Queensland
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The Asian honey bee (*Apis cerana*) and its strains - with special focus on *Apis cerana* Java genotype

Literature review

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Contents

Summary

Under the Biosecurity Queensland, Department of Agriculture, Fisheries and Forestry (DAFF) Asian honey bee Transition to Management (T2M) Plan, a literature review on the Asian honey bees (Indo-Malayan subgroup of *Apis cerana*, referred to as *Apis cerana* Java genotype within this document) was to be written to provide thorough background knowledge of the species in order to (1) aid in developing a suit of control measures for Asian honey bees (*A. cerana* Java genotype) and (2) help limit the impact on honey production. Specifically, the literature review aimed to:

a. review the critical points of current knowledge about *A. cerana* in general and *A. cerana* Java genotype in particular,
b. compare *A. cerana* and *A. mellifera* behaviour and ecology,
c. review *A. cerana* beekeeping practices as well as control measures both overseas and in Australia, and
d. highlight gaps in currently available literature and future research needs.

Numerous hurdles were faced while researching available knowledge, including for example: little information being available about *A. cerana* Java genotype, so that the literature search had to be widened to *A. cerana* in general; literature being written in Japanese, Chinese, German or Indonesian languages and only abstracts, if at all, being available in English; a wide range of genetic, morphological, and behavioural variation being apparent within *A. cerana*, so that great caution is advised when extrapolating how *A. cerana* may behave outside its natural range. Very little is known about *A. cerana* Java genotype in Australia and so unless otherwise stated information relates to *A. cerana* in its natural range in Asia.

Following is a summary of the information found in the scientific literature covering the main sections of this literature review. Detailed information and references for each statement can be found in the respective sections and subsections.

A. cerana versus *A. mellifera*

A. cerana, termed the 'Asian honey bee' in Australia, is one of nine currently recognised honey bee species of the genus *Apis*. Eight of these, including *A. cerana*, are endemic to Asia. The only *Apis* species naturally occurring outside Asia is *A. mellifera,* the 'European honey bee'. *A. cerana* has been termed the Asian equivalent of *A. mellifera* (Friedrich Ruttner, 1988), as both are cavity nesting bees that build a series of parallel combs with identical life cycles. Both can be domesticated and cover huge geographical areas with a large range of ecological and climatic conditions. Furthermore, both species can be morphologically and genetically subdivided into several strains, with tropical strains being smaller than, and different in behaviour to, temperate strains. Tropical strains of both species have very similar behaviours, in that they collect less honey and are more prone to swarming and absconding.

A. cerana differs from *A. mellifera* in that *A. cerana* is generally slightly smaller, lives in smaller colonies and nests in smaller cavities. *A. cerana* is often found nesting in human-made structures where available (possibly due to their smaller colony size and cavity requirements), whereas wild *A. mellifera* tend to nest in tree cavities. *A. cerana* also has a smaller foraging range, possibly due to its smaller size. *A. cerana* is more prone to swarming and absconding when disturbed, whereas managed

European *A. mellifera* tends to hoard large amounts of honey and is less prone to absconding.

A. cerana shows greater hygienic behaviour, making it more disease resistant and enabling it to coexist with *Varroa* mites. Diseases and parasites have been exchanged in both directions between *A. mellifera* and *A. cerana* where they have come into contact.

A. cerana general ecology and behaviour

A. cerana occupies a large range of climatic conditions, from cool regions in higher latitudes and altitudes, to dry, semi-desert environments as well as tropical climates. *A. cerana* is genetically and morphologically subdivided into several strains that differ in their ecology and behaviour, particularly between temperate and tropical strains. One such strain includes *A. cerana* Java genotype, which naturally occurs across tropical Indonesia, Malaysia and Borneo.

A. cerana Java genotype was introduced, by human transport, to Papua New Guinea, the Solomon Islands, and north-eastern Australia. Negative impacts of *A. cerana* Java genotype on managed *A. mellifera* on the Solomon Islands sparked fears that it may become a pest species in Australia that could potentially compete with and affect native flora and fauna, as well as commercially kept *A. mellifera*. An additional concern is the potential spread of the destructive *Varroa* mite throughout the Australian *A. mellifera* population should it be introduced.

A. cerana has been described as docile, mild, tolerant and timid with a gentle temperament and relatively low stinging tendency. However, it does sting when cornered or disturbed. It is a cavity-nesting honey bee that nests in all habitats (including rainforest as well as highly disturbed areas such as human settlements) except where it co-occurs with another cavity-nesting honey bee species. In those areas it prefers disturbed habitats. *A. cerana* forages mostly within one kilometre of the hive. *A. cerana* builds multiple parallel combs in a wide variety of available cavities, including, for example, tree or palm hollows, rock crevices, and house wall cavities.

Tropical *A. cerana* absconds and swarms more readily, due to the year-round favourable environmental conditions and high predation pressures in the tropics. Reproductive swarming is highly variable but generally occurs several times a year.

Pollination and beekeeping

A. cerana is regarded as an excellent crop pollinator in Asia, and the species is an important pollinator of wild, native flora, particularly in dipterocarp, lowland rainforest. *A. cerana*, including *A. cerana* Java genotype, is also successfully kept in hives for honey production, and is particularly important for poor communities. However, *A. cerana* produces distinctly less honey than *A. mellifera*, particularly the tropical *A. cerana* subspecies. This has led to an increased use of *A. mellifera* for commercial honey production and pollination services across Asia, which in turn has led to dramatic local declines (and sometimes local extinction) of *A. cerana*.

A. cerana control measures

As *A. cerana* is native to Asia and has only been introduced to a limited number of areas, there is little information about its control as a pest species. Various control measures have been trialled on the Solomon Islands and in Australia with limited success.

Future research needs

The literature review has highlighted gaps in the current knowledge, particularly of *A. cerana* Java genotype in Australia. Very little published information is available on the basic ecology and behaviour on *A. cerana* Java genotype, and how it may interact with Australian native flora and fauna, and so it is of upmost importance not only to conduct research into the species' general ecology but also into its pollination behaviour, competition with Australian native flora and fauna, and competition with *A. mellifera*. *A. cerana* is also difficult to detect in non-urban areas, and further research is needed to improve detection and control methods. Findings of this research need to be widely disseminated to the scientific, management and conservation community.

Introduction

A. cerana is one of nine currently recognised honey bee species of the genus *Apis* (Family Apidae, Subfamily Apinae, Tribe Apini) (Arias & Sheppard, 2005; Raffiudin & Crozier, 2007). The European honey bee, *Apis mellifera*, is the only *Apis* honey bee species that naturally occurs outside of Asia. All other *Apis* species, including *A. cerana*, naturally occur in Asia.

A. cerana, also known as the Asian honey bee, Asiatic bee, Asian hive bee, Indian honey bee, Indian bee, Chinese bee, Mee bee, Eastern honey bee, and fly bee, is endemic to most of Asia where it has been used for honey production and pollination services for thousands of years. *A. cerana* has been described as the exact equivalent of its European/African sister species *A. mellifera*, the European honey bee, showing as wide a range and capacity for variation and adaptation (Friedrich Ruttner, 1988). Similar to *A. mellifera*, *A. cerana* occupies a large range of climatic conditions, from cool regions in higher latitudes and altitudes, to dry, semi-desert environments as well as tropical climates (Friedrich Ruttner, 1988). And similar to *A. mellifera*, *A. cerana* is also genetically and morphologically subdivided into several strains that differ in their ecology and behaviour, particularly between temperate and tropical strains.

However, since the 1980s, incursions of *A. cerana* have occurred in areas outside the species' natural range (namely New Guinea, Solomon Islands and Australia), and the fear is that it may become a pest species that could potentially compete with native Australian fauna (especially insects) and affect pollination of native flora. It is also feared that it may compete with *A. mellifera*, which is commercially used for honey production and crop pollination services. Substantial impact of introduced *A. cerana* on *A. mellifera* hives have indeed been reported in the Solomon Islands (D. Anderson, 2010; D. L. Anderson, 2004; D. L. Anderson, Annand, Lacey, & Ete, 2012), raising concern that *A. cerana* may have the same devastating effect on *A. mellifera*, and consequently on honey production and pollination services, in Australia.

This literature review is a response to these concerns and aims to review the scientific literature to determine what is known about the ecology and behaviour of *A. cerana*, to aid the development of targeted surveillance and control measures of this introduced species in Australia. The specific strain that was introduced to Australia is thought to be *A. cerana* Java genotype (D. Anderson, pers. com.), i.e. from the recognised Indo-Malayan strain of *A. cerana*, a tropical strain of the species found in Indonesia, Malaysia, Borneo and Sulawesi (Figure 1; see sections on Distribution and Morphological and genetic diversity). Although the literature review aims to clarify the ecology and behaviour of this tropical strain in particular, very little is known and published about it. Therefore, the literature search was widened to *A. cerana* in general, with a focus (where possible) on tropical *A. cerana*, which includes *A. cerana* Java genotype.

It is important to keep in mind that although *A. cerana* may behave in a certain way where it is endemic, one cannot assume that it will behave in the same way elsewhere. Similarly, differences in behaviour may be found between different strains. Therefore, where information on a specific strain is lacking, one should not assume it may behave as a different strain would.

Specifically, this review aims to clarify the following questions:

(1) What is known about the ecology and behaviour of *Apis cerana* (Java genotype)? How are tropical and temperate strains different?

(2) What is known about honey production and pollination services in *A. cerana*? How does this differ between tropical and temperate strains?

(3) How does *A. cerana* ecology and behaviour compare to *Apis mellifera*, and what is the likely ecological overlap between these two species?

(4) What has been the impact of introduced *A. cerana* elsewhere? How is *A. cerana* controlled and managed elsewhere?

(5) What are the most important gaps in knowledge and what research needs to be done to fill these gaps?

This literature review is broadly divided into several sections, covering the distribution of *A. cerana*, its ecology and behaviour, pollination, beekeeping, *A. cerana* versus *A. mellifera*, a summary of potential impacts on the Australian environment, control strategies in place in Australia and elsewhere, and recommendations for future research.

Distribution

Natural and introduced range

The natural range of *A. cerana* is very widespread across temperate and tropical Asia, reaching from Afghanistan to Japan, north into the foothills of the Himalayas, and south through Indonesia (Figure 1; Crane, 1999; C. Hepburn & Radloff, 2011; Friedrich Ruttner, 1988). *A. cerana*'s range covers many climatic zones, from tropical rainforest and tropical savannah to mid-latitude grasslands, moist continental deciduous forests to taiga (C. Hepburn & Radloff, 2011).

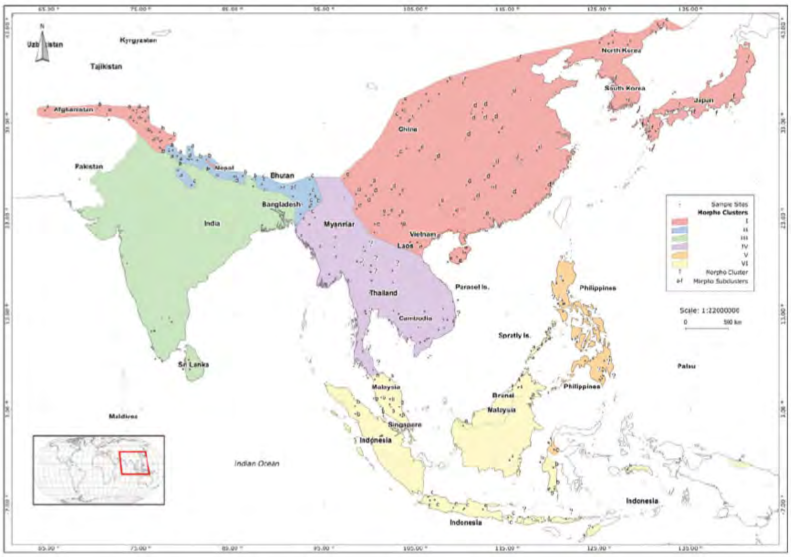

Figure 1 **The distribution of *Apis cerana*. Different colours depict different *A. cerana* morphoclusters based on complex morphological differences (Sarah E. Radloff et al., 2010). The 'Plains' variety within Morphocluster III (previously *A. cerana indica*) has recently been genetically split into a new species (*A. indica*) (Lo, Gloag, Anderson, & Oldroyd, 2010). Yellow regions refer to *A. cerana* Java genotype (morphocluster VI).**

No honey bee species (*Apis*) naturally occur in the Americas, Australia, New Zealand or Pacific islands (Bradbear, 2009). However, *A. mellifera* has been introduced by humans to all of these areas, and *A. cerana* has been introduced to some.

A. cerana was intentionally introduced from Java into the Indonesian province of Papua New Guinea in the late 1970s. It then established throughout New Guinea (D. L. Anderson, 1994). In 1993, swarms of *A.* cerana were detected on Boigu, Saibai and Dauan islands in the Torres Strait (Dunn, 1992). *A. cerana* has been intercepted and destroyed on vessels at Australian seaports since 1995, namely Cairns, Brisbane, Melbourne and South Australia (Barry, Cook, Duthie, Clifford, & Anderson, 2010). A nest was found in Darwin in 1998 – it was destroyed and an eradication and surveillance program established (D. Anderson, 2010). In 2003, *A. cerana* was detected over 1000 kilometres further east on the Solomon Islands (D. Anderson, 2010; D. L. Anderson et al., 2012). In 2007, a nest was found in Cairns, Australia. Although it was destroyed, over 800 nests and swarms have been detected and destroyed since. In 2011, the eradication of *A. cerana* in Cairns was deemed not feasible by the National Management Group (formed by the Australian Government specifically to deal with *A. cerana* in Australia), and so an *A. cerana* population is now establishing in the Cairns region.

The incursions into PNG and Australia clustered genetically with *A. cerana* of the Indo-Malayan region using mitochondrial DNA (CO I gene; Anderson, pers. com). A recent genetic study using more sensitive microsatellite genetic markers revealed that Australian *A. cerana* appear distinct from *A. cerana* in the Torres Strait and the Solomon Islands, as well as from *A. cerana* from Thailand (Oakey, 2012). However, sample sizes were limited and did not include samples from the Sundaland group.

Other, less well documented *A. cerana* incursions have also occurred in New Zealand and possibly Hawaii (mentioned in Friedrich Ruttner, 1988). No further documentation of either incursion could be found in the scientific or common literature.

