- 19. Sowig, P., Oecologia, 1989, 78, 550.
- 20. Johnson, L. K. and Hubbell, S. P., Ecology, 1975, 56, 1398.
- 21. Feinsinger, P., Ecol. Monogr., 1976, 46, 257.
- 22. Fleming, T. H., in Effects of Resource Distribution on Animal-Plant Interactions, (eds. Hunter, M. D., Ohgashi, T. and Price, P. W.), Academic Press, New York, 1992, pp. 355.
- 23. Paton, D. C., Bio Science, 1993, 43, 95.
- 24. Janzen, D. H., Science, 1971, 171, 203.
- 25. Bronstein, J. L., in Mosaic Landscapes and Ecological Processes, (eds. Hansson, L., Fahrig, L. and Merrian, G.), Chapman and Hall, New York, 1993 (in press).
- 26. Rathcke, B., Ecology, 1988, 69, 446.
- 27. Haber, W. A., in Biology and Conservation of the Monarch Butterfly, (eds. Malcolm, S. B. and Zalucki, M. P.), Nat. Hist. Museum of Los Angeles County, Los Angeles, California, 1993, 201.
- 28. Haber, W. A. and Frankie, G. W., Biotropica, 1989, 21, 155.
- 29. Doak, D. F., Marino, P. C. and Kareiva, P. M., Theor. Pop. Biol., 1992, 41, 315
- 30. Frankie, G. W., in Coevolution of Plants and Animals, (eds. Gilbert, L. E. and Raven, P. H.), University of Texas Press, Austin, Texas, 1975, pp. 192.
- 31. Gilbert, L. E., in Coevolution of Animals and Plants, (eds. Gilbert, L. E. and Raven, P. H.), University of Texas Press, Austin, Texas, 1975, pp. 210.

- 32. Aizen, M. A. and Feinsinger, P., Ecol. Applic., 1993, (in press).
- 33. Menges, E., Conserv. Biol., 1991, 5, 158.
- 34. Linhart, Y. B. and Feinsinger, P., J. Ecol., 1980, 68, 745.
- 35. Spears, E. E., J. Ecol., 1987, 75, 351.
- 36. Williams, N. H. and Dodson, C. H., Evolution, 1972, 26, 84.
- 37. Campbell, D. R. and Motten, A. F., Ecology, 1985, 66, 554.
- 38 Kwak, M. M., in Disturbance in Grasslands, (eds. van Andel, J., Bakker, J. P. and Snaydon, R. W.), Dr W. Junk, Dordrecht, Netherlands, 1987, p. 273.
- 39. Waser, N. R. and Real, L. A., Nature, 1979, 281, 670.
- 40. Rathcke, B., J. Ecol., 1988, 76, 975.
- 41. Rathcke, B. J., in Effects of Resource Distribution on Animal/Plant Interactions, (eds. Hunter, M. D., Ohguishi, T. and Price, P. W.), Academic Press, New York, 1992, pp. 113.
- 42. Saunders, D. A., Hobbs, R. J. and Margules, C. R., Conserv. Biol., 1991, 5, 18.
- 43. Real, L. A. and Rathcke, B. J., Ecology, 1991, 72, 149.
- 44. Zimmerman, M., Oikos, 1983, 41, 57.

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## India's buzzy biodiversity of bees

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The historical background of research on the bees or Apoidea of India is reviewed. Current knowledge of these important pollinating insects is compared with that in other parts of the world. Recommendations for further research in India are made, with suggestions regarding the conservation of bee species and the management of their populations to benefit both agriculture and wildlife in India.

A millennium ago, India was a place of floral bounty, where people relaxed in beautiful public gardens. At that time, bees were extolled in Sanskrit poetry, especially the bhramara (Xylocopa, or carpenter bees). These big, acrobatic, noisy bees symbolized virile male lovers, voluptuously kissing the dainty, fragrant, feminine flowers. In religious poetry, bees represented seekers of knowledge or wisdom, which is symbolically hidden in flowers (usually the lotus, which may nocturnally close, to trap any lazy bees). Bees were admired and cherished for their musical humming, their persistent attraction to beauty, their epicurean taste in food, their love of fragrances, their dynamic and farranging flights, and their preference for fair weather. In the Ramayana, when Hanuman found Ravana's

beautiful ladies asleep, 'On their soft limbs, the marks of their ornaments sat like bees...'. They were '... like garlands of flowers attended by lovesick bees, ... like the intertwined branches of great forest trees, full of clouds of swarming bees ...'. The behavior of bees was related to the seasons<sup>1</sup>: 'With tumbled hair of swarms of bees, and flower-robes dancing in the breeze, with sweet, unsteady lotus-glances, intoxicated, Spring advances.' Also, 'This season of erotic fragrance, of wistful love, has maddened the sporting bees.' Bee sport, or bhramara vilasita, evidently refers to the territorial hovering, courtship and fighting of male Xylocopa, which happens during Spring. Sri Guru Granth Sahib states: 'In Chet, agreeable is the Spring, and beautiful the bhowra'. (=bhramara). However in the rainy season (Bhadon), 'The bees have forgotten all about honey and the fragrance of flowers, and are hiding themselves in heaps'. Male solitary bees often cluster together to sleep in nooks.

