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APIS DORSATA,
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LANDSCAPE FORAGING ECOLOGY OF GIANT HONEY BEES, *APIS DORSATA*, IN AN INDIAN FOREST

By

Puja Batra

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ABSTRACT

LANDSCAPE FORAGING ECOLOGY OF GIANT HONEY BEES, *APIS DORSATA*, IN AN INDIAN FOREST

By

Puja Batra

I conducted a study of the spatial and temporal foraging dynamics and pollen foraging of giant honey bees, *Apis dorsata*, in Karnataka, India. Through observations of the honey bee dance language over the course of two flowering seasons at several nesting aggregations I inferred that bees forage at maximum distances of over nine km from the nest, thus covering an area of over 250 km^2. Ninety five percent of their flights occur at distances within 2.7 km from the nest. They did not exhibit predictable expansions or contractions of flight range according to the type of forest they were nesting in, year in which data were collected, or week in the flowering season. Instead, flight range variation was due to week* site differences, and week* colony (site) differences. This suggests that colonies adjust their flight distance according to local fluctuations in resources, and shift their foraging locations such that they do not overlap with neighboring colonies.

I examined the feces of colonies over the course of two flowering seasons to discover which plants *A. dorsata* utilizes as its pollen resources, and also to examine whether they exhibit preferences for certain plants. I used data on the relative frequency of the major tree species to quantify whether bees used pollens in proportion to their occurrence in the environment. Across several sites and weeks, bees overutilized pollen of *Catunaregam spinosa* (Rubiaceae) relative to its abundance in the forest, overused the relatively rare genus *Schleichera* (Sapindaceae), and underused the dominant genus *Terminalia* (Combretaceae). When phenological variation in plants was taken into account, bees still exhibited a preference for the same taxa. These results suggest that *Schleichera* and *Catunaregam* may be important for maintaining the population of *A. dorsata*, which in turn provides pollination to many other plant taxa.

I used Geographic Information Systems (GIS) to examine how the spatial and temporal heterogeneity in food plant distribution influence bees' flight range and pollen usage. Stepwise and multiple regression revealed that the flight range of *A. dorsata* is negatively correlated with *Terminalia* flowering availability. Though they do not overuse it for pollen, bees' apparent tracking of *Terminalia* may be due to the importance of this genus as a nectar source. Pollen preferences remained largely similar to the results above, although some site-specific patterns of preferences for pollens of different plants emerged when spatio-temporal heterogeneity was accounted for. These results demonstrate the power of using GIS methods alongside field observations to understand spatio-temporal variation in ecological systems.

Finally, I quantified visitation rates of *A. dorsata* to flowers of *C. spinosa* at distances within two km from the nest aggregation, and at distances beyond two km to test the hypothesis that trees within the typical foraging range of bee nest sites experience greater visitation than trees outside the foraging range, ultimately structuring the bee plant community around nest sites. There were no differences among visitation rates to the two distances, but a trend in the expected direction suggests that a more detailed study may be a promising avenue of research. This research sheds new light on the ecology of a crucial pollinator, and will be useful for conservation corridor planning in Asia.

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CHAPTER 1: INTRODUCTION

WHY STUDY HONEY BEES IN TROPICAL ASIA?

A major challenge in understanding the maintenance of biological diversity in tropical forests is to comprehend the role that is played by animals in the pollination of forest plants. In the Neotropics, an estimated 98% of forest tree species are dependent on animal mutualists for pollination, with bees representing the largest fraction of that fauna (Bawa 1990). The behavior of pollinators has a major influence on interconnections among organisms in these complex and threatened ecosystems. For example, distances traveled by pollinators will determine distance of pollen flow, and thus can profoundly influence the genetic structure of a plant population. At the community level, because the majority of tropical pollinators are generalists and not specialists on specific plant species (Roubik 1993), seasonal differences in food plants utilized by one pollinator species may create linkages between different plant species. Therefore, population changes in one food plant may have cascading effects on the forest community via its effects on a shared pollinator.

Most studies of tropical plants and their pollinators have been conducted in the New World; however, the bee faunas of the tropical regions differ markedly. Whereas pollination in the Neotropics is mediated by a highly diverse bee fauna, in Asian tropical forests pollination is presumably dominated by the two to four sympatric species of eusocial honey bees (genus *Apis*) in any given locale (Ruttner 1988; Roubik 1990). Perhaps because behavioral specializations of *Apis* confer superior competitive ability, the Asian tropics are relatively depauperate in solitary bees when compared to the New World, in which there are no native species of *Apis* (Roubik 1990). Thus, pollination ecology, and therefore population and community ecology, of forest plants in the Asian tropics may substantially differ from the situation in the Neotropics, simply due to differences in behavioral attributes of pollinators, such as whether they have a colonial or a solitary lifestyle, and their nesting requirements, foraging ranges, and degree of dietary generalism.

An understanding of pollination by *Apis* will have ramifications for forest management, conservation and reforestation plans. Generalizations made solely on the basis of Neotropical studies are likely to be inappropriate in Asian forests. We currently know very little about the actual role of honeybees in the reproduction of Asian tropical plants. In order to make predictions about the impact of major habitat fragmentation or alteration on loss of biodiversity and regeneration, it is crucial to have baseline data from a relatively contiguous forest. In particular, it is important to have data on the dynamics of flight range and foraging area, and the consequent distances of potential pollination by *Apis* throughout the flowering season, and on their use of food plants over the course of the flowering season. How those two attributes interact as resource levels vary over time will in large part determine the ability of *Apis* to absorb larger scale habitat changes. I report here my findings on a study of the pollen foraging ecology of giant honey bees, *Apis dorsata* Fabricius in a tropical forest of southern India.

Various aspects of giant honey bee ecology and behavior have been studied, including their mating behavior (Koeniger et al. 1990); seasonal movements (Koeniger and Koeniger 1980; Venkatesh and Reddy 1989; Dyer and Seeley 1994); nocturnal foraging behavior (Dyer 1985); ecophysiology (Dyer and Seeley 1987); colony defense behavior (Seeley et al. 1982; Kastberger et al. 1996; Kastberger et al. 1998); agricultural importance (Abrol and Kapil 1996); beekeeping (Nguyen et al. 1997) #49; nest site preferences (Starr et al. 1987). However, the pollination ecology of these bees has scarcely been studied in non-agricultural systems. Although visitation by bees does not ensure pollination, an understanding of their patterns of resource usage provides the foundation for explicit studies of the bees' role in pollen transfer. If it is indeed true that *Apis dorsata* are pivotal pollinators in these forests, identification of major components of their pollen diet may identify plant species which serve as "keystone" links by maintaining honeybee populations at sizes large enough to serve the diverse forest community as a whole.

Honeybees are ideal organisms for studying foraging behaviors because a great deal of information can be obtained at the nest. Their unique system of communication via the dance language is easily interpreted and provides the observer with information about the distance and direction of food sources exploited by the colony (Frisch 1967). I have constructed daily "forage maps" (Visscher and Seeley 1982) from hourly dance observations to identify the locations and number of patches being visited by a colony. In addition, I identified pollens utilized by the bees by sampling feces under the nests on a weekly basis. When taken over the course of entire flowering seasons, these data reflect the seasonal changes in foraging range and preferences of several colonies in different areas of the habitat. When the data were used in combination with the extensive maps and data compiled on the area's flora by local collaborators, I was able to address a number of questions. First, I could determine the typical foraging ranges of giant honey bees, and thus, not only the scale of possible pollen mediated gene flow, but also the amount of forest area that is necessary to maintain that bee population size. Secondly, I was able to identify what *Apis dorsata* is using as its important pollen food plants, thus which plant species they are potentially pollinating, and also which plant species are crucial in maintaining the bee population. Third, I could examine how the variation in the distribution and availability of their heavily utilized resources influences their foraging behavior.

The specific aims of my research were to conduct a study of the foraging distances of *Apis dorsata* across different spatial and temporal scales, a topic I address in chapter 2. In chapter 3, I elucidate the major pollen components of the bees' diet relative to what is available in the environment. In chapter 4 I use Geographic Information Systems (GIS) to explore the bees' foraging dynamics in the context of the spatial and temporal heterogeneity in the distribution of their resources, and finally, in chapter 5 I begin to address how the above findings may have interesting ramifications for forest community structure.

THE STUDY SPECIES: GIANT HONEY BEES

Apis dorsata Fabricius, commonly referred to as the "rock bee" or "giant honey bee," is a large open-nesting species which hangs a single large comb from high tree limbs and rock cliffs, and lives in colonies of 40,000 to 60,000 bees (figure 1.1). The species ranges throughout tropical and parts of subtropical Asia and is believed to be among the most important pollinators of trees in areas where they occur. Moreover, they are important pollinators of many economically important fruit, oilseed, and fiber crops (Sidhu and Singh 1962; Sihag 1986; Verma 1987; Crane 1991; Abrol and Kapil 1996; Sinha and Atwal 1996).

Like the other eight described species of honey bees, *A. dorsata* is a eusocial species in which there is only one reproductive female, commonly referred to as the queen. All other female bees in the colony are workers that perform tasks needed for colony maintenance, such as feeding and grooming the queen and larvae, cleaning the empty comb cells of debris and parasites, thermoregulating and guarding the nest, and foraging for and storing food (Winston 1987). Honey bees maintain perennial colonies, and are largely considered to have a generalist diet in that many different plants can be exploited for nectar and pollen.

As with all honey bees, colonies reproduce by fission after the parent colony has reached a critical size. This phenomenon is referred to as swarming, and is not to be confused with the dramatic colony migrations that are a unique aspect of the natural history of *Apis dorsata* and its Himalayan sister species, *A. laboriosa*. The migrations, in which colonies presumably track resources according to the rainy/dry season cycle, are not well understood, but they may occur over a distance of 100 km or more (Koeniger and Koeniger 1980). Another fascinating aspect of the biology of giant honey bees in some parts of their range including India, is their large nesting aggregations of up to one hundred colonies on a single tree or cliff face (figure 1.1b). The implications of the yearly migrations and nesting aggregations on individual colony foraging behaviors and pollination remain unexplored and fascinating questions. Before such questions can be investigated however, a clear understanding of relationships between *Apis dorsata* and its forest food plants is necessary.

Past studies on the foraging range of pollinating insects have relied on inference of potential flight range by displacement and return of marked insects released at various distances from their nests (e.g., Janzen 1971; Roubik and Aluja 1983). Such studies estimate an upper bound for foraging range, but do not help to resolve the question of how the insects are typically foraging in the environment throughout the course of the flowering season. Honey bees are ideal for study of this question, as an enormous amount of information about their resource use can be obtained by behavioral observations at the nest itself. Various aspects of pollinator foraging behavior, here most importantly the distance and direction of a foraging location, are readily obtained through observations of activity at the nest (Visscher and Seeley 1982). In the following chapter I rely heavily on the techniques and insights from the classic work of Karl von Frisch on the unique communication system of *Apis*, known as the dance language (Frisch 1967), to infer the foraging locations of giant honey bees.

THE STUDY SITE: ECOLOGICAL AND HUMAN LANDSCAPE

Along the western coast of peninsular India runs the Western Ghats, a hill range that has been designated as one of the global "hotspots" of biodiversity, due to its high levels of plant endemism as well as the high degree of threat it faces from human activities (Myers et al. 2000). Along the eastern coast of the peninsula runs another hill range, the Eastern Ghats, a much drier region due to its position in the rain shadow of the Western Ghats. I conducted this work in the Biligiri Rangaswamy Temple Wildlife Sanctuary (BRT), located between 11° 40'-12° 09' N and 77° 05'-77° 15' E in the Biligiri Rangan (BR) Hills of Karnataka, India (figure 1.2). The BR Hills are a low hill range that forms a saddle between Eastern Ghats and Western Ghats. Although they contain floristic elements of both regions, and form a stepping stone between different floristic regions of Asia (Ramesh 1989), their floral affinities more closely overlap with the Western Ghats, especially in the dry deciduous forest, the predominant vegetation type (Murali et al. 1996). For this reason BR Hills are often considered the easternmost spur of the Western Ghats, and mark the eastern range edge of many Western Ghats species.

BR Hills experiences both of the monsoons of southern India, and thus has two rainy seasons in addition to "summer showers," convectional storms which occur prior to the onset of the Indian southwest monsoon. The southwest monsoon is responsible for most of the rainfall in the region and spans the period from June through September. Following that, BR Hills also experiences the retreating northeast monsoon, primarily caused by cyclonic activity off the Bay of Bengal, which hits the regions during the period from October through December (Ramesh 1989). In the deciduous forest, leaf shed and new leaf flush occurs during the dry season from February to April. This is also the main flowering season for trees, and the season during which *Apis dorsata* migrates into and forages in the area.

Biligiri Rangaswamy Temple Wildlife Sanctuary (BRT), a protected area covering 540 km^2 within the BR Hills region, reflects much of the heterogeneity of habitats and history of the Western Ghats (figure 1.2). Among the predominant vegetation types is the low elevation (700-900 m) scrub forest, dominated by low, dense undergrowth and a canopy height of 10 m or less. The scrub forest is characterized by relatively low average annual rainfall (750 ± 130 mm), and mainly occurs on the periphery of the sanctuary. It is typified by thorny vegetation in the families Mimosoideae, Rubiaceae, Rhamnaceae, and Euphorbiaceae (Shankar et al. 1998). *Apis dorsata* can sometimes be found nesting on the large trees that occur along riparian zones, but does not commonly nest in this forest type (pers. obs.).

The second of the major habitat types in BRT is the dry deciduous forest, occurring at elevations between 1000-1400m (Ramesh et al. 1998). This type is dominated by *Anogeissus* and *Terminalia*, both in plant family Combretaceae, as well as *Grewia*, *Dalbergia*, *Pterocarpus*, and other genera. The canopy structure is relatively open, and includes trees of 20 m or more in height. This forest type occurs across a variety of rainfall regimes, and hosts several large aggregations of giant honey bees. The majority of my research was conducted on colonies nesting in the dry deciduous forest.

A third major vegetation type is evergreen forest which occurs mainly in narrow bands and patches in the higher elevations of BRT (1200-1400 m). The average annual rainfall in this type is between 1400-1800 mm depending on the hill chain and slope upon which the patch resides. Evergreen forest here includes areas with a canopy height of more than 20 m. The evergreen forests are very similar in physiognomy and composition to the riparian forests that occur throughout BRT, dominated by *Elaeocarpus*, *Canarium*, and *Michaelia* (Ramesh 1989). *Apis dorsata* colonies can often be found in the tall evergreen forests, although large aggregations are uncommon.

Another category of evergreen forest occurs above 1400 m elevation. The stunted *shola* forests are high elevation patches of evergreen forest which occur in hydrogeological pockets of moisture surrounded by grasslands. Their physiognomy differs markedly from that of evergreen forest, with a canopy of around 15 m maximum, and relatively little understory. The shola forest tree community composition is dominated by the family Lauraceae (Ramesh 1989). Although bees are seen foraging on plants in sholas, they are rarely, if ever, seen nesting in these patches.

Amidst the matrix of these main types of habitats are many patches of smaller native habitat types such as the high elevation grasslands, tree savanna, riparian zones, and others (figure 1.2). Besides the complex floral communities that it harbors, BRT Wildlife Sanctuary is home to healthy populations of a great number of the charismatic Indian megafauna, including tigers, leopards, elephants, langurs, macaques, the elk-like sambar, spotted deer, barking deer, gaur, sloth bear, wild dogs, wild boar, giant squirrels, and many others.

The human landscape in the area is as heterogeneous as its habitats, reflecting several centuries of varied types of human use. The Soliga people are the traditional inhabitants of the BR Hills, and although many have moved away to cities and towns nearby, about 5000 Soligas live within the boundaries of BRT and depend on the forest for fuelwood, fodder, and non-timber forest products (Shankar et al1998). Originally they were shifting agriculturists whose land use practices involved clearing small patches of land by setting ground fires, farming it for 8-10 years, and then leaving it fallow for 50-60 years (Rudrappa 1996). They actively managed the forest as well as the lands they cultivated, most directly by rotational burning of small patches. They set fires in order to control the thorny undergrowth which impeded movement through the forest, and to control the build up of fuel on the forest floor such that highly destructive fires could not occur. Rudrappa (1996) reports that their management of the forest through fire selected for the growth of certain useful plants, and created grazing patches which attracted species of herbivores that they hunted. The forests here, as perhaps most of Asia's forests, are products of centuries and generations of management by humans whose absolute dependence on the products of their ecosystem required an intimate familiarity and coexistence. Although major traditional land use practices have changed, Soligas living in BRT continue to depend on the wealth of the forest for food, medicine, and spirituality.

As in much of Western Ghats, BR Hills underwent commercial logging by the British colonialists, which then continued into post-colonial era. By 1987, all tree felling was banned and the area was designated as the Biligiri Rangaswamy Temple Wildlife Sanctuary, to be administered by the Karnataka State Forest Department. Most of the people living within the boundaries were resettled to an area in the northern part of the sanctuary. The Soligas continue to have usufruct rights to harvest non-timber forest products (NTFP) such as fruits, lichen, medicinal plants and honey; however, they do not have hunting or fishing rights, nor do they practice shifting agriculture anymore, and at present almost all families subsist at least in part on the cash economy that sales of forest products and temporary employment brings them.

Among the most significant NTFP's that are collected for both personal use and for sale is honey from *Apis dorsata*. Honey collection by Soligas is a major seasonal undertaking, and a dramatic scene to witness. Collection from *A. dorsata* occurs at night at heights of up to 40m or more; thus, it is a vocation practiced only by a few highly skilled people, and honey collecting season is typically opened with a prayer ceremony by the collectors. Although collection requires destruction of the comb, it does not typically result in destruction of the colony; thus, it is not clear what, if any impact the collection of honey has on the population of *Apis dorsata*. Honey collection is a practice that has occurred sustainably for several thousands of years in Asia (Crane 1999); however, present day changes in economic imperatives are altering the traditionally sustainable harvesting practices of many forest products around the world. Studies are ongoing in BRT as to whether the honey collection practices and harvest levels will ensure the persistence of the resource in perpetuity.

Because of the presence in this area of a 500 year old Hindu temple which once belonged to the Prince of Mysore, and which is now heavily visited by worshippers from surrounding regions, the approximately 4 km^2 area in which the indigenous people were resettled is not technically part of the wildlife sanctuary (figure 1.2). Instead it is designated as revenue land in which people can settle, purchase land, grow crops, etc. In addition to the Soliga settlements in this area, there exists a hospital and school run by a local NGO working with the Soligas called the Vivekananda Girijana Kalyana Kendra (VGKK), the temple and its surrounding administrative bodies and visitor facilities, forest department housing and outpost, a place for religious study called an ashram, a few small public works offices which are or were in the past involved in government development schemes with the local people, and a research field station operated by Ashoka Trust for Research in Ecology and the Environment (ATREE) from which I conducted this work.

In addition to Soliga settlements in the above described area, a few Soliga settlements are scattered in some areas inside the actual sanctuary. Here, houses are typically made of thatch, and the people cultivate small kitchen gardens that include bananas, tubers, and gourds. In addition to these settlements, there are other human influences inside the sanctuary boundaries. Much of the original range of evergreen forest was replaced by coffee plantations by British colonialists in the early 20th century, and these still exist as functioning plantations today. Tree plantations of *Eucalyptus* and Teak were planted in a number of small isolated patches by the forest department, and although they are no longer maintained, they persist as discrete types in the landscape and have not yet been overgrown by native vegetation.

Amidst this varied biotic and human landscape, a study of honey bees has even greater relevance. Our scientific knowledge of rock bees is somewhat scant, and human knowledge of it is rapidly disappearing as the wisdom accumulated by indigenous Asian cultures transforms to keep pace with the demands of the modern world. A forest such as BRT that has been inhabited and managed by humans for millennia represents the situation that is typical of forests throughout South Asia (Gadgil 1992). It is not a pristine habitat, but one in which the forces of human alteration have acted and continue to act at a pace much slower than the changes presently occurring around it. People throughout Asia depend on *A. dorsata* directly, for the products they derive from bees, and indirectly, through their pollination services to forests and croplands. Thus, I believe that research which sheds light on aspects on the ecological role of *Apis dorsata* and pollination in the Asian tropics could have potential widespread value in many areas of Asia in which similar networks of dependency exist among people, honeybees, and forests.

Figure 1.1. a. *Apis dorsata* nest b. *Apis dorsata* nest aggregation of over 80 colonies.

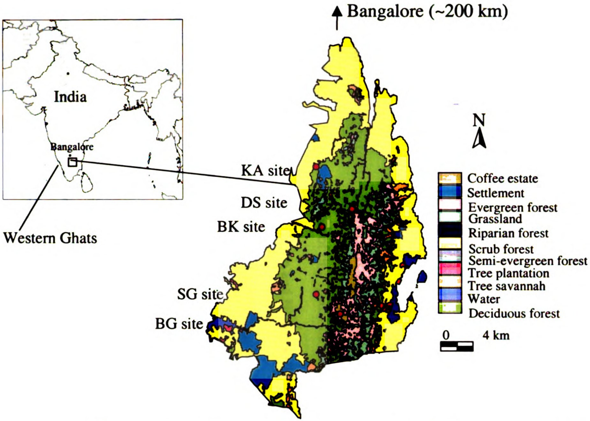

Figure 1.2. Map of India and landscape map of Biligiri Rangaswamy Temple (BRT) Wildlife Sanctuary, Karnataka, India. Map of BRT: Ramesh, B.R., S.Menon, and K.Bawa, 1998. Some legend entries from the latter have been changed to be consistent with wording in the text. Red circles mark locations of study areas with site names on left side of map.

CHAPTER 2: DYNAMICS OF FLIGHT RANGE ACROSS SPATIAL AND TEMPORAL SCALES

INTRODUCTION

Insect pollinators have recently become focal points in applied ecology for their role as crucial links in the long-term integrity of ecosystems (Buchmann and Nabhan 1996; Allen-Wardell et al. 1998; Kearns et al. 1998). Consequently, a number of research efforts are underway to assess the effects on the pollination mutualism of habitat changes such as fragmentation. These implicitly spatial problems are somewhat limited by our lack of information regarding the foraging distance of pollinating insects. The foraging ranges of insects are especially of interest since insects are presumed to be limited in their ability to effectively cross-pollinate as the spacing between conspecific plants increases. The consequences of this spatial limitation on insect foraging have implications for fruit and seed set (Nason and Hamrick 1997; Nason et al. 1998; Steffan-Dewenter and Tscharntke 1999), levels of inbreeding depression and seed viability (Hall et al. 1996), population genetic structure (Murawski and Bawa 1994; Dayanandan et al. 1999), and plant community composition (Nason and Hamrick 1997), all via their effects on pollinator foraging.

In contrast to the Neotropics where honey bees are introduced, Asian tropical forests host from one to three sympatric and native species of *Apis* in any given area (Ruttner 1988). In Asia, where the bee fauna is less diverse than in the Neotropics, and where the native fauna and flora have evolved alongside *Apis*, it has been hypothesized that the highly eusocial bees have largely "pre-empted" the insect pollinator niche (Michener

1979; Roubik 1990), in part due to the unrivaled efficiency with which they recruit nestmates to resources over long distances. Thus, although habitat fragmentation has negative effects on plant populations in some Neotropical plants (Aizen and Feinsinger 1994), such effects may be mitigated in Asia by the recruitment system and relatively long foraging distances of honey bees. Consequently, these forests may be somewhat "immune" to the effects of spatial disruption of the habitat as they affect pollinator foraging. There have been findings in support of this idea from studies in the Neotropics: studies of fruit set, seed set, and even genetic variation has shown that the introduced European honey bee, *Apis mellifera scutellata* is in fact now assuming the role of an dominant tree pollinator in fragmented or highly disturbed habitats, in some cases where the native pollinator fauna has dwindled (Aizen and Feinsinger 1994; Dick 2001). This suggests that the genus *Apis* may indeed possess unique traits that allow it to exploit resources in a way that is less limited by spatial configuration of habitat. However, before being able make predictions about the impact of large scale habitat alteration on loss of biodiversity and habitat regeneration, it is crucial to have baseline data from a relatively unfragmented forest: the dynamics of flight range and foraging area, and thus distances of potential pollination throughout the flowering season must be documented. These parameters may vary in response to resource fluctuations, so estimates made over an extended time period will allow for a distribution of flight ranges reflective of the variation in natural systems.