Morphological and genetic diversity

Not surprisingly, given its wide range covering many climatic zones, considerable genetic and morphological variation has been shown within *A. cerana* (Sarah E. Radloff et al., 2010; Friedrich Ruttner, 1988; Smith, Villafuerte, Otis, & Palmer, 2000). In order to place the *A. cerana* introduced to Australia within geographic and genetic context, this variation and the subgroupings or strains suggested for *A. cerana* will be summarised. It needs to be noted that there has been extensive debate, re-classification and re-naming of *A. cerana* subgroups since the species was first described by Fabricius in 1793. Recent use of more sophisticated morphological and genetic techniques have started to shed light into the taxonomy and sub-groupings of *A. cerana*.

Morphological divergence

A. cerana is morphologically and genetically subdivided across its range. Most recent studies found that there are six “morphoclusters” (Figure 1), i.e. groupings within *A. cerana* based on complex statistical analyses of 12 morphological characters (Sarah E. Radloff et al., 2010). The genetic strain of *A. cerana* found in Australia, New Guinea and the Solomon islands (as determined by D. Anderson, pers. com.) falls within morphocluster VI, which is distributed across southern Thailand, Malaysia and Indonesia (also called Indo-Malayan *A. cerana*; Figure 1)(Sarah E. Radloff et al., 2010). Morphoclusters V and VI (Philippine and Indo-Malayan clusters, respectively) also occur in tropical wet climate. All other morphoclusters occur outside wet tropical climates, although some subclusters may fall within wet/dry tropical or subtropical climates (within morphocluster I: Indus, central and eastern China, and Japonica subclusters; within morphocluster IV: Thailand subcluster).

Subtle morphological differentiation has been detected within some of the morphoclusters, which is generally linked to biogeographical and climatic boundaries (Sarah E. Radloff et al., 2010). Within the Indo-Malayan morphogroup VI (containing *A. cerana* Java genotype), three main subgroups were found (Sarah E. Radloff et al., 2010; S. E. Radloff et al., 2005): (1) Palawan (Philippines), North Borneo (Malaysia) and Kalimantan (Indonesia); (2) Malay Peninsula, Sumatra, and some Sulawesi; (3) Indonesia (Java, Bali, Irian Jaya, some Sulawesi and Sumatera (Figure 2).

It must be noted here that morphological subdivision, particularly based on extremely subtle changes as found in *A. cerana*, does not imply division into strains, nor changes in behaviour or genetics.

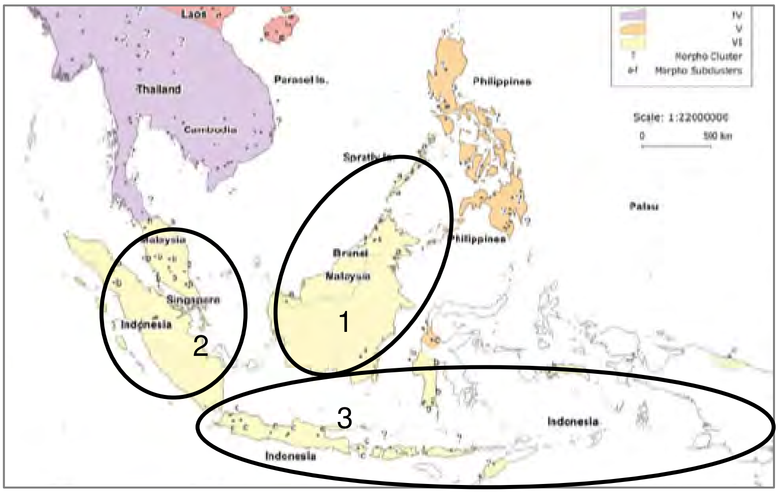

Figure 2 **The subgroupings found within morphocluster VI, the Indo-Malayan *Apis cerana* according to (Sarah E. Radloff et al., 2010). (1) Palawan (Philippines), North Borneo (Malaysia) and Kalimantan (Indonesia); (2) Malay Peninsula, Sumatra, and some Sulawesi; (3) Indonesia (Java, Bali, Irian Jaya, some Sulawesi and Sumatera).**

Genetic divergence

Most recent genetic studies generally agree with these morphological studies. They divide the species into four main genetic groups (Figure 3; Smith, 2011; Smith et al., 2000). One of these groups (the Sundaland group) corresponds with morphogroup VI (= Indo-Malayan *A. cerana*) that contains *A. cerana* Java genotype (Figures 1 & 3). This genetically and morphologically distinct subgroup is confined to the Asian tropics south of 10˚N latitude (Rueppell, Hayes, Warrit, & Smith, 2011; Smith, 2011; Smith et al., 2000; Songram, Sittipraneed, & Klinbunga, 2006).

Further genetic subdivision can be found within the Sundaland/Indo-Malayan group. Relevant here is the fact that *A. cerana* samples from Java, Bali, Flores, Timor and Sulawesi cluster together, as do samples from Bali and Lombok (Smith, 2011; Smith et al., 2000). Genetic clustering within the Sundaland/Indo-Malayan group seems to be linked to location upon the Sunda continental shelf and sea level fluctuations during Pleistocene glaciations. Islands on the Sunda shelf (Sumatra, Java, Bali, Lombok, Timor and Flores) would have been connected by dry land during glaciations periods, whereas Borneo and Sulawesi remained separated by deep channels (Smith, 2011).

It needs to be noted here that sharp genetic boundaries between populations (e.g. between the Mainland Asia group and the Sundaland/Indo-Malayan group) are linked specifically to the genetic marker used. Mitochondrial DNA is maternally inherited, and so any gene flow and admixture between populations represents female gene flow (migration), whereas drone gene flow is “invisible” using this marker. Differences in the nuclear genome, which evolves much more slowly and is both maternally and paternally inherited, would be much less than those observed in the above studies (Smith, 2011). In addition, mitochondrial DNA gives a good picture of past population genetic events, while it gives little or no information about adaptation to local environments (Smith, 2011). This means that differentiation within the Sundaland/Indo-Malayan group (as, indeed, between and within other morphogroups) is very slight, and broad habitat differences rather than genetic differences may explain differences in behaviour.

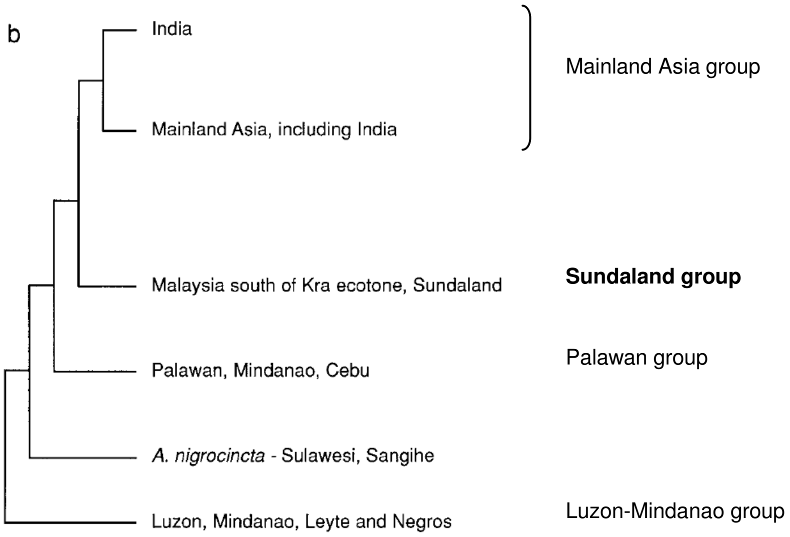

Figure 3 **Phylogenetic tree of the main *A. cerana* haplotypes (mitochondrial DNA subgroupings) and their corresponding geographic regions (from Figure 6b in Smith et al., 2000). Also shown is the placement of *A. nigrocincta* within the tree.**

Ecology and behaviour

Appearance

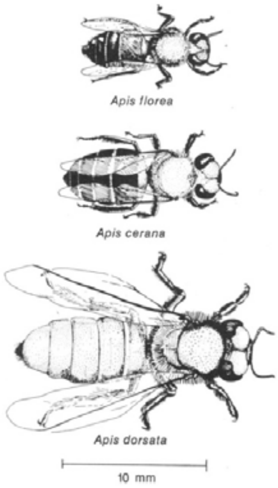

Figure 4. Workers of three Asian honey bee species *A. florea, A. cerana,* and *A. dorsata* (from Seeley, 1983)

There are nine *Apis* honey bee species worldwide, eight of which are native to Asia. *A. mellifera* is the only *Apis* honey bee species outside of Asia. Among the Asian honey bee species, *A. cerana* is a medium sized honey bee – smaller than the giant Asian honey bees (*A. dorsata* and *A. laboriosa*) but larger than the dwarf Asian honey bees (*A. florea* and *A. andreniformes*; Figure 4) (Oldroyd & Wongsiri, 2006). *A. cerana* is the smallest of the four cavity-nesting Asian honey bees (including *A. koschevnikovi*, *A. nuluensis*, *A. nigrocincta* and *A. cerana*) (Oldroyd & Wongsiri, 2006).

A. cerana are generally smaller than *A. mellifera* (Oldroyd & Wongsiri, 2006). However, remarkable morphological variation has been found within both *A. cerana* and *A. mellifera*, with non-tropical bees being larger than tropical bees, and bees at high altitude being larger than those at low altitude (Ken, Fuchs, Koeniger, & Zan, 2003; Friedrich Ruttner, 1988; L. R. Verma, Mattu, & Daly, 1994). Although *A. cerana* tend to be smaller in general, there is some overlap between larger, cool-climate *A. cerana* and smaller, warm-climate (African) *A. mellifera* (Friedrich Ruttner, 1988). In Queensland, Australia, *A. cerana* tend to be smaller than *A. mellifera* (Biosecurity Queensland, unpublished data) but this has yet to be quantified.

A. cerana have more prominent and consistent striping on their abdomen with even black bands across the entire abdomen, whereas *A. mellifera* tend to have uneven black stripes with thinner stripes at the front of the abdomen and thicker black stripes towards the back of the abdomen (making it appear more yellow at the front and darker at the back). However, colouration is notoriously variable in nature, and the most reliable morphological characteristic that distinguishes *A. cerana* from *A. mellifera*, used for taxonomic species identification, is the extension of the radial vein on the hind wing, which is absent in *A. mellifera* (Figure 5; Friedrich Ruttner, 1988).

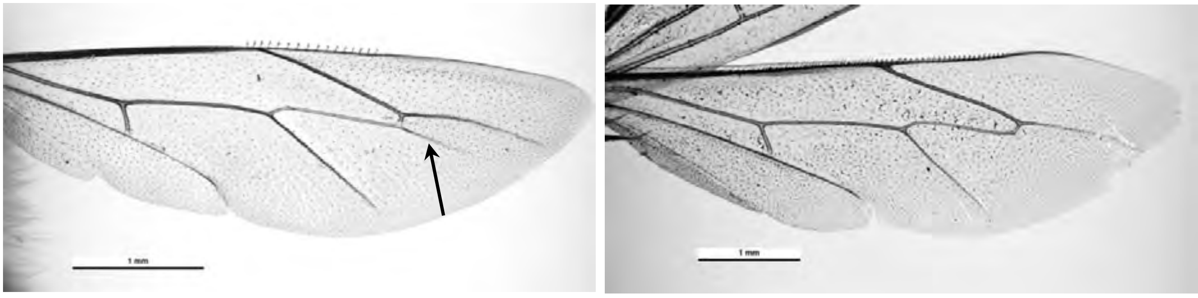

Figure 5 **Hind wing venation in *A. cerana* (left) and *A. mellifera* (right). Radial vein in *A. cerana* indicated by an arrow (photos from http://www.padil.gov.au, accessed 10/10/2012).**

Foraging

Honey bees collect nectar and pollen, which are needed for bee nutrition. Pollen is a source of protein, nectar is a source of carbohydrates, and together they provide all the food necessary for larval growth and metamorphosis, and for adult function and development (Winston, 1987). While bees collect nectar and pollen, they provide one of the most important ecological services -pollination. Pollination will be covered in more detail further on. Here, general foraging and its importance to the bee colony will be covered.

On a single foraging trip, *A. cerana* foragers tend to collect either pollen or nectar (not both) from a single species of plant, continuing to collect pollen or nectar from that plant throughout the day (Bakker, 1999; Corlett, 2011).

Foraging ranges

Foraging ranges of *A. cerana* vary between different studies, but generally honey bees prefer to forage within 200-300m of their nest (Partap, 2011). In all studies reviewed here, half of the observations showed *A. cerana* foraging within 250m from the hive, and most (95%) *A. cerana* foraged within 500-900m (Punchihewa, 1985 in Bakker, 1999; Bhuiyan, Hossain, & Bari, 2002; Dhaliwai & Sharma, 1974; F. C. Dyer & T. D. Seeley, 1991; Hyatt, 2011; Kevan, Punchihewa, & Greco, 1995). Maximum foraging ranges of 1500m to 2500m have been observed (Dhaliwai & Sharma, 1974; F. C. Dyer & T. D. Seeley, 1991; Hisashi, 2010).

In comparison, *A. mellifera* tends to forage across much larger distances, with maximum distances of over 10km (D.P. Abrol, 2011; Beekman & Ratnieks, 2000; Visscher & Seeley, 1982). Half of all foragers were found within 1650m, and most foragers (95%) were found within 6km in a natural deciduous forest in north-eastern US (Visscher & Seeley, 1982).

Foraging times

The time of day when honey bees start and finish foraging often depends on ambient temperature, humidity and/or light levels, as well as the availability of floral resources – the specific combination of factors is species-specific (reviewed in D.P. Abrol, 2011). In addition, these conditions can change dramatically from day to day, between seasons, and also depend on the geographical location. In general, *A. cerana* tend to start foraging earlier in the day than *A. mellifera* (D. P. Abrol, 2006; Bakker, 1999; Kevan et al., 1995; L. R. Verma & Dulta, 1986), as *A. cerana* require slightly lower temperatures, light intensity and solar radiation levels to commence flight activity than *A. mellifera* (subtropical India: *A. cerana* – 15.5˚C, 76% relative humidity, 600 lx light level & 9mW/cm^2 light intensity; *A. mellifera* – 16˚C, 75% relative humidity, 800 lx light level & 10mW/cm^2 light intensity; Abrol, 2006).

