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REPRODUCTIVE BIOLOGY OF POINTLEAF MANZANITA (*ARCTOSTAPHYLOS PUNGENS*) AND THE POLLINATOR-NECTAR ROBBER SPECTRUM

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Abstract—Floral visitor species are often assumed to act either mutualistically towards plants (as pollinators) or to exploit them (as nectar-robbers or as nectar or pollen thieves). We investigated the reproductive biology of pointleaf manzanita (*Arctostaphylos pungens* K. Kunth), a regionally abundant North American shrub, in relation to the wide spectrum of behaviours displayed by its flower-visiting insects. We recorded *A. pungens* population-level flowering phenology and nectar standing crop, and conducted experiments documenting its breeding system, in an Arizona upland habitat in 1998 and 1999. Floral visitors were observed over 38 hr. We recorded frequencies of six foraging behaviours within and among individuals of each visitor species.

Arctostaphylos pungens flowers in late winter. During this period it is the only abundant floral resource for a diverse array of generalist insects in its habitat. We observed 1206 floral visits by 46 taxa. Most floral visitors pursued mixed behaviours: at the species and/or individual level, they foraged both legitimately and as nectar-robbers or thieves. The most commonly mixed behaviours were legitimate pollen collection (which likely resulted in pollen transfer) and secondary nectar-robbing (which was highly unlikely to do so). As *A. pungens* was found to be largely self-incompatible, robbing and thieving visits should be detrimental to reproductive success.

Although theoretical analyses often assume that exploiters must be punished or excluded for mutualism to persist evolutionarily, exploitation is in fact ubiquitous within cooperative interactions in nature. In manzanita, very few floral visitor species could be classified as exclusively beneficial or detrimental to plants: rather, they exhibited multiple foraging strategies, with no evidence of plant control. Such pollinator-nectar robber spectra appear to be common, and constitute an important challenge to current understanding of how mutualism can persist.

Keywords: Arctostaphylos, cheating, exploitation, foraging, manzanita, mutualism, nectar-robbing, pollination.

INTRODUCTION

Mutualisms involve a mutually profitable exchange of commodities between two species. One phenomenon common to virtually all mutualisms, however, is the presence of exploiters (often termed cheaters or parasites). These are organisms that obtain the commodities mutualists offer, but that deliver none in return (Yu 2001; Bronstein 2001, 2003). The exploitation of mutualism has recently attracted extensive attention because of its potential evolutionary significance. Individuals that obtain the benefits mutualists offer while avoiding investment into mutualistic commodities should experience a fitness advantage. Unless exploitative strategies are countered, they are therefore expected to replace mutualism over evolutionary time. Paradoxically, however, mutualisms are ubiquitous in nature, and exploitation seems ubiquitous within them (Bronstein 2001, 2003). These observations underscore the need for further empirical studies of exploitation, particularly those devoted to understanding how mutualism can persist in its presence.

Plant/pollinator interactions have become model systems for studying exploitation. In particular, a great deal is known about the natural history of nectar-robbing (Irwin et al. 2010). Nectar-robbers are floral visitors that collect nectar from punctures in the corolla, made either by themselves or by other individuals. In so doing, they usually bypass direct contact with the stamens and stigmas. Nectar-robbing exhibits two features typical of exploitation. First, exploitation varies widely in the costs it inflicts upon the partner. Many robbers neither pick up nor deposit pollen during a visit; pollinators may subsequently avoid robbed flowers, with consequent reductions in seed set and/or pollen donation (e.g., Irwin & Brody 1999, 2000). Other robbers, however, do move pollen, or else cause changes in pollinator behaviour (e.g., inducing pollinators to leave flowers earlier than they otherwise would) that lead to greater pollen transfer. In those cases, exploitation may actually benefit plants (e.g., Navarro 2000; Maloof 2001; Richardson 2004). Second, what appears to be one form of exploitation is actually a suite of related phenomena. The most thoroughly studied nectar-robbers never visit the

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species that they rob as legitimate pollinators. However, in some floral visitor species, certain individuals exclusively rob and others exclusively pollinate the same plant species; in other visitor species, each individual both robs and pollinates the same plant (Irwin et al., 2010). Although mixed pollinating-robbing strategies have been reported previously (e.g., Free 1968; Rust 1979; Morris 1996; Villalobos & Sherry 1996; Olesen 1996; Dedej & Delaplane 2005; Newman & Thompson 2005), little is known of their causes, consequences, or ecological distribution.

