CONSPECIFIC POLLEN LOADS ON INSECTS VISITING FEMALE FLOWERS ON PARASITIC *PHORADENDRON CALIFORNICUM* (VISCACEAE)

William D. Wiesenborn¹

ABSTRACT.—Desert mistletoe, *Phoradendron californicum* (Viscaceae), is a dioecious parasitic plant that grows on woody legumes in the Mojave and Sonoran Deserts, produces minute flowers during winter, and is dispersed by birds defecating fruits. Pollination of desert mistletoe has not been examined despite the species' reliance on insects for transporting pollen from male to female plants. I investigated the pollination of *P. californicum* parasitizing *Acacia greggii* (Fabaceae) shrubs at 3 sites at different elevations in the Mojave Desert of southern Nevada during February 2015. I examined pollen from male flowers, aspirated insects landing on female flowers, and counted pollen grains in insect pollen loads. Desert mistletoe's tricolpate pollen differed from a previous description by being oblate instead of subprolate in equatorial view. Female flowers were visited by 13 species of Diptera in 10 genera and 6 families and 3 species of Hymenoptera in 3 families. Almost all (98.5%) of the pollen carried by insects was from desert mistletoe. Five species of phytophagous fruit flies in Tephritidae were frequently found on flowers, comprising 53% of the insects collected, but carried low amounts of *P. californicum* pollen. Two species of blow flies in Calliphoridae, both larval decomposers of animals, were also relatively abundant on flowers and carried moderate to high pollen loads. Flies in Syrphidae, 2 predators and 1 plant-decomposer, carried varying amounts of conspecific pollen. Conspecific pollen loads also varied on a species of native bee in Halictidae and on naturalized honey bees in Apidae. Desert mistletoe appears to be pollinated mostly by tephritids, due to their abundance on female flowers, and by calliphorids. Blow flies would be more likely than fruit flies to carry pollen between male and female plants on different host shrubs due to their larger size and stronger flight. Parasitic, dioecious *P. californicum* plants appear to rely on a web of mutualism between fruit-eating birds and flower-fertilizing insects.

RESUMEN.—El muérdago del desierto, *Phoradendron californicum* (Viscaceae), es una planta parásita dioica que crece en leguminosas leñosas en los Desiertos de Mojave y de Sonora. Esta planta produce flores diminutas durante el invierno y son dispersadas por aves que defecan las semillas. La polinización del muérdago del desierto no ha sido estudiada, a pesar de la dependencia a los insectos para transportar polen de plantas macho a plantas hembras. Estudié la polinización de *P. californicum* que parasita los arbustos *Acacia greggii* (Fabaceae) en tres sitios a diferentes elevaciones en el Desierto de Mojave al sur de Nevada, durante febrero del 2015. Examiné el polen de flores macho, insectos sucionados al aterrizar en flores hembras y conté los granos de polen en las cargas de polen de los insectos. El polen tricolpado del muérdago del desierto difirió de una descripción anterior por ser achatado en lugar de subprolado en vista ecuatorial. Las flores hembra fueron visitadas por 13 especies de dípteros (Diptera) en 10 géneros y 6 familias, y 3 especies de himenópteros (Hymenoptera) en 3 familias. Casi todo el polen (98.5%) llevado por los insectos pertenecía al muérdago del desierto. Encontré con frecuencia cinco especies de moscas de la fruta fitófagas en las flores, comprendiendo el 53% de los insectos colectados, pero llevaban cantidades bajas de polen de *P. californicum*. Dos especies de moscas verdes Calliphoridae, ambas descomponedoras de animales en etapa larval, fueron relativamente abundantes en las flores y transportaron tanto cargas moderadas como cargas grandes de polen. Las moscas Syrphidae, dos depredadoras y una descomponedora de plantas, transportaron cantidades variables de polen conespecífico. Las cargas de polen conespecífico también variaron en una especie de abeja nativa Halictidae y en abejas melíferas Apidae. El muérdago del desierto parece ser polinizado principalmente por los tefritidos, debido a su abundancia en flores hembras y califóridos. Las moscas verdes serían más propensas, que las moscas de la fruta, a transportar el polen entre plantas macho y plantas hembras en diferentes arbustos de refugio debido a su tamaño mayor y a su vuelo más firme. Las plantas parásitas dioicas *P. californicum*, parecen depender de una red de mutualismo entre aves que se alimentan de frutas e insectos fertilizadores de flores.

