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The Striped Squirrel (*Tamiops swinhoei hainanus*) as a Nectar Robber of Ginger (*Alpinia kwangsiensis*)[1]

ABSTRACT

Nectar robbing by squirrels is reported for the first time in the striped squirrel (*Tamiops swinhoei hainanus*), which was found robbing nectar from ginger plants (*Alpinia kwangsiensis*) in tropical forests of south Yunnan, China. We describe the behavior of squirrels visiting inflorescences, and we compare the fruit set of inflorescences visited by squirrels with that of inflorescences not subject to nectar robbing by squirrels. Most of the styles of robbed flowers were damaged and the affected plants exhibited reduced fruit set.

Key words: Alpinia kwangsiensis; nectar robber; *plant–animal interactions; rodent; squirrel;* Tamiops swinhoei hainanus; *tropical forest; Xishuangbanna.*

NECTAR ROBBERS ARE FLORAL VISITORS that remove nectar from flowers through a hole pierced or bitten in the corolla of angiosperm species (Inouye 1980, Maloof & Inouye 2000). Nectar robbing by birds and insects is commonly reported in the literature, but rodents have not been routinely identified as nectar robbers. We report here for the first time nectar robbing by a rodent, the striped squirrel (*Tamiops swinhoei hainanus*), which robbed nectar from the flowers of a native tropical ginger (*Alpinia kwangsiensis*) in the tropical rain forests of southern China.

Rodents are primarily seed dispersers or predators and may play an important ecological role in the process of plant community succession by regulating the demography of some plants and the spatial structure of the community (Jensen 1985, Jensen & Nielsen 1986). Results presented here, however, demonstrate that rodents can also play another role in plant demography by robbing nectar from tropical plants, thereby influencing the reproductive success of these plants.

The study was conducted from 16 April to 2 July 2002, in a protected forest at the Xishuangbanna Tropical Botanical Garden (21°45′N, 101°02′E; 580 m elev.) in southern Yunnan Province, China. Annual precipitation in the area is 1600 mm, and annual mean temperature is *ca* 21.6°C. The vegetation at the research site consists of a 30-year-old secondary rain forest.

Alpinia kwangsiensis T. L. Wu & Senjen (Zingiberaceae) is a perennial herb that inhabits tropical forest gaps and roadsides. Plants are usually 1.5–3.0 m tall with many-bladed leafy shoots. Inflorescences are terminal on leafy shoots and composed of congested bracteoles, with each bracteole subtending a single flower. The petaloid, red and yellow, showy labellum is fused with the single stamen on the base to form a tube, the free part of which is expanded and forms a landing platform for legitimate visitors. During blooming, each inflorescence produces two to ten flowers that undergo anthesis daily, each flower lasting only one day from 0600 to 2000 h. The flowering season extends for about two months from mid-March to early May, and the most common pollinators are carpenter bees (*Xylocopa magnifica* and *X. tenuiscapa*) and bumblebees (*Bombus* spp.; Li *et al.* 2002).

The striped squirrel (*T. s. hainanus* Allen, Sciuridae) is a small-bodied squirrel *ca* 10 cm in body length with a weight of 60 g. It is easily recognized because of characteristic light yellow stripes on either side of the gena (extending from nose to neck) and white tufted hair on the posterior tip of the ears. The striped squirrel is widely distributed in southern Asia and is very common in southern China. The squirrel is known to feed on fruits, seeds, and insects (Huang *et al.* 1995).

The behavior of squirrels visiting ginger flowers was observed from a concealed position in nearby shrubs. Observations were carried out from 0600 to 2000 h over four successive days in three different patches of *A. kwangsiensis.* Some details of squirrel behavior were recorded with a Sony video camera. We also recorded the visiting frequency and behavior of legitimate pollinators (mainly carpenter bees *X. magnifica* and *X. tenuiscapa*) on robbed and non-robbed inflorescences of *A. kwangsiensis.* In each patch, 50–60 inflorescences were randomly checked to assess floral damage caused by visiting squirrels. We measured fruit set in the three patches after 40 days, when the fruits would normally be mature.

