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Foraging Behavior of Honeybees (Hymenoptera: Apidae) on *Jatropha integerima* (Euphorbiaceae) in Upolu, Western Samoa

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Abstract—Honeybees foraging on monoecious *Jatropha integerima* primarily (90%) sought nectar, but some foraged on pollen. Staminate and pistillate flowers were not distinguished from a distance but close-up, bees rejected pistillate flowers even though these had abundant nectar. Apparently the nectar is less accessible in pistillate flowers. Individual bees characteristically foraged along one level of *J. integerima* canopies. Foraging rythmns of honeybees were regulated by closure of petal platforms. Bees were not effective pollinators becuase the stigma lobes were approximately 3 mm above the backs of the foraging bees.

Introduction

Foraging behaviors of insect pollinators are inextricably linked to the reproductive biology of their host plants. Therefore, a foraging system cannot be fully evaluated without reference to the floral anatomy, physiology and phenology (Proctor & Yeo 1972): specific attributes of entomophilous (insect-loving) flowering plants subtly influence foraging behaviors of anthophilous (flower-loving) insects. As a contribution to the fragmented knowledge of evolutionary biology and food ecology of insular insects, I have investigated the foraging behavior of honeybees, *Apis mellifera* L., on the ornamental shrub, rose-flowered Jatropha, *Jatropha integerima*. This bushy, monoecious native of Cuba is extensively grown in the two main islands of Western Samoa (13°S 173°W). The honeybees of the Samoan archipelago are also exotic: Perkins & Cheeseman (1928) stated that the bees were probably introduced by European settlers about the middle of the last century.

Materials and Methods

REPRODUCTIVE SYSTEM OF *J. INTEGERIMA*

The external morphology of flowers, pollen complement, residual pollen grains on shed petals and anthers, number of fruits, flowers and flower buds per inflorescence, number of leaves on flowering twigs recruited since the last flowering episode and the length of floral stalks were investigated on four shrubs at Siusega, three shrubs at Alafua Campus, School of Agriculture, USP, and one shrub at Pesega. These shrub sites were approximately 3–4 km apart.

Pollen grains on 3 randomly detached anthers per flower were counted in situ if they were loosely packed in the lateral grooves (Fig. 3D) or gently dislodged from such anthers onto grid paper using a needle and counted. Counting was done under a fiber optic light on a Wild M5A microscope using a hand tally counter. Grains on 3 petals per flower were counted in situ within 5 consecutive zones demarcated by horizontal lines of needle pricks on the petals.

Measurements of the external floral morphology emphasized the architectural display of staminate and pistillate reproductive structures and the location of nectary tissues on the flowers randomly picked from the eight *Jatropha* shrubs. Floral population characteristics and associated structures were measured on two of the Siusega shrubs. Similarly, continuous observation of floral recruitments from 1 Jan. 91 to 15 Feb. 91 was carried out on marked twigs on the same Siusega shrubs.

STUDY PLOTS

Knowledge of *Jatropha* reproductive biology was used to design investigations into the foraging behavior of honeybees at Siusega. Two study sites were established on the canopies of *Jatropha* shrubs: a natural arena on shrub I (hereby designated as Arena I) (Fig. 6A) and a manipulation arena on shrub II (Arena II) (Fig. 6B). Shrub I was located in the midst of four flowering ornamental shrub spp., two of which were also foraged on by the bees. Shrub II was located near several flowering herbs, of which none was a forage plant for the honeybee. Arena I was approximately 1.5 × 3 m containing 11 flowerheads. On 30 Dec. 1990 all the fruits, flowers and flowerbuds were counted. The number of new floral heads developed after the first count was noted and added to this pool. Arena II consisted of 7 blocks of flowers isolated by removal of all the neighboring flowerheads. Blocks 1–5 comprised 2 flowerheads (twigs) each, while block 6 had a flowerhead on a single twig. The apex (block 7) was made up of 8 twigs (flowerheads). The arena was established on 7 Jan. 91 and the blocks were kept separate by removal of newly developed flowerheads.

