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THE IMPORTANCE OF POLLINATOR BEHAVIOR IN THE REPRODUCTIVE BIOLOGY OF TROPICAL TREES

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ABSTRACT

Most pollination studies in the tropics have dealt with mechanisms of pollen pick up and deposition by anthophilous animals; few have been concerned with intra-and inter-plant flow of pollen via these vectors. Herein, we examine the behavioral patterns of flower-visiting bats and bees with respect to the role they may play in the outcrossing of widely spaced tropical trees. Suggestions for future studies regarding the relationship between pollinator behavior and outcrossing are offered.

RESUMEN

La mayoría de los estudios sobre polinización en los trópicos han abordado los mecanismos de recolección y deposición de polen por los animales antóforos, pero pocos se han abocado con el flujo de polen intra e inter individuos vegetales a través de estos vectores. En este trabajo, se examinan los patrones de comportamiento de los murciélagos y abejas que visitan flores con respecto al papel que puedan desempeñar en la cruza de árboles tropicales ampliamente esparcidos. Se sugieren estudios futuros enfocados a las relaciones entre el comportamiento del polinizador y el cruzamiento de los árboles.

INTRODUCTION

Pollination studies in the tropics have been largely concerned with the mechanisms of pollen pick up and deposition on flowers (see Frankie et al. 1973 for references). Few studies have dealt with intra— and interplant foraging patterns of pollinators as they relate to outcrossing. Exceptions include the studies by Frankie et al. (1976) on bees in Costa Rica; Gilbert (1975) on butterflies in Trinidad; Baker (1973) and Heithaus et al. (1974) on bats in Costa Rica; Janzen (1971) on bees in Mesoamerica; Linhart (1973) and Stiles (1975) on hummingbirds in Costa Rica.

The following discussion will consider some of the movement patterns of Old and New World bats and the foraging patterns of Central American solitary bees as they relate to outcrossing in tropical trees.

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BAT STUDIES

The usually-accepted syndrome of flower-characters typifying pollination by bats (for example, Faegri and van der Pijl 1971, p. 154) was set up on the basis of experience in the Paleotropics where the bats that visit flowers all belong to the suborder Megachiroptera. However, this suborder of bats is missing from the Neotropics and their place is taken by smaller bats of the suborder Microchiroptera. Recent studies (for example, those by Vogel 1968-9; Baker 1970, 1973; Heithaus et al. 1974) have shown that the behavior of these bats and consequently the structure and physiology of the Neotropical bat-pollinated flowers, do not fit exactly with the syndrome built up on Old World experience.

Thus, the anthophilous Megachiroptera tend to be "opportunists", concentrating their attention on a single freely flowering tree or on a small number of trees in close proximity to each other (cf. Baker 1973, pp. 153-155). In addition to published accounts (Baker and Harris 1957, 1959; Harris and Baker 1958, 1959; Baker 1973, pp. 153-155, etc.), observations and photograhps of *Pteropus tonganus* (Megachiroptera-Pteropinae) in Fiji and "flying foxes" of the same genus in Australia reveal the same concentration at any one time on a single tree or group of trees (Baker, unpub.). These bats are pure vegetarians. By contrast, the anthophilous Microchiroptera of the Neotropics are, to varying degrees, insectivorous and they spend some of their time catching insects, as well as getting nitrogenous food material from pollen or fruit. But their greater agility, and retention of a sonar guidance-system. have made it possible for them to adopt to varying degrees a "trap-lining" habit. Singly (Baker 1973), or in groups (Heithaus et al. 1974), they travel a fixed path between trees, epiphytes or vines that bear only a few flowers (or even only one) on any particular night, but may continue to flower for weeks or even months.

Moving rapidly on their rounds, the anthophilous Microchiroptera make only fleeting contact with the flowers that they visit. An open cup shape is the most appropriate for the flowers in this case, with anthers and stigmas in such a position that the head of the bat will brush against them as it makes its fleeting contact. This is to be seen in *Markea neurantha* (Solanaceae) (tentatively identified erroneously as *Trianaea* sp., of the same family, in Baker 1973). In *Mucuna andreana*, the flowers are explosive and the bat is showered with pollen when it touches a newly mature flower. By contrast, many flowers and inflorescences of Paleotropical trees are constructed so that the bats are encouraged to land and grasp the flowers (cf. *Parkia clappertoniana*, Baker and Harris 1957, and *Ceiba pentandra*, Baker and Harris 1959).