Due to the difficulties of gathering such information, there are very few estimates of the foraging ranges of insects, despite their crucial importance in all terrestrial ecosystems.

Past estimates of pollinator flight range have relied on indirect methods to estimate the upper bound of potential flight range (Janzen 1971; Roubik and Aluja 1983; Dramstad 1996; Saville et al. 1997; Roubik 2000) due to the impossibility of tracking individuals as they perform foraging flights over several kilometers (but see Osborne et al. 1999).

Honey bees (genus *Apis*) present a unique opportunity to investigate flight range due to their communication system known as the "dance language" (Frisch 1967). Foragers communicate to nestmates the distance and direction of a food source via means of the "waggle dance" which occurs on the nest surface. Across the entire genus *Apis*, the dance language works in the following way. A forager that finds a profitable source of forage returns to the nest and informs her nestmates of the location of the patch by running in a straight line on the vertical surface of the nest comb, while rapidly waggling her abdomen back and forth. The angle relative to the upward direction at which she runs corresponds to the horizontal angle between the solar azimuth, the patch of forage, and the nest (figure 2.1). She waggles for some period of time, usually on the order of a few seconds, then returns to her original position, repeats the run, and may continue to repeat it several more times. The distance signal is encoded by the duration of the waggle run such that the duration of each run translates into distance flown. The relationship between waggle run duration and distance flown is referred to as a "dialect" because, as with human linguistic dialects, it varies across geographically isolated populations (Frisch 1967). In *Apis*, the distance dialect also varies across species (Lindauer 1957; Dyer and Seeley 1991), and can be calibrated by researchers for any given species or population. Thus, by observing dances one can use the bees' own communication signals to infer direction and distance flown without the need to track individual bees as they fly.

This method has been used by past researchers examining foraging organization and strategies of *Apis mellifera* in both native (Schneider 1989; Schneider and McNally 1992a) and non-native environments (Visscher and Seeley 1982; Waddington et al. 1994). Although there are estimates of the foraging range of *Apis mellifera* from the above studies, other species of Asian *Apis* (Punchihewa et al. 1985; Dyer and Seeley 1991), some stingless bees (Roubik and Aluja 1983), and some bumblebees (*Bombus* spp.) (Saville et al.1997; Osborne et al.1999), until now there have been no estimates for any pollinating insect across various spatial and temporal scales, and none that accounted for intercolonial variation by examining several colonies over the same extended time period.

The giant honey bee, *Apis dorsata*, is ubiquitous throughout tropical Asia, and like all other honey bees, possesses the ability to communicate via dance language. *A. dorsata* nests hang in the open from tree limbs or rock cliffs, often in large aggregations (Deodikar et al. 1977) (figure 1.1b). These aggregations occur at sites which are recolonized by migrating colonies of *A. dorsata* year after year. Nests consist of a single comb covered by a "curtain" of bees (Ruttner 1988) and waggle dances occur on the surface of the curtain, visible to the naked eye or through a spotting scope (Dyer and Seeley 1991). I observed the dances of several colonies in different nesting sites over the course of the flowering seasons of 1997 and 1998 in the Biligiri Rangaswamy Temple (BRT) Wildlife Sanctuary in Karnataka, India.

In this study, I used the dance language signals to infer locations of foraging patches throughout the entire flowering season for two consecutive years in order to examine flight range distributions across a range of spatial and temporal scales. An estimate of flight range and its variation will allow me to estimate the area of a given forest type which is needed to support colonies in nesting aggregations of *A. dorsata*, and in turn how much forest area a nesting aggregation provides pollinator services to. I expected that different habitat types, microhabitat characteristics associated with the nesting site, and colony differences to contribute to variation in flight range. Furthermore, I expected to find that flight range contracts and expands in response to resource availability when examined chronologically across the season as the flowering season progresses.

METHODS

DISTANCE DIALECT CURVE

The translation of circuit duration-distance to flight distance was made by obtaining a "dialect curve" for the population using standard methods (Lindauer 1957; Frisch 1967; Dyer and Seeley 1991). Data for dialect curve calibration were collected in Bangalore, India (12.58 N, 77.35 E) during October 1998. We located an *A. dorsata* nest on a partially constructed building with a fairly long stretch of open, flat land in front of it, ideal for this type of data collection. The nest was on the second story of the building, and thus was within the normal range for nesting height of *A. dorsata*. Since it was constructed in a window space, it was possible to approach from inside the building in order to "bait" the bees. On the first day of data collection and every morning subsequently, we baited the nest with concentrated sugar solution scented with orange essence. This technique of spraying the nest with the same solution used in the training feeders induces the bees to search for that scent elsewhere.

We trained bees from the above colony to forage at a feeder with scented sugar solution by initially placing it close to the nest. Once a few bees had found it and recruitment of nestmates was in progress, the feeder was progressively moved further away from the building, and we marked recruits with acrylic paints as they fed. By marking each bee with a unique color combination on the thorax and/or abdomen, we ensured that dance measurements would only be taken from foragers seen at the feeder, and we also were able to avoid resampling the same individuals when measuring their dances.

After marking several recruits, the feeder was moved to a distance of 100 m from the nest and we began data collection. One person was stationed at the feeder, marking new recruits and noting the identities of feeder foragers. One person was stationed near the nest, measuring the dance angle and waggle circuit duration of foragers returning from the feeding station as described below. We communicated with each other via two-way radios to confirm identities of bees seen at the feeder and whose waggle dances were therefore to be timed.

Observations were made by watching each marked dancer bee through a Swift 15-60x spotting scope. To measure the distance signal in the dances, we timed the entire waggle circuit duration, as opposed to only waggle run duration. By timing a minimum of three continuous circuits, average circuit duration could be obtained while minimizing the error associated with starting and stopping the stopwatch, thus improving precision as well as accuracy in the distance estimate. Waggle circuit duration is often used as a surrogate for waggle run duration because the two measures are highly correlated (Frisch 1967).

After at least 20 different bees' dances were measured, the feeder was again moved out in gradual steps to the next 100 m increment, and the process was repeated. Over the course of two weeks, we trained the bees to a distance of 1100 m, beyond which it was impossible to entice them to the feeder. Sample sizes associated with the 1000 m and 1100 m training distances are less than 20, as it appears that fewer bees were motivated to recruit to the sugar solution at distances so far from the nest.

I ran a least squares linear regression of circuit duration vs. feeder distance to describe the waggle circuit duration-distance relationship. I used this regression equation to infer distances flown by dancers whose dances were observed for forage mapping.

FORAGE MAP DATA COLLECTION

Forage map data were collected in BR Hills during the dry seasons of 1997 and 1998. In 1997, I observed the foraging activities of *A. dorsata* in both deciduous forest and evergreen forest, the two habitat types in which they are known to occur predictably every year in B R Hills. In each habitat, two nest aggregations of >20 colonies were chosen on the basis of their accessibility. The nesting aggregations are a convenient spatial unit in which to choose replicates because all colonies in an aggregation experience the same surrounding environment. At each aggregation (or "site") I chose three or four representative colonies from which to collect data throughout the season. The selection of colonies at a site was largely determined by the accessibility of a clear line of sight perpendicular to the planar surface of the comb, and a ground surface level enough to support the spotting scope at a distance of 10-30 meters from the nest. In 1998, for logistical reasons I restricted the study to three deciduous forest sites.

Forage maps were constructed by observations of the dance language of the bees, measuring waggle angle and waggle circuit duration. On each focal colony, I randomly chose dancer bees for observation. I watched each bee with one eye through the spotting scope, and looked at a carpenter's protractor (an instrument with a mechanical plumb line) while holding it against the scope with the other eye. Binocular vision creates the appearance of the bee dancing along the edge of the protractor, and thus, I was able to measure the vertical angle of the waggle dance. Waggle duration was timed using the methods described in the dialect calibration section of this chapter. Other necessary pieces of information needed were those that affect the position of the solar azimuth: the date, and exact time (HH:MM) at which the observations were being made, longitude, and latitude of the site. The latter two were taken using a Magellan Trailblazer GPS unit.

Each site was visited for one full day per week. During each observation day, each colony was observed for twelve minutes every hour starting at approximately 0600 or with the first sign of dance activity after 0600. Observations continued until the time at mid-day when flight and dance activity by the bees stopped, usually around 1200. We then resumed dance observations from approximately 1600 until 1800, at which point the bees were often still dancing, but light levels became too low to see them through the spotting scope. During 1997, the Beduguli site was observed every week from 1600-1800 on one day, and from 0600-1200 the following day. The end of the observation season was when colonies started migrating and/or honey harvesting (and therefore colony comb destruction) began. In 1998, observations at Sige Gudi site ended earlier in the season than those at the other two sites because two of the three colonies under observation absconded for unknown reasons in mid-season. Appendix 1 summarizes the site characteristics, dates of observation, number of colonies and weekly sample sizes of dances measured.

FORAGE MAP CONSTRUCTION

I constructed forage maps by first plugging the average circuit duration for each dance observed into the regression obtained from the dialect calibration to obtain distance flown by each dancer. Second I translated the dance angle into the bee's flight angle using a Microsoft Excel macro programmed for calculation of the sun's azimuth. Based on site latitude and longitude, date, and time of data collection, the program calculates the position of the azimuth with the following equation:

$Azimuth = \arccos [(\sin D - \cos Z \sin L) / \sin Z \cos L]$

D = *solar declination*

L = *latitude*

Z = *zenith distance* $= \arccos (\sin D \sin L + \cos L \cos D \cos H)$

H = *hour angle, i.e., time in hours relative to local noon* $* 17°/hr$[1]

Using the position of azimuth, the program translates dance angle into the bee's actual flight direction relative to geographic north.

The flight direction and distance for each dance were converted into (x,y) coordinates using the following set of formulas:

Flight angle radians = Radians (90-compass flight direction[2]*).*

$x = \cos$ *radians * flight distance in meters*

$y = \sin$ *radians * flight distance in meters.*

The (x,y) coordinates were plotted relative to the origin (0,0) which indicates the honeybee nest site aggregation.

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[1] 17 degrees per hour is the rate of the sun's movement at the latitude of the study site.

[2] In a compass angle, 0° occurs in the forward (or upward) position, but in a mathematical angle it occurs in the right hand horizontal position. Thus, the compass angle first had to be transformed into a mathematical angle using the formula (90-flight angle).

STATISTICAL ANALYSIS

In order to determine whether flight range varied between years or according to time in the flowering season, and whether various levels of spatial differences (habitats, sites within a habitat, colonies within a site) accounted for variation in flight range, flight distances were compared by performing a repeated measures nested analysis of variance (ANOVA). Using SAS 8.0 software to run the general linear models procedure, model factors were defined as year, site (year), colony (site, year), week (year), week* site (year) and week*colony (site, year). I designated year, site, colony (site, year), week* site (year) and week*colony (site, year) as random variables. Initially, 1997 data were analyzed separately with habitat type as the highest level in the nested hierarchy to determine whether colonies nesting in evergreen vs. deciduous habitats varied in flight range. Since there was no significant difference due to habitats ($p = .8041$) (figure 2.10 inset), the 1997 data were pooled with the data from 1998 in which I studied nests only in deciduous habitat. Sites BK and KA were used in both years, but they were considered in the ANOVA to be separate, hence the site term is nested within year. Flight range was non-normally distributed, therefore all ANOVA's were performed on natural log transformed values. The data were still non-normally distributed, but ANOVA with large sample sizes is considered to be robust to non-normality (Sokal and Rohlf 1981).

To distinguish whether colonies forage in a manner that results in segregation of foraging locations from week to week, a two-way multivariate analysis of variance (MANOVA) was performed for each site data set on the (x, y) coordinates of each foraging location as they varied with colony, week, and colony*week. Using JMP 3.2 statistical software (SAS Institute 1999), the response design used was the identity matrix, utilized in order to keep the integrity of each variable separate instead of summarizing the two dependent variables. I report F ratios and p-values from Pillai's Trace test since this is the test considered to be the most robust to unequal sample sizes (Tabachnick and Fidell 1983).

RESULTS

DISTANCE DIALECT CURVE

The calibration curve for the distance dialect reaches to 1100 m from the nest, with a clear linear fit of circuit duration vs. distance ($y = 1.39 + 0.0030\ x$, $r^2 = .86$) (figure 1.2). I used this equation in forage map construction to calculate the distance flown by dancers observed at BRT. For dances with circuit durations greater than that observed for the longest training distance (1100 m), I assumed that the slope of the dialect curve could be extrapolated to greater flight distances. This assumption has been supported for *A. mellifera* (Frisch 1967).

FORAGE MAPS

Forage maps for all sites on a weekly basis are given in figures 2.3-2.9. An examination of the forage maps alone suggests certain patterns: flight range is largely concentrated within a few kilometers from the nest, but there are some occasional longer distance flights; distance does not appear to contract and expand in a linear chronological progression; any given colony does not restrict its entire season's flight activity to a certain distance or a certain direction, but instead seems to shift its use of the landscape on a weekly basis; and colonies appear to be using patches in roughly different places. These patterns are examined statistically in greater detail below.

FLIGHT RANGE DISTRIBUTION AND FORAGING AREA

Figure 2.10a inset illustrates the similarity of flight range in the two habitat types examined in 1997. Figures 2.10 and 2.11 illustrate the overall flight ranges of *A. dorsata*, in 1997 and 1998 separately and combined, respectively. Results of the two years combined indicate that 90% of foraging locations occur within 2278.8 m from the nest (figure 2.11), corresponding to a circular area of 16.3 km^2. The results also indicate, however, that bees occasionally advertised a location that was close to ten kilometers away (figure 2.11); thus the maximum circular foraging area covered by any colony was 289.2 km^2. Images in this dissertation are presented in color.

ANALYSIS OF VARIANCE

ANOVA results (table 2.1) reveal that flight range did not vary temporally, either between years, nor between weeks within a year. A significant portion of the variation was, however, explained by the interaction between week and site, and by the interaction between week and colony. The latter suggests that there may be some separation of foraging locations among colonies in the same aggregations, a point which is further investigated below by a MANOVA on the coordinates of foraging locations. Site and colony main effects were significant, but confounded by their significant interaction terms with week. It appears then that the above foraging range distribution does not vary across different temporal scales or according to habitat characteristics, and is representative of a typical *Apis dorsata* colony's foraging movements over the course of an entire flowering season.

MULTIVARIATE ANALYSIS OF VARIANCE

MANOVA results for each site confirmed that colonies are not foraging in the same patches (table 2.2). In only one site (BG 97) were there significant colony main effects; that is, in six of the seven sites, colonies did not "specialize" on a particular segment of the landscape throughout the season. In most sites there was a significant effect of week on location of foraging patch, that is, the flowering patches used shifted significantly between weeks. In all sites, there was a significant effect of colony* week interaction, that is, in any given week, colonies foraged in different locations relative to each other, confirming the ANOVA result that colonies within sites varied relative to each other in the distances they foraged among weeks.

DISCUSSION

The forage maps in figures 2.2-2.9 illustrate the areas of terrain that are covered over the course of a flowering season by an aggregation of *Apis dorsata*. Colonies send foragers out over a maximum area of close to 300 km^2, a figure that rivals and even exceeds home range estimates made in the same or similar habitats for several large mammals (Batra et al, in prep.).

Despite the enormous maximal range, however, most flights were concentrated within two kilometers from the nest, as was also found in *Apis mellifera* in both native and non-native habitats (Visscher and Seeley 1982; Schneider 1989). Furthermore, the maximum *A. dorsata* flight distance was approximately the same as that of *A. mellifera*, but the 90% quantile for *A. mellifera* was much greater (6 – 6.5 km), indicating that the flight range distribution of *A. dorsata* shown in fig 2.11 is less evenly distributed, that is, far more skewed than that of *A. mellifera*. A similarly skewed flight range distribution was found by Dyer and Seeley (1991) for a single colony of *A. dorsata* in Thailand, suggesting that my conclusions may indeed be applicable throughout tropical Asia where *A. dorsata* occurs.

The results of the statistical analyses suggest a picture of flight range that is fairly stable when viewed over large spatial and temporal scales, but one that undergoes constant dynamic shifts at smaller spatio-temporal scales. As evidenced by the ANOVA, neither year nor week, the two temporal factors, had significant effects on distance flown in foraging flights by *A. dorsata*. Flight range data for two consecutive years did not show any differences in overall distribution, suggesting that there may be little inter-annual variation, and that *A. dorsata* may be constrained in its flight distance by factors that have little to do with large scale environmental fluctuations that occur between years. Ideally, such findings would be confirmed over several more years, and thus span a greater range of climatic or other conditions that may vary among years.

Flight distance also did not vary across shorter time periods. During any week in the season, the entire distribution of flight range was exhibited when all colonies were examined together; that is, flight range does not undergo predictable expansions and contractions which respond directly to progression of the flowering season. Thus, the hypothesis that flight range would respond uniformly across all colonies to changes in floral resource availability is not validated. It is possible that although flowering density increased and then decreased over the season, colonies' energetic needs changed in tandem, such that the simple equation of being able to fly shorter distances due to an abundance of resources could not compensate for the increase in numbers of brood and adults as reproductive swarming time approached. Instead, an interaction between changing resources and changing needs resulted in no net change in flight distance over the weeks of the study.

Results of the spatial influences on flight range reveal that on the large scale level of "habitat type" flight range does not vary, as evidenced by the ANOVA on 1997 data. Similarly, neither site differences nor colony differences explain variation in flight range. Instead, the significant week*site and week*colony interaction terms suggest that flight range is far more dependent on individual site and colony conditions as they change from week to week. The weekly site differences most likely reflect local availability of flowering patches influenced by microhabitat variation, and are highly site-specific. I address this issue further in chapter 4.

The statistically significant week*colony term suggests that foraging range expansions and contractions occur on a more colony specific basis over short temporal scales. A similar finding was reported by Waddington et al (1994), who found the colony* day interaction to be highly significant in a study of two *A. mellifera* colonies placed side by side and studied in two habitats for four days each. Waddington et al suggested that different nutritional demands might result in different foraging patches being preferred. Flight range may be influenced not only by a colony's discovery of resources, but also by "colony state," that is, its availability of workers, its need for incoming pollen and/or nectar as demanded by the adult to brood ratio and potential for swarm production (Schneider and McNally 1992a, 1992b), and factors such as disease, parasite load, and predation losses by wasps or birds—all dynamic influences that may interact and vary between colonies and between weeks.

Estimates made by Visscher and Seeley (1982) of flight range for *Apis mellifera* in a temperate forest showed a flight range distribution in which 90% of all flights occurred within a 6600 meter distance, clearly exceeding the 90% quantile of 2280 m that I observed for *A. dorsata*. Their estimate, however, was based on intensive sampling of only one colony spread out over a three month period, but it did not cover the early and late parts of the season, nor did it not account for intercolonial or interannual variation. If the statistical results that I report here for *Apis dorsata* are applicable to *A. mellifera* as well, Visscher and Seeley's estimate may nonetheless be an accurate indicator of the region's *A. mellifera* population on the whole, since I found no interannual, intercolonial, or weekly differences. However, in a study of *A. mellifera scutellata* in southern Africa by Schneider and McNally (1992a, b), there did appear to be differences based on seasonal availability of food, with flight range showing strong (although not statistically analyzed) increases as the dearth season approached. It remains unclear as to what extent the tropical race of *A. mellifera* studied by Schneider and McNally and the European race studied by Visscher and Seeley are comparable, nor do we know to what extent the results I report for *A. dorsata* may be generalized to other species of honey bees.

A further implication of the significant week* colony interaction is that during any given observation period, colonies were not foraging at the same distances from the nest site. The suggestion that distances and hence foraging patch locations were different is confirmed by the consistent results of MANOVAs performed on the (x,y) coordinates of all inferred foraging locations. The coordinates are a combination of the distance and direction of a foraging patch. If colonies nesting at the same site are utilizing distinct patches, the MANOVA results should show a significant effect of week*colony on (x,y) coordinate combinations. This is indeed the case in all seven sites, confirming the results of the ANOVA which examined distance alone. I observed only a small proportion of the colonies nesting in each site, so it is possible that the particular colonies observed incidentally happened to be visiting locations widely separated from each other. However, this "sampling artifact" scenario is unlikely to be an adequate explanation for my results given that all seven sites showed the same result quite strongly. Additionally, since there was a significant main effect of colony in only one of the seven sites, there is no evidence that colonies generally separate their foraging locations by "specializing" on a certain segment of the surrounding environment and staying within it throughout the season.

A similar result implying spatial separation of foraging effort was found by Waddington, et al. (1994) in a study of *Apis mellifera* in suburban habitats in which two colonies were placed side by side and foraging locations mapped. Although they examined only flight distance, the divergence in the colonies' distance distributions was clear enough to lead them to conclude that colonies were not utilizing the same patches simultaneously. They point to the possibility of differences in initial discovery that are then reinforced by recruitment and eventual segregation between colonies. Precedence at a patch, they point out, also may result in decline of the patch's resources, causing foragers from other colonies to find it less attractive. Waddington et al. also consider that colonies may choose different patches based on different nutritional needs.

Another possible mechanism for patch segregation may involve interactions at the patch itself using chemical cues. Colony specific odors at floral resources, in addition to attracting nestmates looking for the patch (Winston 1987), might additionally serve as a deterrent to scouts from other colonies. Once a newcomer "recognizes" that the patch is already being exploited and thus depleted, the patch may become less attractive as a potential food source for their own colony. The use of pheromones for avoidance competition is likely to be less costly than interference competition because it would prevent the cost to both colonies of losing foragers and expending energy involved in fighting among their workers. Such a mechanism may be important in allowing *A.*

dorsata colonies to minimize competition at resources while coexisting in aggregations that sometimes exceed 100 nests, all of which forage over the same expanse of forest.

Apis dorsata's ability to forage over enormous areas of terrain, an overall flight range distribution that typically stays within a few kilometers of the nest, and short term micro-segregation of habitat among neighboring colonies, when taken together, suggest several implications for the pollination of plants in the vicinity of nest aggregations. Areas surrounding the nest sites are well covered by foraging pollinators coming from one colony or another, although the occasional long distance flight may indeed be important in long distance pollen flow and maintenance of genetic diversity in plant populations. In addition to providing a glimpse at how the ubiquitous giant honey bee interacts with the landscape, foraging area estimates provide a spatial baseline from which to formulate hypotheses regarding pollen mediated gene flow and population genetic structure of plants pollinated by *A. dorsata*, effects of habitat fragmentation on genetic, population, and community level properties, and finally, the evolution of plant-pollinator relationships in Asian forests.

Table 2.1. Analysis of variance results. The dependent variable was normalized using a natural log transformation. y = ln flight distance. Random variables are year, site (year), colony (site, year), week* site (year) and week*colony (site, year).

SOURCE OF VARIATION	DF	MS	F	p
year	1	6.27	.51	.5068
site (year)	5	14.44	4.17	.0056 **
colony (site, year)	18	2.58	2.87	.0004 ***
week (year)	12	2.83	1.25	.2975
week*site (year)	28	2.55	2.56	.0004 ***
week*colony (site, year)	84	1.04	2.06	.0004 ***
residual	2372			

Table 2.2. MANOVA results. Dependent variables are the x and y coordinates of foraging location. For each site, the Pillai's Trace F ratio is reported with p-value in parentheses.

