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continued on the back inside cover

Cover: Himalayan Gray Langur *Semnopithecus ajax* (adult female) © Rupali Thakur.



Nectar robbing by bees on the flowers of *Volkameria inermis* (Lamiaceae) in Coringa Wildlife Sanctuary, Andhra Pradesh, India

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Abstract: Floral traits that shape the floral architecture are important to allow or disallow flower visitors to access nectar and effect pollination. Specialization in floral architecture is vulnerable to flower visitors that exploit nectar by robbery without effecting pollination. In Coringa Wildlife Sanctuary in Andhra Pradesh, India, studies on the exploitation of nectar by robbery in plant species with specialized flowers are completely lacking. We carried out a study on the foraging activity of insect foragers and nectar robbing by bees on the specialized nectariferous flowers of an evergreen shrub, *Volkameria inermis* growing in the landward side of this sanctuary. Field observations indicated that the flowers of this species facilitate legitimate probing only by butterflies and diurnal moths which while seeking nectar effect pollination. However, two bee species *Anthophora dizona* and *Xylocopa pubescens* seek nectar illegitimately as primary nectar robbers by making a slit/hole into the corolla tube from outside bypassing the flower front. Additionally, *A. dizona* gathers pollen legitimately from the stamens which are exposed and placed outside the corolla tube. The stigma is also placed outside the corolla tube but this bee indiscriminately makes attempts to collect pollen from the stigma, as a result of which pollination occurs. Nectar robbing by these bees leads to a reduction in nectar volume in robbed flowers and brings about variability in the standing crop of nectar. As a result, the pollinating butterflies increase the number of nectar foraging visits and shuttle between populations of *V. inermis* in quest of more nectar to meet their daily metabolic requirements. Such a foraging behavior increases pollination rate in general and cross-pollination in particular, which in turn increases plant fitness in *V. inermis*. Therefore, the nectar robbing by bees appears to have a positive effect on plant fitness through change in seed set rates.

Keywords: *Anthophora dizona*, butterflies, nectariferous flowers, plant fitness, tubular corolla, *Xylocopa pubescens*.

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INTRODUCTION

Floral adaptations that promote pollen transport by pollinators are treated as evidence of specialization to a particular pollinator type (Castellanos et al. 2003, 2004). Specialization in floral architecture is vulnerable to exploitation by flower visitors which remove or steal nectar without effecting pollination which in turn may show detrimental effects on plant fitness (Navarro 2001). Nectar robbers display a particular behaviour to steal nectar. A common form is primary nectar robbing in which the flower visitor makes a hole, slit, or tear in corolla tissue to steal nectar bypassing the floral opening used by legitimate pollinators; this form of robbing is most common on flowers with hidden nectar. The flowers with tubular corolla are vulnerable to nectar robbing (Rojas-Nossa et al. 2016). Another form is secondary nectar robbing in which the flower visitor acquires nectar through holes made by primary nectar robbers bypassing the floral opening used by legitimate pollinators (Irwin & Maloof 2002). Irwin et al. (2010) reported that all flower visitors are not pollinators. Some visitors rob nectar bypassing the contact with the anthers and/or stigma and the effects of this nectar robbing behaviour by robbers range from negative to positive on female and male components of plant reproduction. Rojas-Nossa et al. (2021) reported that nectar robbing behavior has negative, neutral and positive consequences according to life history traits of the interacting animals and the ecological mechanisms involved. These authors reported that nectar robbing has neutral effects on the reproduction of *Lonicera etrusca*. In this species, the nectar robbers act as pollinators and decrease the visitation rates of legitimate foragers.

