

Pollination Ecology and Mating System of the Weedy Mint *Leonotis nepetaefolia* R.Br. in India

RAJU J S ALURI and C SUBBA REDDI

Department of Environmental Sciences, Andhra University,
Visakhapatnam 530 003

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The scarlet or orange-flowered *Leonotis* (Lamiaceae), a weedy species and a self-compatible and self-pollinating, produces large and small flowers (in the same verticil) with large amounts of nectar with low sugar concentration. The lower lip of the corolla withers immediately after the flower opens. The plants have facultatively autogamous mating system and produce completely viable seed from both large and small flowers in the complete absence or presence of pollinators like sunbirds of the genus *Nectarinia* and a stingless bee, *Trigona* sp. The plant's facultatively autogamous mating system is considered to produce weedy populations in India. Indian *Leonotis* is suggested to have evolved from an intermediate flower form that might have originated by natural hybridization between a large- and a small-flowered form that occur at different elevations in Africa and pollinated by sunbirds.

Key Words: *Leonotis nepetaefolia*, Flower size, Pollination, Facultative autogamy, Sunbirds, *Trigona*, Weed

Introduction

Leonotis nepetaefolia (Lamiaceae) is a scarlet or orange flowered weedy species that is pantropical and widely distributed in the warmer parts of north America (Freeman et al. 1985). Cruden (1976) believes this species varies in flower size/floral features and originated in Africa and was introduced into North America recently. He also believes that there are three distinct flower forms in Africa, each of which is represented by weedy races in either the New World or elsewhere in the Old World. He provides some fragmentary data on the floral biology and speciation of the large- and small-flowered forms and based on pollen-ovule ratios, reports that the large-flowered form is a xenogamous race in the New World. An autogamous race may have evolved from this

form as an escape from horticulture. He also states that there is a third flowered form of *L. nepetaefolia* in eastern Africa undoubtedly giving rise to weedy populations in India, Southeast Asia, Indonesia, Australia, etc.

The large-flowered form of *L. nepetaefolia* is pollinated by sunbirds of the genus *Nectarinia* in Africa (Gill & Wolf 1975, Gill & Conway 1979) and by large bees in the central highlands of Mexico (Cruden 1976). The small-flowered form in the coastal tropics of the New World is pollinated by humming birds and small bees (Cruden 1976). There is no information available on *L. nepetaefolia* in other parts of the Old World. In India, *L. nepetaefolia* is widely distributed along the east coast and also occurs in the elevational range 1-800m in different parts of South India. In the present

study, we describe the flower form of *L. nepetaefolia* in India, its pollination ecology and its mating system.

Materials and Methods

Leonotis nepetaefolia (*Phlomis nepetaefolia* L.) is an annual weed occurring at elevations below 800 m. It is frequent along roadsides and open forests in Visakhapatnam (17°42'N and 82°18'E) and confined to banks of irrigation canals in Turimella (15°10'N and 18°45'E) in the State of Andhra Pradesh, India. Flowering plants occur in moist shaded and sunny places. In both habitats, the plants flower simultaneously. After preliminary observations made in November 1983, intensive studies were carried out in October-January 1984 and 1985. To determine flowering phenology, 10 inflorescences, selected at random, were tagged before the initiation of blooming and recorded daily for the number of open flowers. These were then removed to avoid recounting on the next day. Tagged inflorescences were followed until they ceased flowering to obtain data on the lifetime of the inflorescences and the rate of flower production each day. In the first year of our observations, we noticed differences in flower size between the first and last flowers within a verticil. In the second year floral morphometric differences were recorded. Following preliminary observations on diurnal anthesis, flowers anthesing each hour during the total period were counted from 10 randomly selected inflorescences marked before anthesis. The same procedure was used to measure the rate of anthesis on rainy, cloudy, and clear days. Concurrently, prevailing air temperatures, RH were recorded. Time of anther dehiscence on each of these days were recored (by observing the anthers with a 10 × h and lens three hours before anthesis and until floral dehiscence). Undehisced mature anthers, immersed separately in a drop of lactophenol

