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Pollination ecology of *Helicteres isora* Linn. (Sterculiaceae)

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The flowers of *Helicteres isora* are large, bisexual and zygomorphic with robust corolla. The elongated staminal column is adnate to the gynophore and the ten anthers are grouped at the tip of this column. The ovary with a short style ending in a simple stigma projects beyond the anthers and stays in an erect position. The flowers open daily at 0300–0330 h and are visited by birds and insects during daytime. The flowers characteristically change their colour, being bluish-grey on day one (d_1), changing to light red on day two (d_2) and dark red on day three (d_3). Birds collect nectar more frequently from d_2 and d_3 flowers. Bees collect nectar and pollen mostly from d_1 flowers. The flowers are not apomictic, but compatible for auto-, geitono- and xenogamy. The bees *Ceratina* and *Trigona* mediate autogamy and geitonogamy by remaining mostly on the same flower while *Pseudapis* and *Amegilla* promote xenogamy by their frequent inter-tree movement. The birds quaker babbler *Alcippe poioicephala* and Indian myna *Acridotheres tristis* largely promote xenogamy because stigma receptivity continues up to the second day of flower life. Since the two bird species implicated in pollination are not entirely nectarivorous, total dependence on them for pollination may not be an ideal strategy, and receiving pollen-collecting bees may help in the reproduction of *H. isora*. Floral damage caused by the red-vented bulbul, *Pycnonotus cafer* and by the blister beetle and the insect larvae is detrimental to *H. isora* reproduction. Natural fruit production is very low which may be due to the inadequancy of pollinators.

THE East Indian screw tree *Helicteres isora* is distributed gregariously throughout India. The plants are exploited for the stem bark from which fibre is obtained. The fibre is known for its durability and is used for making bags and as supplementary raw material in paper mills. Apart from the fibre, tender branches and leaves are used as fodder. Fruit in the dried form and the bark of root and stem are of medicinal use. Despite such usefulness of the plant, little information is available on the pollination ecology and the breeding behaviour. Santharam[1] described the visits by birds to the flowers of *H. isora* and mentioned that the flowers are red fading to lead (blue) towards the end of the day. Our observations contradict this sequence of colour change. We report here the details of pollination ecology together with the flower colour changes and their relevance to the prevailing breeding system(s) and cross-pollination.

Natural populations of *Helicteres isora* Linn. occurring on the hill slopes and the hills located opposite to the Zoo Park about 10–12 km from Visakhapatnam city (17°42′N and 82°18′E) and adjoining NH5, were utilized for the present study. Flowering phenology at the plant level was recorded for 15 randomly selected plants distributed at weekly intervals. Inflorescence phenology was followed through daily observations on 15 inflorescences distributed on five plants. Simultaneously, the time of flower opening (anthesis) and the time of anther dehiscence were noted by tagging 25 mature flower buds. The number of pollen grains contained in an anther was determined following Subba Reddi *et al.*[2]. Twenty anthers selected from different flowers were used for determining the pollen output per anther. A mature undehisced anther was placed on a clean microscope slide and dabbed with a squashing needle until all the pollen grains were released on to the slide. After removing the anther tissue the pollen mass was spread. A drop of glycerine jelly with lactophenol analine blue was put on the pollen preparation and covered with 22 mm^2 cover glass. The pollen were counted under a compound microscope (40× objective, 10× eyepiece) and pollen characters were noted. Based on pollen and ovule number per flower, the pollen to ovule ratio was calculated following Cruden[3]. The pollen viability period was assessed by *in vitro* (using 20% sugar solution) and *in vivo* methods detailed by Dafni[4]. Stigma recep-

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tivity was tested with hand-pollinations. Batches of fresh flowers (each batch consisting of 5 flowers from three different plants) emasculated previously were pollinated with fresh pollen at different time intervals for 48 h, then bagged and observed for fruit set. Two types of nectar measurements were made, one immediately after anthesis and another two hours after anthesis; micropipettes were used for this purpose. Nectar sugar concentration was recorded using a hand refractometer. The nectar was analysed for the sugar types using paper chromatography following Harborne[5]. Tests for autogamy, geitonogamy, xenogamy and apomixes were conducted on 25 flowers distributed on 10 plants for each mode of reproduction and fruit set recorded. During all the visits made to the plants under observation, representative samples of flower visitors were collected, and later identified by our research group. The bird foragers were observed using binoculars and identified by referring to the book by Salim Ali[6]. Further, the type of food collected by different visitors, the daily foraging period and the number of visits made per unit time were recorded by close observation. Body washings of bee species collected after foraging on pollen which had contacted the anthers and the stigma were taken to record the number of pollen grains that could be picked up by their bodies. The numbers were counted as per the procedure used for determining the pollen number per anther and for each bee species 5 individuals were examined.

