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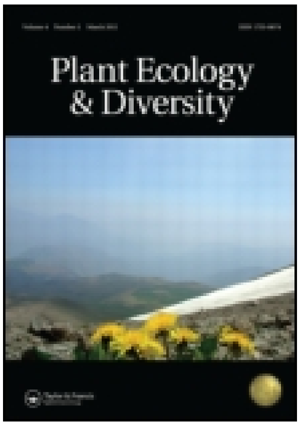

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Alpine *Codonopsis convolvulacea* (Campanulaceae) provides multiple rewards to its main pollinator

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Background: In addition to being a food source, flowers provide non-obvious rewards to their pollinators, such as heat or shelter. However, these rewards have seldom been studied.
Aims: Plant–pollinator interactions between an alpine plant *Codonopsis convolvulacea* and its main pollinator, a bee (*Andrena* sp.) were characterised.
Methods: We recorded the floral biology and floral visitors in three populations of *Codonopsis*. Pollination treatments were conducted to evaluate the importance of insect visitors.
Results: The bee was the only visitor to two populations, and the main visitor to a third population. Females visited flowers to collect pollen, while males had a multi-faceted relationship with flowers. Nectar was the food resource of males. When the air temperature was <18 °C, they slept on flowers. During the day flowers were bowl-shaped solar collectors (1–3 °C warmer than the ambient air), and flowers were closed at night. Copulation was occasionally observed on flowers. Although flowers lasted 2 days and males were active for 3 h per day, the high visiting frequency (19.8 per flower per hour) guaranteed pollination of each flower.
Conclusions: We suggest that the combination of multiple rewards protect males from cold and unstable weather conditions and encourage them to visit more flowers, and that the specialised pollination system is promoted by the harsh alpine environment.

Keywords: alpine habitat; *Andrena*; copulation; floral closure; heat reward; pollination; shelter

Introduction

Plants are location-bound and need pollen vectors to complete their reproductive cycle, so it is no surprise to find that zoophilous plants have a large diversity of floral traits linked to pollinator attraction strategies (Baker and Hurd 1968; Proctor and Yeo 1973; Kevan and Baker 1983; Kevan 2001).The visual and scent cues of flowers are effective attractants (Faegri and Van Der Pijl 1980; Ishii and Sakai 2001; Passarelli and Bruzzone 2004), and are usually linked to visitor rewards. The most common rewards are food resources, such as nectar, pollen, oil or other substances (Simpson and Neff 1983). In fact, plants might use a wide range of strategies that benefit their pollinators and also themselves as a consequence of efficient pollen transfer, potentially resulting in non-obvious rewards. For example, some flowers act as a shelter for floral visitors, offering protection from predators (Faegri and Van Der Pijl 1980; Alcock 1998), and possibly hostile weather conditions. Heat has also been considered as a reward for floral visitors in a cold climate (Kevan 1975; Dafni et al. 1981; Herrera 1995; Seymour et al. 2003; Sapir et al. 2006). Heat can be generated by active thermogenesis of flowers (Seymour and Schultze-Motel 1997; Thien et al. 2000; Seymour et al. 2003; Luo et al. 2010) or by specialised organs that act as solar collectors, such as concave mirror-shaped corollas (Heinrich and Raven 1972; Kevan 1975; Totland 1996; Galen and Stanton 2003), and large dark-coloured corollas (Monty et al. 2006; Sapir et al. 2006). Although such rewards might be quite ubiquitous, they have seldom been studied.