Not all the flowerheads in each arena were visible from each other. In Arena I, the following flowerheads were visible from each other: 6-3-8-4; 2-5-4; 1-2; 1-3; 1-6; 1-9. (Fig. 6A). In Arena II flowers in blocks 1, 2, 3 and apex were visible while those in blocks 3, 4, 5, 6 and apex were also omindirectionally visible from one another. Flowers in blocks 4, 5 and 6 were not visible from blocks 1 and 2 (Fig. 6B). A bee leaving an inflorescence had three options: ascend, descend or make horizontal flight in order to visit the nearest and/or next flower head. This was especially marked on Arena II (Fig. 6B).

FORAGING BEHAVIOR

Within these arenas, the following honeybee behaviors were noted: (1) resource (nectar vs. pollen) and flower type used, (2) time spent foraging on a flower, (3) number of flowers on a multiflowering head (> 2 flowers) visited by a bee before flying to the next head, (4) locomotive methods used between visitations within an inflorescence, (5) flight traffic between two inflorescences, and (6) visitation patterns as a function of both resource distribution and energy conservation. In this study, vertical flight was assumed to require more energy than horizontal flight (Kevan & Baker 1983). Diurnal foraging activities were also observed on 24, 25, 26 and 27 of January 1991. Observation began at 6 a.m. and was terminated at 6 p.m. or abandoned if 30 minutes elapsed without bee visitation.

MORPHOMETRICS

Foraging preferences could have resulted from differences in body sizes, or sizes of the foraging appartuses. To evaluate the importance of bee size the following dimensions were recorded: inter-antennal distance, lengths of tongue, labial palp, distal segment of maxilla (galea) and mandible, and width and length of pollen basket and the right wing pair. All the measurements were made with an eyepiece micrometer on a Wild M5A microscope.

Results

FLORAL SYSTEMS AND MORPHOLOGY

Virtually every *J. integerima* twig produced a cymose inflorescence, composed of either pure pistillate or staminate flowers, or a mixture (Fig. 1). Thus, there were three types of flower bearing twigs: staminate, pistillate and bisexual twigs. Comparatively, staminate flowers were more numerous than pistillate flowers on the trees used in this study (Fig. 2). Twigs grew similar numbers of leaves

Figure 1. Honeybee foraging on the nectar of a staminate flower of *Jatropha integerima.*

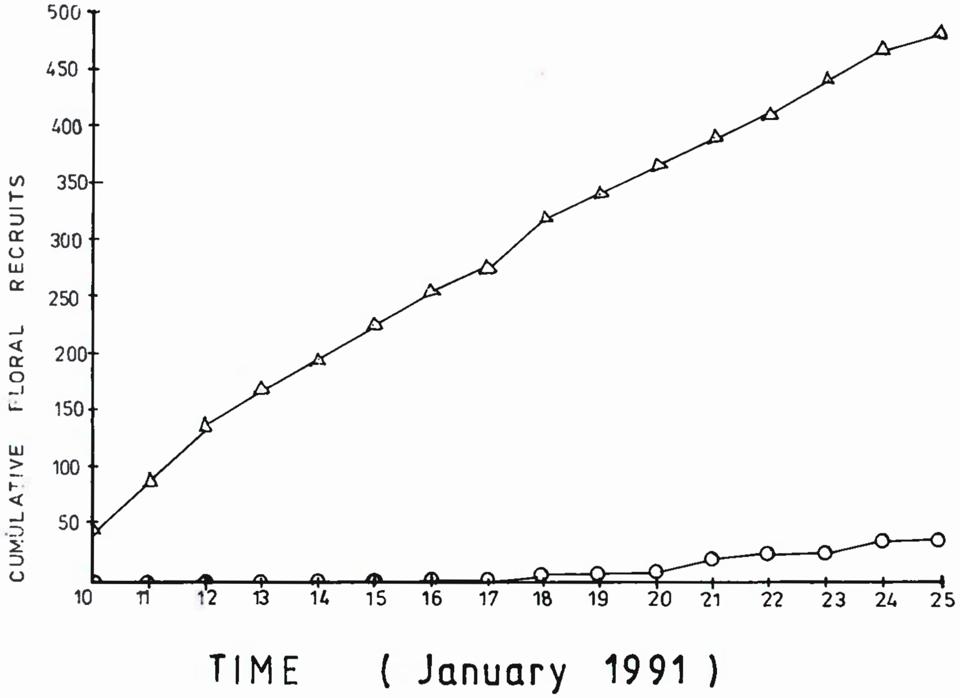

Figure 2. Cumulative number of female (O) and male (△) flowers on Arena I established on *Jatropha* shrub at Siusega, W. Samoa.

