

CONSPECIFIC POLLEN LOADS ON INSECTS FROM *PRUNUS FASCICULATA* (ROSACEAE) FEMALE FLOWERS IN SOUTHERN NEVADA

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ABSTRACT.—Desert almond, *Prunus fasciculata* (Rosaceae), is a Mojave Desert shrub that primarily produces male and female flowers on different plants. I investigated the plant's pollination by examining pollen loads on insects aspirated from female flowers on 3 dioecious shrubs, growing near male-flowering shrubs, at one locality in southern Nevada during March 2014. Pollen loads were analyzed on 9 species of Diptera in Bombyliidae, Syrphidae, Calliphoridae, and Tachinidae and 4 species of Hymenoptera in Andrenidae (all female *Andrena*). All but 4 of the 65 flies and 38 bees aspirated carried *P. fasciculata* pollen grains, recognized by their tricolpate shape in polar view and oblate shape in equatorial view. Two species of syrphid flies in *Copestylum* were frequently aspirated and carried high *P. fasciculata* pollen loads and moderate proportions of conspecific pollen. High conspecific pollen loads on the tachinid *Chaetogaedia* also indicated potential for pollinating *P. fasciculata*. Three of the 4 species of *Andrena* bees carried large amounts of *P. fasciculata* pollen. Conspecific pollen also comprised most of the pollen load on *Andrena* bees, suggesting high flower constancies to the plant. Pollinators of *P. fasciculata* would vary over the plant's range, and likely between years, because of the localized populations or narrow larval diets of many of the insects collected from flowers. The female desert almond shrubs examined in southern Nevada during 2014 appeared to be pollinated by a variety of native flies and bees, especially syrphid flies in *Copestylum* and andrenid bees in *Andrena*.

RESUMEN.—Las almendras del desierto, *Prunus fasciculata* (Rosaceae), es un arbusto del desierto de Mojave, que produce flores masculinas y femeninas en diferentes plantas. Investigué la polinización de la planta examinando la carga de polen aspirada en insectos de flores femeninas en tres arbustos deciduos, creciendo cerca de arbustos de floración masculina, en una localidad al sur de Nevada durante marzo del 2014. Las cargas de polen fueron analizadas en 9 especies de dípteros en Bombyliidae, Syrphidae, Calliphoridae y Tachinidae y 4 especies de himenópteros en Andrenidae (todas hembras *Andrena*). Todos menos 4 de las 65 moscas y 38 abejas llevaron de polen de *P. fasciculata*, reconocido por su forma tricolpada en vista polar y su forma achatada en vista ecuatorial. Dos especies de sírfidos en *Copestylum* aspiraron frecuentemente polen de *P. fasciculata* y proporciones moderadas de polen de conespecíficos. Altas cargas de polen conspecifico en *Chaetogaedia* indicaron un potencial polinizador de *P. fasciculata*. Tres de las 4 especies de abejas *Andrena* lleva a grandes cantidades de polen de *P. fasciculata*. El polen conespecifico también compone la mayor parte de la carga de polen de las abejas *Andrena*, sugiriendo constancia de flores en la planta. Los polinizadores de *P. fasciculata* varían a lo largo de la planta, y es probable que entre años, debido a las poblaciones localizadas o a la estrecha dieta de larvas de muchos de los insectos encontrados en las flores. Las hembras, de los arbustos examinadas en el sur de Nevada en 2014 parecían ser polinizadas por una variedad de moscas y abejas nativas, especialmente los sírfidos *Copestylum* y abejas *Andrena*.

Desert almond, *Prunus fasciculata* A. Gray, is an intricately branched, deciduous, stiff-stemmed shrub in Rosaceae that is widely scattered in and around the Mojave Desert of southeastern California, southern Nevada, southwestern Utah, and western Arizona (Mason 1913, Benson and Darrow 1954). The plant's common name comes from its frequently abundant, small (8–10 mm long), ovoid, pubescent fruit, and its species name is derived from its clusters of bundled, 9–18 mm long, oblanceolate leaves (Jaeger 1941, Benson and Darrow 1954). Desert almond usually grows to 2 m in height on hillsides

and in washes between 760 m and 1800 m elevation (Munz 1974).

