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Pollen resource partitioning by *Apis dorsata*, *A. cerana*, *A. andreniformis* and *A. florea* in Thailand[1]

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SUMMARY

The sympatric congeners *Apis dorsata*, *A. cerana*, *A. andreniformis* and *A. florea* were observed foraging for pollen on the nocturnally-dehiscent king palm (*Archontophoenix alexandrea*). The larger *A. dorsata* and *A. cerana* foraged earliest but in low numbers, presumably exploiting the resource at its most productive time. The smaller *A. andreniformis* and *A. florea* followed in large numbers. Although there was minimal separation of *A. andreniformis* and *A. florea* foragers in either space or time, no aggressive interactions between the species were observed.

Keywords: *Apis dorsata*, *Apis cerana*, *Apis andreniformis*, *Apis florea*, pollen, foraging, competition, *Archontophoenix alexandrea*, *Trigona*

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INTRODUCTION

Four species of honey bees are sympatric and apparently successful in south-east Thailand near the Cambodian border. They are *Apis dorsata* Fabricius, *A. cerana* Fabricius, *A. andreniformis* Smith and *A. florea* Fabricius. Ruttner (1988) suggested that *A. andreniformis* is a subspecies of *A. florea*, but recent studies confirm its species status (Wu & Kuang,1986, 1987; Wongsiri *et al.*, 1990; Koeniger *et al.*,1991). Several species of *Trigona* are also abundant in the area. All species are highly eusocial and found semi-permanent nests which have a high energy requirement (Ruttner, 1988).

The ability of these species to successfully coexist depends on adequate partitioning of the available food resources. Mechanisms for distribution of bee species among available resources are thought to be related to an interaction between food availability and the energy requirements of the foragers, rather than aggressive interactions (Roubik, 1989). Thus larger bees with a larger energetic requirement tend to forage on rich resources while smaller bees can profit from more dispersed resources. The changing quantity of food available from a particular floral resource during the course of a day (caused in part by exploitation) means its profitability for different bee species changes with time (Hubbell & Johnson, 1978; Real, 1981). This often means that peak abundance of foraging bees of different species will vary with time on one floral resource (Real, 1981; Schlising, 1970). However, there exists at least one case of similar-sized *Trigona* bees specializing on dispersed and clumped plants of the same species (Johnson & Hubbell, 1975). In these cases, aggressive interactions among foragers may have caused different foraging strategies to evolve.

Here we report on the changing array of four *Apis* species and at least two *Trigona* species foraging on a single source of natural pollen. The partitioning of resources by *A. andreniformis* and *A. florea* is of great interest since the two species have very similar natural histories and size (Wu & Kuang, 1986, 1987).

MATERIALS AND METHODS

Our observations were made at the Chanthaburi Horticultural Centre, Chanthaburi, Thailand (12°N, 103°E) in February 1992. Here intensively cultivated coastal flats abut densely wooded hills of natural vegetation.

Observations of bee interactions and counts of foraging bees were made on four inflorescences of the exotic, monoecious king palm (*Archontophoenix alexandrea*), which is extensively planted at the research station as an ornamental. Each inflorescence occupied an approximate volume of 0.5 m^3 and contained 150–200 open flowers. The flowers

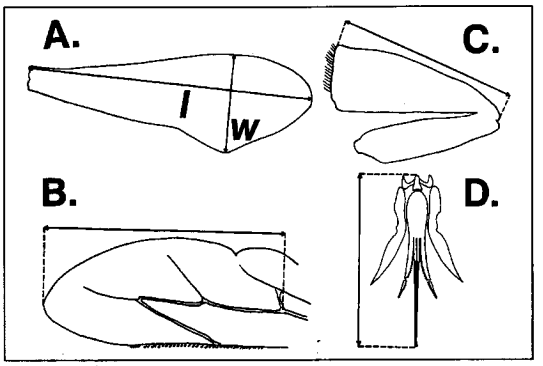

FIG. 1. Morphological measurements. A. Forewing length (*l*) and width (*w*); B. Hindwing length; C. Tibia length; D. Tongue length.

are nocturnally dehiscent, producing abundant pollen but no nectar.

Observations commenced at 06.00 h. At least one of us walked between the observation points so that for three days bees were counted at inflorescences 1 and 2 approximately every 30 minutes. Inflorescences 3 and 4 alone were observed on day four. Observations continued until few or no *Apis* bees remained foraging (approximately 11.00 h). Counts were made of the number of bees of each species with the aid of a mechanical counter. When few foragers were present (≤ 10 of a particular species), one count was sufficient to accurately estimate the number of bees of that species. When foraging was more intense, we counted the bees of each species three times and took the average as an estimate of the number of foragers present.

The four *Apis* species are easily distinguished when foraging. *A. dorsata* is much larger than *A. cerana*, which is in turn larger than the other two species. *A. florea* appears slightly larger than *A. andreniformis* and has a yellow integument, while that of *A. andreniformis* is black.

