected that tree heights in the rainforest would exceed those available in gardens and semi-natural land, but average nest heights within the rainforest (5.35 m) were lower than those in gardens and semi-natural land.

Caution must be exercised in interpreting these nest height results as nest heights were visually estimated rather than measured, and nests at low heights had a greater chance of being detected and reported by the public. Future researchers should seek to employ a more meaningful habitat classification scheme than that applied herein to facilitate more informative conclusions. For example, measured nest heights could be accompanied by data regarding the maximum height of structures within the habitat and the relevant Australian Land Use and Management (ALUM) classification code (Australian Bureau of Agricultural and Resource Economics and Sciences, 2011).

Nest characteristics

On average, *A. cerana* nests in the Cairns region had 3.76 combs (range 1 to 11, $n = 37$), with established nests being 101.37 mm high, 69.72 mm wide, 18.52 mm thick, weighing 40.09 g, and occupying 13 455.53 mm^2. In all respects, *A. cerana indica* nests in Indonesia were larger than *A. cerana* nests in the Cairns region. Similarly, *A. cerana* nests in Bangladesh were larger than those analysed in the Cairns region, with average nests having 6.4 combs (Karlsson, 1990). This is an important discovery, given that Koetz (2013a) indicates that the *A. cerana indica* described by Inoue *et al*. (1990) may in fact be *A. cerana* Java genotype. Furthermore, these results suggest that resources (that is, floral resources or nest cavities) are more abundant in the Cairns region than in Indonesia and/or Bangladesh, thereby allowing *A. cerana* to maintain a greater number of smaller nests in an area. Alternatively, available nest cavities may be larger in Indonesia and Bangladesh than in the Cairns region since nest sizes are smaller (Gordon, 2000). Operational resource constraints meant that insufficient data was available to determine nest volume for *A. cerana* in the Cairns region.

In an established *A. cerana* nest in the Cairns region, the number of cells varied between 0 and 6 for queens (average 0.14), 0 and 288 for drones (average 19.73), and 0 and 878 for workers (average 179.53) per comb face. Initially, it seems reasonable to conclude that these nests were much smaller than the *A. cerana indica* nests described in Inoue *et al*. (1990), which had an average of 26 000 worker cells in tree nests and 66 000 worker cells in a storage room nest. Assuming the maximum number of each caste cell type (expressly 6 queens, 288 drones and 878 workers per comb face) and maximum number of combs per nest (that is, 11 combs per nest, 2 faces per comb) was present for the nests in our study there would be a maximum of 25 784 cells per *A. cerana* nest in the Cairns region. Since approximately 24% of cells were empty for the nests analysed herein, it is reasonable to extrapolate that Cairns *A. cerana* nests would have a maximum of 33 926 cells. This was calculated as (*maximum number of occupied cells [i.e. 25 784] divided by percentage of cells occupied [i.e. 76] multiplied by 100)*. While this is an estimation only and facilitates a comparison of average *A. cerana indica* cell numbers with maximum *A. cerana* cell numbers, it does suggest that maximum number of *A. cerana* cells may somewhat approximate those of *A. cerana indica*.

Although they were more variable, the *A. cerana* drone and worker cell diameters of nests detected in the Cairns incursion did approximate those described in Inoue *et al*. (1990) for *A. cerana* in Sumatra. Specifically, cell diameters averaged 5.51 mm for queens, 4.61 mm for drones and 3.97 mm for workers in the Cairns incursion. Reported average diameters in Inoue *et al*. (1990) were unavailable for queens, 5.00 mm for drones, and 4.30 mm for workers.

Established *A. cerana* nests had between 0 and 136 honey cells per comb face (average 11.01 cells), and between 0 and 135 pollen cells per comb face (average 9.82 cells). These approximately equivalent proportions for *A. cerana* are vastly different to those of *A. cerana indica* in Sumatra where 24 percent of cells contained honey and 3 percent held pollen (Inoue *et al*., 1990). Since bees use the protein sourced from pollen for brood rearing, the *A. cerana* nests analysed in this study may have been growing more so than the *A. cerana indica* nests described by Inoue *et al*. (1990), potentially because pollen and nest site availability was not constrained (Crane, 1984; Gordon, 2000).