Alpine insects face multiple physical constraints, such as low temperature, strong wind and unpredictable storms, and many studies have documented low insect pollen vector diversity, abundance, and activity in alpine ecosystems (Cruden 1972; Levesque and Burger 1982; Arroyo et al. 1985; McCall and Primack 1992; Totland 1993; Bingham and Orthner 1998). Many alpine plant species are self-compatible and/or can autogamously self-pollinate (Baker 1966; Kelso 1992; Zhang and Li 2008), and are thus less dependent on pollinators. However, obligate or predominantly outcrossing species exist commonly, even in such adverse pollination environments (Spira and Pollak 1986; Gugerli 1998). For these species, increases in attraction and reward for pollinating insects are important to maintain pollination success (Kudo and Molau 1999; Fabbro and Körner 2004), such as relatively large flowers and bright colouration (Billings and Mooney 1968; Bliss 1971). A generalised pollination system might be favoured due to the unpredictable availability of effective pollinators from year to year in alpine regions (Johnson and Steiner

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2000). However, there is a possibility that alpine plants provide not only food rewards but also other non-obvious rewards which aid insect vectors to overcome the physical constraints of the environment, resulting in specialised pollination systems. For example, at low ambient temperatures, solitary bees are usually inactive and exhibit a sleep-like behaviour, so warmer and more inhabitable flowers are presumed to have an advantage to attract them (e.g. Herrera 1995; Kaiser 1995). Plants and their insect pollen vectors might develop very tight mutualistic relationships in harsh alpine environments. More studies into these pollination systems are needed to assess their importance.

Flowers of *Codonopsis convolvulacea* Kura (Campanulaceae) are conspicuous, with a bowl-shaped corolla. In Shangri-La county, north-west of Yunnan, China, we observed a solitary bee, *Andrena* (*Melandrenan*) sp., regularly visiting flowers of *C. convolvulacea* when the air temperature was high, and males sleeping on flowers when the temperature was low (during the whole night and most of the day). In addition, we noted males copulating with females on the flowers. Almost every flower set fruit, which is usually explained by efficient pollination or autonomous self-pollination. The sexual presentation of the flower in the genus *Codonopsis* shows mechanisms of protandry and secondary pollen presentation, indicating the impossibility of autonomous self-pollination (Yeo 1993; Wang and Tan 2011). We hypothesised that *C. convolvulacea* and the solitary bee comprised a specialised system. To comprehensively understand this pollination system, we carried out a 3-year experiment to answer (1) whether the bee was an effective pollinator of *C. convolvulacea*, (2) which rewards the plant provided to the bee, and (3) which factors promoted a specialised pollination system.

Materials and methods

Study area and species

The study was conducted in 2007, 2008 and 2010, with preliminary observations conducted in 2006. The study sites were located at the Zhongdian Plateau, Shangri-La County, Yunnan Province, China (27° 50′ N, 99° 40′ E, 3260 m a.s.l.). In this area, the annual average air temperature is 5.4 °C, and the yearly precipitation is 620 mm. We based our observations and experiments on three populations of *C. convolvulacea*: Nairi (NR), Hamugu (HMG), and Shangri-La Alpine Botanical Garden (SABG). The former two sites are alpine scrub habitats which are dominated by *Quercus* sp., and the third site is a species-rich meadow. The distance between the sites is about 5 km. *Codonopsis convolvulacea* is a twining perennial, and is distributed widely in the south-west of China. Flowering occurs from mid-July to late September. Flowers are radially symmetrical with five blue petals and solitary at the ends of stems/branches (Hong 1983). Using urine glucose test strips, we confirmed that there was nectar at the surface of ovaries.

Floral biology

Fifteen flowers from separate individuals were randomly chosen at NR in late August of 2007 and at SABG in early August of 2008. The flowers were marked in the bud stage, and pollen and stigma presentation were monitored daily. We observed that flowers closed at night and reopened the next morning. To evaluate whether this pattern was correlated with air temperature, we recorded the air temperature and the corolla diameter of each marked flower every 20 min during the process of closing and reopening at NR. We made a regression analysis, with the air temperature as the independent variable and the corolla diameter as the dependent variable.

