Comparative biology of *Apis andreniformis* and *Apis florea* in Thailand

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The existence of two species of dwarf honey bees has only recently generally been accepted. Since they coexist in many locations, this leads to the question of how they differ so that they can both be present. This article presents a comparison of the biology of these species, particularly as they occur in Thailand. We do this to highlight what we *do not* know about these two very similar species, as well as what we *do* know.

Introduction

The dwarf honey bees *Apis andreniformis*[38] and *A. florea* have recently been determined to be separate species[20,43,44]. They are almost the same size, both build a single, exposed comb and may utilize similar resources in the same or similar habitats. The two species have only a limited known range of overlap (sympatry) (figs 1 and 2) and descriptions of one species are similar to descriptions of the other. These reasons may account for why *A. andreniformis*, although it is widely distributed, has only recently been recognized as a true biological species. Hence, prior to 1991, reports concerning *A. florea* that derive from research in areas having *A. andreniformis* may inaccurately identify the species studied.

A. florea is an excellent pollinator[6] and is easy to maintain in orchards. Their honey and nest products have increased the income of villagers in Thailand[1]. The economic importance of *A. andreniformis* has not been assessed, but it may be very significant in areas where the species is common.

This article describes differences observed primarily in Thailand, with limited information from other parts of the ranges of these two species. The thesis by Whitcombe[41] has a particularly extensive discussion of *A. florea* in Oman.

Distribution

Both species occur in tropical and near subtropical regions of Asia (figs 1 and 2)[27]. However, the range of overlap is in south-eastern Asia. Exact distributions are not known, but thus far *A. andreniformis* has been found in at least seven Thai provinces (fig.1). *A. andreniformis* was also found in southern China, India, Burma, Laos, Vietnam, Malaysia, Indonesia and the Philippines (Palawan)[1,4,20,27,43,44]. In contrast, *A. florea* is distributed throughout Thailand, but has not been found in the southern Malay peninsula or Indonesia, Borneo, the Philippines or the surrounding islands. Specimens collected in Java have been reported, but these may be the result of a human-assisted introduction[28].

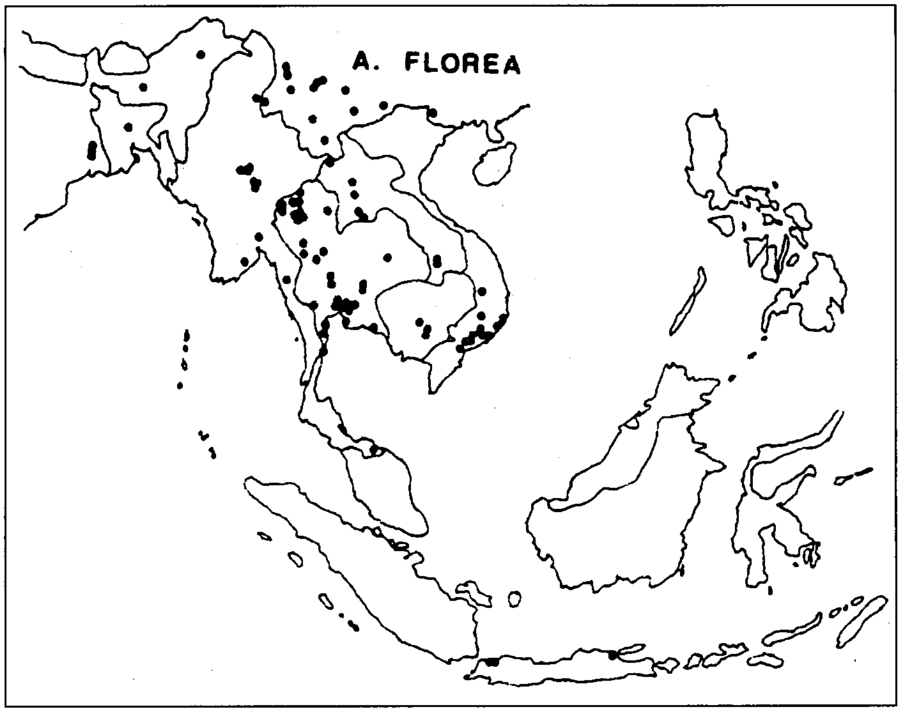

FIG. 1. Distribution of *Apis florea* in south-east Asia.

