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Short communication

Diverse nectar robbers on *Alpinia roxburghii* Sweet (Zingiberaceae)Xiaobao Deng^a, Wen Deng^b, Alice Catherine Hughes^c, Dharmalingam Mohandass^{a,*}^a Key Laboratory of Tropical Forest Ecology, Chinese Academy of Sciences, Menglun Town, Yunnan, PR China^b Kunming Institute of Zoology, Chinese Academy of Sciences, Jiaochang Donglu, Kunming, Yunnan, PR China^c Centre for Integrative Conservation, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun Town, Yunnan, PR China

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ABSTRACT

This study records for the first time three mammal species as nectar robbers on the ginger *Alpinia roxburghii* Sweet. We examined the behavior of nectar robbers and compared with earlier studies on a single plant species. We recorded seven species of nectar robbers: three squirrels, one bird, and three bees. Timing of robbing nectars were similar; however, robbing behavior differed among robbers. In particular, squirrels damaged the flower parts while robbing the nectar.

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Introduction

Numerous species of insect, in addition to various birds and some mammals fail to pollinate flowers as legal pollinators, by changing their behavior to remove nectar without pollinating various plant species (Adler and Irwin 2006; Arizmendi et al 1996; Castro et al 2008; Hernandez and Toledo 1979; Lyon and Chadek 1971; Irwin 2003; Roubik 1982; Zhang et al 2013). Nectar robbing of various plant species is common in tropical and temperate forests (Irwin et al 2010; Mayer et al 2014; Singh et al 2014; Zhang et al 2013). Although nectar theft is not uncommon by insects or birds, it has not been recorded in many legitimate mammal pollinators (i.e., bats) (Devy and Davidar 2003; Sazima et al 1999).

However, some rodents have previously been shown to display nectar robbing behavior, with ginger species bringing a frequently victimized taxa for nectar theft. In an earlier study *Alpinia roxburghii*'s sister species *Alpinia kawengensis* was also found to be the subject of nectar theft by striped squirrels (Deng et al 2004). Nevertheless, some earlier studies report different nectar robbers victimizing a single plant species (Guitan et al 1993; Roubik 1982; Wilmer and Corbet 1981), but this phenomena has not been

studied in detail. Therefore, nectar robbers on ginger species could be a relevant topic to understand ecological consequences.

Several studies have reported negative, positive, and neutral effects of nectar robbing on male and female fitness. For instance, nectar robbing bees have been shown to have positive (Malooof and Inouye 2000; Singh et al 2014), neutral (Navarro 2001), and negative effects (e.g., Irwin et al 2001; Irwin and Brody 1999; Roubik 1982; Traveset et al 1998; Zhang et al 2007), on reproduction in a number of plant species. Some studies report that nectar robbers may cause floral damage in certain situations, but little is known or has been recorded about the nectar theft by mammals. This study aims to determine how species actively steal nectar from *A. roxburghii*, and their interactions and timing of nectar stealing events by different robbers.

Materials and methods

Study site and species

The study was conducted in Caiyanghe Provincial Nature Reserve (22°30'N, 101°22'E), south west China at 1200 m above sea level. The *A. roxburghii* population in the study area extends over a large area of the evergreen broad leaved forest along several valleys and is a dominant understory species. *A. roxburghii* Sweet (Zingiberaceae) is a hermaphrodite flexistylous perennial herb, usually 1–3 m tall (Deng et al 2005; Zhang et al 2003), with a large inflorescence on leafy shoots 20–40 cm long. The peak flowering period is from March to late April and fruiting lasts from April to

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September, with a single flower lasting 1 day (5:30 AM to 20:00 PM). It is a self-compatible species and attracts diverse pollinators due to high secretion of nectar throughout the day (Deng et al 2005). This species has large corollas that facilitate a comfortable platform for many pollinators (Zhang et al 2003).

Interestingly, *A. roxburghii* shows flexistylous floral dimorphism evolved through changing the position of the style and separating maturation of male and female organs, which differ in the direction of style movements (Cui et al 1995; Takano et al 2005; Zhang et al 2003). Two types of flexistylous are used by *A. roxburghii*, i.e., cataflexistylous (protandrous) style and anaflexistylous (protogynous) style. Cataflexistylous involves upwards curved styles when pollen is dispersed in the morning. During this time, stigmas are spatially separated from anthers and pollinators have no chance to contact stigmas, which may additionally be unreceptive. In anaflexistylous, the styles move downward during afternoon. During this stage,

pollinators can contact stigmas may cross-pollinate. Therefore *A. roxburghii* uses cataflexistylous and anaflexistylous adaptations to promote higher outcrossing that enhance fruit set (Zhang et al 2003; Sun et al 2007), the effect of such adaptations on various aspects of reproductive success has been published in several previous studies (Li et al 2001; Li et al 2002; Sun et al 2007; Zhang et al 2003).

