

in the areas of pollination biology such as reproductive isolation and differential pollinator visitation<sup>24</sup>, origin of floral colours<sup>25</sup>, experimental embryology and *in vitro* techniques of pollination<sup>5</sup>. These studies besides contributing substantially to the area of pollination biology have served a tangential but an equally or even more important purpose of instilling confidence among the young generation of workers. They have demonstrated that the logistic difficulties faced by the workers in countries such as India shall never be a hindrance; especially in the areas such as pollination ecology that requires the biological diversity as an important resource which our country is abound with.

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## Plant-pollinator interactions

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**In this article we review studies by Indian workers on plant-pollinator interactions and discuss the evolution of floral traits in relation to pollination and the foraging behaviour of pollinators. In the process, we identify the contributions of these studies to several conceptual issues in pollination biology.**

POLLINATION biology in India started mostly as a descriptive science aiming at understanding plant morphology and anatomy in relation to pollination. Most of the early work was restricted to documenting the kind, number and time of floral visitors on various plant species. Consequently a few investigators have studied plant-pollinator interactions with a right emphasis on the mutual adaptations of the two partners and interactions between them.

In this article we have attempted to sketch a few important discoveries regarding plant-pollinator interactions in the Indian context. In the process, we have also

attempted to identify the Indian contribution to the conceptual issues in the area of pollination biology. In the first part, we trace the early works emphasizing anatomical and morphological basis of pollination, and in the second we review studies aimed at identifying floral rewards and attractants as factors molding the foraging activity of pollinators. The third and final part focuses on environmental parameters influencing pollinator activity.

### Floral anatomy and morphology in relation to pollination

Among the early workers, Rao<sup>1</sup>, Parija and Samal<sup>2</sup>, and Narayana<sup>3</sup> studied the anatomical features in relation to pollination. Rao<sup>1</sup> described modification of epidermis as extrafloral nectaries in *Spathodea stipulata* Wall. and found that these nectaries were abundant on the abaxial side of all the floral and foliar parts. The

nectaries were observed to secrete both 'cane' and 'grape-sugars' which act as an attractant to pollinators. Pre-anthesis secretion of extra floral nectaries as a mechanism to divert ants from visiting flowers in *Tecoma capensis* was reported by Parija and Samal<sup>2</sup>. Further they hypothesized that selfing is favoured by excluding ants from visiting flowers. Narayana<sup>3</sup> also reported ants as potential pollinators of coconut. Based on the histological studies, he identified the presence of sepal hydathodes which are involved in the secretion of nectar which, upon desiccation, would attract ants and the bees. Diwan and Rao<sup>4</sup> observed an interesting behaviour of *Apis cerena* on the flowers of *Synadenium grantii* where bees were found regurgitating the water in order to feed on the crystallized nectar. Chakravarty<sup>5</sup> suggested that ants attracted by the extrafloral nectaries in cucurbitaceous plants perform defensive function apart from aiding pollination.

Probably the first study in India suggesting the adaptive significance of floral morphology was reported by Iyengar<sup>6</sup> in 1922. He studied two species of *Monochoria*; *M. hastaefolia* and *M. viginalis* commonly found in marshy habitats. The flowers of both the species showed an interesting form of dimorphism with respect to the orientation of stamen and styles. Two types of flowers were recognized by him: i) those in which the stamen bends to the right and the style to the left and ii) those in which the bending is reversed. The flowers of both the types were observed to occur on the same inflorescence. Insects like *Xylocopa* sp., *Vespa cincta* and *Apis florea* feed on the nectar and while doing so, one side of the body of the insects is rubbed against anthers and the other against stigma. Insect visiting one type of flower will deposit pollen grains only if it had visited the opposite type of flower in its previous visit. Because on a single day an inflorescence mostly consists of one type of flower, he inferred that this dimorphism is an adaptation to ensure cross pollination. He also observed the bending down of the entire inflorescence of *Monochoria* following fruit set and argued that it may be an adaptive strategy to disperse the seeds through water.

Maheshwari and Singh<sup>7</sup> and Maheshwari and Maheshwari<sup>8</sup> described floral dimorphism in two species of *Commelina* (*C. bengalensis* and *C. forskaelaei*). Generally three flowers were observed to be enclosed in a spathe; among them the first flower is long pedicelled and exclusively male, the second is bisexual and self-pollinated. The third flower is chasmogamous or occasionally pure male. Underground branches of these species were also described to bear cleistogamous flowers, the seeds produced by which are fertile and are self-sown.