Samples of these bees were taken by sweep-netting the flowers (*A. andreniformis*, *A. florea* and *Trigona* spp.) or nearby colonies (*A. dorsata* and *A. cerana*). Specimens were preserved in alcohol prior to dissection and making the morphological measurements shown in figure 1. The *Trigona* specimens were not measured morphometrically, but were identified to species.

RESULTS

Temperatures recorded during observations varied between 21°C at dawn and 33°C at noon on each of the four days of observation. No rain was recorded.

No aggressive interactions (biting or pushing) were seen during the course of these observations.

TABLE 1. *Apis* and *Trigona* species foraging on *Archontophoenix alexandrea* inflorescences. Abundance distributions shown in figures 2 and 3 are compared with Kolmogorov-Smirnov (KS) two-sample tests. Numbers on the above right of the matrices are the values of *D* from the K-S test. Symbols below the diagonal indicate the probability that the observed species distributions were the same with respect to time (n.s. = not significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$). Numbers in brackets on the diagonals are counts of that species on that day and location. *A. dorsata* numbers are not presented as they are too low for valid comparison.

Inflorescence 1

	A. andreniformis			*A. cerana*			*A. florea*			*Trigona* spp.		
February:	24	25	26	24	25	26	24	25	26	24	25	26
A. andreniformis	(40)	(36)	(31)	0.7	0.8	0.5	0.1	0.2	0.0	0.4	0.2	0.2
A. cerana	n.s.	***	**	(2)	(17)	(18)	0.8	0.6	0.5	0.7	0.7	0.3
A. florea	n.s.	n.s.	n.s	n.s	***	**	(346)	(938)	(922)	0.3	0.3	0.2
Trigona spp.	**	n.s.	n.s.	n.s.	***	n.s.	n.s.	n.s.	n.s.	(51)	(101)	(122)

Inflorescence 2

	A. andreniformis			*A. cerana*			*A. florea*			*Trigona* spp.		
February:	24	25	26	24	25	26	24	25	26	24	25	26
A. andreniformis	(130)	(102)	(235)	0.5	0.7	0.4	0.1	0.1	0.1	0.6	0.8	0.3
A. cerana	***	***	***	(24)	(109)	(76)	0.4	0.6	0.3	0.6	0.7	0.4
A. florea	n.s.	n.s.	***	**	***	***	(310)	(652)	(2649)	0.5	0.7	0.3
Trigona spp.	n.s.	***	n.s.	n.s.	***	*	n.s.	***	n.s.	(4)	(10)	(11)

Inflorescences 3 and 4

	A. andreniformis		*A. cerana*		*A. florea*		*Trigona* spp.	
Inflorescence:	3	4	3	4	3	4	3	4
A. andreniformis	(653)	(909)	0.4	0.5	0.2	0.2	0.2	0.2
A. cerana	***	***	(41)	(65)	0.3	0.3	0.3	0.4
A. florea	***	***	**	***	(616)	(512)	0.1	0.3
Trigona spp.	***	***	**	***	**	***	(200)	(154)

TABLE 2. Lengths (mm) of various body parts of *Apis andreniformis*, *A. cerana*, *A. dorsata* and *A. florea*. Values are based on 10 individuals per species.

Character	*A. andreniformis*		*A. cerana*		*A. dorsata*		*A. florea*	
	Mean	s.e.	Mean	s.e.	Mean	s.e.	Mean	s.e.
Forewing length	6.39	0.03	7.83	0.04	12.72	0.10	6.44	0.02
Forewing width	2.16	0.02	2.76	0.04	4.23	0.02	2.26	0.04
Hindwing length	3.16	0.02	5.84	0.03	5.85	0.04	3.16	0.02
Tibia length	2.11	0.01	2.82	0.02	4.07	0.13	2.26	0.02
Tongue length	2.81	0.02	4.53	0.01	6.14	0.04	3.41	0.02

A. dorsata bees were rarely seen on our flowers. On those occasions when they were seen, they foraged between 06.15 h and 07.30 h. The earliest foragers were invariably *A. cerana*, which were seen in low numbers from before dawn, declining rapidly after 08.00 h, although at inflorescence 3 their abundance peaked at 09.30 h. On other inflorescences, they were rarely seen after 09.00 h. Peak abundance of *A. florea* and *A. andreniformis* followed *A. cerana*, leading to significantly different abundance distributions (figs 2 and 3, table 1). The distributions over time of *A. florea* and *A. andreniformis* did not differ significantly at inflorescence 1 on any day (table 1), but the abundance of *A. andreniformis* peaked later than that of *A. florea* at inflorescence 2 on February 26 (fig. 2) and at inflorescences 3 and 4 on February 28 (fig. 4). This led to significant differences in the abundance distributions over time (table 1) for these two species. Two *Trigona* species, *T. geissleri* Cockerell and *T. scintillans* Cockerell, had highest proportions of foragers after foraging by *Apis* species was reduced (figs 2 and 3), with abundance