The available information on the foraging activity and pollination in mangrove plant species of Coringa Wildlife Sanctuary indicates that different insect species act as pollinators there. *Ceriops decandra* is pollinated by bees and wasps, *C. tagal* by flies and honey bees (Raju & Karyamsetty 2008), *Avicennia alba*, *A. marina*, *A. officinalis* by insects (Raju et al. 2012), *Caesalpinia crista* by bees (Raju & Raju 2014), *Derris trifoliata* by bees (Raju & Kumar 2016a), *Scyphiphora hydrophyllacea* by bees and wind (Solomon Raju & Rajesh 2014), *Suaeda maritima*, *S. monoica*, *S. nudiflora* by wind and insects (Raju & Kumar 2016b), *Brownlowia tersa* by carpenter bees and honey bees (Raju 2019a), *Sarcolobus carinatus* by insects (Raju 2019b), *Xylocarpus granatum* and *X. moluccensis* by hawk moths (Raju 2020). In all these plant species, none of the insects have been reported as nectar robbers. Inouye (1983) reported that among

insects, bees, wasps and ants are the most common primary nectar robbers of which bees make up the vast majority, and include carpenter bees, bumble bees, stingless bees, and some solitary bees. These bees also act secondary nectar robbers. These bees use their mouthparts to pierce the floral tissues. Bumble bees use their maxillae, proboscis, or toothed mandibles to make holes. Gerling et al. (1989) reported that carpenter bees use their maxillae to make slits in the sides of the flowers. The insects that act as nectar robbers in some plants pay legitimate visits to the flowers of others growing in the same area and act as pollinators.

The aim of the present study was to carry out field studies on legitimate and illegitimate foraging visits to the flowers of a mangrove associate, *Volkameria inermis* L. (Lamiaceae) to collect nectar in Coringa Wildlife Sanctuary, Andhra Pradesh, India.

MATERIALS AND METHODS

The Coringa Wildlife Sanctuary is a wildlife sanctuary and estuary situated near Kakinada (16.716 °N, 82.245 °E) in Andhra Pradesh State, India. It is the second largest expanse of mangrove forest ecosystem in India with several viviparous, crypto-viviparous, oviparous mangrove plant species, and also with several mangrove associate plant species. In this sanctuary, *Volkameria inermis* is a mangrove associate that grows well with bushy habit in landward locations. It is a perennial with leaf shedding taking place year-long but this phenological event is quite prominent during summer season (March–May). The flowering occurs during rainy season from August to October but prolific flowering occurs during September. The study was carried out during the flowering season of 2019 and 2020 to observe the foraging activity of flower visitors in the collection of pollen and/or nectar. The flower visitors were observed on five sunny days in each month of the flowering season for their flower approaching, probing and forage collection behaviour. Nectar volume was measured by using a graduated pipette while its sugar concentration was recorded by using a hand sugar refractometer (Erma, Japan); twenty flowers were used for recording these two aspects. For the analysis of sugar types, paper chromatography method described by Harborne (1973) was followed. Nectar was placed on Whatman No. 1 of filter paper along with standard samples of glucose, fructose and sucrose. The paper was run ascendingly for 24 hours with a solvent system of n-butanol-acetone-water (4:5:1), sprayed with aniline oxalate spray reagent

and dried at 120 °C in an electric oven for 20 minutes for the development of spots from the nectar and the standard sugars. Then, the sugar types present were recorded.

The foraging activity was observed from sunrise to sunset to record the flower-visiting schedules of individual species. Bee species visiting the flowers were captured and identified by Zoological Survey of India, Howrah. Butterfly species visiting the flowers were identified instantaneously by consulting the book of Kunte (2007). The field methods described in Dafni et al. (2005) and Suvarnaraju & Raju (2014) were followed for the collection of data on foraging visits made, foraging schedule, foraging mode and flower handling time. The number of foraging visits made by each insect species were recorded for 10 minutes at each hour throughout the day from 0600 to 1800 for five days at random in July and August 2019 and again for five days at random in August and September 2020. Based on these visits, the mean number of total foraging visits made per day were calculated. The foraging mode employed for forage collection were also recorded while the insects were probing the flowers. The time spent for probing and collecting the floral reward by each insect species was counted in seconds by using a stop watch; the number of observations made was according to the foraging visits made to the flowers during observation period. Based on the data, the mean time for handling flowers to collect the forage by each insect species was calculated to understand the flower to flower mobility rate. Among the flower visitors, bees were found to exhibit nectar robbing behaviour; this behaviour was carefully observed in the field in order to quantify the number of flowers robbed from the total standing stock of flowers. A sample of 650 flowers from five populations was observed for recording the percentage of unrobbed and robbed flowers. The flower morphological characters were also noted to evaluate their specialized traits that contribute to the exploitation by nectar robbing bees. Further, the observations on the foraging activity of these bees on other plant species growing in the same area were also made to note whether they are resorting to display illegitimate or legitimate foraging behaviour to collect nectar.