	BK 97	**KA 97**	**DS 97**	**BG 97**	**BK 98**	**KA 98**	**SG 98**
colony	2.1350 (.0747)	.3685 (.8312)	1.0011 (.3686)	4.4560 (.0126)	2.1392 (.0745)	.2103 (.8105)	.9904 (.4129)
week	5. 8435 (<.0001)	8.3514 (<.0001)	2.5784 (.0365)	16.8849 (<.0001)	9.7952 (<.0001)	4.8423 (<.0001)	1.5970 (.1748)
colony* wk	2.3771 (<.0001)	2.5730 (<.0001)	2.1594 (.0036)	1.8464 (.0005)	3.3532 (<.0001)	2.4285 (.0010)	3.9738 (<.0001)

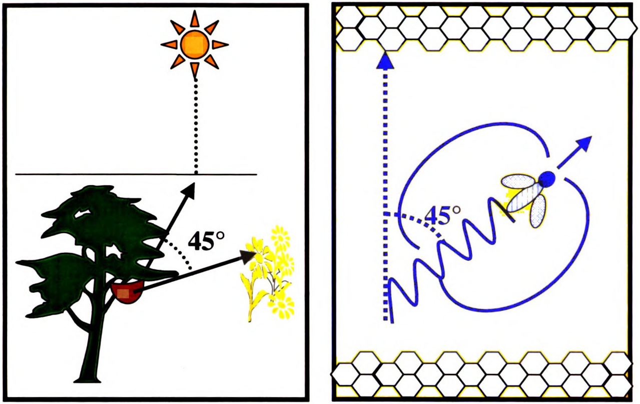


Figure 2.1. Dance language. The vertical angle relative to the upward direction at which a dancer runs (right panel) corresponds to the horizontal angle between the solar azimuth, the patch of forage, and the nest. She repeats this waggle run several times, by stopping, returning toher original position and starting again. Distance is encoded by the duration of the waggle run.

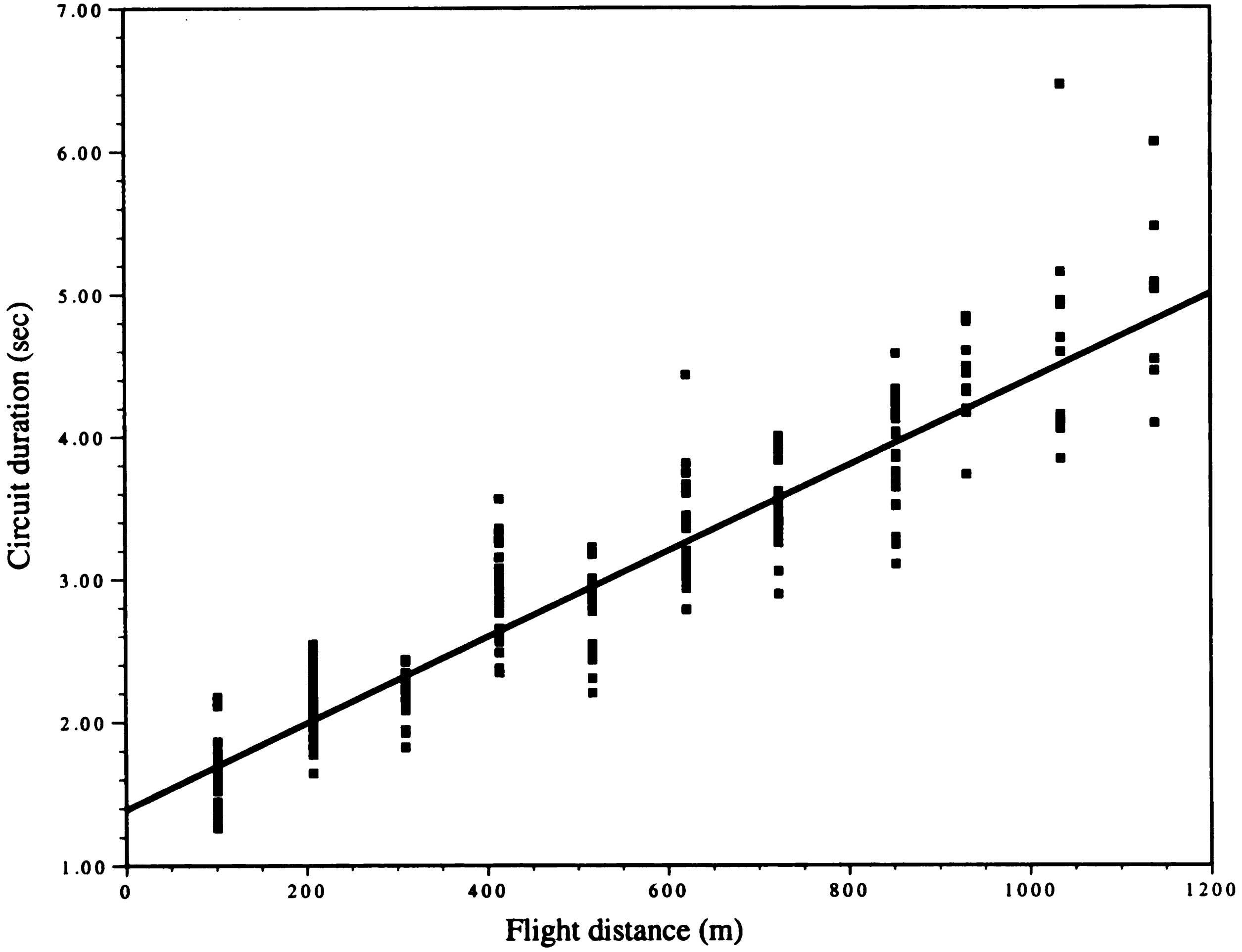


Figure 2.2. Distance dialect curve for the waggle dances of *Apis dorsata*.

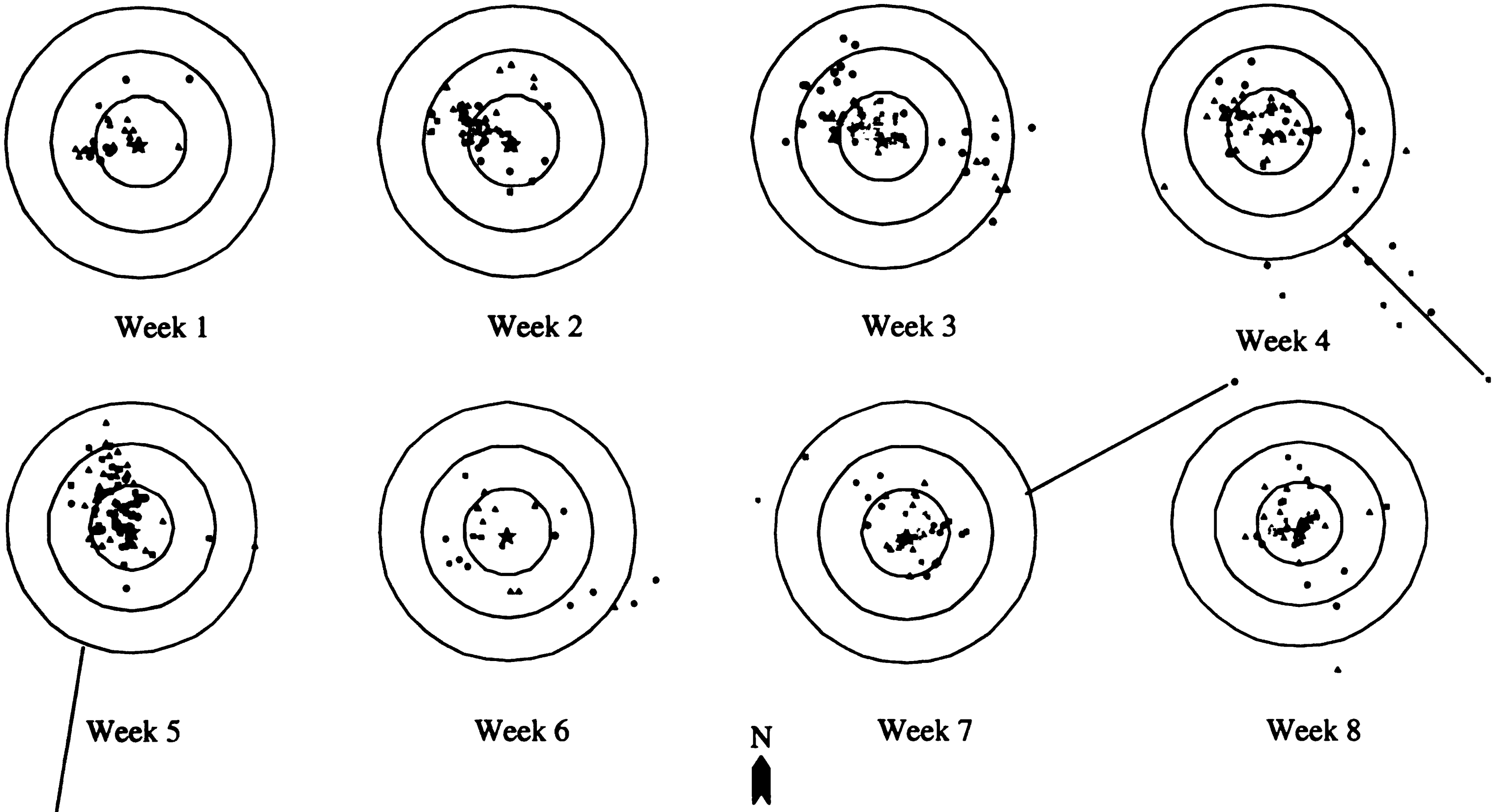


Figure 2.3. Basavanakadu (BK 97) site forage maps throughout 1997 flowering season. Symbols indicate different colonies. Circles are placed at 1 km increments.

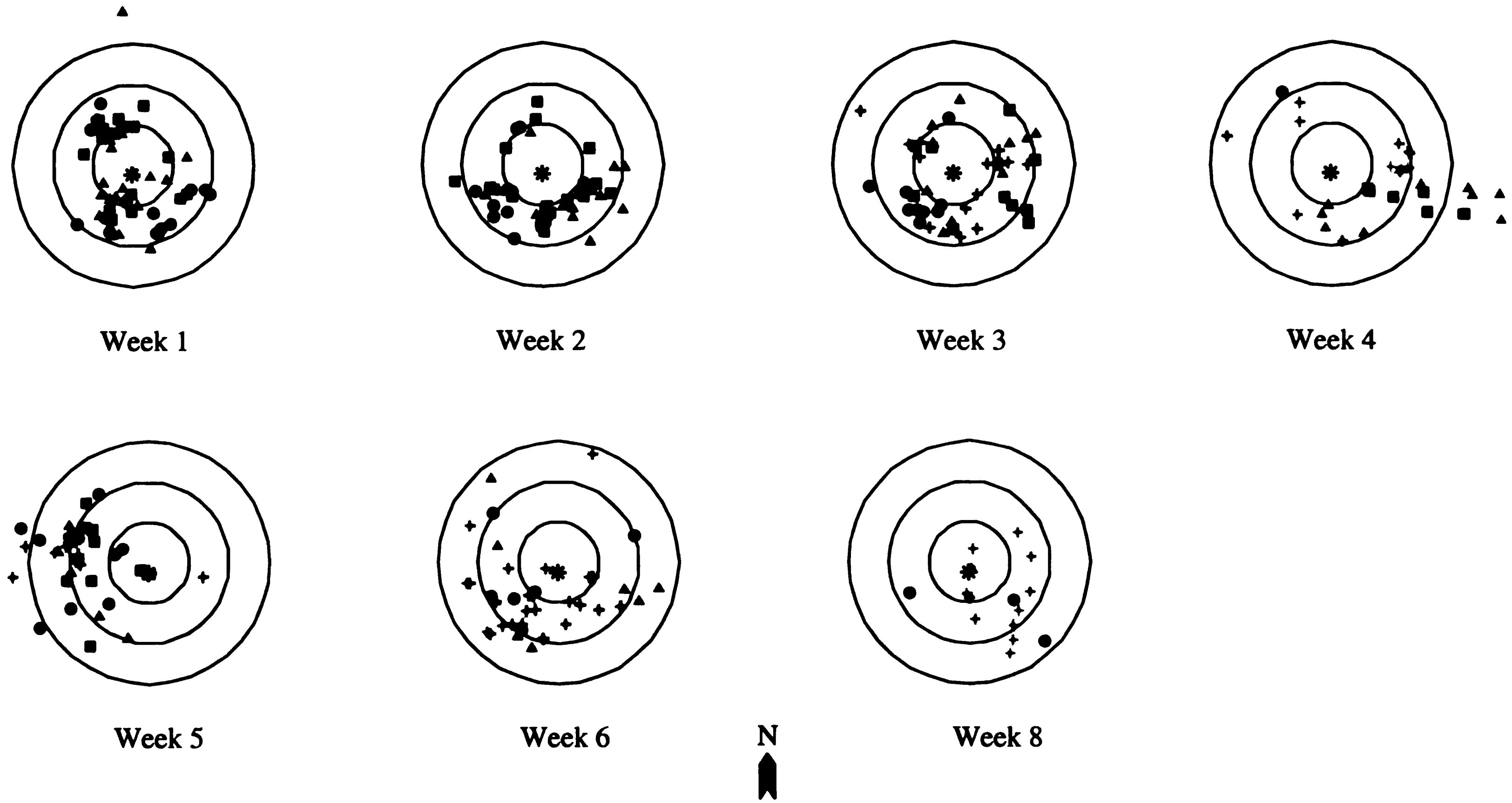


Figure 2.4. Beduguli (BG 97) site forage maps throughout 1997 flowering season. Symbols indicate different colonies. Circles are placed at 1 km increments.

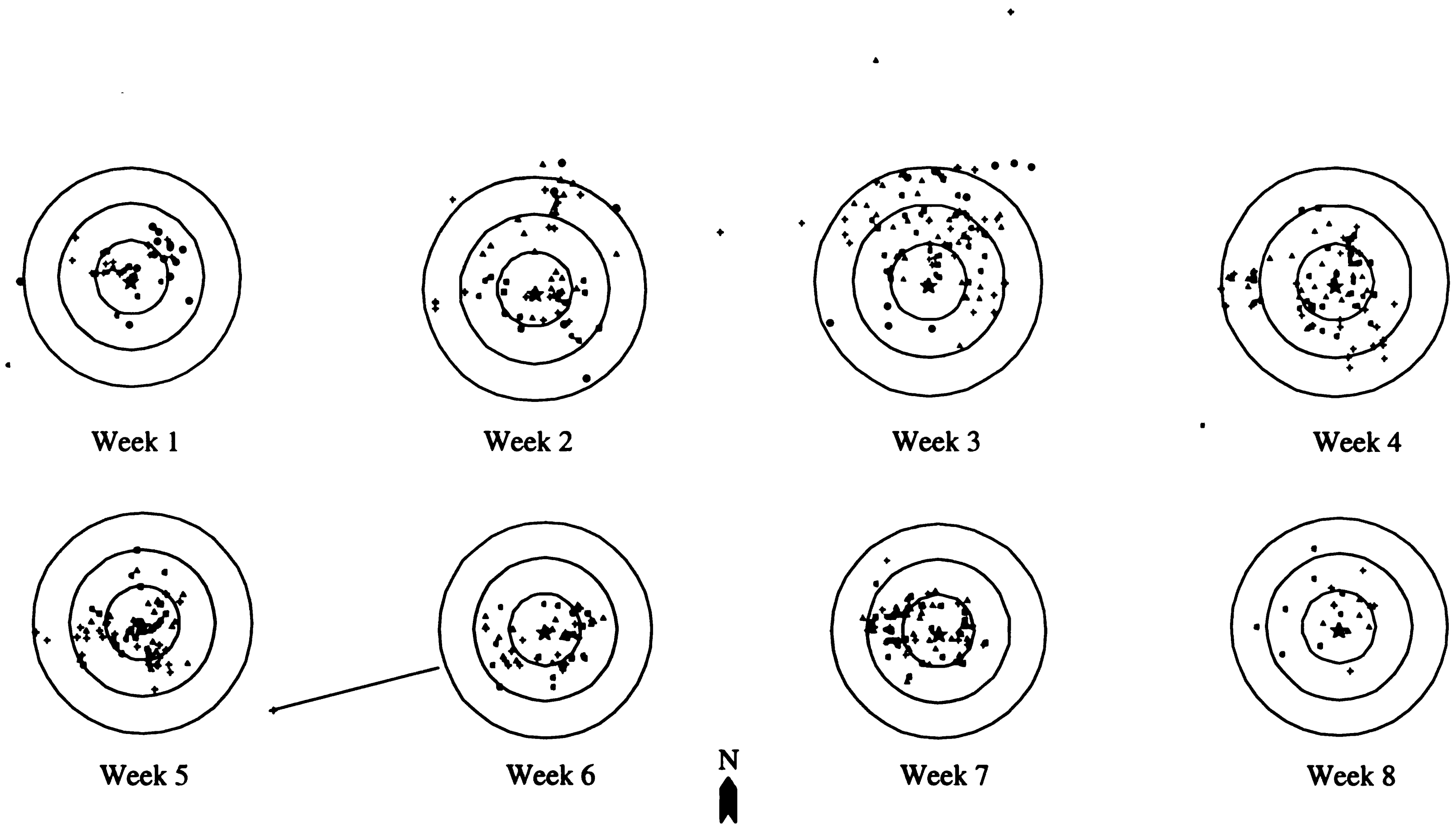


Figure 2.5. Doddesampige (DS 97) site forage maps throughout 1997 flowering season. Symbols indicate different colonies. Circles are placed at 1 km increments.

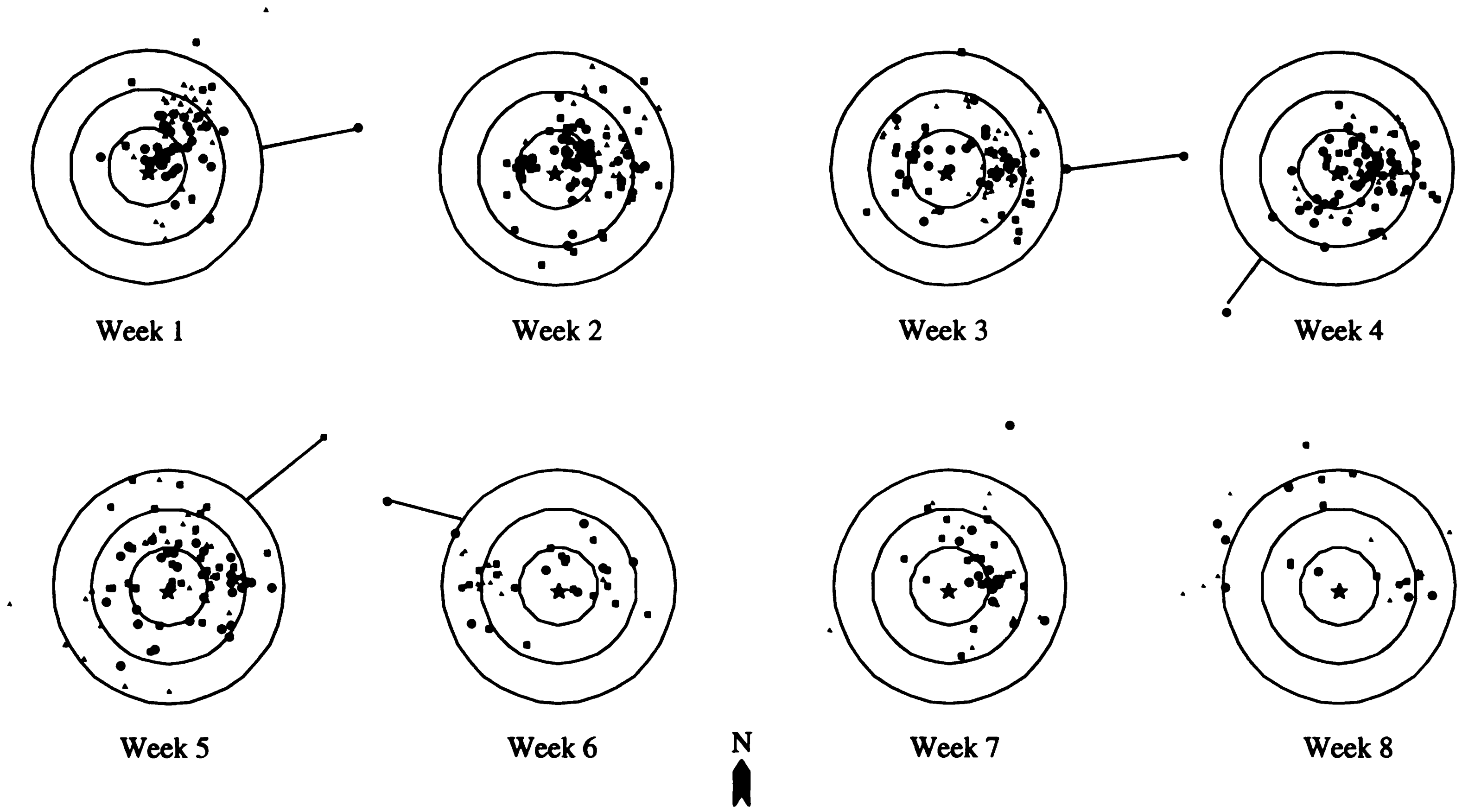


Figure 2.6. Kamari (KA 97) site forage maps throughout 1997 flowering season. Symbols indicate different colonies. Circles are placed at 1 km increments.

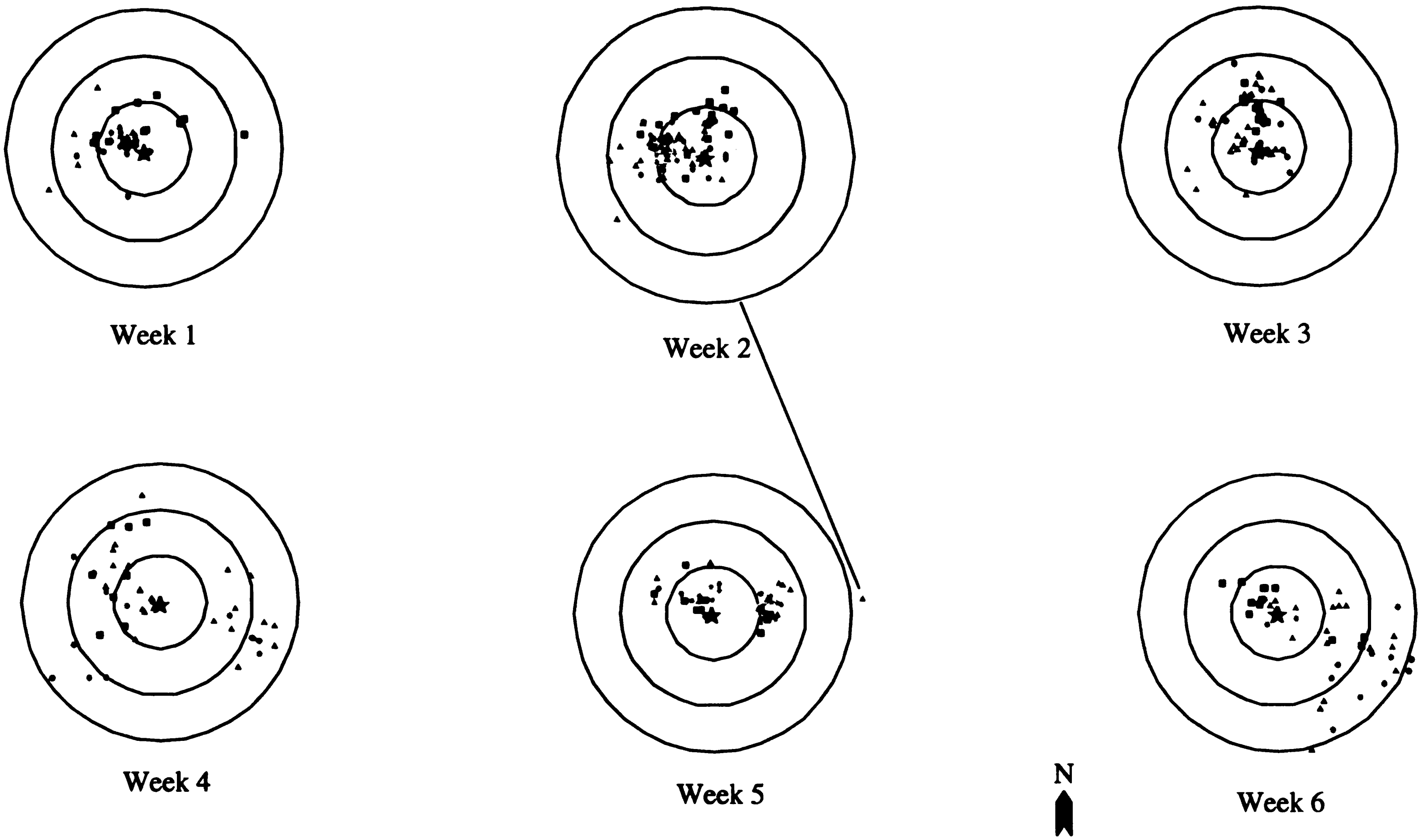


Figure 2.7. Basavanakadu (BK 98) site forage maps throughout 1998 flowering season. Symbols indicate different colonies. Circles are placed at 1 km increments.

