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SHORT COMMUNICATION

Sexually deceptive pollination of the non-native *Ophrys fuciflora* (Orchidaceae) in Japan by the native bee *Eucera nipponensis* (Hymenoptera: Apidae)

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Key words. Diurnal bees, pollinator, pseudocopulation, sexually deceptive pollination, non-native plant, Japan

Abstract. A study on the pollination of *Ophrys fuciflora* (Orchidaceae), which is not a native orchid of Japan, was carried out in a botanical garden in Japan, where the flowers attracted the solitary bee, *Eucera nipponensis*. Six male bees were observed visiting the flowers over a period of 8 h. The pollinia of *O. fuciflora* became attached to these bees and four were successfully transferred to the stigmas of nearby flowers. The present study verifies that a species of *Ophrys* can attract pollinators in Japan, which is at least 8,700 km far from their natural habitat. Thus, it is likely that species of *Ophrys* could potentially extend their distribution by forming new alliances with other species of bees.

INTRODUCTION

Orchidaceae with approximately 28,000 species (Christenhusz & Byng, 2016) is one of the largest families in the plant kingdom. During the evolution and divergence of Orchidaceae, differences in the provision of a reward and sexual deception of pollinators developed (Jersáková et al., 2007). No reward is common and reported in genera such as *Disa*, *Calopogon*, *Cypripedium*, etc. (Firmage & Cole, 1988; Johnson et al., 1998; Pemberton, 2013). In addition, pollination via sexual deception is also reported in orchids. The flowers imitate the mating signals of a target insect and are pollinated by sexually aroused insects. Species of *Ophrys* are sexually deceptive and the pollination of these species was first documented over a hundred thirty years ago (Darwin, 1885; Kullenberg, 1961; Vereecken & Patiny, 2005). The genus *Ophrys* includes nine 'macrospecies' recognized primarily by DNA barcoding and several hundred 'microspecies' identified mainly by the specificity of the pollinator (Bateman & Rudall, 2023). These species are distributed throughout Europe, North Africa, the Canary Islands and the Middle East, extending as far east as Turkmenistan (Delforge, 2006). The primary pollinators of this group of orchids are Hymenoptera with Diptera and Coleoptera also reported as pollen carriers (Reihard et al., 1991; Stökl, 2005; Tyteca et al., 2006). Male insects exclusively mediate the transfer of pollinia in orchids, particularly in the case of species of *Ophrys*, where pollination via "pseudocopulation" has been confirmed (Paulus & Gack, 1990; Schiestl et al., 1999). The 'microspecies' within *Ophrys sphegodes* Mill. vary in the composition of their pseudo-pheromones (Sedeek et al., 2016), and Kellenberger et al. (2019) reported similarly small genetic modification that affect anthocyanin synthesis. High genetic diversity is a notable characteristic of the genus *Ophrys*. All previous studies, on pollination in *Ophrys* were carried out in their natural habitat. This study reports the sexually deceptive ability of *Ophrys fuciflora* (F.W. Schmidt) Moench far from its natural habitat. This orchid is distributed from Britain and Spain to Turkey and Romania and Libya and the Middle East as far east as Iraq (Delforge, 2006) but does not occur in the East Asian region. This study reports the pollination of cultivated *O. fuciflora* in Japan.

MATERIAL AND METHODS

Two mature tubers of *O. fuciflora* were obtained from a website, http://www.myorchids.de and imported with a permit from the Convention on International Trade in Endangered Species (CITES) along with a Phytosanitary Certificate from Germany. The two tubers were planted in the same plastic pot and cultured outdoors in Tsukuba Botanical Garden, Ibaraki, Japan (36°06′04″N, 140°06′41″E, alt. 26 m). The total area of the botanical garden is approximately 14 ha and plants belonging to 56 families, 102 genera and 134 species bloomed on 2 May 2015 (Table 1). Two other species of orchid, *Calanthe discolor* Lindl. and *C. sieboldii* Decne. ex Regel, were also present and planted near the flower bed (within 200 m), which flowered from 30 Apr. to the 10 May in 2015. The two *O. fuciflora* plants started to bloom on the 15 April 2015, and all flowers were open on the 1 May. In order to prevent pollination before this experiment, two inflorescences were covered with non-woven fabric until the 2 May 2015. Pollination of the *O. fuciflora* flowers by the bees were observed between 09:00 snd 17:00 on 2 May 2015, and the frequency of visits, behaviour, staying times, the number carrying pollinia away from flowers, and the number of pollinia attached

Table1. Plants in bloom at the Tsukuba Botanical Garden at the time the experiment was conducted (2 May 2015).