RESULTS

Volkameria inermis flowers throughout the year with intense flowering during rainy season from July to September (Image 1a). It produces 3-flowered

cymes in leaf axils (Image 1b) which open on the same day (Image 1c) or in 2–3 days, between 1500–1800 h depending on the stage of the bud development. The flowers are pedicellate, large, fragrant, zygomorphic and functionally hermaphroditic. Calyx is green, cup-shaped at base and valvate apically. Corolla is white and tubular with 4–5 lobes separated from each other and reflexed. The stamens are 4 or 5, epipetalous and protrude out of the corolla mouth at flower-opening. The ovary is bicarpellary with 2–4 ovules and extended into a long style tipped with stigma. The flowers initiate nectar secretion soon after flower-opening but its secretion continues until the noontime of the third day. Individual flowers produce $3.6 \pm 1.3 \mu\text{l}$ of nectar with $17 \pm 2.13\%$ (sugar concentration made up of three sugar types, sucrose, glucose and fructose, and it is stationed around the ovary which is completely concealed due to tubular corolla.

The floral architecture is highly specialized and the stamens and stigma are exposed far beyond the rim of the corolla tube in synchrony with the unfolding of the petals. A diurnal hawk moth, *Macroglossum gyrans* Walker began visiting the flowers for nectar almost immediately after flower-opening (1530 h) and continued its activity until sunset (1800 h), again started visiting the flowers the next day during dawn hours from 0430 h to 0600 h and stopped its foraging activity thereafter; its foraging activity favors both self- and cross-pollination. The butterflies *Pareronia valeria* Cramer (Image 1d), *Danaus genutia* Cramer (Image 1e), & *Borbo cinnara* Wallace (Image 1f), the digger bee *Anthophora dizona* Engel (Image 2a,b), and the carpenter bee *Xylocopa pubescens* Spinola (Image 2c), visited the flowers regularly during day time (Table 1).

Of these, only butterflies probed the flowers legitimately from the flower-opening side to insert their proboscis to reach the location of nectar; their proboscis length facilitated to access and collect nectar with great ease (Table 1). In bees, *A. dizona* foraged for both pollen and nectar while *X. pubescens* foraged for nectar only. Both bee species rob nectar by making a slit/hole into the corolla tube from outside bypassing the flower front. This nectar robbing behavior indicates that they are primary nectar robbers. *A. dizona* slit the corolla tube tissue nearly at the flower base to rob nectar during which the flower did not bend downwards due to its light body weight. On the contrary, *X. pubescens* made a hole in the middle portion of the corolla tube to rob nectar; the hole is usually at the origin point of the epipetalous stamens which are covered by short hairs. During this activity, the flower hangs downwards

Table 1. List of insect foragers on *Volkameria inermis*.

Order	Family	Insect species	Foraging period	No. of foraging visits/day* (n = 10 days)	Mode of foraging	Forage sought	Flower handling time (in seconds)
Hymenoptera	Apidae	<i>Xylocopa pubescens</i> * Spinola	08:30–17:00	35 ± 5.3	Illegitimate Primary nectar robber	Nectar	2.8 ± 0.09 (n = 42)
		<i>Anthophora dizona</i> Engel	08:00–17:00	28 ± 4.2	Illegitimate Primary nectar robber	Nectar + pollen	3.2 ± 0.06 (n = 38)
Lepidoptera	Pieridae	<i>Pareronia valeria</i> Cramer	09:00–16:30	54 ± 3.4	Legitimate	Nectar	2.5 ± 1.2 (n = 32)
	Nymphalidae	<i>Danaus genutia</i> Cramer	09:30–16:00	42 ± 2.5	Legitimate	Nectar	2.1 ± 1.1 (n = 39)
	Hesperiidae	<i>Borbo cinnara</i> Wallace	09:00–15:30	32 ± 1.9	Legitimate	Nectar	2.8 ± 1.3 (n = 27)
	Sphingidae	<i>Macroglossum gyrans</i> Walker	15:30–18:00; 04:30–06:00	63 ± 6.7	Legitimate	Nectar	2.1 ± 0.04 (n = 46)