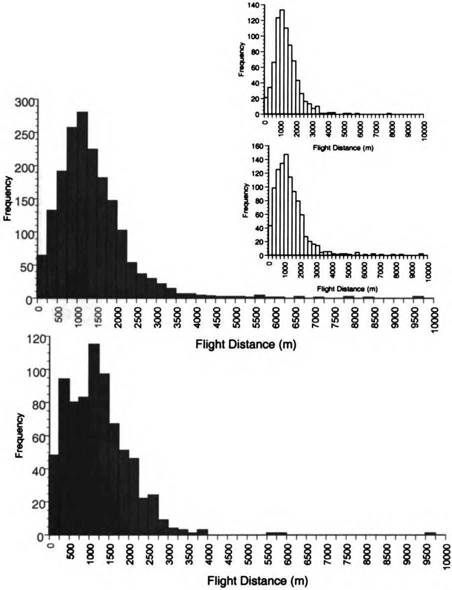


Figure 2.10. a. 1997 flight range distribution combined over two habitat types and all colonies. Inset shows flight range in evergreen (upper) and deciduous (lower) habitats.b. 1998 flight range distribution

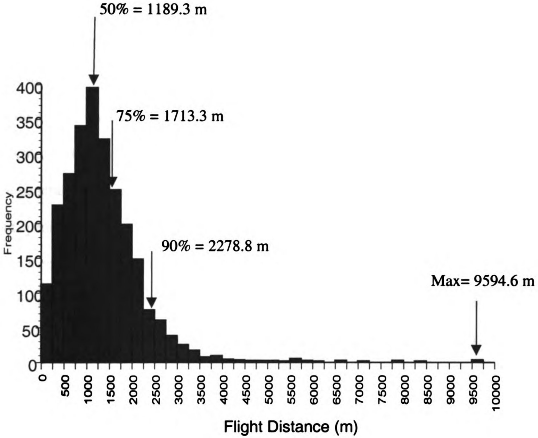


Figure 2.11. Flight range distribution 1997 and 1998 combined. 50th, 75th, and 90th quantiles are indicated.

CHAPTER 3: POLLEN DIET COMPOSITION AND FOOD PLANT PREFERENCES

INTRODUCTION

Apis dorsata, like other honey bees, is assumed to be a generalist forager. Its large body size, the need to sustain large, perennial colonies, and its ability to occupy a range of different habitat types over a broad geographic range all imply an ability to consume nectar and pollen from a wide diversity of food plant species. Understanding the patterns of food plant utilization by this important pollinator is critical for evaluating its role in the ecology of Asian forest communities. Recent studies in non-agricultural habitats have generally supported the assumption that *A. dorsata* exploits a wide diversity of plant species (Kiew 1997; Devy 1998; Momose et al. 1998), but it has proven difficult to obtain a comprehensive picture of the pattern of exploitation of different plant species over time in a given habitat. In this chapter, I address this question through analyses of pollens found in the feces deposited in the vicinity of nesting aggregations in the BR Hills

Even if a species can be characterized as a generalist, foragers in a single population may not forage on all plants available in a given area, and may not forage equally across all the plants that it does use. Such apparent "preferences" may emerge as a by-product of the sequential exploitation of plants according to their phenology and their flowering density at any given time in the season (Kiew 1997). However, true preferences may also exist depending on the economic trade-off experienced by the forager between the nutritional content of various food plants and the energy expended on searching and foraging for them. Such trade-offs are known to be important in *A. mellifera* colony level foraging strategies (Visscher and Seeley 1982; Seeley et al. 1991). There have been many studies which have experimentally attempted to discern the decision making criteria and sensory biases of bees for particular flower colors (Daumer 1958; Chittka et al. 1993; Giurfa et al. 1995), shapes (Frisch 1914; Free 1970; Wehner 1971), floral display arrays (Pyke 1978; Pleasants and Zimmerman 1979; Zimmerman 1981), scents (Frisch 1919), energetic trade-offs (Heinrich 1979), and so on. It is an extremely complex task however, to determine how those factors interact in a natural setting, with all of its complexity, to result in biased resource exploitation. In fact, simply discerning if a preference exists has scarcely been done in a forested setting even without considering the multiple mechanisms which act to produce it. A dietary "preference" in nature can only be discerned if a food plant is used disproportionately more than expected when compared to its availability. Here I will explore this question as it relates to *A. dorsata* pollen foraging in BRT, and its possible implications for the forest community.

The importance of knowing the components of an animal's diet depends on the role that such consumption patterns play in structuring an ecosystem. Bees are by far the most important of all insect taxa involved in the pollination mutualism between insects and flowering plants (Bawa 1990), and the process of pollen transfer among conspecific plants is dependent on bees' consumption of floral resources. The diet of bees therefore provides a partial window into knowing which plants may depend on them for pollination, and also provides a list of the plant species which maintain the bee

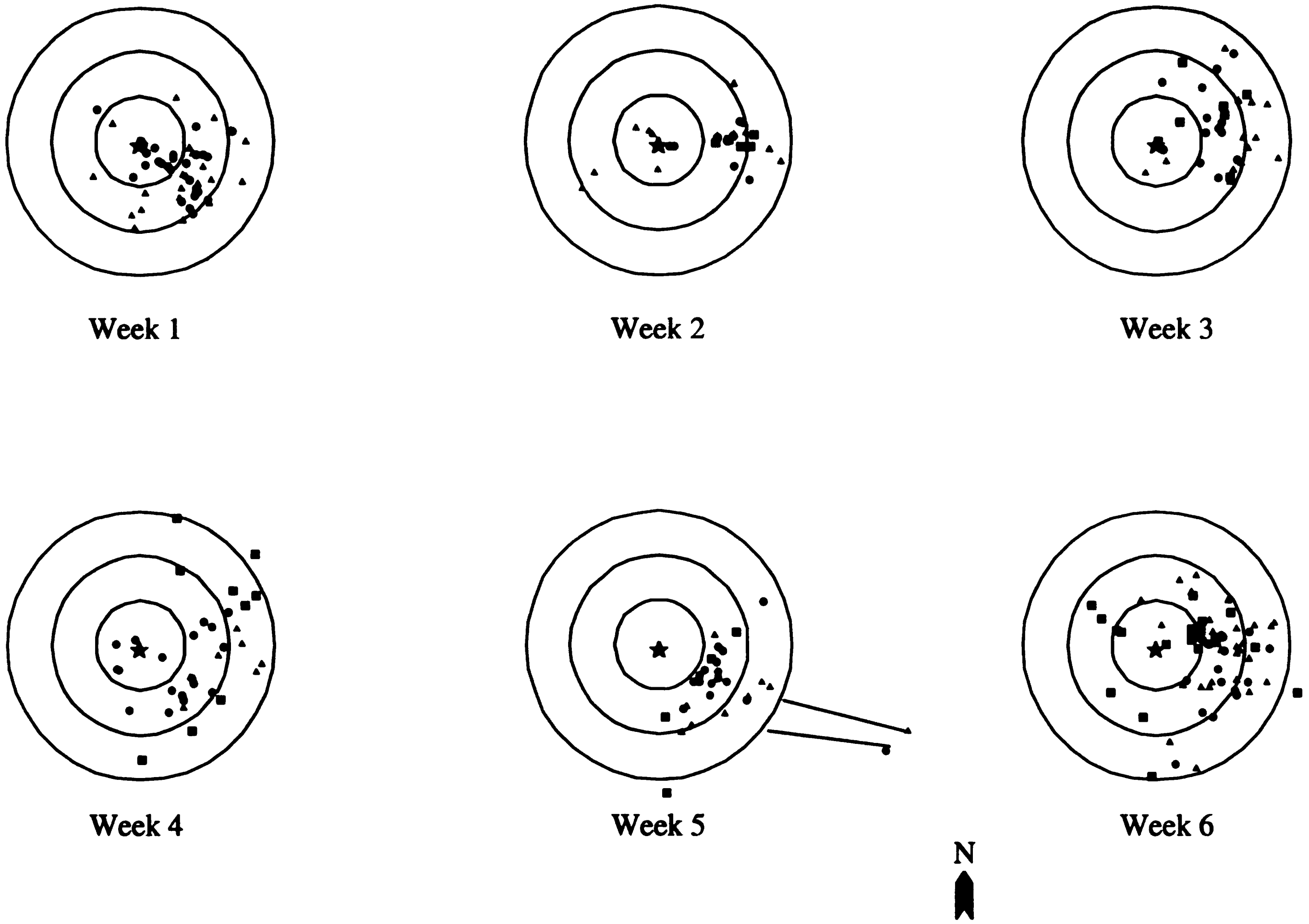
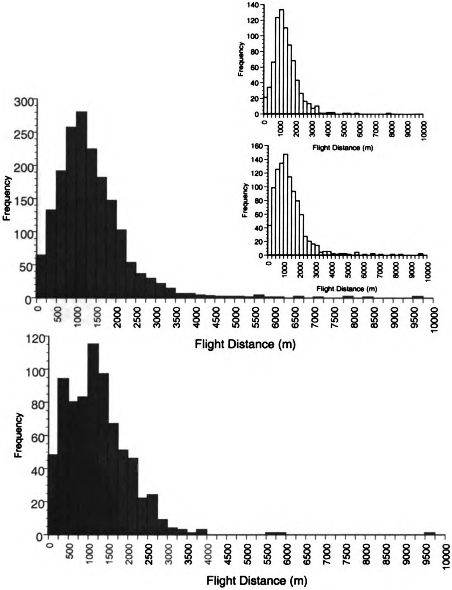


Figure 2.8. Kamari (KA 98) site forage maps throughout 1998 flowering season. Symbols indicate different colonies. Circles are placed at 1 km increments.



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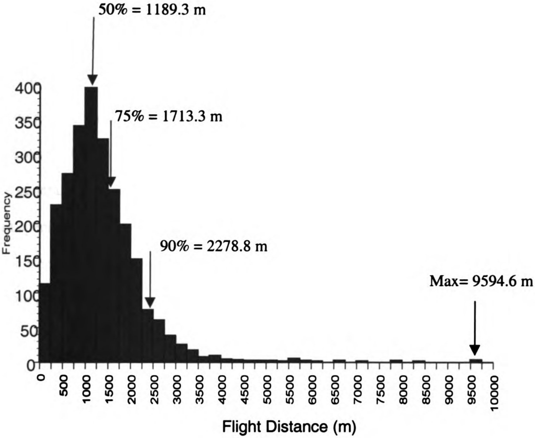

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Visitation and foraging by bees on a flower does not necessarily guarantee pollen transfer, seed set or actual plant reproductive success (Waser 1983). However, compiling lists of plant taxa visited is a necessary first step in identifying the possible species which may depend on *A. dorsata* for pollination. Indeed, such lists are especially useful in tropical forests where plant species richness can be staggeringly high. There is a long tradition of identifying of a forager’s food plants based solely on the suites of floral traits known as “pollination syndromes.” However, several studies have shown us that floral morphology does not tell the entire story of the plant-pollinator relationship, and they may in fact leave out important plant species (Waser et al. 1996; Johnson and Steiner 2000). Thus, a comprehensive examination of the entire diet of a putative pollinator is the only way to bypass these assumptions and begin to get an accurate picture of how plants interact with their pollinators.

Apis dorsata's utilization of food plants outside agricultural areas is known for two forest areas through observations of visitation to flowers. In Lambir Hills, Indonesia, researchers have found that giant honey bees forage on, and possibly pollinate about 30% of the species of canopy trees observed during mast flowering periods (S. Sakai, pers. comm.). In a wet evergreen forest in the Western Ghats of India, Devy (1998) found that *A. dorsata* visited about 20% of the tree flora, and actually provided pollination services to around 15%. These studies were conducted by observation of visitation to flowers of selected tree species. Other researchers (e.g., Jhansi et al. 1991; Kiew 1997) have examined the honey and pollen stores from honey bee combs after the combs were cut for honey harvest, but these late season analyses may exclude those taxa whose pollen was collected and fully consumed early in the flowering season, and thus may not give an accurate picture of relative proportions of the food types collected by the bees. Virtually all bees rely on both pollen and nectar from flowers, and the process of gathering either may result in fertilization of the flower. While it would be ideal to know which plants comprise the entire set of food plants, pollen provides protein needed for colony growth and reproduction and is a far more tractable resource to investigate than nectar.

Apis dorsata presents a unique opportunity to study the pollen diet of a population of bees in an unbiased and comprehensive manner. Giant honey bees' perform "cleansing flights," in which most or all individuals fly off the comb and defecate *en masse* only a few meters from the nest, a behavior that may be adaptive for efficiently dissipating heat from the colony (Mardan and Kevan 1989). This behavior, further amplified by giant honey bees' large colony sizes and nest aggregations, allows for investigation of pollen foraging activities because the feces can be collected very efficiently from the forest floor and consist primarily of the exine shells of consumed pollen grains. These outer shells do not break down in the digestive tract of honey bees, and their shape, size, and microscopic sculpturing are diagnostic characters which can be traced to family, genus, and sometimes species of the plant from which they came (Faegri and Iverson 1964). Analyzing the diet by analyzing the feces relies on information taken directly from the bees, and not on the subjective observer-biased process of choosing species of plants at which to quantify bee visitation, or on the overgeneralizations of the pollination syndrome concept. In this chapter I report the first detailed characterization of the pollen diet of *A. dorsata* from a forest habitat, and provide a picture of weekly changes in the composition of the diet throughout the flowering season.

After characterizing the diet contents, the only way an actual preference can be discerned is by comparing composition of the diet to the relative availability of those resources in the environment. In order to get good estimates of relative abundance of the tree species in BRT, I rely on data from collaborators at Ashoka Trust for Research in Ecology and Environment (ATREE) which characterizes the tree community composition in the major forest types of BRT. They uniformly sampled trees from a total of 125 plots, totaling five hectares overall. The community structure revealed by these plots overall closely matches the structure of other sampling plots in BRT whose community was characterized for different studies (e.g., Murali et al. 1996), thus appears to capture the major elements of the tree community quite well. Taking relative abundance of a floral resource as the null expectation, I examine here, using data from 1997 and 1998, whether *A. dorsata* collects pollen types in proportion to their availability or whether they exhibit preferences by foraging disproportionately more on some plant species and less on others. The availability of a floral resource depends not only on the relative abundance of that species in the forest, but also on its flowering status at any given time in the flowering season. Weekly flowering phenology data taken during the 1998 season, combined with the above data on relative abundance of tree species in one forest type, provides for an even more accurate assessment of the relative availability of food plants utilized by *A. dorsata*. I incorporate temporal variation in floral resources in asking the question of whether *A. dorsata* utilizes trees in a manner that suggests foraging preferences.

METHODS

FECAL SAMPLING

During the flowering seasons of 1997 and 1998, I collected samples of honey bee feces by taking advantage of their mass defecation flights, which occur within a few meters from the nest (Mardan and Kevan 1989). Approximately once a week, I laid out ten sheets of plastic or newspaper underneath a nesting aggregation. Appendix II lists the dates of sampling at each site, and the corresponding week numbers with which I refer to them. The locations of the sampling sheets were most often arbitrarily chosen, but in some areas the terrain excluded certain spots (for example, many of the feces under the cliff colonies actually landed on the cliffside itself.) The sheets remained in place for one week and on occasion more than one week, and then were changed. They accumulated yellow spots of fecal matter which I scraped from the paper and later processed for light microscopy as described below.

The samples may be considered random samples of the diet of all colonies in that particular nest aggregation, but the method does not guarantee equal representation of the feces of all colonies. This sampling method does not standardize the number of grains that landed on each sheet of plastic or paper; similarly, it is impossible to know from how many colonies the feces had come, as the defecation may occur up to 20 meters from the nest, and sometimes even farther (pers. obs.) Furthermore, in some weeks the sampling sheets may have accumulated more feces simply due to more defecation by the colonies at that aggregation, an activity that may be correlated with ambient temperature (Mardan and Kevan 1989). Some locations in some weeks were not sampled due to removal or destruction of the plastic or newspaper sheets by passersby, rain, or wildlife. In spite of these difficulties, there is no reason to suspect that the proportional representation of specific pollens should be skewed towards one plant taxon or another.

VEGETATION SAMPLING PLOTS

Data on the abundance and distribution of the major tree species were made available to me through collaboration with ATREE. The data were collected by ATREE researchers by first subdividing the entire BRT Wildlife Sanctuary into 125 2 x 2 km grid squares.

All trees above 10 cm diameter at breast height (DBH), i.e., 1.3 m above ground, which occurred along 80m x 5m line transects running through the center of each grid square were identified and DBH measured. Sampling was spread uniformly across BRT. Thus, the data provide a good measure of the community composition of the major vegetation types for all but the rarest species of trees.

FLOWERING PHENOLOGY

In 1998 from 12 March - 7 May I recorded weekly (sometimes biweekly) assessments of flowering phenology of the major species of deciduous forest trees using a transect of previously identified and tagged adult trees. Appendix II gives the sampling dates and the week numbers to which they correspond, and Appendix III lists tree species on the transect. The flowering status of each tree was defined according to the following categories: "bud" when only flower buds were present on the tree, "early flowering" when the number of buds exceeded the number of open flowers, "peak flowering" when the number of open flowers exceeded the number of buds or old flowers, "late flowering" when the number of old flowers and/or fruits exceeded newly opened flowers, and "fruit" when only fruits but no flowers were present. The categories were given numerical values as relative quantitative measures of pollen availability, or standing crop. The relative numerical values assigned to different floral stages are 1 for bud, 2 for early flowering, 3 for peak flowering, 2 for late flowering, and 0 for fruit. The bud stage still offers visual and/ or olfactory cues for bees to forage on the plant, and mature buds at the time of measurement may well have opened later that day or in the evening. For these reasons, trees in this stage were not given a score of "0". The values assigned to each flowering category are relative measures only, and do not account for any differences that exist between numbers of flowers per tree or volume of pollen produced per flower.

PALYNOLOGY

The fecal samples were analyzed for pollen types in the palynology laboratory of the French Institute of Pondicherry in Pondicherry, India. This lab is well equipped with microscopes and wet lab facilities, and with an extensive reference collection of Western Ghats pollens. I prepared the samples by using the standard acetolysis technique, which extracts the cell contents, leaving the hollow pollen exine intact (Kearns and Inouye 1993). Contents of each sample were first thoroughly crushed through a wide mesh sieve to remove all debris. They were then washed with glacial acetic acid in order to remove all water from the sample, and centrifuged for approximately three minutes at 2000 revolutions per minute (rpm). A 9:1 mixture of acetic anhydride: concentrated sulfuric acid was prepared by slowly adding the sulfuric acid to the acetic anhydride. Approximately five ml of this solution was added to the sample test tubes, and the test tubes were put in a hot water bath and maintained at a temperature of 85 to 90 C° for five to ten minutes. Samples were stirred during this time, taking care to keep stirring rods separate so as not to mix sample contents. The tubes were removed from the water bath and the reaction stopped by adding glacial acetic acid to the test tubes. After centrifuging again for 3-5 minutes, and removing the liquid, samples were washed with distilled water, centrifuged, and drained 3 to 5 times to remove all traces of acid in the test tubes. After determining with pH paper that samples were no longer acidic, test tube contents were mixed with 50% glycerine, stirred and then transferred with a pipette to a vial for storage. Slides were prepared by transferring a drop of the sample suspended in 50% glycerine onto a slide, covering it with a coverslip and sealing the slip edges with paraffin wax. The glycerine underneath the slip allows the examiner to rotate a grain, if desired for better viewing, by pressing gently on the cover slip with the point of a pencil.

In total there were 43 samples of fecal pollens. Detectability of pollens used by insects is equally high for all taxa, as the size ranges generally above 10 microns. I identified three hundred grains on each slide by arbitrarily choosing (x,y) coordinates at which to start a sampling line and traveling along the vertical direction. I repeated the process as many times as necessary to count three hundred grains. The number of grains sampled was determined by plotting saturation curves (cumulative number of pollen types vs. number of grains sampled) for several samples from different locations and dates as I counted. Three hundred grains adequately captured the diversity of the samples and the point at which sampling effort no longer revealed many new types (figure 3.1). Pollen types were identified with assistance of Mr. S. Prasad, slides from the reference collection, and several illustrated books (Huang 1972; Vasanthy 1976; Nayar 1990; Tissot et al. 1994).

Due to our knowledge of the flora of BRT, many grains were identified to species level, and most were identified to genus or probable genus. Palynologists usually can make no distinction between the families Combretaceae and Melastomataceae, and identify them only as "Comb/Mel " type (Anupama et al. 1999). In my samples, however, I identified such pollens as the Combretaceae genus *Terminalia* due to the dominance of this family in BRT, the relative rarity of Melastomataceae in all of BRT (ATREE, unpublished data), and due to the fact that the only other genus in Combretaceae that occurs in BRT, namely *Anogeissus*, does not flower simultaneously with the species of *Terminalia* which flower during the peak of bee season (pers. obs; ATREE, unpublished data.)

STATISTICAL ANALYSIS

Any taxon in the pollen samples that did not amount to at least two percent of the overall total for a site combined across weeks was put into the category "other". Each taxon that constituted two percent or more of the total for a site was left in its own category, and all analyses were done using these categories. Hereafter, taxa are also sometimes referred to as genera.

A Shannon-Weiner diversity index for pollen diet was calculated for each site combined across weeks (table 3.1) using the equation: $H' = p_i \Sigma \ln p_i$, where p_i is the proportion of the *i*th pollen taxon (May 1975).

In order to test the null hypothesis that bees forage in an opportunistic manner and that their pollen diets conform to an ideal free distribution, several G-tests were employed. First, 1997 and 1998 data were tested keeping sites separate and pooling pollen frequencies across weeks. I compared the composition of fecal pollens to the overall forest composition based on the dominance values of those taxa across all forest types combined. Dominance values were generated by dividing the total number of stems in each genus of interest occurring across all the sampling plots, by the total number of stems sampled (n = 2042).