Bee counts revealed that established nests of *A. cerana* had between 0 and 1 queen (average 0.41), 0 to 67 drones (average 12.16) and 8 to 9 765 workers (average 1 812.63), giving an average colony or nest size of 1 825.20 bees. These figures may have been slightly overestimated as queens and drones were not removed before estimating the total number of bees which was then used as a proxy for the number of workers. In future,

queens and drones should be removed before weighing the bees and calculating the number of workers. Given an average colony size of 1 825.20 *A. cerana*, it is evident that colonies in the Cairns region are smaller than those of *A. cerana* in Thailand (average 6884 to 9200; Dyer and Seeley, 1991) and *A. cerana indica* in Sumatra (average 14745; Inoue *et al*., 1990). Potentially, greater colony sizes may be related to increased cavity volume, as shown in Inoue *et al*. (1990) for *A. cerana indica.*

Nest seasonality

A. cerana in the Cairns region did not display any seasonality in nest size by month between February 2012 and November 2012. No other studies discuss this for *A. cerana*.

Population size is determined by climate, availability of food and nesting sites, competition and predation (Andrewartha and Birch, 1954; Krebs, 1972; Connell, 1983). That the *A. cerana* examined were able to maintain constant colony sizes reinforces (i) that there was a minor degree of climatic variability in the study period as is expected in tropical ecosystems, (ii) that food and nest site availability was not constrained by physical variables such as light or temperature, and (iii) that competition and predation were not intense.

Swarming

Swarm site selection

Swarms were detected in ten different land uses amongst highly disturbed areas, human settlements and forests. Specifically, and in order from most frequently detected to least frequently detected, these land uses were residential, commercial, industrial, rural, cropping, parkland, gardens and semi-natural areas, rainforest, bushland and grazing paddocks.

Over half of the *A. cerana* swarms were located in non-natural structures including permanent buildings and their fixtures; residential backyard structures; land transport vehicles, parts or machinery; marine transport vehicles; marine structures; and miscellaneous objects and structures. The remaining swarms were found on natural structures including trees, shrubs, fallen palm fronds and sugar cane paddocks.

Mean *A. cerana* swarm height in the Cairns region was 2.56 m (range 0 m to 25 m). Swarm heights differed amongst the ten habitats that swarms were detected in, forming three groups. None of the three groups identified could be clearly distinguished as having higher or lower swarm heights than the others, suggesting that the findings were not meaningful. This may have been because the habitat classifications were not established according to a predetermined focal variable since they were assigned arbitrarily in the field.

Swarm characteristics

Median *A. cerana* swarm size in the Cairns region was 1 750 bees (range 45 to 12 225 bees), made up of 1 queen, 24.50 drones and 1 740 workers per nest. Although it is unknown whether the Cairns' swarms were reproductive swarms or absconding swarms, the overall swarm size was smaller than that observed in northern Pakistan, where reproductive swarming does not commence until a colony reaches 20 000 bees (Koeniger 1976a in Ruttner, 1988). Assuming that the Cairns swarms were in fact reproductive swarms, and that about 70% of the colony relocated to a new nest site with the old queen as described in

Koetz (2013a), the Cairns' *A. cerana* swarms were substantially smaller than the colonies described earlier for northern Pakistan, with total colony sizes approximating 2 500 bees.

Swarm seasonality

A. cerana swarm size did vary temporally both throughout the year and between years in the Cairns region. Swarm sizes in July differed from those in all other months for the period 1 August 2008 to 28 August 2012, but were not obviously smaller or greater than the other months. Consequently, these differences do not appear to be meaningful. When considering swarm size variation between years, we found that 2011 differed to all other years examined, specifically 2008, 2009, 2010 and 2012. This may have been associated with the environmental disturbance, altered light, temperature and moisture schemes, and associated resource depletion caused by Tropical Cyclone Yasi in February 2011 (Turton, 2011). Temporal variation in swarm size (between months and between years) is consistent with previous reports that *A. cerana* do not store large amounts of honey (Oldroyd and Wongsiri, 2006) and seasonally abscond when the availability and/or quality of essential resources such as pollen, nectar or nest sites decline (Koetz, 2013a). However, given that this study was conducted in a tropical environment where climatic conditions remain relatively constant, the swarms observed may have been reproductively swarming if their original nest site was no longer large enough to support colony growth. Alternatively, the colonies may have been absconding due to disturbance, if they were severely disturbed by fire, flood or human interference (Koetz, 2013a). Since *A. cerana* nests often coincide with human settlements, such interference absconding is likely.