Phoradendron (Viscaceae) is a large genus of perennial plants called mistletoe that parasitize a wide variety of woody plants (Trelease 1916, Kuijt 2003). The genus includes 234 species found in the Americas from the northern United States to northern Argentina and from

eastern Pacific islands to throughout the Caribbean (Kuijt 2003). *Phoradendron* plants penetrate trunks or branches with their haustorium, a root-like structure that taps into host-plant xylem. Plants obtain water and other inorganic nutrients from their hosts and produce

¹E-mail: wwiesenborn@fastmail.fm

organic nutrients from photosynthesis in leaves and stems (Kuijt 1969, 2003). Insects and other invertebrates may feed and develop on mistletoe as observed in *Phoradendron tomentosum* Engelm (Whittaker 1984).

Flowers on *Phoradendron* (Kuijt 2003) are very small, typically around 1 mm in diameter, and unisexual. Male flowers are spherical with 3 or 4 petals that enclose an open space, and each petal supports a minute sessile anther. Female flowers are similar but contain a short style with an indistinct rounded or faintly bilobed stigma atop an inferior ovary. Both sexes of *Phoradendron* flowers contain a vestigial nectar gland described by Trelease (1916) as "apparently adapted to pollination by such short-tongued insects as flies and small bees."

Phoradendron californicum Nuttall, or desert mistletoe, is a dioecious species with scale-like leaves found in the Mojave and Sonoran Deserts of the southwestern United States and northwestern Mexico (Trelease 1916, Kuijt 2003). The species mainly parasitizes trees and shrubs in Fabaceae including *Acacia*, *Cercidium*, *Olneya*, and *Prosopis* (Hawksworth and Wiens 2002). Desert mistletoe grows to 2 m in diameter and contains hanging clusters of branching 0.4–1.0-m-long, grayish or reddish green stems (Hawksworth and Wiens 2002, Kuijt 2003). Flowers are borne on inflorescences, 5–25 mm long on male plants and 5–10 mm long on female plants, that branch oppositely along stems. Scanning electron micrographs of *P. californicum* pollen show tricolporate grains with a rounded-triangular shape in polar view and a subprolate shape in equatorial view (Kuijt 2003). Grains measure 31 μm along the polar axis and 24 μm across the equatorial axis. Flowering by *P. californicum* occurs during January–March (Hawksworth and Wiens 2002).

Desert mistletoe is an important food source for vertebrates. Fruits of *P. californicum* are eaten by a variety of birds, and one species, the Phainopepla (*Phainopepla nitens* [Passeriformes: Ptilonotidae]), is dependent on desert mistletoe fruits. Defecation of fruits on host plants disperses the plant, resulting in a mutualistic symbiosis between *P. californicum* and *P. nitens*. Preferential landings by birds on host plants that are already parasitized likely cause desert mistletoe plants to become aggregated (Larson 1996).

The unisexual flowers in *Phoradendron* require insects to transport pollen from male to female flowers. Dioecious flowering in *P. californicum* and many other species of mistletoe further requires insects to carry pollen from male to female plants. Studies on pollination in *Phoradendron* are lacking despite the genus's parasitic habit, unusually small flowers, myriad species, wide distribution, and importance to wildlife. Insect pollination in *P. californicum* is even more obscure due to its winter flowering. The only observation of the species' pollination has been by Kuijt (2003), who writes that flowers are, "very fragrant, on warm days attracting numerous insects in a season when few other local plants are in flower."

Pollination of *P. californicum* within the Mojave Desert in southern Nevada was investigated by examining pollen loads on insects visiting female flowers. I considered the following questions: (1) What species of insects carry *P. californicum* pollen to female flowers? (2) Do individuals of these species carry different amounts of *P. californicum* pollen? (3) How specific are insects to desert mistletoe flowers based on pollen loads? (4) Which taxa of insects are more likely to pollinate *P. californicum* female flowers?

