

*Attraction of males of the cupreous polished chafer *Protaetia pryeri pryeri* (Coleoptera: Scarabaeidae) for pollination by an epiphytic orchid *Luisia teres* (Asparagales: Orchidaceae)*

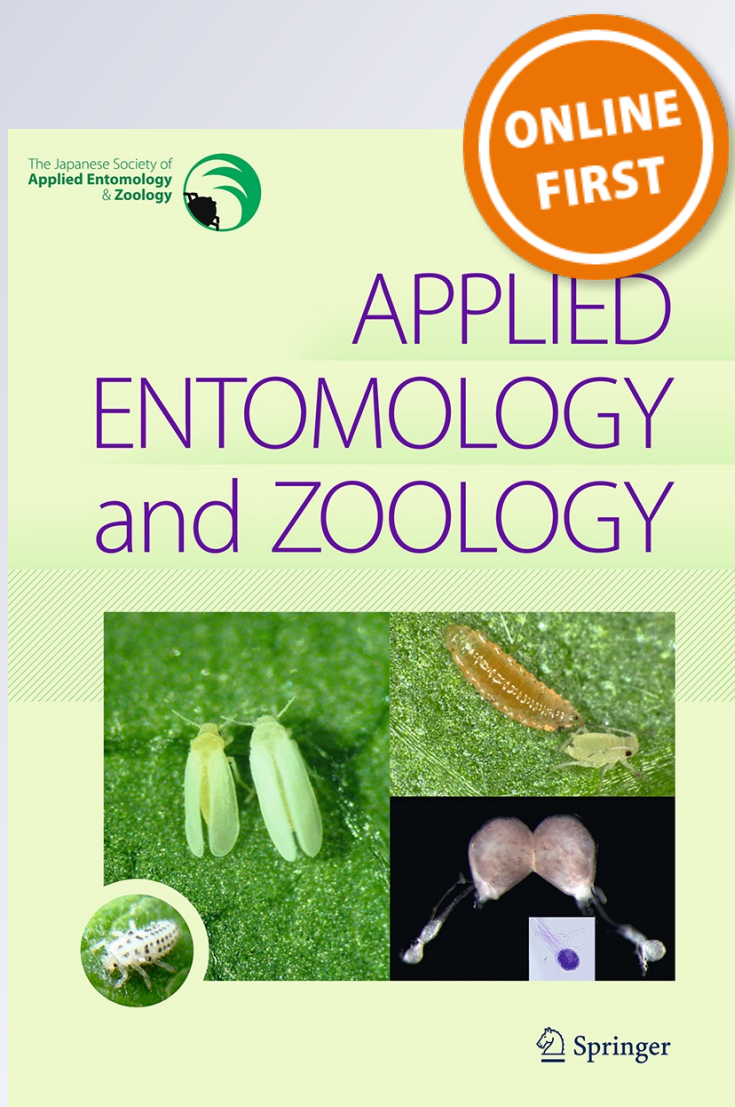
**Norio Arakaki, Keiji Yasuda, Shoko Kanayama, Sakiko Jitsuno, Masahiro Oike & Sadao Wakamura**

**Applied Entomology and Zoology**

ISSN 0003-6862

Appl Entomol Zool

DOI 10.1007/s13355-016-0396-5



**Your article is protected by copyright and all rights are held exclusively by The Japanese Society of Applied Entomology and Zoology. This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your article, please use the accepted manuscript version for posting on your own website. You may further deposit the accepted manuscript version in any repository, provided it is only made publicly available 12 months after official publication or later and provided acknowledgement is given to the original source of publication and a link is inserted to the published article on Springer's website. The link must be accompanied by the following text: "The final publication is available at [link.springer.com](http://link.springer.com)".**

# Attraction of males of the cupreous polished chafer *Protaetia pryeri pryeri* (Coleoptera: Scarabaeidae) for pollination by an epiphytic orchid *Luisia teres* (Asparagales: Orchidaceae)

Norio Arakaki<sup>1</sup> · Keiji Yasuda<sup>2</sup> · Shoko Kanayama<sup>3</sup> · Sakiko Jitsuno<sup>3</sup> · Masahiro Oike<sup>3</sup> · Sadao Wakamura<sup>3</sup>

Received: 13 September 2015 / Accepted: 5 January 2016  
© The Japanese Society of Applied Entomology and Zoology 2016