The plants set full vegetative growth following monsoonal rains in June and start flowering during late July to late October. Flowering is synchronous in a habitat and lasts for 32 ± 3 days (R 18–58) (Table 1). The flowers are borne in axillary fascicled cymes. A fascicle contains 7.5 ± 1.45 flowers (R 5–10) developing over a period of 7–16 days (Table 2).

The flowers are large, odourless, bisexual, and zygomorphic with green calyx. The corolla is robust, the two lower petals are large and broad while the three upper ones are small and narrow. The stamens form an elongated column adnate to the gynophore. The 10 anthers are grouped at the tip of the column. The syncarpous ovary is situated at the top of the column; it is five-lobed and contains 90 ± 10.7 ovules (R 78–108). The style is short and has a simple stigma that projects beyond the anthers and lies is an erect position.

The flowers open daily during 0300–0330 h in association with air temperature ranging between 28 and

Table 1. Flowering phenology of *H. isora*

Plant No.	Flowering period	Total number of days of flowering
1	22 July–07 August	18
2	22 July–14 September	54
3	22 July–29 August	39
4	22 July–18 August	28
5	28 July–17 September	52
6	28 July–12 August	47
7	28 July–08 September	53
8	02 August–06 September	36
9	02 August–08 September	38
10	02 August–18 September	48
11	18 August–22 September	36
12	18 August–13 October	58
13	18 August–18 September	32
14	18 August–28 September	42
15	18 August–24 September	38

Table 2. Fascicle blooming phenology in *H. isora*

Fascicle number	Number of flowers opened on each day from 9 to 24 August 1995																
	d_1	d_2	d_3	d_4	d_5	d_6	d_7	d_8	d_9	d_{10}	d_{11}	d_{12}	d_{13}	d_{14}	d_{15}	d_{16}	Total
1	1	1	0	1	0	0	0	0	0	1	0	0	0	0	0	1	5
2	1	3	1	0	1	0	1	0	0	0	0	0	0	0	0	0	7
3	1	1	2	1	0	0	1	0	0	0	0	0	0	0	0	0	6
4	2	0	2	0	0	1	1	0	0	0	0	0	1	0	0	1	8
5	1	0	1	1	0	1	1	0	0	1	0	0	0	0	1	0	7
6	1	0	2	2	0	1	0	0	1	0	0	0	0	0	0	0	7
7	1	0	1	3	0	2	0	1	0	0	0	0	0	1	1	0	10
8	1	2	2	2	1	0	0	0	0	0	0	0	0	0	2	0	10
9	1	1	1	1	2	2	0	0	0	0	1	0	0	0	0	0	9
10	1	2	0	0	2	0	0	0	1	0	0	1	0	0	0	1	8
11	4	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	7
12	1	3	0	1	0	0	0	0	0	0	0	0	0	0	2	0	7
13	1	1	2	0	2	0	0	1	0	0	0	0	0	0	1	1	9
14	2	1	0	2	0	0	0	0	1	0	0	0	0	0	0	0	6
15	3	1	1	0	0	0	1	0	0	0	1	0	0	0	0	0	7
Total	22	17	15	14	8	7	5	3	3	3	2	1	1	1	7	4	

27°C and RH 74–71%. The anthers dehisce synchronously by longitudinal slits at anthesis.

The pollen grains are smooth, yellow, 30 µm in size on the equatorial axis and 19 µm on the polar axis. Their number per anther averaged 9770 ± 328 (R 8210–10,730). About 2% of the total pollen appeared sterile as they did not stain. The pollen–ovule ratio approximated to 1085:1. While *in vitro* pollen germination tests indicated 17 h of viability for pollen, the *in vivo* tests revealed 15 h of viability. *In vitro* there was 50% germination of pollen stored up to 12 h and *in vivo* there was 40% fruit set with pollen of 15 h storage. The stigmas pollinated by hand with fresh pollen set 100% fruit; those with 9-h-old pollen set 80% and those with 15-h-old pollen gave 40% fruit set. Pollination with pollen grains of further age was ineffective. The total period of pollen viability was 15 h.

The 6-h-old stigmas gave 100% fruit set; afterwards the fruit set percentage decreased – 9 h, 80%; 12 h, 56%; 15 h, 40%; 24 h, 32%; 36 h, 20%; and 42 h, 8%. Visually the stigmas are shiny from anthesis onwards up to late evening the next day. Thus, the stigma receptivity period lasts for about 40 h after anthesis.