In an apple orchard in Northern India, *A. cerana indica* foraged earlier in the day compared to *A. mellifera*, being most active between 9am and 11.30am when temperatures were between 15.5 and 21˚C (compared to *A. mellifera*, which were most active between 11am and 1.30pm, 21-25˚C; Verma & Dulta, 1986; Verma, 1995; in Bakker 1999). In Kathmandu, Nepal, there were two peak foraging times, which corresponded with temperatures of 20-21˚C (Singh, 2008).

Subtropical *A. cerana* in India also tended to start foraging earlier and finish slightly later than *A. mellifera*. However, the single peak foraging times seemed to overlap between the two species (D. P. Abrol, 2006).

No information on foraging times could be found for *A. cerana* Java genotype in its native range or in Australia.

Nesting

Nest site selection

Nesting habitats

Four of the eight Asian honey bee species nest in cavities, including *A. cerana* (C. Hepburn & Radloff, 2011; Oldroyd & Wongsiri, 2006). In areas where *A. cerana* is the only cavity nesting species, it can be found nesting in all habitats, including primary forests (forest that has never been cleared, e.g. old-growth rainforest) (Corlett, 2004; Thomas D. Seeley, Seeley, & Akratanakul, 1982). Where *A. cerana* is found co-occurring with other cavity-nesting *Apis* species, it tends to prefer nesting in secondary forest (regrowth forest that has previously been cleared), agricultural or disturbed areas (reviewed in Bakker, 1999; Hadisoesilo, 1997; Otis, 1996; Phiancharoen, Duangphakdee, & Hepburn, 2011). In Central Sulawesi, where *A. cerana* co-occurs with the cavity-nesting *A. nigrocincta*, *A. cerana* has only been found nesting in agricultural areas and villages (Bakker, 1999; Hadisoesilo, 1997). However, in north-eastern Thailand where *A. cerana* is the only cavity-nesting *Apis* species, Seeley & Seeley (1982) found *A. cerana* nesting in a variety of habitats, predominantly in primary and secondary rainforest as well as cleared areas. *A. cerana* is also found in the rainforests of Western Ghats and Sri Lanka (Corlett, 2004). Furthermore, in a review of beekeeping history and practices by Crane (1999), mention is made of Javanese beekeepers taking log-hives into the jungle to catch swarms. These studies show that *A. cerana*, in the absence of other cavity-nesting *Apis* species, can be found across a variety of habitats, including rainforests.

It has been noted that observations of nest site preferences can be biased, particularly for *A. cerana*, as open areas are more easily searched, and nests in human structures are often more obvious than in forests (Oldroyd & Wongsiri, 2006). However, both Bakker (1999) and Hadisoesilo (1997) studied both *A. cerana* and *A. nigrocincta* in areas where they co-occur – *A. cerana* was only found in villages and disturbed areas, whereas *A. nigrocincta* was generally found inside rainforest but also in disturbed areas. Important to note here is that both authors searched across habitats (forest and disturbed areas) and so would have been likely to find *A. cerana* in the forest. These studies also confirm that *A. cerana* avoids the rainforest when in competition with another cavity-nesting species (e.g. *A. nigrocincta* as reported in Bakker (1999) and Hadisoesilo (1997), but that it can live in forests when not in competition with another species.

The majority detections of *A. cerana* in Australia were made in open and disturbed habitats (Hyatt, 2011). However, this does not indicate a preference for such habitats, but rather is likely to be due to substantially greater search effort in residential, industrial and agricultural areas compared to difficult-to-search habitats (such as mangroves, rainforest and Eucalypt woodland). Indeed, a number of nest detections in mangroves, rainforest and Eucalypt woodland (Biosecurity

Queensland, DAFF, unpublished data) confirms that *A. cerana* can and does exploit these habitats in Australia.

Nest sites

A. cerana nests are generally found in tree hollows, rock crevices, caves and house cavities. In Padang, Sumatra, as well as in Bangladesh, *A. cerana* mostly nested in tree hollows (Inoue, Adri, & Salmah, 1990; Karlsson, 1990), whereas in Thailand, the majority nested in caves (Thomas D. Seeley et al., 1982). In West Pakistan, wild *A. cerana* were mainly found in tree hollows or rock crevices (F. Ruttner, Woyke, & Koeniger, 1972) but also cavities in house walls (Muzaffar & Ahmad, 1990). Hollow trunks of coconut palms as well as piles of coconut husks seem to be a preferred nesting site in areas where coconut plantations abound (Oleh, 1989). In one study, an *A. cerana* nest was found in the ground (Karlsson, 1990). In Queensland, Australia, *A. cerana* nests have been found equally in human and natural structures, including, for example, wall and roof cavities, garden sheds, compost bins, letter boxes, vehicles and machinery, as well as trees (Hyatt, 2011).

Nest height

In its natural range, *A. cerana* tend to nest at relatively low heights, with average nest heights of one to two metres (Karlsson, 1990; Thomas D. Seeley et al., 1982) and maximum nest heights varying between two and ten metres depending on the study (Inoue et al., 1990; Oleh, 1989; Thomas D. Seeley, 1983; Thomas D. Seeley et al., 1982). *A. cerana* Java genotype in Queensland, Australia, have been found nesting at a much higher average height of 4.45m and up to 30m (N = 327; Hyatt, 2011). It is unknown whether this difference is due to different nesting behaviour in Australia, or whether nest height data may be biased due to the difficulty of finding nests at large heights.

Nest cavity volume

Nest cavity volumes of *A. cerana* vary greatly, from 2.75 to 110 litres (Inoue et al., 1990; Karlsson, 1990; Oleh, 1989). Due to this variation, averages also varied between studies and need to be regarded with caution – from 10-15 litres in general (Phiancharoen et al., 2011) to 23.5 litres and 45.9 litres in West Sumatra, Indonesia (Inoue et al., 1990; Oleh, 1989). The smallest and largest cavity volumes found in the literature were found in West Sumatra, Indonesia (Inoue et al., 1990; Oleh, 1989), the home of *A. cerana* Java genotype.

In comparison, *A. mellifera* nest cavity volumes have been found to vary between 12 and 443 litres with most being approximately 35 litres (T.D. Seeley, 1977) and a preference for cavities between 20 and 80 litres (T.D. Seeley & Morse, 1978).

Nest characteristics

A. cerana build multiple comb nests in dark cavities (Phiancharoen et al., 2011), although open nests (e.g. built underneath building eaves) have also been observed (Koetz, pers. obs.; Oldroyd, pers. com.). Combs are built parallel with a uniform distance between them (the bee space; Phiancharoen et al., 2011). Honey is stored in the upper part of the combs as well as in the outer combs adjacent to the cavity walls; the remaining comb space is taken up by brood of various ages (Phiancharoen et al., 2011; R. W. K. Punchihewa, 1994).

The number of combs in *A. cerana* nests varied from three to fourteen combs (Inoue et al., 1990; Karlsson, 1990; Lavrekhin, 1958 in Friedrich Ruttner, 1988; Thomas D. Seeley et al., 1982) with an average of 6.4 in Bangladesh (Karlsson, 1990), 5.6 in Thailand (Thomas D. Seeley et al., 1982) and 7.9 in West Sumatra, Indonesia (Inoue et al., 1990).

A. cerana cells are of two sizes: smaller worker cells (diameter of 4.2-4.8mm, depth of 1.01mm; Tingek, 1996 in Inoue et al., 1990; Karlsson, 1990; Phiancharoen et al., 2011; Friedrich Ruttner, 1988) and larger drone cells (diameter of 4.7-5.3mm; Karlsson, 1990; Phiancharoen et al., 2011; Friedrich Ruttner, 1988). In comparison, *A. mellifera* worker cell sizes were approximately 4.9 mm average (Berry & Delaplane, 2001). Drone cells have a distinctly raised cap with a pore at their apex (Hadisoesilo & Otis, 1998; Phiancharoen et al., 2011). The size difference between worker cells and drone cells is less pronounced in *A. cerana* than in *A. mellifera* (Friedrich Ruttner, 1988). Queen cells are large conical cells built on the lower edge of the combs (Phiancharoen et al., 2011). However, just as body size varies geographically, so does worker cell size. Worker cells are larger in colder regions (e.g. Japan: 4.7-4.8mm, High Himalaya: 4.9mm, central India: 4.5mm, southern India: 4.3mm, Phillippines: 3.6-4.0mm; Crane, 1993 in Phiancharoen et al., 2011; Friedrich Ruttner, 1988).

Inoue et al (1990) reported in great detail nest site and nest characteristics of 10 *A. cerana* nests in West Sumatra (reported as *A. cerana indica* but more likely to be *A. cerana* Java genotype according to current classification). Nests had on average 7.9 (3-14, SE ± 3.9) combs, and combs were on average 51.6 ± 21.6 cm high and 18.2 ± 7.1 cm wide with a volume of 22.3 litres and a weight of 1.7kg. Average number of cells was 28352 (5315-69515) (Inoue et al., 1990).

Nest size and nest density

Reported nest sizes (number of bees/colony) vary greatly in *A. cerana*, ranging from 1400-2000 bees when lacking in cavities of sufficient size (Friedrich Ruttner, 1988), and up to 34000 bees (Inoue et al., 1990). Average sizes vary also, from 6884 to 9200 bees (wild colonies; Fred C. Dyer & Thomas D. Seeley, 1991; Thomas D. Seeley et al., 1982), to 13164 bees (hived; Tong & Boot, 2005) and 14745 bees (wild colonies; Inoue et al., 1990) to list a few. In Australia, rather small average nest sizes of 2182 bees (wild colonies; 41 up to 10706 bees) were reported (Hyatt, 2011). In comparison, *A. mellifera* colony sizes have been reported between 15000 bees (Tong & Boot, 2005) and up to 50000 bees (reviewed in Suwannapong, Benbow, & Nieh, 2011).

In general, animal abundances are influenced by climate/weather and vegetation, by availability of food and nesting sites (e.g. in cavity nesting bees), as well as by competition and predation (Andrewartha & Birch, 1954; Connell, 1983; Krebs, 1972). There are few studies that estimate nest density in *Apis* species in general (Kajobe & Roubik, 2006), and in *A. cerana* in particular. One single study on *A. cerana* nest density found it to be 22 nests/km^2 in Padang, Sumatra, with a mean distance between nests of 104 meters (67-244m, SE ± 36; Inoue et al., 1990). No information on nest densities in Australia is currently available.

A. mellifera densities vary greatly and have been estimated from 0.17-0.96 nests/km^2 in Russia (Galton, 1971 in Oldroyd & Wongsiri, 2006) and 0.5 nests/km^2 in a temperate forest near Ithaca, New York (Thomas D. Seeley, 1983), to 107 nests/km^2

in a dry tropical forest in Brazil (Michener, 1975 in Kajobe & Roubik, 2006). Kajobe and Roubik (2006) reviewed nest densities in stingless bees (Meliponini) and *A. mellifera* across 20 studies, seven of which reported nest densities for tropical *A. mellifera.* These ranged from two to 107 nests/km^2 although most were found to be between six and 15 nests/km^2. *A. mellifera* density in a Ugandan tropical forest reserve was 12 nests/km^2 (Kajobe & Roubik, 2006).

In South Australia, Paton (1996) found *A. mellifera* densities to vary greatly, from 0.1 nests/km^2 (mallee heath) to 10-40 nests/km^2 (Eucalypt woodland), with localised densities of 1000 nests/km^2. Oldroyd et al. (1994; 1997) reported densities from 50 to 150 nests/km^2 in Wyperfield National Park, Victoria. However, their estimates were restricted to a narrow strip of riparian woodland within the National Park (Oldroyd et al., 1994). When converting this to a density per square kilometre, the density was 7.7 nests/km^2 (Baum, Rubink, Pinto, & Coulson, 2005). A more recent study found *A. mellifera* nest densities of 4.4 to 27.7 nests/km^2, with significantly higher densities in undisturbed habitat (Hinson, 2011).

Mating and reproduction

As in all other *Apis* species, mating behaviour characteristics of *A. cerana* include: (1) large numbers of drones trying to mate with each queen (effective sex ratio during mating flights is highly skewed towards males), (2) drones dying shortly after mating, (3) queens mating with many drones on the mating flight, (4) drones and queens mating on the wing, and (5) drones aggregating at specific locations (drone congregation areas) (reviewed in N. Koeniger, Koeniger, Gries, & Tingek, 2005).

The mating season of *Apis* species is inevitably linked to the swarming season and the seasonal blooming cycles. Because of this, in many areas, different *Apis* species reproduce simultaneously, which could lead to reproductive overlap (N. Koeniger & Koeniger, 2000). Reproductive barriers are important in order for two species to maintain isolation and coexist. Differences in the timing of mating flights, sex attractants (pheromones) and drone congregation areas are important in establishing and maintaining isolation between different *Apis* species (N. Koeniger & Koeniger, 2000; Friedrich Ruttner, 1988). However, there seems to be some overlap between *A. cerana* and *A. mellifera*.

Timing of mating flights

Different *Apis* species generally have distinctly different drone flight timings, and this characteristic has been used for recognition of new species (N. Koeniger & Koeniger, 2000; Friedrich Ruttner, 1988). However, flight timing shows great intraspecific variation and seems to be under great selective pressures, particularly in areas where several *Apis* species naturally overlap (Otis, 2000). In areas of overlap, flight timings for each species were found to be shorter than in areas of non-overlap (Otis, 2000).

A. cerana and *A. mellifera* have been found to have very similar drone flight timings in Europe and Japan, generally occurring between noon and mid to late afternoon (3-5pm) although the exact timings change between study locations (N. Koeniger & Koeniger, 2000; Oldroyd & Wongsiri, 2006; Otis, 2000; Friedrich Ruttner, 1988)(Punchihewa, 1994). No information is available on drone flight timing of *A. cerana* Java genotype in the published literature. However, drones have been observed to fly between 13:00 and 15:00 on one occasion in Cairns, Australia (Biosecurity Queensland, DAFF, unpublished data).

Sex attractants (pheromones)

Apis drones are specifically attracted to 9-oxodec-trans-2-enoic acid (9-ODA) queen mandibular pheromone, which does not seem to be species specific, leading to mating interference (drones being attracted to and attempting to mate with queens of other *Apis* species) (reviewed in N. Koeniger & Koeniger, 2000).

Drone congregation areas

Similar to other *Apis* species, *A. cerana* gather in well-defined drone congregation areas (DCA) that are perennial and can stay in the same location for up to 25 years (reviewed in Oldroyd & Wongsiri, 2006). Such DCAs facilitate rapid mating of young queens with many drones in each short queen mating flight (Woyke, 1975 in N. Koeniger et al., 2005).