Although the ancients romanticized carpenter bees, they also found two unusual practical uses for them. The *bhramara* were apparently used to carry messages, as homing pigeons are used today. These bees can return to their nests when released as far away as 4 km

and they are large enough to carry small pieces of paper glued to the thorax. Another ingenious technique was used by thieves, who kept some of these bees in a small box, bhramara-karandaka, from which they were released at night, to fly into and extinguish lamps in the houses to be robbed<sup>2</sup>.

Honey or madhu was the only sweet available at the time of the Rig-Veda, sugarcane not yet having been domesticated. It was produced by two kinds of honeybees, arangara, a big bee (probably Apis dorsata) and saragha, a small bee (?Apis florea). The honey of the small bee was considered to be of the best quality; today A. florea honey is believed to have medicinal properties. Eight kinds of sweets and honeys were used medicinally during later periods<sup>3</sup>. There are many Sanskrit terms referring to honeybees, which indicate considerable ancient knowledge of their behavior, such as madhurajan, queen bee; madhugana, swarm; madhupatala, hive; madhuja, wax, made from honey; madhukosa, comb; madhunadi, cell. There are several terms referring to different kinds of honeybees or insects associated with them: madhukara, madhukesata, madhunoleha, madhupa, madhumakshika, madhuaka (honeybees); madhupakhaga, a large black honeybee; madhumaraka, honey-destroying insect, perhaps wax moth<sup>2</sup>.

The ferocity of A. dorsata is legendary, surpassing the notorious African honeybee. Colonies of A. dorsata routed the vandalizing armies of Aurangzeb from temples where their combs hung; once an entire army fled before a swarm of angry bees<sup>4</sup> for 8 km. The British colonists had similar encounters; Sleeman<sup>4</sup> described how six companies of his infantry, with a train of artillery and a squadron of horse, were routed by a single colony and driven off several kilometers. In another encounter, three companies of a regiment were forced by irritated bees to jump into the Ganga, abandoning everything, including their clothing and treasure. Horses and men went mad, broke their limbs, and died.

## A review of bee research

India is blessed with a great variety of climates, with a wide range of flora and fauna, including diverse bees (Apoidea, over 20,000 species worldwide: families Apidae, Anthophoridae, Megachildae, Melittidae, Andrenidae, Halictidae and Colletidae). Most of this region is in the tropical Indomalayan Realm, which includes biogeographic zones ranging from the arid western Thar desert to the rainforest zones. The biogeography of north and northwestern India is also much influenced by elements from the Palearctic and Africotropical Realms.

Studies of the systematics, biology, and flower relationships of the diverse Apoidea in India have been relatively neglected; thus there surely remain numerous

undescribed species. For example, Roubik's otherwise excellent book on tropical bees worldwide<sup>5</sup> cites some 1400 references, but only 89 of these refer specifically to bees of South and Southeast Asia, including 38 that refer only to Apis. Early research on bees in India has been reviewed by Atwal<sup>6</sup>, Batra<sup>7</sup>, and Kapil<sup>8</sup>. Most systematics work during the past century was conducted by visiting or resident European and Japanese scientists, with some brief notes on bee biology and pollination studies. Pollination studies were of necessity first directed toward improving the productivity of agricultural crops. Many early references to the pollination of non-agricultural plants and nesting biology of bees are scattered in obscure publications on taxonomy. Species that range into India may also occur as far away as Israel, Egypt, China, and Southeast Asia. Thus it is necessary to be aware of the literature on the bees and their hosts in these areas. North America has about 3500 species of bees; the Indian subcontinent should have at least as many. The inconvenience of the literature search and the usual deposition of specimens in foreign museums have rendered bee research difficult for Indian scientists. There remains great potential for the discovery of new bee species, new and unusual host-pollinator interactions, and new information on nesting habits, parasites, and sociobiology.

Honeybees (Apis spp.) are conspicuous, abundant, and valued for their products, thus they have been much studied, but research on other bees has been neglected. Only recently has pollination research in South Asia begun to carefully and critically analyse the mutualistic relationships between native bees and their native host plants, so admired by the observant old Indian poets<sup>1</sup>. These studies have found that, contrary to the usual earlier assumptions, honeybees are not always present, nor, when present, may they be the most numerous, nor may they be the most effective pollinators. For example, teak is pollinated by small solitary bees<sup>9</sup>, indigo (*Indigofera* spp.) is best pollinated by species of Nomia and Pithitis bees<sup>10</sup>, Garcinia is pollinated by Trigona stingless bees<sup>11</sup>, and Alangium and Calotropis are best pollinated by carpenter bees  $(Xylocopa)^{12}$ . These studies include information on the numbers and species of pollinators; their behavior on the flowers; their effectiveness in transferring the pollen; the roles of floral morphology and abundance of nectar and pollen; the phenology of hosts' flowering; and the effects of the time of day, weather, season, and environmental surroundings on pollination.