Second, I conducted a G-test to compare the distribution of fecal pollens to the expected dominance values. In this test, I used the dominance values that would result if the forest were composed only of the plants utilized by bees, that is, each genus' dominance relative to only the other bee plants. The total number of stems sampled in those genera (n=479) does not account for anything that fell into the category "other," thus the "other" category is not included in the G-test. This tests, within the few taxa that bees do use, whether they forage in an unbiased manner.

Phenological data from 1998 was incorporated into a third G-test by averaging the weekly phenology score for each genus of interest on the transect per week, and using that average phenological score to weight the relative abundance values of each genus of interest. The G-test then compared the weighted frequencies of flower types to diet composition. The expected weighted frequencies were standardized to one, so as to be proportions.

RESULTS

The overall results of the analyses of fecal pollens point to strong foraging preferences exhibited by *A. dorsata*, despite the plasticity that generalism confers on them as a species. Colonies use a small fraction of the available species richness, and even within those taxa that they use, they heavily overutilize only a few tree species for the bulk of their pollen diet. Shannon-Weiner indices calculated for dietary diversity (table 3.1) do not reveal any broad patterns of diversity with respect to habitat type. One reason for this may be simply due to the differences in number of weeks sampled. However, even when the weeks sampled are equalized such that the same four weeks of all pollen samples in 1997 only are included in the analysis, the result does not change. Thus, it does not appear that the predominant habitat surrounding the nest site determines dietary breadth. When the same two sites (BK and KA) were sampled across two years, 1998 shows a higher diversity of dietary pollens in both sites, although this result may be confounded with the variation in number of weeks sampled and/or dates of the weeks sampled.

Figure 3.2 is a light micrograph showing some of the more common pollen taxa which I found in the samples of bee feces. Figure 3.3 illustrates that the pollen diet was heavily skewed toward a few taxa by illustrating the relative contributions of each to the cumulative percent total. Figure 3.4 illustrates the breakdown among taxa of pollen composition found at each site pooled across weeks, and figures 3.5 and 3.6 further dissect the components of the diet and show the weekly pollen composition for each site. The composition of the pollen diet overall was restricted to 10 genera, excluding pollen types which occurred at a frequency of less than 2% of the total. These ten genera comprise a maximum of 18 species of the total 216 species of trees that were documented in the vegetation plots. Appendix IV lists all species in BRT that occur in these ten genera, and thus are potentially food plant species of *A. dorsata*. Appendix V lists the 27 pollen genera that were found at extremely low frequencies in fecal samples, and were put into the category of "other". In addition to the taxa listed in Appendix V, there were several instances in which one or a few grains were simply classified according to an unidentified morphotype. None of these unidentified types were major contributors to the sample.

The vegetation plots give a conservative estimate of the number of tree species since the rarest tree species are not likely to have been captured in the sampling. *A. dorsata* is only utilizing a maximum of 8% (that is 18 out of 216) of the tree species richness of BRT for the bulk of its pollen diet. The samples also contained pollen from *Eucalyptus,* coffee (*Coffea arabica*) and an unidentifed type either in the Combretaceae or the Melastomataceae (referred to as "Comb/Mel 2" in figure 3.6), which differed strongly from that of *Terminalia*. These three taxa were each found in only one site's samples, and for a brief period in the season. *Eucalyptus* occurred in the BG 97 site, which is a coffee estate site surrounded by evergreen forest. The estates contain stands of *Eucalyptus* (pers. obs.), an exotic to India planted as a fast growing shade tree. Although these three taxa comprised more than 2% of the total pollen from that site, they are excluded from the G-test analyses for the following reasons. First, the density of neither *Eucalyptus* nor *Coffea* can be quantified since they were not found in the vegetation sampling plots, and because the sampling plots did not include the coffee estates where both of these occur. Second, the Combretaceae/ Melastomataceae cannot be identified even to family, and therefore its dominance cannot be extracted from the vegetation plot data.

Among the ten genera that contributed to the bees' pollen diet, representation of pollen is heavily skewed toward six genera (table 3.2, figures 3.3 and 3.4). *Catunaregam* and *Terminalia* were the only genera found in feces at all sites. *Grewia* and *Syzygium* were at all but one site, and *Schleichera* and *Canthium* were at all but two sites. Relative to their abundance in the forest, use of these plant taxa was highly disproportionate. *Terminalia* is in the family Combretaceae, which dominates the dry deciduous forest (Ramesh 1989), and has four member species in BRT. Of these four, there are three species of *Terminalia* which flowered during the time span of fecal sampling, and thus could have accounted for their presence in the fecal samples. These three species, *T. bellerica, T. crenulata,* and *T. chebula* comprised over seven percent of the total stems in BRT across all sampling plots, and over 31% of all bee plants in the plots. *Terminalia* pollen in the feces accounted for between 3.5% and 24.62% of the fecal samples, pooled across weeks for each site. Thus, it was consistently lower than the expected value of 31%. *Catunaregam* accounted for almost 13% of all bee plants in the forest, and except in one site, its representation in the bees diet was consistently much higher than expected, with a range of occurrence in the fecal pollens from 11.02% and 85.60%. Of the other commonly utilized taxa, the *Schleichera* taxon (which may be either *S. oleosa* or the closely related *Dimocarpus longan)* was relatively rare in the forest, accounting for only 1.25 % of all bee plants. However, in the sites where it was used by bees, it was overutilized relative to its abundance in the forest, ranging from 6.2% to 26.85% of fecal pollen samples at different sites. The G-scores for these data, totaled across weeks but keeping sites separate, all were highly significant, indicating that pollen resources were not used in proportion to their occurrence in the forest, even when compared to distribution of bee plants only (table 3.2, fig 3.4.).

Similar conclusions arise from analyses of data which used more precise estimates of relative flowering availability by incorporating phenological variation. G-tests for 1998 pooled data across sites but kept weeks separate, and thus examined whether bees foraged in proportion to the actual floral occurrence, as determined by flowering status in any given week, weighted by the abundance of that plant in the dry deciduous forest relative to other bee plants. The results, shown in table 3.3 are consistent with above G-tests showing that taxa of pollen were used disproportionate to their occurrence, with *Catunaregam* and *Schleichera* contributing heavily to the positive G-scores, indicating their overuse, and *Syzygium* also contributing mostly large positive values. Negative contributions to G-scores, i.e., those taxa that were underused relative to expectations, were *Terminalia* and *Grewia*, although their negative values were not as large or consistent as they were in the previous G-tests.

Figure 3.7 shows the phenological status weighted by relative abundance of those species which belonged to bee plant genera, and which occurred in the dry deciduous forest. Three species emerge from this picture as having long flowering periods: *Catunaregam spinosa*, *Grewia hirsuta*, and *Terminalia crenulata*. These three also have high flowering indices relative to the other bee plants. Of the three, *Catunaregam spinosa* has the lowest floral index at any given time, but is also the most overused taxon of all the bee plants. Images in this dissertation are presented in color.

DISCUSSION

Apis dorsata, while known to be a species capable of exploiting a great diversity of food plants, appears to utilize a very restricted set of plant taxa for most of its protein diet. The findings of Devy (1998) and those of Momose, et al (1998) whose observations of floral visitation led them to conclude that *Apis dorsata* uses relatively small fraction of the available flora, are confirmed and extended here. Their studies, which did not distinguish between nectar and pollen food plants, found that approximately 20% of the tree species they observed were being used by *A. dorsata* as food plants. Kiew (1997) also looked at pollen and honey in combs at different times of season. My approach, while more effective in identifying all the pollen sources being used without having to choose which trees to watch for potential activity, could not identify nectar sources. The pollen diet of the population of *A. dorsata* in BRT showed that they utilized less than 10% of the tree species available, and that within that group of utilized plants, they relied primarily on three genera, comprising a maximum of six species (figure 3.4).

The most common pollen by far in the samples belonged to the genus *Catunaregam*. This genus is monospecific in BRT (R. Ganesan, unpublished data), and thus all pollen belonging to this genus came from a single species, *C. spinosa*. This species has been formerly classified as *Randia dumetorium* and *Gardenia spinosa*, and has recently been combined with what was previously classified as *Randia brandisii* (R. Ganesan, pers. comm.). *Catunaregam spinosa* is a small, thorny understory tree which appears to be dioeceous (K. Bawa, pers. comm; P. Batra, unpublished data). Flowers are actinomorphic, and male flowers are approximately 1 cm in diameter (fig. 3.8, 3.9). Both male and female flowers produce nectar, which is also collected by *A. dorsata* (pers. obs.), and both male and female flowers are white when new and begin to turn yellowish after one day. Interestingly, its floral morphology describes a typical "moth syndrome" (Faegri and van der Pijl 1979)(K.S. Bawa pers. comm). Indeed its second most frequent visitor after *A. dorsata* is a diurnal sphingid moth (P. Batra, unpublished data), thus confirming recent arguments that generalizations based on criteria associated with classical pollination syndromes may not be useful in identifying the true food sources of a forager, nor the true pollinators of a plant (Waser, Chittka, Price, Williams and Ollerton 1996), (Johnson and Steiner 2000). The male flowers open in the early morning, between 0400 and 0500, and the females open approximately two hours later (P. Batra, unpublished data). This is a common phenomenon in dioecious plants, and helps to ensure that visitation to males, and thus pollen collection, occurs before visitation to females (K.S. Bawa, pers.comm.). Male flowers open with their pollen actually having already dehisced from the anthers before opening and having been deposited onto a central pseudo-stigma (figure 3.8).

A somewhat unusual feature of the relationship between *C. spinosa* and *A. dorsata* is the manner in which bees collect pollen from the anthers. The bees' usual method on most plants is to cover the body hairs with pollen by walking around among the anthers, comb their bodies of the pollen, and then pack it into balls which they then carry in their hind leg corbiculae (Winston 1987). By contrast, all foraging on *C. spinosa* was seemingly for nectar, but except in the very early morning when foraging first began, bees were almost always seen with pollen balls 1-2 mm in size stuck on their heads (fig 3.9). The pseudo-stigma from male flowers appeared to deposit pollen in a location on the bees that would greatly facilitate pollen deposition onto stigmas of female flowers by bees foraging for nectar. Observations of visitation to female flowers confirmed that the heads with pollen balls made strong contact with the stigma (pers. obs.). Balls of deposited pollen, presumably from *C. spinosa*, could be seen very often through the spotting scope while measuring waggle dances, confirming that bees did not remove them before returning to the nest. An interesting question that arises from this phenomenon is whether the floral resource was evaluated by dancers for its nectar value or for its pollen value. Even if it was the nectar that was being advertised by bees, clearly the pollen is a critical resource, as we can see from its abundance in the feces. Indeed one might speculate that one of the advantages behind *C. spinosa*'s preferential appearance in the diet could be the ease and passive efficiency with which bees collect it.

In some weeks, *C. spinosa* pollen comprised more than 80% of the pollen in the fecal samples, although the rank importance of this tree in the forest is sixth overall. *C. spinosa* accounts for 3% of all the trees in the forest, and almost 13% of all bee plants (table 3.2). The importance of this species to *A. dorsata* in BRT is disproportionately large relative to its occurrence in the forest and also relative to its occurrence even when only bee food plants are considered. In fact it is *C. spinosa*'s frequency in the pollen samples that appears to be the most influential on the overall G-scores in both the site by site comparison (table 3.2) as well as the weekly weighted comparisons of 1998 (table

3.3). In all instances, this species contributes an extremely large positive number to the overall G-score, indicating its consistent overuse relative to expectation. Given that they are dioeceous, the population size of trees from which honey bees may collect pollen will actually be lower than that reflected in the plot surveys since the plot surveys counted both male and female trees. This means that its true expected values for the G-tests should be even lower than the values reported here, making the overabundance and ubiquity of *C. spinosa* in the fecal samples even more indicative of a preference.

Appanah (1981) found that *A. dorsata* in dense forest are canopy foragers, cueing in on colors, large floral displays, and utilizing species which have brief flowering periods. Similar to my findings, Devy (1998), in her study on the pollination biology of trees visited by *Apis cerana* and *A. dorsata* in an evergreen forest in India, found that *A. dorsata* used flowers from canopy trees, but that the flowers did not necessarily conform to morphological "syndromes" expected to be used by honey bees. She also found that the bees relied very heavily on only two species, and in contrast to the findings of Appanah (1981) found that the most important of them, *Palaquium ellipticum* had the longest flowering period of any of the trees utilized. Additionally, the second most important species, *Elaeocarpus munronii* had a flowering period that did not overlap in time with that of *P. ellipticum*, and in fact acted to extend the duration of *A. dorsata*'s stay in the forest before its migration. Both of the two tree species flowered annually and produced high volumes of nectar, unlike many of the supra-annual flowering species that were used less heavily by the bees. Devy found further that honey bees' migration into the study area always coincided with the onset of *P. ellipticum* flowering. She concluded from all of these observations that *A. dorsata* utilized those species whose reliability was high, both within and between years. Like *P. ellipticum*, *Catunaregam spinosa* has a flowering period that lasts almost throughout the dry season (fig 3.7); thus its reliability as a food source may make up for its lack of dominance in the forest, and for the fact that its stature as an understory tree means it may not be easily visible to scouting bees despite the relatively open canopy. Furthermore, since passive collection of *C. spinosa* pollen seems to be an added benefit of active nectar collection as explained previously, it may actually be a preference for the nectar from this tree that is the most important factor in explaining its overuse.

It does not appear that the abundance of a floral type in the forest over an extended portion of the flowering season is enough to explain its abundance in the bees' diet. The genus *Grewia* is actually slightly more abundant in the forests of BRT than *C. spinosa* (fig 3.4) and exhibits a flowering season that is also extended over several weeks. In fact, its flowering status is higher at any given time than in that of *C. spinosa* (fig 3.7). Its pollen was indeed used by *A. dorsata*, but was consistently underutilized relative to expectations (table 3.2, 3.3). This is a surprising result, but one perhaps explained in part by the fact that *Grewia* flowers are orange, and thus may not produce a display that attracts *A. dorsata* more than other flowers that are in the preferred color spectrum of bees (Barth 1991). Bees can and do learn to associate rewards with colors other than those that stimulate their peak wavelength receptors, but may not do so readily if floral resources that fall within the peak wavelengths are concurrently available; that is, bees' ability to learn depends also on the changing ecological context (Barth 1991).

Similar to *Grewia*, upon further examination of figure 3.7, it is clear that *Terminalia crenulata* also experiences a long flowering peak and yet its abundance in the pollen diet is surprisingly low. In fact, *Terminalia* is the most common genus in the forests of BRT, with the three species accounted for in this study comprising close to ten percent of all adult stems, and 30% of all bee-utilized plants (fig 3.2). Its utilization, however, is consistently lower than expected based on its frequency (table 3.2). The flowers of the genus are small and arranged in spikes which occur together in clusters (fig 3.10), and the trees often exhibit large floral displays. Such characteristics are amenable to *Apis* foraging behavior in which they may move between flowers rapidly. Indeed the genus appears to be extremely important as a source of nectar (M. Kethegowda, pers comm.; pers obs.) With respect to pollen foraging however, there is some evidence to suggest that although *Terminalia* flowers appear to be hermaphroditic, they may be cryptically monoecious or even dioeceous (A. Sinha, unpublished data.) If this is the case, the number of individual *Terminalia* stems producing pollen may be much smaller than reflected in the plot surveys, and the hence the expected values reported in the G-tests may be gross overestimates.

Schleichera oleosa (and its close relative *Dimocarpus longan*, whose pollen is indistinguishable) might be considered a keystone resource, in that it is an early resource (fig 3.2) utilized by immigrating *A. dorsata* colonies. It provides pollen protein at a time in the season when flowering is not yet abundant and is needed by colonies settling in to build their combs and start brood production. Indeed, it fits the qualitative definition of a "keystone species" in that it is a relatively rare species whose utility is disproportionate to its occurrence (Power et al. 1996). Given the generalist diet of the species as a whole, it is not likely that *A. dorsata* in BRT is obligately reliant on any one resource. The sites in which *Schleichera* pollen was never found (DS 97 and BK 97) also correspond to sites where the first week was not sampled. However, in both of those cases, week two was sampled, which is the week during which *Schleichera* peaked in the other two samples that year. Despite the fact that *Schleichera* forest types occurred within the areas of DS and BK sites, the possibility remains that the flowering times in those areas may have exhibited enough variation from the other two areas for the pollen not to have shown up in the samples that began in week 2. It may also be the case that there simply is spatial heterogeneity in reliance on various pollen types.

The results here do not account for differences inherent in amount of pollen per flower, or the variation between species in the number of flowers per tree. I account for temporal variation in flowering by using phenological variation to weight abundance, but here I do not deal with any spatial variation in availability. Thus, all species are assumed to occur evenly across the forest. The next chapter will account for both spatial and temporal variation with the use of GIS.

Although giant honey bees occur across a wide geographic range, their food plants vary across that range in presence or frequency, and bees' use of these food plants may vary in different areas. For example *P. ellipticum*, which was of primary importance in Devy's study area in a wet evergreen forest southwest of BRT (Devy 1998), does occur in low densities in the evergreen forests of BRT (Ramesh 1989), but its pollen did not appear in the fecal samples. Kiew (1997) examined the pollen stored in combs of *A. dorsata* in Malaysia and found a dominance of *Eugenia*, which is synonymous with *Syzygium*, a taxon that was commonly found in my samples as well. Jhansi et al (1991) found many of the same genera I found in their analysis of honey in another part of southern India, although they did not report finding of *Catunaregam*. It may simply not occur in their study area. However, a heavy contributor to the pollen found in the honey was *Cassia*. This is a taxon which occurs in BRT, but requires sonication, or high frequency "buzzing," for pollen removal. Honey bees are incapable of wing buzzing at frequencies high enough to dislodge the pollen, thus they probably only collect the pollen that remains after sonication and pollen foraging by *Xylocopa* (K.S. Murali, pers. comm.). Jhansi et al's findings of it may simply reflect bees collection of nectar from *Cassia*. In summary, there do appear to be some taxa that are used across different parts of the geographic range of giant honey bees, as well as others that may not be of equal importance in different areas.

Based on the results observed here, it appears that *A. dorsata* does exhibit preferences for certain pollen resources, and that these food plants may be disproportionately important in maintaining the population size of honey bees in BRT such that they also forage on, and pollinate, several other species. Since nectar sources were not accounted for in my study, there remains another set of food plants whose pollination also may depend on *A. dorsata*; thus the indirect links between plants in the forest become even more complex. If *Schleichera oleosa* can be considered a keystone resource, that implies that more common taxa like *Terminalia* spp. are actually indirectly dependent on it via its maintenance of the common pollinator pool. Murali and Sukumar (1994) found in a study in a forest very similar in composition and structure to BRT, that rarer tree species tended to flower earlier than more common ones. They postulated that this may be an adaptive strategy for avoiding competition for pollinators. Phenological divergence as a mechanism for avoiding competition for pollinators has been hypothesized by a number of authors (e.g., Frankie et al. 1973; Gentry 1974). Especially in ecosystems such as BRT where species share a pool of generalist pollinators, such a strategy may indeed prevent the diluting effects on pollination that flowering by the more dominant species may have. Additionally, such a phenological schedule may act to extend the season used by the bees, although it is still unknown as to what resources they rely on prior to their immigration to BRT. If the relatively rare species *S. oleosa* were suddenly absent from the forest, the question then would be whether *A. dorsata* would time its inward migration to be later in the season when other flowers are available, or instead just exercise a "generalist" strategy of relying on something else that may occur in other strata, be of less nutritional value, or be less conspicuous. Many of the other tree species that flower simultaneously with *Schleichera* produce large, red flowers (ATREE, unpublished data; pers. obs.) mostly used by birds (Murali and Sukumar 1994) and may actually be visible to bees (Chittka et al. 1993) but perhaps not highly stimulating or preferable (Giurfa et al. 1995). Bees, however can learn to associate rewards with colors (Dukas and Real 1991; Waser et al. 1996), thus adding another level of complexity to their ability to adapt in ecological time.

Catunaregam spinosa also may be considered a keystone resource in BRT due to its heavy usage by giant honey bees. However, *A. dorsata* clearly can and does utilize other species and their preferences may not be based on nutritional preferences but on a complex combination of sensory and reliability (risk-aversion) factors (Barth 1991). These factors may result in lower prioritization, but not exclusion, of less useful food plants, e.g., *Grewia*. Hence, despite the complex links, forests such as this with large populations of generalist pollinators may be largely buffered from cascading extinctions that could result from the breakdown of the pollination mutualism. In order to distinguish whether the diet of bees in BRT is flexible enough to accommodate dramatic changes in forest structure, long term documentation of changes in bee diet corresponding to interannual variation in flowering phenology would need to be done across multiple sites which have some overlap in their plant composition. Measures of actual colony growth and reproduction also would be needed in order to examine the true adaptive nature of dietary flexibility.

Intriguing mysteries remain regarding *A. dorsata*'s ability to respond opportunistically to sudden and aseasonal bursts of forage. In some instances, such as the dramatic and supra-annual general flowering periods in the Dipterocarp forests of Southeast Asia, bee colonies appear to respond immediately to the increase in forage by a drastic increase in inward migrating colonies (Sakai et al. 1999). It is these species that they most often provide pollination to in these forests and not the more reliable but less abundant ones. Similarly, anecdotal reports from India state that the supra-annual flowering of *Strobilanthes* spp. (Acanthaceae) results in a much larger number of colonies than in non-flowering years despite the fact that it occurs in the herbaceous stratum of the forest. Somewhat in contrast to Devy's finding (1998) that *A. dorsata* utilizes reliable and relatively constant sources of forage over more ephemeral or acyclical ones, Sakai et al (1999) reason that it is unpredictability of resources that allows highly social, generalist bees to dominate in Asian forests as opposed to the more specialized bee pollination guilds present in the Neotropics. Perhaps both are true. The generalist ability of *A. dorsata* combined with its migratory ability may make it a forager and pollinator that depends on constant reliable resources and persists in the forests in relatively low numbers most of the time; however, it may also be an effective pollinator of less reliable species which produce massive flowering bursts, unpredictable in time and space, due to its ability to track resources and respond to them immediately.

Although honey bees are generalists and are not thought to have undergone strict coevolution with a restricted set of plants, they may exhibit tendencies to specialize locally. The ecological consequences of such facultative preferences may have important implications for how Old World tropical forests may be structured, while also buffering against the loss of the pollinator community during periods of rapid change. By examining how this generalist forager and important pollinator may link its food plants together into a complex web of indirect mutualism, we can begin to generate hypotheses about how behaviors such as foraging preferences scale up levels of biological organization to community and ecosystem properties.

Table 3.1. Shannon-Weiner indices for pollen diet diversity.

SITE AND YEAR	HABITAT	H' (N WEEKS)	H' (4 WEEKS STANDARDIZED)
DS 97	Evergreen	1.40 (7)	0.99
BG 97	Evergreen	1.71 (6)	1.43
BK97	Deciduous	0.56 (4)	0.56
KA 97	Deciduous	1.31 (8)	1.20
BK 98	Deciduous	1.58 (5)	--
KA 98	Deciduous	1.69 (9)	--
SG 98	Deciduous	1.86 (5)	--

Table 3.2. Composition of forest tree community, overall bee pollen diet, and individual plant genus contributions to total G-score for sites pooled across weeks. Percent of a site's fecal pollens is given in parentheses. Total G-scores for each site are given. G-tests compare each site's values, except "other" category, to the composition of % bee plants.