Prunus fasciculata is unusual in producing flowers that mature to become unisexual. Male flowers contain 10–12 stamens and an infertile ovary with a stunted pistil, and female flowers contain a single ovary and pistil and stunted stamens without pollen (Mason 1913). Perianths also differ between sexes, with male flowers having slightly wider calyxes and longer petals (Mason 1913). Some flowers on *P. fasciculata* may develop to include stamens and pistils. Munz (1974) described flowers on the species as perfect or imperfect, and

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Benson and Darrow (1954) described its flowers as “tending to be unisexual with staminate and pistillate flowers on different plants.” This suggests that desert almond is to some extent dioecious. Dioecious angiosperms have the advantage of reducing inbreeding but the disadvantage of relying on animal vectors, typically insects, capable of transporting pollen from male plants to female plants (Willmer 2011). Flowers on *P. fasciculata* are nearly sessile on stems and small, being 2 mm long with 2–3 mm long, white petals (Benson and Darrow 1954, Munz 1974). Fruits in *Prunus* usually contain one seed (Munz 1974), suggesting that female flowers on *P. fasciculata* may be completely pollinated by a single pollen grain.

Few studies have examined the pollination of uncultivated Rosaceae in North America. Most information regarding pollination is limited to insect taxonomy studies that list species of flowers visited by a particular insect (e.g., Ribble 1968, La Berge 1977, Hurd 1979, La Berge and Thorp 2005). Flowers on cloudberry (*Rubus chamaemorus* L.)—a dioecious, perennial herb in Rosaceae found in subarctic Canada—are visited by a variety of insects but pollinated primarily by bees in Apidae and Halictidae and flies in Muscidae and Syrphidae (Brown and McNeil 2009). Incongruously, the single study (Pendleton and Pendleton 1998) that examined pollination of a North American desert shrub in Rosaceae (*Coleogyne ramosissima* Torrey) found the plant’s perfect flowers to be self-incompatible but wind-pollinated. *Prunus fasciculata* provides an opportunity to study the pollination of a dioecious plant inhabiting the Mojave Desert, a region that produces a unique and diverse array of potential insect-pollinators.

I investigated the pollination of desert almond by examining pollen loads on insects visiting female flowers at one locality in southern Nevada. The following questions were posed: (1) What species of insects carry *P. fasciculata* pollen to female flowers? (2) Do amounts of *P. fasciculata* pollen on insects differ among insect taxa? (3) Do proportions of pollen loads consisting of *P. fasciculata* pollen, estimations of flower constancies, or plant specificities differ among insect taxa? (4) Which taxa of insects are most likely to pollinate *P. fasciculata* female flowers?

METHODS

I conducted the study at the southern end of the Iretaba Peaks in the Eldorado Mountains, 4.4 km northeast of Searchlight, Clark County, Nevada. I collected insects from *P. fasciculata* shrubs (35.49° N, 114.88° W; elevation 1096 m) growing in a southward-draining wash surrounded by outcroppings of weathered granite. Predominant plants surrounding the shrubs were *Yucca brevifolia* Engelmann and *Yucca schidigera* Roezler ex Ortgies (Agavaceae), *Larrea tridentata* (DC) Coville (Zygophyllaceae), *Salvia mohavensis* Greene (Lamiaceae), *Hymenoclea salsola* Torrey & Gray (Asteraceae), and *Baileya pleniradiata* Harvey & Gray (Asteraceae). Maximum air temperatures at Searchlight during 1913–2013 averaged 12 °C in January and 36 °C in July (DRI 2014). Yearly rainfall during the same period averaged 196 mm and occurred mostly during December–March from regional storms and July–September from convective storms (DRI 2014). Rainfall at Searchlight totaled 173 mm, mostly from summer storms, from 1 March 2013 to 1 March 2014 (CCRFCD 2014).