Observation of nectar robbers were made in 2005–2007. We observed and randomly photographed nectar robbers from 5:30 AM to 20:00 PM in the study site where the area is about 30 ha during our observations. Bees and squirrels were the most common nectar robbers and bird species were rarely found. Robbing species were identified to species level using faunal key character and confirmed at the Kunming Institute of Zoology museum. We observed robbing visits of striped squirrels and recorded the number of robbed flowers and broken styles in three successive

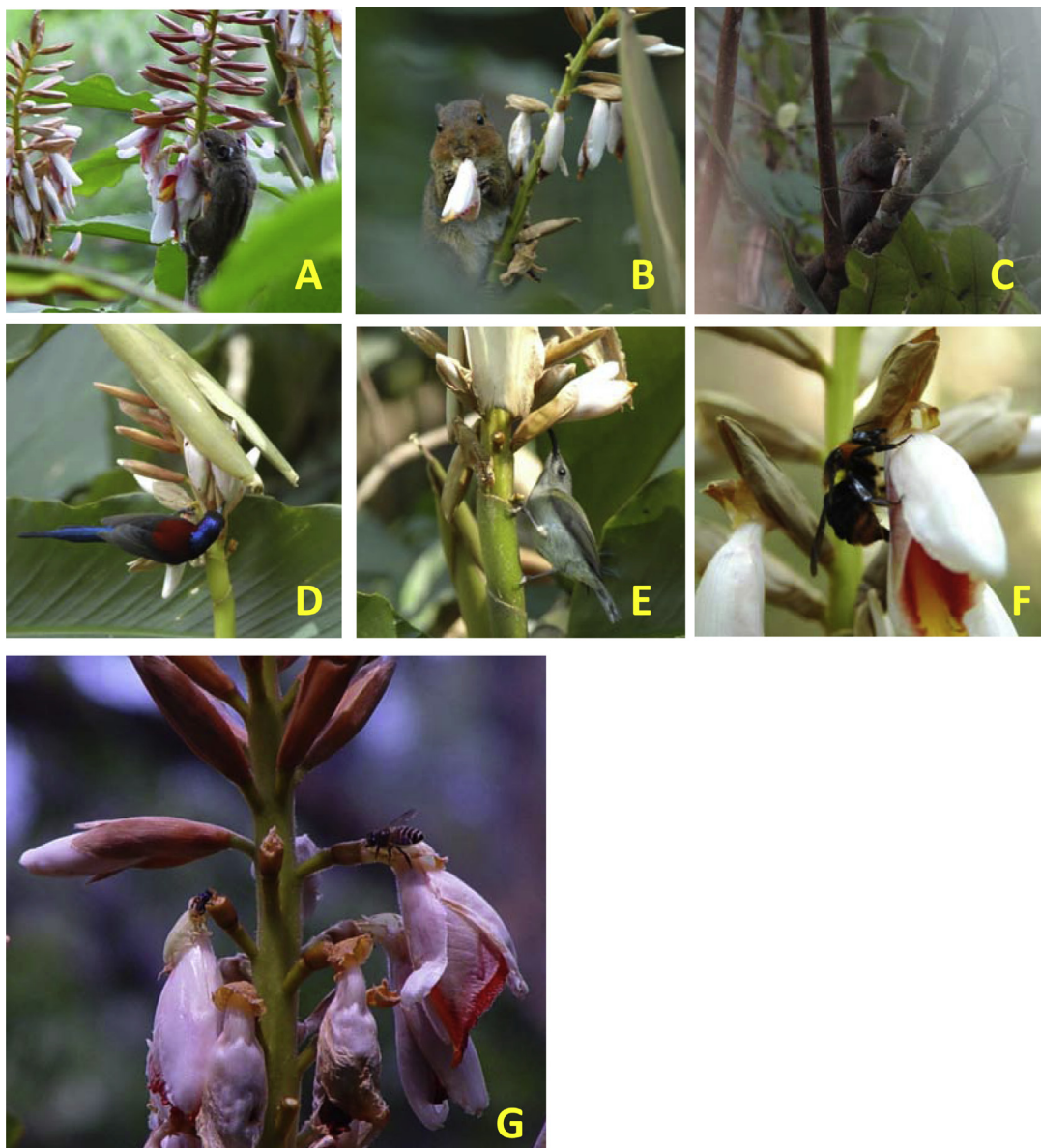


Figure 1. Photographs of diverse nectar robbers on *Alpinia roxburghii*: A, *Tamiops swinhoi* (the important primary nectar robber striped squirrel); B, *Dremomys rufigenis* (accidental primary nectar robber); C, *Callosciurus erythraeus* (Mountain Red-bellied Squirrel, accidental primary nectar robber); D, *Aethopyga siparaja seheriae* (male sunbird, primary nectar robber but not very often); E, *Aethopyga siparaja seheriae* (female sunbird, primary nectar robber but not very often); F, *Bombus richardsi* (big size bumble bee acts as primary nectar robber); G, *Apis cerana* (on the right) and *Trigona (Heterotrigona) pagdeni* (stingless bee on the left), both act as secondary nectar robbers.

days for fifteen hours on each occasion. We did not record the bees and birds because we predicted that squirrels might be effective robbers that cause more significant floral damage than the bees and birds. Mean and standard error was used to compare the number of flowers robbed and styles broken by striped squirrels. Percentage of robbing visits was calculated from the total number of floret visits.

Results

Diverse nectar robbers on ginger species

A total of seven species were recorded as nectar robbers on *A. roxburghii*, including three species of squirrel, three species of bee, and one species of sunbird. Nectar robbing behavior was recorded for the first time in three squirrel species: *Tamiops swinhoi hainanus* Allen (Sciuridae; Swinhoe's striped squirrel), *Callosciurus erythraeus* Pallas (Sciuridae; Pallas's squirrel also known as Red-bellied tree squirrel), and *Dremomys rufigenis* Blanford (Sciuridae; Asian Red-cheeked squirrel). Additionally, three bee species includes a primary nectar robbers (by drilling directly into the nectary to extract nectar), *Bombus richardsi* Frison (Apidae), and two as secondary nectar robbers, *Apis cerana* Fabricius (Apidae) and *Trigona (Heterotrigona) pagdeni* (Apidae; Stingless bee) by feeding on nectar leaking from holes made by primary thieves. One bird species *Aethopyga siparaja seheriae* (Nectariniidae) (male and female) were found as nectar robbers (Figure 1) in the study site.