Here, we document the spectrum of potentially mutualistic and antagonistic behaviours exhibited by floral visitors to a regionally abundant North American shrub, pointleaf manzanita (*Arctostaphylos pungens* HBK, Ericaceae, Vaccinoideae). We first present data on the phenology, floral biology, and breeding system of *A. pungens*. These features have not previously been described, and are necessary for examining implications of its floral visitors' foraging behaviours. We then describe those behaviours, based on over 38 hours of observation of 46 insect species over two years. We document (1) the range of foraging behaviours that floral visitors use, (2) the frequency with which single visitor species and single individuals mix behaviours, and (3) the behaviours that are most commonly mixed at the species and individual level. We then combine data on plant breeding system and visitor behaviour to discuss the implications of the foraging spectrum from the perspective of the insects themselves, the plants they visit, and the mutualisms they sometimes form.

MATERIALS AND METHODS

Study system

Arctostaphylos pungens (pointleaf manzanita) occurs over much of the southwestern United States and as far south as Oaxaca, Mexico (Kearney & Peebles 1960; Diggs 2009), often forming a significant component of Madrean evergreen woodland and chaparral vegetation types (Brown 1982). It is a sprawling evergreen shrub with simple ovate leaves and distinctive, smooth red stems. Flowering occurs from Jan-Apr at most sites; however, sporadic flowering can take place at almost any time of year. Flowering is minimal to absent in drought years (L. Richardson and J. Bronstein, pers. obs.). The small, pendulous flowers are borne in dense inflorescences. A single plant can bear several hundred open flowers at one time during peak flowering. Flowers are bell-shaped, with fused corollas. Flowers range from white to deep pink and average 6 + 1 mm in length and 3 + 1 mm at their widest point; they are constricted at their apical ends to about 2 mm in diameter when fully open (n = 485 flowers). Nectar is produced in depressions in a basal part of the corolla slightly occluded by the ovary. The 10 stamens bear distinctive burgundy-coloured anthers. Pollen is produced in tetrads and is dehisced toward the style via apical pores on the anthers. The superior ovary contains 5-10 ovules. The fruit is a fleshy berry with 1-5 stony segments, each containing 1-3 seeds.

Study Sites

This study was conducted at two locations in the Santa Catalina Mountains, Arizona, USA (32.3374, -110.6918) where *A. pungens* was the dominant shrub species: Molino Basin (1280 m elevation) and the Gordon Hirabayashi Recreation Site (1500 m elevation). Both sites receive ~35-40 cm of precipitation per year (Sabino Canyon, the nearest weather station, receives a yearly average of 33.1 cm of precipitation at 840 m elevation; Western Regional Climate Center, 2012). Most precipitation falls during summer monsoons and a mid-winter rainy season. Summer temperatures typically exceed 35°C, and winter temperatures below 0°C have been recorded annually since record keeping began (Western Regional Climate Center, 2012).

Floral Biology

Population-level floral phenology was documented at Molino Basin during Jan- Mar 1998 and 1999. Plants (4 in 1998; 12 in 1999) were haphazardly chosen at 10 meter intervals along a roughly linear transect. On each plant, stems were arbitrarily chosen (2 in 1998; 1 in 1999) and marked. Every 2-10 d, the following information was recorded for individually marked inflorescences on these stems: number of flowers open, number of flowers with corolla perforations, number of flowers missing (flower and/or pedicel abscised due to abortion or herbivory), and number of fruits initiated. Similar numbers of flowers were censused each year. In 1999, a severe drought cut short the flowering season. Censusing ended in early March, as flowers were no longer opening or abscising from the plant.

Nectar standing crop was measured from open flowers between 0930 and 1045 on 1-2 February 2001 at Hirabayashi, using a 1 μl micropipette. On 17 plants, 1-3 pairs of adjacent flowers, in which one flower of the pair was undamaged while the other had been perforated by a nectar-robber earlier the same morning, were sampled.

Breeding System

In 1998, the mating system of *A. pungens* was studied at Molino Basin. Before flowers opened, a group of inflorescences (~75 flowers) were bagged on 4 stems of each of 4 plants to exclude floral visitors. A fifth stem was randomly chosen to serve as an unbagged control. Flower buds on all inflorescences of the 5 stems were counted before anthesis. Four treatments were performed on the bagged branches; on each plant, each bag received a different treatment. In the bagged control treatment, bags were removed and then immediately replaced in order to test for autogamous reproduction. The outcrossing treatment involved collecting pollen from three or more donor plants located 5-50 m away by sonicating anthers with a tuning fork, then using a pinhead to apply this pollen to stigmas. The geitonogamous self-pollination treatment involved collecting pollen by sonicating flowers within a bag, then distributing that pollen onto stigmas of other flowers within the same bag. Finally, in the buzz self-pollination treatment, all open flowers within a bag were sonicated with a tuning fork. Each treatment was repeated periodically as new flowers opened within the bags. Fruits were collected approximately 6 wk after flowering ceased. The number of fruits produced was divided by the total number of flowers to calculate fruit set for that treatment. Counting seeds to measure reproductive success was not feasible: in *A. pungens*, the persistent, woody endocarp surrounding seeds often causes them to adhere so tightly to one another that individual seeds cannot be distinguished. Instead, fresh fruits were weighed individually to the nearest hundredth of a gram with an electronic balance. Fruit weights were compared among treatments with analysis of variance, followed by Tukey-Kramer post-hoc tests.

