

The pollination ecology of *Bletilla striata* (Orchidaceae)

NAOTO SUGIURA*

Graduate School of Science and Technology, Kobe University, Kobe, 657 Japan

Anthecological observations of an orchid *Bletilla striata* were carried out in Kobe, Japan. The purplish pink flowers were visited by 26 species of insects belonging to Hymenoptera, Diptera and Lepidoptera, although the flower did not offer food rewards of any kind. Candidates for pollination were seven species of aculeate Hymenoptera with a body size that well fitted the space in between the column and labellum. The most effective candidate was the male of the longhorn bee *Tetralonia nipponensis*, judging from its abundance and legitimate intrafloral behavior. The female of *T. nipponensis* and the other six species also contributed to promote out-crossing, but to a lesser extent than the male *T. nipponensis*, since they occasionally exhibited illegitimate intrafloral behaviors for pollination and also, their flower visitation rate was lower.

Key words: *Bletilla*; intrafloral behavior; longhorn bee; pollination.

INTRODUCTION

The Asian genus *Bletilla* is represented by nine species, and one of these, *Bletilla striata* (Thunb.) Reichb. fil. is distributed in Japan, Taiwan and China (Tan 1969; Satake *et al.* 1982). In Japan, this terrestrial orchid is rarely seen naturally but is commonly cultivated in gardens and parks. In spite of such a commonplace species, anthecology of *B. striata* is not fully understood to date. Ishikawa (1968) and Tanaka (1990) described the floral features of *B. striata*, and recorded the honey bee, *Apis mellifera*, attached the pollinia on its body surface. Dressler (1990) reviewed the orchid pollination mechanism, and stated pollination by bees was reported for *Bletia*, *Arundina*, *Phaius* and *Calopogon* of Bletinae and expected for most genera in the subtribe.

Observations on the pollination of *B. striata* and the intrafloral behavior of the insect visitors were carried out. The results are presented here as a contribution to our understanding of insect – orchid relationships.

MATERIALS AND METHODS

Observations on the pollination were conducted at Kobe Municipal Arboretum, Hyogo Prefecture, Japan, during the three consecutive flower seasons (mid-May to early June, 1992–1994). The orchids were planted in patches in open, sunny areas. For the study, one flower clump (2.5 m × 1.0 m) was chosen. The study site was neighbored on secondary forest where *Quercus* and *Pinus* trees dominated.

A total of 9.65 h observation (5.45 h in 1992 and 4.20 h in 1993) and some additional sporadic observations were carried out between 13 : 17 and 15 : 56 to assess the composition and abundance of flower visitors. Flower visiting insects were counted and their intrafloral behavior observed in the flower clump where about 50–260 flowers bloomed. Some insects were netted for identification and counting pollinaria attaching on them.

On 14 May 1994, to assess the site fidelity of the male longhorn bee (*Tetralonia nipponensis*), all four bees visiting the orchid flowers were captured, and then marked with paint before their release. On 20 and 24 May, the presence of the marked bees was checked.

On 4 July 1992 and 1993, the number of young fruits and the number of flower scars on each of the 54 scapes were counted to estimate the proportion of flowers that received pollinia.

Received 13 April 1994.

Accepted 20 December 1994.

*Address all correspondence to Naoto Sugiura, Division of Environmental Biology, Faculty of Agriculture, Shimane University, Nishi Matsue 690, Japan.

RESULTS

Floral morphology

Structure

Flowers are 4.2–5.9 cm long and 4.5–6.4 cm wide (Fig. 1a), and arranged in a raceme of 2–19 flowers on an erect scape (Fig. 1b). They have no detectable scent as perceived by humans and do not offer food rewards of any kind although extrafloral nectaries are present at the base of the bract. The extrafloral nectaries attract ant workers of the genera *Formica*, *Lasius* and *Pristomyrmex*. Three sepals and two petals, except for the labellum, which are frequently ascending, are nearly equal in size and shape. The labellum is free and is composed of three lobes. The middle lobe serves as a landing platform for insect visitors, and its inner surface has 5-parallel ridges from anterior parts of which are waved. Two lateral lobes of the labellum lightly embrace the column, and thus form a chamber (hereafter referred to as the labellum chamber) into which the insect visitors enter. The column is slightly incurved over the labellum with anthers (covered with anther cap) in the ventral tip, with four mealy pollinia which more or less are bilobed (Tan 1969), or with eight soft pollinia (Satake *et al.* 1982). The stigma produces viscid material that receives the pollinia or permits the pollinia to glue the pollinating agents. The rostellum separates the fertile stigma from the anther and prevents natural self-pollination.