before setting identical inflorescences, althought pistillate flowers were generally borne on significantly shorter floral stalks (Table 1). Qualitatively, only the colors of petal and sepal were similar in both sexes: petal widths, platforms, nectarine tissues and hairs differed between the two sexes. First and second generation flowerbuds (Fig. 3A) developed in succession. Third generation flowerbuds (Fig. 3A) never matured into flowers before stalks fell off. On average, the inter-pistillate or -staminate distances of the open flowers on an inflorescence was 47.2 ± 21.2 mm (mean ± SD, n = 106). There was considerable overlap of petals amongst adjacent flowers which remained open diurnally for approximately 10–11 hours. On inflorescences bearing both sexes, pistillate flowers bloomed earlier than staminate flowers. Occasionally, one female flower of a bisexual inflorescence produced a fruit (Fig. 6A).

Staminate flowers have 10 stamens arranged in two equal (n = 5) whorls on a central shaft (column). Anthers of the upper whorl are recurved to form a platform (Fig. 3C) for pollen-foraging bees. The anthers of the lower whorl are displayed to create 5 inverted V-shaped windows through which nectar foraging can occur (Figs. 1, 3B). This structural design ensures that the pollen grains (dia = 0.1 ± 0.01 mm, Mean ± SD; n = 100) on the adjacent anthers were simul-

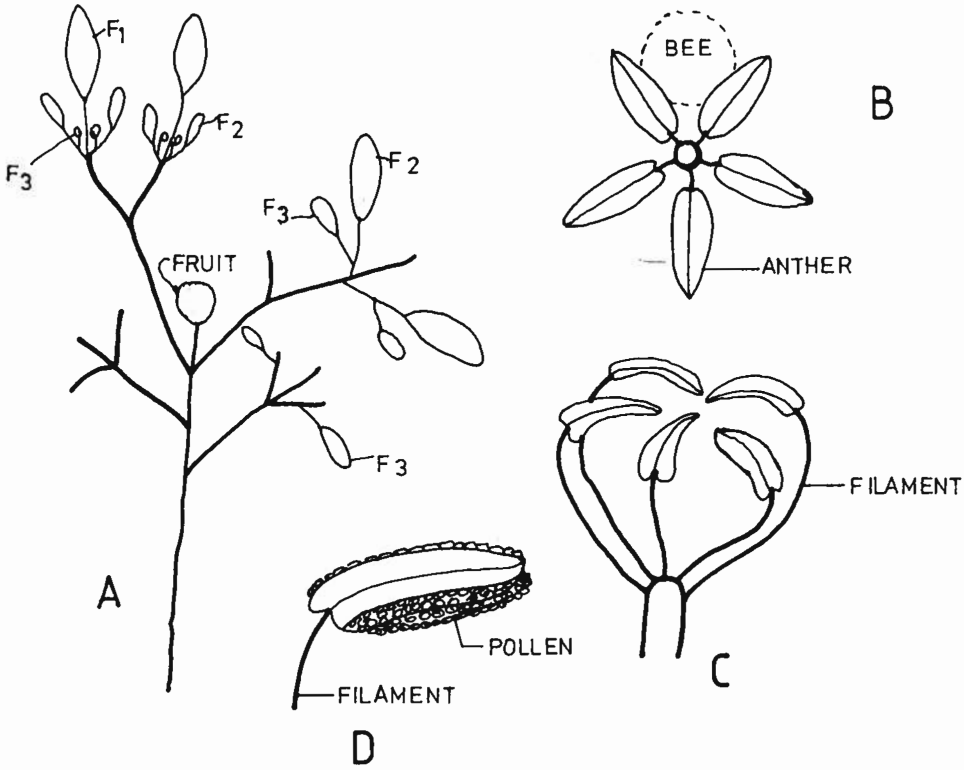

Figure 3. Diagrams of (A) cymose inflorescence, (F_1, first, F_2, second and F_3, third generation flower buds); (B and C), stamens of the lower and upper whorl respectively; and (D) pollen grains on the anther of *J. integerima*.

