

POLLINATION OBSERVATIONS OF THE AFRICAN VIOLET IN THE TAITA HILLS, KENYA

Dino J. Martins

Museum of Comparative Zoology, Harvard University
26 Oxford Street, Cambridge, MA 02138, USA
dinojmv@oeb.harvard.edu

ABSTRACT

The African violet, *Saintpaulia teitensis* (Gesneriaceae), is an Eastern Arc global biodiversity hotspot endemic. Forest fragments on the Taita Hills in south-eastern Kenya hold the only known wild populations of this plant. The pollination ecology of *S. teitensis* was investigated through direct observation. *S. teitensis* flowers show enantiostyly which may promote xenogamy. Pollinators of this endangered plant species were found to be exclusively wild bee species of the genus *Amegilla* (Apoidea: Apoidea: Apidae). Four different species of *Amegilla* were recorded visiting *S. teitensis*. Observations of bee floral visitors showed distinctive floral manipulation (buzz pollination) for release of pollen by pollinating bees. *Amegilla* spp. visiting *S. teitensis* were observed to feed from other forest-floor plant species (Acanthaceae and Lamiaceae) and on crops in adjacent small-scale mixed agriculture farms. Future conservation and management of this endangered plant needs to take into account the needs and biology of its pollinators.

Keywords: Buzz pollination, enantiostyly, *Saintpaulia*, Eastern Arc, Gesneriaceae, *Amegilla*

INTRODUCTION

The Taita African Violet, *Saintpaulia teitensis* B.L.Burt, is endemic to the Taita Hills (Burt, 1958; 1964), which are part of the Eastern Arc biodiversity hotspot. East of the main range is Mbololo Hill (1779 m) where the largest remnant patch of forest is located (Bennun & Njoroge, 1999). The only known populations of this rare plant are found on Mbololo Hill in the higher parts of the forest (Faden *et al.*, 1988; Darbyshire 2006). This biodiversity hotspot consists largely of highly fragmented and relict forest patches on hills and mountains with smaller areas of forest along the coast of Kenya and Tanzania. The Taita Hills in Kenya are considered the northernmost outlier of the Eastern Arc biodiversity hotspot. The term 'Eastern Arc' was introduced in 1986 by Lovett to describe this exceptionally species-rich area spanning southern Kenya and eastern Tanzania (Lovett 1986). It has been suggested that as much as a third of the flora of forest regions of Eastern Tanzania and Kenya is endemic to the floristic regions that cover the Eastern Arc (Lovett 1990).

The hills are surrounded by flat plains covered in dry, arid bushland dominated by *Acacia* spp. (*Acacia tortilis* (Forssk.) Hayne, *A. siebierana* DC., *A. senegal* (L.) Willd.,

A. nilotica (L.) Delile, *A. zanzibarica* (S.Moore) Taub.) and *Commiphora* spp. This bushland with scattered trees (*Melia* and *Ficus* spp.) extends up onto the flanks of the hills giving way to intensive small-scale agriculture. The farms are typically small and grow a wide range of subsistence crops alongside fruit trees, climbers such as passion-fruit (*Passiflora edulis* Sims) and tubers, primarily cassava (*Manihot esculenta* Crantz) and yams. Maize (*Zea mays* L.) is the most conspicuous and dominant crop. The land is intensively cultivated with almost no natural forest habitat left in the farming zone. Many farms have strips of wildflowers along hedgerows and small orchards with fruit trees.

As a result of many decades of intensive farming, the forests of the Taita Hills survive only as fragmented patches on the hilltops and in general on slopes and areas inaccessible for cultivation. The forest patches on the Taitas range in size from a few hectares to over 200 hectares (Beentje & Ndiang'ui, 1988; Bennun & Njoroge, 1999).

The genus *Saintpaulia* H.Wendl. is of regional interest to conservation especially as a potential flagship species for the Eastern Arc. Several efforts have been made to improve the first comprehensive treatment of the genus by Burtt (1958; 1964), including through the use of molecular systematics (Möller & Cronk, 1997a, b; Smith, 1997; Linqvist & Albert, 1999; Harrison *et al.*, 1999). The taxonomy of the genus remains controversial at the species level but has been recently revised and incorporated into the published Flora of Tropical East Africa (Darbyshire, 2006).