Coloration

The perianth segments except for the labellum are purplish pink. Most parts of the labellum are pale (whitish) purplish pink but the apex of the lateral lobes and the anterior margin of the middle lobe are deep purplish pink. The ridges of the middle lobe are white. Thus, the labellum is conspicuous due to its complex coloration and contrast with other floral parts. Coloration of the column is similar to that of the labellum, and most parts are pale purplish pink but with its apex deep purplish pink. The pollinia are pale yellow.

Flower visitors

Flowers of *B. striata* attracted diverse insects, that is, 26 species in 13 families belonging to Hy-

menoptera, Diptera and Lepidoptera (Table 1). The number of species was relatively high in Hymenoptera (16 species, 61.5%), followed by Diptera (6 species, 23.1%) and Lepidoptera (4 species, 15.4%). The relative abundance of individuals was also larger in Hymenoptera (77.5% of all) than in Diptera (15.3%) and Lepidoptera (7.2%). *Tetralonia nipponensis* was the most abundant species, which occupied 36.9% of the total individuals. All insect visitors exhibited a comparatively low flower visitation rate (individuals/h per clump) (Table 1), that is, the rate was less than 1.0 except for the following species: *T. nipponensis* (4.2), the small syrphid flies (1.3), the small carpenter bee *Ceratina japonica* (1.1) and the sweat bee *Lasioglossum occidens* (1.0). In the long-horn bee, the rate was higher in males (2.6) than in females (1.7).

Males of *T. nipponensis* appeared to visit the flower clump of *B. striata* to encounter receptive females, since it was observed that a patrolling male which had noticed a flower-visiting female tried to grasp her and on another occasion, a copulating male with pollinia was found on the labellum. Mate-seeking males patrolled among inflorescences with a brief inspection (by hovering) in front of each flower. The patrolling was occasionally interrupted by flower visits. One patrolling bout lasted for 3.0 min on average ($n = 7$, range 0.2–7.0 min), visiting up to eight flowers during a single bout. Several males, some of which had received pollinia of *B. striata*, also patrolled other flowering plants, for example *Rhododendron macrosepalum* (Ericaceae).

On 20 May 1994, three out of four marked males were found in the flower clump where the bees had been marked. They repeatedly appeared in the flower clump to patrol at the intervals of 2–29 min. On 24 May, however, marked males were no longer seen although several newly visited males were patrolling.

Intrafloral behavior

The insects seemed to visit flowers of *B. striata* to seek nectar since it was observed that many of them extended their proboscis on various parts of the flower such as the inside of the labellum chamber, furrows formed between ridges on the labellum, and the basal part of the column.



Fig. 1. (a) Flowers of *Bletilla striata*. (b) Inflorescences of *Bletilla striata*. (c) and (d) Pollinia transfer from anther to female *Tetralonia nipponensis*. The bee moving backward in the labellum chamber, pushing up anther cap. (e) The bee attaching pollinia (more than one pollinarium but partly removed by legs) on the body surface. (f) A worker *Apis mellifera* searching for nectar at the basal part of the column.

Hymenoptera

The body size, which largely determined removal or delivery of pollinia, differed among species, and

could be classified into two groups: small (body length 1.0 cm or less) and large (body length more than 1.0 cm). The small group included the andrenid bee *Andrena dentata*, *L. occidentis*, *L. proxima-*

Table 1. Insect visitors and their effectiveness as pollinators of *Bletilla striata*.