taneously in contact with the head and thorax of a foraging bee (Fig. 3B), where pollen grains are deposited. During foraging bouts, bees deposited substantial numbers of pollen grains on petals so that together with the quantity of grains left on the anthers, approximately 50% of pollen resources were wasted (Table 1).

The pistillate flower consists of a green naked ovary superiorly protruding above 5 red petals and a style. There are 6 reflexed, pointed stigma lobes each apically twisted about 30–45° to the left to face outside. White hairs borne on the bases of petals coalese into a ring at the bottom of the ovary. A similar, but more profuse ring of hairs is located at the base of the shaft bearing the stamens in staminate flower. The function(s) of these hairs is unclear. At first they appear to obstruct the gap leading to the nectarine tissues on the receptacle. But the length and chaetotaxy (arrangement of hairs on) of the tongues of some bees (see later) and presence of short-tongued foragers among insect visitors (eg. Diptera) suggest that they are probably nectarine hairs (Proctor & Yeo 1972), which draw and present nectar to the foraging insect from the deeply set tissues.

Table 1. Floral characteristics of *Jatropha integerima*.

Parameters	Staminate	Pistillate	F-Value	df
1. No. pollen grains on				
live anthers	419.6 ± 191.5		38.61***	1,68
shed anthers	162.5 ± 149.0			
shed petals	244.2 ± 184.3(n = 12)			
2. Ht. above nectarine hairs				
Lower anthers (mm)	7.9 ± 2.2	—		
Stigma (mm)	—	11.1 ± 0.5	16.43***	1,18
3. Petal				
length (mm)	22.8 ± 1.7	21.6 ± 1.7	2.23	1,18
width (mm)	14.9 ± 0.7	13.3 ± 1.4	10.29**	1,18
4. No. flowers	2.8 ± 1.8	1.8 ± 0.9	2.56	1,41
5. No. flower buds	21.5 ± 12.7	27.6 ± 4.9	1.76	1,41
6. Floral stalk length (cm)	15.4 ± 0.7	13.2 ± 0.7	28.37***	1,11
7. No. leaves on floral twigs	9.4 ± 0.9	9.0 ± 0.9	0.59	1,11

, * Significantly different at $P < 0.01$ and $P < 0.001$ respectively, one way ANOVA.

The relative positions of stigmas and anthers above the nectarine hairs were significantly different (Table 1). Clearly, the pollen transfer/contact ratio (1.4, Table 1) suggests that the dorsum of a bee was too low to transfer pollen.

FORAGING STRATEGY

A significant ($X^2 = 88.81$, df = 15, $P<0.05$) percentage of every sample of honeybees foraging at Siusega between 10 Jan. 91 to 25 Jan. 91, rejected pistillate flowers. Bees approaching pistillate flowers behaved in two distinct ways: Few alighted on their petals while the majority rejected them outright. Of those landing, only a few proceeded to forage beneath the ovaries and the rest flew off very quickly without surveying the flowers. This rate of rejection was difficult to explain. Apart from the obvious absence of pollen in these flowers, the petals of pistillate flowers were slightly smaller (Table 1). But it is doubtful (Kevan & Baker 1983) whether this was the cause for such massive rejection of pistillate flowers. Staminate flowers were favored. But even on these flowers, honeybees never foraged indiscriminately. Over 90% of bees foraged predominantly on nectar and of the rest, some foraged exclusively on pollen while others foraged on both nectar and pollen.

