POLLINATION ECOLOGY OF *ANTHYLLIS VULNERARIA* SUBSP. *VULGARIS* (FABACEAE): NECTAR ROBBERS AS POLLINATORS[1]

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This paper examines the hypothesis that nectar robbing can affect plant reproductive success either positively or negatively. To this end, I investigated various aspects of the pollination ecology of a population of the herb *Anthyllis vulneraria* subsp. *vulgaris* in northwest Spain over 5 yr. By observing floral visitors, I found that the most important pollinator species was the long-tongued bee *Anthophora acervorum,* which accounted for ~45% of recorded insect visits. However, just over 45% of visits were by the nectar-robbing bumble bees *Bombus terrestris* and *B. jonellus.* Although the incidence of robbing differed considerably over 5 yr of study, the frequency in every season was very high (66.4–76.5% of robbing) except for 1997 (0% robbing). Despite this high frequency of robbing, robbed flowers had a higher probability of setting fruit than nonrobbed flowers in all years of the study (mean: 82.0 vs. 51.0%; excluding 1997). This increased fruit set in robbed flowers is directly related to bumble bee behavior because the robbers' bodies came into contact with both the anthers and stigmas while robbing. Thus, the robbers effect pollination. These results suggest that the effect of nectar robbers on plant reproductive success is dependent both on the robbers' behavior and on flower/inflorescence structure. The importance of nectar-robbing bumble bees on the reproductive success of *A. vulneraria* and its yearly high frequency suggest that the relationship between robbers and this plant is part of a successful long-term mutualism.

Key words: *Anthyllis*; *Bombus*; bumble bees; Fabaceae; nectar robbing; pollinator behavior.

Some floral visitor species are able to bypass the restriction imposed by flowers with long and narrow corolla tubes, by making an incision at the base of the corolla tube to rob the nectar; such species have been referred to as "primary robbers" (Inouye, 1980). It seems likely that nectar robbing would have negative implications for plant reproduction. Some studies show either damage to floral tissues inflicted by robbers (McDade and Kinsman, 1980) or reduced attractiveness of robbed flowers to legitimate pollinators (Heinrich, 1975; Gill, Mack, and Ray, 1982; Roubik, 1982; Roubik, Holbrook, and Parra, 1985). However, a number of studies also have revealed that robbing may actually contribute to reproductive success as their bodies come into contact with the plant's sexual organs during robbing (Free and Butler, 1959; Hawkins, 1961; Macior, 1966; Koeman-Kwak, 1973; Waser, 1979; Higashi et al., 1988; Navarro, Guitián, and Guitián, 1993; Scott, Buchmann, and O'Rourke, 1993; Guitián, Sánchez, and Guitián, 1994; Morris, 1996). Robbers also could promote an increase either in the number of flowers visited by legitimate pollinators (Heinrich and Raven, 1972; Soberón and Martínez del Río, 1985; Cushman and Beat-

tie, 1991) or an increase in foraging distances (Zimmerman and Cook, 1985).

In contrast with other plant-animal interactions, little attention has been given to the effect of nectar robbers. However, as mentioned above, the activity of nonlegitimate floral visitors, such as nectar robbers, can have different (i.e., positive or negative) effects on fitness. Consideration of all types of flower visitor activities may clarify the adaptive value of traits such as breeding systems, morphology, flower disposition, and mode of pollen or nectar presentation (see Roubik, Holbrook, and Parra, 1985).

The aims of this work were to describe the pollination ecology of *Anthyllis vulneraria* subsp. *vulgaris,* exploring the frequency of nectar robbing during five consecutive years and to examine the hypothesis that nectar robbing could affect either positively or negatively plant reproductive success (measured as female success). To this end, I investigated the behavior, and its consequences on plant reproduction, of all floral visitors to a population of *A. vulneraria* subsp. *vulgaris* in northwest Spain. I described the pollinator assemblage and its temporal variation for the study population. For each major flower-visiting species, I determined mean duration of flower visits and mean number of flowers visited per capitulum visit. Finally, I estimated, during five consecutive years (1993–1997), the proportion of flowers that were nectar robbed and investigated the effect of nectar robbing on fruit set probability.