Only a few microliters of nectar will be available at any moment in such Neotropical bat-flowers as those of *Mucuna* and *Markea*, a striking difference from the usual idea of abundant nectar production based on such Paleotropical bat-flowers as these of *Ceiba pentandra* (0.3 milliliters per flower, in Ghana, Baker, unpub.), *Musa* (0.15 milliliters per flower, Percival 1965) and *Parkia clappertoniana* (up to 5 milliliters per flowerlike inflorescence, Baker and Harris 1957). This difference is probably related to the much shorter period of time during which Microchiroptera are at the flowers. However, the amounts of nectar such Neotropical bat-flowers as those of *Ceiba pentandra* (as it occurs in the New World) and *Ochroma pyramidale* (both Bombacaceae) and *Parkia* spp. (Leguminosae mimosoideae) are considerably more like those of their Paleotropical relatives and this should be examined in relation to the history of the evolution of bat-pollination in hemispheres (see discussion in Baker 1973, pp. 151-158). At least as far as *Ochroma* is concerned, concentrated attention to a single tree, on the Paleotropical, Megachiroptera model, does not seem to be the rule despite the abundance of nectar available.

Recent discovery that nectars of most flowers contain significant quantities of amino-acids (Baker and Baker 1973) as well as the familiar sugars, means that Paleotropical and Neotropical bat-flowers should be examined to see whether biochemical rewards to the two kinds of visitors are different. This is now being done.

In both hemispheres, the pollination of any flower must be looked at in an ecosystem context. The way toward this has been pointed by observations such as those by Baker, et al. (1971) on the bat-pollinated species *Ceiba acuminata,* the thorn-scrub of north-western Mexico. Here, "irrelevant" small flower-visitors (Hymenoptera and Lepidoptera), which are ineffective as pollinators of the large *Ceiba* flowers are, nevertheless, nourished by them at the end of the dry season when little else is in flower and remain active in the ecosystem to perfom valuable functions as pollinators of other plant species at other seasons. Such "involuntary altruism" should be looked for carefully elsewhere.

BEE STUDIES

In a recent study by Frankie et al. (1976) in the dry forest in Costa Rica, foraging patterns of solitary bees were examined in relation to certain aspects of the floral biology of the leguminous tree *Andira inermis* (Swartz) HBK. Because trees of this species are self-incompatible (op. cit.), the observed foraging patterns involving inter-tree movement assumed particular importance in providing transport of pollen in this obligate outcrossing species. In addition to this species, many others in the same forest (belonging to several families) have been found to possess breeding systems that also demand outcrossing (Bawa 1974).

One of the unanswered questions of the Frankie et al. (1976) investigation is why the bees expend energy to move from one apparently inexhaustible resource site (one tree) to another. In the same study (op. cit.), 70 different bee species (each species varied in relative abundance) were collected on *A. inermis* during the investigation period. It seems possible that it is the concentration of such a large number ob bees (with all the consequent interactions) that may determine the movement patterns. *Energetics*: In the case of *Andira inermis,* simultaneous foraging of a wide variety of bee species results in the gradual diminution of pollen and nectar resources through time. Owing to inherent behavioral differences among visiting bees, it seems reasonable to assume that certain species will respond before others to the decline in floral resources. Responses may be manifested in increased movements of bees on the same tree in order to obtain the necessary quantity of resources. Interactions of this sort are thought to increase the inter-plant movement of honeybees in field crops (Levin 1961; Weaver 1956, 1957). In Butler's (1945) work on honeybees, he has stated that, . . . "provived the degree of competition is sufficiently great, there is a further population of 'wandering bees' which have not yet settled down in any particular area" . . . "which is composed mostly of young bees which have only just reached the foraging age, that are responsible for the cross-pollination of the fruit trees". Jaycox (1964) made a similar observation on honey bee behavior in apple orchards. With regard to foraging behavior of solitary bees on *A. inermis*, if it is energetically feasible, the lowering of a resource by competing insects may cause certain species to seek other food sources by increasing their search areas to include adjacent trees. In California, Thorp (1969, pp. 11-12) documented a significant increase in foraging area of marked *Andrena chalybaea* (Andrenidae) females on flowers of *Camissonia ovata* as the plant's pollen resources were lowered through the day. Free (1970, pp. 43-46) provides a limited discussion of the relationship between be foraging area and floral resource diminution.

