

THE POLLINATION ECOLOGY OF *RHODODENDRON FLOCCIGERUM* FRANCHET (ERICACEAE) IN WEIXI, YUNNAN PROVINCE, CHINA

Elizabeth Georgian^{*1,2}, Zhendong Fang³, Eve Emshwiller¹, Anna Pidgeon⁴

¹Department of Botany, University of Wisconsin-Madison, U.S.A.

²Department of Botany and Genetics, Vilnius University, Vilnius, Lithuania

³Shangri-La Alpine Botanical Garden, Shangri-La, China

⁴Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, U.S.A.

Abstract—Identifying the pollinators of *Rhododendron* species is of great interest due to potential conservation threats in the native range of the genus, but the pollinators of species in *Rhododendron* subgenus *Hymenanthus* section *Pontica* subsection *Neriiflora* are unknown. Bees (Hymenoptera; family Apidae) are thought to be the pollinators of many *Rhododendron* species; however, species in subsection *Neriiflora* have ornithophilous floral morphology. We studied *R. floccigerum* (subsection *Neriiflora*) to determine the identities of visiting, potentially pollinating, and robbing species through in-person and time lapsed camera trap observations. We compared floral morphological characteristics of *R. floccigerum* with visitor morphological measurements to determine if visitors could fit inside the corolla. Thirteen species were observed visiting *R. floccigerum* (two insects, two mammals, and nine birds) and this study provides the first empirical evidence of both bird and mammal visitors to *Rhododendron* species. We determined that the following species are potential pollinators: *Bombus* sp. (an insect genus), *Aethopyga gouldiae*, *Garrulax affinis*, *Heterophasia melanoleuca*, and *Yuhina diademata* (all bird species), and we suspect that *Apis* sp. (an insect genus), *Dremomys pernyi*, *Tamiops swinhoei* (two mammal species), *Minla ignotincta*, *M. strigula*, *Parus major*, and *Phylloscopus affinis* (four bird species) likely rob *R. floccigerum*. All visitors were able to fit their heads/bodies into the corolla. We also found that though predation is frequent, the number of robbers and variety of robbing methods is unlikely to contribute to floral morphological evolution or speciation. Further understanding of the pollination biology of species in subgenus *Hymenanthus* will allow for effective conservation.

Keywords: *Rhododendron*, robbers, ornithophily, pollination syndrome, potential pollinators

INTRODUCTION

Rhododendron L. (Ericaceae) is a large genus with about 1,000 species of woody shrubs, trees, and epiphytes (Wu et al. 2005). Bees (Hymenoptera; family Apidae) are thought to be pollinators of many *Rhododendron* species (Kudo 1993; Ono, Dohzono, & Sugawara 2008). For example, the most frequent and important visitors to *R. ferrugineum* in Austria are bumblebees (*Bombus* spp.) and honeybees (*Apis* spp.; Escaravage & Wagner 2004). *Rhododendron semibarbatum* in Japan is pollinated by *Bombus eximus* and *Apis cerana* (Ono, Dohzono, & Suguwara 2008). Six species of *Rhododendron* in Hong Kong, including one species in subgenus *Hymenanthus* (*R. simiarum*), are pollinated by *Apis* sp., *Bombus* sp., and *Xylocopa* spp. (Ng & Corlett 2000). Additionally, *R. reticulatum* and *R. macrosepalum* in Japan are reportedly visited by several species of insects including species of Hymenoptera, Lepidoptera, Diptera, and Coleoptera (Sugiura 2012).

Despite the evidence for insect pollination, observations suggest bird pollination in rhododendrons with morphological characters including possession of large, red,

tubular-campanulate flowers that produce copious amounts of nectar (e.g., species in subsection *Neriiflora*; Stevens 1985; Argent et al. 1988; Steinheimer 1999; Kingdon-Ward 2007). Bird pollinated flowers are typically red, unscented, with a prominent nectar display that produce dilute nectar, and in the Old World, provide a perch for non-hovering birds (Liu et al. 2013). Birds can be effective pollinators because their eyesight allows them to see long distances and accurately fly to flowers (Cronk & Ojeda 2008). Bird pollination is common in aseasonal climates; however, it is often rare in regions with a long winter, as well as in Asia north of the Himalayas, where there are few food options for nectivorous birds (Cronk & Ojeda 2008).

The present study investigates the pollination ecology of the ornithophilous-flowered *R. floccigerum* Franchet in *Rhododendron* subgenus *Hymenanthus* section *Pontica* subsection *Neriiflora* (27 species in this subsection), which grows in alpine regions of northern Yunnan Province and the southern portion of the Tibetan Autonomous Region of south China at an elevational range of 2,300 to 4,000 m (Wu et al. 2005; McQuire & Robinson 2009). *Rhododendron floccigerum* is a shrub 0.6 m to three m tall with leathery, evergreen leaves that have a thick indumentum (a layer of hairs) on the abaxial surface (Wu et al. 2005). *Rhododendron floccigerum* has a red or occasionally yellow to pink tubular-campanulate, five merous corolla with five

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*Corresponding author: egeorgian@gmail.com



FIGURE 1: A compilation of photographs taken by E.G. in 2012 of *R. floccigerum* in Weixi: (A) shrub in bloom, (B) *R. floccigerum* habitat, (C) an inflorescence, (D) last year's capsules, and (E) evidence of robbing, note the holes at the base of the corolla over the nectaries.

basal nectar pouches, and ten stamen, and it flowers between May and June (Wu et al. 2005). The corollas are with or without a darker red basal blotch, or nectar guides (smaller spots that typically lead to a source of nectar), and the flowers are organized in pendant umbels of four to eight flowers, which often fall below the leaves (Fig. 1). The calyx of *R. floccigerum* is minute, just one to four mm long. It is unknown whether or not *R. floccigerum* is self-compatible. The floral morphology of *R. floccigerum* suggests that it is pollinated by birds.