To elucidate the evidence for co-evolution of plant and pollinator, Reddi and Reddi<sup>9</sup> analysed morphological features of flower of *Jatropha gossypifolia* and

their pollinators. They concluded that floral morphology is clearly tailored for manipulation by several kinds of insects. Chaturvedi and Pant<sup>10</sup> studied the morphology of pollinia and their attachment to various body parts of insect visitors (mainly Hymenoptera and Lepidoptera). The observation indicated that the ratio of length of retinacula to that of pollinia and the site of opening of stigmatic notches influence pollinia insertion. Pollinia of *Calotropis procera*, *Sarcocostemma secamorne*, *Asclepias curassavica* and *Pergularia daemia* were reported to be carried horizontally on the body parts while those of *Wattakaka volubilis* were carried vertically in the mouth parts.

Ali<sup>11</sup> observed that the pollen grains of ornithophilous *Loranthus* sp. are well suited to hold on to the body parts/barbules of bird pollinators. In a detailed study Davidar<sup>12</sup> identified mutual adaptation between seven species of mistletoes (Loranthaceae) and their avian pollinators such as sunbirds, flowerpeckers and white eye. Though she did not analyse strictly for mutualism between the bird and plants, she observed little overlap of the nectar plants for any avian pollinators and vice versa suggesting specific adaptations. This appears to be the lone study of co-evolution between plant and avian pollinators in India.

### Floral coloration, reward and pollinator activity

Dronamraju<sup>13</sup> observed that two sympatric varieties of *Lantana camara* differing in their floral coloration preferentially attracted different species of lepidopteran butterflies. He observed that *Lantana* varieties with yellow flowers, which changes colour to red, exclusively attracted *Precis almana* L. while that with white flowers (which changes to pink) was visited by *Catopsilia pyranthe pyranthe* L. (Table 1). Discussing its evolutionary consequences, he suggested that abundant presence of one species of butterfly would favour the selection of a specific colour variety preferred by it.

Later in a detailed study Dronamraju<sup>14</sup> confirmed the earlier observation of preferential visitation of butterflies to one of the colour morphs except *Danais chrysippus* L. which was found to visit two morphs equally (Table 2). Such selective visits of butterflies to flower morphs were argued to be a means of sympatric speciation.

Dronamraju and Spurway<sup>15</sup> conducted choice experi-

Table 1. Number of insect visits to flowers of *Lantana camara* L.

Butterfly species	No. of visits to red-yellow-flowered plants	No. of visits to white-pink-flowered plants
I <i>Precis almana</i> L.	12	0
II <i>Catopsilia pyranthe pyranthe</i> L.	2	25

(alter Dronamraju, ref. 13).

**Table 2.** Butterfly visitation pattern to flowers of *Lantana camara*

Species	Family	No. of days	Number of times observed to feed on:	
			Orange	Pink
<i>Prectis almana</i>	Nymphalidae	16	218	13
<i>Danaus chrysippus</i>	Danaidae	18	142	152
<i>Papilio demoleus</i>	Papilionidae	4	15	31
<i>Papilio pyranthe</i>	Pieridae	13	42	98
<i>Catopsilia pyranthe</i>	Pieridae	27	40	603
<i>Baris mathius</i>	Hesperiidae	12	1	108

(after Dronamraju, ref. 14).

ments with laboratory grown *Papilio demoleus* to understand the preferences of naive individuals. Freshly emerged butterflies were offered pink or orange flowers alternatively and it was shown that most individuals of *P. demoleus* emerging fresh from pupa preferred to feed on pink rather than orange *Lantana* flowers. They have also reported contrasting individual preferences among closely related kins of *P. demoleus* for colour morphs. They showed that a mother, one of its daughters and sons preferred pink; contrastingly, the father, another son and daughter preferred orange flowers. This observation indicated the presence of 'behavioural polymorphism' for colour preference. They rightly pointed out that such preferences exerts a selection pressure on the plant population comparable to that of 'sexual selection' among animals. Finally they suggested that flower type visitation constancy of anthophilous insects might lead to sympatric speciation in plants.

In *L. camara* the flower colour is known to change from yellow or pink to shades of red with age. Such floral colour changes is believed to have evolved widely among angiosperms to increase the pollinator efficiency. In an interesting study, Mathur and Mohan Ram<sup>16</sup> showed using yellow-coloured artificial panels that thrips (one of the important pollinators of *Lantana*) prefer yellow compared to red-coloured morphs, indicating a preference for fresh flowers. When thrips were offered *Lantana* flowers of different developmental stages from bud to deep red flowers, they were shown to move towards freshly bloomed yellow flowers. Mohan Ram and Mathur<sup>17</sup> showed that petal colour change in *Lantana* is mediated by pollination and synthesis of delphinidin monoglucoside which is responsible for red pigmentation of the older flowers. Probably this is a significant contribution towards the understanding of biochemical basis of floral colour change following pollination.