Locations of *A. cerana* DCAs vary between studies (N. Koeniger & Koeniger, 2000). *A. cerana* drones were observed to gather close to trees and restrict their flight to the open space between the trees in Sri Lanka and Borneo (Koeniger & Koeniger 2000 in Oldroyd & Wongsiri, 2006; R.W.K. Punchihewa, Koeniger, & Koeniger, 1990). In Japan, *A. cerana* drones were observed using prominent trees as landmarks where they assembled under the branches (Fujiwara et al., 1994). In Germany, *A. cerana indica* imported from Pakistan congregated in an open valley far from trees (F. Ruttner et al., 1972), similar to the open-air DCAs in *A. mellifera* (N. Koeniger & Koeniger, 2000). No information is available on *A. cerana* drone congregation areas in Australia.

Brood development

A. cerana development is generally very similar to that of other *Apis* species in general, and that of *A. mellifera* in particular, including the four stages of egg, larva, pupa and adult. *A. cerana* brood development is slightly faster than that of *A. mellifera*, except for *A. cerana* queens (Table 1) (G. Koeniger, Koeniger, & Phiancharoen, 2011; Oldroyd & Wongsiri, 2006). As in other cavity-nesting species, the larva's brood cell is capped by the workers just before the last of the five larval instars (molts) (Oldroyd & Wongsiri, 2006). Unique to *A. cerana*, the raised, hardened caps of drone larvae have a pore at their apex (Boecking, Rosenkranz, & Sasaki, 1999; Hadisoesilo & Otis, 1998; Friedrich Ruttner, 1988).

Table 1. Duration of the life cycle (days) of different castes of *A. cerana* and *A. mellifera* (modified from Oldroyd & Wongsiri, 2006)

Stage	Worker		Drone		Queen	
	A. cerana	*A. mellifera*	*A. cerana*	*A. mellifera*	*A. cerana*	*A. mellifera*
Egg to larva	3	3	3	3	3	3
Larva to pupa	5	6	6	7	4-5.5	5
Pupa to adult	11	12	14	14	6-7.5	5
Total	19	21	23	24	13-16	13

Swarming and absconding

There are two types of swarming in all *Apis* species: reproductive swarming, and absconding. Reproductive swarming involves the splitting of a colony and movement of the old queen (with >70% of the colony) to a new nest site, while the new queen stays with the remaining colony and all its resources (honey, pollen, brood) in the old nest site. It generally occurs when conditions are favourable and floral resources are abundant (e.g. Tong & Boot, 2005). Absconding is also a behavioural trait common to all honey bee species, including *A. mellifera* (H. R. Hepburn, Reece, Neumann, Moritz, & Radloff, 1999).

There are two types of absconding: seasonal absconding or migration, which is the movement of a whole colony due to resource depletion, declining nest site quality and/or chronic disturbance; and disturbance-absconding caused by acute disturbance (natural, e.g. fire, flooding; or anthropogenic, e.g. intervention by beekeepers) (C. Hepburn & Radloff, 2011). Seasonal absconding involves a period of time preparing for the move (lasting days to weeks) prior to moving, when foraging, honey and brood levels are reduced. No such preparation occurs before disturbance absconding.

In general, tropical honey bee species (*Apis*), including African strains of *A. mellifera*, are more prone to absconding than temperate species due to the fact that environmental conditions (temperature, humidity and resource levels) are more variable and patchy (C. Hepburn & Radloff, 2011; H. R. Hepburn et al., 1999; Friedrich Ruttner, 1988). In general, environmental conditions are more favourable for survival year-round, which means that unlike temperate honey bees, tropical honey bees are able to move the whole colony throughout the year in response to change or disturbance, and to follow the honey flow (H. R. Hepburn et al., 1999), both of which increase fitness and survival (Friedrich Ruttner, 1988; Oldroyd, 1996 in Suwannapong et al., 2011). In contrast, temperate honey bees had to evolve in conditions that are favourable only during a short period of time with long periods of food shortage and freezing temperatures, leading to hoarding of large honey stores and “staying put” in thermally stable nests in order to survive the unfavourable conditions of winter (e.g. temperate A. mellifera; H. R. Hepburn et al., 1999; Friedrich Ruttner, 1988; Thomas D. Seeley, 1983).

Seasonal absconding

Seasonal absconding is strongly related to resource depletion and adverse environmental conditions in the current location. *A. cerana* do not store large amounts of honey, and so they do not have sufficient stores to last through a long period of unfavourable conditions (Oldroyd & Wongsiri, 2006). Instead, they move to find better conditions elsewhere, and so they have been seen to move, for example, during periods of high temperatures, after abatement of prolonged heavy rains, and during the dry season (reviewed in C. Hepburn & Radloff, 2011). In the mountainous Sichuan Province in China, temperate and tropical climates occur in close proximity depending on altitude, leading to flower blooms that are short and widely spread geographically (Chen 1995 in C. Hepburn & Radloff, 2011) – here, *A. cerana* migrate all year, following the flower blooms. Absconding has also been found highest in areas with high environmental uncertainty (e.g. drought; S. Verma & Attri, 2008), and when nest cavities are too small for the growing colony (S. Verma & Attri, 2008). However, studies on *A. cerana* in Southern China, Sumatra and India have also observed absconding irrespective of colony size, congestion or food supply (reviewed in H.R. Hepburn, 2011), or without an apparent external cause (Friedrich Ruttner, 1988). *A. cerana* in temperate areas seem to abscond less than those in tropical areas. For example, in Kashmir, Northern India, absconding is less likely, whereas in Thailand, all colonies absconded after the honey harvest (Akranatakul, 1984 in Friedrich Ruttner, 1988).

A. cerana preparing for migration (seasonal absconding) are characterised by decreasing numbers of pollen-carrying workers, greatly reduced brood feeding and rearing, and reduced predator and parasite defence (C. Hepburn & Radloff, 2011; Oldroyd & Wongsiri, 2006). In addition, honey and pollen stores, eggs and open and closed brood decrease dramatically, leading to large changes in colony demography prior to absconding (Dulta, Rana, Verma, & Mattu, 1988; Pokhrel, Thapa, Neupane, & Shrestha, 2006; R.W.K. Punchihewa et al., 1990). Methods to prevent absconding and swarming include supplementary feeding, removing combs to reduce the number of brood needing to be reared (H.R. Hepburn, 2011) as well as selective breeding and removal of newly constructed queen cells during active swarming season (L.R. Verma, 1992).

A. cerana abscond less often than open-nesting Asian honey bee species (Oldroyd & Wongsiri, 2006) but much more often than temperate *A. mellifera*. Temperate *A. mellifera*, especially wild colonies, may abscond in response to the same reasons as tropical honey bees do – depleting resources and starvation, predation, disturbance, adverse environmental conditions and disease/parasitism (Friedrich Ruttner, 1988).

The only information on absconding in *A. cerana* Java genotype includes observations by Biosecurity Queensland DAFF operations staff who reported a nest absconding when attacked by green ants, and another after strong disturbance by humans (Hyatt, 2011).

Predation (disturbance absconding)

Tropical honey bee species seem to be under more severe predation pressure than temperate honey bee species. Predation is thought to be an important and powerful force in the evolution of Asian honey bees, shaping choice of nest site, nest architecture, population size, worker morphology and behaviour (Thomas D. Seeley, 1983; Thomas D. Seeley et al., 1982).

In a study on three co-occurring honey bee species in a semi-evergreen rainforest in north-east Thailand, each month, 10% of all observed *A. cerana* nests were forced to abandon their nest due to predation (Thomas D. Seeley, 1983; Thomas D. Seeley et al., 1982). Each *A. cerana* nest was destroyed every 10 months (Thomas D. Seeley, 1983; Thomas D. Seeley et al., 1982). Main predators included tree shrews, rhesus monkeys, Eurasian honey buzzards, Malayan honey bears and giant social wasps, and also agamid lizards and green (weaver) ants found also in Australia (Thomas D. Seeley, 1983; Thomas D. Seeley et al., 1982).

Reproductive swarming

Reproductive swarming generally occurs when floral resources have been abundant, and a colony is performing well and outgrowing its hive space. When this occurs, reproductive swarming is likely to occur (Chinh, Boot, & Sommeijer, 2005; Seeley, 1985 in N. Koeniger & Koeniger, 2000; R. W. K. Punchihewa, 1994; Suwannapong et al., 2011). Little is known about swarming behaviour of *A. cerana* – most knowledge comes from *A. mellifera* (Oldroyd & Wongsiri, 2006). From *A. mellifera,* it is known that soon after a swarm has left the old nest and settles tens of meters away, scouts will start searching for suitable nest sites. Similarly, *A. cerana* have been seen to settle 20-30m away from the old nest, stay for several days, and then move to the new nest site (Oldroyd & Wongsiri, 2006). An *A. cerana* swarm also tended to settle on a near-by tree after emerging from a hive in West Pakistan (F. Ruttner et al., 1972). In a study on co-occurring *A. cerana* and *A. nigrocincta* in Sulawesi, Indonesia, dancing *A. cerana* scouts indicated distances of potential nest sites up to 1420m, but final distances that swarms actually travelled to their new nest site were found to be between 99m and 780m (Bakker, 1999). Nothing further is known about distances travelled to form a new nest.

Managed *A. mellifera* colonies are generally prevented from swarming by good hive management, removing new queen cells, re-queening and using queen excluders (Warhurst & Goebel, 2005). Wild, temperate *A. mellifera*, however, swarm nearly every year (and sometimes up to three times per seasonal cycle) in late spring or early summer when resources are highest (Winston, 1990 in Chinh et al., 2005; Thomas D. Seeley, 1983). When and how often *A. cerana* swarm is highly variable and depends on the geographic location and climate. *A. cerana* can swarm several times a year (Friedrich Ruttner, 1988). In northern Pakistan, swarming will start once a colony reaches 20000 bees, with an average of eight swarms per colony (Koeniger, 1976a in Friedrich Ruttner, 1988). In western Pakistan, Ruttner et al. (1972) found *A. cerana* to swarm twice a year, with up to 10 swarms produced per swarming season (average of six swarms).

As reviewed in Hepburn (2011), timing of swarming has been found to vary from no seasonal rhythm (Sumatra & Southern India), biphasic (Sumatra, Southern India, Pakistan, Japan & China; Vietnam, Tong & Boot, 2005), to distinct times of the year (Plains of India – April-May; Kashmir Valley – June-July; Pakistan – February/March and August/September, F. Ruttner et al., 1972). In Punjab, northern India, most swarms issued before 1pm, with an average weight of 1kg and a maximum weight of 1.8kg (equalling approximately 16000 bees; Friedrich Ruttner, 1988; P. L. Sharma, 1960).

Reproductive swarming is thought to be linked to flowering intensity and nutrient flow into the colony (Chinh et al., 2005). When foraging conditions are good over extended periods of time (as for example in the tropics), swarming will occur more frequently, and swarming and the production of queens and drones will be asynchronous. For example, Africanised honey bees swarmed up to 12 swarms per cycle (Winston, 1990 in Chinh et al., 2005), and *A. cerana* produced up to eight swarms in northern Pakistan (Koeniger, 1976 in Chinh et al., 2005). When foraging conditions are good only at certain times of the year (e.g. spring and summer in temperate zones), swarming will occur during those specific times, and swarming and the production of queens and drones will be synchronous (as seen in temperate *A. mellifera*) (Chinh et al., 2005).

Little is known about frequency and timing of swarming of *A. cerana* Java genotype in Australia. Swarms were reported in any month of the year between 2009 and 2011 in Cairns, Australia (Hyatt, 2011). No seasonal rhythm was apparent. However, it is unknown which of these swarms were reproductive and which were absconding swarms (Hyatt, 2011). In Australia, swarms had an average size of 2676 bees (466-6800 bees; N=65) (Hyatt, 2011), which appears much smaller than reported in the literature for within the natural range of *A. cerana* (Tong & Boot, 2005).

Other behaviour

Temperament

A. cerana has been described as docile (Hisashi, 2010), mild (Bhuiyan et al., 2002), tolerant and timid (Friedrich Ruttner, 1988) with a gentle temperament (Verma, 1990 in Partap, 2011) and low stinging tendency (Friedrich Ruttner, 1988), although it will sting when cornered or highly disturbed, just as *A. mellifera* does. *A. cerana* is said to be less prone to stinging than *A. mellifera* and has less alerting pheromone in its sting (half the amount of *A. mellifera ligustica*, the Italian bee) – resulting in fewer additional stings by defending bees (Friedrich Ruttner, 1988). In a simulated attack on their nest, *A. cerana* guards simply retreated into their nest cavity (Friedrich Ruttner, 1988; Thomas D. Seeley, 1983). When destroying nests as part of the previous eradication (now Transition to Management) program in Australia using aerosol spray in close proximity to the nest, bees rarely sting despite being in uproar (Koetz, pers. obs.).

Diseases and hygiene

Where honey bees coexist they are bound to interact in some way (e.g. robbing) and so parasites and pathogens can be transmitted between species (Kojima et al., 2011). This is particularly worrisome where species that would not naturally come into contact are forced to coexist (e.g. *A. mellifera* and *A. cerana*)(Kojima et al., 2011; Mack et al., 2000). Diseases and parasites have been introduced from exotic *A. mellifera* to native *A. cerana* and *vice versa* (e.g. Varroa from A. cerana to A. mellifera, and the tracheal mite A. woodi as well as Israeli Acute Paralysis virus from A. mellifera to A. cerana; Kojima et al., 2011; Oldroyd, 1999).

A. cerana diseases include bacterial infections (American and European foulbrood), protozoan and fungal infections (*Nosema ceranae* and *N. apis*; and chalkbrood) and virus infections (Denis L. Anderson, 1995; Fries, 2011; Kojima et al., 2011; Apis Iridescent Virus, Deformed Wing Virus, Kashmir Bee Virus, Thai Sacbrood Virus, Black queens cell virus, Israeli acute paralysis virus; Oldroyd & Wongsiri, 2006; Suwannapong et al., 2011). *A. cerana* parasites include *Varroa* (*V. destructor, V. jacobsoni,* and *V. underwoodi*) and tracheal mites (*Acarapis woodi*) as well as non-parasitic mites (reviewed in Oldroyd & Wongsiri, 2006; Suwannapong et al., 2011; Warrit & Lekprayoon, 2011). In addition, wax moth is also found in *A. cerana* (reviewed in Oldroyd & Wongsiri, 2006). Diseases of *A. cerana* Java genotype in particular and *A. cerana* Java genotype in Australia are as yet unknown. All nests and swarms detected in the Cairns area in north-east Queensland, Australia, since 2007, have been checked for the presence of *Varroa* spp, tracheal mites, *Tropilaelaps* spp. and *Nosema* spp. No *Varroa*, *Tropilaelaps* or tracheal mites have so far been found in the Cairns population. However, *Nosema* is present in some colonies (Biosecurity Queensland, DAFF, unpublished data).