Floral visitors and their behaviour

We observed floral visitors from 9:00 a.m. to 8:00 p.m. for four successive days, at NR and HMG in late August of 2007 and 2008, and at SABG in late August of 2008 and 2010. We recorded the air temperature and the time when males changed their behaviour from sheltering to foraging on flowers, and from foraging to sheltering. When they were active, we recorded their foraging behaviour. Meanwhile, we also recorded any other insects landing on flowers. Each visitor species was photo-recorded and preserved in the insect collections of Xishuangbanna Tropical Botanical Garden. In total, we made 35–40 h of floral visitor observations of three to five flowers at each site. In late August of 2007, when the air temperature was low enough and males were sleeping on flowers, we investigated every flower for eight successive days to examine whether sheltering occurred at the three populations. In total, we carried out 14 sampling sessions at NR, 19 at HMG, and 21 at SABG. The ratio of total flower number to total sheltering bee number was calculated for each session. A one-way ANOVA test was used to compare the sheltering frequency among the three populations.

Temperature measurement within flowers

To illustrate whether the bowl-shaped flowers of *C. convolvulacea* functioned as solar collectors and heated their inner part, we measured the temperature at the bottom of flowers where males slept, using thermocouples and data loggers (TR-71) with an accuracy of ±0.5 °C. To measure ambient temperature, thermocouples were placed at the edge of corollas. Five randomly chosen flowers were used for the measurement at SABG between 31 August and 1 September 2008, and the temperature was automatically recorded every 10 min.

Pollination treatments

To investigate whether *C. convolvulacea* was capable of apomixis and autonomous self-pollination and to evaluate the importance of insect visitors, we performed three treatments in September 2008 at NR: (1) isolation without emasculation (15 flowers), (2) supplemental pollination without isolation (50 flowers), and (3) open pollination control (50 flowers). Flowers with isolation treatment were prevented from receiving visitors by nylon mesh bags for the duration of flowering. At harvest time, we collected all the fruits before dehiscence to count seed number per fruit. In late August of 2010, we repeated treatments (2) and (3).

For statistical analyses seed number per fruit was log-transformed to achieve normality. We carried out a two-way ANOVA with treatments (2 and 3) and years (2008 and 1010) as fixed factors to examine if the population suffered pollen limitation.

Results

Floral biology

Codonopsis convolvulacea has hermaphroditic flowers which terminate on main stems or branches. In all three populations, we found that each plant had no more than one open flower on a single day. A flower usually lasted 2 days, and extended to the third day if the weather was cold. During the process of floral development, the style and the staminal tube fused into a column. Once a flower opened, the anthers dehisced and all the pollen grains stuck to the reversed surface of the stigma. Meanwhile, the filaments moved downward and close to the petals. The male phase usually lasted just 1 day (Figure 1(b) and 1(d)). The following morning, the stigma lobes unfolded and the flower was in female phase (Figure 1(a) and 1(c)); the flower usually withered in the evening.

Corollas tended to move inward when ambient air temperature was <23 °C. However, flowers closed completely only when the temperature was <9 °C. We usually observed completely closed flowers from 8:00 p.m. to 9:00 a.m. During the process of closing and reopening, the corolla diameter and the ambient air temperature were positively correlated ($y = 0.393x - 3.662$, $r = 0.66$, $P < 0.001$, $N = 249$; Figure 2).

Floral visitors and their behaviour

In the flowering season, the solitary bee *Andrena* sp. was the only floral visitor at HMG and NR, and made 93% of total visits at SABG. Males took nectar, and females collected pollen grains (Figure 1(a)). It was easy to find a pollen-collecting female on the reversed surface of the stigma, especially on newly opened flowers (Figure 1(b)). We observed males and females mating on flowers 12 times in total in the three populations (Figure 1(c)), and the mating frequency was 0.1 per flower per hour. When the air temperature was high (>20 °C) and the bees were active, the visiting frequency was always high at about 19.8 per flower per hour in the three populations, and males made about 95% of the visits. At SABG, other floral visitors included the bumblebee *Bombus richardsi*, house fly *Musca* sp., and two syrphid species *Episyrphus balteatus* and *Syrphus ribesii*. Bumblebees and house flies visited flowers

Figure 1. The behaviour of *Andrena* sp. on flowers of *Codonopsis convolvulacea*, Zhongdian Plateau, Shangri-La County, Yunnan Province, China. A, male feeding on nectar; B, female collecting pollen; C, sheltering male on a flower; D, copulating male and female.