**Abstract** Males of the cupreous polished chafer *Protaetia pryeri pryeri* (Janson) (Coleoptera: Scarabaeidae: Cetoniinae) were observed to fly toward, hover around, and land on flowers of an epiphytic orchid *Luisia teres* (Thunberg) Blume (Orchidaceae). Female chafers were never attracted. When on a flower, a male chafer held the lip with his legs, and then inserted his head deep into the base of the flower column, where pollinia stuck onto his frons. Subsequently some *P. p. pryeri* males showed pseudocopulation on the lips: downward elongation of the abdomen and extrusion of the copulatory organ. When the chafer carrying pollinia visited another flower, the pollinia were found deposited on the flower stigma. Thus this chafer was considered to be an effective pollinator for this orchid. Males were also attracted to orchid flowers covered with loose cloth that eliminated their visibility, and to a solvent extract of the flower treated on a cotton ball. Therefore, we concluded that the chafer can use olfactory cues released from the orchid flower. Chemical analysis of the nectar secreted from the flower showed that sugar content was about 2–5 %. The pseudocopulation behavior by the pollinator and the presence of nectar on the flower are intriguing and may indicate an evolutionary transitional step between rewarding and rewardless species in deceptive pollination.

**Keywords** Pseudocopulation · Cetoniid beetle · Mouthpart · Pollinium · Nectar · Reward

## Introduction

It is estimated that one-third of approximately 25,000 orchid species are food deceptive flowers, and an additional 400 species are sexually deceptive and pseudocopulatory (Cozzolino and Wildmer 2005; Nilsson 1992). Deceptive flowers attract pollinators by visual and/or olfactory mimicry but do not offer any reward such as nectar or pollen (Bergström 1978; Schiestl et al. 1999). In deceptive rewardless orchid flowers, in contrast to those in rewarding species, there is often higher pollinator specificity, resulting in more efficient pollen transfer in a single pollinator visit (Dafni 1984).

In epiphytic orchids, the genus *Luisia* contains about 40 species found in tropical Asia, the Indian subcontinent, China, Japan, Malaysia, Philippines, Australia, Micronesia, and Melanesia (Seidenfaden 1971). The orchids of this genus are sometimes named the “bee orchids” because of the bee-like appearance of the flower. Specific bee species are attracted to these flowers and show pseudocopulation behavior (Kullenberg and Bergström 1976). Endress (1994) suggested that pseudocopulation on the orchid flower might play a role in the pollination of many unstudied tropical groups of orchid, such as the genera *Luisia*, *Haraella*, and *Lepanthes*.

One of the authors (K.Y.) noticed that several beetles flew persistently around orchid stalks of *Luisia teres* that had many flowers. These were the cupreous polished chafer *Protaetia pryeri pryeri* (Janson) beetles, suggesting an attraction to floral scent. The orchid *L. teres* is distributed in the Ryukyu Islands, southwestern Honshu, Shikoku, and

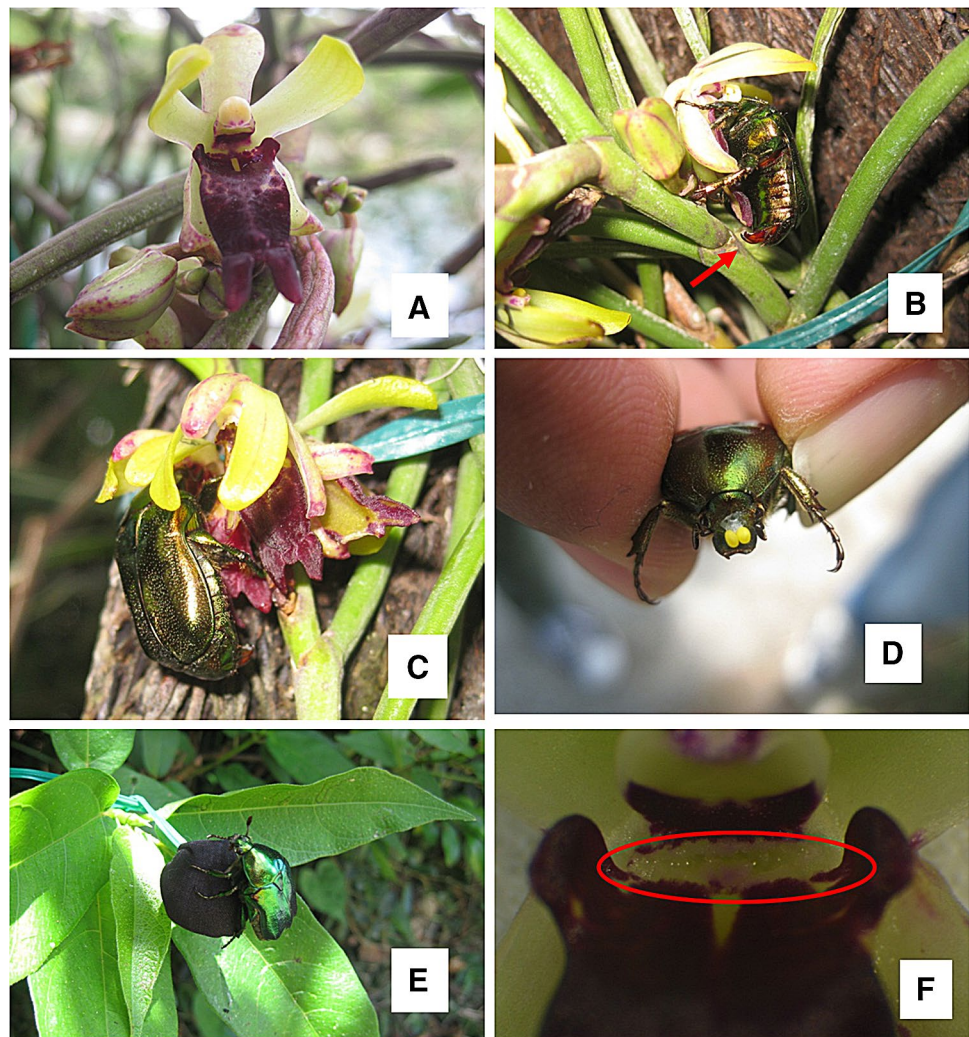
✉ Norio Arakaki  
arakkinr@pref.okinawa.lg.jp