Floral resources

Honey bee nutrition relies on workers collecting pollen and nectar, which provide protein and carbohydrates respectively and supply sufficient energy for larval development, metamorphosis, and adult activities such as movement, foraging and reproduction (Winston, 1987). In this study, *A. cerana* and *A. mellifera* were both observed foraging on a wide variety of native Australian and introduced flora. *A. cerana* were encountered on 27 of the 74 floral host species surveyed in the floral preference field trials, while *A. mellifera* were detected on 73 of the 74 species. The only floral species that attracted *A. cerana* but not *A. mellifera* was Koster's curse (*Clidemia hirta*). The vegetation surveyed included a variety of native and exotic species. This study has identified 16 native and exotic floral host species that have not previously been associated with *A. cerana* in the published literature.

Of the *A. cerana* observed in the field trials, most were found in Cairns city (urban) and, by far, the least in Kuranda (rural/rainforest) and in the rainforest. Some regard must be given to the fact that floral sources were more plentiful at road level in Cairns city than in the rainforest and that treetops were not searched when they exceeded heights that were easily accessible to staff unaided by equipment. This may have meant that the counts were not entirely representative of the actual distribution of *A. cerana* within the rainforest. Otherwise, since the experimental design meant that equal search effort was applied to each of these environments, an ecological determinant for this species' preference for highly disturbed urban sites is suggested. Such ecological factors may include reduced competition with other bee species like *A. mellifera*, reduced predation pressures, greater presence of preferred floral resources, or more favourable physical variables such as ambient temperature, humidity and light levels (Koetz, 2013a).

A. mellifera numbers were greatest at Kuranda (rural/rainforest) and Gordonvale (urban/rural) and lowest in Cairns city (urban). Given this, the proportion of *A. cerana* found in urban areas was approximately four and a half times greater than *A. mellifera* for the same habitat. The proportion of *A. cerana* found in the habitat in which *A. mellifera* were most abundant, that is rural/rainforest, was thirteen and a half times greater for *A. mellifera* than *A. cerana*. Interestingly, the proportions of *A. mellifera* and *A. cerana* detected in the urban/rural sites were approximately equivalent. The proportion of *A. mellifera* found in the rainforest sites was around 38 times higher than that of *A. cerana*.

The number of *A. cerana* was always much lower than the number of *A. mellifera* present, regardless of habitat type. In fact, the number of *A. mellifera* present at a site was able to predict the number of *A. cerana* present. There was no relationship between the number of *A. cerana* detected and the number of floral species surveyed across all sites. This means that under current ecological conditions *A. mellifera* may be able to reduce the ability of *A. cerana* to persist in a given area within the Cairns region by being present in the same area. It is possible that when *A. mellifera* reach a certain density that *A. cerana* may no longer be able to compete for resources. By contrast, *A. cerana* may be unable to regulate the presence of *A. mellifera* in this context.

It is important to consider that the much lower floral diversity recorded for the rainforest sites was potentially because areas being surveyed were on the edge of the rainforest and along road verges rather than the rainforest interior. Also, field staff may not have been as skilled in floral identification of rainforest species as they were with more common exotic household garden plants. It has also been suggested that *A. cerana* numbers may be lower as their colonies are much smaller and because the Cairns' *A. cerana* does not appear to be healthy and thriving (David Guez, pers. com.).

Behaviour of *Apis cerana* in the Cairns region

Foraging times

Peak foraging times

A. cerana in the Cairns region displayed a peak pollen foraging time in the morning, but no peak nectar foraging time. In other honey bee species, such differences in foraging activity have been shown to strongly coincide with environmental peaks in pollen and nectar availability. For example, in a Queensland (Australia) study, Rhodes (1979 in Bakker, 1999) found that *A. mellifera* collected pollen from sunflowers in the morning when it was most abundant in the environment, with nectar collection from sunflowers being distributed more evenly throughout the day.