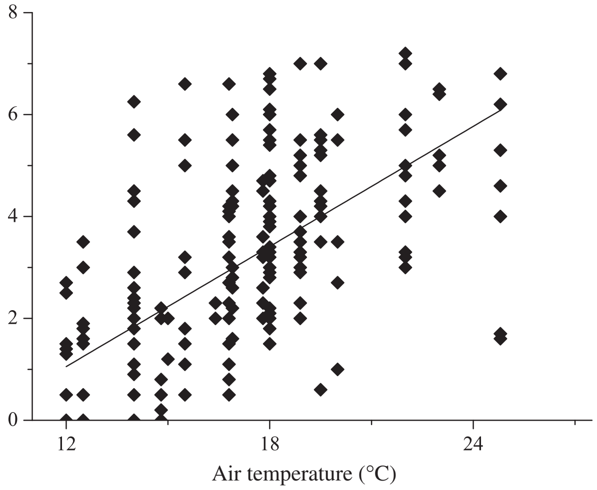

Figure 2. Correlation between air temperature and corolla diameter of *Codonopsis convolvulacea* in *Codonopsis convolvulacea*, Shangri-La Alpine Botanical Garden, Yunnan, China, 31 August and 1 September 2008. The correlation equation was $y = 0.393x$-3.662, $r = 0.660$, $P < 0.001$, $N = 249$.

for nectar and syrphids for pollen; visiting frequencies were 0.6, 0.4, and 0.4 per flower per hour, respectively.

When the air temperature was <18 °C, males became completely immobile and used flowers as shelter. Females were more tolerant to cold conditions and were observed collecting pollen when the air temperature was <14 °C. Males were active for only 3.1 ± 1.3 h per day. When males slept on flowers, the ratio of total flower number to total sheltering bee number was 5.25 ± 0.88, 5.45 ± 0.81, and 5.01 ± 0.77 at NR, HMG, and SABG (Figure 3). The sheltering frequency was not significantly different among the three populations ($F_{2,61} = 2.36$, $P = 0.13$). We further made a regression analysis, with the total number of flowers as the independent variable and the total number of sheltering male bees as the dependent variable, using data from the three sites, and the regression equation was $y = 0.126x + 4.262$, $r = 0.772$, $P < 0.001$, $N = 64$.

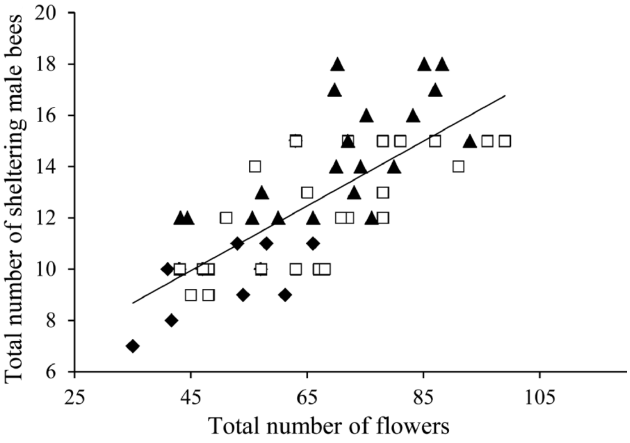

Figure 3. Correlation between the total number of observed *Codonopsis convolvulacea* flowers and the total number of sheltering males of the bee *Andrena* sp. in three populations of *Codonopsis* Nairi, NR (◆); Hamugu, HMG (□); and Shangri-La Alpine Botanical Garden, SABG (▲), Zhongdian Plateau, Shangri-La County, Yunnan Province, China. The correlation equation was $y = 0.126x + 4.262$, $r = 0.772$, $P < 0.001$, $N = 64$.

Temperature measurement within flowers

There was little difference between the air temperature and the temperature within flowers at night, but flower temperatures were 1–3 °C higher than daytime air temperatures. The hourly variation of mean difference (flower temperature vs. air temperature) showed a unimodal distribution, with the highest value at midday (Figure 4).