Family	Genus	Species	Author(s)
Pinaceae	*Larix*	*kaempferi*	(Lamb.) Carr.
Schisandraceae	*Illicium*	*anisatum*	L.
Magnoliaceae	*Magnolia*	*obovata*	Thunb.
Calycanthaceae	*Calycanthus*	*floridus* var. *glaucus*	(Willd.) Torr. & A. Gray
Lauraceae	*Machilus*	*thunbergii*	Siebold et Zucc.
Acoraceae	*Acorus*	*calamus*	L.
	Acorus	*gramineus*	Sol. ex Aiton
Colchicaceae	*Disporum*	*sessile*	D. Don ex Schult.
	Disporum	*smilacinum*	A. Gray
Smilacaceae	*Smilax*	*nipponica*	Miq.
Liliaceae	*Fritillaria*	*camtschatcensis*	(L.) Ker-Gawl.
	Maianthemum	*japonicum*	(A.Gray) LaFrankie
	Tulbaghia	*fragrans*	I. Verd.
Orchidaceae	*Bletilla*	*striata*	Reichb. fil.
	Calanthe	*discolor*	Lindl.
	Calanthe	*sieboldii*	Decne. ex Regel.
	Cremastra	*appendiculata* var. *variabilis*	(Blume) I.D. Lund
	Cymbidium	*goeringii*	(Rchb.f.) Rchb.f.
	Cypripedium	*japonicum*	Thunb.
Iridaceae	*Iris*	*sanguinea*	Donn ex Hornem.
	Iris	*laevigata*	Fisch.
	Iris	*japonica*	Thunb.
	Iris	*rossii* f. *purpurascens*	Y.N. Lee
Asphodelaceae	*Hemerocallis*	*fulva*	(L.) L.
Amaryllidaceae	*Allium*	*schoenoprasum* var. *orientale*	Regel
	Leucojum	*aestivum*	L.
Asparagaceae	*Convallaria*	*majalis*	L.
	Polygonatum	*odoratum*	Mill.
	Polygonatum	*humile*	Fisch. ex Maxim.
	Ruscus	*aculeatus*	L.
Papaveraceae	*Chelidonium*	*majus*	L.
Lardizabalaceae	*Akebia*	*trifoliata*	(Thunb.) Koidz.
	Stauntonia	*hexaphylla*	(Thunb.) Decne.
Ranunculaceae	*Anemone*	*stolonifera*	Maxim.
	Anemone	*flaccida*	F. Schmidt
	Caltha	*palustris*	L.
	Pulsatilla	*cernua*	(Thunb.) Bercht. et C.Presl
	Ranunculus	*grandis*	Honda
Trochodendraceae	*Trochodendron*	*aralioides*	Siebold et Zucc
Altingiaceae	*Liquidambar*	*styraciflua*	L.
Hamamelidaceae	*Rhodoleia*	*championii*	Hook.f.
Saxifragaceae	*Saxifraga*	*nipponica*	Makino
	Tiarella	*polyphylla*	D.Don
	Tiarella	*cordifolia*	L.
Crassulaceae	*Sedum*	*tosaense*	Makino
Fabaceae	*Wisteria*	*floribunda*	(Willd.) DC.
	Cercis	*chinensis*	Bunge
	Cytisus	*scoparius*	(L.) Link.
Rosaceae	*Padus*	*buergeriana*	(Miq.) T.T. Yü et T.C. Ku
	Prunus	*serrulata*	Lindl.
	Rosa	*rugosa*	Thunb.
	Rosa	*banksiae*	R.Br.
	Sorbus	*commixta*	Hedl.
	Spiraea	*dasyantha*	Kuntze
	Spiraea	*cantoniensis*	Lour.
	Kerria	*japonica*	(L.) DC.
	Stephanandra	*tanakae*	Franch. et Sav.
Elaeagnaceae	*Elaeagnus*	*umbellata*	(Nakai et Masam.) Masam.
Rhamnaceae	*Rhamnus*	*davurica* var. *nipponica*	Maxim.
	Rhamnus	*aponica* var. *decipiens*	Maxim.
Moraceae	*Morus*	*australis*	Poir.
Fagaceae	*Quercus*	*serrata*	Murray
Juglandaceae	*Pterocarya*	*rhoifolia*	Siebold et Zucc.
Coriariaceae	*Coriaria*	*japonica*	A. Gray
Celastraceae	*Euonymus*	*oxyphyllu*	Miq. f.
	Euonymus	*alatus*	Thunb.