The restricted distribution in highly-threatened and isolated fragmented forest is typical of the genus (Johansson, 1978; Clarke, 1998; Eastwood *et al.*, 1998; Kohlemainen & Mutikainen, 2006). Mbololo Hill holds the largest contiguous area of forest in the Taita Hills and is also home to a number of other endemics, including several birds, butterflies and an amphibian (Collins & Morris, 1985; Faden *et al.*, 1988; Simiyu *et al.*, 1996). The Taita African Violet is a shade-loving plant that grows in sheltered spots on rocks, amongst tree-roots and occasionally on the lower trunks of moss-covered trees.

Saintpaulia pollination biology has been little studied in the field (Kohlemainen & Mutikainen, 2006). Given the restricted range of *S. teitensis* in a fragmented habitat, the maintenance of pollination services could potentially be one of the main areas of concern for the persistence of the species. Plants in forest fragments that are impacted by human activities are particularly vulnerable to pollination deficits (Buchmann *et al.*, 1997). In order to establish the necessity of pollination to the survival of this species, information on the floral visitors and their behaviour is required.

The aim of this study was to document the floral visitors (hence potential pollinators) of the African Violet, *S. teitensis*. The main questions asked were: What insects are visiting the flowers of *S. teitensis*? What are the patterns of visitation? And, how many different kinds of visitors come to the flowers and what does their behaviour at the flowers tell us about the interactions of the pollinators with this plant species *i.e.* if only a few species of insect pollinators are involved, does this suggest a specialised guild? An additional aim of the study was to observe closely the behaviour of floral visitors to the flowers of *S. teitensis* in order to confirm the hypothesis of buzz pollination being the means of displacing pollen from the anthers in this species. Once the identity of the floral visitors to *S. teitensis* was established, a further question of what other species of plants the same insects are visiting was also asked. This would help link the pollination of the plant with the broader context of the floral community and put this information into the context of state of the fragmented habitat and adjacent small-scale agriculture.

MATERIALS AND METHODS

Morphological observations of floral form and variation were made in order to better inform observation during fieldwork. Herbarium specimens of *Saintpaulia teitensis* and other species of Gesneriaceae were studied at the East African Herbarium and at the Harvard University Herbarium in order to determine the structure of the flowers *e.g.* enclosed anthers. Close observations were also made of a number of species of *Saintpaulia*, including *S. teitensis*, maintained in cultivation at the National Museums of Kenya and in the collections of plant-enthusiasts. A number of flowers were bagged, to exclude pollinators, so as to determine the role played by flower-visitors in pollination.

Individual plants of *S. teitensis* were watched in the wild for visitors. All observations were carried out on Mbololo from 15 July to 10 August 2001, 15 May to 10 August 2003 and 15 to 17 June 2004. Plants were visited on 10 days, and watched closely for visitors on three days. Individual plants bearing flowers were searched out and carefully observed from early morning *ca.* 7.00 am to mid-afternoon. This time period was observed to correspond with the main activity patterns of flower-visiting diurnal insects based on pilot day-long observations in July–August 2001.

Plants were watched from a short distance in order not to disturb the pollinating bees. Some observations were carried out through a pair of close-focusing binoculars (Nikon Pentax 8 x 40). Dull-coloured clothing was worn and unnecessary movement avoided when conducting the observations. Close observations were made of bee behaviour at flowers. The duration of visits as well as the number of flowers visited were recorded and tabled in spreadsheets. Analysis of *S. teitensis* flower-visitation patterns was carried out using spreadsheets in Excel.

Small numbers of bees were also captured by netting them as they approached or departed from *S. teitensis* flowers and at other flowers near by when the same species had been seen visiting the *S. teitensis* flowers earlier. No netting of bees was done at the flowers being studied so as not to negatively impact on visitation rates and/or startle and scare the bees away. This approach was found to be effective in studies of pollinator communities in the adjacent Tsavo ecosystem and of hawkmoths pollinating orchids (Martins, 2004; Martins & Johnson, 2007).