Of the many possible factors that contributed to the large number of species in the genus *Rhododendron*, we investigated whether pollinator specificity or robber pressure could have contributed to floral morphological evolution. Pollinator specificity has been shown to be a driver of evolution in other mountain genera (e.g., *Fuchsia*; Berry et al. 2004). Robber pressure could have contributed to morphological changes within populations over time, for example, on the lengths of corolla tubes (Lara & Ornelas 2001). Moreover, nectar robbery is common in bird pollinated plant species (Arizmendi 2001).

It has been proposed that elevational differences in a population are associated with the speciation of *Rhododendron* subsection *Neriiflora* species (Hu 1990). It is thus possible that visiting species vary between separate higher and lower elevation populations. It is also possible that different factors, such as habitat disturbance due to human impact, could affect species visiting *R. floccigerum* (Parsche et al. 2011). We framed our study to determine if visiting species vary over the elevation range of *R. floccigerum* in our study area.

We investigated the following questions. 1) What are the visitors, potential pollinators, and robbers of *R. floccigerum* and what pollinating or robbing behaviours do they display? We sought evidence to support or refute the hypothesis that pollinators of subsection *Neriiflora* are nectivorous birds. Additionally, we aimed to determine if pollinator specificity or robber pressure could have contributed to speciation in *Rhododendron* subsection *Neriiflora*. 2) Do the visitors, pollinators, and robbers of *R. floccigerum* vary at different elevations on the same mountain? We looked for both qualitative and quantitative evidence to support the hypothesis that visiting species to *R. floccigerum* varied over our study site.

MATERIALS AND METHODS

Study Area

We conducted a pollination biology study of *R. floccigerum* from March 15, 2012 through March 28, 2012 on the outskirts of Weixi City, Weixi County, Diqing Prefecture, Yunnan Province, China (27°09'39.474" N 99°15'59.339" E). The mountain on which we conducted our research, hereafter referred to as Weixi, is outside of Hao Zhu Qing village of Weixi City. The habitat was disturbed at lower elevations (2,400 m) by human impact (compacted paths, occasional parked motorbikes, herded livestock, and frequent presence of people), but was minimally disturbed at higher elevations (fewer and smaller paths, no access via motorbikes, and infrequent presence of people). At both low and high elevations there were some trails, which were predominately used by goat herders.

Rhododendron floccigerum was blooming in March in Weixi (Fig. 1), much earlier than dates documented in Wu et al. (2005) and was flowering both at the lower and higher elevations throughout the period of study. A voucher specimen of *R. floccigerum* was collected in Weixi and is deposited at the Wisconsin State Herbarium (WIS; EMG 70 v0264933WIS). During this study, at 2,580 m and above no plants other than *R. floccigerum* were flowering. At elevations below 2,580 m, in addition to *R. floccigerum*, *R. rubiginosum* and *Berberis* sp. were flowering, and *Vaccinium* sp. were present but not yet flowering. At our study site *R. floccigerum* frequently grew interspersed with *Pinus yunnanensis* at all elevations. *Rhododendron floccigerum* and *P. yunnanensis* were the predominate woody species growing in the study site at the higher elevation and *P. yunnanensis*, *R. floccigerum*, and *R. rubiginosum* were the main woody species growing at the lower elevation.

In this study we defined 'pollinator' as an organism that touches the anther and stigma, presumably transferring pollen, and 'robber' as an organism that removes nectar and/or pollen and/or destroys the corolla without providing the service of pollination (Stein & Hensen 2011). We also suggest that a visiting species could potentially act as both 'pollinator' and 'robber' (Stein & Hensen 2011).

Fieldwork

First-hand observations were made for 24.5 hours over nine days (March 18-21 and 23-27, 2012), and were conducted at various times between 6:00 am and 8:10 pm and at various elevations. Three camera traps were also used to record visitors to *R. floccigerum*, one placed in each of three locations (lower elevation 2,450 m, middle elevation: 2,580 m, and higher elevation 2,660 m) for the duration of the study. The cameras at the middle (placed on March 17) and high elevations (placed on March 19) recorded pictures every ten seconds from dawn until dark (7 am – 8 pm; Day 6 Outdoors Plotwatcher time lapse HD video camera, Day 6 Outdoors, Columbus, Georgia, USA). The camera at the low elevation (placed on March 18) recorded photographs when the motion sensor was triggered and was capable of 24-hour photos using infrared technology (Moultrie M80; Moultrie Products LLC Alabaster, Alabama, USA). Cameras were placed over three days to safeguard against losing them all to theft, but we found this was not a concern. Having concurrent observation at all elevations minimized variation seen in visitors due to weather conditions, and throughout the field period sunny, cloudy, and rainy days occurred. Though the weather at this time of year in Weixi is not hot (daytime temperature of ~50°F), *Bombus* spp. have been shown to be active in cooler weather (Owen, Bale, & Hayward 2013).