Nectar secretion begins an hour before anthesis and continues even after anthesis for ca. 2 h. The fully open flower contains 45 ± 8.7 µl of nectar and the nectar secreted thereafter amounts to 160 ± 17.6 µl. Thus in total a flower secretes 205 ± 12.7 µl of nectar. Sugar concentration at anthesis is 10% and later it varies between 11 and 16% probably due to water evaporation during bright sunlight hours. Glucose, fructose and sucrose are present, the former being dominant.

The flowers last for ca. 3 days. At anthesis the corolla is bluish-grey; it turns gradually to light red by the same evening. The next day it is red in the morning and by evening it is dark red. On the third day it begins to wither in the evening. On the fourth day the pollinated flowers drop off their corolla and anthers while the unpollinated ones begin to abscise.

Tests for apomixis are negative. There is no instantaneous autogamy suggesting that the flowers require external agents for pollination. Manipulated autogamy has given 92% fruit set, and geitonogamy and xenogamy 100% each (Table 3). The fruit set rate in open-pollination is 5–12%.

Table 3. Fruit set in different modes of reproduction in *H. isora*

Treatment	No. of flowers pollinated	No. of flowers set fruit	Fruit set percentage
Apomixis	25	0	0
Autogamy	25	23	92
Geitonogamy	25	25	100
Xenogamy	25	25	100

Table 4. Flower visitors, their floral reward and daily visits on *H. isora*

Visitor species	Floral resource sought: Pollen	Floral resource sought: Nectar	Total no. of visits (average of 3 censuses)	% of total visits	Foraging hours
Apis indica	–	+	18	3	0700–1600
A. dorsata	–	+	22	4	0700–1600
Trigona sp.	+	+	63	11	0600–1000
Ceratina sp.	+	+	52	9	0600–1000
Unidentified bee species	+	+	72	13	0600–1000
Pseudapis sp.	+	–	37	6	0600–1000
Amegilla	+	+	88	16	0600–1000
Delta conedus	–	+	9	2	0800–1500
Rhynchium metallicum	–	+	11	2	0800–1600
Vespa sp.	–	+	12	2	0800–1600
Catopsilia pomona	–	+	21	4	0700–1600
C. pyranthe	–	+	14	2	0700–1600
Euploea core	–	+	18	3	0700–1600
Alcippe poioicephala	–	+	79	14	0600–1700
Acridotheres tristis	–	+	27	5	0600–1700
Pycynonotus cafer	–	+	23	4	0600–1700

About 11% of flower buds and 4% of open flowers were infested with unidentified insect larvae. The larvae also cut and fed on the basal part of the corolla containing nectar. The blister beetle *Mylabris pustulata* made holes at the floral base and sucked nectar from about 6% of flowers. Both categories were not visited by pollinators. Thus, in all 21% of the total buds/flowers were damaged to the point of producing no fruit.

The flowers were foraged during daytime by bees, wasps, butterflies and birds for nectar and/or pollen (Figure 1, Table 4). While *Apis dorsata* and *A. indica* exclusively concentrated on nectar *Pseudapis* sp. foraged on pollen. Other bees foraged on both nectar and pollen. Wasps, butterflies and birds foraged on nectar only. In general flower visitors were low in density and of the total visits, bees made 62%, birds 23%, butterflies 9% and wasps 6%. The first foragers to the flowers were bees. Excepting honey bees, the other bees foraged during 0600–1000 h. The honey bees began foraging from 0700 h up to 1500 h. Wasps collected nectar occasionally during 0800–1500 h and butterflies during 0700–1600 h. Birds foraged between 0600 and 1700 h almost throughout the flowering period.

Data on the number of flower visits made in a minute and the time spent at a flower by an insect species are shown in Table 5. *Amegilla* sp. was more mobile and foraged a large number of flowers per minute. It was followed by *A. indica*, *Ceratina* sp., *Pseudapis* sp., *A.*

Figure 1. *Helicteres isora* with flowers and flower visitors. *a*, The honey bee *Apis indica* sucking nectar from d_1 flower; *b*, The bee *Pseudapis* collecting pollen from d_1 flower; *c*, The stingless bee *Trigona* collecting pollen from d_1 flower; *d*, The bird quaker babbler *Alcippe poioicephala* drinking nectar.