Violaceae	*Viola*	*grypoceras*	A. Gray
Euphorbiaceae	*Euphorbia*	*jolkinii*	Boiss.
	Phyllanthus	*flexuosus*	Müll. Arg.
Staphyleaceae	*Staphylea*	*bumalda*	DC.
Rutaceae	*Zanthoxylum*	*piperitum*	(L.) DC.
Brassicaceae	*Cardamine*	*leucantha*	(Tausch) O.E. Schulz
	Raphanus	*sativus* var. *hortensis* f. *raphanistroides*	Makino
Polygonaceae	*Bistorta*	*officinalis*	Delarbre
	Bistorta	*suffulta*	(Maxim.) H. Gross
	Rumex	*acetosa*	L.
Hydrangeaceae	*Deutzia*	*scabra*	Thunb.
	Deutzia	*crenata*	Siebold et Zucc.
	Deutzia	*gracilis*	Siebold et Zucc.
Cornaceae	*Cornus*	*controversa*	(Hemsl. ex Prain) Soják
	Cornus	*canadensis*	L.
	Cornus	*florida*	L.
	Davidia	*involucrata*	Baillon
Polemoniaceae	*Phlox*	*subulata*	L.
Primulaceae	*Lysimachia*	*thyrsiflora*	L.
	Primula	*sieboldii*	E. Morren
	Primula	*japonica*	A. Gray
Theaceae	*Camellia*	*japonica*	L. f.
Symplocaceae	*Symplocos*	*sawafutagi*	Nagam.
Ericaceae	*Cassiope*	*lycopodioides*	(Pall.) D. Don
	Enkianthus	*sikokianus*	(Palib.) Ohwi
	Enkianthus	*campanulatus*	(Miq.) G.Nicholson
	Enkianthus	*perulatus*	(Miq.) C.K. Schneid.
	Pieris	*japonica*	(Thunb.) D. Don ex G. Don
	Rhododendron	*reticulatum*	D. Don ex G. Don
	Rhododendron	*tashiroi*	Maxim.
	Rhododendron	*kaempferi*	Planch.
	Rhododendron	*serpyllifolium*	(A. Gray) Miq.
	Rhododendron	*molle*	(Blume) G. Don
	Rhododendron	*ripense*	Makino
	Rhododendron	*yedoense* var. *poukhanense*	(H. Lev.) Nakai
	Vaccinium	*vitis-idaea*	L.
Garryaceae	*Aucuba*	*japonica*	Thunb.
Gentianaceae	*Gentiana*	*zollingeri*	Fawc.
Apocynaceae	*Vinca*	*major*	L.
Oleaceae	*Forsythia*	*japonica*	Makino
	Fraxinus	*lanuginose*	Koidz.
	Jasminum	*mesnyi*	Hance
	Ligustrum	*japonicum*	Thunb.
	Syringa	*microphylla*	Diels
Lamiaceae	*Ajuga*	*decumbens*	Thunb.
	Ajuga	*nipponensis*	Makino
	Glechoma	*hederacea*	L.
	Lamium	*galeobdolon*	(L.) Crantz
	Meehani	*urticifolia*	(Miq.) Makino
Helwingiaceae	*Helwingia*	*japonica*	(Thunb.) F. Dietr.
Aquifoliaceae	*Ilex*	*cornuta*	Lindl. & Paxton
Campanulaceae	*Peracarpa*	*carnosa* var. *circaeoides*	(Fr. Schm.) Makino
Menyanthaceae	*Menyanthes*	*trifoliata*	L.
	Nymphoides	*peltata*	(S.G. Gmel.) Kuntze
Asteraceae	*Aster*	*savatieri*	Makino
	Chrysanthemum	*rupestre*	Matsum. et Koidz.
	Erigeron	*thunbergii*	A. Gray
	Taraxacum	*albidum*	Dahlst.
	Taraxacum	*platycarpum*	Dahlst.
	Tephroseris	*pierotii*	(Miq.) Holub
Viburnaceae	*Viburnum*	*erosum*	Thunb.
	Viburnum	*plicatum var. tomentosum*	Miq.
	Viburnum	*sieboldii*	Miq.
Caprifoliaceae	*Abelia*	*tetrasepala*	(Koidz.) H. Hara et S. Kuros.
	Lonicera	*morrowii*	A. Gray
	Valeriana	*flaccidissima*	Maxim.
	Weigela	*decora*	(Nakai) Nakai
	Weigela	*floribunda*	(Sieb. et Zucc.) K. Koch.