MATERIALS AND METHODS

Description of the plant and the study area—*Anthyllis vulneraria* subsp. *vulgaris* (Koch) Willk. (Fabaceae) is a biennial herb of 15–30 cm in height that is widely distributed throughout most of Europe and the Mediterranean basin east to the Caucasus. Its aerial parts consist of

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TABLE 1. Results of the survey of insect visits to the *A vulneraria* subsp. *vulgaris* population (total of 32 h of field observations). In column 1, the average proboscis length of the most important visitors is shown in brackets (cm). In columns 6 and 7, means are shown with standard deviation, and sample size in brackets. Within each column, values with the same letter do not differ significantly (Tukey's test: $P \leq 0.05$). Note that only data from pollinator species that were recorded at least 15 times were included in the statistical analysis.

Visitor	Number of recorded capitulum visits				Mean number of flower visits per capitulum	Mean duration of flower visits (s)
	1993	1994	1996	Total		
Hymenoptera						
Anthophora acervorum (1.2)	118 (46.6%)	81 (34.9%)	217 (49.9%)	416 (45.2%)	2.0 ± 1.1 (416)[a]	2.9 ± 1.6 (54)[a]
Anthophora robusta	12 (4.7%)	6 (2.6%)	—	18 (2.0%)	2.3 ± 1.1 (18)[ab]	3.1 ± 1.5 (22)[a]
Andrena fulva	—	—	28 (6.4%)	28 (3.0%)	1.9 ± 0.7 (28)[a]	2.7 ± 1.5 (28)[a]
Eucera longicornis	—	8 (3.5%)	14 (3.2%)	22 (2.4%)	1.7 ± 0.8 (22)[a]	3.0 ± 1.6 (22)[a]
Melecta luctuosa	—	9 (3.9%)	—	9 (1.0%)	2.1 ± 0.8 (9)	
Megachile sp.	—	2 (0.9%)	7 (1.6%)	9 (1.0%)	2.1 ± 0.9 (9)	
Bombus terrestris (0.8)	63 (24.9%)	97 (41.8%)	110 (25.3%)	270 (29.3%)	2.7 ± 1.4 (270)[b]	5.7 ± 2.7 (48)[b]
Bombus jonellus (0.7)	60 (23.7%)	24 (10.4%)	59 (13.6%)	143 (15.5%)	2.4 ± 1.3 (143)[b]	5.5 ± 2.3 (42)[b]
Diptera						
Bomylius canescens	—	5 (2.2%)	—	5 (0.5%)	1.0 ± 0.0 (5)	

2–4 shoots. The flowers are 0.7–1.2 cm long, protandrous, zygomorphic, stenotribic, and arranged in a capitulum (see Weberling, 1989, for details of inflorescence typology). Flowers bloom for 7.8 ± 2.6 d (Navarro, 1999). Pollen is shed into the conical end of the keel, whose edges are adhered except for a small hole at the tip. The base of the capitulum is enclosed by an involucrum comprising two multipartite leaves. Each shoot may bear several capitula. In the study area, flowering starts by mid-March and continues until July. Flowers produce ~0.20 µL of nectar in 24 h. Once flowers are robbed, they do not produce nectar for the rest of their lifespan. Note that nectar robbers do not damage the nectaries, thus stopping nectar production after robbing could be a floral response to fertilization. Insect pollination is necessary for fruit production, but this species is not strictly xenogamous. The strong protandry exhibited by flowers usually prevents autogamy although geitonogamous fruits may be produced (Navarro, 1999). The fruit is a monospermic legume, which matures ~2 wk after fertilization. In the study area, grazing (largely by domestic goats) causes significant losses of capitulum, shoots, and, occasionally, whole plants. More information about the floral biology and breeding system of this taxon is given by Couderc (1971a, b), Couderc and Gorenflot (1978), Navarro (1996b), and Navarro (1999). Voucher specimens of *Anthyllis vulneraria* subsp. *vulgaris* from the study site are deposited at the herbarium of the Santiago de Compostela University (Santiago de Compostela, La Coruña, Spain).

This study was carried out in Vilardesilva (Concello de Rubiana, Orense Province) in the El Bierzo region of Northwest Spain. The study population occupied low calcareous grassland communities, at an altitude of ~600 m. Climate in this area is typically Mediterranean.