<sup>1</sup> Okinawa Prefectural Agricultural Research Center, Itoman, Okinawa 901-0336, Japan

<sup>2</sup> Okinawa Prefectural Forest Resource Research Center, Nago, Okinawa 905-0012, Japan

<sup>3</sup> Faculty of Bioenvironmental Science, Kyoto Gakuen University, Kameoka, Kyoto 621-8555, Japan

**Fig. 1** **a** A flower of the orchid *Luisia teres*. **b** Pseudocopulation by *Protaetia pryeri pryeri* male on an orchid *L. teres* flower, with elongation of the abdomen downward to extrude the copulatory organ (arrow). **c** Pseudocopulation and probably licking the nectar at the base of flower column by *P. p. pryeri* male on an orchid *L. teres* flower. **d** Pollinia of *L. teres* on the frons of *P. p. pryeri* male. The pollinia cap was lost soon afterwards. **e** A *P. p. pryeri* male landing on a black cotton ball treated with an ether extract of *L. teres* flowers. **f** Base of flower column (red oval), where nectar secretion can be increased by mechanical stimulation with forceps or glass capillary



Kyushu in Japan, and in Taiwan (Ono et al. 1997). It has fleshy, rod-shaped leaves and is epiphytic on trees or rocks. The *L. teres* flower has a rather strong smell and insect-like appearance (Fig. 1a). It has an elongated oval lip with two triangular lobules. The lip is thick, mechanically stable, and dark reddish-purple in color. The chafer *Protaetia pryeri* is distributed in the southwestern islands of Japan and is divided into six subspecies. Among these subspecies, *P. pryeri pryeri* (Janson) occurs on Okinoerabu, Yoron, and Okinawa Islands (Sakai and Fujioka 2007). Adults emerge to fly from May to October and this period extends through the flowering season of *L. teres*. Adults feed on the mature fruits of fig trees (Sakai and Fujioka 2007) or sap of citrus trees (Hori 1987). Adults of this species are important pests of tropical fruits, such as papaya, guava, and wax apple (Arakaki et al. 2009). Adults were attracted to a ripe banana fruit as bait (Sakai and Fujioka 2007).

The pollination biology of *Luisia curtisii* Seidenfaden was studied in northern Thailand by Pedersen et al. (2013). They observed that two beetle species, *Lema unicolor* Clark

(Chrysomelidae) and *Clinteria ducalis* White (Scarabaeidae), pollinated *L. curtisii* and suggested that only these two beetles visit the flower and carry pollinaria of this orchid. Because this orchid flower offers no nectar for the visiting beetles, the pollination system seems to function as food or brood site deception according to Pedersen et al. (2013).

The purpose of our study was to reveal whether *L. teres* is pollinated by *P. p. pryeri* or other beetles. If so, we also intended to examine whether *L. teres* offers a floral reward or deceives the pollinators.