aniline-blue, were observed under the microscope, and the number of pollen grains/anther and pollen production per flower were estimated. Simultaneously, structural characters of pollen grains were observed, and their size was measured with a calibrated ocular micrometer. Pollen-ovule ratios were determined by dividing the number of pollen grains per flower by the number of ovules per flower. Pollen-viability was tested after hand-pollinations using relatively fresh stigmas and stigma receptivity was determined by hand-pollinations at regular short intervals with relatively fresh pollen and by visual examinations (Aluri 1989). Flower lifetime was taken as the time interval between flower-bud opening and dehiscence of the corolla along with the stamens and style. To quantify the nectar produced by the flower, ten flowering verticils were enclosed with paper bags. When flowers started production of nectar, measurements were made on a succession of flowers until nectar production stopped at hourly intervals by squeezing the nectar from the base of the corolla into a capillary tube. The same procedure was used for measuring the nectar in large and small flowers. The total amount of nectar production per flower was then calculated. The concentration of sugar in nectar was recorded in the field in sucrose equivalents with a temperature-compensated hand refractometer. The sugar composition of nectar was determined by paper chromatography using a butanol-acetone-water solvent and aniline hydrogen phthalate as developer. Standard solutions of glucose, fructose and sucrose were run simultaneously for comparison. The presence of aminoacids was determined with 0.2% ninhydrin developer and the presence of proteins with a bromophenol-blue developer.

Breeding behaviour by apomixis, autogamy, geitonogamy and xenogamy was tested through controlled pollinations.

Apomixis was tested by bagging the emasculated flowers, autogamy by bagging the flowers and by pollinating the flowers with the pollen of the same flower, geitonogamy by pollinating the flowers with pollen of the same plant, and xenogamy by pollinating the flowers with pollen from a different conspecific plant. The percentage of fruit and seed set was also calculated for the plants at Turimella and Visakhapatnam. Fecundity was expressed as percentage of seed set for the flowers pollinated.

Flower visitors were sunbirds, a bee, an ant and some butterfly species. Sunbirds were identified by referring to Salim Ali (1988). The bee and the ant were identified by a comparison with the specimens collected from Turimella and identified by the Zoological Survey of India, Howrah. The butterflies were identified by referring to Wynter-Blyth (1957) and Varshney (1983). Foraging activity of these visitor species together with their foraging behaviour, forage resources sought, pollination potential and their ability in depleting and depositing pollen were thoroughly investigated by visual means. The ability of

the bee species in pollen transfer was separately quantified. The depletion and deposition rates under total foragers activity were also quantified at two-hourly intervals. All the data collected are presented in tables. Photographs for the sunbirds foraging at *Leonotis* flowers are presented in figure 1.

Results

The results on the plants of *Leonotis nepetaefolia* at Turimella and at Visakhapatnam are presented separately.

Turimella

Plant phenology: It is an annual herb. It depends on local rains for seed germination and growth. It starts vegetative growth after heavy local rains in September and flowers from mid-October to December mid-January. Plants in moist shaded places are usually 1-2 m tall and have vigorous stems and dark green leaves. Plants in moist, sunny places are 0.5-1 m tall with thin stems and light green leaves. In both places, the plants grow in patches, may reseed themselves and persists for several years. They die after



Figure 1 *LEONOTIS NEPETAEFOLIA* AND SUNBIRDS

A : Illegitimate flower probing by *Nectarinia zeylonica* for nectar

B : Conventional flower probing by *N. asiatica* for nectar

setting seed and their dried vegetative and flowering stalks remain erect. The total life period of an individual plant from seed germination to dispersal of newly produced seeds is about 4 months.

Flowering phenology: The individual plant consists of 5-8 upright stems each bearing terminal, whorled inflorescence. Each inflorescence bears flowers in three or rarely four or five dense, globular verticils. Within each verticil the flowers are arranged in whorls and open in basipetal succession for 63 ± 15 days. The basal verticil flowers earliest, the second verticil two days after the first, and the third a week after the second. About 500 ± 128 flowers are produced per

verticillaster (table 1). Of the total flowers per verticillaster, 46% are produced in the first 15 days, 36% during the next 15 days and the rest (18%) during the last 25 days of its flowering.