Pollination treatment

None of the isolated flowers set fruit, indicating that apomixis or autonomous self-pollination did not occur in *C. convolvulacea*. All individuals in the supplemental pollination treatments and in the natural control set fruit. A two-way ANOVA showed neither pollination treatment ($F_{1,196} = 0.18$, $P = 0.67$), or year ($F_{1,196} = 0.33$, $P = 0.57$), nor their interaction ($F_{1,196} = 0.30$, $P = 0.59$) had a significant effect on the seed number per fruit, indicating the population did not suffer from pollen limitation (Table 1).

Discussion

Codonopsis convolvulacea was not capable of apomixis and autonomous self-pollination, and there was no more than one open flower on each plant on a single day. We can therefore infer that this species has an obligatory outcrossing breeding system and its reproduction relies on

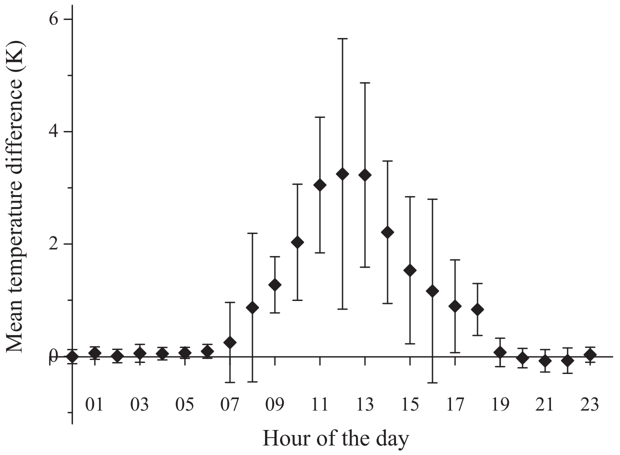

Figure 4. Mean temperature difference between inside the flowers of *Codonopsis convolvulacea* and free air, Shangri-La Alpine Botanical Garden, Yunnan, China.

Table 1. Natural flowers and flowers with extra pollen added did not significantly differ in seed number per fruit in two flowering seasons ($P > 0.1$).

Treatments	2008	2010
Natural flowers	237.0 ± 69.1	253.8 ± 83.0
Extra pollen added flowers	249.4 ± 75.0	248.7 ± 72.0

pollen transfer between flowers of different individuals by pollinators. In alpine pollination systems, plants usually prolong the duration of flowering to compensate for the insufficiency of floral visitors (Primack 1985; Bingham and Orthner 1998; Blionis et al. 2001). However, flowers of *C. convolvulacea* lasted only 2–3 days, which is a much shorter period than reported cases from other alpine plants (e.g. Arroyo et al. 1982; Utelli and Roy 2000; Duan et al. 2007). The solitary bee was the only floral visitor at HMG and NR, and the main visitor at SABG. We observed large numbers of pollen grains of *C. convolvulacea* on the hairs of both males and females by using a dissecting microscope, but the pollination service was provided by males, since females visited flowers in male phase to collect pollen. To our knowledge, all studied *Andrena* species are ectothermic insects and they would be active only when their thoracic temperature was higher than a threshold value (Schemske 1978; Motten 1986; Herrera 1995). Although our observations suggest that this species is active for only 3 h per day, high visiting frequencies meant that each flower set seed (Table 1). There were some other floral visitors at SABG, but *Andrena* sp. was far more important than the others, considering relative visiting frequencies. From our combined obsevations, we suggest this *Andrena* sp. is a very effective pollinator of *C. convolvulacea* at the studied populations. Moreover, we observed that the bee frequently visited flowers of *C. convolvulacea* at three other populations far from Shangri-La (Lijiang of Yunnan, Xiangcheng of Sichuan, and Yanyuan of Sichuan), so it is very likely that *Andrena* is the main pollinator of *C. convolvulacea* across its distribution range.