Floral damages by striped squirrel

Our results suggest that on average $91.3 \pm 39.47\%$ (mean \pm standard error) of visits of squirrel species to flowers was for nectar theft (total floret 384 from 160 inflorescences). Of the robbed flowers, $73.67 \pm 30.83\%$ had broken styles (damaged flowers) (Figure 2), 71.4% (274) had robbed flowers, and 81% (221) of flowers were damaged by striped squirrel over 3-days observation. None of the insect and bird species damaged the floral parts during nectar theft.

Robbing behavior of striped squirrel, bees, and birds

Robbing behavior in the three squirrels differed in timing both in terms of when the theft occurred, and the duration of the activity. The striped squirrel was very active and our video recording demonstrates robbing of nectar from one inflorescence with five flowers for less than 15 seconds. Pallas's squirrel and Asian Red-

cheeked squirrel flowers after 10:00 AM, and soon after midday both species ceased to be active. Striped squirrels were the more frequent nectar robbers than other squirrels (Pallas's squirrel and Asian Red-cheeked squirrel), but on some days no squirrels were present. We did not make records of individual thefts by bee species; however, bees were observed as nectar robber from 10:00 AM to 16:30 PM, which cooccurs with peak legitimate pollination activity. Birds were usually observed robbing nectar between 10:00 AM and 15:00 PM but did not visit every day.

Discussion

Though former studies have largely concentrated on single plant robbing species within a study, a diverse group can act as nectar robbers on a single plant species (*A. roxburghii* in this study). Earlier studies recorded six to seven nectar robbing species on a single plant species includes stingless bees, birds, and ants (Table 1). However, the diversity of species recorded in the present study includes three squirrels, three bees, and one bird species, and their robbing behavior varied greatly: only squirrels were observed to damage flowers during nectar robbing incidents. In this study, striped squirrels, sunbirds, and bumblebees act as primary nectar robbers by making a hole in the nectary of the flower to extract nectar directly, and the honeybee and stingless bees acted as secondary nectar robbers which foraged for nectar through the hole made by a primary nectar robber during the flowering season. The other two species of squirrel (*Callosciurus erythraeus* and *Dremomys rufigenis*) robbed nectar and foraged nectary and sexual organs of the flower, which eventually caused significant floral damage. However, these two squirrels were rarely recorded stealing nectar.