Importantly, the time of the day when honey bees commence and cease foraging cannot be attributed to a single variable, but is instead a species-specific combination of floral resource availability, ambient temperature, humidity, and light (Abrol, 2011). In subtropical India *A. cerana* foraging flights commenced at lower temperatures, relative humidity and light levels than required by *A. mellifera* (Abrol, 2006). While the same pattern may also exist in the Cairns region, it is not prudent to assume so without appropriate data. Cairns' temperatures, relative humidity and light levels varied to such a degree during both the morning observation period and throughout the day in this study that no conclusion can be drawn. To facilitate a meaningful comparison with *A. cerana*, further research is required to establish the climatic conditions required for *A. mellifera* foraging in the Cairns region.

Foraging seasonality

There were no seasonal differences in *A. cerana*'s pollen foraging, in that the number of workers returning to the nest with pollen did not differ significantly between September 2012 and January 2013.

Seasonal differences in *A. cerana*'s nectar foraging were evident, with peak nectar collection occurring in October and November. This timing coincides with the onset of the wet season (November to March) within the Wet Tropics bioregion (Sumner and Bonell, 1988), and the synchronous annual community-level peak in flowering that correlates with increased rainfall and temperature (Boulter *et al.*, 2006).

Mating and reproduction: Drone flight times of *Apis* species in the Cairns region

A. cerana drones were found to conduct their mating flights between 1258 hours and 1528 hours, with a clear peak at 1413 hours. In comparison, *A. mellifera* drones commenced drone flights earlier and finished later, with a much less clear peak. Importantly, drone flight times of both species overlap, leading to the possibility of mating interference. In other areas, *A. cerana* drones have been observed flying slightly later (with peak times between 1440 and 1655hrs depending on the area in India, Thailand, Japan and Sri Lanka; Koeniger and Wijayagunasekera, 1976; Rinderer *et al.*, 1993; Yoshida *et al.*, 1994; Oldroyd *et al.*, 2006). *A. cerana* drone flight times in this study correspond with those in Sulawesi (Hadisoesilo and Otis, 1996) and Sabah, Borneo (Koeniger *et al.*, 1988). The overlap in drone flight times greatly increases the potential for interspecific mating between *A. cerana* and *A. mellifera* in the Cairns region. Despite this, Ruttner & Maul (1983) explain that while interspecific mating and fertilisation between these species can occur, genetic incompatibility means that the hybrid zygote disintegrates and complete development never results.

Interspecific competition with *Apis mellifera* in the Cairns region

When multiple species share the same limited resources and have overlapping distributions, there are two possible patterns of resource use that may result from competitive interactions, namely competitive exclusion or resource partitioning (Krebs, 1972; Gordon, 2000). In competitive exclusion, one species outcompetes the other so that the dominant species flourishes while the less competitive species disappears from the area (Krebs, 1972; Gordon, 2000). With resource partitioning, the two species respond to selection pressures by dividing common resources spatially or temporally so that both species' needs are met and coexistence is possible (Krebs, 1972; Gordon, 2000).

This study revealed a relationship between *A. mellifera* abundance and *A. cerana* abundance when *A. mellifera* are present. In the presence of *A. mellifera*, the number of *A. cerana* attending was always lower than the number of *A. mellifera*. Similarly, in Nepal and India, *A. cerana* were found to forage on a different array of floral species and spend longer foraging on each flower when *A. mellifera* were absent (Partap 1988 in Partap, 1998; Sharma *et al.*, 2000; Yang *et al.*, 2011). Our results suggest that *A. mellifera* may respond to competition for resources by attempting to exclude other honey bees, such as *A. cerana*. This possibility would be consistent with earlier studies that have found that *A. mellifera* aggressively and consistently exclude *A. cerana* when both species compete for a sugar feeding station (Dhaliwai and Atwal 1970 in Sakagami, 1959; Yang *et al.*, 2011).