METHODS

The study was conducted in the Eldorado Mountains along State Highway 165 near Nelson, Clark County, Nevada. Insects were collected from *P. californicum* plants parasitizing *Acacia greggii* A. Gray (Fabaceae) shrubs that grew within sand and gravel washes at 3 sites at different elevations. The lowest site (35.706° N, 114.786° W) was at an elevation of 643 m and supported mostly *A. greggii*, *Larrea tridentata* (DC) Coville (Zygophyllaceae), *Hymenoclea salsola* A. Gray (Asteraceae), and *Encelia farinosa* Torrey & A. Gray (Asteraceae). The middle site (35.702° N, 114.820° W) was 2.8 km west at an elevation of 871 m and dominated by *A. greggii*, *L. tridentata*, *H. salsola*, *Chilopsis linearis* (Cavanilles) (Bignoniaceae), and *Chrysothamnus* sp. (Asteraceae). The highest site (35.740° N, 114.839° W) was 4.4 km north of the middle site at an elevation of 1037 m and supported mostly *A. greggii*, *L. tridentata*, *Ephedra nevadensis* S. Watson (Ephedraceae), and *Prunus fasciculata* A. Gray (Rosaceae). Maximum air temperatures

Fig. 1. *Phoradendron californicum* on *Acacia greggii* near Nelson, southern Nevada, 5–9 February 2015: **a**, male flowers; **b**, pollen from male flowers in equatorial view (top) and polar view (bottom); **c**, female flowers, dark structures at centers are red styles; **d–e**, lateral views of dried *Eupodes volucris* female aspirated from female flower on 20 February 2015; **d**, head and proboscis; **e**, labellum at end of proboscis with pollen or other material attached to setae at lower left. Scale bars in panels **a**, **c**, and **d** are 1 mm; scale bar in panel **b** is 10 μ m; scale bar in panel **e** is 0.1 mm.

averaged 12 °C in January and 36 °C in July, and yearly rainfall averaged 196 mm, 27 km south at Searchlight during 1913–2013 (DRI 2015). Rainfall near Nelson totaled 115 mm during 2014 and 67 mm during December 2014 and January 2015 (CCRFCD 2015), the 2 months preceding the study.

Insects were collected from 2 female-flowering *P. californicum* plants (or clumps of plants) around 1 m in diameter on different *A. greggii* shrubs at each site. Each *A. greggii* shrub also supported at least one male-flowering *P. californicum* plant that was next to, or separate from, the sampled female plant. I collected insects from the same plants on 6 dates during

2–12 February 2015 at the lower site, 8 dates during 2–18 February 2015 at the middle site, and 7 dates during 9–20 February 2015 at the upper site. Male flowers (Fig. 1a) were open and producing pollen during collections. Insects on open, female flowers (Fig. 1c) were individually aspirated into a 125-mL plastic screw-capped flask containing a 4-dram glass vial with 4 mL of 70% EtOH. I aspirated each insect through a 4–13-cm-long tube with a 3-, 7-, or 10-mm-diameter opening (dependent on the size of the insect) to the top of the flask where it dropped into the alcohol. Insects were aspirated from each plant for 20–85 min on each date, for a total 31.5 h,

during 09:40–15:55 Pacific Standard Time. Air temperature during collections was 15–28 °C, relative humidity 24%–29%, cloud cover 0%–90%, and wind speed <10 km · h⁻¹. Plants other than *P. californicum* were not observed flowering except for a few distant *E. farinosa* plants and one nearby *Bebbia juncea* (Bentham) E. Greene (Asteraceae) plant at the lower site. A pressing (UNLV 64206) of a host shrub, a sampled female plant, and an adjacent male plant were deposited at the Wesley E. Niles Herbarium, University of Nevada, Las Vegas.