## Materials and methods

### Plant

*Luisia teres* were collected from epiphytic colonies on dead pine trees on northern Okinawa Island in May 2005 and May 2012, planted on tree-fern boards, and grown in a greenhouse or on tree branches until use. For repeated use

in experiments, the stalks were covered with a mesh bag made of polyester (38 cm diameter, mesh size 3.5 mm; “Marugata-sentakunetto”, LEC Inc., Tokyo) in order to prevent insect pollination, unless otherwise specified.

### Flower visitors

Insects attracted by *L. teres* flowers were examined and sexed at a shelter belt at Nashiro, Itoman City, Okinawa, from 10:00 to 12:00 on 28–29 August 2009. One orchid stalk was hung on the twig of a shelter tree and at a height of 1 m. As a comparison, three peeled bananas in the nylon mesh bags (knee-length sheer stocking) were placed on twigs at ca. 5-m intervals and a height of 1 m. To avoid the mutual influence of attraction of chafers between the orchid stalk and bananas, the banana baits were set at a different time; immediately after the orchid stalk was removed. The attracted insects were collected from 12:30 to 16:30. In the laboratory, chafer specimens were sexed on the basis of morphological differences in the protibia (Sakai and Fujioka 2007) or in reproductive organs by dissection under a binocular microscope.

In order to investigate nocturnal visitors on the orchid flowers, a field attraction test was conducted. Traps were made from corrugated cartons (45 × 35 × 33 cm) baited with orchid stalks with ca. 20 flowers. The traps had four plastic mesh funnels (entrance 16 cm diameter, exit 2 cm diameter, 17.5 cm height, mesh size 3 or 6 mm) in each side. Three traps were placed at Urasoe-dai-kôen Park, Urasoe, Okinawa, Japan on 29–31 June 2015.

### Attraction of *P. p. pryeri* males by *L. teres* flower

To confirm that the chafer attraction to orchids was evoked by the odor emitted by the flowers, chafer behavior around each of three orchid stalks with and without flowers was observed at a shelter belt at Nashiro from 14:00 to 16:00 on 23 June 2013. Although the stalks were in a mesh bag, plants and flowers were slightly visible. Orchid stalk locations were changed with 1-h intervals to eliminate any possible effect of trap locations.

To exclude the slight possibility of visual orientation in the chafer, the orchid stalks were completely covered with black polyethylene netting (80 % light shield rate, “Hutidori-tuki-hiyoke”, Morishita Inc., Okayama), such that the plants and flowers were not visible, but odor still passed through the netting. This follow-up experiment was conducted in the same manner on 24 June 2013.

### Behavior of male chafers around and on orchids

Male chafer behavior on the orchids was observed at a shelter belt at Nashiro, Itoman City, Okinawa from 14:00

to 16:00 on 13 June 2013. Three orchid stalks with flowers and without mesh covering were hung on the twigs of shrubs at a height of 1 m above the ground. Behaviors of chafers were visually observed around and on the orchids. We noted whether the pollinia had been removed by these chafers and whether the pollinia had been deposited on the stigma. Some of the insects landing were collected to confirm their sex. Flowers visited by the chafers were marked with numbered vinyl tape to examine subsequent seed production.

### Behavioral response of chafers to ether extract of orchid flowers

Four orchid flowers were soaked in ca. 0.8 ml ether in a glass vial (1.6 cm diameter × 6.0 cm height) for ca. 4 h at ca. 26 °C and stored in a refrigerator (0–2 °C) until use within ca. 24 h. A wad of absorbent cotton was wrapped with black polyester cloth and tied with plastic-coated wire to form a ball of 1.5 cm diameter (cotton ball; Fig. 1e).

Field attraction tests of the chafer to an ether extract of *L. teres* were conducted at Urasoe-dai-kôen Park on 6 July 2014. Ether extract of the orchid flower was impregnated onto an absorbent cotton ball 10 min before the observation. Then the cotton ball lures were mounted on twigs of undergrowth plants at a height of 20–30 cm from the ground. Equal volumes of solvent were applied to cotton balls in the same manner as field controls. The experiment had six replications.