Order, family and species	Sex or caste	Flower visitation rate (individuals/h per clump)	Pollinia deposition
Hymenoptera			
Scoliidae			
<i>Campsomeris prismatica</i>	F	0.1	Yes
Vespidae			
<i>Polistes mandarinus</i>	Q	0.1	Yes
<i>Vespa simillima xanthoptera</i>	Q	0.1	No
Halictidae			
<i>Lasioglossum occidens</i>	F	1.0	No
<i>L. proximatium</i>	F	0.1	No
Andrenidae			
<i>Andrena dentata</i>	M	0.1	No
Megachilidae			
<i>Megachile tsurugensis</i>	M + F	0.5	
	M	0.2	Yes
	F	0.3	Yes
<i>Osmia taurus</i>	F	0.2	Yes
Anthophoridae			
<i>Nomada japonica</i>	F	0.2	Yes
<i>N. sp.</i>	?	0.1	No
<i>Tetralonia nipponensis</i>	M + F	4.2	
	M	2.6	Yes
	F	1.7	Yes
<i>Anthophora pilipes villosura</i>	F	0.4	No
<i>Ceratina japonica</i>	F	1.1	No
<i>Xylocopa appendiculata circumvolans</i>	F	0.2	No
Apidae			
<i>Bombus ardens</i>	W	0.2	No
<i>Apis mellifera</i>	W	0.2	Yes
Diptera			
Acroceridae			
<i>Oligoneura sp.</i>		0.2	No
Syrphidae			
<i>Episyrphus balteatus</i>	}	1.3	No
<i>Sphaerophoria sp.</i>			
<i>Melanostoma scalare</i>			
<i>Tubifera virgatus</i>		0.1	No
Conopidae			
<i>Myopa buccata</i>		0.1	Yes
Lepidoptera			
Hesperiidae			
<i>Potantbus flavum</i>		0.1	No
<i>Parnara guttata</i>		0.2	No
Papilionidae			
<i>Papilio protenor demetrius</i>		0.3	No
Satyridae			
<i>Ypthima argus</i>		0.2	No

Each species belonging to Hymenoptera shows the sex or caste division. M, male; F, female; M + F, both sexes; Q, queen; W, worker.

The value is calculated collectively in three species of small syrphid flies. The most dominant species is *E. balteatus*.

tum, the cuckoo bee *Nomada sp.* and *C. japonica*. These bees were too tiny and thin to contact the stigma and the anther even if they entered in the labellum chamber.

The other 11 species (Table 1) were classified as the large group. Their body size was large enough to

contact the stigma and the anther. The seven out of 11 species, the scoliid wasp *Campsomeris prismatica*, the paper wasp *Polistes mandarinus*, the leaf cutter bee *Megachile tsurugensis*, the mason bee *Osmia taurus*, the cuckoo bee *Nomada japonica*, *T. nipponensis* and *A. mellifera* were observed to receive

pollinia on their body surface, and the most common pollen-carrier was the longhorn bee. Pollinia transfer from the anther to the insect surface occurred only when the visitor moved backward into the labellum chamber; a retreating insect received the glue from the rostellum on the thorax, and then received pollinia (usually a pollinarium) on the glue. Furthermore, pollinia transfer from the pollinator body surface to the stigma of another flower was observed one time in a male longhorn bee.

Females of *T. nipponensis* usually exhibited the same intrafloral behavior (Fig. 1c–e) as the males did. The mean time from entering inside the labellum chamber to escaping outside was 12 s ($n = 10$, range 6–22). However, the females almost always removed the pollinia on their body by forelegs, resting on the flowers where they had just visited. Moreover, the bee intermittently vibrated thoracic flight muscles while its wings tightly closed over the body. One female spent 2 min to rake off the pollinia until the pollinia were almost completely removed. Such behavior might be the reason why 12 (92.3%) out of 13 females studied were observed not to receive the pollinia on the body. Many of these bees (58.3%, 7/12) reattached new pollinia during the flower visits but five out of seven bees removed the received pollinia before they flew away. Interestingly, females sometimes groomed their body to probably remove the viscid material from the rostellum even if they did not receive pollinia.

An individual honey bee that successively visited 11 flowers often entered the labellum chamber of those flowers, receiving pollinia on the body surface, but such flower visits were occasionally interrupted by illegitimate behaviors that did not lead to pollinia removal (Fig. 1f). Another individual removed the pollinia on its body surface by middle legs.

The shaggy fuzzyfoot bee *Anthophora pilipes villosura*, the carpenter bee *Xylocopa appendiculata circumvolans*, and the bumble bee *Bombus ardens* were never seen entering the labellum chamber. The shaggy fuzzyfoot bee and the bumble bee, both of which had a long proboscis, alighted on the labellum apex and introduced their proboscis in the labellum chamber rather than entering. The carpenter bee tried to enter the labellum chamber but its large body size prevented it from doing so. The hornet *Vespa simillima xanthoptera* entered but did not receive pollinia because the pollinarium had already been removed from the flower.