Visiting species were observed and photographed. Identification of all visiting vertebrate animals was confirmed by comparing photos with specimens at the American Museum of Natural History (AMNH; NY, NY). A species was tallied as a potential pollinator if we observed the head of an individual deep in the corolla, and was tallied as a robber if the visitor was observed stealing nectar, pollen, or portions of the corolla.

Measurements and analyses

Detailed morphological measurements were conducted on 12 randomly sampled individual flowers on different individuals of *R. floccigerum* in Weixi. Flowers that were badly damaged by predation or were not in full bloom were not measured. Corolla length was measured from the opening to the base of the flower where it meets the pedicel (and the curve was excluded). We measured corolla width at the opening and corolla width at the base, because both play a role in limiting access by pollinating species. Also recorded of the 12 measured flowers, were the presence/absence of basal blotches or nectar guides and the number of flowers in the inflorescence in which the measured flower was found. Additionally, we measured stigma and anther exertion length (the length of the stigma and anthers outside of the corolla) because they play a role in pollen transfer (Kearns & Inouye 1993).

We also recorded instances of robbing in a random sample of individual flowers throughout the field site on March 17, 2012 ($N = 176$ flowers), as robbing has been frequently observed in *Rhododendron* (Ng & Corlett 2000; E.G. pers. obs. 2011). We recorded a robbing event if a hole in the base of the corolla or destruction of part of the corolla was present (De Waal et al. 2011). For each instance in which an animal visited a flower, we estimated the number of flowers present. This was aided by photographs taken using the camera traps.

Measurements of visiting mammal and bird species were conducted at the American Museum of Natural History in New York City to compare to the floral morphology measurements. Morphological measurements were not made of the visiting insect species due to the difficulty identifying to species. The many of the measured vertebrate species were originally collected in Yunnan Province or neighbouring provinces in China. Thirty individuals of each of the two mammal species visitors (*Dremomys pernyi* and *Tamiops swinhoeri*) were measured and morphometric values were averaged and a standard deviation was calculated. We made the following measurements on the mammals: 1) nares (nostrils) to posterior base of external pinnae (ears), 2) width of the head at the external edge of the nares, 3) depth of the head at the external nares, 4) width of the head at the external pinnae, 5) depth of the head at the external pinnae, 6) total body length, and 7) vibrissae (whisker) length. We measured ten individuals of each species of the nine bird visitors and these measurements were averaged and the standard deviation was calculated. *Aethopyga gouldia* is a sexually dimorphic species, thus all 12 individuals (ten males and two females) in the collection were measured and averages and standard deviations were reported separately for the sexes. Thirty individuals of each mammal species were measured compared to ten of each bird species because the preservation of mammal species can change the dimensions of the animal (AMNH staff pers. comm.). We made the following measurements: 1) bill length, 2) distal tip of the bill to the back of the head, 3) width of the head at the eyes, 4) depth of the head at the eyes, 5) width of the bill at the nares, and 6) depth of the bill at the nares. The bird and mammal measurements that were conducted were chosen based upon previous studies (Kearns & Inouye 1993).

We compared floral measurements with visitor morphological measurements to determine whether the visitor's head was small enough to fit within a flower without destroying it, and thus would be likely to facilitate pollen adhering to fur or feathers. All head measurements were taken into account because flowers and visitors are three-dimensional. Bird measurements that correspond with floral morphological measurements include: 1) bill length and bill to back of the head with corolla length, 2) width and depth of the bill at the nares with corolla width at base, and 3) width and depth of the head at the eyes with corolla width at opening. Mammal measurements that correspond with floral morphological measurements include: 1) nose to external pinnae with corolla length, 2) width and depth of head at nose and vibrissa with corolla width at base, and 3) width and depth of head at external pinnae and vibrissa with

corolla width at opening. If any of the visiting species measurements did not physically fit inside the corolla (i.e., the size of the visitor was greater than the floral morphological measurements) we excluded that species as a legitimate pollinator.

We calculated the visitation rate of all species that visited *R. floccigerum* using the following equation, $[(\# \text{ of flowers visited} / \text{total } \# \text{ of flowers on the shrub}) / \text{time of visitation in seconds}] \times 100$ (Klassen 1989; Grindeland, Sletvold, & Ims 2005). Visitation rates were calculated for each visitor individually and were then averaged by species and elevation (low, middle, high). The average length of visitation time in seconds was calculated. We compared species visitation rates at different elevations in a generalized linear model framework using R statistical environment (R Core Team 2013). Our null hypothesis was that species visitation rates did not vary over different elevations. The generalized linear model was chosen to compare visitation rates at different elevations because it compares the likelihood of the null hypothesis with the hypothesis that elevation is significant and because the data was not normally distributed. The variables included in the generalized linear model were elevation, number of visits, observation duration, and species, and calculations were conducted separately for each species.