GENUS	% IN FOREST	% BEE PLANTS	BK97	BK98	KA97	KA98	BG97	DS97	SG98
Dalbergia	2.60	11.06	0 (0.00)	0 (0.00)	-90.87 (2.85)	-99.47 (4.65)	0 (0.00)	-84.71 (3.92)	0 (0.00)
Elaeocarpus	0.34	1.46	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	40.79 (2.69)	0 (0.00)	0 (0.00)
Grewia	3.43	14.61	0 (0.00)	-84.52 (2.89)	-99.15 (2.20)	-132.58 (4.03)	-77.73 (3.73)	-67.14 (10.43)	-39.31 (8.45)
Terminalia	7.39	31.52	-92.99 (3.56)	-195.09 (14.57)	-229.33 (5.58)	173.79 (21.61)	-130.62 (16.25)	-237. 19 (13.30)	-11.05 (24.62)
Lagerstromia	0.98	4.18	0 (0.00)	-19.54 (2.68)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	-8.17 (2.72)
Syzygium	3.09	13.15	-48.09 (2.32)	-77.57 (6.70)	-111.19 (5.18)	211.31 (18.42)	-63.30 (2.25)	0 (0.00)	248.09 (22.98)
Schleichera	0.29	1.25	0 (0.00)	1073.26 (20.25)	2058.91 (26.85)	992.96 (14.40)	206.02 (6.20)	0 (0.00)	361.55 (10.88)
Canthium	1.18	5.01	-13.91 (3.56)	75.97 (7.93)	-38.53 (2.57)	-42.97 (2.38)	0 (0.00)	-35.55 (2.49)	0 (0.00)
Catunaregam	3.04	12.94	1972.56 (85.60)	870.86 (39.69)	1682.88 (49.23)	581.29 (26.56)	699.83 (33.10)	1402.42 (47.97)	8.39 (11.02)
Olea	1.13	4.80	-15.36 (3.15)	0 (0.00)	0 (0.00)	0 (0.00)	411.87 (15.92)	531.03 (18.01)	0 (0.00)
Other	76.54		(1.82)	(5.30)	(5.54)	(7.95)	(13.45)	(3.88)	(6.94)
G-score (* p<.001)**			**3604.42*****	**3286.75*****	**6345.43*****	**2673.50*****	**2173.69*****	**3017.70*****	**1119.00*****

Table 3.3. Partial G-scores for 1998 pollen diet composition compared to forest composition with plant taxa weighted by flowering status per week.

POLLEN TYPE	**WEEK 1**	**WEEK 2**	**WEEK 3**	**WEEK 4**	**WEEK 4.1**	**WEEK 5**
Dalbergia	-27.97	-4.50	-9.72	-7.34	-3.15	0.00
Grewia	-9.52	-42.88	-87.36	-81.48	-79.66	-138.36
Terminalia	-144.18	-19.10	-67.92	50.96	-23.50	-70.82
Lagerstromia	-0.0002	-0.0002	-12.10	-19.40	-18.40	7.41
Syzygium	-3.00	-8.70	76.47	383.90	667.27	571.57
Schleichera	1011.19	639.78	1000.63	561.69	198.41	114.85
Catunaregam	762.80	427.64	947.04	380.79	107.80	574.58
Canthium	68.90	39.68	12.99	4.73	-3.50	0.00
G-score (*p<.001)**	**3316.43 *****	**2063.81 *****	**3720.04 *****	**2547.6966 *****	**1690.5083 *****	**2118.4531 *****

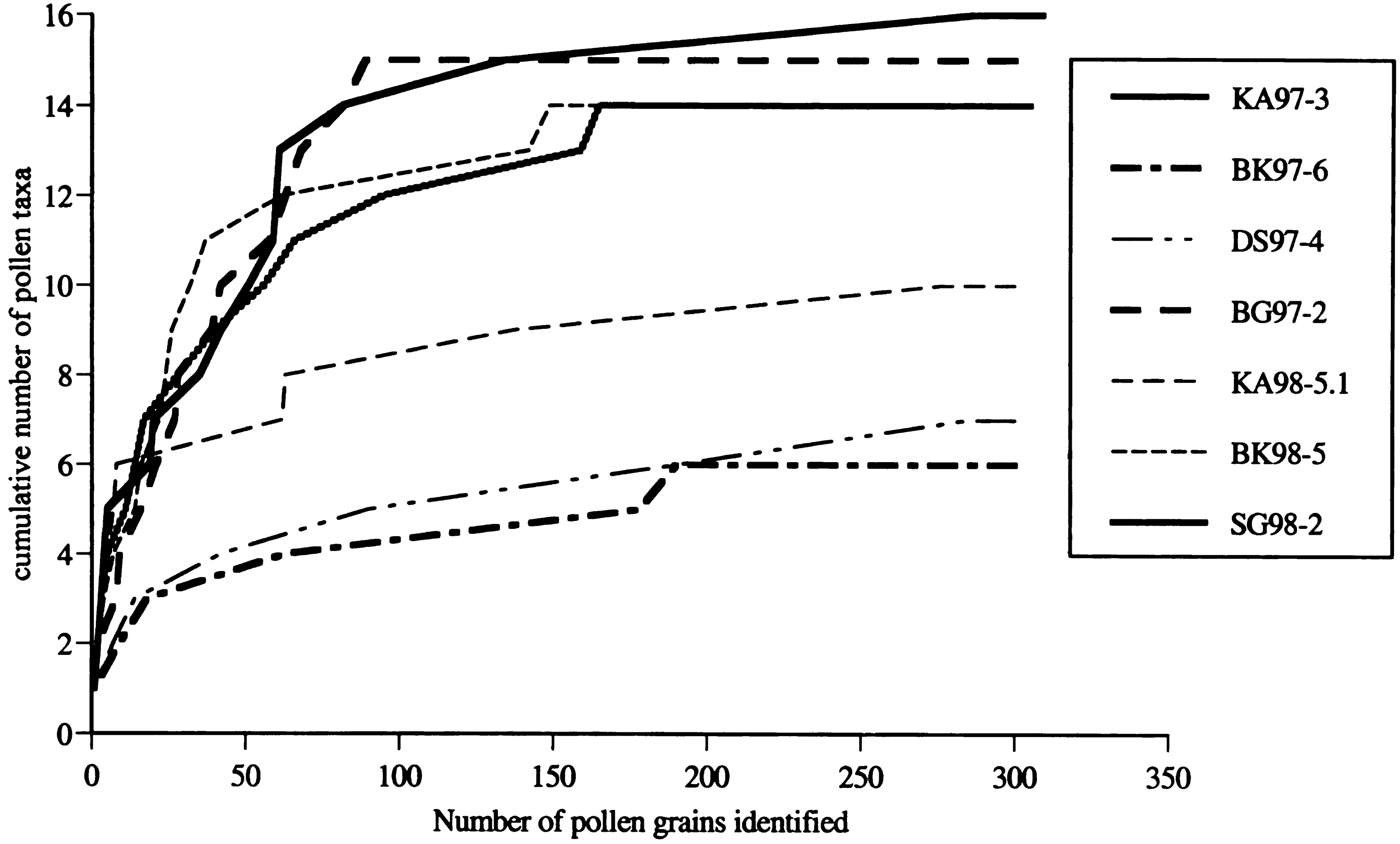

Figure 3.1. Saturation curves for randomly selected pollen samples. Sampling effort of 300 grains captured most of the diversity in pollen taxa.

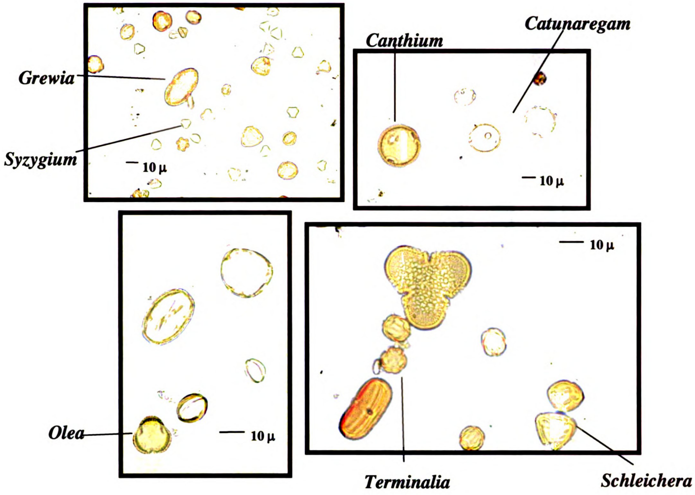

Figure 3.2. Light micrographs of pollen taxa which were common in fecal samples.

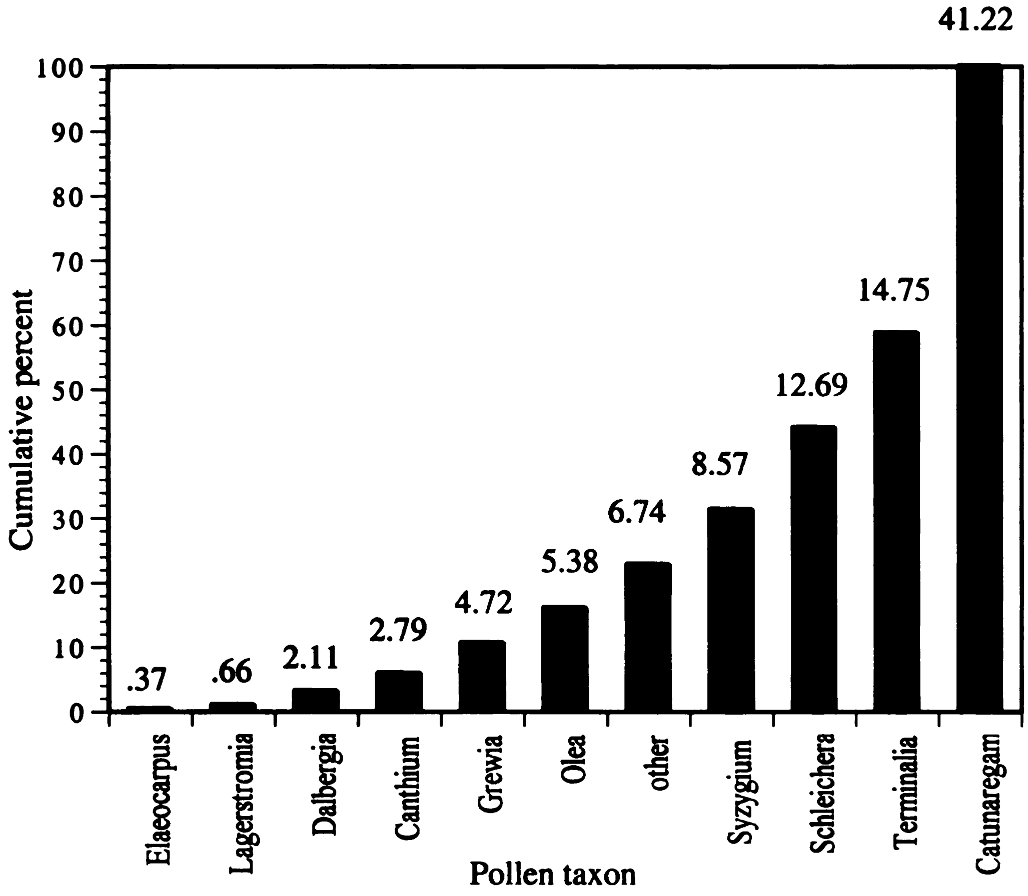

Figure 3.3. Contribution of each pollen taxon to the total pooled across sites and weeks. Numbers above bars indicate percent of total, y-axis values indicate cumulative percent of total.

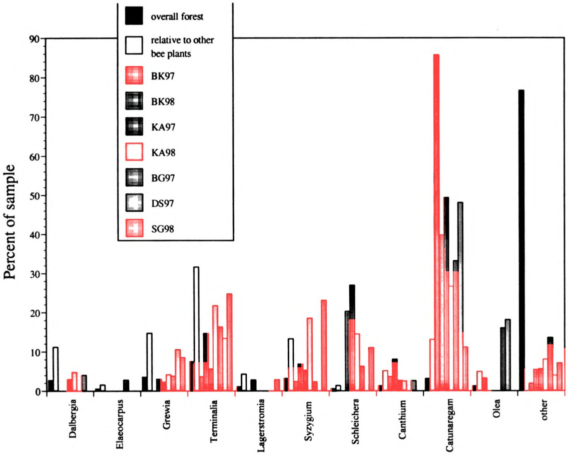

Figure 3.4. Frequencies of pollen types found in feces sampled at each site, pooled across weeks. First two bars respectively show frequencies of beepollen plants in the entire BRT sanctuary overall, and frequencies of those plants relative to other bee plant taxa.

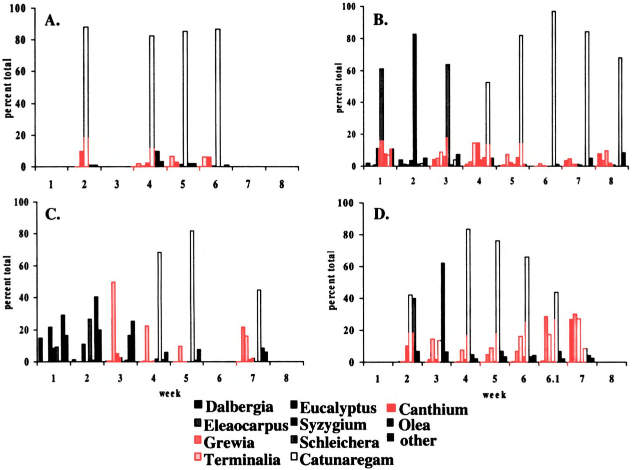

Figure 3.5. Weekly fecal samples' pollen composition. A. BK 97 site B. KA 97 site C. BG 97 site D. DS 97 site.

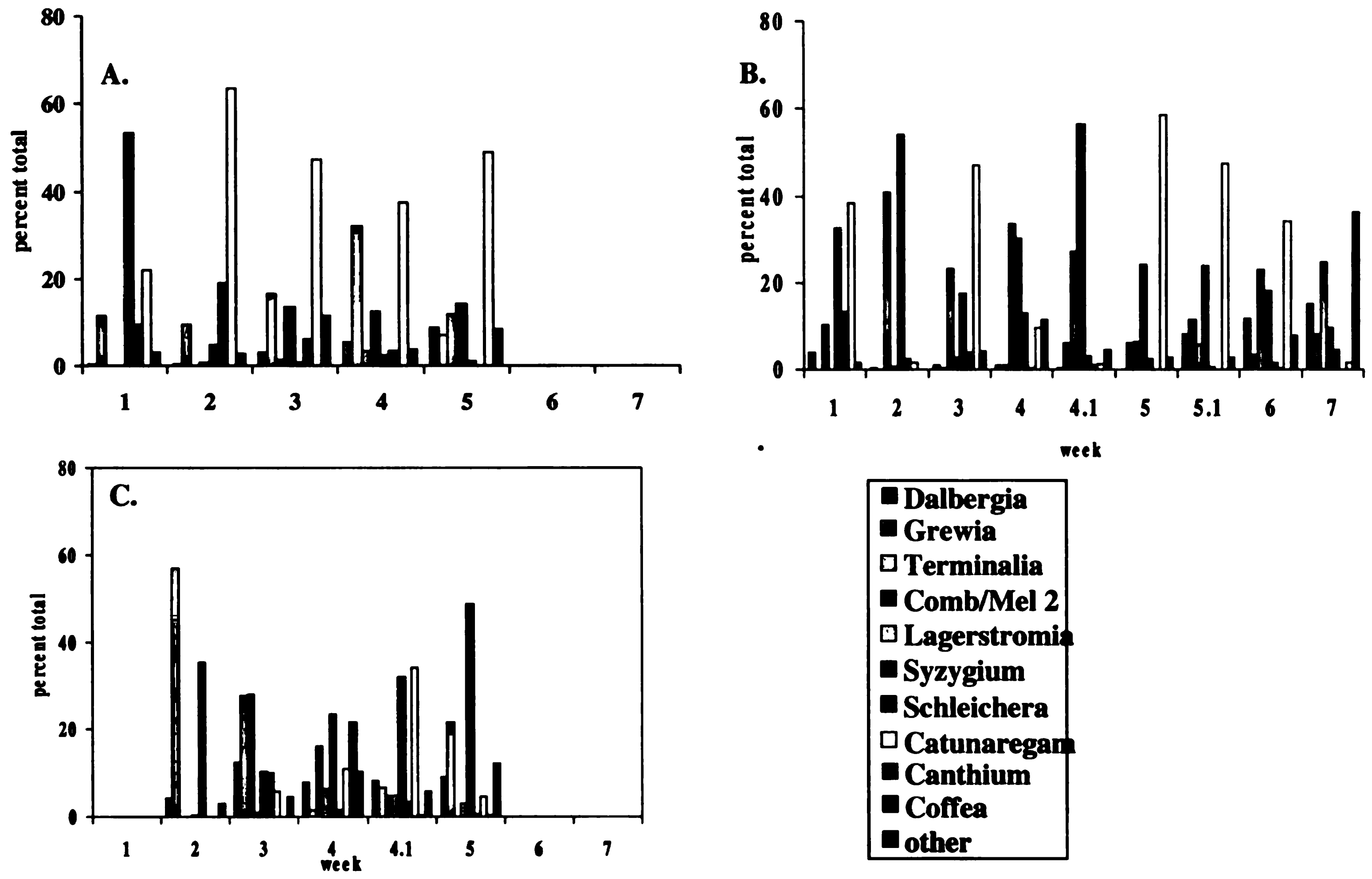

Figure 3.6. Weekly fecal samples' pollen composition. A. BK 98 site B. KA 98 site C. SG 98 site.

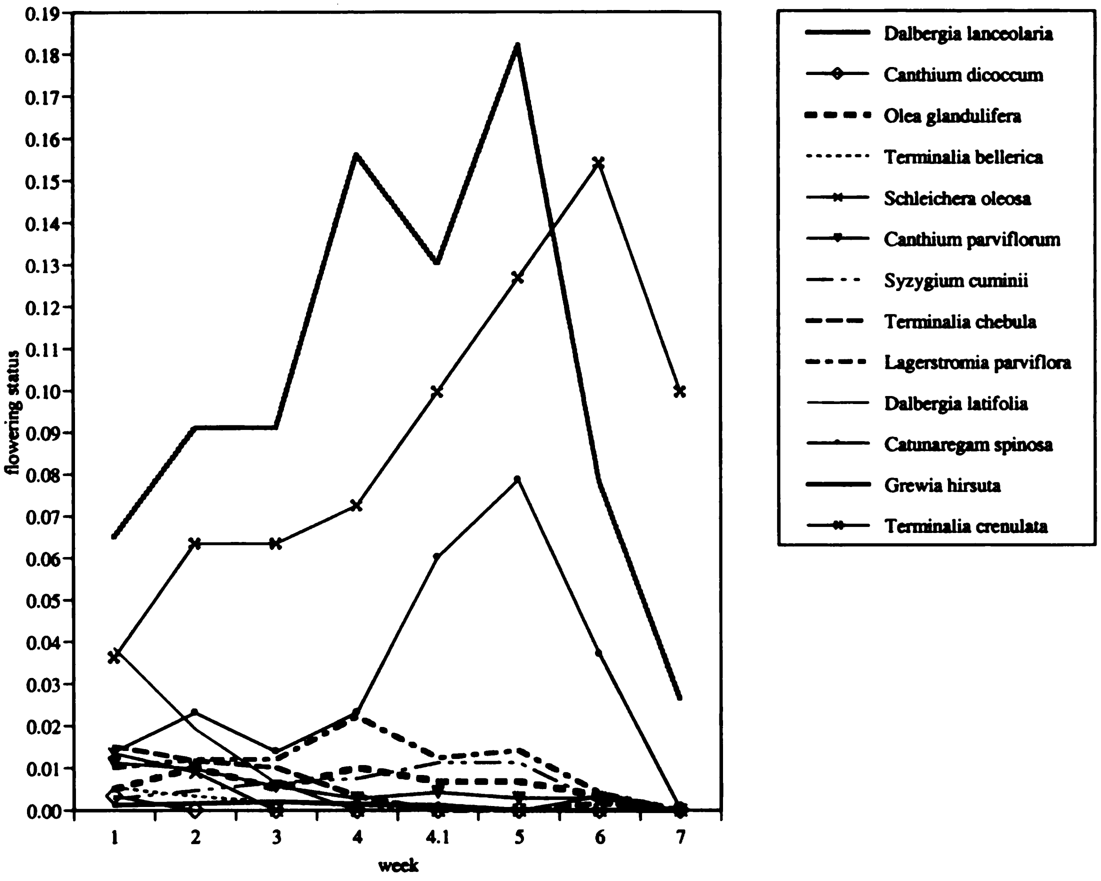

Figure 3.7. Comparison of flowering phenology weighted by relative abundance of major bee plants in dry deciduous forest. Numbers on y-axis represent the mean flowering status of all individuals on the transect per species where flowering values fall between 0 and 3 (see text for details.)

Figure 3.8. *C. spinosa* male flower. Note pollen on the central pseudo-stigma.

Figure 3.9. *Apis* dorsata foraging on male *Catunaregam spinosa* flowers. Note pollen deposited on the head.

Fig 3.10 *Terminalia crenulata* flowers.

CHAPTER 4: SPATIO-TEMPORAL DYNAMICS OF FORAGING

INTRODUCTION

There is abundant evidence that the spatial distribution of resources should affect animal movements, and that such movements in turn affect ecological landscape patterns. Some of the more important patterns affected by animal movements include the distribution of herbivorous insects across the range of host plants (Turchin 1991), habitat patch selection (Ims 1995) and coevolution of geographically structured populations (Thompson 1997), interactions between species in a guild (Danielson 1991), conservation corridor effectiveness and spread of disturbance (Lima and Zollner 1996), and the plant-pollinator relationships (Bronstein 1995). Theoretical and empirical work on insect movements and their ecological consequences has mainly addressed patch selection by herbivorous insects (e.g., Kareiva 1982; Turchin 1991). Far less work has focused on the landscape-scale ecological consequences of the movement patterns of pollinators, whose relationship to plants is of a very different nature than that of herbivores. Bronstein (1995) argues that the patchy and ephemeral nature of floral resources and the importance of pollinators in structuring plant communities should have great influence at the landscape scale on the persistence of different types of pollinator mutualisms. Her call for attention to the "plant-pollinator landscape" provides a sketch of the types of traits in both plant and animal mutualist that will determine whether the mutualism persists over time, and if so, the processes that will influence it. Critical to the study of the plant-pollinator landscape are the phenological variation of food plant populations across space and time, the foraging and searching behaviors of the pollinating animals, and the relative spatial scales of these two processes.

The movement patterns of central place pollinators, such as honey bees, are certain to have spatial consequences that differ greatly from the movements of widely dispersing insects. In fact, it may be true that central place foraging makes the study of heterogeneity of resources and the correlated movement patterns of insects more tractable over large spatial scales than dispersal types of movements because central place foraging provides a natural center from which to search for pattern.

While a voluminous body of literature exists on foraging behavior and decision making by animals at small spatial scales (e.g., Pyke 1978; Schmid-Hempel 1984; Stephens and Krebs 1986), it is extremely difficult to scale these results up to large spatial scales and complex foraging environments (Bronstein 1995; Lima and Zollner 1996). One difficulty is simply to observe large scale foraging patterns, but I have shown in an earlier chapter that honey bees afford unique opportunities to gain insights into landscape-scale foraging patterns through observations at their nests. Another difficulty is to integrate information on foraging behavior with data on spatial and temporal variation in food availability. However, this second difficulty can be met through the use of spatially explicit databases and modeling tools available through Geographic Information Systems (GIS).