Robbing and direct fighting are a form of competitive exclusion. Upon entering another colony's nest, robbing bees kill the inhabitants and remove their honey stores (Partap, 2011). This strategy is employed during low floral resource availability, or when the infiltrated colony is weak or diseased (Yang *et al.*, 2011). Unlike *A. mellifera*, *A. cerana* are not inclined to rob pollen and nectar stores from other honey bee colonies, instead weakly defending the colony against intruders and feeding the robber bees (Sakagami, 1959; Ruttner, 1988; Carr, 2011). This is consistent with reports from Japan, where *A. mellifera* displayed stronger and more aggressive behaviour toward *A. cerana* than vice versa when the two species were confined together (Sakagami, 1959). Similarly, *A. cerana* always lost aggressive interactions with *A. mellifera* when competing for sugar syrup (Sakagami, 1959). By contrast, *A. cerana* were reported as being superior fighters to *A. mellifera* in the Solomon Islands (Annand, 2009).

A. mellifera and *A. cerana* have previously co-occurred in Taiwan, Japan, China, Vietnam, Cambodia, Pakistan and the Solomon Islands with divergent outcomes (Koetz, 2013a). In Vietnam, populations of *A. mellifera* and *A. cerana* are successfully maintained with *A. mellifera* inhabiting higher altitudes while *A. cerana* occupy coastal coconut plantations (Tan and Binh, 1994), an example of spatial resource partitioning.

In 2003 *A. cerana* were detected in the Solomon Islands (Dietemann *et al.*, 2012). Within five years, 99.75% of the *A. mellifera* hives on the main island, Guadalcanal, had been decimated (Koetz, 2013a). At first the *A. mellifera* decline was attributed to the concurrent introduction of the *Varroa* mite, *V. destructor*, however this was later found to be incorrect (Koetz, 2013a). The *Varroa* mite that had accompanied the *A. cerana* incursion were *V. jacobsoni*, a species which does not usually reproduce on *A. mellifera* brood and which accompanied an *A. cerana* invasion in the 1970's (Anderson, 2004). It is important to note that it has recently been discovered that *V. jacobsoni* in Papua New Guinea and the Solomon Islands is able to host switch and exploit *A. mellifera* broods (Anderson *et al.*, 2012). Since then, CSIRO has ascribed the *A. mellifera* declines in the Solomon Islands partially to civil unrest amongst the human population, but also to intensified competition for floral resources, robbing of *A. mellifera* hives by *A. cerana*, and the introduction of the pathogen *Nosema ceranae* with the *A. cerana* incursion (Anderson *et al.*, 2012). This microsporidian pathogen has been connected with substantial losses of *A. mellifera* colonies and Colony Collapse Disorder in the United States (Cox-Foster *et al.*, 2008; Higes *et al.*, 2008; Bromenshenk *et al.*, 2010; Anderson *et al.*, 2012). Given that *A. cerana* do not tend to rob *A. mellifera* nests (Sakagami, 1959; Ruttner, 1988; Carr, 2011), the likelihood seems greater that it was severe competition for floral resources or *A. mellifera*'s lack of resistance to *N. ceranae* (Higes *et al.*, 2008) that produced this outcome.

In Cambodia, apiarists have attempted to maintain domesticated *A. cerana* and *A. mellifera ligustica* in close proximity within mixed colony hives by feeding *A. mellifera* sugar syrup while allowing *A. cerana* to forage naturally (Yoshikawa and Ohgushi, 1965). Eventually, *A. cerana* were able to completely outcompete the *A. mellifera*, with the mixed colony becoming an *A. cerana* colony only (Yoshikawa and Ohgushi, 1965).

In Pakistan, *A. cerana* and *A. mellifera* have overlapping distributions (Muzaffar and Ahmad, 1990). Since, the sex attractant 9-oxo-2 decenoic acid is common to all *Apis* species, *A. cerana* and *A. mellifera* drones and queens are mutually attracted to each other when inhabiting the same geographic location (Muzaffar and Ahmad, 1990). Where *A. mellifera* drones were plentiful in the study area, the *A. cerana* population was suppressed via mating interference from *A. mellifera* (Muzaffar and Ahmad, 1990).