Morphological and behavioural data were combined to determine the potential pollinators, visitors, and robbers. Our use of two lines of evidence allows us to make robust inferences about the ecological role of flower visitors. However, we realize that without exclusionary experiments (to limit access by a subset of visitors) followed by germination trials, or single visit deposition of pollen experiments (methods described in King, Ballantyne, & Willmer 2013) we cannot be certain which species are effective pollinators.

RESULTS

Over a period of 498.5 hours of observation (cameras plus in-person observations), 13 species were observed visiting *R. floccigerum* flowers (Fig. 2). A total of 363 visits were observed; however, individuals were not marked, thus some visits may have been made by the same individual visiting multiple times. Camera traps proved to be the most successful way to collect data about visitors to *R. floccigerum* because they registered images of all 13 visitors, though *Apis* sp. were impossible to detect unless the camera was within two feet of a flower. Visiting species ranged from insects (*Apis* sp. and *Bombus* sp.) to mammals (*Dremomys pernyi*, *Tamiops swinhoeri*), to birds (*Aethopyga gouldia*, *Brachpteryx montana*, *Garrulax affinis*, *Heterophasia melanoleuca*, *Minla ignotincta*, *Minla strigula*, *Paris major*, *Phylloscopus affinis*, and *Yuhina diademata*), with birds being the most prevalent visitor taxon (Fig. 2; Tab. 1).

Through our fieldwork we observed *R. floccigerum* in detail and the morphological description agrees with that in Flora of China (Wu et al. 2005; Fig. 1; Tab. 2); however further morphological measurements should be conducted to determine intra-specific variation. We can add that the stamens vary in length, the stamens and pistil are recurved,