A. cerana has been found to clean itself and each other more thoroughly than *A. mellifera* (Boecking, 1999; Boecking & Spivak, 1999; Rath, 1999; Rath & Drescher, 1990). In addition, infected brood is either removed before capping (e.g. larvae infected with American foulbrood or worker brood with Varroa; Fries, 2011; Rath & Drescher, 1990), or it is entombed (e.g. drone larvae infected with Varroa; Boecking, 1999; Boecking & Spivak, 1999; Rath, 1999). Experiments also showed that the presence of *Varroa* semiochemical compounds result in immediate cleaning behaviour in *A. cerana* but not in *A. mellifera* (Rosenkranz, Tewarson, Singh, & Engels, 1993; Sasagawa, Matsuyama, Leal, & Peng, 2000).

A. cerana are generally regarded as much more hardy and disease-resistant than *A. mellifera*, making it a better honey bee species in many poorer areas of Asia as *A. cerana* requires less management and no treatment for diseases (Hisashi, 2010; L. R. Verma, 1990; S. Verma & Attri, 2008).

Natural predators

Natural predators of honey bees are attracted to all parts of the colony, including adult bees, larvae and pupae, pollen, honey and wax (Fuchs & Tautz, 2011). Natural predators of *A. cerana* include wasps and hornets (Oldroyd & Wongsiri, 2006; F. Ruttner et al., 1972), which tend to prey on foragers but also at times attack colonies (Oldroyd & Wongsiri, 2006). Ants also attack *A. cerana* colonies, including Green ants (*Oecophylla smaragdina*) and smaller ant species (Oldroyd & Wongsiri, 2006). Vertebrate predators of *A. cerana* include toads, frogs, lizards and geckos, rats, honey badgers, macaque monkeys, tree shrews, most Asian bears (such as Malayan honey bear, Sloth bear and Asiatic black bear), martens, tigers and many birds (e.g. honey buzzards, bee-eaters, swifts, drongos and honeyguides) as well as humans (Fuchs & Tautz, 2011; Oldroyd & Wongsiri, 2006). Amongst this list, the predators that also occur in Australia include ants (including Green ants), possibly some Australian native wasps and/or hornets, lizards, frogs and toads, Rainbow bee-eaters, swifts and drongos. Of these, all but wasps, hornets and drongos have been observed preying on *A. cerana* (Koetz, 2012).

In cavity-nesting *Apis* species, the main defence against predators is living in a protected cavity with a small entrance that can be easily guarded (Fuchs & Tautz, 2011; Oldroyd & Wongsiri, 2006). Colony defence behaviours include abdomen shaking, hissing (through wing vibrations), group defence (including grasping, pulling and biting, as well as forming a “bee-ball” around wasps, killing it by over-heating and/or asphyxiation), and stinging, which is the bees’ main defence against vertebrates (Fuchs & Tautz, 2011; Oldroyd & Wongsiri, 2006; Friedrich Ruttner, 1988; K. Tan et al., 2012).

Other

One recognisable difference between *A. cerana* and *A. mellifera* is the fanning position of workers at the hive entrance – *A. cerana* workers ventilate the hive by fanning with their heads away from the entrance, whereas *A. mellifera* fan with their heads turned towards the entrance (Friedrich Ruttner, 1988). As entrances of hived bees are generally at the bottom of the nest/hive, this results in *A. cerana* workers facing upwards, whereas *A. mellifera* workers face downwards (Hisashi, 2010; Friedrich Ruttner, 1988).

Pollination

One of the most important (but less obvious) services provided by bees is pollination. Pollination has two important consequences: it maintains biodiversity of flowering plants, and it maintains ecosystem function. Reduced pollination can lead to local extinction of plant species, a decline in fruit and seed-eating animals, loss of vegetation cover and, ultimately, the loss of a healthy ecosystem and its services. In agriculture, lack of adequate pollination can lead to deformed fruit and reduced crop yield (Partap, 2011).

Pollination is a prerequisite for plant fertilisation and fruit/seed-set (Partap, 2011). However, not all plants are pollinated by bees. Other pollination modes include abiotic agents (wind, water, gravity), as well as a variety of other animals (biotic agents) including other insects, birds and mammals (Partap, 2011). Biotic pollination usually involves a relationship between the plant and its pollinators – pollinators are attracted to and given a reward for visiting a flower (e.g. nectar, pollen), and while visiting flowers, pollinators inadvertently move pollen from flower to flower – leading to pollination (Kevan, 1995).

Approximately 80% of all flowering plants depend on biotic pollinators (Partap, 2011), and an estimated 75% of the world's crops benefit from biotic pollination (A.-M. Klein et al., 2007). About one-third of the global food production depends on biotic pollinators, particularly bees (Genersch, 2010). Bees also play an important role in tropical areas – social bees were found to pollinate 32% of plant species in lowland dipterocarp rainforest in Sarawak, Malaysia (Momose et al., 1998) and 72.7% of cultivated tropical plant species were pollinated by bees (21.3% by honeybees; Roubik 1995 and Nabhan & Buchmann 1997 in Pritchard, 2005).

Wild bees also play a vital role in pollination, particularly in Australia where farmers rely mostly on the free services of feral bees (*A. mellifera*) for pollination (Cunningham, FitzGibbon, & Heard, 2002; De Barro, 2007).

Pollination services – crops

In Asia, *A. cerana* is regarded as an excellent crop pollinator for a large variety of fruit and vegetable crops, sometimes outperforming *A. mellifera* (Khan, 1995; Matsuka, Verma, Wongsiri, Shrestha, & Partap, 2000; Partap, 2011; Partap & Verma, 1994; Sihag & Mishra, 1995; L.R. Verma, 1992; L. R. Verma & Partap, 1994; L. R. Verma & Rana, 1994). This is thought to be due to the fact that *A. cerana* begin foraging earlier in the day and cease later in the day, pollinating flowers for longer than *A. mellifera,* and also because *A. cerana* employ relatively larger numbers of pollen collectors (compared to nectar collectors) than *A. mellifera* (Matsuka et al., 2000; Partap, 2011; Partap & Verma, 1994; L.R. Verma, 1992; L. R. Verma & Partap, 1994; L. R. Verma & Rana, 1994).

A. cerana has been reported as pollinating fruit and nuts, vegetables, pulses, oilseeds, spices, coffee, as well as fibre and forage crops, and has been found especially important in pollinating cauliflower, onion and okra in India (reviewed in A.-M. Klein et al., 2007; A. M. Klein, Steffan-Dewenter, & Tscharntke, 2003; Partap, 2011; Sihag & Mishra, 1995). Studies specifically undertaken to show the impact of *A. cerana* on crop yield and productivity showed that pollination by *A. cerana* increased fruit and seed set, increased the quality of fruit and seeds, and reduced premature fruit drop (reviewed in A.-M. Klein et al., 2007; A. M. Klein et al., 2003; Partap, 2011). Apple, peach, plum, citrus and strawberry all showed a marked increase in fruit set (10 to 112% increase) and weight (33 to 48% increase). Similar results were also shown for a broad range of vegetables, oil rape seed, sunflower, buckwheat, soybean, cotton (reviewed in Partap, 2011) and coffee (A. M. Klein et al., 2003).

However, most of the studies reviewed in Partap (2011) were conducted in temperate climates on temperate *A. cerana*. Few studies could be found on crop pollination of *A. cerana* Java genotype. One study on pollination of the non-food crop *Jatropha curcas* in Java, showed both *A. cerana* (presumably Java genotype) and *A. mellifera* to be pollinators (Atmowidi, Riyanti, & Sutrisna, 2008). Although *A. mellifera* seemed to be better pollinators than *A. cerana* for this particular crop, there was no statistical significance and sample sizes were very small (Atmowidi et al., 2008).

Pollination services – wild flora

A. cerana is an important canopy pollinator in the rainforests of Western Ghats and Sri Lanka, but little is known about the relationship between wild *A. cerana* and wild flora in other parts of Asia or the world (reviewed in Corlett, 2004). At high altitudes in the Asian tropics, and in north-eastern Asia, *A. cerana* is the only social bee present and so is likely to be an important if not the main pollinator (reviewed in Corlett, 2004). For example, on the Amami Islands (300km off the southernmost tip of Japan), *A. cerana* is the only bee pollinator during winter months (Kato, 2000 in Corlett, 2004). In Hong Kong, *A. cerana* is a very important pollinator as it is the dominant visitor to 55% of the 83 woody plant species studied (Coreltt, 2001, in Corlett, 2004). *A. cerana*'s ability to thrive in disturbed landscapes may also give it an important role as a pollinator, compensating for loss of other pollinators, similar to the role of *A. mellifera* in tropical America (Corlett, 2004).

Controversy surrounds whether (and how) introduced honey bees impact on Australian native ecosystems. Research has found that some native flora are negatively impacted by honey bees (*A. mellifera*), some flora was positively impacted and some not at all (Gross, 2001; Gross & Mackay, 1998; Paton, 1997). It is also thought that *A. mellifera* is a less effective pollinator of Australian flora than native bees, may remove pollen without pollination occurring (pollen robbing), and that generally *A. mellifera* will cause changes to the abundance of native flora and fauna (reviewed in Pyke, 1999). No studies have been conducted on the effect of *A. cerana* on the Australian native flora, or whether it is a more or less effective pollinator than *A. mellifera* or native bees (see also Impact on the Australian environment section below).

Furthermore, little is known about the role of *A. cerana* in pollinating and hence helping the spread of unwanted flora (weeds). However, it has been shown that, for example, the spread of *Phyla canescens* (Lippia) and *Cytisus scoparius* (Scotch Broom) in Australia is greatly facilitated by *A. mellifera*, as it is the primary floral visitor of these weeds that require insect pollination for successful seed set (Gross, Gorrell, Macdonald, & Fatemi, 2010; Simpson, Gross, & Silberbauer, 2005). *A. cerana* may play a similar role and may facilitate the spread of some weeds.

Beekeeping

Overview and history

A. cerana has been used for beekeeping and honey production for over two thousand years. The first references of *A. cerana* in relation to beekeeping appear from the 300s BC in northern India and from 200s BC in China and Vietnam (Crane, 2004). In tropical south-east Asia, bee-hunting seemed to be more common than beekeeping due to the larger number of open-hive bee species living in the favourable, warm conditions (see tropical vs. temperate below). However, in some areas (e.g. Java), widespread deforestation led to a decrease of open-nest species, which subsequently resulted in an increase of log-hive beekeeping of *A. cerana* Java genotype from 1800s (Crane, 1999). Box-hives were also introduced around this time, probably by Chinese traders, and frame hives appeared from 1900, introduced by European and American missionaries (Crane, 1999). Today, *A. cerana* are kept traditionally as well as in modern, top-bar removable frame hives (Crane, 1999).

A. cerana beekeeping is common across Asia (Ahmad, Joshi, & Gurung, 2007; Bradbear, 2009; Crane, 1999; Oldroyd & Wongsiri, 2006; Partap & Verma, 2000; N. Q. Tan & Binh, 1994; S. Verma & Attri, 2008), although *A. cerana* has declined dramatically in some areas since the introduction of the non-native *A. mellifera* (Oldroyd & Nanork, 2009; Partap & Verma, 2000; L. R. Verma, 1990). In many areas, *A. cerana* beekeeping is an integral part of social and cultural heritage (L. R. Verma, 1990) and a valuable part of rural livelihood (Bradbear, 2009). How *A. cerana* is kept varies greatly and ranges from finding and harvesting natural nests in forests, to keeping simple hives made of grass or bamboo, hives in walls of houses, logs, pots or boxes, cavities gauged out of trees and closed with a wooden board, to modern beekeeping techniques including movable frame or comb (top-bar) hives (Bradbear, 2009; Crane, 1999; F. Ruttner et al., 1972; S. Verma & Attri, 2008).

A. cerana is prone to abscond, and Asian beekeepers have developed methods to deal with this problem. Methods of reducing absconding and managing swarming include caging or tethering the queen of a new colony until some comb is built, clipping the queen’s wings after her mating flight, removing new queen cells, and managing the amount of brood comb and available space within the hive by splitting colonies (Crane, 1999; R. W. K. Punchihewa, 1994).

Asian honey bee products and services include honey and brood for consumption, beeswax, and pollination services (Oldroyd & Wongsiri, 2006; Partap, 2011).

Tropical versus temperate *A. cerana* beekeeping

There seems to be a marked difference between temperate versus tropical *A. cerana* in terms of their suitability for beekeeping and honey production. The majority of beekeeping literature refers to temperate *A. cerana,* which seem to be more profitable for beekeeping than tropical *A. cerana* including *A. cerana* Java genotype, just as temperate *A. mellifera* are more suitable than tropical *A. mellifera*. Nevertheless, tropical *A. cerana*, including *A. cerana* Java genotype, can be successfully kept in hives for the purpose of honey production and pollination (see below).

The main differences between temperate and tropical *A. cerana* relate to the tropical strains' tendency to swarm and abscond, which is a result of adaptation to the variable conditions of the tropics, as well as to the increased predation pressure on tropical strains (see Swarming and absconding above).

Nevertheless, tropical *A. cerana* has been used successfully for beekeeping purposes.

A. cerana Java genotype beekeeping

Historically, beekeeping techniques were more developed in temperate than tropical regions due to the ease of domestication of temperate strains of *A. mellifera*. Such beekeeping developments did not readily spread into tropical areas, which may be explained by several reasons: Open-nest species that can be hunted are more common in tropical regions, precluding the need to keep bees in hives; tropical *A. cerana* have smaller population sizes and seem to be more prone to absconding; and the availability of palm sugar as an alternative to honey (Crane, 1999).

Crane (1999) reviewed beekeeping techniques of *A. cerana* across Asia, including Indonesia and Malaysia, the home of *A. cerana* Java genotype. Records from Kalimantan (West Borneo) during colonial times describe the use of bamboo and bark hives, as well as log hives (approx. 45-60cm long and 15-30cm across) smeared with honey and hung in the forest to entice a swarm to build a nest, which was then taken into the village (Low 1848 and Hoekman 1929 in Crane, 1999).