In Taiwan, Japan and China, the introduction of *A. mellifera* has resulted in the widespread decline of *A. cerana* (Sakagami, 1959; Ruttner, 1988; Juntawong and Pechhacker, 1994; Yu and Han, 2003; Yang, 2005; Yang *et al.*, 2011). *A. mellifera*'s aggressive competitive

interactions with, and tendency to rob the nests of *A. cerana* causing starvation and absconding have been used to explain this outcome (Moritz *et al*., 2005).

Conclusion

Although this study has increased our current knowledge of *A. cerana*'s ecology and behaviour in the Cairns region, it is not possible to assert with certainty whether *A. cerana* will outcompete or displace *A. mellifera* in the Australian context. From this perspective, it is important that government bodies, scientists and apiarists redirect their focus toward reducing the likelihood and severity of any potential *A. cerana*-related impact, such as those associated with bee pests and diseases, as these cause the most significant concern amongst industry and the community.

Several ecological findings from this study indicate that competition for resources has not reached the critical threshold at which either *Apis* species' population in the Cairns region may be constrained through intense competition with the other species. For competition to occur, a mutual resource must be limited (Krebs, 1972). The essential resources for cavity-nesting honey bees are floral sources for foraging and suitable nesting sites (Winston, 1987).

Firstly, the proportion of cells within *A. cerana* nests in the Cairns region that stored pollen was approximately equal to the proportion containing honey, rather than 1:8 pollen:honey ratio reported in Inoue *et al*. (1990). This suggests that pollen is widely available within the environment such that *A. cerana*, a species which typically does not store large quantities of pollen or honey, has been able collect considerable supplies without being outcompeted by *A. mellifera*. As protein sourced from pollen is used for brood rearing, the *A. cerana* nests in our study may have had a higher reproductive rate than the *A. cerana indica* nests outlined by Inoue *et al*. (1990), possibly because pollen and nest site availability was not constrained (Crane, 1984; Gordon, 2000). Secondly, *A. cerana* nests are smaller in the Cairns region than in West Sumatra and Bangladesh, indicating that there are ample nesting sites available within the Australian environment enabling bee colonies to split earlier, form reproductive swarms and establish additional colonies (Koetz, 2013a). Some Australian bee experts have ascribed these smaller *A. cerana* nests to local Cairns' populations being weak and unhealthy, possibly as a result of inbreeding (Ben Oldroyd and David Guez, pers. com.). Thirdly, colony size did not vary throughout the year, suggesting that not only was the climate relatively stable as expected in a tropical environment, but that food and nest site availability was not negatively impacted by physical factors such as rainfall or sunlight, and that competition and predation were not intense. Until floral resources and nest site availability start to become limited, it is unlikely that *A. mellifera* and *A. cerana* will compete intensively enough that the population size of either species will be adversely impacted.

When competition for floral resources does occur, the evidence from Australia indicates that *A. mellifera* would outcompete *A. cerana* through behaviours leading to competitive exclusion. This hypothesis is supported by two results from this study. *A. cerana* are less abundant in the Cairns region when *A. mellifera* are present than when they are absent, suggesting either that *A. mellifera*'s aggressive behaviours drive *A. cerana* away from the resource being competed for, or that *A. cerana* preferentially partition the resources temporally or spatially. One potential consequence of both of these ecological strategies is that *A. cerana* may respond by expanding their distribution more rapidly within Australia in an effort to access sufficient floral resources and nest sites than it would in less competitive conditions. Additionally, *A. cerana* were found to visit less floral species than *A. mellifera* in the Cairns region, with *A. mellifera* exploiting nearly three times as many native and introduced floral species as *A. cerana*. This also indicates that *A. cerana* is less adaptive to

floral resources than *A. mellifera* and is unlikely to affect *A. mellifera*'s access to floral resources, including access required for commercial honey production.

A pollen study is underway to establish whether *A. cerana* has the potential to utilise a wide range of plants as pollen resources. However, if floral visitation is assumed to be a proxy for pollen and/or nectar collection, then it is reasonable to assert that *A. cerana* use a more narrow range of floral species as pollen and/or nectar resources than *A. mellifera* in the Cairns region.