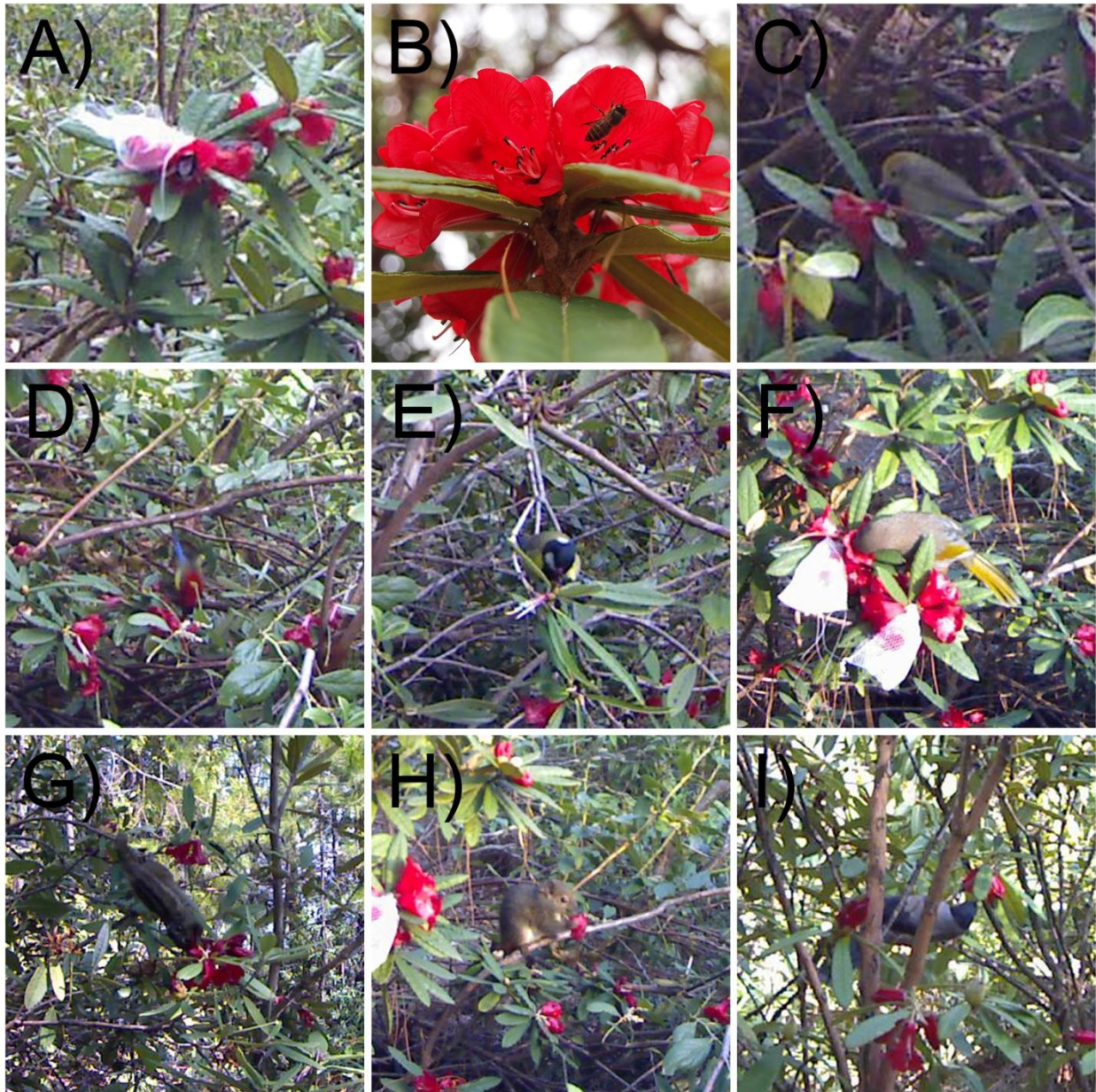


FIGURE 2: A compilation of photographs taken of visitors of *R. floccigerum* in Weixi: (A) *Bombus* sp., (B) *Apis* sp., (C) *Phylloscopus affinis*, (D) *Aethopyga gouldia*, (E) *Parus major*, (F) *Garrulax affinis*, (G) *Tamiops swinhoi*, (H) *Dremomys pernyi*, (I) *Heterophasia melanoleuca*.

individual shrubs have between five and >50 inflorescences depending on shrub size, and the flowers are unscented (to the human nose). At our field site, in 2012, *R. floccigerum* began blooming before March 17 and continued past March 28. Approximately 26% of randomly sampled *R. floccigerum* flowers were robbed on or before March 17, 2012 (N robbed flowers = 46; Fig. 1). By March 28, about 50% of flowers showed signs of robbing including holes at the base of the corolla, partial removal of or damage to the corolla, or both.

Comparative morphological measurements suggest that all vertebrate visitors we observed were capable of fitting all or part of their heads into the corolla of *R. floccigerum* (Tabs. 2, 3, and 4). However, the ability of *D. pernyi* to reach the nectar depends on tongue length, which we were unable to measure. Of the visitors we noted, only *Apis* sp.

are excluded as a potential pollinator of *R. floccigerum* due to morphological constraints.

Even though the morphology of the larger visiting species indicates they are able to fit their head into the corolla of *R. floccigerum*, we observed numerous instances of visiting species displaying robbing behaviors (Fig. 2). The mammal visitors, *D. pernyi* and *T. swinhoi*, were observed removing pieces of, or the entire corolla. The bird visitors, *M. ignotincta*, *M. strigula*, *P. major*, and *P. affinis*, were observed stealing nectar by completely removing nectaries and/or damaging corollas.

We recorded 193 visits by insects (173 of these by *Apis* sp.), 145 visits by the nine bird species (72 of these by *Phylloscopus affinis*), and 25 visits by the two mammal species (Tab. 1). At the low elevation, where the rate of

TABLE I: Visitation rates of species visiting *R. floccigerum* at low, middle, and high elevations were presented as an average with standard deviations in parenthesis. P indicates whether species visitation rate varies at different elevations, which was calculated using a generalized linear model. A *P*-value of < 0.05* was considered significant and a *P*-value of < 0.001** was considered highly significant. Note that the calculations for visitation rate for *Apis* sp. was calculated from 32 individuals at the low elevation and eight individuals at the middle elevation.

Species	Visitation rate (% of flowers visited per shrub/per second)			<i>P</i>
	Low elevation 2450 m	Middle Elevation 2580 m	High Elevation 2660 m	
Insect				
<i>Apis</i> sp.	0.20 (Std dev = 0.11)* <i>N</i> = 63	0.13 (0.02) <i>N</i> = 68	insufficient data <i>N</i> = 48	0.159
<i>Bombus</i> sp.	<i>N</i> = 0	0.09 (0.03) <i>N</i> = 13	0.33 <i>N</i> = 1	< 0.001**
Mammal				
<i>Dremomys pernyi</i>	<i>N</i> = 0	0.12 (0.06) <i>N</i> = 11	0.09 (0.07) <i>N</i> = 12	0.322
<i>Tamios swinhoi</i>	<i>N</i> = 0	0.151 (0.08) <i>N</i> = 2	<i>N</i> = 0	0.141
Bird				
<i>Aethopyga gouldiae</i>	<i>N</i> = 0	0.07 (0.02) <i>N</i> = 5	0.14 (0.02) <i>N</i> = 13	< 0.001**
<i>Brachpteryx montana</i>	<i>N</i> = 0	0.14 <i>N</i> = 1	<i>N</i> = 0	0.297
<i>Garrulax affinis</i>	<i>N</i> = 0	0.11 (0.11) <i>N</i> = 4	0.12 (0.04) <i>N</i> = 6	0.084
<i>Heterophasia melanoleuca</i>	<i>N</i> = 0	0.29 <i>N</i> = 1	0.12 (0.07) <i>N</i> = 10	< 0.001**
<i>Minla ignotincta</i>	<i>N</i> = 0	<i>N</i> = 0	0.09 <i>N</i> = 2	0.022*
<i>Minla strigula</i>	0.5 <i>N</i> = 1	0.04 <i>N</i> = 2	0.06 <i>N</i> = 2	0.744
<i>Parus major</i>	<i>N</i> = 0	0.06 <i>N</i> = 1	0.01 (0.09) <i>N</i> = 2	< 0.001**
<i>Phylloscopus affinis</i>	<i>N</i> = 0	0.17 (0.01) <i>N</i> = 38	0.145 (0.06) <i>N</i> = 34	0.014*
<i>Yuhina diademata</i>	<i>N</i> = 0	0.14 (0.06) <i>N</i> = 6	0.15 (0.06) <i>N</i> = 17	< 0.001**

visitation was lowest, only *Apis* sp. and *M. strigula* were observed visiting *R. floccigerum*. All visitors except for *M. ignotincta* were observed in the middle elevation. At the high elevation, 11 species were observed visiting *R. floccigerum*. Only *T. swinhoi* and *B. montana* were not observed in the high elevation.