In chapter two, I used foraging locations inferred from bee dances to examine overall patterns of flight distance over time in the flowering season. The conclusions which emerged from that set of analyses suggested that besides dynamics between colonies, foraging distances might be mediated by different levels of resources that were not detectable by the broad scale surrogate of "week in flowering season"; that is, changes in flight range when compared across weeks may be related to differences in site-specific resource levels. In chapter three, I found preferences for certain pollen-providing food plants both with and without temporally explicit differences in floral availability. In this chapter, I draw upon the forage maps, fecal pollen composition, and phenological variation from two 1998 deciduous forest sites. Combined with baseline distribution maps of important bee plants, I use an integrated GIS environment to examine whether colony foraging distance and selectivity in pollen foraging varies as a function of the spatio-temporal variation in site-specific resource availability of the bees' preferred plant taxa.

METHODS

Geographic Information Systems (GIS) provide a powerful tool for ecological analysis by integrating several spatially referenced data sets onto the same map. By overlaying different layers of data, for example, bee movements and plant distribution, it is possible to visually examine and illustrate spatial correlations between different factors. If numerical values such as flight distance and flowering intensity are associated with each point on the map, the numbers of the data sets that correspond to a given area or point on the map can pulled out and subjected to statistical analysis.

SPATIO-TEMPORAL CORRELATES OF FLIGHT DISTANCE

The following analyses rely on a combination of data gathered using methods presented in earlier chapters. These include the forage maps (Chapter 2), phenology measurements (Chapter 3), and pollen diet composition (Chapter 3). Since phenology was measured only in 1998 and can be expected to vary between years, forage maps from 1998 only were used. Data sets used for analyses in this chapter are the forage maps from sites KA 98 and BK 98, 1998 phenology numerical weights as described in the previous chapter, and the frequencies of six genera in the vegetation plot sampling done by ATREE. In each of the 125 2 x 2 km sampling grid cells, the frequencies of stems >10 cm DBH of *Canthium* (summed across *C. dicoccum* and *C. parviflora*), *Catunaregam spinosa, Grewia* (summed across *G. hirsuta* and *G. tiliaefolia*), *Schleichera* (summed across *S. oleosa* and *Dimocarpus longan*), *Syzygium* (summed across *S. cuminii* and *S. malabaricum*), and *Terminalia* (summed across *T. bellerica, T. chebula,* and *T. crenulata*) were multiplied by the average phenology index for each of the six weeks of phenology sampling. This resulted in a weekly matrix of relative flowering availability per cell per genus.

The vegetation plot sampling design, as described in chapter 3, was at the scale of 2 x 2 km; however honey bee flights mostly occur at a radius less than 2 km (see chapter 1). Therefore, I wanted to know the relative flowering status of each taxon at a finer spatial scale than that available from the plot sampling data. By using the Geographical Information System (GIS) software Arc View 3.2 and Spatial Analyst 1.2 (Environmental Systems Research Institute 1996), I interpolated values between the sampling plots in the center of each grid cell at a spatial resolution of 1 x 1 km. Arc View has two different computational functions available in the “interpolate surface” option. These functions interpolate between data points in different ways. One method uses the regularized spline function fitted with neighboring points. This method allows for smoothing of the interpolated surface, which is achieved by minimizing the curvatures between the input points (Environmental Systems Research Institute 1996). The alternative method is the inverse distance weighted interpolation, in which the values at points between the input points are computed as a function of the distances separating the input points. The spline function was preferable in this analysis because it allows for values to exceed or fall below the input values, as opposed to returning an interpolated surface whose values always fall between the input minimum and maximum. Since the values in the grids are relative flowering indices, and not absolute numbers of trees or flowers, it was more useful to have values that were not constrained be the maximum and minimum of the other cells. Thus, some values in the grids are negative values, meaning only that they are expected to have relatively less flowers of a particular taxon than other cells with less negative values. Figure 4.1 shows an example for *Catunaregam* of the interpolated weekly surface, as well as the overlain forage maps, explained further below.

One weakness of the approach of using relative and not absolute phenology measures is that it relies on the assumption that all tree taxa are equal in the size of their flowering display and rewards per flower. In nature, this is not likely to be the case, but is an issue which requires a large amount of data on the relative amounts of pollen produced per anther, number of anthers per flower, and number of flowers per tree for each taxon.

Such data sets are not available for the flora of BRT, nor are they available in a comprehensive fashion for any other bee flora. The approach I have used does not address the fine scale differences in levels of pollen availability, but addresses the issue at a larger spatial scale, that of floral patches produced by the distribution of trees and relative visitation and foraging at those patches. Furthermore, from a plant's perspective, the relative amount of visitation by a generalist pollinator is what matters more for the process of pollination than the energetic efficiency of pollen foraging.

A second assumption that the following analyses rests on is that there is no variation across space in flowering phenology. The phenology data were taken on a transect that ran through one area of BRT; thus by using those ranks for any given week in two different sites in BRT, I assume that there is there is little spatial heterogeneity between sites, or between the sites and the transect with respect to flowering status. Personal observations confirm that this assumption is generally valid in the dry deciduous forest; however, no data exist regarding actual levels of variation.

I selected forage maps for BK 98 and KA 98 by week and overlaid them onto the corresponding week's interpolated surface for each of the six plant taxa. I then extracted flowering index values from the surface at the intersection of bee foraging location. Finally, I averaged the flight distances per colony per week at each site, and also averaged the corresponding flowering indices for each plant taxon. Thus, the resulting numbers were average flight distance flown by a colony for each week, and the flowering availability averaged across each of the foraging points for that colony. Colony level differences in flight range appear from the analyses in chapter 2 to be due to indirect interactions between colonies by which they avoid using the same patches as other colonies, thus resulting in flight ranges that shifted relative to each other. Since the analyses here are not concerned with the differences between colonies, summarizing at the colony level removes variation that is attributable to those differences, and leaves in the variation associated with the level of overall site.

To address the question of whether the six preferred plant taxa had any influence on flight range, I performed a stepwise regression with flight range as the dependent variable, and flowering status of each taxon as the six predictor variables. The stepwise procedure was done using JMP software (SAS Institute 1999)] as a "mixed" stepwise, that is, the iterations of computing the best model by adding and removing x's were done in both the forward and backward directions using a value of $p = .25$ as the entry and removal criterion. A p-value greater than .25 resulted in a variable being removed from the model, and a p-value less than .25 resulted in a variable being added to the model. A stepwise regression is most often used when the number of x variables needs to be reduced to only those that explain the majority of the variation in an independent variable (Sokal and Rohlf 1981).

I used the Mallow's C_p criterion of model selection to determine the cutoff number of variables. This approach finds the point at which C_p approaches p, where p is the number of model parameters (SAS Institute 1999). I used this method of model selection instead of simply using all the variables returned by the stepwise regression because in order to perform a multiple regression using the x variables "chosen" by the stepwise, there should be roughly a 5 to 1 ratio of sample size to number of x variables (Tabachnick and Fidell 1983). The sample size in the KA 98 site was N = 17, and thus not large enough to accommodate four predictor variables. The Mallow's C_p criterion actually resulted in limiting the number of x's to three, and I used the same criterion in the BK 98 (N = 23) for the sake of methodological consistency. Once the stepwise regression eliminated the plant taxa which did not explain a significant portion of the variation in flight range, I ran a multiple regression of flight range on the flowering indices of the remaining taxa to determine the predictive value that those taxa have on flight distance.

SPATIO-TEMPORAL VARIATION IN FOOD PLANT PREFERENCE

In the previous chapter I tested whether the representation of pollens in the bees' diet was associated with floral availability in the environment, as determined from the phenology data. Here I expand on this question by explicitly integrating spatial and temporal variation in floral availability in the GIS environment, and then asking whether the bees' diet varied in association with changes in local density of particular floral species. As in the previous chapter, the null hypothesis is that bees have no food plant preference.

To carry out this analysis, I generated an average flowering index for each week that took into account the densities of each plant taxon only in the actual places where the bees were flying, as opposed to assuming homogeneity in the distribution of plant taxa across all bee nest sites. To do this, I averaged, for each site, the interpolated flowering index scores for each taxon across all foraging locations per week. The proportion of the total sum of these indices per week per site generated each taxon's expected value for a G test. In this test, the null expectation was that pollen use was proportional to floral availability. In the BK 98 site I added 1 to each index value in order to eliminate several negative values. This was necessary because G tests use a natural logarithmic function in the computation of G-scores. The observed value for each taxon was its number of pollen grains in each site's weekly sample.

RESULTS

Spatial and temporal variation in flowering status appeared to be linked to variation in flight distance, a pattern that was not detected in the previous coarse grained analysis (chapter 2). Results of the pollen diet analyses here largely confirmed the pollen preferences found in the chapter 3, with some new site-specific patterns emerging as well. I discuss each of these analyses in turn. Images in this dissertation are presented in color.

CORRELATES OF FLIGHT DISTANCE

The stepwise regressions of flight distance on six different taxa originally returned four variables as explaining a significant portion of the variation at both sites (table 4.1, 4.2). Using Mallow's criterion, I determined that each model should restrict the number of variables to the top three. In both sites, *Terminalia* and *Grewia* were chosen by the stepwise procedure; additionally, the BK 98 site model included *Schleichera* and the KA 98 site model included *Syzygium*.

The multiple regression yielded results which showed consistency across sites, as well as site-specific divergence (table 4.3). *Terminalia* emerged as the most important predictor of flight range, with its flowering availability having a highly statistically significant on, negatively correlated with, flight distance in both sites. Other taxa did not show consistent effects across the two sites, and thus may be indicative of locally specific phenomena. Although *Grewia* was significant in both sites' models, it was positively related to flight distance in BK 98, but negatively related in KA 98. In BK 98, *Schleichera*, the third taxon chosen by the stepwise regression, was not statistically significant in the full model, but in KA 98, a third taxon *Syzygium*, was statistically significant and negatively correlated to flight range.

FOOD PLANT PREFERENCE

With respect to pollen diet composition, the results were largely similar to those found when diet was examined without accounting for spatial variation in resource abundance, but also yielded some new insights (table 4.4). *Catunaregam* in BK 98 was overused relative to expectations, but was not a particularly heavy contributor to the partial G-scores in KA 98. Instead in the KA 98 site *Syzygium* appeared to be more overused in weeks when *Catunaregam*'s importance was low. *Terminalia* was mostly underused, although its G-values do not differ strongly from the null expectation of zero, thus indicating that it was used according to expectations. *Schleichera* was overused in both sites early in the season, used according to expectations late in the season in KA and for most of the season in BK, indicated by its small positive and small negative G-scores. It was never grossly underused. At its peak time of availability, it is overused, and it at other times it is used according to expectations. However, since the flight range data analyses do not indicate that *Schleichera* was a correlate of flight range, it appears that the apparent preference for *Schleichera* is mediated by its availability and is not something for which the bees will expand their flight range in order to seek out when its availability drops.

DISCUSSION

By incorporating spatial and temporal variation into the analyses of flight distance and pollen preference, the complexity of the relationship between *Apis dorsata* and its forest food plants begins to emerge. Indeed the heterogeneity in the distribution of bee plants across the forest and through time does appear to influence flight range of colonies as well as result in site-specific patterns of floral utilization.

When results of the spatially explicit pollen preference analyses are compared to those that did not incorporate spatial variation in resource levels, it becomes clear that preferences for taxa do exist, but they are diffuse and mediated by relative availabilities of a few selected food plants. For example, the strong preference for *Catunaregam* shown in the previous chapter is somewhat diluted once the pollen distribution is made spatially explicit. Feces at the KA 98 site in fact showed little deviation from expected values for *Catunaregam* but instead showed an overuse of *Syzygium* (table 4.4). While *Syzygium* was a highly preferred taxon in the weekly 1998 analysis of chapter 3 which used phenological variation and pooled across sites (table 3.3), it was not overused in the BK 98 site when analysis pooled across weeks. That is, at no level of pooling was

Syzygium preferred in BK. Therefore, the BK results across the board are different from KA results with respect to *Syzygium*. Such site-specific preferences may be due to initial discovery and learning of different food sources, differences in tree size and thus floral displays and crown attractiveness of certain tree taxa over others in some environments, or other factors that are particular to the local environment beyond differences in relative abundance.

The site-specific pollen preference results are confirmed independently when the flight range predictors are examined. At KA 98, *Syzygium* floral availability had a strong influence on flight distance. The relationship was negative, suggesting that when *Syzygium* flowers were readily available, bees did not travel as far as when *Syzygium* flowers were rare. At times when *Syzygium* was rare in the forest, bees flew further from the nest. This was not the case in the BK 98 site, which is also consistent with its lack of importance in the pollen diet at that location.

Catunaregam was a preferred plant in BK 98 and mildly so in KA 98 (table 4.4). Somewhat surprisingly, however, its floral availability was not a predictor of flight range variation; that is, bees are not tracking the resource, despite its overall importance in the diet. Even if they were more reliant on *Catunaregam* as a nectar source and not a pollen source, as postulated in the previous chapter, the floral index would remain the same and any tracking behavior should be apparent.

Schleichera was among the four chosen factors in the stepwise regressions, indicating its marginal importance, but was eliminated from the model as the least important of the four in KA 98. It was not eliminated from the BK 98 model, but did not turn out to be a strong predictor of flight range according to the multiple regression. Thus, from a combined interpretation of both the fecal pollen results and the flight distance results, it appears that *Schleichera* did appear to be used preferentially when it was available, but bees did not track it when its peak flowering declined. *Schleichera* is one of the first trees to flower as the immigrating colonies come in to BRT (chapter 3; figure 3.6). Thus, it is an important early resource, perhaps only because there is less to choose from early in the season. Once other pollen sources begin to flower, giant honey bees no longer seek out *Schleichera*. Thus as a relatively rare plant in the forest, its importance lies in the timing of its floral display, and perhaps less in its total contribution as a nutritional or energetic resource.

Grewia was a pollen resource that was used in proportion to its occurrence in both locations. Although *Grewia* was among the strongest of the six predictors of variation in flight range at the two sites, its relationship to flight range differed in sign across locations; thus, its influence in flight range may reflect site-specific differences.

The most surprising result of the combined spatio-temporal analyses was the unintuitive result of *Terminalia*. As a pollen resource, it was most often strongly underused (table 4.4). This is consistent with the results from chapter 3 where *Terminalia* had a negative G-score in almost all cases (table 3.2, 3.3). In the multiple regressions, however, *Terminalia* was a statistically significant correlate of flight distance, showing a negative relationship to flight distance. That is, when *Terminalia* flowering index was low, flight range was high, suggesting that bees are foraging close to the nest when this resource is frequently encountered, and flying further when it is not readily available in the vicinity. This is somewhat puzzling given that they did not exhibit any preference for its pollen; however, bees are known through much anecdotal evidence and observation (A. Sinha, unpublished data; Soligas, pers. comm; pers. obs.) to rely strongly on *Terminalia* for nectar. Most of the *Terminalia* flowers in the forest belong to the species *T. crenulata* (ATREE, unpublished data), and the peak in these flowers occurs in the latter part of the flowering season (fig 3.7). The bees may be tracking this nectar source in preparation for their long migratory flights, which may be as far as 100 km or more (Koeniger and Koeniger 1980). Pollen is crucial for brood production, which necessarily stops prior to migration; thus, it is possible that giant honey bees temporally shift the preference of food category according to season, and are willing to fly further in search of this food resource than they appear to be for any of the major pollen resources.

The complex picture that this plant-pollinator landscape analysis reveals poses some interesting questions for further exploration. One question which may be particularly valuable in understanding how the phenomenon of generalist foraging impacts the forest is whether the same taxa will emerge as preferred food plants if the study were replicated across years. The site-specific preference for *Syzygium* in KA 98, for example, may be a phenomenon particular to the conditions of the year it which the data were collected. Given that the signal was the same in both the pollen analysis and the foraging range analysis, the question of its generality across years is an intriguing one. One mechanism by which the site-specific patterns may emerge could be that bees learn to find profitable resources, and do not learn new ones until the old ones begin to wane (Barth 1991). This bias in searching is reinforced by odor cues at the nest, visual cues in the form of floral display, and several other factors that may be due to differences in initial conditions between sites. However, these initial conditions may not vary over years since floral display is related to crown sizes of trees, and learning of a floral source will depend on the timing of its first flowering relative to other resources, which is roughly the same every year. In combination with the overarching preferences for *Catunaregam*, and influence of *Terminalia* on foraging distance, the site-specific results suggest that there may be local phenomena occurring that, if they hold up across years, could have important influences on forest community structure and seed production via differential patches of pollination associated with certain locations.

Another avenue for study is whether the relationships between plant taxa based on the timing of their flowering and relative importance in the bees' diet is a general phenomenon in different parts of the range of giant honey bees. Is it often the case, for example, that early season resources such as *Schleichera* are relatively rare in the forest, and overused only for a short duration despite the low level presence of other taxa at the same time? Is the relationship between giant honey bees and *Grewia* an opportunistic one such that the correlations of opposite sign seen in the two locations actually do indicate the flexibility of their foraging movements? Are there plant taxa in other parts of tropical Asia which are not used as pollen resources but seem to drive foraging distances?

Why is *Catunaregam* not an influence in predicting the flight range, given the overabundance of its pollen in the bees' diet?

Spatio-temporal heterogeneity of resources is the rule in ecological systems, not the exception, although the problem of understanding the large scale patterns and processes associated with such heterogeneity has remained largely intractable until recently. However, the use of new, high technology tools such as GIS, along with old, low technology tools, such as observations of bee behavior, flowering phenology, and vegetation transects holds great promise in uncovering new patterns in the ecology of plant-animal relationships. Although many questions remain incompletely answered in the analyses presented here, they have provided an unprecedented time series picture of the landscape scale correlations between trees and their pollinators. Equally importantly, I believe they have demonstrated the power of such approaches to detect otherwise unobservable phenomena.

Table 4.1. Results of stepwise regression for BK 98 site. These three out of the original six taxa emerged as being the most valuable predictors of flight range. Here, "sig prob" is the theoretical significance probability, because in stepwise regression it cannot be determined absolutely. Cp is Mallow's criterion, and "p" is the number of parameters. Based on the results here, *Canthium* was removed from the model before performing multiple regression. (See text for details.)

PARAMETER	"SIG PROB"	SEQ SS	R^2	Cp	p
Terminalia	.0008	16372070	.4221	6.3239	2
Grewia	.1172	264868.6	.4904	5.3314	3
Schleichera	.1172	245365.4	.5537	4.5591	4
Canthium	.1697	176703.3	.5992	4.5627	5

Table 4.2. Results of stepwise regression for KA 98 site. These three out of the original six taxa emerged as being the most valuable predictors of flight range. Here, "sig prob" is the theoretical significance probability, because in stepwise regression it cannot be determined absolutely. Cp is Mallow's criterion, and "p" is the number of parameters. Based on the results here, *Schleichera* was removed from the model before performing multiple regression. (See text for details.)

PARAMETER	"SIG PROB"	SEQ SS	R^2	Cp	p
Terminalia	.0067	944856.3	.3967	12.873	2
Syzygium	.2213	150602.9	.4599	12.161	3
Grewia	.0056	589394.6	.7074	3.5488	4
Schleichera	.2132	87724.71	.7442	3.9692	5

Table 4.3. Results of multiple regression for sites BK 98 and KA 98.

	BK 98	**KA 98**
Regression equation	y = 1416.71 + *Grewia* (245.98) + *Schleichera* (-57531.69) + *Terminalia* (-319.81)	y = 4328.31 + *Grewia* (-578.708) + *Syzygium* (-2350.80) + *Terminalia* (-640.84)
Model F-ratio (p value)	7.86 (p=.0013)	10.48 (p = .0009)
Model R^2	.55	.71
Grewia F-ratio (p value)	4.44 (p=.0486)	10.99 (p = .0056)
***Schleichera* (BK 98) / *Syzygium* (KA 98) F-ratio (p value)**	2.69 (p=.1172)	11.79 (p = .0044)
***Terminalia* F-ratio (p value)**	10.79 (p=.0039)	26.62 (p = .0002)
N	23	17

Table 4.4. G-tests for KA 98 site and BK 98 site comparing spatio-temporally explicit forest floral composition to pollen diet composition. DF = 5, G critical = 11.07 ($p<.05$); G critical = 20.515 ($p<.001$).

BK 98

POLLEN TYPE	**WEEK 1**	**WEEK 2**	**WEEK 3**	**WEEK 4**	**WEEK 5**
Catunaregam	45.64	217.24	105.13	47.75	90.43
Canthium	-30.45	-1.02	-23.09	-14.94	0
Grewia	-9.12	-4.78	-25.23	-30.68	-13.23
Syzygium	-4.35	-5.00	78.05	-47.31	-51.15
Schleichera	413.58	-19.72	-7.03	-12.93	-5.96
Terminalia	-157.32	-62.61	-79.28	-2.29	-14.24
G-score	**515.97**	**248.23**	**97.10**	**-120.80**	**11.71**

KA 98

POLLEN TYPE	**WEEK 1**	**WEEK 2**	**WEEK 3**	**WEEK 4**	**WEEK 5**	**WEEK 6**
Catunaregam	166.94	-14.1	129.82	-23.73	36.99	-24.75
Canthium	20.68	0.64	22.65	-1.21	0	-0.08
Grewia	0	0	-4.30	-10.75	-26.74	-19.27
Syzygium	0	-1.32	8.26	155.05	88.77	125.95
Schleichera	403.21	3653.78	520.84	384.58	54.45	26.60
Terminalia	-56.44	-15.84	-53.77	34.45	-15.60	43.33
G-score	**1068.76**	**7246.3**	**1247.01**	**1076.76**	**275.74**	**303.54**

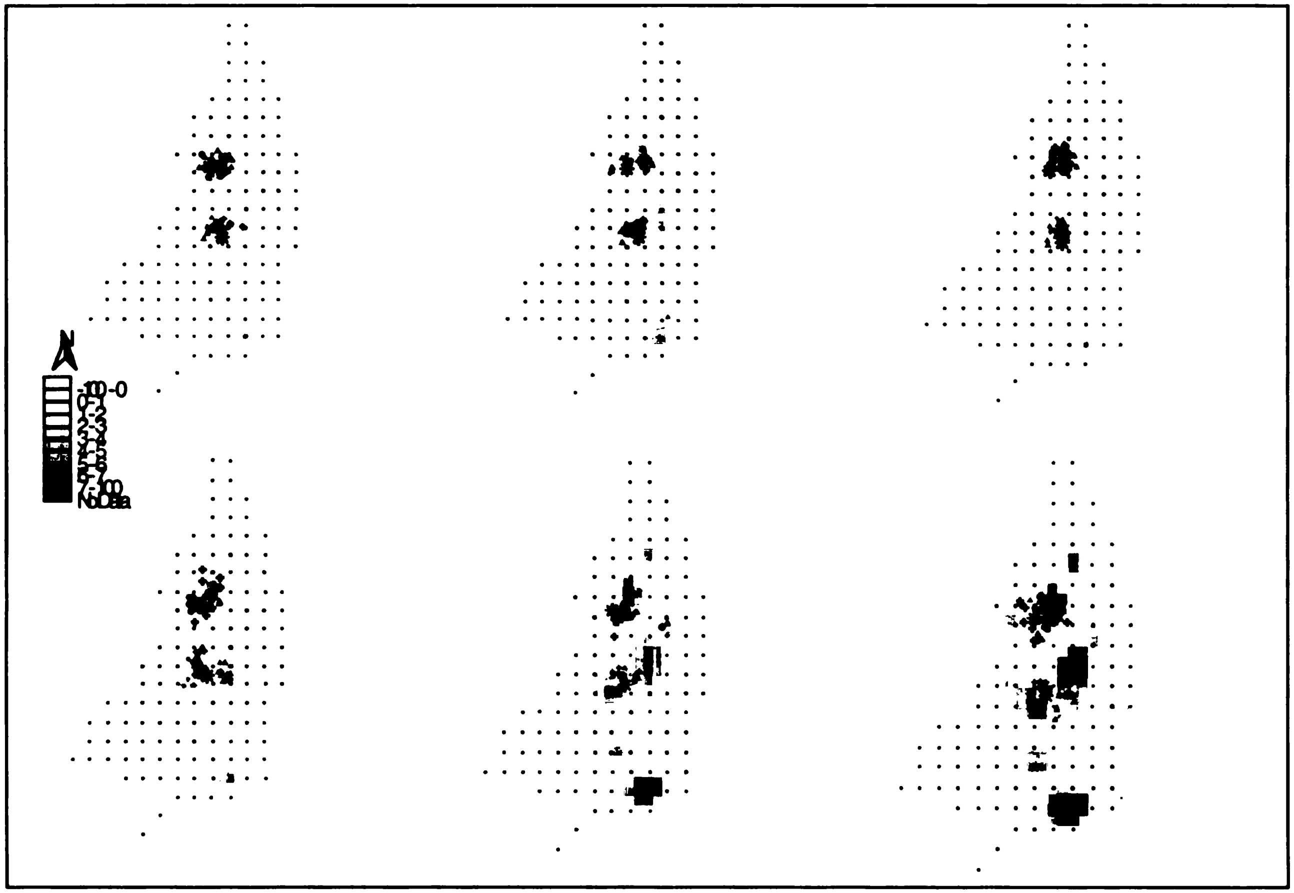

Figure 4.1. Example of weeks 1-6 of forage maps for KA 98 and BK 98 overlain onto weekly interpolated flowering index surfaces for *Catunaregam spinosa*. Darker shades of grey indicate increasing pollen availability. Equally spaced dots are two kilometers apart, and denote the vegetation sampling grid. Different symbols are foraging points for different colonies. The upper aggregation is KA, and the lower is BK.