Desert mistletoe pollen was examined after mounting in polyvinyl alcohol (Dafni 1992). I collected male inflorescences at the middle site into 70% EtOH on 9 February 2015 and shook pollen from flowers. Alcohol containing pollen was centrifuged at 3400 revolutions · 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. Hydrolyzed polyvinyl alcohol (1 mL of 12% solution) was added to the water, vortexed, and dried 2 h at 55 °C. Pollen grains embedded in the resulting circular clear-plastic film were viewed in brightfield microscopy, measured with an eyepiece reticle at 40×, photographed through a 100× oil-immersion objective lowered onto the film, and described following Faegri et al. (1989).

Pollen on insects aspirated from female flowers was extracted, mounted, and examined. I added 4 mL of water to each collection vial and vortexed the vial for 30 s. All of the alcohol solution was drawn from the vial and its suspended pollen embedded in polyvinyl alcohol as described above. I mounted smaller insects such as fruit flies (Tephritidae) on points after drying in hexamethyldisilazane (HMDS) to prevent shrinkage (Brown 1993). Larger insects were pinned. One-quarter of each circular film was sampled for pollen. I pressed the film between 2 microscope slides with the top slide marked with 2 lines delineating a 24 × 25-mm rectangle. I scanned this area at 100× 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 counted pollen grains and categorized each as *P. californicum* or as differing from *P. californicum*. Pollen that could not be distinguished as *P. californicum* at 100× was viewed at 200×. High pollen loads on 3

of the 5 naturalized honey bees (*Apis mellifera* L. [Apidae]) I collected required pollen to be sampled differently. I scanned once across the film and multiplied the number of pollen grains by 14 (the typical number of scans) to estimate the pollen count in one-quarter of the film. Predominant pollen other than *P. californicum* on insects was also described following Faegri et al. (1989).

Insects collected on *P. californicum* were identified to the lowest taxonomic rank possible. I only identified insects with >1 specimen in a species. Diptera in Syrphidae, Anthomyiidae, Muscidae, Calliphoridae, and Sarcophagidae were keyed to genus with Vockeroth and Thompson (1987), Hockett (1987), Hockett and Vockeroth (1987), and Shewell (1987a), Shewell (1987b), respectively. Flies in Syrphidae, Muscidae, and Calliphoridae were further identified to species by comparing specimens with those of the genus at the Entomology Research Museum, University of California, Riverside. Species of Tephritidae were keyed with Foote et al. (1993) and checked against specimens at the museum. Species descriptions in Cole (1969) and Miranda et al. (2013) were also used to identify Diptera. For specimens of Hymenoptera, I keyed a species of Halictidae to subgenus with Michener (2000), and a species of Pteromalidae was identified to genus by R. Burks. Vouchers of insects (UCRC ENT 456-366–377, 456-432, 456-485–488, 456-801, 456-820, 456-893–894, 456-992) other than *A. mellifera* were deposited at the museum.

Desert mistletoe pollen loads were compared among insect species excluding *A. mellifera*. The first quartile (containing the lower 25% of observations), median, and third quartile (containing the lower 75% of observations) of the pollen counts from each species were calculated with Systat (version 10.2, Chicago, IL). I compared pollen counts among insect families with a one-way nonparametric ANOVA. Numbers of *P. californicum* pollen from insects were ranked and analyzed using ANOVA in Systat. Variation among families was decomposed into independent contrasts (Neter et al. 1996) in ANOVA that compared pollen counts between the taxonomic groups (Triplehorn and Johnson 2005) of Diptera and Hymenoptera, muscoid flies and Aschiza within Diptera, and Calyptratae and Acalyptratae within muscoid flies.

Fig. 2. Insects (excluding *Apis mellifera*) aspirated from female flowers on *Phoradendron californicum* parasitizing *Acacia greggii* near Nelson, southern Nevada, 2–20 February 2015; insect taxa along x-axis, with families in bold: a, numbers of aspirated insects with (closed bars) and without (open bars) *P. californicum* pollen in one-quarter of pollen load; b, numbers of *P. californicum* pollen grains in one-quarter of pollen load on each insect. Horizontal bars are medians. Vertical bars connect the first and third quartiles (= pollen counts if $n = 2$).