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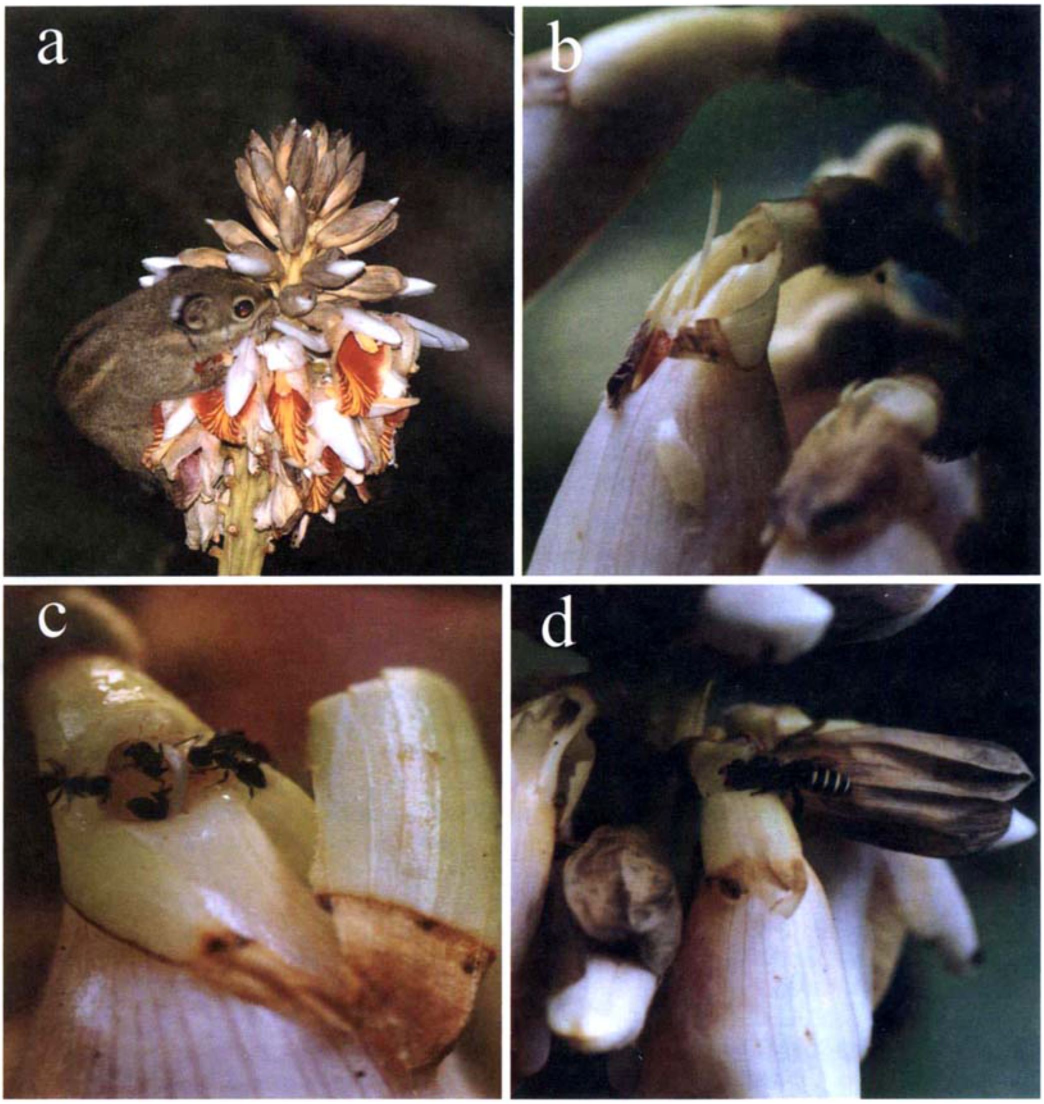

FIGURE 1. Nectar robbing on the ginger plant (*Alpinia kwangsiensis*) by the striped squirrel (*Tamiops swinhoei hainanus*). (a) The squirrel robbing nectar on the inflorescence at 0630 h; (b) Damage to some floral parts caused by a striped squirrel; (c, d) The secondary nectar robbers, ants and honeybees, searching for nectar in the robbed hole.

Hundreds of flowers of *A. kwangsiensis* bloomed in the observed patches. Four striped squirrels were observed foraging each morning during the flowering period, and on average, each squirrel occupied a *ca* 20 m^2 area and robbed 131.8 ± 79.1 ($N = 3$) flowers per day.

Striped squirrels visited the flowers of *A. kwangsiensis* in the early morning and displayed a daily foraging routine from *ca* 0630 to 0700 h throughout the flowering period. They visited every flowering inflorescence on their foraging route, and on each inflorescence, they fed from the majority of the open flowers but ignored the buds and wilted flowers. They removed the coriaceous bracteoles wrapped outside of the corolla, bit a hole at the base of the corolla where the nectarines are located, and lapped up all the nectar in each flower. The duration of visiting on a flower took from three to five seconds (Fig. 1a). Video recordings verified that striped squirrels fed only on nectar and made no attempt to eat floral parts or pollen. They were not observed touching the stigmas and anthers of flowers; however, when they bit

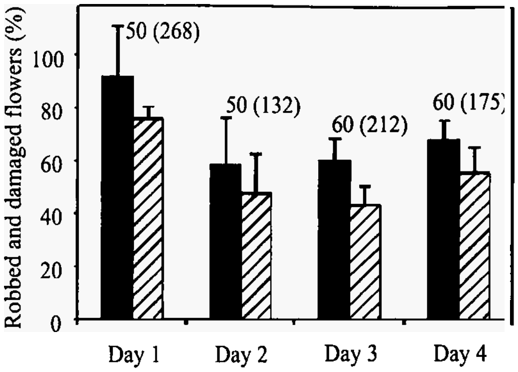

FIGURE 2. The average percentages and standard errors of nectar-robbed flowers (black bars) and broken styles (dashed bars) on the inflorescences in three patches of *Alpinia kwangsiensis* during four observation days. Group sample sizes are given above the bars: inflorescence number (flower number).