Table 5. Activity dynamics of bees at the flowers of *H. isora*

	No. of flower visits/min				Length of a visit/sec			
Visitor species	Sample size	Range	Mean	Standard deviation	Sample size	Range	Mean	Standard deviation
Amegilla sp.	10	9–15	12.0	2.45	10	2–5	2.9	1.28
Ceratina sp.	10	5–8	6.1	1.19	10	5–16	8.3	3.88
Trigona sp.	10	4–7	5.4	1.08	10	6–18	11.1	3.92
Pseudapis sp.	10	4–9	5.8	1.61	10	5–13	9.2	3.38
Apis indica	10	4–10	6.7	2.48	10	6–14	7.8	2.59
A. dorsata	10	3–9	5.5	2.46	10	3–8	5.8	1.81

dorsata and *Trigona* sp. The stingless bee *Trigona* sp. stayed longer at a flower, followed by *Pseudapis* sp. *Ceratina* sp., *A. indica*, *A. dorsata* and *Amegilla* sp.

Body washings of different bees for the pollen grains indicated that *Pseudapis* sp. could pick up more pollen than other visitors (Table 6); then came in order *Ceratina* sp., *Amegilla* sp. and *Trigona* sp.

The tubular nectariferous flowers with a rather wide mouth are probed differently by insects and birds. The insects foraged at the bluish-grey and avoided red and

deep-red flowers. The pollen-collecting bees usually landed at the rim of the staminal column and gathered pollen from the anthers. Sometimes they landed directly on the stigma and moved onto the anthers to gather pollen. In either case, they invariably touched the stigma and the anthers by their ventral surface. The bees which directly landed on the stigma effected cross-pollination if they carried the conspecific pollen from a previously visited flower on their ventral sides. The bees which directly landed at the rim of the staminal column largely effected self-pollination. The nectar-collecting bees, wasps and butterflies used the large petals for landing and then probed the flower. Since the pollination apparatus was away from the petals and nectar source, the foraging visits by these nectar-collecting insects do not effect pollination. Further, *A. indica* also made use of the holes punctured by the blister beetle at the floral base for obtaining nectar easily.

The birds probed the flower from the front for nectar by landing on the nearby twigs. They probed the bluish-grey flowers occasionally, red ones very frequently and deep-red ones frequently. While probing the flowers, *Alcippe* and *Acridotheres* contacted the anthers and stigma with their bill and also the foremost part of their head invariably effecting pollination and getting powdered with pollen on the bill/forehead. Considering their probing behaviour and the manner of effecting pollination, these two birds species could be treated as appropriate pollinators. However, their visits were very low. Cursorial observations on the abundance of these birds in the area also showed that they were numerically very small. *Pycnonotus* cut the anterior part of the staminal column and gynophore containing the anthers and stigma with its beak prior to probing the flower for nectar and thus damaged the sexual apparatus.

The flowers of *H. isora* are scentless, produce copious nectar of low sugar concentration, and possess robust or tough corolla with a rather broad mouth, all characters associated with ornithophily[7–9]. The d_1 flowers of *H. isora* are bluish-grey, turning to light red by the evening of d_1, to red by the morning of d_2, and to dark red by the evening of d_2. These observations of floral colour change in *H. isora* differ from those of Gamble[10] and Santharam[1] who observed that the flowers were red, fading to 'lead' (blue) towards the end of the day. The red coloured flowers are especially attractive to birds and relatively predominant among the bird-flowers in the tropics[11–13], the display of colours other than red by bird-flowers is not totally unusual[9]. According to Jaeger[14], the most highly evolved plants pollinated by the birds are characterized by the purity of the colours red, blue and green. Many bird-visited flowers are white[9]. Thus an absolute correlation between floral colour and bird-pollinations need not always be expected.

Floral colour changes occur in a wide variety of plant taxa[15]. Such changes are often accompanied by changes in nectar production[16,17]. In *H. isora* also a change in nectar production occurs with the change in floral colour. Nectar is secreted in only d_1 flowers which are bluish-grey. There is no production of nectar in d_2 and d_3 flowers which are red and deep-red, respectively. However, because of low density of foragers, the nectar of d_1 flowers was not totally harvested, and consequently flowers of other ages also contained nectar. Interestingly, the two bird species, *Alcippe poioicephala* and *Acridotheres tristris* did not discriminate the bluish-grey flowers of d_1 and the red (d_2) and deep-red (d_3) flowers, but visited red and deep-red flowers rather more frequently than the bluish-grey ones. A similar trend in nectar production occurs in *Combretum farinosum*[17] in which d_1 inflorescences are green changing to orange (d_1 and d_3) and red (d_4 and d_5), and nectar production occurs only in d_1 inflorescences. In contrast with the present observation, the birds (hummingbirds) *C. farinosum* paid sparse visits to red inflorescences.