I flagged desert almond plants at the study site as male or female by examining flowers with a hand lens on 9 March 2014. Male plants were observed producing flowers with only stamens (Fig. 1a), and female plants were observed producing flowers with only pistils (Fig. 1c). Male flowers were also recognized by being slightly larger (4–5 mm diameter calyx) than female flowers (3–4 mm diameter calyx). I selected 3 female shrubs approximately 2 × 2 × 2 m in size for sampling insects. Two shrubs grew in a clump with 2 female plants and 1 male plant, each approximately 1 × 1 × 1 m in size. The third shrub grew 3 m away next to a *Y. schidigera*. These 6 plants were completely flowering, with their entire canopies producing abundant flowers. Other, larger male and female *P. fasciculata* that were partially flowering, with approximately 25% of their canopies producing flowers, grew within 25 m of the sampled plants. I revisited flagged plants on 15 and 17 April and 17 May 2014 while they produced fruits. Fruits were abundant on female plants, with those sampled for insects estimated to support >1000 fruits (approx. 10 fruits per stem). The adjacent male plant supported <20 fruits.

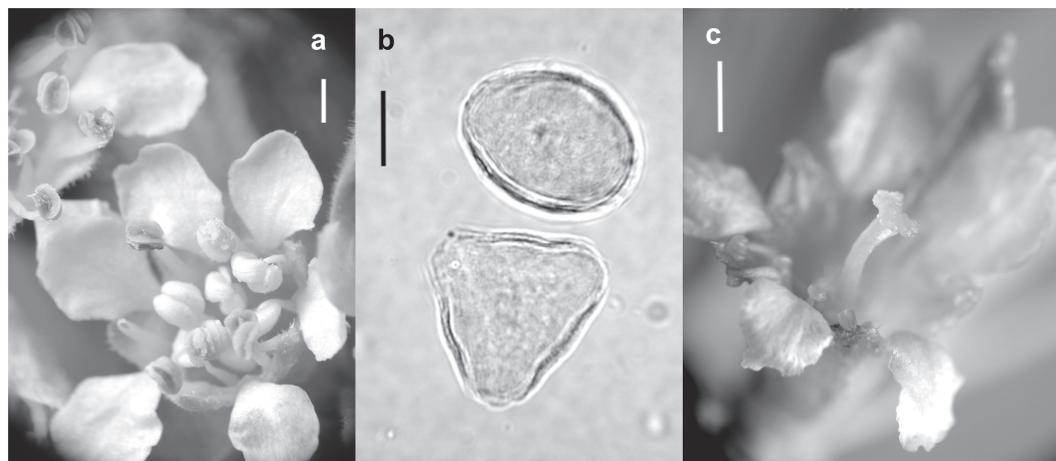


Fig. 1. *Prunus fasciculata* near Searchlight, southern Nevada, on 14 March 2014: a, male flower; b, photomicrograph of pollen grains from male flower in polar (bottom) and equatorial view; c, female flower. Scale bars in a and c are 1 mm; scale bar in b is 10 μm .

Fruits were absent on other plants flagged as male. I deposited a pressing (no. 63552) of *P. fasciculata* with female flowers at the Wesley E. Niles Herbarium, University of Nevada, Las Vegas.

Prunus fasciculata pollen was examined by being mounted in polyvinyl alcohol (Dafni 1992). I collected male flowers into 70% EtOH on 9 and 16 March 2014 and shook pollen from flowers. Alcohol containing pollen was centrifuged at 3400 revolutions \cdot min⁻¹ for 3 min, and the alcohol was drawn off and replaced with 3.5 mL of water. I poured the water and suspended pollen into a teflon evaporating dish with a 5.5 cm diameter bottom. I added hydrolyzed polyvinyl alcohol (1 mL of 12% solution) to the water, vortexed it, and dried it for 2 h at 55 $^{\circ}\text{C}$. I measured pollen grains embedded in the resulting circular, clear-plastic film with an eyepiece reticle, photographed them through a 100X oil-immersion objective lowered onto the film, and described them following Faegri et al. (1989).