No. of flowers under observation: Approximately 150 each day on a different population in each flowering season.

*Collecting nectar legitimately from the flowers of *Acanthus ilicifolius*, *Caesalpinia crista*, *Malachra capitata*, and *Cucumis maderaspatanus*.

due to its heavy body weight. In the standing crop of flowers, the flowers that were not robbed accounted for 61% while the robbed flowers accounted for 39%. *A. dizona* had collected pollen from individual anthers and in doing so they did not discriminate the stigma from the anthers and hence invariably made attempts to collect pollen from the stigma. The inability of this bee to distinguish the anthers from the stigma was considered to be effecting pollination. Butterflies being large in size were able to contact both anthers and stigma with their wings/abdomen and effect self- and cross-pollination while collecting nectar from the flower-opening side on clear sunny days. Flower-handling time (in seconds) for forage collection varied with each insect species (Table 1). *X. pubescens* had collected nectar only legitimately from the flower-opening side from other plant species growing in the same area (Table 1); they include *Acanthus ilicifolius* L. (Acanthaceae) (Image 2d), *Caesalpinia crista* L. (Fabaceae) (Image 2e), *Malachra capitata* (L.) L. (Malvaceae) (Image 2f) and *Cucumis maderaspatanus* L. (Cucurbitaceae) (Image 2g). The flowers of all these species are nectariferous but not specialized and facilitated legitimate foraging behaviour by all insects that seek nectar.

DISCUSSION

Specialized flowers are vulnerable to exploitation by other flower visitors (Mainero & del Rio 1985) by removing nectar without pollinating (Navarro 2001). Nectar robbing takes place in nectariferous flowers; with morphological restrictions for illegitimate foragers but

nectar robbing foragers overcome these restrictions with their behavioural and physical capacity to rob indicating that this nectar robbing activity is an outcome of the ability of some flower foragers to rob nectar without effecting pollination (Inouye 1980; Maloof & Inouye 2000). However, the flower foragers that act as nectar robbers pay legitimate visits and pollinate the flowers of other species growing in the same area indicating that the floral traits of some plants are responsible for triggering this behaviour in some flower foragers (Newman & Thomson 2005).

In the present study, it is found that *Volkameria inermis* flowers are highly specialized as they possess long corolla and abundant nectar with moderate sugar concentration containing all the three common sugars and restrict the nectar access to illegitimate foragers. The flowers are morphologically adapted for visits by moths and butterflies which act as legitimate foragers-cum-pollinators while collecting nectar. Since the long corolla tube of the flowers restricts access to nectar for bees, *A. dizona* and *X. pubescens*, they resort to rob nectar by making slit or hole into the corolla tube from outside bypassing the flower front. Both bee species act as primary robbers as they do not acquire nectar from the slit/hole made by the other bee. Further, the place where each bee species makes slit on the corolla tube is different. *A. dizona* slits at the base of the corolla tube while *X. pubescens* at the middle part of the corolla tube; the selection of the place on the corolla tube appears to be related to the physical strength they exert to cause the nectar to flow to the place where the bees make slit. *A. dizona* is relatively small-bodied when compared to *X. pubescens*; the landing of the former on the corolla



Image 1. *Volkameria inermis* and butterflies visiting its flowers: a—Plant in flowering phase | b—3-flowered cyme in bud stage | c—Simultaneous anthesis of all the three flowers of a cyme | d—Pierid butterfly, *Pareronia valeria* collecting nectar | e—Nymphalid butterfly, *Danaus genutia* collecting nectar | f—Hesperiid butterfly, *Borbo cinnara* collecting nectar. © A.J. Solomon Raju.