Floral Visitors

Floral visitors were observed at both sites. In 1998, visits were recorded only anecdotally, so most of the data reported here are from 1999. Focal plants were chosen haphazardly and a different plant was observed each day. Observers stood 0.5-2.0 m from the focal plant and watched as many flowers as possible (usually several hundred) for 30-180 min. Most observations were made during two daily peaks of insect activity, between 0900 and 1200 and between 1500 and 1700. When an insect arrived at the plant, it was continuously observed until it disappeared from sight or left the plant. A single visitor was observed each time, even if other insects were arriving, departing, and foraging simultaneously. Each observed trip to a flower is subsequently termed a "visit," and a series of visits during which an individual visitor was monitored continually until it left a plant is termed a "bout." In the descriptions that follow, all visits are included, regardless of their sequence within a bout, and each visit is treated as a separate event. We consider this to be appropriate because (a) proportions of each visit type (described below) recorded for the most common visitor species during their first visit were indistinguishable from proportions for the second, third, and fourth visit, and (b) proportions of behaviour types in visits 1-4 were not significantly different from proportions of those behaviours in the entire data set (data not shown).

For each visit, one of six possible behaviours was recorded. We briefly describe them here; further details are provided in the Results. Three types of visits were likely to lead to pollen transfer between flowers. During a *legitimate nectar-collecting* visit, an insect collected nectar by inserting its mouthparts through the corolla opening. In a *legitimate pollen-collecting* visit, an insect reached inside the corolla to glean fallen pollen from the tuft of hairs situated underneath the anthers. In a *buzz pollen-collecting* visit, the insect hung from the corolla and sonicated the flower to release pollen from the poricidal anthers. Three additional types of visits were recorded that were likely not to result in pollen transfer; our terminology follows Inouye (1980). During a *primary nectar-robbing* visit, the insect used its mouthparts to perforate the corolla near the base of the flower, then collected nectar without contacting the stigma or anthers. A *secondary nectar-robbing* visit involved the collection of nectar from a pre-existing perforation. Finally, *nectar thievery* was recorded when the insect forced its mouthparts through the closed corolla of a bud without damaging it, collecting nectar before the flower opened.

Floral visitors were regularly collected during observation periods. The majority of bees were identified to genus; most other insects were identified at least to family with available reference texts (McAlpine 1981-1989; Borror et al., 1989; Michener et al., 1994). Determinations were checked against specimens in the University of Arizona Entomology collection. Although it was not possible to obtain complete identifications for every visitor we observed, all but the Lepidoptera were easily identifiable to operational taxonomic unit on the wing. The > 12 Lepidoptera species have been combined in this analysis, as they displayed similar foraging strategies, and individually, were insignificant as visitors. Voucher specimens have been deposited in the University of Arizona Entomology collection.

RESULTS

Floral Biology

Arctostaphylos pungens individuals typically produced several hundred inflorescences each year. An average of 10.2 (+ 0.2 S.E.) flowers were produced per inflorescence in 1998 (n = 16 inflorescences). Individual flowers remained open an average of 3.3 d (n = 30 flowers). Flowers within an inflorescence usually matured sequentially, although in some cases most were open on the same day. Open, unrobbed flowers sampled at mid-morning contained 0.42 + 0.78 μl of nectar (n = 38 flowers on 17 plants).

In 1998, an exceptionally wet year, flowering began on 1 February, peaked on 4 March, and ended on 25 March. Approximately 36% of marked flowers set fruit. In contrast, 1999 was extremely dry. Flowering began about 2 weeks earlier than in 1998, but there was never a strong population-level bloom. By 1 February most inflorescences were static, neither initiating new flowers nor dropping old, dry corollas. Desiccated flowers remained on the plants for approximately 4 weeks and then abscised. No fruits matured at Molino Basin in 1999.