I sampled the 3 female plants at the study site for insects on 9, 14, and 16 March 2014. I individually aspirated 40 arbitrarily selected insects from flowers on a single plant on each date. I aspirated insects into a 125-mL plastic, screw-capped flask containing an open, 4-dram glass vial that was half-filled with 70% EtOH. Each insect was aspirated through a 10 cm long tube, with a 5 mm

diameter opening, to the top of the flask where it dropped into the alcohol. The vial was then removed, capped, and replaced. I collected insects for 73–94 min on each date between 11:54 and 15:28 Pacific Daylight Time. Air temperature during collections was 19–28 $^{\circ}\text{C}$, relative humidity was 24–27%, cloud cover was 0–60%, and wind speed was <15 km \cdot h⁻¹. Desert almond at the site had ceased flowering by 20 March 2014.

I extracted pollen from aspirated insects by vortexing each vial for 30 s. Insects were removed from the alcohol and pinned. Pollen suspended in all of the alcohol was mounted in polyvinyl alcohol as described above. Half of the circular film was sampled for pollen. I pressed the film between 2 microscope slides, with the top slide marked with 2 lines delineating a 25 \times 48-mm rectangle that approximated half of the film's area. I scanned this area at 40X with a compound microscope by moving the stacked slides with a mechanical stage and recognized pollen grains by their yellow color and symmetrical shape. I classified pollen as *P. fasciculata*, or as differing from *P. fasciculata*, and counted pollen grains in each class. Pollen that could not be distinguished as *P. fasciculata* at 40X was viewed at 100X or 200X. I also described predominant pollen other than *P. fasciculata* following Faegri et al. (1989). I calculated the proportion of each specimen's pollen load that consisted of *P. fasciculata* pollen.

I identified insects collected from female flowers on desert almond. I only identified insects with >1 specimen in a species and females of bees (Hymenoptera: Apoidea), because male bees were rare (4 specimens aspirated) and typically carry less pollen. I keyed Diptera to genus with Hall (1981) for Bombyliidae, Vockeroth and Thompson (1987) for Syrphidae, Shewell (1987) for Calliphoridae, and Wood (1987) for Tachinidae. Species within genera were determined by matching specimens with those at the Entomology Research Museum at the University of California, Riverside (UCRC). I also used the species descriptions in Cole (1969) to identify flies. Andrenidae were keyed to *Andrena* with Michener (2000) and to subgenus with Michener's modification of La Berge (1985). Species in subgenus *Thysandrena* were identified with La Berge (1977) and compared with specimens at UCRC. I was unable to identify a species in subgenus *Derandrena* with Ribble (1968) and instead found its closest match among the *Andrena* species at UCRC. I was also unable to identify a species of subgenus *Onagrاندrena* by using the key in La Berge and Thorp (2005) or by comparing the specimens with *Andrena* at UCRC. Vouchers of flies and bees (443657–443681) were deposited at UCRC.

Desert almond pollen loads were compared among higher taxa of insect species. Numbers of *P. fasciculata* pollen grains, and proportions of pollen loads consisting of *P. fasciculata* pollen, were compared among insect families with a one-way analysis of variance (ANOVA in Systat version 10.2, Chicago, IL). I normalized residuals from each analysis by transforming numbers of pollen grains $\log(Y + 1)$ and proportions of conspecific pollen $2 \arcsin(Y^{1/2})$. Transformed proportions of conspecific pollen were also weighted by $1/s^2$ in each family to balance unequal variances among families due to unequal pollen loads (Neter et al. 1996). Following each analysis, variation among families was decomposed into independent contrasts (Neter et al. 1996) in ANOVA that compared taxonomic groups. I grouped families following the classification in Triplehorn and Johnson (2005). Reported means of numbers of *P. fasciculata* pollen and proportions of conspecific pollen on species and higher taxa were back-transformed.