Image 2. Bees visiting *Volkameria inermis* and other plants: a—*Anthophora dizona* collecting nectar by puncturing the corolla tube (primary nectar robber) | b—*Anthophora dizona* collecting pollen | c—*Xylocopa pubescens* collecting nectar by puncturing corolla tube (primary nectar robber) | d–g: *Xylocopa pubescens* collecting nectar – legitimate pollinator: d—*Acanthus ilicifolius* | e—*Caesalpinia crista* | f—*Malachra capitata* | g—*Cucumis maderaspatanus*. © A.J. Solomon Raju.

tube does not change the orientation of the latter to cause the nectar to flow downwards for its collection while that of the latter changes the orientation of the corolla tube causing the nectar to flow downwards which is then easy for its collection. Since *A. dizona* is unable to bring down the corolla tube by landing, it is

compelled to move to the flower base to make a slit to rob nectar. On the contrary, *X. pubescens* is able to bring down the corolla tube considerably by landing due to which there is a rapid flow of nectar from the flower base to the point where slit is made by it. These findings agree with Inouye (1980) and Maloof & Inouye (2000)

who stated that the nectar robbing foragers overcome the morphological restrictions imposed by nectariferous flowers for illegitimate foragers by changing their legitimate flower foraging behaviour and by using their physical capacity. Further, *X. pubescens* is using certain other plant species located in the same area, *Acanthus ilicifolius*, *Caesalpinia crista*, *Malachra capitata* and *Cucumis maderaspatanus* as nectar sources by probing the flowers legitimately. Such a flower-probing behaviour displayed by *X. pubescens* indicates that it has the ability to use physical capacity and employ legitimate and illegitimate foraging behaviours to exploit the standing crop of nectar from different nectariferous flowers with different floral morphologies for its survival.

Newman & Thomson (2005) reported that the pollinators may need to increase the number of flowers they visit to meet their daily metabolic requirements if they visit the nectar-robbed flowers in which there is usually a reduction in nectar volume. Maloof & Inouye (2000) and Irwin et al. (2001) reported that changes in pollinator behaviour due to nectar robbing may have positive, negative and neutral effects on plant fitness through change in seed set rates. The present study finds that nectar robbing by bees reduces nectar reward and increases variability in nectar standing crop which in turn may make the pollinating butterflies to increase the number of foraging visits and shuttle between populations of *V. inermis* frequently. Further study is needed to evaluate the effect of primary nectar robbing by bees on pollination rate, genetic variation and plant fitness in *V. inermis*.

CONCLUSIONS

In *Volkameria inermis*, the pollinators are butterflies and diurnal moths. However, bees, *Anthophora dizona* and *Xylocopa pubescens* act as primary nectar robbers. *A. dizona* is also a pollen gatherer and its attempts to probe the stigma for pollen results in pollination. Nectar robbing by bees reduces nectar volume in robbed flowers and at the same time brings about variability in the standing crop of nectar. As a result, the pollinating butterflies increase the number of nectar foraging visits and shuttle between populations of *V. inermis* in quest of more nectar to meet their daily metabolic requirements. Such a foraging behavior may promote pollination rate in *V. inermis*. Further study is recommended to evaluate the effect of nectar robbing by bees on the reproductive success and plant fitness in *V. inermis*.