Data collection—To characterize the pollinator spectrum of *A. vulneraria* subsp. *vulgaris*, I monitored insect visits to plants in the same 10-m² patch over 5 d in 1993 (24, 26, and 28 April, and 10, 15 May), 6 d in 1994 (3, 18, 21, 27, and 31 May and 1 June), and 5 d in 1996 (7, 17, 18, and 24 May and 2 June). The patch was monitored for a total of 32 h during the 5-yr period of study, for 30-min periods at various times of day [0900–0930 (sunrise), 1200–1230, 1500–1530, and 1800–1830 (sunset) GMT]. For each capitulum visit, I recorded the visiting species, the number of flower visits, the duration of each flower visit, and the type of flower visitor (legitimate or nectar robbing). Nectar robbing could be readily confirmed by subsequent examination of the flower, because robbers make a visible incision in the corolla tube.

To estimate the incidence of nectar robbing and to investigate its possible effects on fruitset, from 1993 to 1997 I examined 1000 flowers/yr randomly chosen in the population, 2 wk after flowering (when corolla incisions due to nectar robbers were still clearly visible) and recorded whether or not each flower had set fruit.

Data analysis—The significance of among-pollinator differences in mean number of flowers visited per capitulum visit and in mean duration of each flower visit were assessed with the aid of multiple-comparison Tukey's tests. Only pollinator species that were recorded at least 15 times were considered in this analysis. In the text, mean values are cited with standard deviations (SD). The effects of the factors ''nectar robbing'' and ''year'' on the probability of a flower setting fruit were investigated using the procedure Catmod (Categorical Data Modelling) in the statistical package SAS (SAS, 1996).

RESULTS

Visitor assemblage—Based on pooled 1993, 1994, and 1996 data, the most frequent visitor was *Anthophora acervorum*, accounting for 45% of capitulum visits (Table 1). However, *Bombus terrestris* was the most frequent visitor when only data for 1994 were considered (Table 1). Those two visitors and the bumble bee *Bombus jonellus* accounted for >87% of total observed visits each year.

Nectar robbing by *A. acervorum* was not observed. Conversely, all visits observed by *B. terrestris* and *B. jonellus* resulted in robbing. These two species accounted for 44.8% of the total number of capitulum visits (1993, 1994, and 1996 data).

The mean number of flower visits per capitulum varied significantly among visitor species ($F = 13.4$, df = 5, $P < 0.0001$). The two species of bumble bees visited significantly more flowers per capitulum than the other floral visitors (Table 1). Mean duration of flower visits also varied significantly among visitor species ($F = 18.6$, df = 5, $P < 0.0001$). In this case, differences were a consequence of the differential foraging behavior of the robbing bumble bees. To extract nectar, robbers must crawl across the capitulum, making holes in the corolla tubes. Thus, the mean duration of visits by *Bombus* species was about twice that of legitimate visits by *A. acervorum* (Table 1).

Insect visits occurred with maximum frequency at 1500 (37.1% of observations) and with minimum frequency at 1200 (12.4% of observations; Fig. 1). However, *B. terrestris* was a more frequent visitor in the early morning. Early in the morning, sporadic visitors foraged in flowers of *A. vulneraria* subsp. *vulgaris*; however, dur-
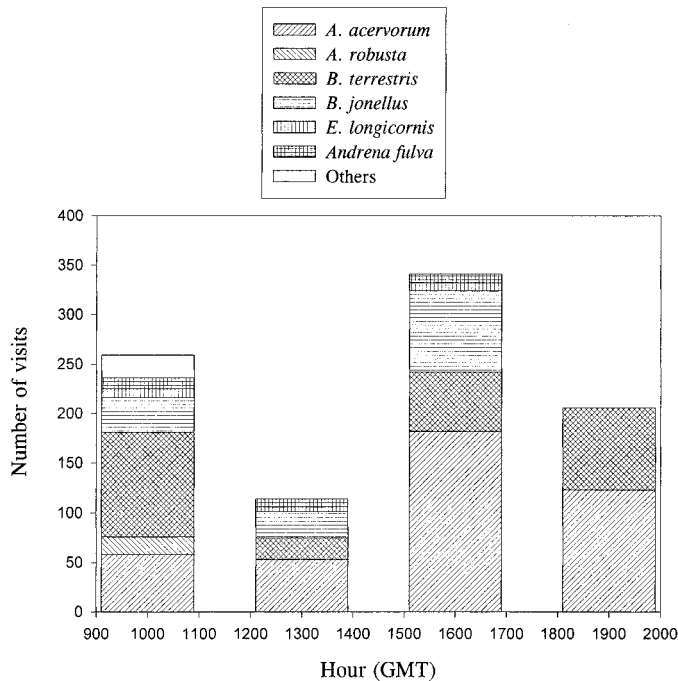
Fig. 1. Relative frequency of observed insect visits from 1993, 1994, and 1996 to the *Anthyllis vulneraria* subsp. *vulgaris* population at different times of day. Also shown, for each time of day, is the number of visits due to each visitor. Under ''other taxa'' are grouped sporadic visitors (see Table 1).
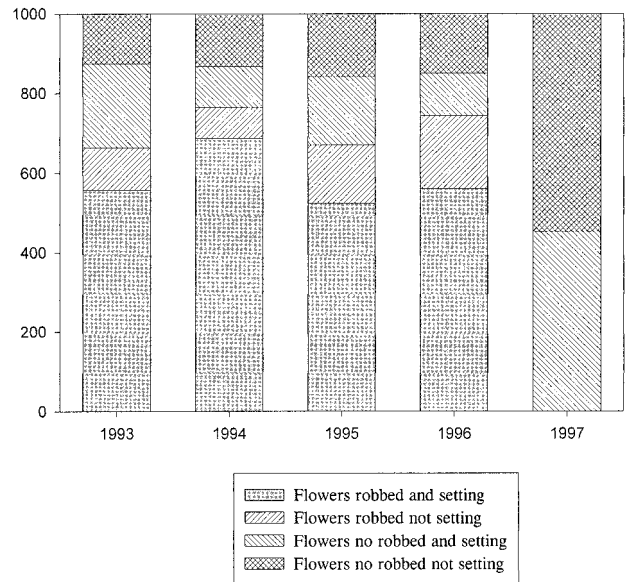