RESULTS

Pollen grains from desert almond were tricolpate. Pollen grain shape was subangular with flat corners in polar view and oblate (longitudinally compressed) in equatorial view (Fig. 1b). Dimensions of pollen grains ($n = 10$) averaged $28 \mu\text{m}$ (range $25\text{--}30 \mu\text{m}$) from corner to opposite side in polar view and 21 ($20\text{--}23$) $\mu\text{m} \times 28$ ($23\text{--}33$) μm in equatorial view. Pollen grains in both views exhibited exines with 2 distinct layers. Most pollen grains differing from *P. fasciculata* were furrowed and prolate-rhomboidal, with the polar axis 3 times longer than the equatorial axis, or spherical with an irregular exine.

Thirteen species of insects in 8 genera and 5 families of Diptera and Hymenoptera, all Apoidea, were collected from female flowers on desert almond (Fig. 2). Flies were more frequently aspirated ($n = 65$) than bees ($n = 38$). Most flies aspirated were in 4 genera of Tachinidae ($n = 25$) followed by 2 species of Syrphidae in *Copestylum* ($n = 21$). All Hymenoptera were *Andrena* bees in Andrenidae. The most frequently aspirated *Andrena* was the species keyed to subgenus *Derandrena*, and specimens most resembled *Andrena californiensis* Ribble at UCRC. Specimens from *P. fasciculata* flowers primarily differed from *A. californiensis* at UCRC by the first transverse cubital vein (first submarginal crossvein) meeting the marginal cell further from the pterostigma and by the fewer hairs along the anterior margin of the propodeal corbicula. The known range of *A. californiensis*, restricted to the western half of central and southern California (Ribble 1968), also does not include southern Nevada.

Numbers of *P. fasciculata* pollen grains and their proportions of pollen loads on insects varied greatly among species (Fig. 2). Mean numbers of pollen grains in half of the pollen load ranged from 2.3 grains on the tachinid *Deopalpus contiguus* (Reinhard) to 39.4 grains on the andrenid *Andrena* sp. near *californiensis*. Mean proportions of pollen loads consisting of *P. fasciculata* pollen ranged from 14.0% on the tachinid *Phasia nigra* (Brooks) to 94.6% on *Andrena* sp. near *californiensis*. Conspecific pollen was absent on 4 specimens representing different species: *D. contiguus*, *P. nigra*, *Andrena* sp. near *californiensis*, and *Calliphora latifrons* Hough in Calliphoridae.