Anthesis and anther dehiscence: Flower buds are fully developed by late evening and open at 2100-0200 hr. Quantitative data on the rate of anthesis under different weather conditions indicate that there is a slight variation in the period and rate of anthesis. On clear days, the anthesis period is between 2100 and 2400 hr with a peak at 2200 hr. On overcast and drizzly days, the anthesis period is from 2200 to 0200 hr, the peak hour of anthesis being 2300 hr (table 2). The flowers

Table 1 Duration of flowering time and total flower production per verticil in inflorescence of *L. nepetaefolia*

Character	First verticil			Second verticil			Third verticil		
	Range	Mean	S.d	Range	Mean	S.d.	Range	Mean	S.d.
Flower number	78-310	162	93	154-219	188	23	89-176	137	31
Productive days	26-70	45	16	39-52	45	5	27-45	36	6
Total flowering life in days	40-83	57	16	43-59	50	6	38-47	42	3

Sampled flowers 10, each whorl; S.d. Standard deviation

Total flowers per inflorescence; Mean 500, Range 321-671, S.d. 128

Inflorescence lifetime; Mean 63, Range 47-79, S.d. 15

Table 2 Daily rate of anthesis as a function of time in *L. nepetaefolia*

Time (hr)	November 4/5, 1983			November 6/7, 1983			November 8/9, 1983		
	i	ii	iii	i	ii	iii	i	ii	iii
2000	0	78	28	0	80	28	0	84	25
2100	0	78	28	0	80	27	7	85	24
2200	13	81	27	18	83	27	65	86	24
2300	38	83	25	58	84	26	21	88	24
2400	24	84	25	8	85	24	7	92	24
0100	13	87	24	10	86	24	0	93	25
0200	12	87	24	6	86	24	0	94	25
0300	0	87	24	0	86	24	0	94	26
	Drizzle			Sky overcast			Sky clear		

i, Flowers anthesed, % of daily total from ten randomly selected individual plants

ii, Relative humidity (%)

iii, Air temperature (°C)

are protandrous with the anthers dehiscing about 30 minutes prior to flower-opening. The stigma becomes receptive following anthesis. The time of anther dehiscence is the same on different weather days.

Flower morphology: The flowers expand in the verticils and orient horizontally to the axis of the verticillaster. The first emerged flowers are significantly larger than those emerging later within the verticil. This flower-size variation occurs gradually. The differences in flower diameter and in floral parts are provided in table 3. These differences are more common in plants growing in exposed places with less moisture. The flowers are bilabiate, scarlet, tubular, nectariferous and gullet-shaped. The calyx is tubular and hairy. The bilabiate corolla has a well developed upper lip with a villous crown and poorly developed tripartite glabrous lower lip. The lower lip fully expands when the flower is open but withers within an hour or two. The tubular portion of the corolla is full of nectar. The proximal third of the corolla tube is characterised by four hairy, fringed partitions. The proximal partition is the most substantial. It consists of

a hard rim supporting a dense, almost impenetrable fringe of short hairs. There is a small opening in the center of the tube. The second, more distal partition also consists of a hard rim attached to the corolla wall. The hairs of this partition are shorter than those of the proximal partition. The third partition is also of a similar somewhat smaller rim with few or no hairs. The fourth partition is rudimentary and with fragments of rim material without hairs. The stamens are held together by hairy filaments. The anthers are oriented towards the upper lip and located within the villous crown. The bicarpellary ovary has four ovules and a gynobasic style terminated by a stigma with unequally divided lobes. The stigma is just below the anthers and covered by the upper lip.

Pollen characters: The mean number of pollen grains per flower is 10412 ± 172 (Range 10,000-10,884). The ratio of pollen production per ovule is 2603:1. The pollen grains are 44 μm in diameter, spheroidal and with a smooth surface and granular cytoplasm.