RESULTS

Pollen grains from desert mistletoe viewed in brightfield microscopy were tricolpate. Pollen-grain shape was semiangular with flat corners in polar view and oblate (longitudinally compressed) in equatorial view (Fig. 1b). Dimensions of pollen grains ($n = 10$) averaged $23\ \mu\text{m}$ (range $22\text{--}24\ \mu\text{m}$) from corner to opposite side in polar view and $18\ (18\text{--}21)\ \mu\text{m} \times 23\ (22\text{--}24)\ \mu\text{m}$ in equatorial view. Pollen grains in both views exhibited exines with 2 distinct layers.

I aspirated and identified 145 insects from *P. californicum* female flowers that included 13

species of Diptera in 10 genera and 6 families and 2 species of Hymenoptera in 2 families other than Apidae: *A. mellifera* (Fig. 2). Fruit flies in Tephritidae were most frequently collected ($n = 77$), with 5 species accounting for 53% of the insects aspirated. The most abundant insect aspirated from female flowers was the tephritid *Euarestoides acutangulus* (Thomson). Other tephritids collected in low numbers were *Trupanea actinobola* (Loew), *T. jonesi* Curran, *T. nigricornis* (Coquillett), and *T. pseudovicina* Hering. Blow flies (Calliphoridae) were the second-most-frequently aspirated insects ($n = 24$) and included 2 species: the

more abundant *Phormia regina* (Meigen) and the less abundant *Calliphora latifrons* Hough. Flower flies (Syrphidae) were third-most-frequently collected ($n = 22$). *Eupeodes volucris* Osten Sacken was the most abundant syrphid on flowers followed by *Copestylum marginatum* (Say) and *Pseudoscaeva diversifasciata* (Knab). A species of small (6–7 mm-long) bee in *Lasioglossum* (subgenus *Dialictus*) in Halictidae was the fourth-most-frequently aspirated insect followed by *A. mellifera*. All bees collected were females. Other species collected in low numbers were the flies *Blaesoxipha* sp. in Sarcophagidae, *Neomyia cornicina* (F.) in Muscidae, female *Delia* sp. in Anthomyiidae, and the parasitic wasp *Heteroschema* sp. in Pteromalidae.

Nearly all (98.5%) of the pollen sampled on insects was from *P. californicum*. Pollen totaling 106 grains from other plant species was found on 53 insects. Most pollen not resembling desert mistletoe was spherical and smaller, or prolate-rhomboidal and furrowed with the polar axis twice as long as the equatorial axis. Desert mistletoe pollen was found on 119 (82%) of the insects that landed on female flowers, and insects in only 4 species lacked conspecific pollen (Fig. 2). Pollen counts on insects with pollen, other than honey bees, varied from 1 grain on a *Heteroschema* wasp to 598 grains on a *C. marginatum* fly. Honey bees carried highly variable pollen loads ranging from 4 grains to an estimated 1.982×10^4 grains, with a median of 1372 grains in one-quarter of the pollen load.

Amounts of pollen in one-quarter of the pollen load differed greatly among insect species other than *A. mellifera* (Fig. 2). Amounts of *P. californicum* pollen on insects (n ; median, 1st–3rd quartiles) did not differ ($F_{1,125} = 2.86$, $P = 0.093$) between Diptera (130; 4.5, 1.0–33 grains) and Hymenoptera (10; 36.5, 3.0–70 grains). Within Hymenoptera, halictid bees in *Lasioglossum* carried more pollen than parasitic wasps in *Heteroschema*. Pollen loads in Diptera were higher ($F_{1,125} = 25.2$, $P < 0.001$) on insects in Aschiza (22; 35.5, 20–50 grains), which lack frontal sutures, than on muscoid flies (108; 2.0, 1.0–13 grains), which possess frontal sutures. Species of flies in Aschiza, all syrphids, carried varying pollen loads, with *C. marginatum* carrying the most followed by *P. diversifasciata* and *E. volucris*. Within muscoid flies, those in Calyptratae

with calypters (31; 63.0, 17–114 grains) carried more pollen ($F_{1,125} = 50.8$, $P < 0.001$) than those in Acalyptratae without calypters, all tephritids (77; 1.0, 0.0–3.0 grains). Pollen loads differed among families and species of Calyptratae, with the calliphorid *P. regina* carrying the most pollen followed by the muscid *N. cornicina*, the sarcophagid *Blaesoxipha* sp., the second calliphorid *C. latifrons*, and the anthomyiid *Delia* sp. Species of tephritids carried similar, low amounts of *P. californicum* pollen that totaled 185 grains.