Likewise, the presence of *A. florea* in Sudan is probably the result of human-assisted introduction[19,21]. However, *A. florea* is found in Iran at high elevations '...within the vegetation range of a temperate zone'[36].

A. andreniformis has been found from the coastal flats and near the foothill areas (1–100 m above sea level) of Chanthaburi province to high mountainous and forest areas at about 1600 m altitude in the northern parts of Thailand. *A. florea* is common in lowlands below 1000 m in areas where forests have been reduced by agriculture and urbanization[20,43,44]. In Yunnan, China, *A. florea* was found below 1000 m[44]. However, during the dry season, it was found at up to 1600 m in northern Thailand.

Morphology

At first glance it is difficult to distinguish *A. andreniformis* and *A. florea*. However, several morphological differences are quite distinct.

Cuticular colour

A species-specific characteristic of *A. andreniformis* identified by Smith in 1858[38] is that of worker bees having black hairs on the hind tibia and dorsolateral surface of the hind basitarsus as opposed to the white hairs of *A. florea*.

A. florea workers have less black pigment in congruence with the general impression that *A. florea* are mostly yellow bees and *A. andreniformis* are mostly black bees. A notable exception to this rule is the

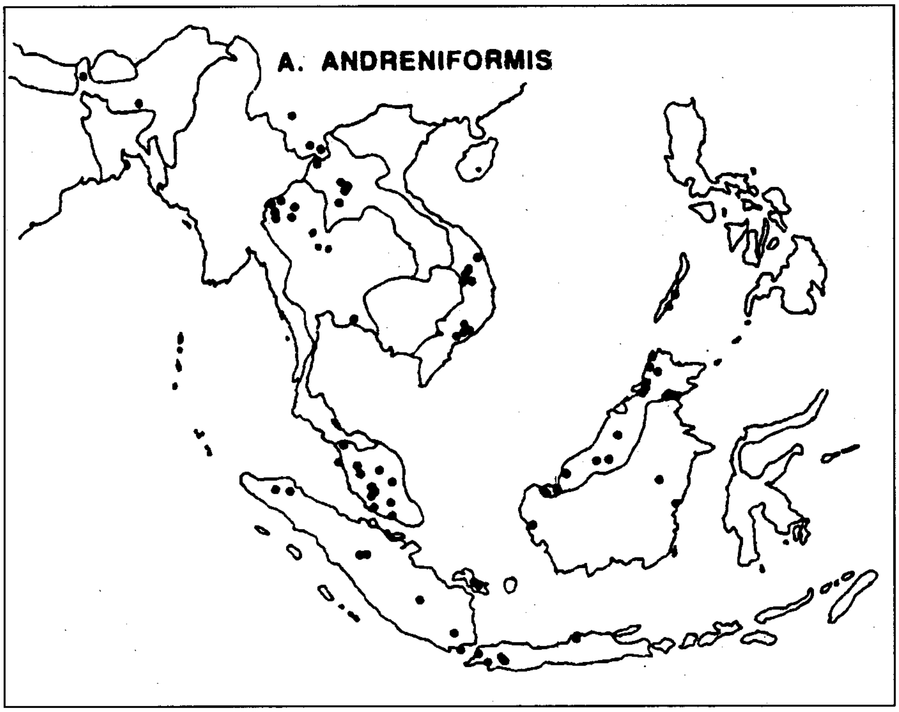

FIG. 2. Distribution of *Apis andreniformis* in south-east Asia.

pigmentation of the scutellum. Scutellum colour for *A. andreniformis* workers tends toward yellow with few exceptions, while the scutellum colour for *A. florea* workers tends toward black.