## The protection and propagation of bees

Currently there is great international concern about deforestation in Latin America. It is easy to imagine the lush forest of tropical Brazil disappearing within a century or two. Only a few centuries ago, India was similarly endowed with forests that teemed with magnificent wildlife. Now little is left but for remnants in a few sacred groves, areas around old graveyards, in wildlife refuges, and in inaccessible mountainous areas. A similar process occurred in Europe where the native forests were long ago replaced with agriculture, including tree farms. The exploitation of coal and oil for energy in Europe, North America and Japan reduced the need to clear land for pastures for draft animals and for yielding fuel wood. This permitted the growth of secondary forests in these areas.

Research concerning the impacts of human activities on bees and their host plants, including deforestation, cultivation, irrigation, revegetation, pesticides, pollution, urbanization and even roadway traffic was pioneered in Europe, where accurate, long-term records on bee population sizes and compositions are available<sup>13</sup>. Similar studies have begun in Japan<sup>14</sup> and Costa Rica<sup>15</sup>.

The European studies<sup>13</sup> found that, in Poland, the diversity of species of bees was positively correlated with the diversity of host plants. Large, intensively cultivated fields had lower populations and fewer (70%) less) species of bees than adjacent small fields after 10 years. However, over an area of thousands of hectares, the total number of species of bees did not change during 60 years (there was no information on population levels). In England, there were twice as many species and individuals of bees in a heath before reforestation with conifers than afterward, believed to be due to the loss of sunlit nesting sites. Bumblebees there have declined significantly in populations and number of species due to intensive cultivation on 80% of the land area, with pesticide use, the removal of nest sites in hedgerows, forest margins, and heath, and the loss of open space with diverse native food plants. This was severe for rare species that were already surviving at the edges of their normal ranges. Heavy highway traffic also killed many foraging bees. The construction of a dam and inundation of a floodplain altered the local composition of bee species. The amelioration of the microclimate by water was beneficial to populations, as was the planting of legumes and the growth of weeds. A rural park of 20 ha in Poland supported 60 species of bees, or 80% of all species in the region. There were three times more bees per unit area inside the undisturbed park than in a similar but cultivated biotype outside.

In towns and cities, the greatest number and variety of bees were in the largest gardens and parks, those with the greatest diversity of flowering plants, forming a mosaic. Cities tended to warm the microclimate, permitting more reproduction by some species. Species that nested in cracks in walls, wooden beams and twigs, and polylectic species with many hosts, became

relatively abundant in urban areas (synanthropic), especially species of Osmia, other megachilids, and Anthophora.

During 10 years in Japan, bees became more dependent on introduced plants, as their native hosts disappeared, and populations of 30 of the 82 bee species, especially woodland-dwelling species, declined<sup>14</sup>. In Costa Rica during 20 years, the number of species and total population of anthophorid bees (Centris) declined sharply due to loss of nesting sites and native host plants through cultivation, urbanization, and the burning of their habitat<sup>15</sup>.

Although no such studies have been conducted in India, it is obvious that India's bees would be similarly affected. India is fortunate in being the homeland of the abundant, highly adaptable Apis dorsata, A. florea and A. cerana. I have seen groups of the large, pendulous combs of A. dorsata, drooping beneath balconies of highrise buildings on a busy main road within about 500 m of bustling, noisy and fumy Connaught Place, in the center of Delhi. India would lose much of her charm if she comes to rely only on these honeybees for pollination, forgetting the bhramara and the many other lovers of her wildflowers.

It is time to pursue more investigations of bees and pollination biology. Some particularly interesting and scientifically rewarding topics in India would be: biogeography and biology of bees and their hosts at various elevations in the Himalayas; orchid-pollinator relationships; management of solitary bees for crop pollination; surveys and conservation of bee populations in agricultural, overgrazed, deforested and urbanizing habitats; surveys of bee species in the remaining undisturbed natural habitats, such as in the wildlife refuges; nesting habits of selected species; sociobiology; and detailed studies of the pollination biology of native wild plants. Many of these research projects take time, but do not require much expensive and delicate equipment. It is urgent that as much as possible be learned, because wild habitats that support rare bees and host plants are more rapidly and widely disappearing in India than elsewhere, yet relatively much less is known about them here.