Codonopsis convolvulacea provided multiple rewards to its dominant pollinator. The plant provided females with a food resource (pollen), but the rewards to males were very broad. Nectar was the food resource, and flowers were served as shelter in cold weather. The temperature at the centre of flowers was higher than the air temperature during the day (Figure 2), indicating that heat was an available reward. Copulation might occur when males came across females on flowers. In addition, we observed that males took food and took refuge only on the flower. These pieces of evidence suggest that the adult life of males is substantially centred on the flowers. It was interesting that the sheltering occurrence had a stable ratio (ca. one male per five flowers). The most plausible explanation is that the number of flowers, as a limited resource, restrained the number of males. Males usually patrol and mate on flowers (Barrows 1978), but to our knowledge there is no convincing case that *Andrena* males show territorial behaviour. Paxton (2005) suggested that large male size was related to territorial behaviour. *Andrena* males are usually smaller than females (Michener 2007). However, the size of males exceeded the size of females for our study species (mean body length: 11.2 mm vs. 9.1 mm, $n = 4$ and 2). Moreover, we observed aggressive behaviour in this *Andrena* species when individuals met each other on flowers, i.e. driving out. It is worth further study to determine if they have territorial behaviour.

The flowering season of *C. convolvulacea* populations in this study lasted from early July to late September. The average air temperature during this period was about 10 °C. However, males were active only when the air temperature was at least 18 °C, which is consistent with other studies (Herrera 1995). The combination of multiple rewards related to feeding, resting and mating protects the males from a cold and unstable environment. Male activity might have been less than 3 h per day without the heat reward presented from *C. convolvulacea* flowers. The concentrated solar heat on the flower centre acts to passively warm up bees that rest in a sleep-like state, and they might be reactivated even when the air temperature is lower than the minimum thoracic temperature for flight (Herrera 1995; Sapir et al. 2006). There are some similar cases (Herrera 1995; Monty et al. 2006; Sapir et al. 2006), but such specialised pollination systems are extremely rare. It would be worth considering in this context an altitudinal gradient study to correlate floral traits and rewards with pollinator community in order to assess how important non-obvious rewards are in alpine regions.

Our observations also showed that flowers of *C. convolvulacea* were closed at night. It has been suggested that flower closure and reopening depend on light and temperature, with some evidence of endogenous rhythms and humidity (Ewusie and Quaye 1977; van Doorn and van Meeteren 2003). We observed that corollas tended to close when the air temperature was low in the daytime. This evidence all but excludes the possibility that closure is controlled by sunlight. On the contrary, our primary experiments suggested that the temporal closure of flowers was controlled by temperature. Bynum and Smith (2001) and He et al. (2006) demonstrated that such closure of flowers was to avoid pollen being washed away by rain and to prevent anthers and stigmas from moisture. However, we observed that stigmas and pollen grains were saturated with water, and males slept on flowers when it was rainy. This suggests that flowers stay open to act as a solar collector to heat their centre during the day, and the temporal closure of flowers is not a waterproofing mechanism. We suggest that the temporal closure of flowers protects males from unknown dangers, such as predators, and harsh weather, such as wind and dew at night, because we found that the temporal closure of flowers occurred only at very low air temperature (<9 °C) and it usually happened at night. However, we need further research to elucidate the ecological and evolutionary significance of the temporal closure of the flower.

Conclusions

Although the alpine plant *C. convolvulacea* has an obligatory outcrossing breeding system and its flower lasted only 2 days, pollen limitation did not occur. The plant provided multiple rewards including food, heat and shelter to its main pollinator, an *Andrena* sp. We suggest that the combination of rewards related to feeding, resting and mating protects males from cold and unstable weather conditions and encourages them to explore flowers, and that the specialised pollination system is promoted by the harsh alpine environment.

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Notes on contributors

Xingfu Zhu is a Ph.D. student and Jiqin Yang is a M.Sc. student. They are partners and working on plant pollination ecology in the alpine region of north-west Yunnan, China.

Qingjun Li is a professor. He currently conducts research in plant reproductive biology and plant–animal interactions.

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