Diptera

The small syrphid *Episyrphus balteatus* usually alighted on anterior parts of the labellum, and introduced its extended proboscis in the furrows formed between ridges on the labellum. In one case, the fly successively visited three different flowers in the same manner but it mostly tended to rest on the labellum. The acrocerid *Oligoneura* sp. that had a long proboscis was observed to enter the labellum chamber but in all cases they left the flower receiving no pollinia. The small conopid *Myopa buccata* also entered the labellum chamber, and then moved backward. The dorsal surface of the abdomen brushed against the rostellum, attaching the pollinia on the glue just removed from the rostellum. However, the fly could not escape from the labellum chamber because it was too weak to completely take out pollinia.

Lepidoptera

The small satyrid *Ypthima argus* and two species of the skippers *Potanthus flavum* and *Parnara guttata* alighted and walked on various parts of the flower, such as the dorsal surface of the column and the inner surface of perianth segments. While walking, they often inserted their extended proboscis in the slit between the column and lateral lobe of the labellum, the labellum chamber, and the basal part of the column. On one occasion, *Y. argus* landed on the labellum and introduced its extended proboscis deeply in the labellum chamber. The black swallowtail butterfly *Papilio protenor demetrius* grasped the tip of the labellum, and inserted its extended proboscis in the labellum chamber, with fluttering wings.

Number and location of pollinaria attached on pollinators

As shown in Table 2, the number of pollinaria attached per individual was usually one but several males and a female of *T. nipponensis*, a male of *M. tsurugensis*, a worker of *A. mellifera* (not presented in Table 2), and a female of *C. prismatica* were found to receive two or more pollinaria which were sometimes piled up.

The pollinaria were usually received on the posterior portions of the thorax (mostly on scutellum and/or metanotum) of bees and wasps, although

Table 2. The number and location of pollinaria attached on the pollinator body surface.

Species	Sex or caste*	No. pollinaria	Location of pollinaria		
			Scutum	Scutellum	Metanotum
<i>Campsomeris prismatica</i>	F	2			○
<i>Polistes mandarius</i>	Q	1		○	
<i>Megachile tsurugensis</i>	M	1		○	○
<i>M. tsurugensis</i>	M	2		○	
<i>M. tsurugensis</i>	F	1		○	
<i>Osmia taurus</i>	F	1		○	
<i>O. taurus</i>	F	1		○	○
<i>Tetralonia nipponensis</i>	M	1		○	○
<i>T. nipponensis</i>	M	1		○	○
<i>T. nipponensis</i>	M	1		○	
<i>T. nipponensis</i>	M	1			○
<i>T. nipponensis</i>	M	1 <	○	○	○
<i>T. nipponensis</i>	M	2		○	○
<i>T. nipponensis</i>	M	2 <	○	○	○
<i>T. nipponensis</i>	M	2 <	○	○	○
<i>T. nipponensis</i>	M	2 <		○	○
<i>T. nipponensis</i>	F	1		○	
<i>T. nipponensis</i>	F	2 <		○	○
<i>Nomada japonica</i>	F	1		○	○
<i>Apis mellifera</i>	W	1		○	

*Refer to Table 1 for abbreviations.

the places slightly differed among species or individuals in relation to size and shape of the body, and the number of pollinaria received.

Fruit set

The mean number of flower scars per scape and the mean number of young fruits per scape in 1992 were 8.2 (range 5–19) and 1.9 (range 0–8), respectively. The mean fruit set for an individual scape was 23.3% (range 0.0–80.0). Approximately 20% (11/54) of the scapes bore no fruits at all. Similar results were found in 1993, that is, the mean number of flower scars was 6.1 (range 2–9), the mean number of young fruits was 1.5 (range 0–4), the mean fruit set was 24.3% (range 0.0–66.7), and the proportion of the scapes bearing no fruits was about 20% (11/54).

DISCUSSION

Flowers of *B. striata* were visited by 26 species of insects belonging to Hymenoptera, Diptera and Lepidoptera, but only seven species of the large bees and wasps were observed to receive pollinia on their body surface (Tables 1, 2). These seven bees and wasps with a body size that well fitted the space in

between the column and labellum, can be regarded as candidates for pollination, and the male *T. nipponensis* appears to be the most effective species in the study site, judging from the following reasons: (i) its visitation rate was the highest among the insect visitors (Table 1); (ii) as the bees always visited flowers in a legitimate manner, pollinia transfer from the anther to the bee body surface commonly occurred; (iii) pollinia transfer from the bee body surface to the stigma was confirmed; (iv) some males visited different flowers at the clump of *B. striata* for several days; and (v) the female of *T. nipponensis* and the other six candidates occasionally showed illegitimate intrafloral behaviors for pollination, and their flower visitation rate was lower than that of the male longhorn bee.