Raizada and Nangia<sup>18</sup> conducted laboratory experiments using flowers of *Nyctanthus*, *Dianthus*, Pomegranate and Jasmine and demonstrated that attraction of thrips is due to combined influence of odour and colour of flowers. Preferential visitation of pollinators such as *Xylocopa* bees on the white over variegated flowers of *Antirrhinum majus* was also observed by Bhaskar and Gopinath<sup>19</sup>. Satyanarayana and Seetha-

ram<sup>20</sup> recorded frequent visitation of honey bees to the pollinator lines (male fertile) than to seed lines (male sterile) in sunflower. The pollinator activity on seed plants was shown to decrease with its distance from the pollinator line.

Deodikar *et al.*<sup>21</sup> reported differential collection of pollen and nectar by worker bees and showed that pollen collectors are more efficient than nectar collectors. They also identified an important pattern of foraging: individual bees were found visiting more than one head of sunflower though a single head can meet the requirements. They inferred that this would increase the possibility of out-breeding though the authors could not point out the reasons for such behaviour.

It is interesting to note that avian pollinators such as mynas, sunbirds have also been recorded to be preferential in their visitation to the flowers. Ali<sup>11</sup> observed that the yellow variety of *Bombax* tree despite having copious amounts of nectar in its flowers was practically unattended while on the conspecific crimson variety, there was continuous 'hustling and rivalry' among birds for feeding on the nectar. This has been attributed as a factor for low seed set in yellow variety of *Bombax*.

Of recently, floral choice by pollinators has been viewed from the point of the energetics of pollinators which has wider implications in floral biology and community ecology<sup>22</sup>. Abrol<sup>23</sup> working with 54 cultivars of apple has clearly shown a positive correlation between calorific reward offered by a cultivar and visitation of honey bees and consequently the level of cross pollination achieved.

For the first time a study regarding the concentration of sugars in the nectar was conducted by Sharma<sup>24</sup> using 25 honey plants of India. Later, Sihag and Kapil<sup>25</sup> identified that quality and quantity of nectar determine the foraging strategies of honey bees.

Factors controlling the synchronization of flowering period and developmental phase of the pollinating thrips were studied extensively by Ananthkrishnan<sup>22</sup>. He showed that larval emergence of *Microcephalothrips abdominalis* coincides with the anthesis and nectar production in *Wedelia chinensis*. However cross pollination takes place only to a modest level by the random flights of adult thrips or by being drifted by wind. Movement of thrips between flowers of the same inflorescence was also confirmed in some Fabaceae members.

Robbing of floral rewards (pollen/nectar) by insects has been observed by several workers<sup>26-28</sup> and some have also attributed this to the reduced seed/fruit set. Bird pollinators like sunbirds have been observed to steal the nectar by making a hole at the base of the flowers. Such 'higher level of intelligence' of visiting birds 'without doing any service in return' has also been reported<sup>11, 26, 27, 29</sup>.

### Environmental factors and pollinator activity

Temperature and relative humidity were identified as important environmental correlates controlling honey bee foraging activity by Bisht and Pant<sup>30</sup>. In a comparative study of Megachilid bees, Kapil and Jain<sup>31</sup> have shown that temperature, humidity and light intensity affect the commencement and cessation of flights and also the tripping efficiency.

In a novel attempt to explain the factors influencing pollination activity of *Apis dorsata*, Abrol<sup>32</sup> conducted a path coefficient analysis of a few environmental factors and nectar content. Bee abundance was shown to be significantly correlated with air temperature, light intensity, solar radiation and nectar concentration but negatively with relative humidity. Path coefficient analysis revealed that the direct effects of air temperature and light intensity were pronounced and positive while the effects of other factors did not substantially affect the bee activity.

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## Pollination by birds and bats

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The available Indian literature on bird and bat pollination has been reviewed. Analysis of the information shows a generalized relationship among flowering plants and their pollinators. We discuss the probable reasons for such generalized relationship. Literature on bat pollination shows that anthesis and phenology in certain plants are cued towards the activity and breeding cycle of bats.

INDIA being a tropical country offers a vast potential for studying the role of birds and bats in pollination. However, except for a few studies<sup>1-6</sup>, the subject has received very little attention. Here we review the available

Indian literature on bird and bat pollination. Our discussions mainly rest on the two appendices generated following our survey of the Indian literature.

#### Flower birds

A total of 58 Indian bird species from 16 different families and four orders are reported to be involved in the pollination (Appendix I) of 93 species of flowering plants belonging to 34 families and 20 orders (Appendix II). Over 80% of the plant species are frequented by more than one bird species (Figure 1). On the other