I was unable to ascertain whether floral visitations on multiflowering inflorescences were random. Very rarely were all the flowers on a head visited by a bee before it flew off to the next inflorescence (Fig. 4), suggesting that exploitation of floral resources on such inflorescences varied significantly ($F_{0.05\,[6,144]} = 14.95$) amongst bees in spite of a marked preference to visit heads with 2 - 6 flowers (Figs. 4 and 5). Bees used specific exit and entry points into the foraging arenas

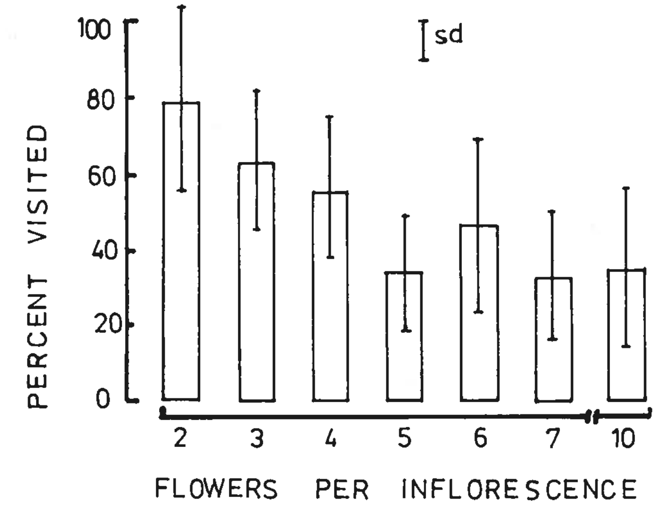

Figure 4. Mean percentage of flowers on an inflorescence visited by individual bees before departing to either forage on the next inflorescence or leave the study Arena II.

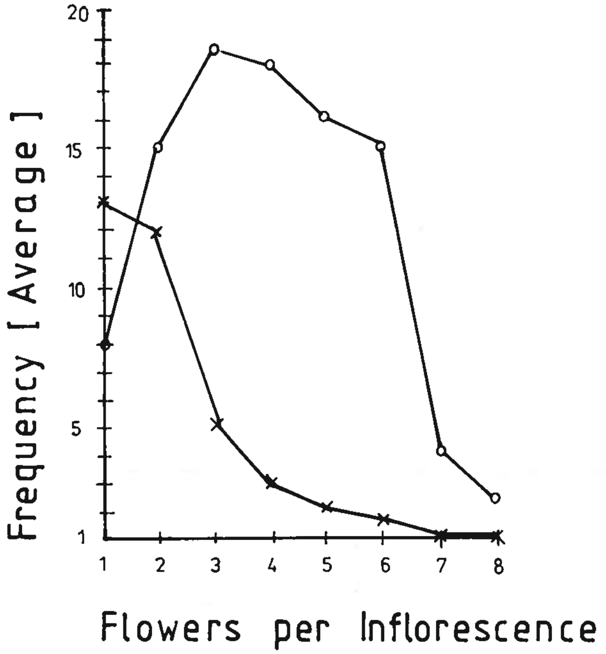

Figure 5. Average frequency visits (0) to inflorescences (x) with varying number of flowers between 5 Jan. 91 and 10 Jan. 91.

throughout the study period. The majority of bees entered and exited arena I at floral heads 1 or 5 and 1 or 4 respectively (Fig. 6A). Similarly, bees frequently entered arena II at floral blocks 1, 2 or Apex and exited at block 1 or 6 (Fig. 6B).

Points of entry more or less determined the directions of foraging bouts (e.g. Fig. 6B). The decision to visit a floral head was apparently based on three factors: (i) the desire not to double back on a foraging path (Fig. 6, dotted lines), (ii) the proximity and/or visibility of inflorescences along a foraging track ($r^2 = 10.5$, $P<0.001$, $n = 94$) and (iii) angle of inclination of the inflorescence from the bee's position (Fig. 6). Nevertheless, bees apparently used these determinants selectively. For example, for the flowers on horizontal plane, a combination of factors 1 and 2 was important. Similarly, irrespective of floral numbers, steep gradients discouraged bees on most occasions so that in real term, bees foraged along one level of the canopies (Fig. 6). This was maintained whether bees were foraging at the bottom, mid or top crowns. These stereotyped behaviors were disrupted when an individual bee encountered intra- or inter-specific competitors (Epila-Otara, unpubl. data), but such encounters rarely occurred because very few bees ever shared an inflorescence. Flight paths for these visitations were also variable. Bees descending to lower flowers literally 'dropped' out of the canopy and looped back to such inflorescences. And when ascending, they flew through the caopy in a zigzag manner. Otherwise bees moving between horizontally located flowers made straight flights and never reversed the directions of such chosen paths before visiting all the visible inflorescences ahead of them; especially if such inflor-