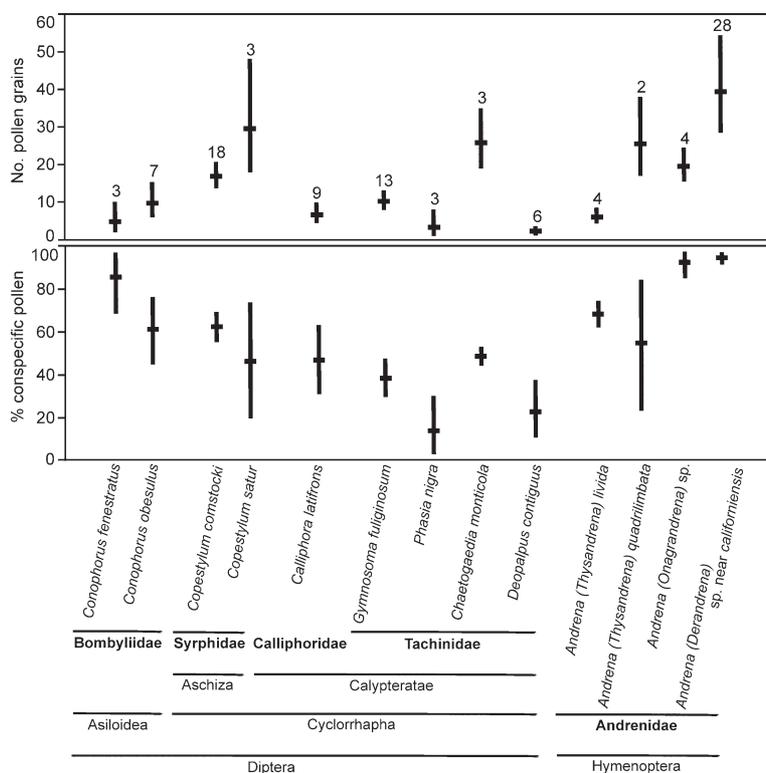


Fig. 2. Mean (\pm SE) numbers of *Prunus fasciculata* pollen grains (upper graph) and their percentages of pollen loads (lower graph) in half of pollen sampled on insects from *P. fasciculata* female flowers in southern Nevada during March 2014. Insect classification is shown along the x-axis, with families in bold and subgenera of *Andrena* (all females) in parentheses. Numbers of pollen grains were back-transformed from counts transformed $\log(Y + 1)$. Percentages of pollen loads were back-transformed from proportions transformed $2 \arcsin(Y^{1/2})$. Numbers of specimens are given in the upper graph.

Amounts of *P. fasciculata* pollen in half of the pollen load on insects differed between taxonomic groups of families and between species within families (Fig. 2). Mean numbers of conspecific pollen differed between orders (Table 1) by being higher on Hymenoptera (29.6 grains) than on Diptera (9.4 grains). Abundances of conspecific pollen on bees were highest on *Andrena* sp. near *californiensis* in *Derandrena*, intermediate on *Andrena quadrilimbata* La Berge and the *Andrena* species in *Onagrarendra*, and lowest on *Andrena livida* La Berge. Among flies, mean numbers of *P. fasciculata* pollen did not differ (Table 1) between Bombyliidae (7.9 grains) and other families in Cyclorrhapha (11.1 grains). Conspecific pollen loads were also similar on the 2 bombyliids collected, *Conophorus fenestratus* (Osten Sacken) and *Conophorus obesulus* (Loew). Mean numbers of *P. fasciculata* pollen were higher (Table 1) on Syrphidae in Aschiza

(18.3 grains), characterized by lacking frontal sutures, than on Calliphoridae and Tachinidae in Calypteratae (7.2 grains), which possess frontal sutures and calypters. The 2 syrphids examined—*Copestylum comstocki* (Williston) and *Copestylum satur* (Osten Sacken)—held similar amounts of conspecific pollen. Mean numbers of *P. fasciculata* pollen did not differ (Table 1) between the single calliphorid species, *C. latifrons* (6.6 grains), and the 4 tachinid species (7.2 grains). Within Tachinidae, *Chaetogaedia monticola* (Bigot) held more conspecific pollen than *P. nigra*, *D. contiguus*, or *Gymnosoma fuliginosum* Robineau-Desvoidy.

Proportions of pollen loads consisting of *P. fasciculata* pollen (Fig. 2) differed between Diptera and Hymenoptera (Table 1). Proportions of conspecific pollen averaged 91.4% on bees and 49.1% on flies. Among *Andrena* bees, those in *Onagrarendra* and the species near *californiensis* in *Derandrena* carried higher

TABLE 1. Taxonomic comparisons of numbers of *Prunus fasciculata* pollen grains and their proportions of pollen loads in half of pollen sampled on insects from *P. fasciculata* female flowers in southern Nevada during March 2014.

Taxonomic comparison ^a	No. pollen grains ^b		% conspecific pollen ^c	
	<i>F</i> ^d	<i>P</i>	<i>F</i> ^d	<i>P</i>
Hymenoptera (Andrenidae) (38) vs. Diptera (65)	17.5	<0.001	32.7	<0.001
Diptera: Asiloidea (Bombyliidae) (10) vs. Cyclorhapha (55)	0.17	0.68	2.56	0.11
Cyclorhapha: Aschiza (Syrphidae) (21) vs. Calypteratae (34)	6.06	0.016	3.28	0.073
Calypteratae: Calliphoridae (9) vs. Tachinidae (25)	0.03	0.84	0.71	0.40

^aANOVA independent contrast; numbers in parentheses are sample sizes.