Pollen viability and stigma receptivity: Hand-pollination tests show that the pollen

Table 3 Morphometric data for flowers within verticils of *L. nepetaefolia*

Floral part	First emerged flowers (large)			Last emerged flowers (small)		
	Range (mm)	Mean (mm)	S.d.	Range (mm)	Mean (mm)	S.d.
Flower length	32-35	33	0.0948	23-24	23	0.0473
Flower diameter	7	7	0.0000	4-6	5	0.0603
Tube length	15-16	15	0.0760	8-11	11	0.0935
Corolla upper lip	15-17	16	0.0707	11-12	12	0.0524
Calyx	23-27	24	0.1173	17-18	18	0.0404
Short stamen	14-16	15	0.0943	10-11	11	0.0032
Long stamen	15-18	16	0.1080	11-13	13	0.0680
Pistil.	24-29	26	0.1813	16-20	18	0.1027

S.d. : Standard deviation

Sampled flowers for each category were 15 from 10 individual plants

is viable following anther dehiscence. It is 100% viable for the first 33 hours, 67% for the next 4 hours, 47% for the next 5 hours, 13% for the next 2 hours and inviable thereafter. The total period of pollen viability is 44 hours (table 4). Stigma receptivity is indicated by spatial separation of its two lobes. It is 100% for the first 16 hours, 80% for the next 16 hours, 25-10% for the consecutive 5 hours and absent thereafter. The total receptive period of the stigma is 37 hours (table 4).

Table 4 Results of hand-pollination tests for pollen viability and stigma receptivity in *L. nepetaefolia*

Treatment	-Flowers pollinated	-Flowers fructed	Fructing (%)
Pollen viability (begins from anther dehiscence)			
after 12 hours	15	15	100
16 hours	15	15	100
33 hours	15	15	100
37 hours	15	10	67
42 hours	15	7	47
44 hours	15	2	13
45 hours	15	0	0
46 hours	15	0	0
Stigma receptivity (following anthesis)			
after 12 hours	20	20	100
16 hours	20	20	100
30 hours	20	20	100
32 hours	20	16	80
33 hours	20	16	80
34 hours	20	5	25
37 hours	20	2	10
38 hours	20	0	0
40 hours	20	0	0

Flower life-time: Flowers remain in place for about 40 hours. The first floral part to wither, within an hour or two after anthesis is the lower lip of the corolla. The remainder of the corolla remains intact until dusk of the 2nd day. The corolla, stamens and style fall off after the stigma loses its receptivity in the afternoon hours of the 2nd day. The calyx is persistent, conceals the developing ovary by

elongation after fertilization and disperses the seeds.

Nectar characters: Nectar secretion begins about 2½ hours before anthesis. Secretion is continuous for 13½ hours. Flowers that open at 2100 hr start producing nectar between 1830 and 1900 hr. This continues into the following day until 0800 hr. No further secretion occurs in the remaining period of flower life (table 5).

Table 5 Rate of nectar secretion in large and small flowers of *L. nepetaefolia* anthesing at 2100 hr

Time (h)	Mean volume of nectar (µl)	
	Large flower	Small flower
1830	0.0	0.0
1900	0.5	0.3
2000	1.0	0.7
2100	0.5	0.5
2200	0.4	0.6
2300	0.3	0.3
2400	0.4	0.5
0100	0.5	0.8
0200	0.9	0.3
0300	0.2	0.4
0400	0.7	0.3
0500	0.4	0.2
0600	0.5	0.3
0700	0.7	0.5
0800	1.0	0.3
0900	0.0	0.0
1000	0.0	0.0
Total nectar volume	8.0	6.0