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Communications

The killing of Fishing Cat *Prionailurus viverrinus* (Bennett, 1833) (Mammalia: Carnivora: Felidae) in Hakaluki Haor, Bangladesh
– Meherun Niger Sultana, Ai Suzuki, Shinya Numata, M. Abdul Aziz & Anwar Palash, Pp. 21903–21917

Feeding ecology of the endangered Himalayan Gray Langur *Semnopithecus ajax* in Chamba, Himachal Pradesh, India
– Rupali Thakur, Kranti Yardi & P. Vishal Ahuja, Pp. 21918–21927

Kleptoparasitic interaction between Snow Leopard *Panthera uncia* and Red Fox *Vulpes vulpes* suggested by circumstantial evidence in Pin Valley National Park, India
– Vipin, Tirupathi Rao Golla, Vinita Sharma, Bheemavarapu Kesav Kumar & Ajay Gaur, Pp. 21928–21935

A comparison of the breeding biology of White-throated Kingfisher *Halcyon smyrnensis* Linnaeus, 1758 in plains and hilly areas of Bangladesh
– Habibon Naher, Noor Jahan Sarker & Shawkat Imam Khan, Pp. 21936–21945

An updated checklist of reptiles from Dampa Tiger Reserve, Mizoram, India, with sixteen new distribution records
– Malsawmdawngliana, Bitupan Boruah, Naitik G. Patel, Samuel Lalronunga, Isaac Zosangliana, K. Lalhmangaiha & Abhijit Das, Pp. 21946–21960

First report of marine sponge *Chelonaplysilla delicata* (Demospongiae: Darwinellidae) from the Andaman Sea/Indian Ocean with baseline information of epifauna on a mesophotic shipwreck
– Rocktim Ramen Das, Titus Immanuel, Raj Kiran Lakra, Karan Baath & Ganesh Thiruchitrambalam, Pp. 21961–21967

Intertidal Ophiuroidea from the Saurashtra coastline, Gujarat, India
– Hitisha Baroliya, Bhavna Solanki & Rahul Kundu, Pp. 21968–21975

Environmental factors affecting water mites (Acari: Hydrachnidia) assemblage in streams, Mangde Chhu basin, central Bhutan
– Mer Man Gurung, Cheten Dorji, Dhan B. Gurung & Harry Smit, Pp. 21976–21991

An overview of genus *Pteris* L. in northeastern India and new report of *Pteris amoena* Blume from Arunachal Pradesh, India
– Ashish K. Soni, Vineet K. Rawat, Abhinav Kumar & A. Benniamin, Pp. 21992–22000

Nectar robbing by bees on the flowers of *Volkameria inermis* (Lamiaceae) in Coringa Wildlife Sanctuary, Andhra Pradesh, India
– P. Suvarna Raju, A.J. Solomon Raju, C. Venkateswara Reddy & G. Nagaraju, Pp. 22001–22007

Contribution to the moss flora of northern Sikkim, India
– Himani Yadav, Anshul Dhyani & Prem Lal Uniyal, Pp. 22008–22015

Short Communications

Firefly survey: adopting citizen science approach to record the status of flashing beetles
– Nidhi Rana, Rajesh Rayal & V.P. Uniyal, Pp. 22016–22020

First report of *Gymnopilus ochraceus* Høil. 1998 (Agaricomycetes: Agaricales: Hymenogastraceae) from India and determination of bioactive components
– Anjali Rajendra Patil & Sushant Ishwar Bornak, Pp. 22021–22025

Notes

A coastal population of Honey Badger *Mellivora capensis* at Chilika Lagoon in the Indian east coast
– Tiasa Adhya & Partha Dey, Pp. 22026–22028

New distribution record of Black Softshell Turtle *Nilssonina nigricans* (Anderson, 1875) from Manas National Park, Assam, India
– Gayatri Dutta, Ivy Farheen Hussain, Pranab Jyoti Nath & M. Firoz Ahmed, Pp. 22029–22031

First report of melanism in Indian Flapshell Turtle *Lissemys punctata* (Bonnaterre, 1789) from a turtle trading market of West Bengal, India
– Ardhendu Das Mahapatra, Anweshan Patra & Sudipta Kumar Ghorai, Pp. 22032–22035

The Fawcett's Pierrot *Niphanda asiatica* (Insecta: Lepidoptera: Lycaenidae) in Bandarban: an addition to the butterfly fauna of Bangladesh
– Akash Mojumdar & Rajib Dey, Pp. 22036–22038

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