This study has highlighted two aspects of *A. cerana* and *A. mellifera* biology that may provide opportunities to develop control measures either for *A. cerana* specifically or to mitigate the potential adverse effects that exotic bee pests and diseases may have on *A. mellifera*. The first opportunity is to exploit mating interference between the two species to suppress *A. cerana* populations, either because the pairing is expected to produce non-viable zygotes or because *A. mellifera* drones can physically damage *A. cerana* queens during copulation (Ruttner and Maul, 1983). This will reduce the number of viable *A. cerana* fertilisations that develop to adulthood, thus suppressing *A. cerana* populations. Before employing this approach, every care must be exercised to consider other potential ecological effects, such as the impact of *A. mellifera* on native Australian fauna.

The second opportunity involves the selective breeding of *A. mellifera* to be more resistant to *V. jacobsoni* and *V. destructor* mites, and *N. ceranae* fungi. This is especially important given that *N. ceranae* is known to be present in Queensland (Shield, 2007; Biosecurity Queensland, DAFF, unpublished data). While *Varroa*-infestation can lead to weakened and malformed adult bees and be catastrophic for *A. mellifera* colonies (Oldroyd, 1999), *N. ceranae* may cause Colony Collapse Disorder which results in the disappearance of adult bees, reduced brood tending, diminished colony vigour and substantial mortality during winter (Higes *et al.*, 2009). To proactively avert the threat that *Varroa* mites present to Australian industry and reduce future disease control expenses, apiarists may be able to replace their less-resistant *A. mellifera* colonies with strains exhibiting heightened *V. jacobsoni* and *V. destructor* resistance, such as those from eastern Russia (Danka *et al.*, 1995; Rinderer *et al.*, 1999; Rinderer *et al.*, 2001). Other studies have also examined the use of more hygienic *A. mellifera* strains that are able to eliminate *Varroa*-infested bee pupae and consequently halt mite reproduction (De Guzman *et al.*, 2002). Although most (>80%) Australian commercial honey bee colonies (*A. mellifera*) have been shown to be non-hygienic, research conducted by Oldroyd (1996) has revealed that it is unnecessary to import overseas *A. mellifera* strains to improve the hygiene of Australian commercial colonies, since two of the ten commercial *A. mellifera* strains used in Australia were shown to be highly hygienic and able to remove dead bee pupae from the nest within 72 hours. While we have been unable to locate any published studies specifically investigating resistance to *N. ceranae* in *A. mellifera* colonies, experimental evidence from Malone *et al*. (1995) on *Nosema apis* suggest that differences in *Nosema* resistance may be present within *A. mellifera* and may be manipulated to fortify the Australian beekeeping industry.

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Appendices

Appendix 1: *Apis cerana* nest characteristics

Characteristics of *A. cerana* nests collected by Biosecurity Queensland between 28 February 2012 and 13 November 2012 in the Cairns region.

		All nests	Newly established nests (1-2 combs)	Established nests (3+ combs)
Number of combs	Mean	3.76 (*n* = 37, SD = 2.53)	1.31 (*n* = 13, SD = 0.48)	5.08 (*n* = 24, SD = 2.17)
	Range	1-11	1-2	3-11
Comb length (mm)	Mean	98.80 (*n* = 123, SD = 50.01)	80.34 (*n* = 15, SD = 47.52)	101.37 (*n* = 108, SD = 50.01)
	Range	9.57-244.31	9.57-188.23	11.38-244.31
Comb width (mm)	Mean	68.37 (*n* = 123, SD = 32.70)	58.67 (*n* = 15, SD = 40.05)	69.72 (*n* = 108, SD = 31.53)
	Range	11.20-150.27	19.01-135.02	11.20-150.27
Comb thickness (mm)	Mean	18.75 (*n* = 122, SD = 5.30)	20.28 (*n* = 15, SD = 12.42)	18.52 (*n* = 107, SD = 3.16)
	Range	8.02-56.11	8.59-56.11	8.02-32.28
Comb mass (g)	Mean	40.11 (*n* = 132, SD = 45.98)	40.20 (*n* = 17, SD = 71.20)	40.09 (*n* = 115, SD = 41.76)
	Range	0.75-274.00	0.90-274.00	0.75-274.00
Comb area (mm^2)	Mean	13 399.78 (*n* = 118, SD = 11 132.28)	12 755.56 (*n* = 10, SD = 13 628.93)	13 455.53 (*n* = 108, SD = 10 967.68)
	Range	1 250.00-40 550.00	1 250.00-38 850.00	1 650.00-40 550.00
Number of honey cells	Mean	10.09 (*n* = 246, SD = 23.00)	4.23 (*n* = 31, SD = 9.24)	11.01 (*n* = 215, SD = 24.35)
	Range	0-136	0-34	0-136
Number of pollen cells	Mean	9.61 (*n* = 243, SD = 19.63)	8.29 (*n* = 29, SD = 18.78)	9.82 (*n* = 214, SD = 19.80)
	Range	0-135	0-75	0-135
Number of queen cells or cups	Mean	0.13 (*n* = 133, SD = 0.66)	0.11 (*n* = 18, SD = 0.32)	0.14 (*n* = 115, SD = 0.71)
	Range	6-133	0-1	0-6
Number of drone cells	Mean	21.52 (*n* = 248, SD = 49.70)	32.48 (*n* = 27, SD = 67.54)	19.73 (*n* = 220, SD = 46.17)
	Range	0-288	0-284	0-288
Number of worker cells	Mean	172.33 (*n* = 249, SD = 209.06)	120.16 (*n* = 29, SD = 196.54)	179.53 (*n* = 220, SD = 210.23)
	Range	0-878	0-586	0-878