The abdominal segments of *A. andreniformis* drones and queens are all black, but *A. florea* drones have grey abdominal segments with white hairs and *A. florea* queens have all orange-yellow abdominal segments[32].

Wing venation

The cubital index of *A. andreniformis* (6.37) is much larger than that of *A. florea* (2.86). The two species differ in all the angles of wing vein intersection except one[32,43].

Male metathoracic legs

The basitarsus of drones carries a thumb-like bifurcation. This structure is a distinct and characteristic feature of both dwarf *Apis* species. However, the basitarsus of *A. andreniformis* is comparatively short and not more than half of the length of the tibia[43,44]. In *A. florea* the basitarsus is quite long, being more than two-thirds of the length of the tibia[44].

Proboscis

The successful coexistence of *Apis* species is dependent on partitioning of available resources. In Chanthaburi, Thailand, the proboscis of *A. andreniformis* (2.797 ± 0.09 mm; mean ± s.d.) is about 15% shorter than that of *A. florea* (3.273 ± 0.18)[32]. This

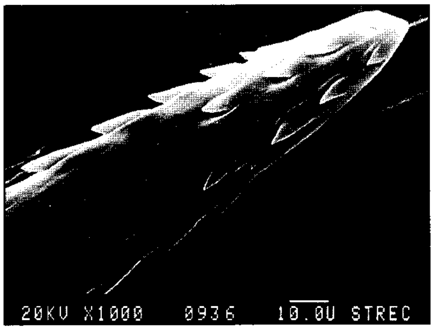

FIG. 3. Stylet barbs of *Apis andreniformis*.

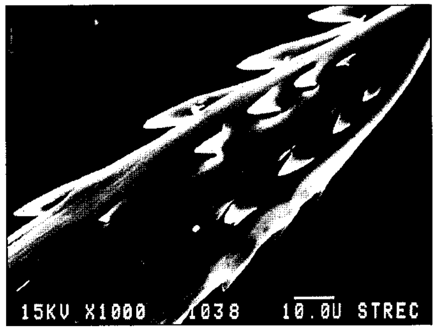

FIG. 4. Stylet barbs of *Apis florea*.

difference may contribute to the partitioning of resources through floral selection and differential temporal harvesting of the same crop as a result of differential nectar availability[25].

Endophallus

The endophalli of *A. andreniformis* and *A. florea* are also distinctly different. The endophalli of both species have a pair of bursal cornua, but in the case of *A. andreniformis*, the fimbriate lobe has six protrusions and a comparatively thick as well as straight terminal. In *A. florea* the fimbriate lobe has only three protrusions, with a comparatively strongly curved terminal[11,43,44].

Sting

Generally the sting is quite similar in both species (figs 3 and 4). Their stylet barbs are the same in number (4–5). However, the distance from the tip of the stylet to the first and second stylet barbs is significantly different between these two species. For *A. andreniformis* the tip to first stylet barb distance is 17.93 ± 3.64 µm (mean ± s.d.) and the tip to second barb distance is 31.27 ± 3.53 µm, while for *A. florea* these distances are 25.39 ± 5.32 µm and 39.56 ± 6.21 µm, respectively[8].

Behaviour

Not only are the two species of dwarf honey bees morphologically separate, they also exhibit vastly different behaviour.

Virgin queen activities

Virgin queens of *A. andreniformis* often produce piping sounds similar to those of *A. cerana* queens (but more rapid in tempo[28,29]) and *A. mellifera* queens. Queen piping sounds induce a cessation of activity in *A. andreniformis* workers. Despite observing many virgin *A. florea* queens, we have never observed queen piping in this species. However, Koeniger has heard *A. florea* queens piping in Pakistan[10]. When he removed the piping queen from the comb, several young queens emerged from their queen cells. One remained on the comb and was chasing the others away. For several days there was one queen on that comb and another one nearby, which from time to time was fed by workers of that colony. Later the colony absconded.

If another virgin *A. florea* queen emerges while the first one is still in the colony, then a fight ensues and finally only one queen survives. None of the sealed queen cells are destroyed by a virgin queen[42].