### Sugar contents in the orchid flower secretion

The base of the column in the orchid flower was gently prodded with a 5- $\mu$ l micropipette (Drummond Scientific Co., PA, USA) until secretion was observed. The secretion was collected, transferred to a vial, and mixed with 50  $\mu$ l of distilled water. The solution (10  $\mu$ l) was injected into the HPLC system in order to determine the sugar concentration. Analyses were conducted with a Prominence HPLC system (Shimadzu, Kyoto, Japan) equipped with a Cosmosil sugar-D column (4.6 mm i.d. × 150 mm, Nacalai Tesque Inc., Kyoto, Japan). The column was kept at 35 °C. The eluting solvent was 70 % acetonitrile in water, and the flow rate was 0.70 ml/min. Sugars were detected with a refractive index (RI) detector, Prominence RIP-10A (Shimadzu).

## Results

### Flower visitors

Fifty-three and 46 *P. p. pryeri* chafers were collected on and around the orchid stalks during each 2-h field observation

**Table 1** Sex ratio of feral *P. p. pryeri* chafers attracted to orchid *L. teres* flowers or ripe banana (28–29 August 2009, Itoman, Okinawa)

	Female	Male	Sex ratio (%) <sup>a</sup>
Chafers attracted to orchid flowers	0	99	0
Chafers attracted with ripe banana	60	76	44

<sup>a</sup> (no. of females attracted)/[(no. of females) + (no. of males)] × 100. The ratios were significantly different by Fisher's exact test ( $P < 0.001$ )

on 28 and 29 August, 2009, respectively. All of the chafers were male (Table 1). In contrast, 44 % of the specimens in the chafers attracted to the banana baits were female ( $n = 136$ ). Among the chafers attracted to the orchid, one male of *Protaetia ishigakina okinawana* Y. Kurosawa was found. No other insects other than these two *Protaetia* species were noted during these field observations.

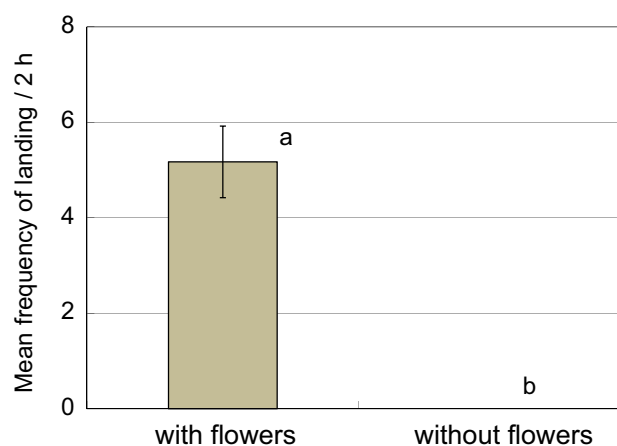
Male *P. p. pryeri* chafers were observed to enter flower-baited carton traps at the frequency of 1–6 chafers per hour during the day, and no chafers or no other insects were observed during the night.

In the subsequent field experiments described below, almost all of the chafers attracted with the *L. teres* flower were *P. p. pryeri* males. A small number of *P. i. okinawana* males were also found.

### Behavior of male chafers around and on orchids

In the field observation conducted on 13 June 2013, *P. p. pryeri* chafer males were observed to approach *L. teres* flowers in zigzag upwind flight, hover, and then land nearby. The male moved to hold the lip with his legs and then inserted his head deep into the space at the base of the column (Fig. 1c). While taking this posture, males were often observed to elongate their abdomen downward to extrude the copulatory organ (Fig. 1b). When the male left the flower, pollinia were found on his frons (Fig. 1d). The pollinia initially had a pollinical cap that fell off within a few minutes of transport. When the male with pollinia entered another flower, the pollinia were deposited on its stigma. In this observation, nine acquisitions of pollinia on *L. teres* flowers by *P. p. pryeri* chafer males were recorded. In three additional cases, chafers visited the flowers but did not acquire pollinia as a result of pollinia-depleted flowers. Five depositions of pollinia on other nearby *L. teres* flowers on the same or different stalk were observed. In the remaining four cases, chafers flew away without deposition. One acquisition of pollinia by a *P. i. okinawana* male was also observed.

The flowers that were visited by chafers were observed to wilt and to lose their unique odor within 5 or 6 days. Subsequently, seed production was confirmed on all five of the flowers marked as pollinated. In contrast, all the flowers



**Fig. 2** Attraction of *Protaetia pryeri pryeri* males to *Luisia teres* stalks with and without flowers. The values indicated are the mean frequency and SE (bar) of visits by males for 2 h visual observation ( $N = 6$ ). The means designated by different letters are significantly different with a Welch's *t* test at the 1 % level

kept from pollination remained fresh and continued to emit odor for more than 2 weeks.