DISCUSSION

The morphology of *P. californicum* pollen viewed in brightfield microscopy differed from the scanning electron micrographs and description in Kuijt (2003). Pollen grains in both descriptions were tricolporate or tricolpate and 23–24 μm across the equatorial axis. In contrast, the pollen described by Kuijt (2003) was 31 μm along the polar axis, producing a subprolate grain in equatorial view, whereas the pollen I sampled was 18 μm along the polar axis, producing an oblate grain in equatorial view. This difference in polar-axis length cannot be attributed to preservation technique, microscopy, or measurement error. Different morphologies likely resulted from variation in *P. californicum* pollen. Genetic specialization of *P. californicum* on different host-plant species has been hypothesized. Desert mistletoes growing on different host-plant species have different allozymes, plant morphologies, and flowering times, and seeds are more likely to establish plants if moved within host-plant species than between host-plant species (Glazner et al. 1988, Overton 1997).

Insects carrying *P. californicum* pollen to female flowers develop as larvae on a variety of foods. The abundant fruit flies collected on flowers are phytophagous and develop on a range of genera mostly within Asteraceae (Foote et al. 1993). One source of food for *E. acutangulus* is flowers on *H. salsola* (Goeden and Ricker 1986), a plant present at the study sites. The species is widespread across western North America (Foote et al. 1993). Fruit flies in *Trupanea* have varying distributions, with *T. pseudovicina* being limited to the Southwest and *T. actinobola* occurring across the United States (Foote et al. 1993). Blow fly

larvae decompose dead animals. Both species of blow flies collected are widespread in North America, with *P. regina* being especially abundant in the West and also occurring in Europe (Cole 1969). Larval diets differ among the Syrphidae aspirated from flowers (Cole 1969). *Eupeodes volucris* is a common species whose larvae eat aphids. Homoptera are likely also eaten by larvae of *P. diversifasciata* (formerly *Ocyptamus diversifasciata*). In contrast, larval *Copestylum* eat decomposing cacti, with *C. marginatum* being a common desert species (Cole 1969). Sarcophagid flies in *Blaesoxipha* include species that parasitize spiders, grasshoppers, or beetles (Cole 1969). Larval diets of Anthomyiidae are mostly unknown, though many species are phytophagous, whereas Muscidae are generally decomposers. Bees in *Lasioglossum* provision solitary or colonial nests of larvae with collected pollen (Michener 2000). The diverse subgenus *Dialictus* contains 340 species in the Western Hemisphere, and many species remain undescribed (Michener 2000). Pteromalidae are minute wasps that parasitize different life stages of insects.

The rarity of pollen on insects from plants other than *P. californicum* corresponded with the near absence of flowers on other species during February. Insects obtain pollen, and likely nectar, from desert mistletoe flowers when little else is available. Pollination of the plant is facilitated by the concentration of available insects on flowers. Not all species of *Phoradendron* flower during winter. Two of the species in California deserts flower during winter (December–March), and the other 3 flower during summer (June–September) (Hawksworth and Wiens 2002). Competition between plant species for pollinators is relatively low during summer and virtually absent during winter, allowing *P. californicum* to produce small flowers with minimal visual displays.