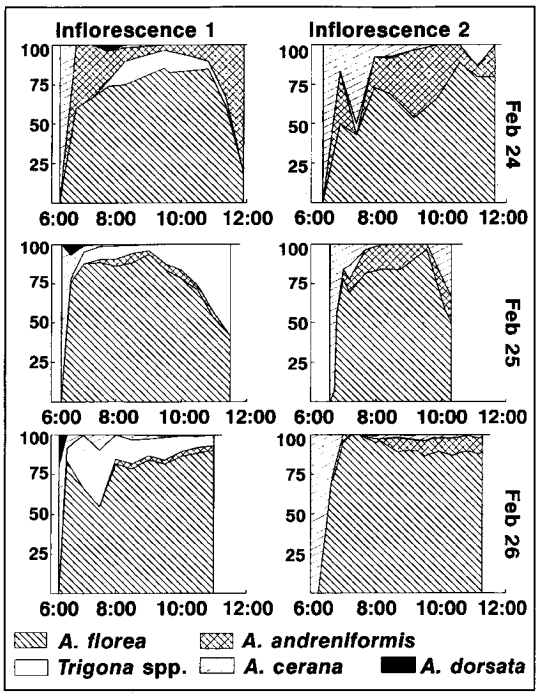

FIG. 2. Proportion (%) of the total number of bees, for each species, at inflorescences 1 and 2 at different times of the day.

distributions significantly different from *A. florea* when numbers of *Trigona* were greater than 10 (table 1).

The numbers of bees observed for each species varied greatly by inflorescence location and by time. *A. florea* was numerically dominant at inflorescences 1 and 2 on all three days of observation, but *A. andreniformis* was numerically dominant at inflorescences 3 and 4 (table 1).

Bees of the four *Apis* species varied greatly in overall size (as estimated by the wing and leg measurements) and in tongue length (as estimated by the combined length of the glossa and post-mentum) (table 2).

DISCUSSION

Aggressive interactions among foragers were not observed. This contrasts with the findings of Koeniger and Vorwohl (1979) who reported frequent intra- and inter-specific interactions between and among *A. florea*, *A. cerana*, *A. dorsata*, and *Trigona iridipennis* foraging on artificial sucrose sources in Sri Lanka. However, Roubik (1989: 106) suggests that such behaviour may be a consequence of the artificial condition of a stable nectar resource inducing nest defence or robbing behaviour which is not normal for foraging bees.

Differences in foraging behaviour of the *Apis* species

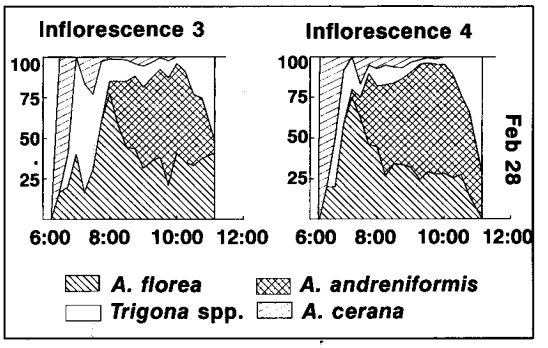

FIG. 3. Proportion (%) of the total number of bees, for each species, observed at inflorescences 3 and 4 at different times of the day.

were observed. There was an inverse relationship between body size and the number of foragers observed. The two largest species, *A. dorsata* and *A. cerana*, foraged earliest, exploiting the resource when it was richest. The actual numbers of foragers of the two larger species was relatively low (table 1). The medium-sized *A. florea* and *A. andreniformis* were numerically dominant by a wide margin, and foraged after the resource had been somewhat depleted by the larger species. The relatively tiny *Trigona* species appeared to be displaced by the medium-sized *A. andreniformis* and *A. florea*, appearing in greatest numbers either before and particularly after the peak of *Apis* foraging.

Our data support the hypothesis that the available pollen resource was partitioned according to bee size, with the two largest *Apis* species exploiting the resource when it was richest, while the smaller bees successfully utilized it when it was less profitable. The two similarly-sized dwarf honey bees (*A. andreniformis* and *A. florea*) appeared to be in direct competition on *Archontophoenix alexandrea*, with no partitioning of this resource between the bee species. The observation that *A. florea* was numerically dominant at inflorescences 1 and 2 and *A. andreniformis* at inflorescences 3 and 4 (table 1) suggests that there is at least some partitioning of resources by space and time among *A. andreniformis* and *A. florea*. The mechanism of this partitioning is not clear. Proximity to nests may cause some heterogeneity in bee numbers. However, the density of both *A. andreniformis* and *A. florea* colonies in this area is so high that this does not seem a likely cause. Perhaps foraging bees of some or all of these species mark resources with species or nest-specific odours which are somewhat repellent to other foragers.

Our observations do not suggest that competition for food resulting in floral specialization has been a cause of speciation of *A. florea* and *A. andreniformis*, although this may be the case in other environments. It is interesting that *A. florea* and *A. andreni-*

formis are of very similar size except for tongue length, which is 18.0% larger in *A. florea* (table 2). Perhaps this difference may allow some resource partitioning when foraging for nectar.

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