### Attraction of *P. p. pryeri* males by the *L. teres* flower

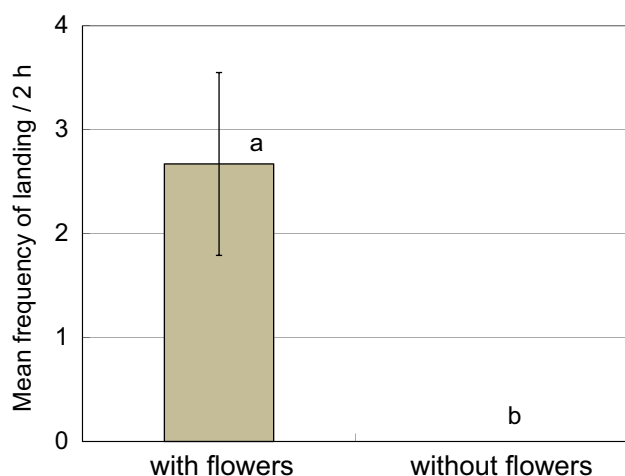
In the field, male *P. p. pryeri* chafers were observed to visit *L. teres* stalks with flowers at a frequency of 5.2 chafers/h. No males were attracted to the stalks without flowers (Fig. 2; Welch's *t* test,  $p < 0.001$ ). In the follow-up experiment in which the stalk was completely concealed from sight, the chafers were observed to approach only the orchids with flowers, at a mean frequency of 2.7 chafers/h (Fig. 3). The difference between the treatment and control was significant (Welch's *t* test,  $p < 0.05$ ).

### Behavioral response of chafers to ether extract of orchid flowers

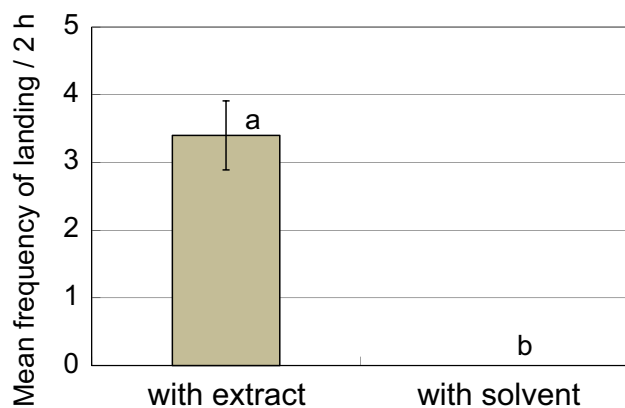
When cotton balls treated with ether extract of *L. teres* flowers were placed on plant leaves, many chafers landed on the leaves within 10 cm from the ball, and then arrived at it by walking (Fig. 1e). The mean number of beetles that arrived at the balls treated with extract was 3.4 chafers/2 h. No chafers were observed to land around the untreated balls (Fig. 4). The difference between the treatments was significant (Welch's *t* test,  $p < 0.05$ ). After arrival the chafers moved on and around the balls and then flew off within a few minutes.

### Sugar contents in the orchid flower secretion

To examine whether a sugar was contained in the flower secretion, liquid from the column base was analyzed by HPLC. When the lip was mechanically stimulated with a



**Fig. 3** Landing by *Protania pryeri pryeri* males on *Luisia teres* stalks with and without flowers. The orchids were covered with black polyethylene netting to completely conceal them from sight. The values indicated are the mean frequency and SE (bar) of visits by males for 2 h visual observation ( $N = 6$ ). The means designated by different letters are significantly different with a Welch's  $t$  test at the 5 % level



**Fig. 4** Landing by *Protania pryeri pryeri* males on cotton balls with and without ether extract of *Luisia teres* flower. The values indicated are the mean frequency and SE (bar) of landing by males for 2 h visual observation ( $N = 5$ ). The means designated by different letters are significantly different with a Welch's  $t$  test at the 5 % level

glass micropipette, approximately 0.1  $\mu$ l of liquid was collected. In the subsequent HPLC analysis, fructose, glucose, and sucrose were detected at a total concentration of ca. 2–5 % in the liquid ( $n = 3$ ). The approximate ratio of fructose, glucose, and sucrose was 1:2:1.

## Discussion

In most orchid pollination systems that use sexual deception, the attracted pollinator species is highly specific; only

one or two pollinators are attracted and these are only male (Gaskett 2011). In our observation, only two chafer species, *Protania pryeri pryeri* and *P. ishigakina okinawana*, were found to be attracted to *Luisia teres* flowers and all of them were male. The former was predominant and the latter was rather infrequent.