Squirrels usually steal nectar in the morning during the catalexistylous stage of flowering. When they steal nectar the flower style movements are effected, which may affect anaflexistylous actions. The regular activity of squirrel robbing behavior observed involves plucking the flowers, breaking the pedicel or style, and sometimes pulling the nectar through base of the flowers without plucking the flowers. Nectar robbing behavior by birds does not affect the flowers reproductive parts, as they normally steal nectar by making a hole through base of the flowers. Similarly, bumblebees, *Apis cerana* and *Trigona*, steal nectar by making a hole under the base of the flower. The stingless bee *Trigona* damages floral parts such as corolla, stamens, and pistils (Roubik 1982). But, honeybees and stingless bees nectar robbers rarely damaged flowers during theft; though, in some cases flower shrinkage and

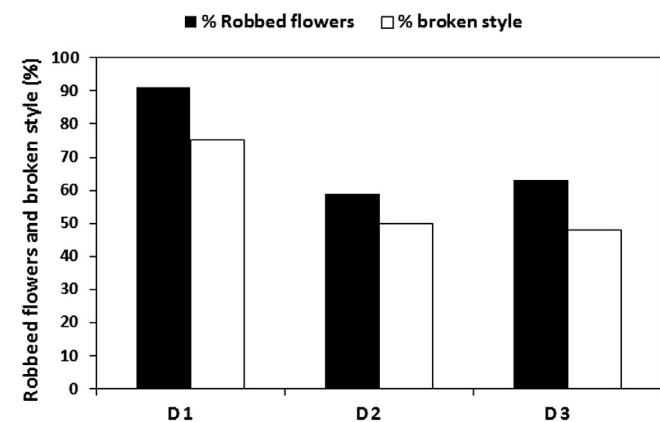


Figure 2. Percentage of robbed flowers and broken style of striped squirrel floral damage visits on *Alpinia roxburghii*.

Table 1. Diverse nectar robbers on single plant species and percentage of flowers robbed on plants of various species, as reported from several literature sources.

Nectar robbers	Plant species	Robbed flowers (%)	References
Multiple species (Squirrels, bumble bee, honey bee, birds; 7 species)	<i>Alpinia roxburghii</i> (Zingiberaceae)	–	This study
Striped squirrels (<i>Tamiops swinhoi</i>)	<i>Alpinia roxburghii</i> (Zingiberaceae)	70	This study
Multiple species (stingless bees, birds; 6 species)	<i>Quassia amara</i> (Simaroubaceae)	83	Roubik et al (1985)
Multiple species	<i>Lonicera etrusca</i> (Caprifoliaceae)	99	Guitian et al (1993)
Multiple species (stingless bees, birds, ants; 7 species)	<i>Justicia aurea</i> (Acanthaceae)	81.1	Willmer and Corbet (1981)
Multiple species	<i>Aphelandra golfodulcensis</i> (Acanthaceae)	0.9	McDade and Kinsman (1980)

withering was recorded. In contrast, squirrel nectar robbing behavior causes withering of flowers, shrinkage, and damage to the style on this ginger, and damage increases with the number of squirrel visits. The visitation rate of nectar robbers differed as thieves vary the timing of robbing across the peak flowering period.

The striped squirrel has two peak times of robbing nectar from the ginger *A. roxburghii* during 8:30 AM to 10:00 PM in the morning and 15:30 PM to 17:00 PM in the late afternoon. In another species from the same genera, *A. kwangsiensis* nectar robbing occurred earlier in the morning at approximately 6:00 AM to 8:00 AM. Because of competition between pollinators (Deng et al 2004), bird pollinators were usually followed by bee visitors in the morning (Carpenter 1979). In this study, the striped squirrels stole nectar before bees and birds, and was a more effective nectar robber compared with bumblebee and *Apis cerana*, though visiting frequency and duration is much lower and shorter (five flowers in less than 10 seconds).

Previous studies have demonstrated that squirrels are generally involved in seed dispersal, or are predators and play a major role on plant community success by regulating the demography of some plants (Jensen 1985; Jensen and Nielsen 1986). Momose et al (1998) recorded squirrels as pollinators in *Ganua sp.*, (Sapotaceae) for nectar reward and Tandon et al (2003) observed three striped squirrel as pollinators in *Butea monosperma*. Therefore, squirrels may involve playing a role on different activities for plant resource collections. However, our present observational study shows that striped squirrels significantly damage the flowers that may influence flexistly movements due to nectar robbing behavior. Though further experimental study is needed to understand the effect of different nectar robber behavior on reproductive fitness in a target species.

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