Fig. 2. Numbers and relative frequencies of (a) flowers robbed and setting fruit, (b) flowers robbed and not setting fruit, (c) flowers not robbed and setting fruit, and (d) flowers not robbed and not setting fruit, in each of the 5 yr studied.

ing the rest of the day, *A. acervorum* and the two *Bombus* species were the most abundant visitors.

Nectar robbing—Nectar robbing was very frequent in the study population, but there was also high variability among years in the percentage of flowers that were nectar robbed. In 1994, the percentage of flowers robbed was 76.5%; however, in 1997 no flowers were robbed (Fig. 2), but flower density did not change greatly in the 1993–1997 period (personal observation). Excluding 1997, >60% of the population's flowers were robbed during the years of this study. When data from the period 1993–1996 were analyzed, results showed that the factor ''year'' was a significant source of variability on the percentage of robbed flowers ($\chi^2 = 39.0$, df = 3, $P < 0.0001$). Data from 1997 were excluded from the analysis by the clear evidence of differences. Despite the high frequency of nectar-robber visitation, robbing had a positive effect on the probability of setting fruit. Robbed flowers had a higher probability of setting fruit than unrobbed flowers (Table 2). Thus, 82.0% of robbed flowers set fruit compared to 51.0% of nonrobbed flowers (data are averaged over all study years, excluding 1997). The interaction ''robbing × year'' was also significant (Table 2), indicating that the effect of the nectar robbing on the probability of a flower setting fruit differed among years. However, yearly differences were a consequence of the change in the magnitude of response but not in the effect, because the effect of nectar robbing on the probability of a flower setting fruit was always positive.

DISCUSSION

Visitor assemblage—*Anthyllis vulneraria* subsp. *vulgaris* probably constitutes an important food source for *Anthophora acervorum*, bumble bees, and other visitors during the early spring flowering season because it is widely distributed.

Although the most frequent visitor was the long-tongued bee *Anthophora acervorum*, just over 45% of capitulum visits were nectar-robbing visits by *B. terrestris* and *B. jonellus*. These two last visitors, like other short-tongued bumble bees, have already been described as nectar robbers of other plant species (Macior, 1966, 1993; Koeman-Kwak, 1973; Kendall and Smith, 1976; Inouye, 1983; Newton and Hill, 1983; Higashi et al., 1988; Jennersten, 1988; Jordano, 1990; Fussell, 1992; Guitián, Guitián, and Navarro, 1993; Jennersten and Nilsson, 1993; Crofton, 1996; Morris, 1996; Pierre et al., 1996). Inouye (1983) showed evidence that *Bombus* nectar robbers are morphologically adapted for nectar robbing (see also Kugler, 1943). *Bombus terrestris* has toothed mandibles used to make holes in the side of corollas (personal observation). Moreover, the proboscis length of the two bumble bee species (~0.7–0.8 cm) permit the bees, in some cases, to take nectar ''legitimately'' because the nectaries in *A. vulneraria* are located at the end of corolla tubes that are ~0.7–1.2 cm in length. How-

TABLE 2. Analysis of variance for the effects of nectar robbing and year on fruit set of individual flowers (CATMOD procedure; SAS, 1996).