Floral colour change is not without any advantage; but there is no consensus among the various workers regarding the advantages[18]. The changes may ensure a reduction in nectar thievery[19], an increase in pollinator efficiency[20], maintenance of pollinator constancy[21], increased attraction of pollinators[17] and maximization of foraging time of the pollinators[18]. In *H. isora*, the bird species implicated in pollination paid relatively more visits to the red and deep-red flowers, a tendency attributable to the increased attractiveness. As will be described later, the increased visits to red (d_2) flowers were not without advantage to the plant, for the stigma receptivity continued until the evening of d_2 and such prolonged receptivity of the stigma enhanced the opportunity for cross-pollination[22]. Thus the visits to red flowers might have contributed to more of out-crossing and the attendant genetic variation, and thus enhanced plant fitness.

Hand pollinations demonstrated that *H. isora* could reproduce through autogamy, geitonogamy and xenogamy, and the pollen–ovule ratio (1085) was a little over than that expected for facultative xenogamy (ca. 800)[3]. Bagged inflorescences did not show any fruit set, thereby indicating the necessity of an external agent to mediate pollination. The flowers were foraged during

Table 6. Pollen pick-up by bees on *H. isora* as revealed by body washings

Visitor species	Sample size	Pollen grains		
		Range	Mean	Standard deviation
Pseudapis sp.	5	36,200–63,200	51,700	10,366
Ceratina sp.	5	18,600–42,700	32,260	11,109
Amegilla sp.	5	4700–8300	6720	1681
Trigona sp.	5	2720–6940	4212	1768

daytime by birds as well as insects. Among the insect visitors of *H. isora*, the bees other the honey bees were only involved in carrying out pollen transfer. They made definite contacts with anthers and stigma during the process of pollen collection. *Pseudapis* was particularly important in that it confined to pollen collection only and very often it first alighted on the stigma and then crawled on to the anthers. If it was coming from other conspecific plant(s), its landing on the stigma should result in xenogamous pollinations. *Amegilla* is known for its swift foraging and thus might transport largely the xenogamous pollen. *Ceratina* and *Trigona* largely concentrated on the same clump and mediated autogamy and geitonogamy. The bird species *Alcippe* and *Acridotheres* exploited the flowers of *H. isora* by perching on the twigs in close proximity to the flowers as against the hovering behaviour of hummingbirds[23]. As already stated the two bird species visited the bluish-grey (d_1), red (d_2) and deep-red (d_3) flowers, but more frequently the red (d_2) flowers. The second day flowers contained no pollen but the stigma remained receptive until the evening. The visits of the two bird species resulted in autogamy, geitonogamy and xenogamy. But the prolongation of stigma receptivity into the second day and the anthers of these flowers containing no pollen, and the higher frequency of the bird visits on this day might have resulted in more of xenogamous pollinations. Utilization of common resources by the birds and insects also occurs in *Combretum farinosum*[17], and *Campsis radicans*[24]. In *C. radicans*, hummingbirds are the main pollinators followed by bumble bees, honey bees, whereas in *C. farinosum* only hummingbirds are implicated in pollination.

Santharam[1] indexed four bird species as the pollinators of *H. isora* in the Western Ghats (Tamil Nadu, India) which included *Turdoises striatus*, *Chloropsis autoforsus*, *Dicrurus leucophaeus* and *D. caerulense*. The two bird species that were pollinators of *H. isora* in the present study did not figure among the 11 bird visitor species listed by Santharam and also among the three bird species mentioned by Subramanya and Radhamani[25]. This indicates that *H. isora* might be visited and pollinated by different bird species in different regions. Even the small generalist or opportunist bees could well be the pollinators depending on the ecological situations as observed in the present study. It may be noted that *Alcippe* and *Acridotheres* are not specialized for nectar feeding[26], and their diet includes insects, grains apart from nectar[6], and therefore total reliance on these bird species for pollination cannot be an ideal and fitting strategy for *H. isora*. The pollen–ovule ratio also indicates that pollinators are unreliable[3]. By offering pollen as a reward to the unspecialized opportunistic bees, *H. isora* derives reproductive benefit.

The flowers partly eaten by the unidentified larvae, and the blister beetle and those damaged by the bird bulbul failed to produce fruit and such failures amounted to about 25%. As such their visits may be detrimental to the reproductive success of *H. isora*. But natural fruit production itself was low, 5–12%. Perhaps the excess flowers allowed the opportunity to take advantage of the favourable conditions as assumed by the bet-hedging strategy[27], or resource boom hypothesis[28], or they were meeting the male function[29]. More probably, the low natural fruit production might be due to inadequancy of pollinators.

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