On the island of Java, Indonesia, a similar technique was used to attract and capture swarms (Hoogeveen 1864 in Crane, 1999). Such hives could yield 12 combs of honey each year, and with careful handling bees remained in these log-hives for several years (Veth 1876 in Crane). Other traditional hives used in Java include hollowed horizontal logs (50-100cm long and 10-25cm across) closed at the ends with wooden boards or half coconut husks containing flight entrance(s), primitive boxes with lids, inverted earthenware cook pots closed with a wooden board containing flight entrance(s), and hives made from bamboo (reviewed in Crane, 1999). Hives were generally hung under the eaves of houses or supported by bamboo posts off the ground, although predation by ants could be a problem in this case. Interestingly, in order to prevent swarming, young queens in existing Javanese hives were killed or tethered (Crane, 1999).

Traditional hives used in other tropical areas include earthenware pots, which at swarming time were rubbed with wax (or smoked using resin and the mouth rubbed with wax and honey) and hung in the forest where swarms would occupy them within 10-12 days (southern India; Crane 1999).

A. cerana Java genotype are also kept in Irian Jaya (west Papua New Guinea) where they were introduced for honey production by transmigrants from Java in the 1970's (Figure 6; Lee, 1995).

Figure 6. *A. cerana* Java genotype log hives in Irian Jaya (PNG) (Lee, 1995)

Other tropical *A. cerana* beekeeping

A. cerana was being successfully kept in Phnom Penh, Cambodia (Yoshikawa & Ohgushi, 1965). Although it was reported as *A. cerana javana* by the authors, it is uncertain whether these bees were indeed *A. cerana* Java genotype or *A. cerana indica* (Sarah E. Radloff et al., 2010). *A. cerana* seemed to be doing better than *A. mellifera* – *A. mellifera* colonies seemed to be smaller, were prone to reported 'tick' (probably mite) infestation, and foraging was much reduced during the rainy season compared to *A. cerana* (Yoshikawa & Ohgushi, 1965). Nevertheless, harvest of honey was still higher in *A. mellifera* (10-20kg per box) compared to *A. cerana* (5-6kg per box; Yoshikawa & Ohgushi, 1965).

Although not generally regarded as a tropical strain, *A. cerana japonica* is successfully kept on the Goto Islands, Southern Japan, a tropical area with distinct wet/dry seasons (Hisashi, 2010). This species was reintroduced to the islands in 2007 after becoming locally extinct during and after the World War II due to deforestation (Hisashi, 2007). *A. cerana japonica* is now successfully established and thriving, and considered docile and a good pollinator. They are kept in box pile hives as it is thought that vertical, long hives mimic tree hollows and encourage the bees' tendency to built very long combs (Figure 7). Honey production has been increasing and in 2009 was approximately 16kg of honey per colony (Hisashi, 2010). *A. cerana* is preferred over *A. mellifera* as *A. mellifera* is more prone to disease and parasite infestation and require more beekeeping equipment than *A. cerana* (Partap, 2011). In this area, *A. cerana* is reported to only forage within two kilometres of the hive (compared to four kilometres in *A. mellifera*), thus covering only one-quarter of the area that *A. mellifera* would (Hisashi, 2010). As *A. cerana* honey sells for four times the price, beekeeping with *A. cerana* is deemed easier and more profitable on these islands (Hisashi, 2010).

Figure 7. Beekeeper amongst his *A. cerana japonica* hives on the Goto Islands, Japan (Hisashi, 2010)

A. cerana versus *A. mellifera* beekeeping

In general, *A. mellifera* are the superior honey collector due to both their need for honey hoarding in order to survive harsh winters, as well as long years of selective breeding for just this trait (Crane, 1984). *A. mellifera* are two to ten times more productive than *A. cerana* (L. R. Verma, 1990; Yoshikawa & Ohgushi, 1965) and are easier to keep due to lower rates of absconding. In Chitwan, Nepal, *A. cerana* produced on average 8.1kg/colony/year whereas *A. mellifera* produced more than three times as much with 28.7kg/colony/year (Suroj & Pokhrel, 2009).

However, *A. cerana* are superior to *A. mellifera* in other aspects. To produce large amounts of honey, *A. mellifera* requires intensive management, standardised equipment and larger foraging areas (Partap, 2011). *A. mellifera* also need to be supplementary fed during lean times, and they dramatically reduce foraging in the tropical wet season, again leading to the need for supplementation (Partap, 2011). *A.*

mellifera are also much more prone to wasp attack, diseases and parasitic mites, which requires chemical treatment that could make their honey less desirable.

On the other hand, *A. cerana* (including *A. cerana* Java genotype) are very hardy, disease resistant honey bees that require little management. Start-up and maintenance costs are minimal, and they can be kept in low-cost box hives or rough containers (Oldroyd & Wongsiri, 2006). Importantly, they are unaffected by mites and diseases such as *Varroa* and *Tropilaelaps clareae* (Lee, 1995; Oldroyd & Wongsiri) that have affected *A. mellifera* colonies around the world.

Due to their resistance to disease and lower capital costs, *A. cerana* tend to be more economic in poorer areas, e.g. Himachal Himalaya, India, where for each *A. cerana,* 4.6 *A. mellifera* are needed to obtain equal financial reward (S. Verma & Attri, 2008). Similarly, *A. cerana* are more economic than *A. mellifera* in southern China (Wongsiri, Lai, & Liu, 1986).

It must be noted that some of these examples refer to the temperate climate *A. cerana* strains, which are better honey producers than tropical strains such as *A. cerana* Java genotype. Nevertheless, *A. cerana* Java genotype has been successfully kept in hives to produce honey (Crane, 1999; Yoshikawa & Ohgushi, 1965).

Although levels of honey production differ in the two species, in the past and before undergoing selective breeding *A. mellifera* was, commercially speaking, a poor honey producer (Crane, 1984), producing similar amounts of honey (2-5kg/year) as *A. cerana* does today (Pechhacker, Joshi, & Chatt, 2001). So *A. cerana* may be termed equivalent to a natural, historical, European *A. mellifera*.

A. cerana versus *A. mellifera*

Competition between *A. cerana* and *A. mellifera*

When species come to overlap geographically and compete for the same, limited resources, one of two things can happen: competitive exclusion, i.e. one species out-competes the other so that one species disappears and the other thrives; or resource partitioning, where the two species partition their resources in such a way that both species can occur together (Gordon, 2000; Krebs, 1972). It is potentially possible that the ecological and behavioural differences of *A. mellifera* and *A. cerana* will result in sufficient niche partitioning that both species can co-occur successfully, as was shown in one study in India (H. K. Sharma, Gupta, & Rana, 2000a). It is also possible that both species can coexist if resources, such as flowers, are not limited. A shared resource must be limited in order for competition to occur (Krebs, 1972).

The two most important resources for cavity-nesting honey bees are floral resources and nest cavities (Winston, 1987). Honey bees can compete for pollen and nectar while visiting flowers or they can attempt to rob honey from other nests (of the same of a different species). Both of these will be examined in turn.

It needs to be noted here that *A. cerana* and *A. mellifera* do not naturally coexist, and so all associations between them are artificial.

Competition for floral resources

Research in Nepal and India found that significantly more *A. cerana* foraged on flowers of different crops, and spent more time on each flower, when *A. mellifera* were absent (Partap, 1998 in Partap, 2000; H. K. Sharma et al., 2000a; M.-X. Yang, Tan, Radloff, & Hepburn, 2011), indicating that *A. mellifera* was the superior competitor. Similar results were found when both species were competing for the same sugar feeding station – *A. mellifera* were more aggressive and successfully and consistently excluded *A. cerana* (Sakagami, 1959; Dhaliwal & Atwal, 1970 in M.-X. Yang et al., 2011).

A. cerana was also found to forage on a number of plant species that *A. mellifera* did not visit, and *vice versa*, and on those plant species that were visited by both species they avoided foraging in the presence of the other species (H. K. Sharma, Gupta, & Rana, 2000b).

Two species may also avoid competition if foraging times differ (e.g. *A. cerana* and *A. mellifera* in India; Verma 1995), or if foraging is partitioned spatially (e.g. foraging at the top, middle or bottom of trees; *A. cerana* vs. *A. koschevnikovi*, Borneo; Rinderer, Marx, Gries, & Tingek, 1996). *A. cerana* had a much higher metabolic rate and foragers made many more trips within the same habitat than other species. Foragers also began foraging earlier in the day and they tolerated lower temperatures than *A. mellifera* (Fred C. Dyer & Thomas D. Seeley, 1991; Partap, Shukla, & Verma, 2000). *A. cerana* are also said to be more industrious while collecting pollen from scattered flowers of a variety of plant species, spending less time on each flower, whereas *A. mellifera* prefer big flower patches of fewer species where they spend more time on each flower (Kuang & Kuang, 2002 in Partap, 2011; Partap et al., 2000; Friedrich Ruttner, 1988; Wongsiri et al., 1986).

Thus, these differences in timing and flower patch preferences may be enough to avoid competitive exclusion. However, further research is needed to confirm this.

Robbing and direct fighting

Robbing bees enter another colony's nest, kill bees and take their honey stores. The smaller the colony the more susceptible it is to robbing (Partap, 2011). Robbing usually occurs only when floral resources are low, when the nectar flow is interrupted or when a colony is weak and/or diseased (reviewed in M.-X. Yang et al., 2011).

Interestingly, *A. mellifera* showed a much stronger defence-response to non-nest mates (of the same or different species) than any of the Asian honey bees examined, which means that *A. mellifera* defended their nest much more strongly than *A. cerana* did (Breed, Deng, & Buchwald, 2007). Studies on robbing behaviour between managed hives of *A. mellifera* and *A. cerana* kept at the same apiary showed that although *A. cerana* initiated robbing during lean times, *A. mellifera* usually won, killing the *A. cerana* colony and taking over their foraging area (Yang, 2001 in Sakagami, 1959; M.-X. Yang et al., 2011). In Japan, robbing of *A. cerana* hives by *A. mellifera* is much more common than robbing of *A. mellifera* hives by *A. cerana* (Sakagami, 1959). *A. cerana* were reported to have a very weak defence against intruders and were observed to feed robber bees (Friedrich Ruttner, 1988; Sakagami, 1959).

Research in Japan on mixed colonies of, and competition between, *A. mellifera ligustica* and *A. cerana*, found that *A. mellifera* behaved much more aggressively towards *A. cerana*, and when placed in confinement together A*. mellifera* were stronger and the superior fighter to *A. cerana* (1959). However, *A. cerana* were reported to deliver a powerful bite. When competing for a sugar syrup station, *A. cerana* always lost (Sakagami, 1959).

However, *A. cerana* appeared to be superior robbers of *A. mellifera* hives on the Solomon Islands (D. Anderson, 2010; Annand, 2009). In the presence of *A. cerana* and *A. dorsata*, *A. mellifera* also did not thrive in a forest ecosystem on the Philippines (Manila-Fajardo & Cervancia, 2003). In addition, there was some anecdotal evidence of single occurrences of *A. cerana* robbing Australian native insects (sugar ants, *Camponotus* sp., and a stingless bee, *Trigona* sp.) (Hyatt, 2011). No literature could be found with comparable evidence of *A. mellifera* robbing native insects, indicating a lack of research into whether or not *A. mellifera* rob nests of native Australian bees. However, research shows that the presence of foraging *Apis mellifera* results in reduced visitation by native bees (Gross, 2001). In addition, in the majority (91%) of interactions between *Apis mellifera* and native bees on the pioneer plant *Melastoma affine* in tropical north Queensland, native bees were disturbed from foraging at flowers by *Apis mellifera* (Gross & Mackay, 1998).

Mating interference

As discussed previously, differences in the timing of mating flights, sex attractants (pheromones) and drone congregation areas are important in establishing and maintaining isolation between different *Apis* species (N. Koeniger & Koeniger, 2000; Friedrich Ruttner, 1988). However, there seems to be some overlap between *A. cerana* and *A. mellifera*. *A. cerana* and *A. mellifera* have been found to have very similar drone flight timings in Europe and Japan (N. Koeniger & Koeniger, 2000;

Oldroyd & Wongsiri, 2006; Otis, 2000; R. W. K. Punchihewa, 1994; Friedrich Ruttner, 1988) as well as in Cairns, Australia (Koetz, pers. obs.).

It has been observed that *A. mellifera* drones are attracted to *A. cerana* queens and *vice versa*, and that *A. mellifera* drones outcompete *A. cerana* drones when mating with *A. cerana* queens, with detrimental effects on *A. cerana* queens (Ruttner & Maul 1983 in Muzaffar & Ahmad, 1990; Friedrich Ruttner, 1988). In Pakistan, in the presence of *A. mellifera* drones in an area, virgin *A. cerana* queens did not lay at all or became drone layers (F. Ruttner et al., 1972). *A. cerana* queens in an *A. mellifera*-dominated area were found to have very low success rate at mating with their own species, especially when *A. mellifera* colonies were in close proximity (Muzaffar & Ahmad, 1990; Friedrich Ruttner, 1988). Similarly, *A. mellifera* queens in an *A. cerana*-dominated area also had very low success rate at mating with their own species (Muzaffar & Ahmad, 1990; Friedrich Ruttner, 1988).

Examples where *A. cerana* and *A. mellifera* coexist (through human introduction)

Solomon Islands

A. cerana Java genotype and *A. mellifera* did not co-exist successfully on the Solomon Islands, where managed *A. mellifera* declined severely and honey production ceased entirely after *A. cerana* Java genotype were introduced to the islands in 2003 (D. Anderson, 2010; D. L. Anderson et al., 2012). By 2008, the number of *A. mellifera* hives on Guadalcanal (the main island) had declined from 2000 to 5. Although initially it was thought that the introduction of parasitic *Varroa* mites on introduced *A. cerana* caused the decline, this was found not to be the case. Introduced *Varroa* mites were *V. jacobsoni*, which do not breed on *A. mellifera* brood (D. L. Anderson, 2004). Losses of *A. mellifera* were attributed to competition for floral resources, *A. cerana* robbing *A. mellifera* hives, leading to starvation in *A. mellifera*, as well as the introduction of the microsporidian pathogen *Nosema ceranae* (D. Anderson, 2010; D. L. Anderson et al., 2012; Annand, 2009).