Eleven species visited 23 times or less. The average longest visit was made by *D. pernyi* (a mammal; mean = 165.65 seconds, *N* = 23). The second average longest visit was by *Heterophasia melanoleuca* (a bird; mean = 138.18 seconds, *N* = 11), the third average longest visit was by *Apis* sp. (an insect; mean = 127.3 seconds, *N* = 179), and the

fourth average longest visit was by *Garrulax affinis* (a bird; mean = 120 seconds, *N* = 10). None of the birds or mammal species visiting *R. floccigerum* were observed attempting to exclude other animals from visiting *R. floccigerum* shrubs.

Our models suggest that for some of the visiting species we can reject the null hypothesis of no significant difference between visitation rates at different elevations. Visitation rate varies significantly at different elevations for *A. gouldiae*, *H. melanoleuca*, *P. major*, *P. affinis*, *Y. diademata*, *M. ignotincta*, and *Bombus* sp. (Tab. I).

TABLE 2: Average and range of floral morphological measurements, in cm measured in 12 fresh flowers at our field site on the edge of Weixi City, Weixi County, Yunnan Province.

	Stigma/Style exertion	Anther exertion	Corolla length	Corolla width at opening	Corolla width at base	Number of flowers per inflorescence
Average	0.55	0.07	3.65	3.87	1.24	6
Range	0 to 1.3	0 to 0.4	3 to 4.2	2.5 to 5	1 to 1.5	5 to 8

TABLE 3: Average measurements in cm and standard deviation of bird visitor morphology measured in 10 individuals of each species at AMNH. *Aethopyga gouldia* is a sexual dimorphic species therefore we measured 12 individuals (the entire collection; 10 males and two females) and the measurements for this species are separated into measurements by sex. Measurements in columns 2 and 3 correspond with corolla length; measurements in columns 5 and 7 correspond with corolla width at base; columns 4 and 6 correspond with corolla width at opening. Data are presented as average, with standard deviation in parenthesis.

Species	Bill length (cm)	Tip of bill to back of head (cm)	Width of head at eyes (cm)	Width of bill at nares (cm)	Depth of head at eyes (cm)	Depth of bill at nares (cm)
<i>Garrulax affinis</i>	1.79 (0.10)	4.98 (0.35)	2.09 (0.14)	0.51 (0.05)	2.04 (0.13)	0.62 (0.05)
<i>Yuhinia diademata</i>	1.33 (0.06)	3.91 (0.20)	1.43 (0.16)	0.44 (0.03)	1.52 (0.23)	0.39 (0.01)
<i>Minla strigula</i>	1.14 (0.07)	3.64 (0.22)	1.57 (0.16)	0.45 (0.05)	15.85 (0.21)	0.43 (0.03)
<i>Minla ignotincta</i>	1.17 (0.05)	3.16 (0.11)	1.57 (0.19)	0.37 (0.01)	1.40 (0.21)	0.36 (0.03)
<i>Heterophasia melanoleuca</i>	1.83 (0.15)	4.35 (0.17)	1.73 (0.18)	0.56 (0.04)	1.74 (0.18)	0.52 (0.05)
<i>Phylloscopus affinis</i>	0.99 (0.07)	2.61 (0.07)	1.08 (0.10)	0.23 (0.02)	1.09 (0.15)	0.25 (0.03)
<i>Brachpteryx montana</i>	1.47 (0.05)	3.78 (0.09)	1.54 (0.28)	0.44 (0.03)	1.60 (0.27)	0.43 (0.02)
<i>Paris major</i>	0.96 (0.06)	2.86 (0.13)	1.4 (0.08)	0.40 (0.03)	1.32 (0.09)	0.43 (0.02)
<i>Aethopyga gouldiae</i> Female	1.47 (0.51)	2.88 (0.68)	1.21 (0.48)	0.31 (0.26)	1.21 (0.25)	0.3 (0)
<i>Aethopyga gouldiae</i> Male	1.48 (1.41)	2.93 (1.00)	1.16 (1.01)	0.33 (0.39)	1.06 (1.74)	0.29 (0.54)

Potential nocturnal visitors include bat and moth species whose ranges include this area. However, no nocturnal visitors were detected in the camera trap data. This could be because there are no nocturnal visitors, or because the infrared sensor was not sensitive enough or quick enough to provide evidence of nocturnal visitors.

DISCUSSION

While birds (Stevens 1985; Argent et al. 1988; Steinheimer 1999; Kingdon-Ward 2007) and mammals (bats; Cruttwell 1988) have been proposed as pollinators of *Rhododendron*, to our knowledge we provide the first empirical evidence in support of this hypothesis.