Heinrich and Raven (1972) and Anonymous (1970) discuss from an energetics standpoint how "flower robbing" by certain visitors (an activity which also lowers floral resources) could cause increased visitation on the part of the "actual" pollinators. Heinrich and Reven (1972) call upon data developed in pollination studies of red clover (Hawkins 1961; Morrison 1961) to support their hypothesis.

In addition to increased movements possibly resulting from declining resources, there are intra- and inter-specific interactions among bees that may also cause inter-plant movement of pollinators. To date, two principal kinds of behavior have been recognized. The first of these deals with group foraging by solitary bees, while the second is concerned with territoriality-related behavior. Both of these behavioral patterns result in interactions that may cause bees to leave one resource site in search of another. This kind of movement may also play a role in the outcrossing of a tree species.

Group Foraging: Three species of anthophorid bees have been observed foraging in close aggregations over the crowns of several Costa Rica dry forest tree species (Table 1). Foraging groups of *Gaesischia exul* and *Centris aethyctera* range in number from 10 to 100 bees. In the case of *C. adani*, aggregations of up to 300 bees have been observed on *A. inermis.* The approximate area occupied by a given group of bees ranges from 0.5 m to 2 m in diameter.

The aggregations move quickly and continuosly from one cluster of flowers to another. The movement takes the form of a smooth-flowing wave in which there is a rather rapid dissipation in numbers from one flowering branchlet to another. These "waves" (which are best seen by continually observing one branchlet for long time periods), are primarily composed of male bees as evidenced by several collections taken from each tree. The exception to this pattern is observed in *Piscidia carthagenesis* where females of *G. exul* predominate over males.

Size and number of "waves" per tree appear to be partly a function of tree crown size and degree of bloom. In general, mature trees in full bloom support a greater number of waves, each with a greater number of bees per aggregation. However, it is of interest that on some flowering individuals (small or large), aggregations have not been observed. On mature forest trees, one to three 'waves" of a single species can be observed, and usually only one species enters into group foraging on a given tree crown.

The particular significance of these foraging aggregations to anthecology may lie in their influence on non-grouped visitors to the same tree (Fig. 1). The general stir caused by these groups as they move over the tree surface in "waves" may provide impetus for at least the more sensitive bee species (and possibly sensitive individuals within a

TABLE 1

ANTHOPHORID BEE SPECIES OBSERVED FORAGING IN GROUPS ON DRY FOREST TREES IN GUANACASTE PROVINCE, COSTA RICA, 1972-73

Tree Species	Gaesischia exul	Centris (Centris) adani	Centris (Centris) aethyctera
Tree Species	*Gaesischia exul*	*Centris (Centris) adani*	*Centris (Centris) aethyctera*
Andira inermis		+	
Caesalpinia eriostachys	+		
Dalbergia retusa	+	+	
Myrospermum fructescens	+		
Piscidia carthagenensis	+[a]		+
Pterocarpus rohrii	+		

[a] Male bees made up the majority of individuals in the aggregations on all tree species with the exception of *P. carthagenensis*. In this species females predominated over males in the foraging aggregations.

given species) to move to other food sources such as neighboring conspecific trees. Behavioral interactions of this sort would be productive in outcrossing provided that non-grouped bees were not unduly harassed to the point where they were continually displaced to other trees.

Territoriality-related Behavior: Territoriality and related aggressive behavior is well known in certain groups of anthophilous animals (for example, bees, butterflies and hummingbirds). However, the relationships of territoriality-related behavior to tropical plant reproductive biology has been only briefly examined. In Costa Rica, Linhart (1973), Stiles (1974), and Stiles and Wolf (1970) describe how clumped food plants of certain hummingbird species may encourage the establishment of hummingbird territories that lead to restricted pollen flow. Dodson (1962) and Dodson and Frymire (1961) reported that males of a *Centris* species in Ecuador set up territories that overlap with the habitat of *Oncidium hyphaematicum* and *O. planilabre* (Orchidaceae). Occasionally, these bees mistake orchid flowers for animal intruders and attack them, bringing about pollination. Recently, one of us (Frankie) initiated studies in the dry forest of Costa Rica on territorial behavior in male *Centris* as it relates to plant reproductive success. Preliminary results suggest that interactions between patrolling males and flower visitors, which result in harassment of reward-seeking visitors, may cause some individuals to move to other resources (neighboring conspecific trees)