We observed that during the first days after emergence, the *A. florea* queen patrolled mainly on the comb beneath the curtain of bees which covered the colony. On days 3 and 4, the queen crossed the top platform several times. The first mating flight time of *A. florea* queens was between 14.00 and 15.00 h[12], but there are no reports of the mating flight time of *A. andreniformis* queens.

Drone flight

During the half-hour before drone mating flights occur, *A. andreniformis* drones appear on the surface of the protective curtain, walk upward and eventually begin flights from the honey storage area at the crown of the nest. Before flying, some drones of *A. andreniformis* run, with wings somewhat extended to the side, in circling loops. Some runs, but not all, end with the drone taking flight. These runs are visually identical in form and tempo to the round dances of *A. mellifera* workers. The dances of drones stimulate other drones in two ways:

- After encountering a dancing drone, other drones will often follow the dance.
- When a dance ends in flight, the following drones often take flight with the lead dancer. *A. florea* drones also fly in groups, but do not dance.

The most likely hypothesis explaining the adaptive value of drone dancing is that it synchronizes group flight by drones. Group flight may enhance mate location, mating or avoidance of predation[30]. Rinderer et *al.*[30] hypothesized that drone dancing, which in some way enhances mating success, is the evolutionary root of the dance communication used by worker honey bees throughout the genus *Apis*.

The timing of mating flights by *A. andreniformis* and *A. florea* are well separated

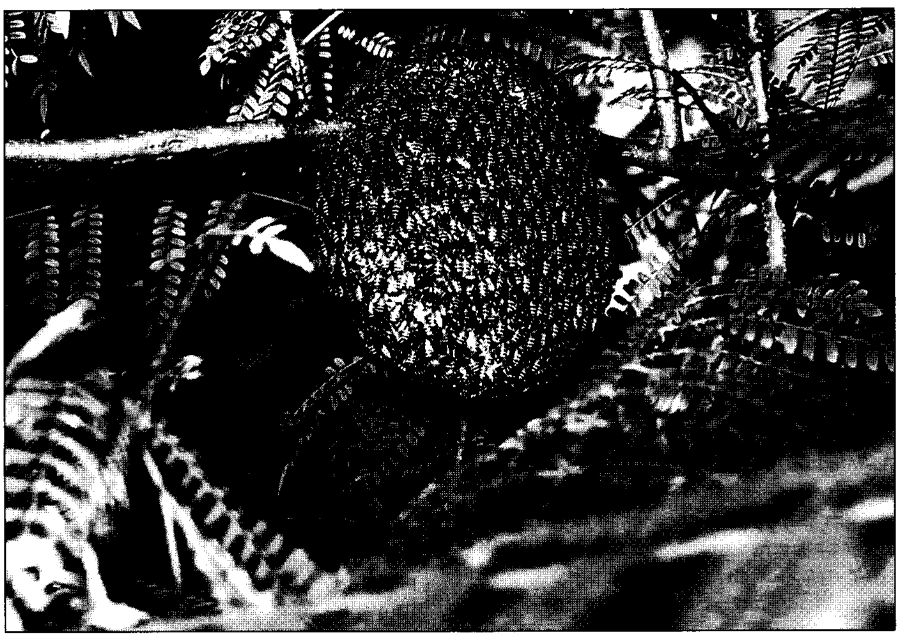

FIG. 5. Nest of *Apis florea* in Thailand.

temporally, with *A. andreniformis* flying just after the sun passes its zenith and *A. florea* flying later in the afternoon. This difference reinforces reproductive isolation and supports the interpretation that the two are separate biological species[31].

Mating and sperm transfer in queens

Based on sperm counts, Koeniger *et al.*[13] estimated that *A. florea* queens copulate with a maximum of four drones. However, recent work based on microsatellite allele distributions in worker progeny demonstrated that *A. florea* queens mate at least 5–14 times[24], compared to 10–20 times in *A. andreniformis*[26]. The number of spermatozoa from a pair of seminal vesicles is $0.13 \pm 0.01 \times 10^6$ (mean ± s.d. $n = 5$) in *A. andreniformis* in Johore, Malaysia[11], compared to $0.44 \pm 0.037 \times 10^6$ (mean ± s.d. $n = 8$) in *A. florea* in Thailand[13].