Species exhibiting pollinating behaviours

Species that were potential pollinators of *R. floccigerum*, based on observations of behavior and morphology, include *Bombus* sp., and the bird species *Aethopyga gouldiae*, *Garrulax affinis*, *Heterophasia melanoleuca*, and *Yuhinia diademata*. We have particularly strong visual evidence for *Bombus* sp. and *G. affinis*, as we captured images of these species with their bodies (*Bombus* sp.) or heads (*G. affinis*) fully in the corolla. Additionally, the morphology of these

five visitors is such that their heads fit into an open corolla making it probable that they can reach the nectar while providing the service of pollination. We do not intend to imply that these species successfully pollinated *R. floccigerum*, we only propose them as potential pollinators. We observed only one visit to *R. floccigerum* by the bird species *Brachpteryx montana*, and thus further studies are need to determine if this bird species plays a role as pollinator or robber of *R. floccigerum*.

Pollinator specificity has been shown to be a driver of evolution in other mountain genera (e.g., *Fuchsia*; Berry et al. 2004). For example, it is possible that closely related *Rhododendron* species are pollinated by different species, which thus prevents extensive hybridization (which is common among *Rhododendron* spp.; see Ma et al. 2010; Milne et al. 2010) by limiting gene flow among populations or species. We think this is unlikely in our study area; however, because *R. floccigerum* has very similar morphology to other species in subsection *Neriiflora* and species in other closely related subsections. *Rhododendron floccigerum* does not appear to have one specific pollinator and in fact, during our study had 13 visitors ranging from insect to bird to mammal.

TABLE 4: Mammal morphology average measurements and standard deviations in cm measured in 30 individuals of each species at AMNH. Measurements in column 2 correspond with corolla length; columns 4, 7, and 8 correspond with corolla width at base; columns 5, 6, and 8 correspond with corolla width at opening. Data are presented as average, with standard deviation in parenthesis.

Species	Nose to back of ears	Total length	Width of head at nose	Width of head at ears	Depth of head at ears	Depth of head at nose	Vibrissa length
<i>Tamias swinhoi</i>	3.14 (0.50)	24.36 (2.49)	1.45 (0.44)	2.91 (0.56)	2.73 (0.53)	1.52 (0.47)	4.12 (0.65)
<i>Dremomys pernyi</i>	3.98 (0.53)	34.03 (4.01)	2.20 (0.46)	3.56 (0.54)	3.25 (0.53)	2.07 (0.62)	5.23 (0.86)

Species exhibiting robbing behaviours

Species displaying behaviour indicative of robbing visits were *Apis* sp., *Dremomys pernyi*, *Tamiops swinhoei*, *Minla ignotincta*, *Minla strigula*, *Parus major*, and *Phylloscopus affinis*. Measurements of the rostrum of *D. pernyi* and *T. swinhoei* suggest that the head of these mammals could fit into the corolla; however, neither species was observed consuming nectar through the corolla opening. *Tamiops swinhoei* is known to be a primary robber of a wild ginger relative (*Alpina kwangsiensis*; Zingiberaceae) in southern Yunnan Province (Deng et al. 2004). In the case of *A. kwangsiensis*, *T. swinhoei* removes the protective calyx and damages the corolla to expose the nectary (Deng et al. 2004). It is possible that the recurved stamens of *R. floccigerum* may help to block the entrance to the floral tube, thus preventing relatively large visitors, like *D. pernyi* and *T. swinhoei* from obtaining nectar through the mouth of the corolla (Cronk & Ojeda 2008); however, this does not explain the behaviour of the bird visitors (discussed further below).

In contrast to the largest visitors (*D. pernyi* and *T. swinhoei*), *Apis* sp. were excluded as potential pollinators based on size. Our observations indicated that *Apis* sp. were too small; they frequently climbed down the side of the corolla to reach the deep basal nectaries but in doing so, did not make contact with the anthers or stigma and thus did not transfer pollen (Fig. 2). Additionally, *Apis* sp. were only observed making contact with the anthers of *R. floccigerum* when collecting pollen. It is possible that *Apis* sp. that primarily act as robbers of *R. floccigerum* rarely provide the service of pollination, but this must be determined by additional studies (see Stein & Hensen 2011). Various aspects of floral morphology, including corolla length, shape, color, scent, or pollen placement on the visitor have been shown to effectively exclude visitors from pollinating (Kearns & Inouye 1993).

The bird species *Minla ignotincta*, *M. strigula*, *Parus major*, and *Phylloscopus affinis* were observed extracting the entire nectary via the base of the corolla (Figs. 1 and 2), even though these species could have physically entered the corolla from the opening and potentially provided the service of pollination.

Robbers can be classified by their robbing behaviors into five groups: 1) primary nectar robbers, who make holes in the flower to access the nectar, 2) secondary nectar robbers who use an already made hole, 3) nectar thieves who obtain nectar through the legitimate opening, but fail to transfer pollen, 4) floral larcenists who rob pollen which causes damage to the flower, and 5) pollen thieves who steal pollen but do not damage the flower (Irwin et al. 2010). Of the five robbing behaviors we observed 1) primary nectar robbers (the bird species *Minla ignotincta*, *M. strigula*, *Parus major*, and *Phylloscopus affinis*); 2) secondary nectar robbers (*Apis* sp.), 3) nectar thieves (*Apis* sp.), and 4) pollen thieves (*Apis* sp.). Primary and secondary nectar robbers in this study behaved slightly differently than described in other studies, in that primary nectar robbers completely removed a nectary, therefore the secondary nectar robber could use the hole to enter the corolla tube and visit one of the four remaining

nectaries. We observed an additional form of robbing in which portions of, or the entire corolla was removed for consumption (floral herbivory; by the mammals *Dremomys pernyi* and *Tamiops swinhoei*).