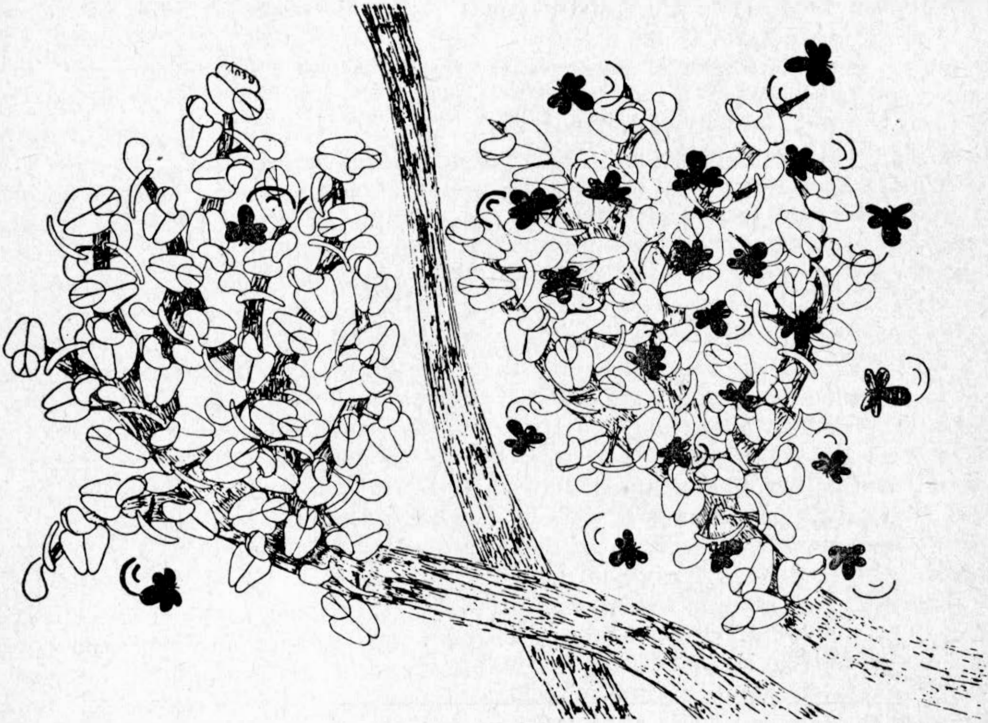

Fig. 1. Artist's conception of group foraging behavior of *Gaesischia exul* on *Pterocarpus rohrii.* Banded bees constitute a foraging group, while nonbanded bees are visiting flowers independently.

thereby increasing chances for outcrossing.

In the Costa Rican dry forest, males of three *Centris* species (*C. eathyctera, C. adani* and *Centris inermis*) regularly set up territories within or to the outside of crowns of flowering trees. Behavior of this sort by one or more of these solitary species has been observed regularly on *Andira inermis, Caesalpinia eriostachys, Cochlospermum vitifolium, Piscidia carthagenensis* and *Pterocarpus rohrii.* These territories generally involve the patrolling of small, well-defined areas interspersed with frequent landings on prominent branches. Occasionally, some individuals maintain patrols for extended time periods without coming to rest. Janzen (1964) observed that territorial xylocopid bees in Mexico may hover for extended periods (several minutes) while patrolling small areas.

Conspecific male interactions. Interactions between males of a single *Centris* species generally involve the chasing away of male intruders by patrolling bees. This activity can occur over a period of three to four hours (A. M.) during which time several intruders may be chased away. However, on some occasions, the bees engage in seemingly nonaggressive pursuing displays that last several minutes before one of the participants[1] leaves. This latter kind of behavior has also been observed in male

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[1] It is unknown if the patroller or the intruder remains after such an interaction occurs.

euglosine bees (Frankie 1965, Janzen, pers. comm.).