Many species of bees are far more gentle than honeybees, and are easily propagated in gardens and on farms<sup>16</sup>. They can be used for nature study programmes. The little, bright green Pithitis bees and the tiny black Braunsapis bees (which have a fascinating social life) nest in the pithy Saccharum reeds commonly used for thatched roofs. Bhramara nest in dry bamboo and wooden beams. Many kinds of andrenid, halictid, colletid and anthophorid bees nest underground, in dry, sunny soil. Kacha walls provide homes for anthophorids and megachilids. Other megachilids nest in holes in wood<sup>7</sup>. Look for the dashing, blue-banded Amegilla, a robust, long-tongued visitor to the sacred tulsi; the shy

Nomicules, as pale and tiny as many sand grains, among which she nests; Colletes, the clever chemist, which spins gossamer brood cells made out of polyester; and the black, rusty-red, and gray Chalicodoma bees, which boldly enter houses, where they make cells out of mud in key holes, cloth rolls, gun barrels, and other such snug spots. When appropriate nest materials are provided, bee populations increase, as do crop yields. Is there not enough space in India to allow such beneficial and fascinating creatures some quiet places to nest in, and enough wildflowers for their sustenance?

- 1. Brough, J., Poems From the Sanskrit, Penguin Books, 1987, pp. 1-151.
- Monier-Williams, M., Sanskrit-English Dictionary, Oxford, 1899, pp. 1-1333.
- 3. Prakash, O., Food and Drinks in Ancient India, Munshi Ram Manohar Lai, Delhi, 1961, pp. 1-360.
- 4. Sleeman, W. H., Rambles and Recollections of an Indian Official, Oxford, 1844, pp 1-667.
- 5. Roubik, D. W., Ecology and Natural History of Tropical Bees, Cambridge Univ. Press, 1989, pp. 1-514.
- 6. Atwal, A. S. (ed.), Insect Pollinators of Crops, Punjab Agr. Univ. Press, Ludhiana, 1970, pp. 1-116.
- 7. Batra, S. W. T., Orient. Insects, 1977, 11, 289-324.
- 8. Kapil, R. P. (ed.), Pollination Biology An Analysis, Inter-India Publ., New Delhi, 1986, pp. 1-300.

- 9. Hedegart, T., Silvae Genet., 1973, 22, 124-128.
- Atmowidojojo, A. H. and Adisoemarto, S., Treubia, 1986, 29, 225–235.
- 11. Richards, A. J., Bot. J. Linn. Soc., 1990, 103, 251-266.
- 12. Bhatnagar, S. and Mishra, R. M., Proc. Nat. Acad. Sci. India, 1987, 57, 171-174.
- 13. Peters, G., Entomol. Ber., 1972, 85-90; Haesler, V., Zool. Jb. Syst., 1972, 99, 133-212; Jacob-Remacle, A., Bull. Ann. Soc. R. Belge Entomol., 1976, 112, 221-242; Haesler, V., Drosera, 1982, 82, 17-32; Banaszak, J., Polish Ecol. Stud., 1983, 9, 421-505; Jacob-Remacle, A., Bull. Ann. Soc. R. Belge Entomol., 1984, 120, 241-262; Banaszak, J., Chronmy Przyr. Ojcz., 1985, 41, 5-9; Tanacs, L., Tiscia (Szeged), 1987, 22, 109-119; Banaszak, J., Badania Fizjogr. Polska Zachodnia, 1987, C36, 67-77; Pawlikowski, T., Acta Univ. Nicolai Copernici Biologia, 1987, 35, 153-167; Pawlikowski, T., Acta Univ. Nicolai Copernici Biologia, 1989, 33, 31-46; Torres, F., Gayubo, S. F. and Asensio, E., Commun. Inst. Nac. Invest. Agrar. Ser. Recur. Nat., 1989, 52, 1-49; Kratochwil, A. and Klatt, M., Zool. Jb. Syst., 1989, 116, 379-389; Wilhams, P. H., in Bumble Bees and their Decline in Britain, Publ. Central Assn. Beekeepers, Ilford, Essex, 1989, pp. 1-11; Archer, M. E., Naturalist (Leeds), 1989, 114, 129-136; Westrich, P., Die Wildbienen Baden-Württembergs, Verlag Eugen Ulmer, Stuttgart, 1990, pp. 1-972.
- 14. Munakata, M., J. Hokkaido Univ. Educ. Sect. 2B, 1984, 34, 53-73.
- 15. Frankie, G. W., Vinson, S. B., Newstrom, L. E., Barthell, J. F., Haber, W. A. and Frankie, J. K., in Reproductive Ecology of Tropical Forest Plants, (eds. Bawa, K. S. and Hadley, M.), UNESCO, Paris, Parthenon Publishing, Carnforth, U.K., 1990, pp. 37-47.
- 16. Batra, S. W. T., Sci. Am., 1984, 250, 120-127.