Mating System

Arctostaphylos pungens appears to be largely self-incompatible. Although selfed flowers produced as many fruits as did hand-outcrossed flowers, an ANOVA revealed that fruit weights differed significantly among pollination treatments ($F_4 = 114.54$, $P < 0.0001$; Table 1), and many fruits derived from selfed flowers apparently did not contain viable seeds. Tukey-Kramer post-hoc tests showed that hand-outcrossed flowers and unbagged control flowers produced significantly heavier fruits than those produced by the three self-pollination treatments (bagged control, geitonogamous self-pollination, and buzz self-pollination). Fruits from two of the self-pollination treatments (bagged control and geitonogamous self-pollination) were of very low weight and not significantly different from each other. Those from the buzz self-pollination treatment were significantly heavier than those of the other self-pollination treatments.

Floral Visitors

Floral visitors were observed for 38 hr. Data from 1206 visits by 46 insect taxa during 565 foraging bouts are summarized in Table 2. Appendix 1 lists data by taxon. Bouts ranged from 1-24 visits in length; mean bout length was 2.1 (+ 0.1) visits. Visits by 12 insect species (10 bees and 2 flies) accounted for 93% of visits and 88% of bouts

TABLE 1. Arctostaphylos pungens produced significantly heavier fruits ($F_{4,387} = 114.54$, $P < 0.0001$) and produced fruits from a greater proportion of flowers ($F_{4,143} = 3.32$, $P < 0.0124$) when experimentally outcrossed than when selfed. Fruit set was calculated as the number of fruits/number of flowers initiated. Data are presented ± 1 S.E. Values with the same lower case postscript are not significantly different.

Experimental Treatment	Sample Size (no. fruits)	Mean Fruit Weight (g)		Sample Size (no. flowers)	Mean Fruit Set	
Hand outcrossed	157	0.35 ± 0.01	a	42	0.51 ± 0.04	d
Hand selfed	97	0.09 ± 0.01	b	24	0.48 ± 0.05	d
Buzz selfed	25	0.17 ± 0.02	c	24	0.33 ± 0.05	e
Bagged control	35	0.08 ± 0.02	b	24	0.36 ± 0.05	e
Unbagged control	78	0.33 ± 0.01	a	34	0.35 ± 0.04	e