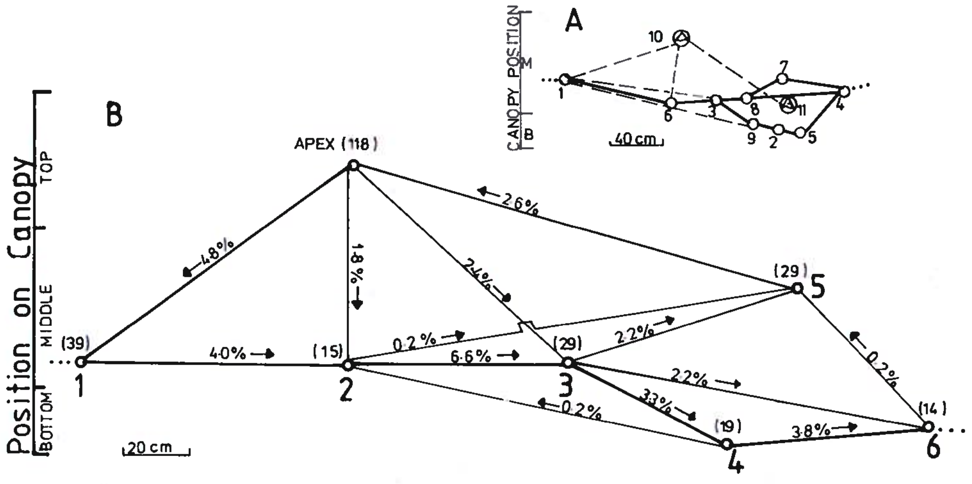

Figure 6. Honeybee foraging patterns on *Jatropha* shrubs at Siusega, W. Samoa. A, Arena I: dashed and solid lines represent respectively, the least and most used foraging tracks, and encircled triangles represent inflorescences located in the midst of thick foliage growth. B. Arena II: arrows show directions of differential percentage preference between blocks and figures in brackets are floral totals observed on 20 days between (7 Jan. 91 and 15 Mar. 91). Dotted lines were the most used exit paths.

escences were on straight lines (e.g., 6-3-8-4; 2-5-4 of Arena I and blocks 1-2-3-5 on Arena II) (Fig. 6).

Flight approach to staminate flowers varied according to the resource exploited. Pollen-foraging bees approached and hovered over every flower while raking pollen grains gathered from previous flowers into baskets before alighting onto the yellow antheral platform (Fig. 3C). Nectar-foraging bees flew and landed straight onto the upper surfaces of petals. Few landed on the leaves, back of petals or on the flowerbuds. However, although once within the head, nectar-foragers predominantly accomplished interfloral visitations through short flights, they occasionally walked from flower to flower.

TIME BUDGET

On an ideal day, honeybees foraged on *J. integerima* from about 6:30 a.m. until the flowers started to close. Floral closure was never a precise physiological event. On some days it began as early as 4:00 p.m. and ended before 5:00 p.m. while some flowers remained open until 6:00 p.m. Regardless of the timing of floral closure, foraging peaked between 11:00 a.m. and 12:00 noon. During the day bees repeatedly foraged on the open flowers and groomed themselves occasionally. On average bees spent 4.4 ± 2.0 sec (Mean ± SD, n = 32) per flower. In the course of a typical day, a bee visited a large number of flowers, (Epila-Otara Unpubl. data) collecting approximately 24 mm^3 of pollen in a single foraging bout. Obviously, such pollen loads, although bigger than the suface area of the baskets (see below) were effectively secured in place by flexible hairs fringing the baskets.