Nest site selection

In Thailand, *A. andreniformis* nests are mostly found in and near undisturbed, mixed deciduous to evergreen forests. Their nesting habitat is usually a dark and shady place (20–35% sun), commonly near or over streams. They usually build their nest on small branches of shrubs, bamboos, bananas or small trees (for example, coffee and tea trees in northern Thailand). They build a single, comparatively small comb from 0.7 to 9.0 m ($\bar{x} = 2.69 \pm 1.13$ m, $n = 16$) above the ground[2].

A. florea nests are found in more disturbed areas, such as urban and intensive agricultural areas and savanna ecotopes[2,6] (fig. 5). They also use a small branch as the support for their nest, which is usually in a shady location. However, they are usually more exposed to sunlight and often have a surface of their comb exposed to direct sunlight for several hours a day. Also, they are more likely to nest in diverse places. For example, in Thailand we have observed *A. florea* nests high in tall trees, on the wall of a building and on the roof of a building at Chulalongkorn University[43]. Typically however, their nesting height is about 1–15 m, ($\bar{x} = 2.22 \pm 1.69$ m, $n = 17$) above the ground in dry evergreen forests[2]. Higher sites, up to 15 m, are common in Bangkok[42].

Comb structure

Both species have a nest comprised of a single exposed comb. Typically, a single branch is used as a support for the nest. The brood area is below the supporting branch and a honey storage area is above and around the supporting branch. In both nests, pollen is stored at the top of the brood-nest area, drone cells are found at the lower margin of the nest, and swarm cells are found protruding vertically from the lower edges of the brood nest. Both have a midrib through the brood nest and pollen storage area, with worker cells from one side meeting worker cells from the other side, and drone cells meeting drone cells. Both species apply sticky resin on support branches near the edge of their nests which aids in defence against ants[34,35].

In almost every aspect, the nests of *A. florea* are larger than the nests of *A. andreniformis*. The height (H) and width (W) of the *A. andreniformis* brood area (H = 10.03 ± 3.29 cm, $n = 17$, W = 12.18 ± 3.62 cm, $n = 18$) are about 25% and 16% smaller, respectively, than the height and width of the *A. florea* brood area (H = 12.00 ± 3.32 cm, $n = 41$, W = 16.85 ± 5.28 cm, $n = 42$). The honey storage area of an *A. andreniformis* nest is less wide and less high (H = 3.70 ± 1.16 cm, $n = 11$, W = 10.19 ± 2.93 cm, $n = 14$) than the width and height of this area in an *A. florea* nest (H = 4.20 ± 1.05 cm, $n = 44$, W = 12.49

± 5.27 cm, $n = 44$). However, the proportional relationships of these measurements are quite similar for the nests of both species, with measurements in the smaller *A. andreniformis* nests being about 13% less than those for the nests of *A. florea*. The breadth, the top depth, and the side depth of the honey storage area are all smaller in the nests of *A. andreniformis*. The estimated branch thickness is about 1 cm larger for the *A. andreniformis* nest[33].

The comparative sizes of cells are generally in accord with the smaller size of *A. andreniformis*. The depth and width of worker cells and the width of drone cells are all significantly larger in nests of *A. florea*. The depth of drone cells is similar for both species, however the shape of the drone cell capping might be sufficiently different to provide more length for developing *A. florea* drones. Both species construct non-perforated dome cappings on drone cells similar to those of *A. mellifera*. The depth of queen cells is numerically larger for *A. florea* and the internal diameter is numerically larger for *A. andreniformis*, although neither reported difference was statistically significant[33]. However, for *A. florea*, the number of cells counted per dm^2 varied from 1190 in northern India to 1560 in southern India[23].