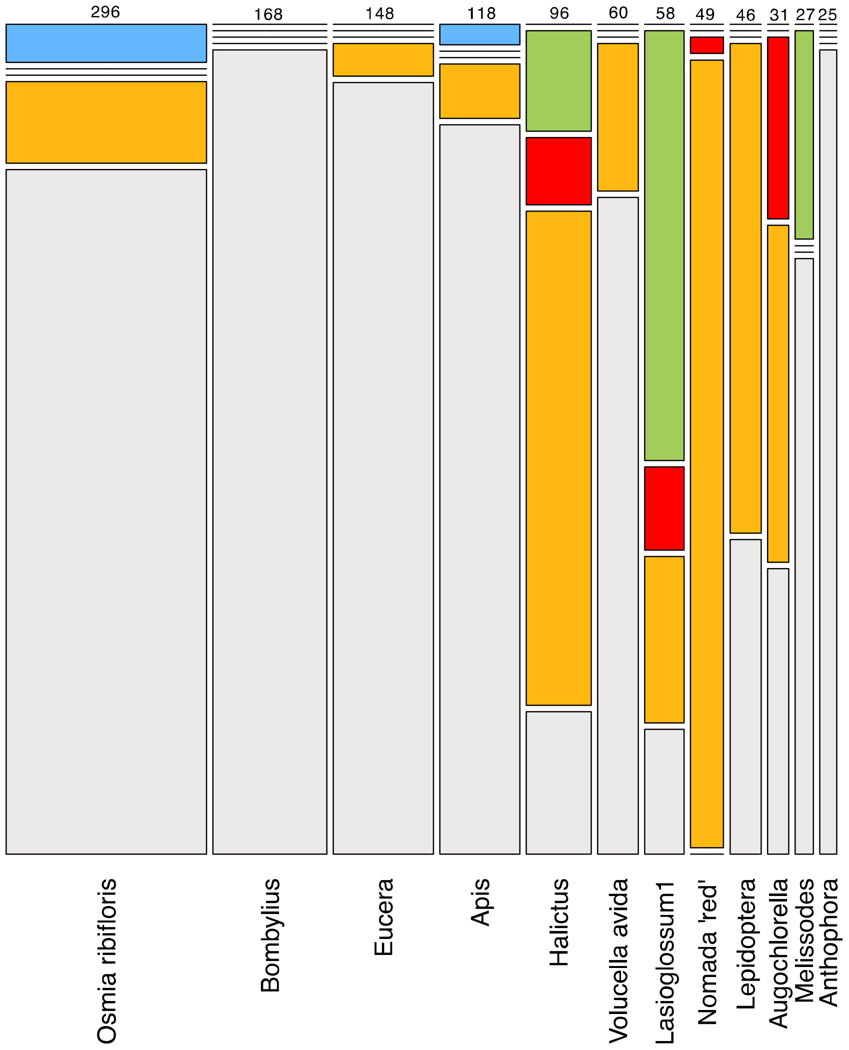

FIGURE 1. Mosaic plot of foraging behaviours of the 12 most common visitors to *Arctostaphylos pungens*, indicating that most flower visitors employed more than one foraging strategy. Visitors are arranged from left to right according to abundance, and sample sizes are given above each bar. From bottom to top, behaviors are: legitimate nectar collection (grey), secondary nectar-robbing (orange), primary nectar-robbing (red), buzz pollination (green), and legitimate pollen collection (blue). A horizontal line indicates that the taxon did not perform a behavior. Observations of nectar thievery have been omitted due to small sample size. All but two of these exhibited mixed foraging behaviours. Details on individual taxa are provided in the Appendix.

observed. The most common visitors were bees of the genera *Osmia, Augochlorella, Lasioglossum, Halictus, Nomada,* and *Eucera*; also common were bee flies (*Bombylius*) and flower flies (*Volucella*). Multiple individuals of all but two of these 12 species exhibited mixed foraging behaviours (Fig. 1).

Legitimate visits for pollen and nectar. -- The most common behaviour (70% of all observed visits) was legitimate nectar collection, i.e., a visit in which an insect inserted its mouthparts through the opening of the corolla tube and probed the nectaries at the base of the ovary. Ten

TABLE 2. Foraging behaviours of insects visiting *Arctostaphylos pungens* flowers. Based on 1202 visits by 46 insect species observed during 565 foraging bouts. Behaviours are defined in the text.

Foraging behaviour	Number of observed visits	As % of all observations	% of insect species employing behaviour
Legitimate nectar collection	846	70,4	65,7
Secondary nectar robbing	263	21,9	65,7
Primary nectar robbing	24	2	14,3
Buzz pollen collection	52	4,3	11,4
Legitimate pollen collection	17	1,4	5,7
Nectar thievery	4	0,3	2,1

bee species and 10 fly species, as well as small butterflies (65.7% of all visitor species), were observed to forage this way (Appendix 1). Five bee species sonicated ("buzzed") the flowers for pollen, accounting for 4.3% of all insect visits (Table 2). When these visitors collected pollen, they usually clung to the flowers and vibrated their flight muscles, causing pollen to rain out of the poricidal anthers. Two other bee species collected pollen by inserting the forelegs into the flower and scraping dehisced pollen from the trichomes on the internal surface of the corolla (1.4% of all visits, Table 2).

Illegitimate visits. -- Six bee species acted as primary nectar robbers. This behaviour was recorded in only 2% of all visits observed in 1998 (Table 2), even though ~ 70-90% of corollas were perforated that year. Primary nectar robbers were observed to cut slits or oval punctures through the corolla, then inserted their mouthparts without contacting the stigma or anthers. They occasionally made a second perforation in the same flower immediately after making the first, possibly because they could not access all of the nectar from the first hole. We assumed that all perforations were observed (which were highly consistent in size, shape, and placement) were due to the actions of primary nectar robbers.

Primary robbing significantly lowered nectar standing crop in 2001, even though nectar-robbing rates were extremely low that year (6% of flowers robbed; n = 302 flowers) relative to the same time period in 1998. By mid-morning, robbed flowers contained 82% less nectar on average than did adjacent unperforated ones (paired t-test, $t = 2.8$, $P = 0.008$, n = 38 flower pairs).

Secondary nectar robbers foraged at the holes made previously by primary robbers. Secondary robbing was the most common foraging behaviour after legitimate nectar collection, representing 22% of observed visits (Table 2). Eleven bee species, 2 wasp species, and 11 fly species, as well as diverse small butterflies (66% of all visitor species), fed this way (Appendix 1).

Nectar thieves fed by forcing their mouthparts through the petal lobes of nearly open, nectar-containing buds. Nectar thievery represented < 1% of visits (Table 2), all of them by the bee *Osmia ribifloris* (Megachilidae), which was overall the most common floral visitor.

Mixed foraging behaviours. -- About half of all floral visitor species exhibited mixed foraging behaviours at either the species or individual level, using two, three, or four of the six foraging strategies we recorded (Appendix 1). Among visitor species exhibiting a single behaviour, six were only seen foraging legitimately for nectar, two only foraged for pollen by sonicating flowers, one acted only as a primary robber, and 10 acted only as secondary robbers. It is likely that many of these species too had mixed foraging strategies, but that they went undetected because these species were relatively rare. Indeed, of the 13 visitor species observed 25 or more times, all but two exhibited mixed behaviours (Fig. 1).