^bTransformed log ($Y + 1$).

^cProportions transformed $2 \arcsin (Y^{1/2})$ and weighted by $1/s^2$ in each family.

^ddf = 1, 98.

proportions of *P. fasciculata* pollen than *A. livida* and *A. quadrilimbata*. Proportions of *P. fasciculata* pollen on flies did not differ between taxonomic groups of families (Table 1). The greatest difference between groups of flies occurred between Syrphidae and the 2 families of Calypteratae (Table 1). Mean proportions of conspecific pollen averaged 60.2% on Syrphidae and 36.2% on Calliphoridae and Tachinidae. Among tachinid flies, proportions of *P. fasciculata* pollen were higher on *G. fuliginosum* and *C. monticola* than on *P. nigra* and *D. contiguus*.

DISCUSSION

Prunus fasciculata at the study site was nearly dioecious. The few fruits produced by the plant flagged as male while in full flower indicates some flowers were perfect, or imperfect and female. Other shrubs classified as male, but partially flowering, lacked fruit and likely supported only male flowers. The abundant fruit on shrubs flagged as female suggests the plants produced mostly, or entirely, female flowers. Dioecious flowering in *P. fasciculata* requires pollinators to transport pollen from male plants to female plants. Insect pollinators of *P. fasciculata* would need to emerge early in the spring coincident with flowering, visit male flowers and acquire pollen from anthers, move to a different plant, and visit female flowers and deposit pollen on stigmas.

Movement by flower-visiting insects between sexes of *P. fasciculata* plants did not appear as a barrier to pollination. Almost all (96%) of the bees and flies aspirated from female flowers carried pollen acquired from male flowers, and female plants became laden with fruit, suggesting a high proportion of fruit set. Segregation of insect species between plant sexes may have occurred, but may not have

been detected, because I did not collect insects on male plants. Transport of pollen from male to female plants was likely facilitated by the close proximity of plant sexes and the strong flight capabilities of the bees and flies collected. Male and female *P. fasciculata* shrubs also appeared to flower concurrently.

Findings from this study indicate that bees in *Andrena*, primarily the 2 species in subgenera *Onagrandrena* and *Derandrena*, may be important pollinators of desert almond in southern Nevada. Both species carried moderate to high numbers of *P. fasciculata* pollen that comprised most of the pollen load, indicating high flower constancies (or specificities) to the plant. *Andrena* sp. near *californiensis* in *Derandrena* was the smallest bee collected (6–7 mm long) but appeared to be the most abundant because it was more frequently aspirated. Female bees feed on pollen and nectar in flowers. They also collect large amounts of pollen that they carry on modified patches of hairs and feed to developing larvae (Willmer 2011). Larvae of *Andrena* develop within nests burrowed in the ground (Michener 2000). *Andrena* bees in *Onagrandrena* are generally considered to be oligolectic (specialized) on flowers in Onagraceae, primarily *Oenothera* and *Camissonia* (La Berge and Thorp 2005). Female *Onagrandrena* are large (10–15 mm long) for the genus and will also visit flowers on a range of other plant families. Although I have observed the annual *Camissonia brevipes* (Gray) Raven flowering abundantly around Searchlight, Nevada, during early March, flowers of the species were not observed at the study site when *Onagrandrena* bees were aspirated. *Andrena quadrilimbata* occurs mostly in the Mojave and western Sonoran deserts and has been collected on a variety of flowers (La Berge 1977),

corresponding with the moderate flower constancy to *P. fasciculata* in this study. *Andrena livida* may have carried less conspecific pollen on account of its polylectic behavior and wide distribution throughout the southwestern United States (La Berge 1977).