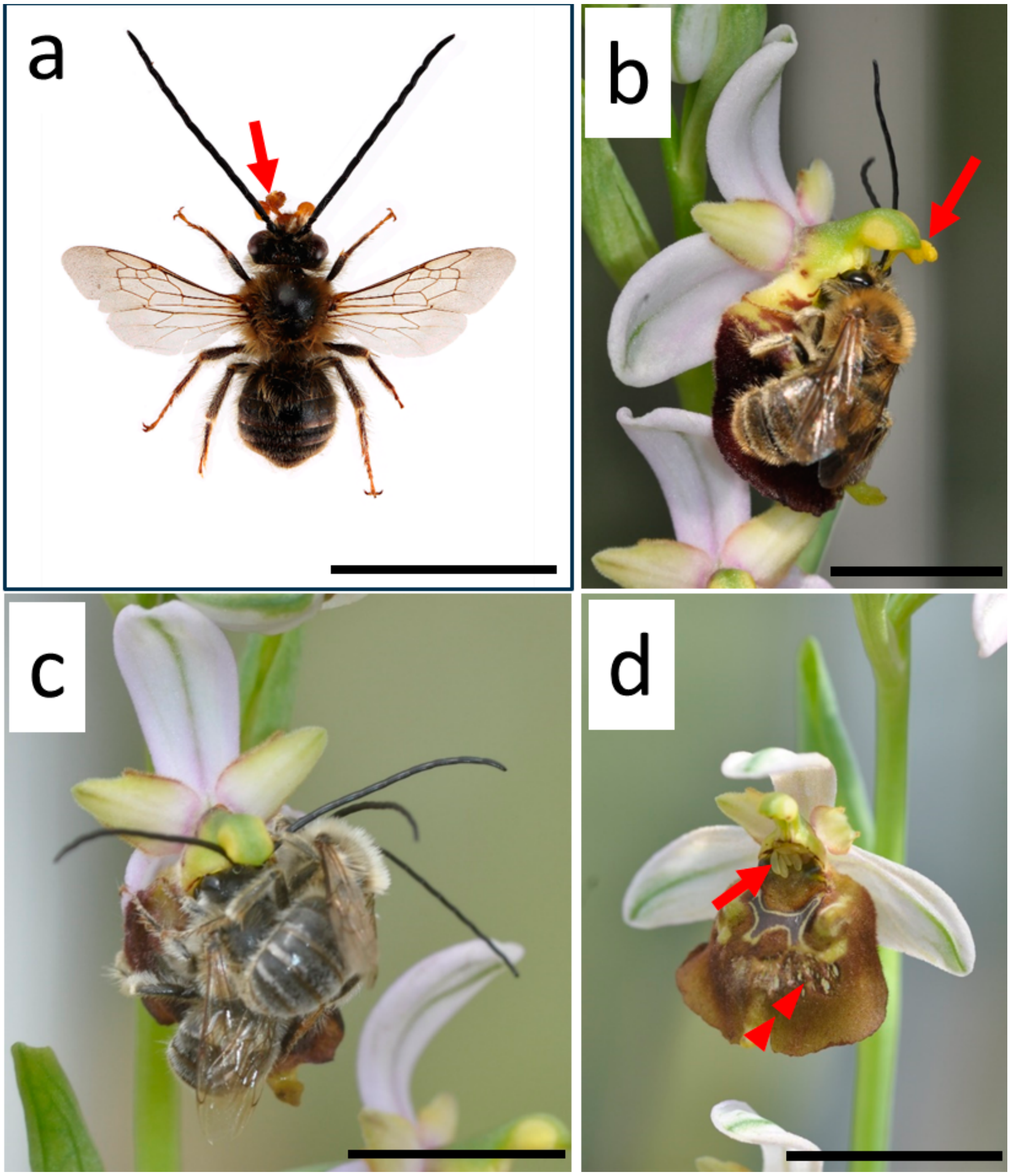

Fig. 1. Pollination of the European orchid *Ophrys fuciflora* in Japan. a: Male of *Eucera nipponensis* with pollinium of *Ophrys fuciflora*. Arrow indicates the location of the pollinium in *Ophrys fuciflora*. b: Pseudo-copulation: male of *Eucera nipponensis* on flower of *Ophrys fuciflora*. Arrow indicates the location of the pollinium attached to head of *E. nipponensis*. c: Two males of *Eucera nipponensis* on a flower of *Ophrys fuciflora*. d: Adherence of a non *Ophrys* species pollinium to the stigma of *Ophrys fuciflora*. Arrow: pollinium of *Calanthe* sp. Double arrowhead: Scratches made by a male of *E. nipponensis* during pseudo-copulation. Bar = 1 cm.

to stigmas were recorded. The total study time was one day, of which 8 h were spent observing the orchids. One month after pollination, the number of fruits on *O. fuciflora* was recorded. In addition, the percentage of seed with embryos was calculated.

RESULTS

The two *O. fuciflora* plants produced nine flowers. Six bees visited the flowers a total of ten times (Table 2). Because all these bees were the same species, two were caught and identified to species level based on their morphological characteristics. Both bees were males of *Eucera nipponensis* Pelez (Hymenoptera: Apidae) (Fig. 1a). The first bee was observed to visit a flower at 10:03 and the last at 15:46. The air temperature over that period of