Flowers sampled 10 for each flower size at each hour of measurement

Flowers that open consecutively follow the same pattern as flowers anthesing at 2400 hr, which secrete nectar until 1100 hr. Anthesis is delayed on days with drizzle and overcast sky and extends flowering until 0200 hr. Consequently, plants having flowers anthesed at 0200 hr secrete nectar until 1300

hr. The total nectar secretion period, irrespective of the hour of flower-opening, falls between 1830 and 1300 hr. The corolla tube is full of nectar when nectar secretion ceases. The total amount of nectar produced per large flower is 8.0 μ l and per small flower is 6.0 μ l. Flowers do not have a definite pattern in the amount of nectar production throughout the period of secretion. The nectar sugar concentration is the same in both large and small flowers, viz., 18% before dawn and from 18 to 22% after sunrise, probably as a consequence of evaporation. Sugar concentration goes as low as 12% when nectar is diluted with drizzle or rain. Sugar components of nectar are sucrose, glucose and fructose in that order of concentration. Aminoacids and proteins are also found in the nectar.

Breeding and mating behaviour: The results of breeding and mating tests are presented in table 6. They show that the plant is not apomictic. It is both self- and cross-compatible and can reproduce through inbreeding and outbreeding. The different mating systems tested indicate that the plants

have the capacity to reproduce by any means of conspecific pollen deposition on the stigma. The success of all experimental mating systems, except for xenogamous pollination, is 100% indicating that a pollen vector is not necessary and that self-pollination occurs when the dry, light pollen drops onto the receptive stigmas. Self-pollination, however, is the predominant system since cross-pollination is less successful. Seeds are smaller in small flowers than those in large flowers. Other morphological features of the seeds are apparently identical.

Flowers visitors: Flowers are visited by foragers during 0600-1800 hr, and a list of all foragers on *Leonotis* recorded in the study period is provided in table 7. Sunbirds, *Nectarinia asiatica* and *N. zeylonica* visit the flowers throughout the day. The same schedule of foraging is maintained by them throughout the flowering period of the *Leonotis*. Sunbirds usually perch before foraging. They probe the flowers legitimately and illegitimately. In legitimate probing they sit on the stalk of *Leonotis* below a

Table 6 Results of breeding experiments for *L. nepetaefolia*

Test	Treatment	Flowers pollinated	Flowers fruited	Fruiting (%)	Seeding (%)	Fecundity (%)
Apomixis	Emasculated, bagged	25	0	0	0	0
Automatic self-pollination	Untreated, bagged	25	25	100	100	100
Effectiveness of self-pollination	Self-pollinated by hand within flower, bagged	25	25	100	100	
Effectiveness of self-pollination	Self-pollinated by hand within individual plant, bagged	25	25	100	100	100
Effectiveness of cross-pollination	Cross-pollinated by hand	25	12	48	62	30
Open-pollinated						
Visakhapatnam	Untreated, not bagged	600	600	100	100	100
Turumella	Untreated, not bagged	500	500	100	100	100

Table 7 Flower visitors on *L. nepetaefolia*, their forage type and body parts with pollen

Forager species	Resource sought	Body parts with pollen
Hymenoptera		
Apidae		
<i>Trigona</i> sp.	pollen	ventral side, legs, head
Formicidae		
<i>Camponotus sericeus</i>	nectar	—
Lepidoptera		
Danaidae		
<i>Danaus chrysippus</i>	nectar	proboscis (?)
<i>Euploea core</i>	nectar	proboscis (?)
Pieridae		
<i>Catopsilia crocale pomona</i>	nectar	proboscis (?)
<i>Catopsilia pyranthe</i>	nectar	proboscis (?)
Papilionidae		
<i>Polydorus aristolochiae</i>	nectar	proboscis (?)
Nymphalidae		
<i>Hypolimnas misippus</i>	nectar	proboscis (?)
Aves		
Nectarinidae		
<i>Nectarinia asiatica</i>	nectar	bill, forehead
<i>Nectarinia zeylonica</i>	nectar	bill, forehead