Asia

A. cerana and *A. mellifera* co-exist across Asia. *A. cerana* and *A. m. ligustica* were kept successfully in close proximity to one another within an apiary in Cambodia (Yoshikawa & Ohgushi, 1965). In Pakistan, *A. cerana, A. mellifera, A. dorsata* and *A. florea* coexist, and both *A. cerana* and *A. mellifera* are kept in hives, although reproductive interference occurs between the species (Muzaffar & Ahmad, 1990).

In some areas across Asia where *A. mellifera* have been introduced, widespread declines of *A. cerana* have been observed, particularly in Taiwan, Japan and China (Juntawong & Pechhacker, 1994; Friedrich Ruttner, 1988; Sakagami, 1959; G. Yang, 2005; M.-X. Yang et al., 2011; Yu & Han, 2003). Such declines have been attributed to *A. mellifera* being a more aggressive competitor and prone to robbing *A. cerana* nests, leaving *A. cerana* to starve or abscond (Moritz, Haertel, & Neumann, 2005).

Similarly, in Vietnam, *A. mellifera* and *A. cerana* are generally kept in different areas – *A. cerana* do well in the coastal coconut plantations, whereas *A. mellifera* are kept at higher altitudes. However, when both species are brought together in lean times, they were reported to fight, with *A. mellifera* killing or chasing away *A. cerana* without exception (N. Q. Tan & Binh, 1994).

Far North Queensland, Australia

A. cerana and *A. mellifera* have been co-existing in the Cairns area of Far North Queensland Australia since *A. cerana* was introduced in 2007. No reports of direct robbing attempts on *A. mellifera* hives could be found. Similarly, the impact of *A. cerana* on the local honey production has not been documented. The only observation of *A. cerana* robbing behaviour has been when *A. cerana* robbed wax and honey off an individual 'sticky frame' (a single, separated hive frame that has had the honey removed from it) with no *A. mellifera* present (M. Damon, pers. com.).

However, robbing and taking-over of weakened *A. cerana* nests by *A. mellifera*, as well as strong and effective nest entrance defence by *A. mellifera*, have been observed on several occasions (pers. obs.) as well as by local beekeepers (M. Damon, pers. com.).

Australian versus Solomon Islands experience

The devastating losses of *A. mellifera* hives on the Solomon Islands resulted in fears that this may also happen in Australia. However, so far there is no evidence of adverse effects of *A. cerana* on *A. mellifera* in Australia. The question remains, why does there seem to be such a difference in impact of *A. cerana* between Australia and the Solomon Islands? Following conversations by the author with Dr. Denis Anderson, who led an ACIAR-funded research project into the effects of *A. cerana* on *A. mellifera* on the Solomon Islands (D. Anderson, 2010; D. L. Anderson et al., 2012), some observations and comparisons are as follows:

- The Solomon Islands are relatively small compared to the available habitat in Far North Queensland. This may have led to fierce resource competition between *A. cerana* and *A. mellifera* on the Solomon Islands. When resources are limited and neither of two species can switch resources or modify its behaviour to reduce competition, one species inevitably declines (see 'competitive exclusion' above).
- The habitat and climate on the Solomon Islands is very similar to that in the Indonesian islands where *A. cerana* Java genotype is endemic. Both areas lie within 12 degrees latitude of the equator, resulting in monsoon tropical climate that supports wet tropical vegetation, e.g. lowland rainforest. The temperate strain of *A. mellifera* kept on the Solomon Islands does not do as well in the tropics as in temperate areas, whereas the tropical *A. cerana* Java genotype is well adapted to tropical conditions. Thus, *A. mellifera* may have been disadvantaged.
- Solomon Islanders may not have had knowledge of, or access to, optimum techniques of keeping and managing *A. mellifera* hives, making them more prone to adverse effects of *A. cerana*.

There have, so far, been no reports on the adverse effects of *A. cerana* on *A. mellifera* in far north Queensland, Australia. This may indicate that the results seen in the Solomon Islands may not be indicative of the future impact of *A. cerana* in Australia.

Impact on the Australian environment

A detailed review of the potential impact of *A. cerana* on the Australian environment has been covered in detail elsewhere (see Carr, 2011) and is beyond the scope of this review. However, a summary of the main impacts and gaps in knowledge are presented here.

Competition with *A. mellifera*

As has been outlined above, *A. cerana* and *A. mellifera* may compete. However, evidence shows that *A. mellifera* generally outcompetes *A. cerana* (Sakagami, 1959; N. Q. Tan & Binh, 1994; M.-X. Yang et al., 2011). The only well-documented case where *A. cerana* outcompeted *A. mellifera* was on the Solomon Islands (D. Anderson, 2010). So far there is no evidence that *A. cerana* outcompetes *A. mellifera* in Australia. Some anecdotal evidence showed that *A. mellifera* outcompetes *A. cerana* in Far North Queensland, Australia (pers. obs.; M. Damon, pers. com.). Nevertheless, competition between the two species needs to be closely monitored and experimentally determined).

Potential for becoming an urban pest

A. cerana tend to live in smaller colonies and nest in smaller cavities than *A. mellifera*. As a result, *A. cerana* readily nests in houses, letterboxes, or any relatively undisturbed cavity in and around human dwellings. As a consequence, greater contact between humans and *A. cerana* than between humans and *A. mellifera* is likely. Therefore, there is a greater probability that humans may be stung by *A. cerana*.

However, *A. cerana* do not seem to be more aggressive than *A. mellifera*. *A. cerana* have been described as docile, mild, tolerant and timid with a gentle temperament (Bhuiyan et al., 2002; Hisashi; Verma 1990 in Partap, 2011; Friedrich Ruttner, 1988). *A. cerana* are also said to be less prone to stinging, and have a less developed stinging apparatus with significantly less venom than *A. mellifera* (Friedrich Ruttner, 1988).

Impact on native fauna and flora

It is thought that introduced *Apis* species, including *A. cerana*, may compete with Australian native fauna such as birds, bees and mammals for nesting sites, pollen and nectar. However, results vary and this topic is still highly controversial (Manning, 1997; New, 1997; Oldroyd et al., 1994; D. Paini, 2004; D. R. Paini, 2004; Paini, Williams, & Roberts, 2005; Paton, 1993; Pyke, 1999; Sugden, Thorp, & Buchmann, 1996).

A. cerana may have an effect on pollination of Australian native flora, and promote pollination of weed species. Any introduced bee may disturb pollination of some species or promote pollination of others. This has been clearly shown to be the case for *A. mellifera* (Gross, 2001; Gross et al., 2010; Gross & Mackay, 1998; Paton, 1997; Simpson et al., 2005). In this sense, *A. cerana* and *A. mellifera* may be rather similar.

Domestication

A. cerana (including *A. cerana* Java genotype) can be kept in hives for honey production and pollination services (reviewed in Crane, 1999; L. R. Verma, 1990; Yoshikawa & Ohgushi, 1965). Tropical *A. cerana* (e.g. *A. cerana* Java genotype) produce less honey than temperate *A. cerana*, and *A. cerana* in general produces much less than *A. mellifera* (Partap, 2011; Suroj & Pokhrel, 2009; L. R. Verma, 1990; Wongsiri et al., 1986; Yoshikawa & Ohgushi, 1965). Thus, *A. cerana* are less suitable for honey production on a commercial level.

A. cerana are reliable pollinators for a large variety of crops in Asia (Matsuka et al., 2000; Partap, 2011; Partap & Verma, 1994; L.R. Verma, 1992; L. R. Verma & Partap, 1994; L. R. Verma & Rana, 1994). Thus, they may, potentially, be suitable for some crop pollination in Australia, e.g. small acre crop pollination. However, no research has been done on pollination by *A. cerana* in Australia.

A. cerana has undergone little domestication and selective breeding compared to *A. mellifera*. However, it is thought that with careful selective breeding, *A. cerana* may be able to produce more honey and become less prone to absconding (L.R. Verma, 1992).

Control strategies

In most areas that *A. cerana* is found, it is a native species and so not considered a pest. Therefore, no control strategies have been developed or are necessary for areas where *A. cerana* is endemic. Surveillance is similarly unnecessary in its native range, except perhaps for monitoring its decline and for conservation purposes. Surveillance and control of *A. cerana* as a pest species is mostly conducted in countries where it has been introduced, i.e. New Guinea, Solomon Islands and Australia. Therefore, the following section is restricted mostly to control strategies in those countries.

Control strategies

A. cerana are, to date, only a pest species in Australia, New Guinea, and the Solomon Islands. The majority of literature found covering the detection and control of *A. cerana* was produced by Biosecurity Queensland DAFF, Australia. Very few other control strategies were found documented in the literature for other countries. No control strategies were found for New Guinea, and only three research reports were found for the Solomon Islands: Anderson (2010); Annand (2009); Anderson, Annand et al. (2012). The following section will provide a summary of these documents.

Australia

The Biosecurity Queensland DAFF Asian honey bee program has been in place to control *A. cerana* in Queensland, Australia, since its first incursion into Cairns in 2007. In 2011, the eradication program changed to a Transition-to-Management (T2M) program as *A. cerana* was deemed not eradicable by a majority decision of the National Management Group (comprised of the chief executive officers of the Australian national and state/territory departments of agriculture and primary industries across Australia, representatives of the Australian Honey Bee Industry Council and managed by Plant Health Australia). The T2M program was designed to hand the response and control of *A. cerana* to the public, pest controllers and the honey industry.

Various surveillance and destruction methods were trialled by Biosecurity Queensland DAFF in the past with varying success (Table 2). Current response measures include passive surveillance (detection and reporting of *A. cerana* nests and swarms by the public), as well as active surveillance in the form of floral sweeping and targeted floral sweeping (sweep netting previously identified and mapped floral sources of *A. cerana*), feeding stations and traps (both offering sugar syrup for bees to feed on), and collecting regurgitated crop-pellets from Rainbow bee-eaters (*Merops ornatus*) that are then checked for the presence of *A. cerana* hind wings (Bellis & Profke, 2003; Shield, 2007; D. Wilson, 2009). Current destruction method involves the use of aerosol insecticidal spray (Biosecurity Queensland DAFF). Remote treatment of *A. cerana* nests using an insecticide containing fipronil is also currently being trialled (Koetz, 2012).

Table 2. *A. cerana* surveillance and destruction methods (including type, purpose, status and reason for ceasing use) that are or have been used by Biosecurity Queensland, Department of Agriculture, Fisheries and Forestry, Queensland, Australia (Biosecurity Queensland DAFF).

Type	Purpose	Status (July 2012)	Reason
Active surveillance			
Floral observations	Finding foragers on flowers	Still in use	
Targeted floral observations	Finding foragers on flowers	Still in use	
Sugar feeding stations	Finding foragers	Still in use	
Sugar feeding traps	Trapping foragers	No longer used	Very low efficacy
Sticky traps	Trapping foragers	No longer used	Did not trap *A. cerana*
Sticky frames	Trapping foragers	No longer used	Did not trap *A. cerana*
Pheromone log traps	Trapping swarms	No longer used	Did not trap *A. cerana*
Bait hives	Trapping swarms	No longer used	Did not trap *A. cerana*
Various other traps (including Lucitraps, lopped palm tree flowers, mashed up palm tree flowers)	Trapping foragers	No longer used	Did not trap *A. cerana*
Scenting	Finding foragers	No longer used	Did not attract *A. cerana*
Odour detection dog	Finding nests	No longer used	Low efficacy
Mega Garden (*A. cerana* preferred floral sources in a movable trailer)	Finding foragers	No longer used	Low efficacy
Bee-eater roosts/pellets	Detect presence of *A. cerana* in a general area	Still in use	
Genetic testing for *A. cerana* in bee-eater pellets and syrup of feeding stations	Detect presence of *A. cerana* in a general area	Being trialled	Efficacy not yet validated
Genetic testing for *A. cerana* in trap liquor	Detect presence of *A. cerana* in a general area	Being trialled	Efficacy not yet validated
Passive surveillance			
Public calls & reports	Find nests, swarms & foragers	Still in use	
Control/destruction methods			
Aerosol insecticide (nest & swarms)	To kill a nest or swarm	Still in use	
Remote treatment using fipronil	To remotely kill a nest	Being trialled	Efficacy not yet validated
Permethrin dusting powder	To kill a nest or swarm	No longer used	Safety reasons

Solomon Islands

On the Solomon Islands, remote poisoning of *A. cerana* nests using the broad-spectrum insecticide fipronil has been shown to effectively suppress *A. cerana* in a half-square kilometre area for approximately four to eight months (D. L. Anderson et al., 2012; Annand, 2009). The strategy was introduced to local *A. mellifera* beekeepers and involved (a) removing all *A. mellifera* hives to a distance of at least 5km, (b) training *A. cerana* onto several sugar syrup stations (500m apart) over a two-week period, (c) remote poisoning *A. cerana* for one hour per feeding station (using 0.05% fipronil solution), and (d) returning the *A. mellifera* hives after a period of four to six weeks (D. L. Anderson et al., 2012; Annand, 2009).

Detection and capturing techniques

Detection

Detection of a newly introduced species is often difficult due to the generally low density of the species in the invaded area (Ashcroft, Gollan, & Batley, 2012; Harvey, Qureshi, & MacIsaac, 2009). Detection of an introduced species at the range boundaries can be even more difficult as populations are often very variable in time and space and at even lower densities (Frey, 2009). Although *A. cerana* has been found in Australia since 2007 and so is not newly introduced, its population density would have been affected by the efforts of the Biosecurity Queensland DAFF eradication program between 2007 and 2011.

Detection of *A. cerana* in Australia appears to be difficult, with the most reliable detection methods being public reporting and floral observations. However, these methods are of limited use in dense rainforest or mangroves and remote bushland as floral sources are high up in the trees and human habitation is very low. However, early detection of newly introduced species as well as detection at the range boundaries of such species is crucial, and so effective sampling methods need to be developed (Ashcroft et al., 2012; Harvey et al., 2009).

Possible detection methods in general include the use of bioclimatic envelope modelling, sampling in close proximity to known populations, utilising the public for detection (‘citizen science’) and targeted surveys in preferred habitats (Ashcroft et al., 2012). Survey methods more specific to bees include the use of coloured pan traps and/or sweep netting, standardised or variable transect walks (e.g. Cane, Minckley, & Kervin, 2000; Gollan, Ashcroft, & Batley, 2011; Grundel, Frohnapple, Jean, & Pavlovic, 2011; Nielsen et al., 2011; Richards et al., 2011; Roulston, Smith, & Brewster, 2007; J. S. Wilson, Griswold, & Messinger, 2008), and species-specific aggregation lures using scents or pheromones to catch workers, drones and/or swarms of bees (e.g. Danka, Williams, & Rinderer, 1990; Williams, 1987).