Source	df	χ^2	P
Robbing	1	391.9	0.0001
Year	3	45.7	0.0001
Robbing × year	3	37.4	0.0001

ever, these bumble bee species usually choose to rob nectar because the majority of flowers have the corolla tubes too long for them to reach the nectaries by a legitimate visit.

Apart from nectar robbing, my observations indicate clear differences in other aspects of the behavior of the principal flower visitors. Bumble bees take longer to extract nectar than *Anthophora acervorum,* the principal and legitimate visitor of *A. vulneraria* subsp. *vulgaris,* because they need to make holes. *Bombus terrestris* was also the most frequent early-morning visitor, in accordance with the well-known thermoregulatory ability of bumble bees and their consequent capacity to remain active at relatively low ambient temperatures (Heinrich and Heinrich, 1973; Heinrich, 1975).

Among-year variation in pollinator assemblage and nectar robbing—The results showed that in 1994, *B. terrestris* was the principal visitor of *A. vulneraria* subsp. *vulgaris.* During this period, the weather was particularly unfavorable for flying insects (low temperatures, strong winds, and rain), and under these climatic conditions, *Bombus* species were practically the only floral visitors. Although I have not investigated the ''quality'' component in this pollination system (i.e., the effectiveness of different species as pollinators), previous studies on other plant–pollinator systems have shown that efficiency of pollen transfer differs among species due to differences in both pollen load and flight distance (Schemske and Horvitz, 1984; Herrera, 1987; and references therein). Temporal variation in the pollinator assemblage observed in the present study could be expected to lead to correspondent variation in plant fitness. In fact, fruit set in 1994 in the studied population was the highest of the period 1993–1997 (76.8, 78.9, 69.6, 66.8, and 45.3% for 1993, 1994, 1995, 1996, and 1997, respectively) and differences with the following years (1995–1997) were significant. Note that in 1994 nectar robbing was also the highest of the studied period (76.5%) (Navarro, 1999).

Differences in nectar robbing among years can also be explained by a diverse and complex number of factors. Unfortunately, with some exceptions (Hawkins, 1961; Navarro, 1996a; Thompson, Ray, and Preston, 1996), there are few studies examining yearly constancy in nectar robbing. In this study, yearly differences in the frequency of robbed flowers were observed. But, excluding 1997 when no robbed flowers were observed, possible causes of which will be discussed below, the percentage of robbed flowers was always >66% (Fig. 2). Therefore, it seems that nectar robbing constitutes an important part of each reproductive event. The yearly differences observed in the frequency of nectar robbing could be a consequence of the variation in both (1) bumble bee abundance and/or (2) bumble bee foraging behavior. Resource (flower) availability (Bowers, 1985, 1986) and the presence of parasitoids (Schmid-Hempel and Durrer, 1991; Müller and Schmid-Hempel, 1992) have both been shown to affect growth and reproduction of colonies of bumble bees and, thus, their abundance. Bowers (1985) and Schmid-Hempel and Schmid-Hempel (1998) demonstrated that when food was scarce, the colonies produced fewer and smaller workers.

In addition, variable environmental conditions could affect foraging strategies of bumble bees. For example, on rainy and cold days it may be possible for bumble bees to forage only during short and unpredictable intervals. As can be seen, food availability, parasitoid damage, or bumble bee foraging behavior respond to variations in environmental conditions, so yearly observed fluctuations in nectar robbing could be a consequence of natural environmental fluctuations among years.

Differences among years in nectar robbing of *A. vulneraria* may also be induced by the variation in relative abundance of other attractive flowers for bumble bees. If some coexisting plant species overlap in flowering period attracting to the same visitors, they can compete for them. In that case, the most abundant species could attract a larger number of visitors that may suppose a disadvantage for the other (see Proctor, Yeo, and Lack, 1996, for a review). However, this may not be the case. Another early-spring-flowering species abundant in the study area, *Petrocoptis grandiflora* Rothm. (Caryophyllaceae), which is also robbed by bumble bees, presented yearly nectar-robbing patterns similar to these observed in *A. vulneraria* subsp. *vulgaris.* No robbed flowers were observed in 1997, and the highest percentage of robbed flowers was observed in 1994 (data from 1992–1997 period; Navarro, unpublished data).