The most remarkable difference between the nests is the presence or absence of a midrib in the honey storage area above the support branch. The honey storage area or 'crown' of an *A. florea* nest has cells that seem to be orientated inward towards the supporting branch when viewed from the outside surface. Because the crown is generally rounded and tapered to the supporting branch at the ends, some of the cells are distorted from the standard hexagon. Three- and four-sided cells and smaller or larger cells as well as cells with unequal sides occur. A cross section of the crown of an *A. florea* nest reveals that three levels of internal organization occur. First, cells from the side are very long and do extend to the supporting branch. Above this area, cells coming from opposite sides have their base at the sides of cells coming from the other side. Cells coming from the top of the crown have this same pattern, however the use of an adjacent sidewall as a base is more extreme, with some cells open to the top surface having their base well away from the base of the supporting cell[33]. The honey storage capacity of an *A. florea* nest has been reported to be 1000 g or more[23,40]. This contrasts with the crown of an *A. andreniformis* nest. This crown has a characteristic crest appearance when viewed from the outside. Each cell has a regular hexagonal shape. Cells are arranged in layers with each layer offset by the width of half a cell, much like roofing shingles. A cross section shows a clear midrib structure where the bases of opposing cells come together in the same way as cells in the brood nest area[33].

Protective curtain

Generally, a large number (approximately 80–90%) of the house bees of both species are engaged in protecting the nest and brood from weather and from predators by hanging over the surfaces of the comb in a thick, protective 'curtain'[42]. In their normal position in a protective curtain, *A. andreniformis* workers have their heads upward and spread their hindwings to 90° and the forewings at 45° downwards. The shape of the wings looks like a diamond. When the ambient temperature is more than 30°C, the protective curtain becomes loose. When the colony is disturbed and prepares to attack an intruder, a tail-shaped group of bees appears at the bottom of the curtain. This tail will disappear as the bees in it take to the air and engage in nest defence.

During rain and early in the morning, the protective curtain is very compact and all curtain-forming bees place their heads

FIG. 6. Nest of *Apis andreniformis* in Thailand, showing the tail-like group of workers hanging from the bottom of the nest.

under the abdomen or wing of other curtain-forming bees above them. With mouth pointed upward, the back of the head of the lower bee touches the prothorax of the bee above. When the bees are in this arrangement, the nest and the bees in the protective curtain are virtually rainproof.

A. florea workers also form a very compact protective curtain, but they do not spread their fore- and hindwings at 90° and 45°, respectively, to form a diamond-shaped pattern. However, they hide their heads under the wings of other curtain-forming workers to provide similarly effective protection from rain. The tail-like group of workers in an *A. andreniformis* (fig. 6) protective curtain is not found in nests of *A. florea* (fig. 5)[42].

Fanning behaviour

Nest cooling behaviour is also different between these two species. At Chiang Mai, Thailand, both species started to fan when the temperature of the brood nest rose above 33°C. However, *A. andreniformis* workers started fanning their comb earlier and stopped later. *A. andreniformis* fanned longer (15 s–2 min) than *A. florea* (5–35 s). Fanning *A. andreniformis* workers face downward and a loose curtain of bees forms under the fanning bees. Fanning *A. florea* workers face upwards and when they fan the comb they usually vibrate their whole body[39].

Absconding behaviour

Both species have the habit of moving their nest location in response to seasonal changes. *A. florea* absconds in response to increased heat or sunlight and usually relocates a short distance away, permitting the bees to collect wax from their old nest and use it in the construction of the new nest[2].

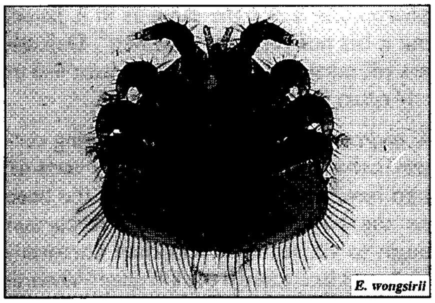

FIG. 7. Ventral view of *Euvarroa wongsirii*.