Appendix 2: *Apis mellifera*-dominated floral resources

Host plants that *A. mellifera* were detected on during timed floral observations and transect walks in the Cairns region, including the number of *A. mellifera* observed on each of these floral species. No *A. cerana* were found on these floral species during this surveillance.

Common name	Scientific name	***Number of A. mellifera observed***
Wild raspberry	*Rubus probus*	39
Purple top or Blue top	*Ageratum houstonianum*	24
Shell ginger	*Alpinia zerumbet*	24
Khaki weed	*Alternanthera pungens*	22
Ginger spp.	*Zingerberaceae*	22
Mock orange	*Murraya paniculata*	18
Grevillea *sp.*	*Grevillea sp.*	15
Plumbago	*Plumbago sp.*	7
Bramble	*Rubus alceifolius*	6
Snakeweed	*Stachytarpheta sp.*	6
Fox tail palm	*Wodyetia bifurcata*	4
Alexandra palm	*Archontophoenix alexandrae*	3
Marigold	*Calendula officinalis*	3
Cosmos	*Cosmos sulphureus*	3
Leucaena	*Leucaena leucocephala*	3
Pentas	*Pentas sp.*	3
Ivory curl tree	*Buckinghamia celsissima*	2
Cat's whiskers	*Cleome gynandra*	2
Cadaghi	*Corymbia torelliana*	2
White oak	*Grevillea baileyana*	2
Hibiscus	*Hibiscus sp.*	2
Lychee	*Litchi chinensis*	2
Lime berry	*Micromelum minutum*	2

Common name	Scientific name	*Number of A. mellifera observed*
Pandanus	*Pandanus sp.*	2
Wattle tree	*Acacia sp.*	1
White lace flower	*Archidendron hendersonii*	1
Lemon myrtle	*Backhousia citriodora*	1
Bauhinia	*Bauhinia sp.*	1
Cobbler's peg	*Bidens pilosa*	1
Orange tree	*Citrus sinensis*	1
Citrus tree	*Citrus sp.*	1
Pumpkin	*Cucurbita sp.*	1
Navua sedge	*Cyperus aromaticus*	1
Poplar gum	*Eucalyptus platyphylla*	1
Spurge	*Euphorbia sp.*	1
Icecream bean tree	*Inga edulis*	1
Ipomea *sp.*	*Ipomea sp.*	1
Leptospermum *sp.*	*Leptospermum sp.*	1
Siratro	*Macroptilium atropurpureum*	1
Meliocope *sp.*	*Meliocope sp.*	1
Basil	*Ocimum basilicum*	1
Date palm	*Phoenix dactylifera*	1
Praxelis	*Praxelis clematidea*	1
Peanut weed	*Senna torra*	1
Devil's fig	*Solanum torvum*	1
Xanthorrhoea *sp.*	*Xanthorrhoea sp.*	1
Golden penda	*Xanthostemon chrysanthus*	1

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