These bees were checked for pollen loads using the fuschin gel method (Beattie, 1971). These fuschin gel pollen extractions were later melted onto glass slides and observed through a simple monocular light microscope to confirm that the pollen was coming from the *Saintpaulia* flowers. Bees were identified by the author up to the genus level on the basis of a key developed for the African Bee Course by Dr Connal Eardley. Species level identifications were done by Dr. Connal Eardley on the basis of digital images and of mounted specimens by the late hymenoptera taxonomist Roy Snelling. Specimens have been sent to Dr Eardley at ARC-PPRI in South Africa and will also be deposited at the National Museums of Kenya.

RESULTS

Floral biology of *Saintpaulia teitensis*

The flowers of *S. teitensis* are borne on short stalks. These extend above or outwards from the rosette of leaves if the plant is growing on a vertical rock or trunk face. Typically 2–3 flowers are open and viable per flowering spike, with up to 10 open flowers on a plant.

S. teitensis bears bilaterally symmetrical flowers. Of a total of 20 bagged flowers, 19 did not set fruit, and one developed a small fruit that withered and aborted before ripening. Of 17 out-crossed flowers in the related *S. ionantha*, 15 set fruit and developed to maturity.

The individual flower consists of an arrangement of five partly fused petals in a bilaterally symmetrical display with the yellow anthers in the middle contrasting with the surrounding light blue-purple petals (Martins, 2005). *S. teitensis* also shows an interesting floral feature known as enantiostyly. Enantiostyly is a form of flower polymorphism where the style projects away from the symmetric plane of the flower. In *S. teitensis* this feature is heteromorphic, with the style projecting either to the left (left-styled) or right (right-styled) to the main axis of the flower (figure 1), with both kinds of flowers on the same plant. Heteromorphic enantiostyly was observed on all individual *S. teitensis* plants studied and is typically in a 1:1 ratio of left-styled to right-styled flowers. (N = 20 plants observed in flower).



Figure 1. Enantiostyly: left- and right-styled flowers of *Saintpaulia teitensis*.

The pollen is contained within the bright yellow anthers, which are a fused structure. This structure needs to be specially manipulated by a pollinator in order for the pollen to be released. In contrast with the bright yellow anthers, the pollen grains of *S. teitensis* are white in colour.

Pollination of *Saintpaulia teitensis*

Pollen grains of *S. teitensis* are spherical and adhere readily to the hairs of the *Amegilla* bees that visit it. Observations of visitors to flowers were made on 10 days, with specific visitation data collected over 8 hour periods for three days (figure 3). We only observed *Amegilla* bees visiting *S. teitensis* flowers. The bees approach the flowers while flying 60–90 cm above the forest floor. When an individual bee has noticed a particular patch of flowers its flight changes from meandering to direct. The bee approaches to within *ca.* 20 cm of the flowers and weaves back and forth in flight (figure 2). This hovering stance is maintained for a few seconds. The bee makes several closer approaches and retreats while weaving from side to side in the air. The bee then flies directly towards a particular flower.

The bee flies towards the flower perpendicular to the flower's 'face'. The bee lands on the flower by seizing it with its legs and grappling with the petals and fused anther structure (figure 2). During this contact with the flower the bee holds part of the flower in its mandibles and vibrates its wing muscles. This transfers the high-frequency vibrations to the flower and pollen is released from the fused anthers. This process takes place very rapidly and lasts 1–3 seconds. During this time, as the bee holds on to the flower, short pulses of a buzzing sound can be heard. This is the result of the vibrating flight muscles that cause the