time ranged from 18°C to 23°C. The attracted bees continually rubbed the tips of their abdomens and hind legs against the lips of *O. fuciflora* (Fig. 1b). The longest and shortest times the bees spent on the flowers were 90 min 10 s and 10 min 5 s, respectively (Table 2). At 16:02, two male bees huddled together on the same flower (Fig. 1c). The pollinia of *O. fuciflora* adhered to all the attracted bees, and four out of the six bees also visited a neighbouring flower of *O. fuciflora.* Adhesions of pollinia to stigma of four *O. fuciflora* flowers were recorded at the end of this experiment. In addition, at 15:23 one of the six male bees carried a pollinium of a non-*Ophrys* species, which adhered to the stigma of one of the *O. fuciflora* flowers (Fig. 1d). The centre of the petal was scratched and surface damaged by the legs of *E. nipponensis*

Table 2. Pollination by solitary bee, *Eucera nipponensis* to *Ophrys fuciflora* in this study.

Individual code of bee[1]	Visited time	Staying time	Adhesion of pollinium to stigma[2]	Fructification
A	10:03	35´10˝		
	10:38	23´01˝	○	○
B	11:12	30´08˝		
	11:42	20´10˝	○	○
C	11:46	10´05˝		
	11:57	60´01˝	○	○
D	13:12	90´10˝		
	14:43	15´03˝	○	○
E	15:23	64´09˝	□	
F	15:56	25´07˝		

[1] Different character shows different individuals of soitary bee, *Eucera nipponensis.* [2] White circle and square show pollinium adhesion in *Ophrys fuciflora* and *Calanthe* sp., respectively.