Overall, 14 of the 15 insect species that foraged legitimately for pollen or nectar also included at least one illegitimate behaviour in their foraging repertoire. The most common behavioural combinations employed by foraging insects were legitimate nectar collection and secondary robbing (13 species); legitimate collection of nectar and sonication to obtain pollen (three species); legitimate nectar collection and primary robbing (three species); and primary and secondary robbing (three species).

Some species that mixed foraging behaviours were doing so at the within-individual level. These individuals switched behaviours within a foraging bout on an individual plant, and occasionally even while visiting a single flower. We observed switches in behaviour in 7.4% of 565 recorded foraging bouts (Table 3); the actual frequency is certainly higher, since many visitors disappeared from view while still foraging. Of these behavioural switches, more than 90% involved shifts between illegitimate and legitimate visits. The large majority of switches were between legitimate nectar collection and secondary nectar-robbing (Table 3).

In the large majority of foraging bouts (92.6%), however, individuals were observed to use a single foraging behaviour. For instance, some *Halictus* species bees were seen to bypass open, unperforated flowers while searching for perforated flowers to secondarily rob; at the same time, other individuals of the same species were foraging legitimately at undamaged flowers on the same plant.

TABLE 3. Switches in foraging behaviours during a bout by the most common floral visitors observed to switch. An "X" indicates that a species was observed to switch between that pair of behaviours during at least 1 bout. The total number of bouts during which a species switched behaviours is given, followed by the percentage of all bouts in which behavioural shifts were observed. Abbreviations: LN = legitimate nectar collection; LP = legitimate pollen collection; BZ = buzz pollination; 1NR = primary nectar robbing; 2NR = secondary nectar robbing; NT = nectar thievery.

Taxon	Behavioural Switches Observed					No. switching Bouts	Switching as % of all bouts
	LN/2NR	LN/1NR	BZ/2NR	BZ/1NR	1NR/2NR		
Augochlorella sp.	1	1			1	3	15
Halictus sp.	2	1	1	1	1	6	13,6
Lasioglossum sp. 1	3	2	1		1	7	23,3
Nomada sp. 'red'					1	1	4,3
Osmia ribifloris	10					10	6,7
Apis mellifera	1					1	2
Bombylius sp.	3					3	4,2
Bombyliadae sp.	1					1	100
Volucella avida	5					5	20
Lepidoptera spp.	3					3	8,8

Other floral visitors. -- Two other groups of visitors were commonly recorded on *A. pungens* flowers. Three species of thrips were frequently observed feeding within flowers. The most abundant of these, *Orothrips kelloggii* (Thysanoptera: Aelothripidae), was found in 68% of all flowers and on every plant. It damaged flowers by laying eggs in the pedicels and by feeding on corolla sap, nectar, and pollen. When males dispersed from their natal flowers, they passively transported pollen between flowers (Richardson 1999). Anna's hummingbirds (*Calypte anna*) defended breeding territories at Molino Basin and occasionally foraged at *A. pungens* flowers. Bill insertions usually resulted in severe damage to floral tissue. Because nectar standing crop was so low, we speculate that these birds were primarily feeding on thrips, a food source reported for other hummingbird species (Bené 1945).

DISCUSSION

Arctostaphylos pungens blooms exceptionally early in the year in the southwestern United States. Even though flower abundance and phenology appear to be strongly influenced by late winter and early spring weather and nectar volumes per flower are rather low, it is apparently a critical resource for a large and diverse community of flower-visiting insects, probably because it is usually the only plant in abundant flower in its habitat at these times of year. As shown here, most of these visitors do not consistently visit in ways likely to result in pollination (i.e., 'legitimate' nectar foraging or buzz pollen collecting). Rather, a significant portion of the time they function as nectar robbers and thieves unlikely to benefit the plant. In many of these insect species, individuals pursue a single behaviour while foraging on an individual plant, even though other individuals (and possibly the same individual at other times) exhibit a different foraging strategy. Individuals of other visitor species shift among as many as four different behaviours within a foraging bout on a single plant. These observations raise a number of issues with regard to the ecological and evolutionary consequences of these behaviours to the plants they visit, to the insects themselves, and to the mutualisms that at times exist between them.

The Plant Perspective

Arctostaphylos pungens produces significantly heavier fruits when it has the potential to outcross (Table 1), underscoring the importance of floral visitors. However, a variety of foraging behaviors were employed by these visitors, and, as in other pollination systems (e.g. Herrera 1987; Irwin et al. 2001), it is likely that some foragers are more effective pollen vectors than others. Although we did not measure the individual contributions of foragers to pollination of this plant, the specifics of the different foraging behaviours permit some reasonable inferences.