The absence of robbed flowers in 1997 may to be a consequence of a dramatic local extinction of bumble bees because of a resource shortage early in the season (see Bowers, 1985). Note that in 1997, when no robbing was observed, the weather at the study area was very atypical, with high temperatures between December and February and unusual low temperatures after February. That atypical weather delayed the flowering of *A. vulneraria* subsp. *vulgaris.* These weather changes altered the normal flowering period of early-flowering species and perhaps the reproductive success of bumble bees in this area. Similar local absence of *Bombus terrestris* during the spring of 1997 was observed in other neighboring areas from the Northwest Iberian Peninsula (M. Medrano, communication personal, University of Santiago de Compostela). The absence of robbing in 1997 may also be explained by a local extinction of bumble bees because of an unusually late and light snowpack, so that the ground and, therefore, hibernating queen bumble bees froze (D. Inouye, personal communication, Rocky Mountain Biological Laboratory).

Nectar robbers as pollinators—A number of other studies have revealed that nectar robbers act as pollinators when their bodies come into contact with the plant's sexual organs during robbing (Macior, 1966; Koeman-Kwak, 1973; Waser, 1979; Higashi et al., 1988; Navarro, Guitián, and Guitián, 1993; Scott, Buchmann, and O'Rourke, 1993; Guitián, Sánchez, and Guitián, 1994). Such contact also occurs during nectar robbing from *A. vulneraria* subsp. *vulgaris* by the two *Bombus* species; both species alight directly on the capitulum and crawl across it in a rather ''heavy-footed'' fashion as they proceed with the robbing. While crawling across the capitulum, bumble bees depress the keel and wings of the flowers that they are robbing and sometimes of the surrounding open flowers on this capitulum. Flowers on the capitulum open by pairs (Navarro, 1999). As bumble bees

visit two or three flowers per capitulum (see Table 1), almost every flower open at a given time is visited. Thus, the stamens beneath act as a piston forcing out a string of pollen onto the underside of bumble bees. Because of synchronic stigma protrusion, pollination can take place. The hypothesis that *Bombus* visits lead to pollen transfer is supported by my findings that the probability of fruit set was significantly higher for robbed than for nonrobbed flowers.

Although morphologically the individual flowers of *A. vulneraria* subsp. *vulgaris* do not appear to be adapted for pollination by short-tongued bumble bees, these nectar robbers may be the most important pollinators. There are several reasons to suggest that this is the case. First, judging from their abundance (45% of total visits) and the large number of flowers visited per capitulum, bumble bees are the most abundant pollinators of *A. vulneraria* subsp. *vulgaris* in this geographic area. Second, bumble bees spend more time in contact with anthers and stigmas while they crawl across the capitulum and therefore may be more effective pollinators. And, third, fruit set in robbed flowers is greater than that obtained in nonrobbed flowers. Higashi et al. (1988) suggest that, terminologically, these robber-bumble bees are not real ''robbers'' but should be called ''robber-like pollinators.''

Proctor and Yeo (1973) suggested ''that protection against nectar theft may have been one factor in the development of dense inflorescences seen, for instance, in *Trifolium.*'' However, the inflorescence plays a fundamental role in favoring pollination by nectar robbers in *A. vulneraria* subsp. *vulgaris* because robbers crawl across the capitulum thereby increasing pollen transfer. Fabaceae are a family of plants whose species are commonly robbed (Kendall and Smith, 1976; Newton and Hill, 1983; Stoddard and Bond, 1987; Fussell, 1992; Crofton, 1996; Pierre et al., 1996). For the family Fabaceae this is the first study showing that robbers act as pollinators when robbing nectar. The maintenance or development of a dense inflorescence, as seen in *A. vulneraria* subsp. *vulgaris,* could enable nectar robbers to act as pollinators in Fabaceae.

In conclusion, the effect of nectar robbers on plant reproductive success is dependent on robber behavior and flower/inflorescence structure (although not exclusively, see Hawkins, 1961; Heinrich and Raven, 1972; Zimmerman and Cook, 1985). This study illustrates the importance of pollination ecology studies examining the activity of all floral visitors and not only the activity of visitors that initially appear to be pollinators (see also Waser et al., 1996). By doing so, we may find that ''robbers'' who pollinate are not as uncommon as once thought.

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