on a corolla, the nectaries and style were frequently damaged. Our results indicate that on average, 72.8 ± 3.04 percent ($\bar{x}$ ± SE) of the flowers were robbed from 220 randomly observed inflorescences, and of them, 78.56 ± 9.7 percent had broken styles (Figs. 1b and 2).

No striped squirrel was observed on the flowers after 0700 h, despite their continuing foraging for other foods throughout daylight hours. Visits to flowers were timed so that nectar was robbed prior to legitimate visitors beginning to visit the flowers at *ca* 0700 h (Li *et al.* 2001). This is the opposite of the visiting schedule exhibited by many pollinator and nectar robber systems. For example, Carpenter (1979) demonstrated that bird pollinators generally forage before bee nectar robbers are active. But considering the visitor types in this nectar robbing system, vertebrate robbers may be able to forage earlier in the day than their competitors, diurnal insects. This foraging behavior of the squirrels allows them to rob nectar prior to the availability being reduced by legitimate pollinators. Presumably, the squirrels' temporal pattern of foraging from flowers may increase their chance of obtaining larger volumes of nectar; moreover, the plants produce nectar at night.

The direct effect of nectar robbing by squirrels on *A. kwangsiensis* is a reduction of fruit set; this is the result of damage to the styles during the nectar robbing. Fruit set in inflorescences robbed by squirrels was 5.9 ± 0.62 percent and was significantly lower than that of 34.8 ± 9.76 percent in non-robbed inflorescences (t = 4.54, df = 1, $P < 0.001$).

Nectar robbing squirrels may also have indirect effects on plants by changing the behavior of the legitimate pollinators (Maloof & Inouye 2000). An indirect effect may be occurring here due to decreased nectar volume after primary nectar robbing by squirrels in the morning and secondary nectar robbing by insects through the damage to the corolla after the squirrels had visited (Fig. 1c, d). Over the three-year period (2000–2002), there was a decline in the visiting frequency of the main pollinator (carpenter bees) and a concurrent increase in nectar robbing by squirrels. The pollinators' visiting frequency dropped from 72.7 ± 31.6 times per flower per day in 2000 when there was no observed nectar robbing (Li *et al.* 2002) to 5.25 ± 2.63 times per flower per day in 2002 when the nectar robbing was most severe (see data above); but we did not find such a decline in non-robbed patches (Li *et al.* 2001).

An increase in nectar robbing in the observed patches over the period 2000–2002 may have been related to the life history of the plants *Alpinia kwangsiensis* invades tropical rain forests when canopy gaps first form and occupies the gaps for several years. As the canopy closes, the ginger gradually disappears from the gaps. Squirrels may require time to learn to forage on what may be a novel food source. Squirrel nectar robbing has also been observed on a congeneric species, *A. blepharocalyx* K. Schum (Deng *et al.* in press).

Nectar robbers play important ecological and evolutionary roles. Although their impact on plant reproduction may be negative, neutral, or positive, the negative effects may be most common (Irwin *et al.* 2001). Some previous studies have reported that nectar robbers have negative effects on fruit set (Navarro 2000) and seed set (Roubik 1982) through direct mechanisms, such as damage to reproductive organs (as reported here) or indirect mechanisms, such as changes in pollinator behavior (Roubik 1982, Irwin & Brody 1998, Maloof & Inouye 2000); however, nectar robbing by bees sometimes has a positive effect because some robbers act as pollinators (Maloof & Inouye 2000) or because altered pollinator behavior improves fitness through increased pollen flow and outcrossing (Maloof 2001), although this may not be the case in all systems (Irwin 2003). Our observations show that nectar-robbing squirrels have a negative effect on plant reproductive success (as judged by fruit set), through direct and indirect mechanisms.

Many aspects of this novel plant–animal interaction remain unknown. Further studies should experimentally manipulate robbing to test the relationship between plant reproduction and levels of robbing, measure the relative importance of nectar consumption in squirrel energetics, and investigate if the nectar of the ginger provides squirrels with any special or extra dietary element (*e.g.*, calcium; Barclay 2002).

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Xao-Bao Deng, Pan-Yu Ren, Jiang-Yun Gao, and Qing-Jun Li[2]

Xishuangbanna Tropical Botanical Garden
Chinese Academy of Sciences
Mengla, Yunnan 666303
People's Republic of China

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[2] Corresponding author; e-mail: qjlixtbg@bn.yn.cninfo.net