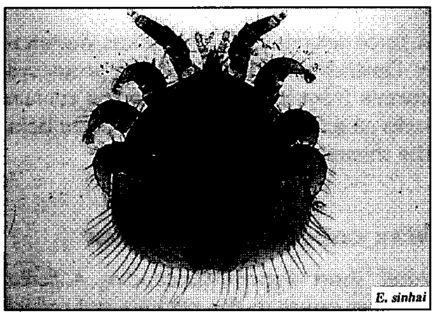

FIG. 8. Ventral view of *Euvarroa sinhai*.

In other cases, *A. florea* appears to make longer moves after absconding. In northern Thailand, *A. florea* is found for two months in the dry season and five months (July to November) in the rainy season[37]. Evidently the colonies migrate, since their location after they have absconded is not known. Before absconding, the protective curtain of *A. florea* becomes disorganized due to movement of the bees toward the crown for flight.

A. andreniformis follows a seasonal migration pattern and is generally found at higher elevations in the rainy season and lower elevations in the dry season. Nests can be found in Chanthaburi (south-east) from January to June and in Chiang Mai (north) from March to April. They usually abscond from June to October. Small swarms from absconding found at high elevations in Chiang Dao in October often have no comb. *A. andreniformis* is hardly found from June to October (rainy season) in lowlands like the coastal flats areas of Chanthaburi.

The absconding behaviour of *A. andreniformis* is quite different from that of *A. florea*. In an *A. andreniformis* colony, only one scout bee begins a wagtail dance for only about 5–15 s on the dance floor of the nest's crown. During her dancing, she opens her mandibles, stretches her antennae forward and walks slowly, almost as if partially disorientated. Sometimes she touches her metathoracic legs together, as in the cleaning behaviour of *A. cerana*. During this time, 4–8 recruit bees, especially guard and house bees present on the dance floor, attend her dance from the posterior of the dancer's abdomen and touch the ventral surface of her abdomen with their antennae. After a few seconds, the recruit bees run in a fast zigzag dance in seemingly random directions throughout the entire nest. After the zigzag dance, the dancers return to the crown of the nest, again attend the wagtail dance, and then repeat the zigzag dance. This process continues until they abscond. We also observed bees that had done a wagtail dance leave the dance floor, run throughout the nest in a zigzag dance and then return to the dance floor and do another wagtail dance. Sometimes, she inserts her head into honey storage cells prior to returning to the dance floor.

A. andreniformis is more likely to abscond upon disturbance than is *A. florea*[42].

From observations of *A. florea* in Oman, a different behaviour was reported. 'On some occasions, apparently in the period before a colony absconded, many bees scattered over the comb surface could be seen holding their wings slightly extended, and moving the raised abdomen vigorously from side to side. This action was performed for several seconds, after which the bee moved a short distance and turned to face another direction, and then repeated the procedure. The behaviour did not seem to be direction oriented, and the performing bees, each of which might have a circle of others facing her, were themselves facing in many different directions[7].

Activity of queenless colonies

In a queenless *A. andreniformis* colony, the bees run randomly across the comb surface. If a queen cell is present, most bees stay near the bottom of the comb near the cell. If a queen cell is not present, they start to bite each other and occasionally we have seen bees stinging the comb. Some bees may walk with their head and abdomen arched ventrally. They never form a protective curtain. Worker *A. andreniformis* have never been observed to lay eggs[42], unlike *A. florea*.

A. florea workers usually form a protective curtain even when they do not have a queen. The workers start to lay many eggs in one cell when a queen has been absent for many days.

Defensive behaviour

A. andreniformis is more defensive of its nest than *A. florea*. Approach by an invader closer than 1–2 m to a nest of *A. andreniformis* provokes an immediate attack by the guard bees. On occasion, a slight disturbance 3–5 m from the nest will provoke a response. During a defensive response, the protective curtain loosens, large numbers of bees join the 'tail' of the protective curtain and quickly take to the air; these bees readily sting. Many bees also fly as defenders directly from the surface of the protective curtain. Some defending bees release their pheromone before stinging. This may increase the intensity of the defensive response. The smell of the alarm pheromone is not the same as in *A. florea*, but it has not yet been identified[42]. Defenders will pursue an intruder for at least 4–5 m and often up to 20 m or more[42].