It is unclear at this time how *Centris aethyctera* and *C. adani* can interact in concert with other males in group foraging behavior in some circumstances and in other situations engage in territorial activity against conspecific males. This apparent conflict in behaviors require further investigation.

Interactions with other than conspecific males. Patrolling males interact with non-conspecific male and female bees (all species) by "buzzing" them continually as they visit flowers that are included within the territories. Owing to difficulties in observing resulting male flight patterns, it is unclear at present as to how intruding males react to this treatment. In the case of females, investigative "buzzing" causes most individuals to merely move to the opposite side of the same tree where they continue to forage. However, studies on young trees of *Cochlospernum vitifolium* (a pollen source producing a limited number of flowers daily) reveal that occasional male-female encounters result in disturbance of the female to the point where she completely leaves the tree canopy. This sometimes occurs when the female has collected pollen from only a few flowers.

An investigation is presently in progress in Costa Rica to quantify this interaction since it may prove to be important in outcrossing of this and other tropical plants. It is also of interest that several examples of this kind of aggressive male behavior[2] exist in the literature on solitary bees; however, its possible function in plant reproductive biology appears not to have been considered (Janzen 1966; Linsley and Hurd 1959; Michener 1953; Rau 1929; Rozen 1958, 1970; Sakagami and Camargo 1964; Stephen et al. 1969; Thorp 1969; Vleugel 1952).

In addition to energetic relationship, group foraging and territorial behavior, there are no doubt other behavioral patterns of anthophilous visitors which may play a role in inter-plant movement of the "actual" cross-pollinators. For example, it would be of interest to know what kinds of interactions result from the interplay of different levels of bee aggression (that is, simple physical aggression which is not related to either group foraging or territoriality), which are inherent among the numerous species visiting massively flowering tropical trees. It seems conceivable that the large aggressive bees may displace some smaller species to less competitive sites (for example, to branches on the same tree with sparsen blooms or to adjacent conspecific trees).

CONCLUSION

Now that investigations of anthecology are being conducted on an ecosystem basis, complexity beyond anything recognized even a few years ago is being revealed. In addition to behavioral studies of flower visitors at the flower, other kinds of behavioral patterns are being examined to evaluate how these anthophilous activities may affect pollen flow among widely spaced tropical plants. Clues to the existence of unique pollinator behaviors are being sought through simultaneous investigations of the plant breeding system, floral behavior and pollinator behavior (Bawa *et al.*, in prep.; Frankie *et al.* 1976). An intensive study of this sort by L. Gilbert (1975) in Trinidad on *Passiflora, Angu-*

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[2] P. F. Torchio (pers. comm.) has observed male alkali bees, *Nomia melanderi* Cockerell, patrolling particular flowering patches of alfalfa in Oregon and sweet clover in Utah in sufficiently large numbers to prevent successful visitation of these plants by females.

ria and *Gurania* pollination by *Heliconius* butterflies has already begun to yield important information on the vast array of animal/plant interactions meaningful to the reproductive success of both groups of organisms.

DISCUSION

Most pollination studies in the tropics have dealt with mechanisms of pollen pick up and deposition by anthophilous animals; few have been concerned with the intra- and interplant flow of pollen via these vectors. In this paper, behavioral patterns of flower-visiting bats and bees are examined in light of the role they may play in the outcrossing of widely spaced tropical trees.

With regard to bats, the anthophilous Megachiroptera of the Paleotropics tend to be "opportunists", foraging on a single freely flowering tree or on a small number of trees in close proximity to each other. By contrast, anthophilous Microchiroptera of the Neotropics are to some degree insectivorous and spend some time catching insects as well as getting nitrogenous food material from pollen or fruit. New World bats also display in varying degrees the "trap linnig" habit in which they travel a fixed path between plants that bear only a few flowers nightly for relatively long time periods.

A recent investigation on solitary bee behavior in the Neotropics has revealed that bees move at low but consistent rates between widely spaced tropical trees. This foraging pattern is important particularly to those species possessing self-imcompatible breeding systems. Further studies on the bees suggest that behavioral interactions, involving energetic relationships, group foraging and territoriality, may be important in increasing the movement of bees not engaged in these activities to the point where they move to adjacent trees, thereby effecting outcrossing.

Suggestions for future studies regarding the relationship between pollinator behavior and outcrossing are offered.

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