Pollinia were found stuck on the frons of male *P. p. pryeri* chafers after they inserted their heads deep into the column base on a flower (Fig. 1c, d). When he visited another orchid flower, the pollinia were left on the stigma. In such flowers, seed production was subsequently confirmed. These observations indicated that *P. p. pryeri* is a predominant pollinator of *L. teres* flowers on the Okinawa Islands.

All known sexually deceptive orchids attract their pollinators via floral odor (Phillips et al. 2014), and this can be partly confirmed by attracting pollinators to covered flowers (Kullenberg 1961). In our field experiments, the chafer was apparently attracted to *L. teres* stalks with flowers but not to those without flowers (Fig. 2). Flowering stalks covered with a sheet of black net (Fig. 3) and cotton balls treated with solvent extracts of flower were attractive (Fig. 4). These facts confirmed that male attraction involves flower odor.

Most species of sexually deceptive orchids have an insectiform floral structure (Kullenberg 1961). Phillips et al. (2014) consider insectiform orchid flowers to have some or all of the following traits: dull colored, inconspicuous flowers; reduced petals and sepals; a large lip relative to the remaining petals and sepals; the presence of hairs and/or pronounced texture. In deceptive orchids, those violet or purple in color are more attractive than light-colored variants (Bergström 1978). In the case of *L. teres*, it is a dull colored, inconspicuous flower with a large elongated, red-purple lip (Fig. 1a). This large thick lip plays a role as a platform at the time of chafer landing. This floral form may be associated with sexual behavior.

*Protania pryeri pryeri* males often showed pseudocopulation behavior on the lip of the orchid flower; they were observed to elongate the abdomen downward to extrude the copulatory organ (Fig. 1b). Generally, a combination of odor, visual orientation, and tactile stimulation is required to evoke full mating behavior in many insect species (Barth 1991). Similar sexual excitation behaviors to those in *P. p. pryeri* were found in male digger wasps (Sphecidae) *Gorytes mystaceus* L. and *G. campestris* L. when they visited orchid *Ophrys insectifera* L. flowers (Bergström 1978). In these cases, wasps landing on the flower tried to copulate with the flower lip, and pollinia became attached to their heads (Bergström 1978). Our finding is, to the best of our knowledge, the first record of pseudocopulation in the chafer on an orchid flower in Asia, while pseudocopulation has been recorded in Europe, Australia, Africa, and South America (Jersáková et al. 2006).

A small amount of liquid was observed on a spot at the base of the *L. teres* flower column (Fig. 1e). Glucose, fructose, and sucrose were detected in the liquid at concentrations of ca. 2–5 %. However, the total sugar content in flower nectar has been measured generally as ca. 40 % (8–76 %) (Barth 1991).

The chafers were observed to lick the lips of flowers with brush-like mouthparts, where they might take the “nectar”. Some orchid species are known to have shallow nectar glands at the location we observed (Stpiczyńska et al. 2003). Plant flowers generally offer pollen in addition to nectar as a reward to pollinators (Barth 1991; Dafni 1984). In the *P. p. pryeri* chafer, however, pollen does not seem accessible as a reward because pollinia were stuck onto the frons and the insects did not attempt to remove them (Fig. 1d).

In *L. teres* flowers, secretion of nectar was observed to increase when a specific spot at the base of the column was mechanically stimulated (Fig. 1f). Some male chafers were observed to extrude prognathous mouthparts on the *L. teres* flowers. This suggested that chafers consume nectar there and stimulate further nectar secretion. This suggestion may contrast a study on the congeneric orchid *L. curtisii* by Pedersen et al. (2013); they observed that beetles entered the flower and consistently probed the base of its column, but no floral nectar was detected. Whether the scanty nectar secreted from the *L. teres* flower may function as a reward for the pollinator would provide an interesting problem to be solved in the future.

Generally, most known deceptive flowers do not offer a reward to the pollinators but attract them by visual and/or olfactory mimicry (Bergström 1978; Cozzolino and Wildmer 2005; Dafni 1984; Nilsson 1992). In the interaction between *L. teres* and *P. p. pryeri*, the male chafers were apparently attracted by flower odor and occasionally adopted a pseudocopulatory posture on the flower lip (Fig. 1b). This suggested that the orchid flower mimics the female chafer. The orchid flower was also observed to secrete sugar-containing liquid, and the secretion was increased by mechanical stimulation. The sugar content of such secretion is only 2–5 %, a scanty reward for the pollinator.