Robber pressure can also drive floral morphological evolution (Arizmendi 2001; Galen & Cuba 2001; Lara & Ornelas 2001). For example, the corolla shape of *Polemonium viscosum* (Polemoniaceae) is influenced by the predation by ants (Galen & Cuba 2001). The variety of robbing species and robbing methods that we observed underscore our conclusion that it is unlikely that robber pressure contributes to floral morphological evolution or speciation in subsection *Neriiflora*.

Some *Rhododendron* species have features that may thwart or discourage robbing such as secondary metabolites or thick protective calyxes (Adler 2000; Goodwillie, Kalisz, & Eckert 2005; Koca & Koca 2007). *Rhododendron floccigerum* does not have a large protective calyx to prevent nectar robbing as found in other species in subsection *Neriiflora* (e.g., *R. beanianum*, *R. catacosmum*, *R. citriniflorum*, and *R. dichroanthum*; McQuire & Robinson 2009). Interestingly, many species of *Rhododendron* are considered toxic due to presence of grayanotoxins in the nectar (Wong et al. 2002; Koca & Koca 2007), which may limit robbing (Irwin et al. 2010). In our study visitation was not prevented, so three options are possible: 1) visitors are unaffected by this toxin; 2) *R. floccigerum* does not produce grayanotoxins; or 3) grayanotoxins are only present in low quantities (Georgian 2014). Further studies should be conducted on the presence and concentrations of grayanotoxins in *Rhododendron* species.

Rhododendron floccigerum flowers are pendant (i.e., the mouth of the corolla faces downward). It has been proposed that *Rhododendron* spp. that are bird pollinated have pendant flowers so that the mouth of the flower is located near a perch (Stevens 1976). Our observations showed that pendant flowers exposed the nectaries from above, which made it convenient for birds perched above the flower to access and completely remove the nectaries, avoiding the anther and stigma altogether.

Nectar and pollen robbing have been described frequently in *Rhododendron* spp. (Stevens 1985; Ng & Corlett 2000) and robbing can negatively affect seed production (Arizmendi, Dominguez & Dirzo 1996; Irwin, Brody, & Waser 2001; Lara & Ornelas 2001). Despite this, in Weixi we observed seedlings of *R. floccigerum* and fruits from previous seasons. Therefore we conclude that robbing does not completely prevent successful pollinations and subsequent fruit formation. Further studies should be conducted on the pollinators and robbers of other species in *Rhododendron* subsection *Neriiflora* to allow for comparative studies among species.

Elevation, habitat disturbance, and visitation

The low elevation *R. floccigerum* had the fewest visiting species (2) and total visits (64) and the difference in number of visits and species at the low elevation compared to the middle and high elevations is notable. We observed only two species (*Apis* sp. and *Minla strigula*) visiting *R. floccigerum*

at the low elevation. We acknowledge that this may be due to the trigger speed on the camera used at the low elevation (Moultrie M80; Moultrie Products LLC Alabaster, Alabama, USA).

Elevational differences are a possible explanation for the variation in the visitation rates of *A. gouldiae*, *H. melanoleuca*, *P. major*, *P. affinis*, *Y. diademata*, *M. ignotincta*, and *Bombus* sp. For *A. gouldiae*, *P. major*, *Y. diademata*, *M. ignotincta*, and *P. affinis* elevation positively affected visitation rate and these species were more frequently observed at higher elevations. The visitation rate for *Bombus* sp. was negatively affected by elevation and it was rarely observed visiting at the high elevation. There is no indication that visitation rate increases or decreases with elevation for *Apis* sp., *D. pernyi*, *T. swinhoei*, *G. affinis*, and *M. strigula*.

Additionally, habitat disturbance caused by frequent human presence at lower elevations at our study site could have contributed to the variation seen in visitation rates of species at different elevations. Low pollinator richness at the lowest elevation site may be associated with the greater amount of human presence and alteration of habitat, relative to higher elevation sites. Plant insect interactions can become disrupted because of habitat damage (Parsche, Frund, & Tschantke 2011), potentially due to the loss of key resources (e.g., sites for nesting) or because food resources fall below a critical threshold. This could explain why we observed few species visiting *R. floccigerum* at the lowest elevation where there was abundant evidence of frequent human disturbance. We conclude that elevation, human presence, and land cover change all affected visitation frequency to *R. floccigerum* to some degree.

Further considerations

In Yunnan many species of *Rhododendron* especially those in subsection *Neriiflora* face increasing threats due to human disturbance and habitat destruction (Ma et al. 2014). As this study shows, there are still many unexplored aspects of *Rhododendron* biology, particularly related to pollination ecology in populations growing in their native range. We hope that this study invigorates future research on *Rhododendron* pollination ecology and conservation in the Himalayas. To further studies on *Rhododendron*, we will share our images of visitors captured by trail cameras and videos upon request.

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