It is likely that the two common foraging behaviours we refer to as "legitimate" – buzz pollen collection and nectar collection via the corolla opening – resulted in pollen transfer and were thus mutualistic in nature, although not necessarily to the same degree. Buzz-pollinating species forage by clinging to the pendulous flowers and vibrating their flight muscles, causing pollen to rain out of the poricidal anthers. These behaviours appear to bring them into contact with the stigma, effecting pollination. Furthermore, female bees that vibrated the flowers for pollen were densely hairy and, when captured, were typically carrying large loads of pollen both in their scopae and dispersed over their bodies (L.L. Richardson, *personal* *observation*). It was more difficult to observe if and when pollen transfer took place during legitimate nectar-collecting visits, due to the flowers' small size and tightly constricted openings. However, most nectar-collecting insects probably made contact with the prominent stigma, as well as with the recurved anther appendages. We did note that the two most common legitimately nectar-foraging bees, *Osmia ribifloris* and *Eucera* sp., commonly had pollen adhering to their facial hairs. The morphology and foraging behaviours of the two flies that made many legitimate nectar visits (*Bombylius* sp. and *Volucella avida*) likely rendered them poor pollinators.

In contrast to its legitimate visitors, the nectar thieves and robbers of *A. pungens* are unlikely to transfer pollen. Nectar thieves force their way into *A. pungens* buds to feed upon nectar. As the anthers do not dehisce until buds have opened (L.L. Richardson, pers. obs.), it is unlikely that these visitors collect pollen, although it is possible that they deposit some if they have recently made a legitimate visit to another flower. Nectar-robbers do pick up and deposit pollen in some plants (Higashi et al. 1988; Scott et al. 1993; Navarro 2000). However, these species generally have stigmas and anthers that are either highly exserted or else that can be contacted via the corolla perforation. The structure of the *A. pungens* flower makes these phenomena unlikely.

It is possible, however, that nectar-robbing visits could lead to changes in pollinator behaviour that would benefit the plant. Nectar-robbing significantly reduced nectar volumes. In some plant species, pollinators make briefer visits to heavily robbed plants (Irwin 2003), increasing outcrossing rates and hence reproductive success (Maloof 2001; Richardson 2004). In other species, however, reduced nectar volumes lead pollinators to abandon heavily robbed plants or even to avoid them entirely, reducing plant reproductive success (Irwin 2000). Reduced nectar levels could even have induced pollinators to shift to robbing strategies (e.g., if robbing is a more effective method of obtaining the last dregs of nectar from nearly drained flowers), but we are unaware of any report of this phenomenon in the literature. Further experimental studies would be necessary to provide evidence for these effects in *A. pungens*.

The Insect Perspective

Research on nectar-robbing has typically focused on its costs and benefits to plants, rather than on its nature as a foraging strategy (Irwin et al. 2010). Perhaps for this reason, it has commonly been overlooked that robbing and pollinating often are not in fact distinct behaviours performed by different visitor species. Rather, many robbers also act as pollinators of the same or other plants, whereas at least some pollinators also rob. Honey bees have repeatedly been noted to function simultaneously as legitimate pollen-collectors, legitimate nectar-collectors and secondary nectar-robbers on a single plant species (Weaver 1956; Free 1968, 1993; Joubert et al. 1977; Villalobos & Shelly, 1996; Dedej & Delaplane 2005), much as they did on *A. pungens* (Appendix 1). Honey bees and other insects may also function as non-mutualist pollen thieves (*sensu* Inouye 1980), even if they sometimes pollinate the same plants when they forage for nectar (Hargreaves et al. 2009, 2012). Similarly, some bumblebee species both pollinate (often via sonication) and act as either robbers or thieves of the same plant (Kwak 1977; Free 1993; Morris 1996; Oleson 1996; Newman & Thomson 2005). Mixed pollinating-robbing behaviours have also been noted in a few other Hymenoptera (Hurd & Linsley 1963; Rust 1979). The present study indicates that complex mixed behaviours may be common in a much broader spectrum of flower-feeding insects, including Diptera and Lepidoptera.

Factors that might favor mixed foraging behaviours within and among floral visitors and the rules that might govern behavioural switches have not yet been investigated in this system, and little relevant information is available from any other system (but see Dedej & Delaplane 2005; Newman & Thomson 2005). Data from other studies generate two observations, however, that may shed light on the nature of these phenomena.