Following is a review of *A. cerana*-specific capture methods used in Asia as well as in Australia and the Solomon Islands. Some further methods have also been discussed previously in the Beekeeping – *Apis cerana* section.

Swarm capture

A. cerana swarms have been captured in order to keep them in hives for thousands of years (Crane, 1999). Traditional methods of swarm capture generally involve a log hive spread inside with honey and/or wax, which is then hung from a tree – year-round in tropical areas or in spring when scouts are observed looking for nests in temperate areas (e.g. Vietnam, Thailand, Burma, India, Indonesia, Malaysia Crane, 1999, 2004). In some areas, scout bees are caught and kept inside a log hive for a few days. Once released, they tend to fly back to their swarm and guide it to the log hive (Crane, 1999). Another method of enticing a swarm into a hive involves tethering or caging a queen inside an empty hive (e.g. after manually removing a queen from her brood comb, or in some areas of India beekeepers sift through swarms with their fingers to find the queen) (Crane, 1999).

In Japan, the orchid *Dendrobium floribunda* (previously *D. pumilum*) attracts drones and foragers (Sasaki, 1992; Sasaki, Ono, Asada, & Yoshida, 1991; Sugahara, Minamoto, Fuchikawa, Michinomae, & Shimizu, 2010), and so the orchid is used to lure swarms to a bait hive (Figure 8).

As part of the eradication program conducted by BQ, DAFF, *A. cerana* swarms were also captured in order to destroy the colony and prevent the species from spreading. However, swarm traps (made from coconut palm logs) used in Cairns, Australia, were unsuccessful (Shield, 2007).

Figure 8. Japanese bait hive using the orchid *Dendrobium floribundum* as a lure (http://www.h6.dion.ne.jp/~kansatu/index.html, accessed 24/07/2012)

Trap attractants - scents

Honey bees can be trained to recognise scents and identify them with a reward. Thus, scent lures can be used to attract honey bees, but they are not particularly suitable to attract untrained, wild bees.

A study on scent preferences in *A. cerana indica* and several strains of *A. mellifera* showed differences between *A. cerana* and *A. mellifera*, as well as slight differences between the different *A. mellifera* strains (Table 2.; Koltermann, 1973). Lavender was highly preferred by both *A. cerana* and *A. mellifera*. Scents preferred by *A. cerana* while disliked by *A. mellifera* included orange, jasmine, fennel and thyme (Koltermann, 1973).

Table 2. Scent preferences in *A. cerana indica*, *A. mellifera ligustica* and *A. mellifera carnica*, listed in order of preference (modified from Koltermann, 1973)

	A. cerana indica	*A. mellifera ligustica*	*A. mellifera carnica*
1	Rosewood oil	Pine needle oil	Rosemary
2	Lavender	Lavender	Benzylacetone*
3	Rosemary	Camomile	Lavender
4	Fennel	Rosewood oil	Benzaldehyde**
5	Cinnamon	Eucalyptus oil	Camomile

*generic flowery smell

**almond-like smell

In the Solomon Islands, the most effective lure was an open flat dish filled with un-scented sugar-syrup placed in sunlight (D. L. Anderson et al., 2012). Offering this lure in the middle of the day seemed to increase bee visitations and reduce visitation by non-target species (D. L. Anderson et al., 2012). Other lures trialled involving scents included acetic acid, isobutanol (odour of molasses), a mix of citral and geraniol (flower odours), none of which attracted *A. cerana* more than simple sugar-syrup (D. L. Anderson et al., 2012). Banana and coconut favoured sugar syrup was also trialled, and it was found that coconut flavour was clearly preferred. However, no more so than sugar-syrup (D. L. Anderson et al., 2012).

Partap (2011) found that honey bees could be attracted to certain crops for pollination by soaking crop flowers in the sugar syrup that bees fed on.

Trap attractants – pheromones

Pheromones in A. cerana

In social insects, pheromones are used for chemical communication. For example, queen mandibular glands produce pheromone messages that, depending on the queen's life-phase (e.g. unmated or mated), attract drones on mating flights, attract a worker retinue, suppress ovarian activation in workers, and are generally involved in controlling colony functioning. Worker pheromones are involved in food preservation and larval nutrition (Wiston & Slesser 1998 in Keeling, Otis, Hadisoesilo, & Slessor, 2001; Pirk, Sole, & Crewe, 2011; Hoover 2003 in Ken Tan, Wang, Yang, Hepburn, & Radloff, 2010).

Pheromones have been used extensively to lure and trap insects, for example to attract and trap *A. mellifera* swarms (e.g. Williams, 1987). Unlike scents that need to be learnt and associated with a food reward, pheromones do not need to be learnt – attraction or repulsion to pheromones is inherent but may depend on the concentration. Pheromones that may help attract workers or swarms include queen mandibular gland pheromones, sting apparatus and venom pheromones, as well as homing/orientation pheromones (e.g. Nasonov pheromones). Developing a pheromone attractant for *A. cerana* would be useful in controlling this species where it is unwanted. However, compared to the extensive research that has been done on *A. mellifera* pheromones, only few studies have been conducted on *A. cerana* pheromones in order to develop a lure.

Plettner et al. (1997) compared the mandibular gland pheromones of *A. mellifera* and four Asian honey bee species, including *A. cerana* (sourced from Kuala Lumpur, Malaysia, presumably *A. cerana* Java genotype; and from Sri Lanka, India, presumably *A. cerana indica*). Pheromones of the cavity-nesting species *A. mellifera* and *A. cerana* were more similar to each other than to the open-nesting species, but distinct differences could be found between *A. mellifera* and *A. cerana*. In particular, they shared all but one component – one of the aromatic components, HVA, was absent in *A. cerana.* HVA and ODA attract a worker retinue around the queen in *A. mellifera* (Plettner et al., 1997). In addition, relative quantities of each component were different between the species (Table 3; Plettner et al., 1997).

Lacey (1999) studied the Nasonov and queen mandibular pheromones in *A. cerana* Java genotype from the Torres Strait. Chemical analysis of two *A. cerana* queens showed similar results to the previous study, including the absence of HVA, but he also found a new compound (4-hydroxy-3-methoxyphenyl ethanone) that has not been found in *A. cerana* in any previous study. Lacey (2000) confirmed his 1999 findings with a further six queens from Java, Indonesia.

The most comprehensive study (Keeling et al., 2001) compared pheromone characteristics of *A. cerana* (presumably Java genotype) and *A. nigrocincta* in Sulawesi, Indonesia. They found the same five components in *A. cerana* queens as Plettner et al. (1997) did (including the lack of HVA). However, not only did they find highly different quantities of the different compounds, but they also found twelve additional compounds in *A. cerana* queens, none of which included the new compound found by Lacey (2000). Keeling et al. (2001) attributed the difference in quantities in *A. cerana* to high geographical variation within this species.

Table 3. Type and amounts of mandibular gland components in queens of *A. cerana* and *A. mellifera* (µg per queen)

Reference	Species (queen status)	ODA*	9-HDA*	HOB*	HVA*	10-HDA**	10-HDAA**
Plettner et al. 1997	*A. cerana* (mated)	28.8	18.1	6.8		1.8	1.1
	A. cerana (virgin)	40.1	2.4	0.9		0.8	0.9
	A. mellifera (mated)	231	164	27.7	4.2	27.3	8.1
Keeling et al. 2001	*A cerana* (mated)	110	61.5	43.6		32.7	4.22
Lacey, 1998	*A. cerana* Java genotype	highest	7%	8%	Not found	Not tested	Not tested
	A. mellifera	highest	47%	15%	11%		
Lacey, 2000	*A cerana* Java genotype (unknown)	54.1-238.6	8.6-51.7	2.6-38.4	5.6-23.7		
Bangyu et al. 2000	*A. cerana*	yes	yes	yes	yes		

*primarily produced by queens (very small quantities produced by workers)

** primarily produced by workers (very small quantities produced by queens)

9-ODA	(*E*)-9-oxodec-2-enoic acid	10-HDA	(*E*)-10-hydroxydec-2-enoic acid
9-HDA	(*E*)-9-hydroxydec-2-enoic acid	HOB	methyl *p*-hydroxybenzoate
10-HDAA	10-hydroxyecanoic acid	HVA	4-hydroxy-3-methoxyphenylethanol

Eicosenol is an oil and pheromone found in large quantities in *A. cerana* venom (Schmidt, Morgan, Oldham, DoNascimento, & Dani, 1997). Eicosenol is also found in *A. mellifera*, although not in the venom itself, and at much lower quantities. This compound can be highly attractive to *A. mellifera* workers (Free 1982 in Schmidt et al., 1997), although mixed results of its attractiveness were found in other studies (Schmidt et al., 1997). Although its function in *A. cerana* is unknown, one suggestion was that Eicosenol may be used by workers to mark particularly rich floral resources so that others can locate those (Schmidt et al., 1997). The use of small quantities of Eicosenol was found to slightly increase the attractiveness of sugar syrup trays to *A. cerana* Java genotype on the Solomon islands (D. L. Anderson & Trueman, 2000). However, this was not rigorously tested.

Orientation pheromones are exuded by bees at the entrance of their nest from the Nasonov gland on the abdomen. It is also responsible for individual bees staying in a swarm and forming a cohesive unit (Pirk et al., 2011). Nasonov compounds differ greatly between *A. cerana* (main constituents: linalool, linalool oxide and citral) and *A. mellifera* (main constituent: geraniol) (Lacey, 1999; Matsuyama, Suzuki, & Sasagawa, 2000; Naik et al., 1988).

Attractiveness of pheromones

Plettner et al. (1997) determined that a mix of the five mandibular gland compounds (ODA, 9-HDA, HOB, 10-HDA and 10-HDAA) attracted *A. cerana* workers – the sixth component (HVA) found in *A. mellifera* was not required to elicit a full response in *A. cerana*.

Kuang et al. (2000) trialled an *A. cerana* queen pheromone blend (20mg on a dummy queen), which succeeded in attracting worker bees within a hive (close-range) and also suppressed egg-laying by workers, the building of queen cells and maintained general colony function. It is suggested to use synthetic queen pheromone in a queenless colony as a method to increase honey yield, as the colony will become eggless and broodless and more workers will go foraging (Kuang et al., 2000).

Lacey (1999, 2000) conducted pheromone experiments on *A. cerana* Java genotype in Papua New Guinea and Java, Indonesia. He tested several pheromones, including a synthetic *A. cerana* Java genotype queen pheromone blend, *A. mellifera* queen pheromone, Nasonov pheromone, and three pheromones present in the sting/venom (11-eicosen-1-ol, 2-octenyl acetate and Z-9-octadecenoate). He found that the *A. cerana* Java genotype queen pheromone blend successfully attracted workers at close-range (15cm) and medium-range (2m). Preliminary long-range field trials in the Torres Strait showed some success in catching *A. cerana* (Lacey, 2000).

Unfortunately, Lacey (1999, 2000) did not elaborate on which components were used, and at what quantities, for the *A. cerana* Java genotype queen pheromone blend. Therefore, the constituent compounds cannot be compared to either Plettner et al.'s (1997) or Keeling et al.'s (2001) studies, which would give an indication of geographic variability in this species.

Anderson, Annand et al. (2012) trialled a range of pheromones on the Solomon Islands (including eicosenol at differing concentrations, Queen aggregation pheromone, Queen and Nasonov pheromone mix, and Nasonov pheromone). Although low levels (<1mg) of eicosenol resulted in more landings of bees than any other pheromone, the sample size was too low to be statistically significant (D. L. Anderson et al., 2012).

Three modified LuciTraps (Miazma Pty Ltd, Queensland Australia) were also deployed on Dauan Island, Torres Strait, two of which contained synthetic *A. cerana* queen pheromone (produced by M. Lacey, CSIRO; Shield J., pers. com.). Two pheromone-baited traps did trap *A. cerana,* whereas the third, pheromone-free trap did not trap *A. cerana* (Shield J., pers. com.). Although the result may seem promising, generalisation is impossible due to the extremely low sample size and a lack of replication. Further research is necessary to determine whether pheromone-baited traps are useful for trapping *A. cerana.*

Conclusion and recommendations

The literature review aimed to review the critical points of current knowledge about *A. cerana* in general and *A. cerana* Java genotype in particular, compare *A. cerana* and *A. mellifera* behaviour and ecology, review *A. cerana* beekeeping practices as well as control measures both overseas and in Australia, and highlight gaps in currently available literature and future research needs.

It is apparent how little knowledge is available on tropical *A. cerana* ecology and behaviour in general, and no peer-reviewed scientific publications are available on *A. cerana* Java genotype in Australia. Most information available on Australian *A. cerana* is in the form of Government reports, which may not be freely available to the scientific community, or indeed anyone wishing to control *A. cerana* in other countries. This highlights an urgent need to publish and disseminate research findings of *A. cerana* in Australia.

There is evidence in the international literature that *A. cerana* can be domesticated for honey production and pollination services. There are also references in the international literature on *A. cerana* being an effective commercially-kept as well as feral pollinator. What is not possible to determine from the international literature is the potential for the strain of *A. cerana* in Australia to act as a feral pollinator or if it is possible to effectively manage this strain for honey production. However, there is anecdotal evidence that the strain in Australia has a high tendency for absconding. To effectively answer this question further research would need to be undertaken.

In undertaking this literature review it has become apparent that research in the following areas would assist those working with *A. cerana* in Australia to better understand the bee and its interaction with the environment. The research recommendations are:

- General ecology and behaviour
  - Foraging ranges and times
  - Confirming nesting characteristics are the same as overseas
  - Determining drone and queen flight times and drone aggregation areas
  - Reasons for swarming and absconding
  - Swarming distances
  - Pre- and post-mating isolation mechanisms between *A. cerana* and *A. mellifera*

- Pollination
  - Pollen analysis to determine floral sources

- Impact on the Australian environment
  - Competition of *A. cerana* with native invertebrates and vertebrates for floral sources and nest sites
  - Impact of *A. cerana* on pollination and reproduction of Australian native plants and weeds
  - Determining the diseases carried by *A. cerana*

- Competition with *A. mellifera*
  - Competition of *A. cerana* and *A. mellifera* for floral sources and nest sites

- Control
  - Developing effective and species-specific bait stations and lures to attract *A. cerana*
  - Increasing efficacy and specificity of feeding stations

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