MORPHOMETRICS OF FORAGING APPARATUSES

The glossa (tongues) of honeybees were of two types: the long hairy (5.6 ± 0.37 mm, Mean ± SD; n = 20) and the short hairless (4.1 ± 0.26 mm, Mean ± SD; n = 15). Surprisingly, however, the accessories of both types of glossa [ie. the mandibles (2.1 ± 0.07 mm, Mean ± SD; n = 18), galea (3.5 ± 0.2 mm, Mean ± SD; n = 35) and labial palps (3.7 ± 0.72 mm, Mean ± SD; n = 35)] were remarkably uniform in lengths. Similarly, differences in the bee tongues were never reflected in the sizes of wings (widest parts; 3.6 ± 0.21 mm and 2.1 ± 0.09 mm, lengths; 11.2 ± 0.25 mm and 7.8 ± 0.22 mm, Mean ± SD; n = 36, for fore and hind wings respectively), transantennal distances (0.98 ± 0.06 mm, Mean ± SD; n = 17), or pollen baskets (1.4 ± 0.08 × 4.4 ± 0.13 mm, Mean ± SD; n = 35). And indeed, the G-test (Sokal & Rohlf 1973) for goodness of fit ($G_{adj} = 0.014$, df = 1, $P > 0.05$) showed that tongue lengths never influenced the type of resources (nectar or pollen) the bee exploited.

Discussion

The basis for the bees' discrimination between pistillate and staminate flowers is difficult to diagnose. From a distance, honeybees approached pistillate flowers in the same manner they would the staminate flowers, only to reject them on close inspection. I speculate that the discrimination was probably based on morphological differences. Firstly pistillate petals were comparatively smaller and duller (Table 1). But above all, the central yellow patch; the equivalent of the platform of the staminates (Fig. 3C) is vividly missing in pistillates. Instead, this central attraction is replaced by a green ovary bearing a set of 6 red stigmas located approximately 3 mm above the dorsum of the visiting bee. The double-grained nectarine tissues of pistillates suggest that these flowers have far greater quantities of nectar than the staminates. But even bees which visited pistillate flowers failed to exploit their nectar resources effectively probably because (i) the ovaries obstructed them and (ii) the scanty nectarine hairs were unable to absorb and present nectar to them in adequate amounts. Wasps, flies and ants apparently exploited these sources more than the bees (Epila-Otara unpubl. information). Thus, staminate flowers provide both more accessible nectar and the opportunity to forage on pollen. Nevertheless, the bees demonstrated a marked polarization in the way they exploited the resources of these flowers on any single foraging bout. Individual bees foraged on either pollen or nectar almost exclusively, and rarely on the two resources concomittantly. The biological significance of this feeding strategy is not quite clear. Is it in some way related to the specific nursing roles individual bees play on their return to the hive? Similarly, the individuals which foraged on pollen did so only from the upper antheral whorls where they normally alighted.

Within the plots established on the shrub canopies at Siusega, bees encountered variable number of uneven-aged flowers, and qualities of pollen and nectar resources each day. But bees hardly changed their basic foraging strategies (Wells & Wells 1984, Adler 1987, Faegri & van der Pijl 1979, Proctor & Yeo 1972). The majority of the bees persistently approached each respective shrub from the same direction, and entered and exited the arenas at specific points (Fig. 6), suggesting that they were probably nest mates. Pollen-foraging bees alighted directly on the antheral platforms (Fig. 3C), spent about 4 seconds on each flower and flew from flower to flower. Bees foraging on nectar landed on the petals first and walked to forage at the nectar for a similar period of time before flying off to visit another flower. Bees rarely walked between flowers of an inflorescence (Wells & Wells 1984). And bees rarely reversed their foraging paths to revisit flowers visited a while ago. This raises the question whether bees know both the locations and quality of every flower on an inflorescence (Figs. 4 and 5). Although no answer was specifically sought for in this study, Wells et al. (1983) and Wells & Wells (1983, 1984) have clearly demonstrated that individual bees are capable of learning location of flowers and constantly forage on such flowers irrespective of their reward volumes and/or values. A similar trait was discovered among hummingbirds (Miller et al. 1985).