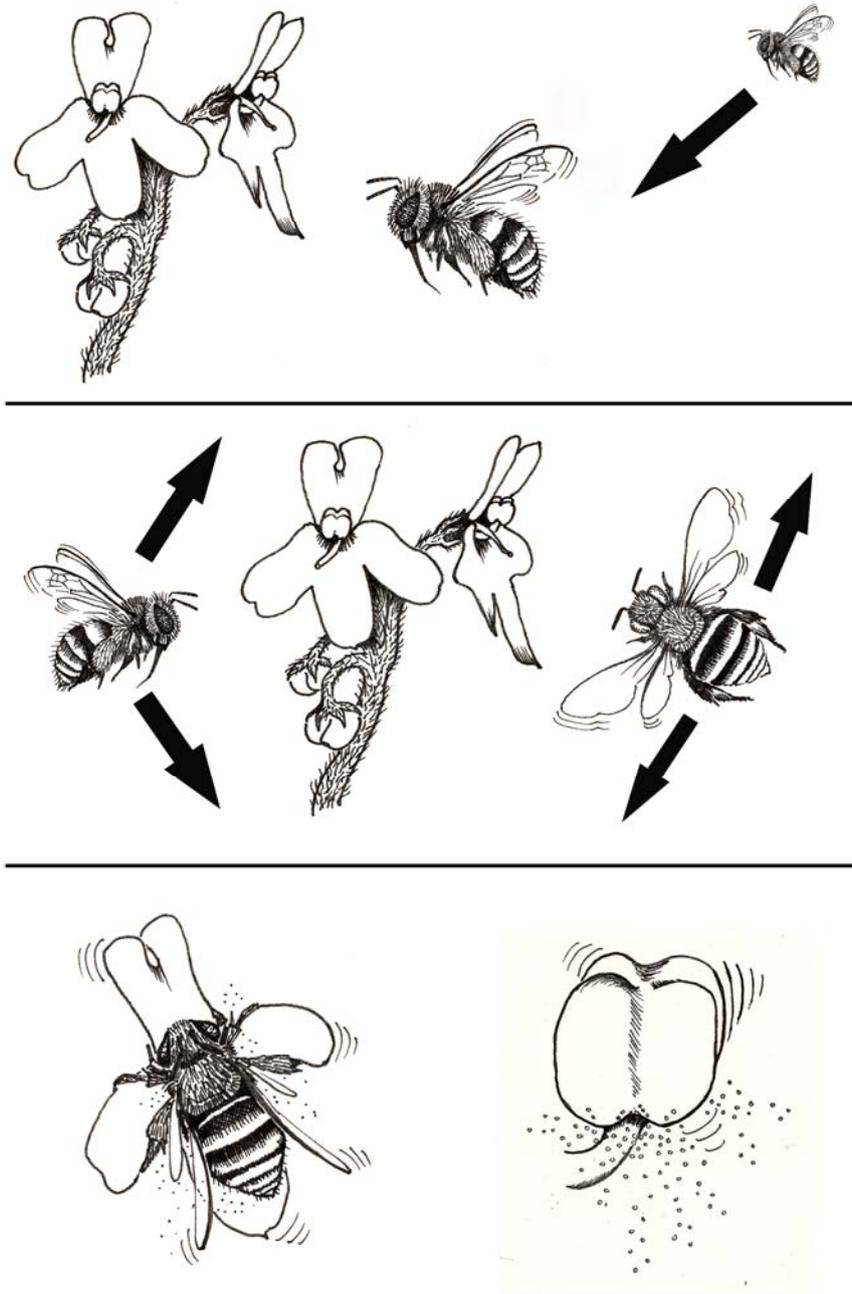


Figure 2. Behaviour of *Amegilla* and pollination of *Saintpaulia teitensis* flowers. Top: bee approaches flower directly from a distance. Middle: bee weaves in front of flower for 2-5 seconds often switching position. Bottom left: bee 'buzz' pollinating flower. Bottom right: detail of anthers shaking and releasing pollen grains.

pollen to be released. This is indicative of buzz pollination (Proctor *et al.*, 1996). During its time on the flower the bee makes circular movements on the flower, which helps more pollen adhere to its body hairs.

The bee then lifts itself into the air and hovers again briefly while combing pollen into its pollen baskets. This motion is very rapid and is followed by a return to weaving flight in front of the flowers. The bee then either drops back onto another flower or flies away. The numbers of flowers visited during a particular visit are variable, but the durations of the visits are always under 1 minute (N=20 timed visits observed, mean=37.25 seconds, st. dev.=13.714 seconds). Visitation rates are variable, bi-modal peaks around mid-morning and early to mid-afternoon were observed in 2003 (figure 3).