CHAPTER 5: NESTING AGGREGATIONS, POLLINATION, AND FOREST STRUCTURE

INTRODUCTION

The field of ecology continues to address the question of what role individual species play in overall ecosystem function, an approach that will be increasingly relevant in developing new approaches to habitat and biodiversity conservation (Balvanera et al. 2001). It is clear that some species are particularly influential in structuring aspects of their environment beyond their role in the trophic web. Such species have been called "ecosystem engineers" (Lawton 1994) whose presence provide structures (such as beaver dams) that affect the rest of the biotic community. In this chapter I begin to explore a hypothesis built on the results of the previous analyses which examines the role of *Apis dorsata* in engineering overall forest structure of the areas in which it forages.

Apis dorsata colonies nest as singletons scattered throughout the forest, but in many areas of its range, giant honey bees also aggregate their nests in groups that may number 100 or even more colonies on a single tree or rock cliff (figure 1.1b) (Morse 1969; Deodikar, 1977). Colony size is on average 50,000 individuals, and an estimated 20% of workers are at any given time engaged as foragers (Morse 1969). *A. mellifera* foragers make an average of 10-15 trips per day, though the number may range up to 150 (Winston 1987) and although it is likely that *A. dorsata* foragers make fewer trips per day (Dyer and Seeley 1991) individuals clearly can and do go on multiple foraging bouts per individual when presented with sugar water feeders (see chapter 2). Thus, a conservative estimate of five trips per forager per day results in approximately 50,000 foraging trips per day from each colony. An aggregation of 100 colonies therefore results in millions of potential pollination events every day, all radiating out from a single point in the forest. Such an aggregation locale then could be considered an "epicenter" of pollination. Moreover, these aggregation locations are known to recur from year to year. That is, despite their migration during the rainy season, giant honey bee colonies always recolonize the same locations in large numbers. In BRT, the trees on which there were nest aggregations were 20 m or higher, and presumably quite old. The cliff faces have potentially been recolonized for hundreds or thousands of bee generations. This nesting behavior, due to the sheer numbers of pollinators it places in a single location, combined with the recurrence of colonization by large numbers of colonies in a single site may have some extremely important implications for forest spatial structure, both at the community composition level as well as population genetic level.

The forage mapping analyses showed that 90% of the time, bees forage within a distance of about 2 km from the nest. Preferred plants such as *C. spinosa* that occur in a forest with radius of 2 km centered around the nest aggregation should receive higher numbers of floral visitors than regions that are at further distances from the central nest aggregation. If visitation rates are directly related to fruit and seed production, the patch centered around the nest site aggregation with radius of 2 km could be a source patch for fruits of preferred bee plants. Since fruit dispersal is assumed to be leptokurtic with distance from parent tree (Howe 1990), over several generations of dispersal and regeneration close to fruit bearing trees, one might hypothesize the development of "contours" of abundance of *C. spinosa*, centered around the stable honey bee aggregation sites.

There are several assumptions inherent in the above scenario, none of which have been tested for *Catunaregam spinosa*, or for any other species. First, it assumes that fruit set in *C. spinosa* is pollination limited as opposed to being limited by other factors such as resource levels. This assumption can only be tested experimentally over a number of years; however, it may not be inconceivable that in dioeceous species, in which typically the number of female flowers is far lower than the number of male flowers (Bawa and Opler 1975), pollination may be limited by visitation rates to the females since the floral display is much smaller and less conspicuous. The hypothesis here is that the bees' foraging range and nesting behavior will result in a landscape mosaic of pollinator limitation, and that this will result in variation in fruit production across the landscape.

A second assumption is that the scale of fruit dispersal will occur over a spatial scale that does not encompass the foraging region of another nest site aggregation. The fleshy fruits of this tree are eaten by large vertebrates, especially the forest bison, or gaur (*Bos gaurus*) (M. Ketha, pers comm.). It is not known whether the fruits need to pass through a mammalian digestive tract for germination to occur or whether those that fall from the parent tree also can germinate. However, gaur range over distances of 2-3 miles a day (Schaller 1967), a scale of movements that could enable dispersal of seeds across the boundaries of the foraging ranges of adjacent bee aggregations (pers obs). Detailed studies on dispersal by gaur would be crucial in setting expectations for spatial structure of this plant species.

Before conjecturing that the spatial distribution of bee plants is controlled indirectly by the foraging limitations of bees themselves, the first step is to quantify whether honey bee and other insect visitation rates to trees within a 2 km radius from the nest sites differs from visitation rates to trees farther away. By measuring visitation by other species of *Apis* and other insect taxa, I begin to explore also whether there are differential zones of competition for floral resources such that in areas that may experience relatively lower densities of *A. dorsata* foragers, other insects are more frequent floral visitors.

METHODS

FIELD METHODS

Ninety percent of all *A. dorsata* foraging flights occur within 2.2 km from the nest site (chapter 2). Therefore, I located *Catunaregam spinosa* male individuals in bud stage in locations within two kilometers from any nest aggregation, here called "proximal"sites, and trees that were beyond two kilometers distance from all nest aggregations, called "distant" sites. There may have been, however, single colonies nesting close to focal trees at either proximal or distant sites. The probablity of such singletons is assumed to be equal for any area of the forest. In total, there were eight trees in each distance category. At each site I chose two trees in approximately the same stage of flowering, with approximately the same crown size. The purpose of this was to minimize differences in floral display between replicates, though because it was done by visual estimation only, it not strictly standardize the patch size.

At each tree, my field assistant and I chose three branches with a varying number of flowers on them, and counted the number of flowers. For five minutes every half hour, we watched each branch of flowers and tallied the number of visits (floral landings by the same or different individuals) by *A. dorsata*, *A. cerana*, *A. florea*, *Trigona*, lepidopterans, and "other" insects. As the period during 1100-1500 has very little insect activity, we counted visits from 0600 until 1100 and again from 1500-1800.

STATISTICAL ANALYSIS

There was an abundance of zeros in all data sets, which is problematic for statistical analysis. In order to try and reduce the number of zeros, I pooled all visits per day to each branch, and then computed the number average of visits per minute per flower on the branch, or visitation rate per flower. This resulted in each branch being treated separately as a replicate unit, so there were 24 units per distance category. I did this for all categories of visitors. The data were still quite non-normally distributed; therefore, I analyzed them using a Wilcoxon's rank sums test, which is the non-parametric equivalent of a t-test. The independent variable here was distance from an aggregation (distant vs. proximal), and the dependent variable was visitation rate per flower.

RESULTS

The results of two-way unpaired comparisons between honey bee and other insect visitation to proximal sites vs. distant sites did not yield any conclusive results. All groups of insects showed higher visitation to the proximal sites (table 5.1). When visitation by *A. dorsata* to distant and proximal sites were compared, the result of the non-parametric test was not statistically significant at the $p<.05$ level. The p-value of 0.08 suggests that there may be a biologically significant trend worth exploring further. *A. cerana* showed virtually no difference in visitation rates to areas that were at different distances from *A. dorsata* nest sites, whereas *A. florea* seemed to visit those areas near to nest aggregations at higher rates per flower. All other insects also visited the proximal sites more often than the distant sites. Thus, it appears that other insects, including the other two species of *Apis*, do not avoid areas that may be dominated by *A. dorsata*.

DISCUSSION

Visitation by giant honey bees was not significantly higher in areas of the forest that were within a two kilometer foraging distance from nest aggregations than in areas further than two kilometers. Interestingly, the response was similar across all insects except for *A. cerana* in which visitation rate was basically equal for the two distance categories.

The rates of visitation were quite low in all cases, thus the statistical results are difficult to interpret with much confidence. There were many counts of zero in the data. This poses a challenge for statistical analysis, a challenge that is further compounded by the fact that some of the zeros are hypothesized to have biological meaning; that is, at the distant site, I hypothesized that there would be more zeros than at proximal sites. There were five proximal site branches out of 24 where the average visitation rate was zero and only six at distant sites where it was zero. Thus it seems there is not much difference in zero visitation rates between the two sites. Other insects had even lower visitation rates to flowers of *C. spinosa* than *A. dorsata*. It was not the case that in areas which were further from giant honey bee nest aggregations, other insects utilized the resource more heavily. From this result I draw two conclusions: First, *A. dorsata* is the most frequent visitor to *C. spinosa* male flowers, and second, if indeed there is variation in visitation rates at different distances from the aggregation, it does not result in a mosaic of different mutualists that may be avoiding competition.

The fact that visitation rates for proximal and distant flowers verged on being significantly different in the hypothesized direction for *A. dorsata* suggests that this hypothesis is worthy of further exploration. The fact that all taxa exhibited higher rates to the proximal sites may mean that those trees chosen were simply more attractive to all foraging insects. In order to fully address the question, the study would need a larger sample size, would perhaps need to incorporate more than two distance categories, and would need to equalize the floral display in a systematic manner, either statistically or by removal of flowers from the focal and neighboring trees such that all sites were of equal attractiveness. It would also need to stratify the sample sizes at various distances, thus controlling for the fact that at longer radial distances, the area searched by the bees is larger and thus any given tree within that radius has a lower probability of being visited. This effect alone could account for the marginally significant results I obtained in the

Wilcoxon test. Furthermore, in light of the findings in chapter 2 that colonies do not seem to share patches, a better design would incorporate many patches of *C. spinosa* near the same aggregation being observed simultaneously, as opposed to this study, which made simultaneous observations only two trees at a time, and those trees were close enough to each other that they may be considered the same patch. Discovery of a patch would in this case be dominated by one colony, regardless of its distance from the nest. The improved design of incorporating several patches also may correct for any singleton colonies that may have been nesting near the focal trees and whose visitation may have swamped out any effects of distance from large aggregations.

Another approach to examining whether *C. spinosa* is structured around nest site aggregations would be to use GIS to map the fine grained distribution of adult trees around several nest site aggregations up to distances that exceed the foraging range of the bees, and compare them with the distribution of *C. spinosa* trees around singleton *A. dorsata* nests. These singletons occur randomly throughout the forest at sites which are not recolonized from year to year (pers. obs.) and therefore would not result in a contour-like organization of trees around them.

The phenomenon which this chapter hypothesizes could have interesting ramifications for the population genetic structure of selected tree species. Gene flow largely within a confined area that has a natural center, the nest site aggregation, may result in a mosaic landscape that can actually be observed as patches of allelic diversity, and one in which plant neighborhood size may be predicted by honey bee flight range.

The implications of such a phenomenon would also have implications for conservation applications and landscape management plans in the Asian tropics. While it is clear that such aggregations of pollinators should be included in preserved habitat regardless, if they actually do act to structure the forest, the bees may be truly considered both an “umbrella” and keystone species (Simberloff 1998) whose nest sites and foraging range delineate natural units of community and genetic spatial organization. The inclusion of a number of these units might be a strategy for preserving a desired level of forest diversity, and would also result in protecting areas in a manner that does not disrupt existing movement corridors of some elements of forest community, including the large frugivorous mammals which act as dispersers.

Table 5.1. Results of Wilcoxon rank sums test of visitation rate to flowers of *C. spinosa.*

	A. dorsata	***A. cerana***	***A. florea***	**other**
Proximal (visits/flower/minute)	.018958	.000186	.000395	.002430
Distant (visits/flower/minute)	.009560	.000075	.000000	.001128
Wilcoxon p-value	**.0870**	**.9828**	**.0410**	**.0620**

APPENDIX I

Forage mapping site characteristics, dates of data collection and their corresponding week numbers used throughout text, and sample sizes (number of dances recorded) per colony per week at each site.

SITE	COLONY	WEEK AND CORRESPONDING FORAGE MAP DATE							
		1	2	3	4	5	6	7	8
Kamari		13-Mar-97	17-Mar-97	24-Mar-97	31-Mar-97	6-Apr-97	14-Apr-97	29-Apr-97	5-May-97
(KA 97)	1	N = 40	40	30	46	30	8	14	8
dry deciduous	2	29	29	36	32	30	11	10	10
11:59.70 N, 77:08.43 E	3	11	34	21	22	32	19	16	10
cliffside; 60-70 colonies									
Basavanakadu		10-Mar-97	18-Mar-97	25-Mar-97	1-Apr-97	7-Apr-97	15-Apr-97	28-Apr-97	6-May-97
(BK 97)	1	9	17	30	16	13	9	14	11
dry deciduous	2	17	26	32	40	35	8	13	23
11:55.69 N, 77:09.12 E	3	1	12	24	16	34	5	14	16
tree; 25-35 colonies									
Doddesampige		11-Mar-97	21-Mar-97	29-Mar-97	5-Apr-97	11-Apr-97	18-Apr-97	25-Apr-97	10-May-97
(DS 97)	1	15	5	10					
evergreen	2	13	18	29	35	25	19	28	8
11:56.94 N, 77:10.97 E	3	12	16	31	27	25	16	16	5
tree; 80-90 colonies	4		21	27	26	21	16	31	7
Beduguli		15-Mar-97	19-20 Mar 97	27-28 Mar 97	4-Apr-97	9-10 Apr 97	16-17 Apr 97	N/A	4-May-97
(BG 97)	1	16	11	9	1	9	6		3
evergreen/coffee plantation	2	20	14	11	9	6	8		1
11:50.07 N, 77:10.18 E	3	17	23	10	7	10			
tree; 70-80 colonies	4			16	13	11	24		11

Appendix I (cont'd)

SITE	COLONY	WEEK AND CORRESPONDING FORAGE MAP DATE 1	2	3	4	5	6	7	8
Kamari		9-Mar-98	16-Mar-98	23-Mar-98	31-Mar-98	13-Apr-98	27-Apr-98		
(KA 98)	1	N =28	9	14	18	16	19		
dry deciduous	2	22	12	13	7	9	28		
11:59.70 N, 77:08.43 E	3		5	7	9	4	21		
cliffside; 60-70 colonies									
Basavanakadu		13-Mar-98	18-Mar-98	26-Mar-98	2-Apr-98	15-Apr-98	28-Apr-98		
(BK 98)	1	20	32	16	13	23	14		
dry deciduous	2	12	29	28	23	13	18		
11:55.69 N, 77:09.12 E	3	14	19	12	8	9	12		
tree; 25-35 colonies	4			9	3	3	4		
	5				5				
Sige Gudi		N/A	17-Mar-98	25-Mar-98	1-Apr-98	N/A	14-Apr-98		
(SG 98)	1		10	10	13				
dry deciduous	2		12	6	24		34		
11:51.58 N, 77:08.25 E	3		13	17	9		25		
tree 30-40 colonies									

APPENDIX II

Dates of pollen samples and phenology observations.

	WEEK										
SITE	1	2	3	4	4.1	5	5.1	6	6.1	7	8
KA 1997	5-17 Mar	18-24 Mar	25-31 Mar	1-6 Apr	N/A	7-14 Apr	N/A	15-29 Apr	N/A	29 Apr-5 May	6-12 May
BK 1997	N/A	19-25 Mar	N/A	1-7 Apr	N/A	8-15 Apr	N/A	16-28 Apr	N/A	N/A	N/A
DS 1997	N/A	22-29 Mar	30 Mar-5 Apr	6-11 Apr	N/A	12-18 Apr	N/A	19-25 Apr	26 Apr-2 May	3-10 May	N/A
BG 1997	16-20 Mar	21-27 Mar	2 Mar-4 Apr	5-10 Apr	N/A	11-17 Apr	N/A	N/A	N/A	N/A	N/A
KA 1998	9-16 Mar	17-23 Mar	24-31 Mar	31 Mar-7 Apr	8-13 Apr	14-21 Apr	22-27 Apr	28 Apr-5 May	N/A	6-12 May	N/A
BK 1998	13-18 Mar	19-26 Mar	27 Mar-2 Apr	3-8 Apr	N/A	9-22 Apr	N/A	N/A	N/A	N/A	
SG 1998	N/A	17-25 Mar	26 Mar-1 Apr	2-8 Apr	9-14 Apr	15-2 Apr	N/A	N/A	N/A	N/A	N/A
1998 phenology	12 Mar	19 Mar	27 Mar	3 Apr	10 Apr	17 Apr	N/A	29 Apr	N/A	7 May	N/A

APPENDIX III

Composition of phenology transect.

FAMILY	GENUS AND SPECIES	LOCAL NAME	N INDIVIDUALS ON TRANSECT
Mimosaceae	*Acacia sinuata*	Sige	1
Mimosaceae	*Albizzia odoratissima*	Sele	5
Combretaceae	*Anogeissus latifolia*	Bejja	14
Caesalpinaceae	*Bauhinia racemosa*	Kanchale	1
Bischofiaceae	*Bischofia javanica*	Neelalu	2
Bombacaceae	*Bombax ceiba*	Buruga	1
Euphorbiaceae	*Bridelia retusa*	Sironne	4
Anacardiaceae	*Buchanania lanzan*	Murki	3
Rubiaceae	*Canthium dicoccum*	Ambe	2
Rubiaceae	*Canthium parviflorum*	Doddakare	4
Barringtoniaceae	*Careya arborea*	Dolli	5
Caesalpinaceae	*Cassia fistula*	Kakke	4
Cordiaceae	*Cordia obliqua*	Selle	4
Fabaceae	*Dalbergia lanceolaria*	Buluga	6
Fabaceae	*Dalbergia latifolia*	Bite	7
Ebenaceae	*Diospyros montana*	Jagalaganti	2
Menispermaceae	*Diploclisia glaucescens*	Urianambu	1
Elaeocarpaceae	*Elaeocarpus serratus*	Bikkilu	1
Euphorbiaceae	*Emblica officinalis*	Nelli	8
Steculiaceae	*Eriolaena quinquelocularis*	Katale	4
Moraceae	*Ficus sp.*	Itchi	5
Burseraceae	*Garuga pinnata*	Arnelli	6
Euphorbiaceae	*Glochidion zeylanicum*	Hanase	5
Verbenaceae	*Gmelina arborea*	Kule	6
Tiliaceae	*Grewia hirsuta*	Dadsalu	5
Malvaceae	*Kydia calycina*	Bende	3
Lythraceae	*Lagerstromia parviflora*	Channangi	5
Euphorbiaceae	*Mallotus phillipensis*	Kesilu	6
Sabiaceae	*Meliosma pinnata*	Mustaka	3
Oleaceae	*Olea glandulifera*	Narvalu	2
Papilionaceae	*Ougenia oogenesis*	Kallumutuga	1
Lauraceae	*Persea macranta*	Karvadi	6
Fabaceae	*Pterocarpus marsupium*	Honne	8
Bignoniaceae	*Radermachera xylocarpa*	Udi	6
Rubiaceae	*Catunaregam spinosa*	Kare	8
Salicaceae	*Salix tetrasperma*	Byese	2
Sapindaceae	*Schleichera oleosa*	Sagade	1

Appendix III (cont'd)

FAMILY	GENUS AND SPECIES	LOCAL NAME	N INDIVIDUALS ON TRANSECT
Oleaceae	*Schrebera sweitenoides*	Gante	6
Sterculiaceae	*Sterculia villosa*	Chouve	5
Bignoniaceae	*Stereospermum personatum*	Padure	2
Myrtaceae	*Syzygium cuminii*	Nerale	6
Myrtaceae	*Syzygium malabaricum*	Neeranchi	5
Combretaceae	*Terminalia bellerica*	Tare	5
Combretaceae	*Terminalia chebula*	Arale	6
Combretaceae	*Terminalia crenulata*	Matti	13
Combretaceae	*Terminalia paniculata*	Uluge	9
Meliaceae	*Trichilia connoroides*	Kanagojjali	3
Caprifoliaceae	*Viburnum punctatum*	Thonde	3
Rubiaceae	*Wendlandia thyrsoidea*	Koli	1

APPENDIX IV

Tree species in BRT which belong to the genera of pollens found in fecal samples.

FAMILY	GENUS AND SPECIES	LOCAL NAME
Fabaceae	*Dalbergia lanceolaria*	Buluga
Fabaceae	*Dalbergia latifolia*	Bite
Eleaocarpaceae	*Elaeocarpus serratus*	Bikkilu
Eleaocarpaceae	*Elaeocarpus tuberculotus*	Kende
Tiliaceae	*Grewia hirsuta*	Udupe
Tiliaceae	*Grewia tiliaefolia*	Dadsalu
Combretaceae	*Terminalia bellerica*	Tare
Combretaceae	*Terminalia chebula*	Arale
Combretaceae	*Terminalia crenulata*	Matti
Lythraceae	*Lagerstromia parviflora*	Channangi
Myrtaceae	*Syzygium cuminii*	Nerale
Myrtaceae	*Syzygium malabaricum*	Neeranchi
Sapindaceae	*Schleichera oleosa*	Sagade
Sapindaceae	*Dimocarpus longan*	Kanasagade
Rubiaceae	*Canthium parviflorum*	Doddekare
Rubiaceae	*Canthium dicoccum*	Ambe
Rubiaceae	*Catunaregam spinosa*	Kare
Oleaceae	*Olea glandulifera*	Narvalu

APPENDIX V

Plant families and genera whose pollens were found in low frequencies in feces, and put into the category designated as "other" for pollen analysis.

FAMILY	GENUS
Acanthaceae	*Strobilanthes*
Anacardiaceae	*unidentified*
Apocynaceae	*Holorrhena*
Asteraceae	*Artemisia*
Asteraceae	*unidentified*
Bignoniaceae	*unidentified*
Bombacaceae	*Bombax*
Burseraceae	*Garuga*
Caesalpinaceae	*Bauhinia*
Caesalpinaceae	*Caesalpinia*
Caesalpinaceae	*Entada*
Celastraceae	*Maytenus*
Ebenaceae	*Diospyros*
Euphorbiaceae	*Bischofia*
Euphorbiaceae	*Glochidion*
Euphorbiaceae	*Mallotus*
Euphorbiaceae	*Phyllanthus*
Euphorbiaceae	*Securinega*
Mimosaceae	*Careya*
Palmae	*unidentified*
Poaceae	*unidentified*
Rosaceae	*unidentified*
Rubiaceae	*Ixora*
Rubiaceae	*Psychotria*
Sabiaceae	*Meliosma*
Ulmaceae	*Trema*
Verbenaceae	*Clerodendrum*

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