The reason(s) why especially the nectar-foraging bees rarely attempted to conserve energy by walking across the overlapping petals was not investigated. Indeed this mystery remains a puzzling paradox (Houston 1990) in the sense that the same bees exhibited a high desire for energy conservation by predominantly foraging along the latitude of the *Jatropha* canopy, while occasionally 'dropping' to forage on the inflorescences lower down these latitudinal paths (Fig. 6). Similarly, although ambient conditions influence foraging behaviours of pollinators directly (Wilmer 1983, Mammod et al. 1989) or indirectly via the nectar secretory systems (Corbet 1978, Adler 1987), the foraging regimes of bees on *Jatropha* were also regulated by the closure of petal platforms. So long as the flowers remained open, bees continued to forage even as late as 6:30 p.m.

Two distinct tongue variants were discovered in the bee populations foraging on *Jatropha* in Upolu, Western Samoa. Tongues were either short and hairless or long and hairy. The biological significance of the differences was not rigorously investigated during this study. Nonetheless, available data suggest that tongue length was probably not a decisive determinant of the floral resources the bee exploited. Undoubtedly, the chaetotaxy of glossa is an adaptation for nectar-foraging (Proctor & Yeo 1972) and the differences in glossa lengths are connected with nectar exploitation. That is, bees apparently exploit *Jatropha* nectar from two sources; nectar on nectarine hairs and nectar from secretory tissues themselves. Short, hairless tongues are predominantly adapted for sponging and siphoning nectar from the hairs while long, hairy tongues use hairs to imbibe nectar as explained by Proctor & Yeo (1972).

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References

Adler, P. H. 1987. Temporal feeding patterns of adult *Heliothis zea* (Lepidoptera:Noctuidae) on pigeonpea nectar. Environ. Entomol. 16, 424–427.

Corbet, S. A. 1978. Bee visit and the nectar of *Echium ovulgare* L and *Sinapis alba* L. Ecol. Entomol. 3, 25–37.

Faegri, K. & L. van der Pijl, 1979. The Principles of Pollination Ecology, 3rd edition. Pergamon Press, Oxford. 244 pp.

Houston, A. I. 1990. Parent birds feeding young—to walk or to fly? J. Theoret. Biol. 142, 141–147.

Kevan, P. G. & H. G. Baker, 1983. Insects as flower visitors and pollinators. Ann. Rev. Entomol. 28, 407–453.

Mamood, A. N., D. T. Ray, G. D. Waller & J. H. Martin, 1989. Foraging activity of honeybees (Hymenoptera:Apidae) on guayule. Environ. Entomol. 18, 1032–1034.

Miller, R., S. Tamm, G. D. Sutherland & C. L. Gass, 1985. Cues for orientation in hummingbird foraging: color and position. Can. J. Zool. 63, 18–21.

Perkins, R. C. L. & L. E. Cheesman, 1928. Insects of Samoa and other Samoan terrestrial Anthropoda. Part V. Hymenoptera, Fasc. I. pp 1–58. BM (NH), London.

Proctor, M. & P. F. Yeo, 1972. The Pollination of Flowers. Taplinger Publishing Company, New York 418 pp.

Sokal, R. R. & F. J. Rohlf, 1973. Introduction to Biostatistics. W. H. Freeman and Company, San Francisco, 368 pp.

Wells H. & P. H. Wells, 1983. Individual honeybee foraging: optimal diet, minimum uncertainty or individual constancy behavior? J. An. Ecol. 52, 827–836.

Wells, P. H. & H. Wells, 1984. Can honeybees change foraging patterns? Ecol. Entomol. 9, 467–473.

Wells, H., P. H. Wells & D. M. Smith, 1983. Ethological isolation of plants. 1. Colour selection by honeybees. J. Apicult. Res. 22, 33–44.

Willmer, P. G. 1983. Thermal constraints on activity patterns in nectar-feeding insects. Ecol. Entomol. 8, 455–469.

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