verticil and insert the bill into the flower frontally (figure 1B). Consequently, the bill and forehead region of the sunbirds are sprinkled with powdery, pollen, and the stigma is usually dusted with either self- or cross-pollen. In illegitimate probing, they slit or depress the middle portion of the corolla from above with their bill and extract the nectar (figure 1A). The stigma and stamens are then diverted from the hooded upper corolla lip without damage and stigma is dusted with pollen resulting in self-pollination only. In both foraging approaches, all the flowers of a ring of the verticil are usually probed during a single sunbird foraging visit. Sunbirds spin quickly around the ring of flowers probing consecutively into adjacent flowers. Sometimes, this spinning by the sunbirds results in skipping of flowers or revisiting the same flowers. Sunbirds do not visit one-day old flowers. Regardless of forager's

behaviour, *Leonotis* in large aggregations is their main nectar source. When *Leonotis* is in full bloom, sunbirds feed only infrequently from other species in the area. When the rate of emergence of new flowers is declined and flower density is reduced, the sunbirds shift to *Anisomeles malabarica* and *A. indica*, the flowers of which are purple and produce high nectar sugar concentration (30-48%) and volume (1.6-1.8 µl). *Anisomeles* species are perennial shrubs and have a patchy distribution in the study area. When the flower density of *Leonotis* is considerably reduced, the sunbirds restrict their visits to *Anisomeles* species.

The bee, *Trigona* is also a regular visitor for pollen on *Leonotis* but forages only during 1100-1500 hr. It avoids foraging on sunbird-perforated flowers. Five or six individuals of this bee often forage around the same verticil. Such groups of bees attract sunbirds which fly rapidly to the verticil and

devour them. Four or five successive foraging visits of a single bee deplete nearly all pollen from the flower and results in deposition of 41-214 pollen grains on the stigma (table 8). The bee gathers pollen by turning its body upside down and moving back and forth between the stigma and the anthers. Its foraging activity, therefore, results in self- and or occasional cross-pollination. Pollen depletion and deposition rates at regular intervals during the foraging period of sunbirds and bees are presented in table 9. At the close of foraging activity, a few pollen grains remain in the anthers and a considerable amount of pollen is deposited on the stigma.

The ant, *Camponotus sericeus* crawls all the time over the entire plant and seldom forages for nectar laterally without contacting the stigma or anthers. It usually

gleans nectar from the nectariferous calyces without corollas. Infrequent butterflies visiting the flowers laterally for nectar touch neither anthers nor stigma, while frontal visits seldom cause the proboscis of the butterfly to contact the stigma or anthers.

Visakhapatnam

L. nepetaefolia has a sparse distribution in Visakhapatnam. There are no other plant species blooming simultaneously with *Leonotis* in its vicinity. Its floral biology is similar to that of *Leonotis* at Turimella except for flower visitors. The flowers are not visited by foragers and consequently, the floral nectar remains in the calyx for several days after the corolla with style and stamens drops off. Each large and small flower sets four nutlets in the complete absence of foragers. Since Janaki Bai and Subba Reddi

Table 8 Pollen depletion and deposition in *L. nepetaefolia* under *Trigona* foraging activity

Visit	Mean – pollen depleted/flower/visit	Pollen depleted/flower (%)	Mean – pollen deposited on stigmas/visit	Pollen deposited (%)
One	6024	58	214	47
Two	2178	21	105	23
Three	1249	12	98	21
Four	961	9	41	9

Mean pollen production per flower = 10412

Table 9 Pollen depletion and deposition in *L. nepetaefolia* under foraging activity of sunbirds and insects

Time (h)	Mean – pollen depleted/flower	Pollen depleted (%)	Mean – pollen deposited	Pollen (%)
0600	2	0	0	0
0700	304	5	18	1
0900	1262	11	392	30
1100	5616	53	455	34
1300	1938	18	204	15
1500	930	8	159	13
1700	360	6	94	7

(1983) found that wind-pollination does not occur, the flowers are self-pollinated gravitationally by powdery pollen grains dropping onto the receptive stigma lying just below.