First, certain generalist pollinators unable to obtain nectar of a certain plant species by legitimate means shift to nectar-robbing after a few visits, rather than abandoning that plant to forage legitimately at other species (Joubert et al. 1977; Rust 1979). When *A. pungens* flowers, small generalist insects have few other floral resources available to them, and they may be forced to forage upon it in any way that they can. Such forced switches may also explain the strategy-switching we commonly observed within individual foraging bouts of certain visitor species. In a second North American *Arctostaphylos* species, *A. pringlei*, flowers vary greatly in corolla width; we observed bees (*Nomada* sp.) foraging legitimately for nectar on flowers with relatively wide corollas and acting as primary robbers on flowers with more restricted entrances (Richardson 1999).

Secondly, among insects unable to chew holes through corollas, shifts from legitimate visitation to secondary nectar-robbing have in some cases been shown to be contingent upon the actions of primary nectar-robbers (Hawkins 1961; Free 1968; Barrows 1980; Villalobos & Sherry 1996). In one detailed study, Free (1968) showed that the abundance of honey bees on runner beans (*Phaseolus multiflorus*) increased greatly in the presence of primary nectar-robbing bumblebees. When bumblebees were present, most honey bees shifted from legitimate nectar collection visits to secondary nectar-robbing, suggesting that secondary robbing was a more efficient strategy, but one constrained to certain community contexts. In *Vaccinium ashei*, Dedej and Delaplane (2005) have demonstrated that honey bees in fact receive higher energetic returns from secondary robbing than from legitimate visits. Secondary nectar robbing, as well as facultative switching from legitimate nectar foraging to secondary robbing, may thus be more common at plants frequented by diverse guilds of generalist foragers that include primary nectar robbers., such as in *Impatiens capensis* (Rust 1979) and *A. pungens*.

Implications for Mutualism

That floral visitors mix beneficial and detrimental foraging behaviours is ecologically interesting, but does it matter to the evolution of pollination mutualisms? We would argue that it does. First, selection for increased specificity within mutualisms is expected to be weak or absent in the face of spatial and temporal variation in mutualist quality (Howe 1984; Schemske & Horvitz 1984). In pollination systems, both across-individual variation in foraging behaviours within visitor species and within-individual, context-dependent behavioural shifts undoubtedly generate low predictability as to which visitors will be the most effective pollinators at a given time and place. Thus, variable foraging strategies may be one more factor that keeps most plant/pollinator interactions highly generalized (Waser et al. 1996).

Second, it has become of great interest to understand how mutualisms can persist at all in the face of exploitation. Theoreticians have argued that without mechanisms to retaliate against or to exclude exploiters, mutualisms cannot be evolutionarily stable (Axelrod & Hamilton 1981; Bull & Rice 1991; Yu 2001). A variety of floral traits have been interpreted as defences against nectar robbing, including thickened calyces, toxic nectar and glandular trichomes (Prys-Jones & Willmer 1992; Agrawal et al. 2000; Irwin et al. 2010), yet many plants have no apparent defences and are heavily robbed. The behavioural spectrum documented here demonstrates that mutualism and exploitation can be intertwined in surprisingly complex ways, perhaps obviating the (theoretical) requirement for such defences. Plants able to deter visits by some exploiters might well experience a net increase in mutualist visits. In the present case, if *A. pungens* floral morphology prevented nectar robbing, behaviourally flexible nectarivores like *O. ribifloris* would presumably forage in a more cooperative fashion (i.e., as legitimate foragers), thereby increasing plant fitness. However, it is equally possible that if *A.* pungens could prevent primary nectar robbing, some facultative secondary robbers would abandon the plant altogether, leading to a loss of legitimate visits that result in pollination. These competing hypotheses should be tested in a plant system where nectar robbing can be effectively manipulated at the population level.

One of the most striking features of the behavioural spectrum exhibited by floral visitors is that species with foraging choices visit flowers legitimately as frequently as they do, even when robbing might be more efficient and plants do not defend against robbing. In this study, 13 of the 14 nectar-robbing species that exhibited foraging flexibility regularly, and indeed more commonly, visited flowers in ways likely to have led to pollination. Theoretical studies of exploitation generally assume that because cheating is often more efficient than foraging legitimately, organisms with choices should cheat whenever possible. Indeed, the only study to date of the relative economics of legitimate vs. robbing visits has shown that the latter are more energetically advantageous to honey bees (Dedej & Delaplane 2005). Further work on the exploitation of pollination mutualisms is needed to explain how these strategies can coexist.

APPENDIX

Additional supporting information may be found in the online version of this article:

Appendix I. Insects observed to visit flowers of *Arctostaphylos pungens* during 1998 and 1999.

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