The absence of food rewards of any kind, the visitation by diverse taxa of insects, and the nectar seeking behavior of the visitors all suggest that *B. striata* is pollinated by generalized food deceit or food deception without a rewarding flower model (Nilsson 1992). Because no obvious rewarding flowers that resembled the flower of *B. striata* were observed during the orchid flowering period, food deception with a specific flower model is ruled out. Also, the possibility of sexual deception is unlikely since both sexes of various species of insects visited the flowers and no males attempting copulations

with the flowers were found. Although the floral stimuli to attract insects is not clear, the five white colored ridges on the (purplish pink colored) surface of the labellum may visually play an important role; they function as the deceptive nectar guide. Besides, scent emitted from the labellum, which is not detectable to humans but is detectable to insects, may be important. Additional studies, especially those for clarifying why the bees and wasps are repeatedly deceived by the orchid flowers, will be needed to further understand the pollination mechanism of *B. striata*, because it is generally known that hymenopteran insects can learn the features of profitable resources and recognize the resources from others (Heinrich 1979; Papaj & Lewis 1993).

The pollination efficiency and fruits set are usually low in deceptive systems (Nilsson 1979, 1980; Calvo 1990; Pettersson & Nilsson 1993), and variation in reproductive success among orchid individuals is often great (Calvo 1990). The results in *B. striata* agree with these tendencies.

In conclusion, the flower of *B. striata* morphologically adapts for pollination by large bees and wasps and it probably adopts generalized food deceit.

ACKNOWLEDGEMENTS

I express my sincere thanks to Mr S. Miyake and other staff of Kobe Municipal Arboretum for allowing me to carry out the research in their facilities and to Dr Y. Maeta and Mr M. Goubara of Shimane University for kindly identifying a conopid fly and some bees, respectively. My cordial thanks are also due to Dr T. Naito of Kobe University for his encouragement during the course of this study.

REFERENCES

- CALVO R. N. (1990) Inflorescence size and fruit distribution among individuals in three orchid species. *American Journal of Botany* 77: 1378–1381.
- DRESSLER R. L. (1990) *The Orchids: Natural History and Classification*. Harvard University Press, Cambridge.
- HEINRICH B. (1979) *Bumble Bee Economics*. Harvard University Press, Cambridge.
- ISHIKAWA M. (1968) The pollination of *Bletilla striata*. *Idea* 22: 30–34 (in Japanese).
- NILSSON L. A. (1979) Anthecological studies on the lady's slipper, *Cypripedium calceolus* (Orchidaceae). *Botaniska Notiser* 132: 329–347.
- NILSSON L. A. (1980) The pollination ecology of *Dactylophiza sambucina* (Orchidaceae). *Botaniska Notiser* 133: 367–385.
- NILSSON L. A. (1992) Orchid pollination biology. *Trends in Ecology and Evolution* 7: 255–259.
- PAPAJ D. R. & LEWIS A. C. (eds) (1993) *Insect Learning: Ecological and Evolutionary Perspectives*. Chapman & Hall, London.
- PETERSSON B. & NILSSON L. A. (1993) Floral variation and deceit pollination in *Polystachya rosea* (Orchidaceae) on an inselberg in Madagascar. *Opera Botanica* 121: 237–245.
- SATAKE Y., OHWI J., KITAMURA S., WATARI S. & TOMINARI T. (eds) (1982) *Wild Flowers of Japan: Herbaceous Plants (including Dwarf Subshrubs) Vol. 1*. Heibonsha, Tokyo (in Japanese).
- TAN K. W. (1969) The systematic status of the genus *Bletilla* (Orchidaceae). *Brittonia* 21: 202–214.
- TANAKA H. (1990) A mystery on the honey bee visitation to *Bletilla striata* flowers. In: *Field Watching, Vol. 1*. (eds S. Kawano & H. Tanaka) pp. 74–75. Hokuryukan, Tokyo (in Japanese).