Discussion

Plants of *L. nepetaefolia* in India which we studied have both large and small flowers borne in the same verticil and the plants are distributed vertical in an altitudinal range of 1 to 800 m. It flowers from mid-October through December or mid-January. Its vegetative growth starts in September after heavy local rains unlike the African large-flowered form which blooms from March through August (Gill & Conway 1979). Anthesis occurs during night hours and is slightly regulated by weather conditions. The Mexican large flower-form seems to anthese similarly (Cruden et al. 1983). The flowers exhibit weak protandry, and the time of anther dehiscence is not regulated by weather. The first-emerged flowers of the verticil are large and nearly similar to the flower size of the African sp. (Gill & Conway 1979) or Mexican large-flowered form (Cruden et al. 1983). The large flowers produce relatively higher amount of nectar than that of the small flowers. The nectar volume in African or Mexican large-flowered forms is nearly the same as that of the large-flowered Indian *Leonotis*. The Mexican small-flowered form produces an amount of nectar that is nearly equal to that of the amount in small flowers of Indian *Leonotis*. The large and small flowers resemble each other in other floral characteristics. The time of initiation and cesation of nectar production in both large and small flowers seems similar to that in the Mexican large-flowered form. The African large-flowerd form, on the contrary, produces nectar between dawn and dusk. It also exhibits variation in the rate of nectar production in different flowers attributed to

the age of verticil, reabsorption of some nectar in unvisited flowers and to the accumulated-nectar falling from the flower. Further, this flower form continues to produce nectar even after the corollas have fallen usually in the early morning (Gill & Conway 1979). Flowers of Indian *Leonotis* have a long period of nectar production during night and until the next afternoon. It occurs as a consequence of the onset time of nectar secretion that varies with individual flowers which open at different times within the anthesis period. The nectary ceases to function permanently while the corolla is still in place. This condition deviates from the African large-flowered form which is reported to produce nectar during daytime when sunbirds do foraging (Gill & Conway 1979). The little variation in the volume of nectar production in large and small flowers of Indian *Leonotis* can be related to the size of the flower. The nectar sugar components are the same as those in the Mexican or African flower forms. The pollen-ovule ratio of the Indian *Leonotis* is the same as that of the small-flowered form of Mexico with a facultative xenogamous mating system which is pollinated by hummingbirds and small bees (Cruden 1976). The Mexican large-flowered form representing a xenogamous mating system has the pollen-ovule ratio five times greater than that of the small-flowered form of Mexico and the large flowered-form is pollinated by large bees (Cruden 1976). Cruden (1977) postulates that the pollen-ovule ratio is correlated with the breeding system of the plant. This is not true with the Indian *Leonotis* which exhibits facultative autogamy with a high pollen-ovule ratio. It is unknown why it produces such a high pollen-ovule ratio?

Fruiting is scanty in flowers pollinated by xenogamous pollen. It shows that the plants limit xenogamic fruiting and seeding in open-pollinations performed by sunbirds and bees. Hand self-pollinated and open-

pollinated flowers produce complete fruit and seed set, which means all four ovules of each flower develop into viable seeds in the complete absence or presence of foragers activity. In natural condition, both large and small flowers of the Indian *Leonotis* in Visakhapatnam, where the plants are not visited by any animal species, result in viable seed. The Indian *Leonotis* is therefore self-compatible and self-pollinating. Self-pollination occurs as a result of powdery pollen grains falling onto the stigma below and is known as "gravitational pollination". The stigma is receptive by spatial separation of its unequal lobes. It shows no movements during its entire receptive phase. Cruden (personal communication) showed that in the Mexican small-flowered form, the stigma recurves into pollen remaining in the anthers after bird or bee visits or remains in the anthers of unvisited flowers for self-pollination after cross-pollination failed. This suggests that in this flower-form, the bilobed stigma situated above the level of the didynamous anthers, moves. This needs to be further investigated. Cross-pollination in the Indian *Leonotis* is effected by intense sunbird foraging activity. Sunbirds of the genus *Nectarinia* employ legitimate and illegitimate approaches exploiting floral nectar. Sunbirds which have 25-27 mm long bills very frequently probe the flowers illegitimately by slitting or depressing the middle portion of the corolla from above with their bill thereby bypassing the pollination apparatus. This foraging behaviour is not due to the difficulty of reaching nectar by the conventional or legitimate foraging approach but appears less expensive in terms of caloric energy expenditure. Other species of the genus *Nectarinia* are reported to exhibit such a foraging behaviour to exploit the floral nectar of the large-flowered form in Africa. There, long-billed sunbirds employ a conventional foraging approach, and the