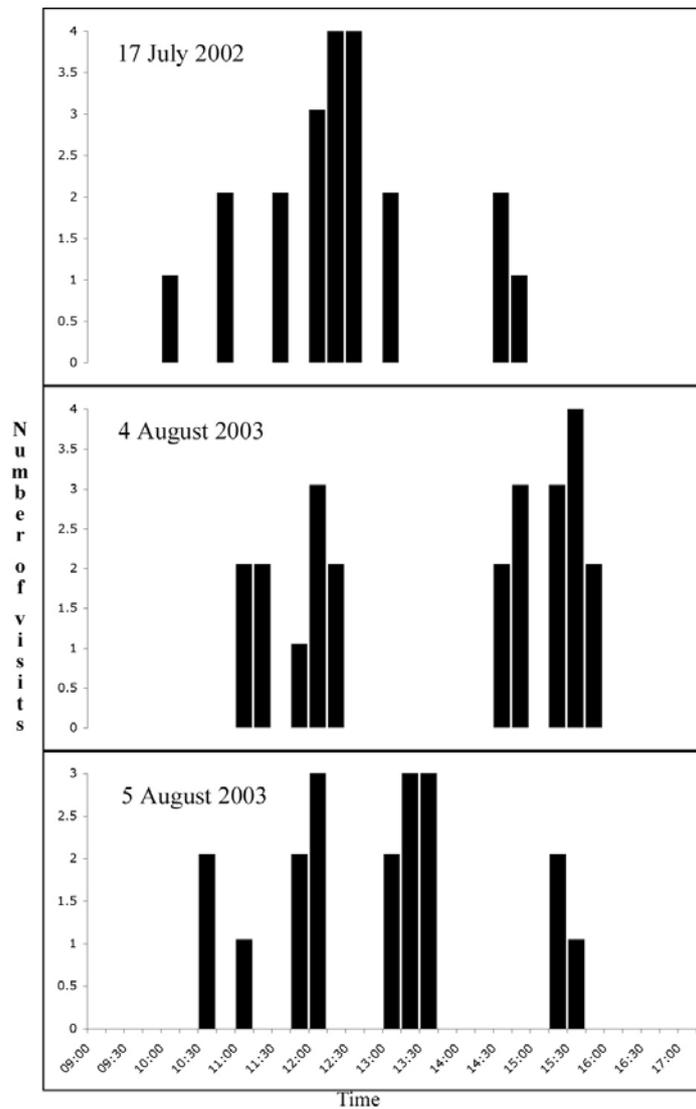


Figure 3. *Amegilla* visitation rates to *Saintpaulia teitensis*.

Four different species of *Amegilla* were recorded on *S. teitensis*: *Amegilla calens* Lepeletier, *A. acraensis* Fabricius, *A. caerulea* Friese and *A. sp.* Of these four, *A. calens* and *A. caerulea* were the most frequent visitors. Initially, only the duration and number of visits were recorded. As it became apparent there was more than one species of bee involved, all from the same genus, more detailed information on visitation was recorded. It was challenging at first noting the species of bee involved due to the speed and short duration of the visits. Observations made later in the study in 2003 and 2004, noted the identity of the bee during recording of visitation. All four species of *Amegilla* were often observed on the same day. More work on the visitation patterns and behaviour of the 4 different *Amegilla* spp. remains to be done in order to determine whether all are equally effective pollinators or engaging in resource-partitioning on *S. teitensis*.

The fuschin gel slides showed pollen grains from *S. teitensis* present on all the flower-visiting *Amegilla* bees' bodies and in their pollen baskets. *Amegilla* spp. were common visitors to other forest floor flowers primarily Lamiaceae and were seen visiting *Streptocarpus* spp., the genus within which *Saintpaulia* is embedded (Möller & Cronk, 1997b), in the Taita Hills forest, Mount Kasigau and in the Aberdares (pers. obs.). In the Taita Hills the same four species of *Amegilla* bees were observed visiting flowers along the forest edge adjacent to cultivated areas (bees were netted and released). They visited the flowers of the following crops being cultivated in small-scale farms bordering the forest: cowpea (*Vigna unguiculata* L.Walp.), eggplant (*Solanum melongena* L.), pigeon pea (*Cajanus cajan* L.Millsp.) and tomato (*Solanum lycopersicum* L.).