Flies may pollinate desert almond as effectively as bees. Many flies visit flowers and feed on pollen and nectar, but in contrast to bees, do not transport pollen to their larvae (Willmer 2011). Both *Copestylum* species in Syrphidae—*C. comstocki* and *C. satur*—carried high *P. fasciculata* pollen loads and exhibited moderate flower constancies to the plant. *Copestylum* flies were large (9–11 mm long) and rotund, had distinctively prolonged proboscises (similar to *Copestylum marginatum*, fig. 182 in Cole 1969), and were the most frequently aspirated insects after *Andrena* bees. Larvae of *Copestylum* (and the similar *Volucella*) feed on decaying plants, especially cacti (Essig 1926, Vockeroth and Thompson 1987), and cacti occur in the study area. A third, unexpected species of Diptera with moderate potential for pollinating desert almond was the tachinid *C. monticola*. The species carried amounts and proportions of *P. fasciculata* pollen similar to *Copestylum* but was less frequently collected. Tachinidae are parasites of arthropods, primarily insects (Wood 1987). *Chaetogaedia monticola* is a widespread tachinid (Cole 1969) that parasitizes larvae of Lepidoptera (Arnaud 1978). The species was the largest tachinid aspirated, being 10–11 mm in length, and its robust body was covered with the short setae and long bristles characteristic of the family.

Four other species of flies with diverse life histories may provide limited pollination to desert almond. The 2 bombyliid species in *Conophorus*—*C. fenestratus* and *C. obesulus*—the calliphorid *C. latifrons*, and the tachinid *G. fuliginosum*, appeared to be fairly abundant, carried low *P. fasciculata* pollen loads, and displayed moderate to high flower constancies. Life histories of Bombyliidae are poorly understood. Larval bombyliids are known to live in bee nests, eat insect larvae or eggs, or parasitize other insects, including Hymenoptera and Tachinidae (Essig 1926). Adults frequently extend their tubular mouthparts into flowers while hovering. Many larvae of Calliphoridae feed on mammal tissues, either as parasites beneath the skin of live animals

or on decomposing carcasses (Shewell 1987). Adult *G. fuliginosum* are widespread nectar feeders with distinctive round, orange abdomens (Cole 1969). Larvae of the species parasitize adult Heteroptera that feed on plants (Arnaud 1978).

The narrow distributions or larval diets of many of the insects collected on *P. fasciculata* flowers in southern Nevada suggest pollinators vary across the plant's geographic range. Widespread pollination would not be expected by *Andrena* bees with localized populations such as *Onagrandroidrena* (La Berge and Thorp 2005). Some flies with specialized diets, such as the dead cacti eaten by *Copestylum* larvae, may also have limited distributions. Other species of bees and flies would be expected to pollinate desert almond at other localities. Species of pollinators likely also vary between years because of changing availabilities of food for larvae and alternative flowers for adults. It is unclear how often *P. fasciculata* shrubs at a given locality produce flowers, especially the profuse flowers (and fruit) observed during this study.

The bees and flies transporting conspecific pollen to female flowers on desert almond shrubs resemble those that pollinate cloudberry (Brown and McNeil 2009). Although both plant species are dioecious, *R. chamaemorus* differs from *P. fasciculata* by producing fruits that contain multiple seeds. Pollination by Syrphidae followed by Halictidae was most effective in producing fruit, but not necessarily seed set, on cloudberry herbs. Halictid and andrenid bees have similar body forms and ground-nesting behaviors. Syrphid flies, and halictid or andrenid bees, appear to be important pollinators of both plants despite their different growth forms and environments.

Further differentiation among insect species in their abilities to pollinate *P. fasciculata* would require determining how they contact flowers and transfer pollen. Desert almond's small and shallow flowers would have prevented the collected species of flies and bees from entering the corolla. Acquisition and deposition of pollen would have instead been facilitated by the plant's exerted stamens and pistils, extending beyond the corolla (Fig. 1a, c). A variety of body parts could have contacted the exposed anthers and stigmas while flies and bees were feeding on the pollen of male flowers or the nectar of male and female

flowers. Rather than coevolving with a particular insect taxon, *P. fasciculata* appears to ensure pollination by exploiting the diversity of flies and bees produced by its Mojave Desert environment.

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