shorts-billed ones probe the flowers illegitimately by slitting the sides of the base of the corolla as they have difficulty in reaching the nectar by the legitimate approach (Gill & Conway 1979). Humming birds also apply an illegitimate foraging approach and slit the corolla or depress it from above to exploit the nectar from the large flower-form of Mexico (Cruden 1976). Sunbirds exhibit discriminatory power and avoid visiting day-old flowers of the Indian *Leonotis*. The foraging behaviour of the pollen-feeding *Trigona* on *Leonotis* suggests that the bee has limited hours of foraging and usually visits a few flowers on the same plant. Insect activity thus results in early self-pollination, which in natural conditions occurs when the pollen is dry and powdery. *Trigona* bees are the usual prey of sunbirds and when foraging in groups at one verticil attract the birds. This predator-prey relationship reduces *Trigona* activity considerably. This situation may influence negatively on the percentage of outcrossing fruit and seed.

The large-flowered form in Africa is self-compatible, and flowering inflorescence protected from sunbird visits set seed that germinated as well as that produced by flowers visited by sunbirds. Several inbred generations have also produced total viable seed (see Gill & Gonway 1979). The large- and small-flowered forms in Mexico, when grown in a green house excluding pollinators, set seed thus suggesting that they are self-compatible and self-pollinating (Cruden, 1976). Flower forms in Africa, Mexico and India are self-pollinating suggesting that *L. nepetaefolia* in both New and Old World is facultatively autogamous with a certain amount of outcrossing achieved through continued foraging activity of sunbirds and small bees in the Old World and of hummingbirds and small bees in the New World. Floral characteristics such as scarlet colour, lack of odour,

concealed nectar, absence of landing platform and nectar guides characteristic of insect-pollinated flowers, and nectar with low caloric value suggest ornithophily. Nectar concentrations of *L. nepetaefolia* are comparable to those of other sunbird flowers such as *Aloe graminicola* (17.4%) (Wolf 1975), *A. kedongensis* (Liliaceae) (18.9%) (see Gill & Conway 1979), *Phragmanthera dshallensis* (Loranthaceae) (21.0%) (Gill & Wolf 1975), *Leonotis mollissima* (25.0%) (see Gill & Conway 1979), and *L. leonurus* (Lamiaceae) (23.4%) (Frost & Frost 1980) in Africa. Sunbirds at Turimella restrict their visits to *Anisomeles malaburica* and *A. indica* with nectar concentrations between 30-48%, after the flower density of *Leonotis* starts to decline. The range of sugar concentrations in nectars of various plant species visited by sunbirds in Africa is 9-48% (Stead 1967) and in humming bird flowers is 13-35%, averaging 20-25% (Baker 1975).

The success of facultatively autogamous mating system in Indian *Leonotis* seems consistent with viable seed production from cultivated plants in Africa without outcrossing through several generations (see Gill & Conway 1979). This mating system can be considered essential for *L. nepetaefolia*'s colonizing of many different niches found in weedy habitats (Allard

1965). The plant may have produced the many different inbred intra-specific populations occurring in different flower forms and certainly could provide its ability to occupy rapidly heterogenous habitats (Mulligan 1972). The widespread *L. nepetaefolia* in South India, where it occurs below 800 m, is a weedy race maintaining limited genetic variation by inbreeding which may cause extinction of the plant. This observation is corroborated by gradual decline of *Leonotis* populations at Visakhapatnam, where its flowers are never visited by animals so that self-pollination and the continuous inbreeding may reduce the population.

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