DISCUSSION

The Taita African Violet appears to be pollinated in its natural habitat by a limited number of bee species from a single genus. Pollination is required for fruit set, even if it is self-pollen landing on the stigma of the same flower, it still needs to be mechanically displaced from the anthers (Kolehmainen & Mutikainen, 2006). *Amegilla* bees are also visiting other *Saintpaulia* spp. in Tanzania (J. Kolehmainen, pers comm.). The limited number of bee species involved, and the manipulation of the flowers suggests a more specialised pollination system (Roubik, 1989). The *Amegilla* bees, if confirmed as the sole pollinators of all other *Saintpaulia* spp., suggests a pollination guild. The Taita African Violet can only be adequately conserved if both its pollinators and habitat are protected. The pollinators themselves, such as the *Amegilla* bees in the forest fragments and their edges, require a wide range of flowering plants so as to access enough nectar and pollen resources throughout the year and therefore sufficiently provision their nests and larvae (Roubik, 1989). The limited numbers of bee species available to pollinate this Eastern Arc endemic indicates that the conservation of specialised interactions is just as crucial as that of protecting individual species and habitats.

The pollination mechanism, buzz-pollination, is in itself interesting and worth further investigation to determine if this is a unique feature of the genus *Saintpaulia* within the Afro-tropical Gesneriaceae, or if it occurs in other species of Gesneriaceae as well. Preliminary observations of other plants in cultivation indicate that both heteromorphic enantiostyly and buzz-pollination are common features of *Saintpaulia* spp. Enantiostyly has evolved in at least ten different angiosperm families (Jesson & Barret, 2002). More detailed observations of the behaviour of the floral visitors will indicate the role of enantiostyly in the pollination ecology of *S. teitensis* and other *Saintpaulia* spp.

Dispersal of pollen between sub-populations of the plant and movement by bees across forest fragments and adjacent cultivation is key to both survival of the plants and their pollinators (Kolehmainen & Mutikainen, 2006). This study suggests that even small highly fragmented and impacted forests can support pollination services for endangered plants as has been found in some orchids (Murren, 2002; Martins & Johnson, 2007). However, fragmentation can also lead to a potential collapse of pollination services even within protected areas (Pauw, 2007).

The observation of *Amegilla* bees on crops and forest-edge/agricultural matrix areas need to be investigated further. This feature represents an opportunity to link the pollination ecology and conservation of a flagship endemic species with the sustainable farming practices and rural livelihoods of small-scale farmers living adjacent to forest fragments. Given the current focus on the conservation of the Eastern Arc forests and the wider issue of sustainable development in the region, the specialised interactions between *Amegilla* bees and the Taita African Violet could serve as an example of the necessity of conserving forest fragments for this flagship endangered species.

ACKNOWLEDGMENTS

This study was conducted as a parallel project to an analysis of bee diversity and interactions in the Tsavo ecosystem while based at the Taita Discovery Centre. Thanks are due to the staff and management of Origins Safaris and Taita and Rukinga Ranches for logistical support. Dr. Connal Eardley of ARC-PPRI, South Africa and the late Roy Snelling of the Los Angeles County Natural History Museum helped provide the bee identifications. Assistance, useful comments and various insights were provided by Edwin Selempo, Dr. Paula Kahumbu, James Mwang'ombe, Peter Greste, Dr. Gerard Hertel, Dr. Henk Beentje, Dr. Stella Simiyu, Anne Powys, Job Ballard, Dr. Ian Gordon, Dr. Barbara Gemmill, Anne Robertson, Dr. Benny Bytebier, Gordon Boy, Dr. P. Siro Masinde and the scientists and staff of the East African Herbarium, the National Museums of Kenya, and the Taita Hills project team of the East African Wildlife Society. Useful comments on this manuscript were provided by Dr. Benny Bytebier and Dr. Timo van der Niet and an anonymous reviewer, I thank them for their time and efforts.

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