Why does this orchid *L. teres* adopt two strategies, sexual deceit and reward, for pollinator attraction? We are familiar with only one similar case in *Diuris pedunculata* R. Br.; this Australian orchid attracts only males of a small black bee *Halictus lanuginosus* Smith and offers nectar (Coleman 1932). In the case of sexual deceit, Ames (1937) and Meeuse (1973) assumed that pollinators were originally rewarded by food. Kullenberg and Bergström (1976) postulated that floral odor was already present as a pollinator attractant before the loss of reward occurred and before

the lip acquired a female-like structure. The orchid *L. teres* appears to be at an evolutionary transitional step, as considered by Jersáková et al. (2006).

**Acknowledgments** We thank Takashi Kuriwada of Kagoshima University for his support with statistics. Thanks are also due to S. Glushkoff for editing the manuscript.

## References

- Ames O (1937) Pollination of orchids through pseudocopulation. *Bot Mus Leaflet* 5:1–28
- Arakaki N, Shimoji Y, Wakamura S (2009) Camphor: an attractant for the cupreous chafer, *Protaetia pryeri pryeri* (Janson) (Coleoptera: Scarabaeidae). *Appl Entomol Zool* 44:621–625
- Barth FG (1991) *Insects and flowers: the biology of a partnership*. Princeton University Press, New Jersey, p 408
- Bergström G (1978) Role of volatile chemicals in *Ophrys*-pollinator interactions. In: Harborne JB (ed) *Biochemical aspects of plant and animal coevolution*. Annual Proceedings of the Phytochemical Society of Europe. Academic, London, pp 205–231
- Coleman E (1932) Pollinations of *Diuris pedunculata* R. Br. *Vic Nat* 49:179–186
- Cozzolino S, Wildmer A (2005) Orchid diversity: an evolutionary consequence of deception? *Trends Ecol Evol* 20:487–494
- Dafni A (1984) Mimicry and deception in pollination. *Ann Rev Ecol Syst* 15:259–278
- Endress PK (1994) *Diversity and evolutionary biology of tropical flowers*. Cambridge University Press, London, p 511
- Gaskell AC (2011) Orchid pollination by sexual deception: pollinator perspectives. *Biol Rev* 86:33–75
- Hori S (1987) *Colleoptera*. In: Azuma S, Hori S, Minato K, Uesugi K, Kinjo M, Murayama N (eds) *Field guide to the insects of Okinawa*. Okinawa Shuppan, Okinawa, pp 78–79
- Jersáková J, Johnson SD, Kindlmann P (2006) Mechanisms and evolution of deceptive pollination in orchids. *Biol Rev* 81:219–235
- Kullenberg B (1961) *Studies in Ophrys pollination*. *Zool Bid Upps* 34:1–340
- Kullenberg B, Bergström G (1976) Hymenoptera Aculeata males as pollinators of *Ophrys* orchids. *Zool Scripta* 5:13–23
- Meeuse ADJ (1973) Co-evolution of plant hosts and their parasites as a taxonomic tool. In: Heywood VH (ed) *Taxonomy and ecology*. Academic, London, pp 289–316
- Nilsson L (1992) Orchid pollination biology. *Trends Ecol Evol* 7:255–259
- Ono M, Ohba H, Murata J, Nishida M (eds) (1997) *Revised Makino's illustrated flora in colour*. Hokuryukan, Tokyo, p 926
- Pedersen HÆ, Watthana S, Kocyan A, Srimuang K (2013) Pollination biology of *Luisia curtisii* (Orchidaceae): indications of a deceptive system operated by beetles. *Plant Syst Evol* 299:177–185
- Phillips RD, Scaccabarozzi D, Retter BA, Hayes C, Brown GR, Dixon KW, Peakall R (2014) Caught in the act: pollination of sexually deceptive trap-flowers by fungus gnats in *Pterostylis* (Orchidaceae). *Ann Bot* 113:629–641
- Sakai K, Fujioka M (2007) *Atlas of Japanese Scarabaeidae*. Phytophagous Group I, vol 2. Roppon-Ashi Entomological Books, Tokyo, p 173
- Schiestl FP, Ayasse M, Paulus HF, Löfstedt C, Hansson BS, Ibarra F, Francke W (1999) Orchid pollination by sexual swindle. *Nature* 399:421–422
- Seidenfaden G (1971) Notes on the genus *Luisia*. *Dan Bot Ark* 27:1–101
- Stpiczyńska M, Davies KL, Gregg A (2003) Nectary structure and nectar secretion in *Maxillaria coccinea* (Jacq.) LO Williams ex Hodge (Orchidaceae). *Ann Bot* 93:87–95