A. andreniformis displays a 'shimmering curtain' behaviour. When a predatory wasp or bird hovers near their nest, all of the bees on the surface of the protective curtain begin to vibrate their abdomen dorsoventrally and face toward the intruder. When all of the bees vibrate their body at the same time, they produce a wave-like movement.

A. florea defends its nest much less intensively. Defending workers leave the protective curtain from its surface since the curtain lacks an extended 'tail'. Also, *A. florea* lacks the shimmering curtain behaviour.

Wax collecting behaviour

After 'short distance' absconding, *A. florea* workers return to the old nest and collect wax from the old comb. Only a few bees come to collect the wax from the old comb. They usually collect the wax from the crown of the nest and sometimes from old queen cells. These locations probably have wax less connected to pupal castings and it may be easier to harvest and reuse.

Wax collecting behaviour has not been observed in *A. andreniformis*. This may be because they are less likely to make short distance shifts of nest location after absconding.

Parasitic mites

A. andreniformis and *A. florea* are parasitized by separate species of brood infesting mites of the genus *Euvarroa*. *E. wongsirii* (fig. 7) is found only on *A. andreniformis*[15]. *E. sinhai*[5] (fig. 8) is found on its original host, *A. florea*, and also on *A. mellifera* imported to Asia[9].

These two mites are morphologically and biologically different. The female of *E. wongsirii* has a triangular-shaped body, wider posteriorly, which bears 47–54 long, slender lanceolate setae (bristles)[16,22]. The female of *E. sinhai* has a pear-shaped body, bearing 39–40 very long lanceolate setae.

Both species of these brood mites are obligate parasites on their own host. Both *A. andreniformis* and *A. florea* show very aggressive cleaning behaviour toward foreign mites and kill them[14,16,18].

Conclusion

Although both are dwarf honey bees that inhabit a single exposed comb, *A. andreniformis* and *A. florea* are very different in morphology, behaviour and natural history. *A. florea* is an excellent orchard and field crop pollinator[3,6,35]. They excel in their ability to pollinate mango flowers (Thai Department of Agriculture, unpublished report). Clearly, *A. florea* is important for food production in the tropics and its use can be easily increased[6].

Thus, *A. florea* is an economically important *Apis* species in Thailand[17]. However, in Thailand more than 10 000 colonies of *A. florea* are annually harvested by bee hunters. People eat the larvae and pupae as well as the honey. Currently, *A. florea* is abundant throughout the country. However, if harvesting continues or increases, this very important agricultural and natural resource may be threatened.

The economic value of *A. andreniformis* is not well documented. However, important segments of the naturally occurring flora in the range of *A. andreniformis* probably depend on this species for pollination. Resource partitioning is fundamental to the sympatric existence of species of honey bees. One mode of resource partitioning is for bee species to specialize in collecting food from separate suites of plants in the ecosystem.

There is no evidence that colonies of *A. andreniformis* are commonly harvested, but the populations of *A. andreniformis* are perhaps more threatened than the populations of *A. florea*. Populations of *A. andreniformis* seem to be gradually declining, especially due to habitat loss and forest fires. The villagers of Chiang Dao in northern Thailand stated that the *A. andreniformis* population around their village has declined[12].

It is becoming urgent to find ways to protect both of these dwarf *Apis* species in Thailand. Both are under adverse pressure and both are essential for pollinating cultivated and wild plants. Both species are important for agricultural production and for the maintenance of the natural ecosystem with its critical biodiversity.

The main result of a survey of previous studies of these two species is the realization that there are major gaps in our knowledge. What are the ecological differences that affect their distribution? Why is *A. andreniformis* but not *A. florea* found in Malaysia? What variation is present within each species throughout its range? How do they compete for resources? With their great similarities, but yet differences, these two species provide the opportunity for much exciting and interesting research.

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