(Fig. 1d) One month after the observation, four pods on the two plants of *O. fuciflora* were mature (Table 2). Percentage of seed in pods with embryos was 65%.

DISCUSSION

The reported pollinators of *O. fuciflora* in its natural habitat are males of the beetle, *Phyllopertha horticola* (L.) (Coleoptera: Scarabaeidae) (Tyteca et al., 2006) and males of the solitary bees, *Eucera* spp., *Tetralonia* spp. (Hymenoptera: Apidae) and *Chalicodoma erivetorum* (Hymenoptera: Megachilidae) (Kullenberg, 1961; Ågren et al., 1983; Paulus & Gack, 1986). *O. fuciflora* is characteristically pollinated by very different taxa, including wild bees of the genus *Eucera*, as well as hoverflies and a beetle (Claessens & Kleynen, 2011; Joffard et al., 2019). This indicates it is potentially capable of attracting a wide range of different species of pollinator.

Dorchin et al. (2018) changed the classification of the genera, *Tetralonia, Peponapis, Xenoglossa, Cemolobus* and *Syntrichalonia* to sub generic rank within *Eucera* based on the analysis of 6,700 aligned nucleotide sites in six gene fragments and 120 morphological characters. Therefore, the pollinator of *E. nippoensis* is monophyletic and belongs to the subgenus *Synhalonia* so it is likely they have similar physiological characteristics. This indicates that it is likely that the chemical structure of the female sex pheromone produced by *E. nipponensis* could be similar to that of the bees that pollinate *O. fuciflora* in its natural habitat. In this study, the pollinia of *O. fuciflora* adhered to *E. nipponensis* and were transported to the stigmas of other *O. fuciflora* flowers. Furthermore, this resulted in fructification and formation of seed containing embryos. This confirms that *E. nipponensis* can pollinate *O. fuciflora* cultivated in Japan and the method of pollination was similar to that reported for this orchid in its natural habitat, which is located at least 8,400 km away from its most eastern part of its range in Iraq. In the present study, the sexually deceptive ability of *O. fuciflora* was recorded for the first time in a country well outside is normal range.

One of the six males of *E. nipponensis* carried the pollinium of another species of orchid to the stigma of *O. fuciflora.* From its morphological characteristics, this pollinium could be that of a species of *Calanthe* (*C. discolor* or *C. sieboldii*) growing in the same flower bed. Their pollination strategies involve food deception and in natural habitats the pollinator is the solitary bee, *E. nipponensis* (Suetsugu & Fukushima, 2013). The male bees may initially have been attracted by the food deception strategy of the species of *Calanthe* and then more strongly by the sexual deception strategy *O. fuciflora*. Currently there are no native sexually deceptive orchids in Japan. The longest time *E. nippoensis* spent on flowers of *O. fuciflora* was 90 min 10 s and it was easy to collect the two bees by hand. Because males of the Japanese endemic species, *E. nippoensis*, have no opportunity to encounter orchids with sexually deceptive pollination strategies, the odour of *O. fuciflora* may have been a powerful attractant for this solitary bee.

In previous studies the specificity of the pollinators of species of *Oprhys* was determined. Reproductive efficiency of *Ophrys* is not affected by climate change, because it can attract other solitary bees that are adapted to the new environmental conditions (Breitkopf et al., 2013; Bateman, 2022). Changes in preferred pollinators from among 67 species of solitary bees in the genus *Andrena* is confirmed for *O. sphegodes*, which ensures that populations of this orchid remain resilient (Stroh et al., 2022). Pollination of this orchid may be more opportunistic than described in the literature, with one main pollinator and one or several secondary pollinators in the range of each species (Schatz et al., 2021). *Ophrys* with its unique floral traits and high genetic diversity could extend its distribution by forming new alliances with other species of bees.

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