Pollen loads on insects visiting flowers generally corresponded with body size. Greatest pollen loads were on 2 of the largest species, *P. regina* and *C. marginatum*. Lowest pollen loads were on the smallest flies, tephritids, and on the minute wasps in *Heteroschema*. Two fly species contradicted this trend; the second calliphorid *C. latifrons* and the sarcophagid *Blaesoxipha* sp. both carried relatively low pollen loads despite larger body

sizes. Pollen loads would also be affected by insect morphology and behavior. Pollen on flies would be most likely picked up by the labella during feeding. Pollen, or other material, could be seen attached to the labellum of an *E. volucris* syrphid (Fig. 1d, e) that was dried in HMDS (without being vortexed) and photographed at different focal planes with CombineZP (Hadley 2013). Flies with large setose labella would be expected to transport more pollen between male and female flowers. Flies spending more time on male flowers, increasing their contact with stamens, would also be expected to collect more pollen. Pollen on female bees (e.g., *Lasioglossum* and *Apis*), is mostly transported among hairs on the hind legs (Michener 2000). The *Lasioglossum* females collected from *P. californicum* possessed long hairs on their hind tibiae and femora.

Desert mistletoe in southern Nevada appears to be pollinated by a variety of insects primarily composed of flies. The 2 families of insects most likely to pollinate the plant are Calliphoridae and Tephritidae. Blow flies, especially *P. regina*, were relatively abundant on female flowers and carried large numbers of conspecific pollen. Other dioecious, parasitic plants appear to be pollinated by Calliphoridae. Blow flies visit flowers on *Pilostyles* (Bellot and Renner 2013), a widespread genus of plants in Apodanthaceae with flowers similar to *P. californicum* that occurs in California deserts (Hawksworth and Wiens 2002). Blow flies on female desert mistletoe plants were also observed flying or walking from flower to flower. Tephritidae may significantly contribute to *P. californicum* pollination due to their high relative abundances. Although fruit flies carried less pollen than other families of flies, numbers of pollen grains transported may be adequate for fertilization given the single minute stigma in each desert mistletoe female flower. The 77 tephritids collected would have carried a total pollen load of 740 grains, estimated from the proportion of each pollen load sampled. The abundance of fruit flies on *P. californicum* flowers may be partly due to the fruit fly's life cycle. One of the species collected, *T. pseudovicina*, overwinters as long-lived adults (Goeden and Teerink 1998), possibly enabling flower visitation during late winter. A third family of insects, Syrphidae, may also be important pollinators of desert mistletoe. One species, *E. volucris*, was relatively abundant

with moderate pollen loads, whereas a second species, *C. marginatum*, was less abundant but with more pollen. Pollen loads on bees, such as *Lasioglossum* and especially *A. mellifera*, are less predictive of pollination capability. Only pollen on mouthparts, and not the hind legs, would be likely to contact the stigmas within the small flowers of *P. californicum*.

Phoradendron californicum is dependent on animals both for pollination and seed dispersal. Seed dispersal by birds would affect the proximity of male plants to female plants, especially if sexes occurred on the same or different host plants. Distances between male and female flowers may affect pollination efficiency. Large, strong-flying insects such as Calliphoridae would likely transport pollen between widely separated male and female plants. Small, weak-flying insects such as Tephritidae may only be able to carry pollen from male flowers to nearby female flowers. Visitation by fruit flies to female, but not male, flowers is suggested by the large number of *E. acutangulus* without pollen. Plant clumping by birds defecating fruits on parasitized host plants (Larson 1996) may facilitate pollination by insects, which in turn would increase fruit set and food production for birds. Successful pollination and reproduction of desert mistletoe would also increase availabilities of food (pollen and nectar) for adult insects during the plant's atypical winter-flowering period. *Phoradendron californicum* is an unusual parasite of North American desert trees and shrubs whose male and female plants appear to support a web of mutualism between birds and insects.

ACKNOWLEDGMENTS

I thank Doug Yanega and Serguei Triapitsyn at the Entomology Research Museum, University of California, Riverside, for making the collection available to me. I also appreciate the pteromalid identification by Roger Burks of the university's Entomology Department.

LITERATURE CITED

- BELLOT, S., AND S.S. RENNER. 2013. Pollination and mating systems of Apodanthaceae and the distribution of reproductive traits in parasitic angiosperms. *American Journal of Botany* 100:1083–1094.
- BROWN, B.V. 1993. A further chemical alternative to critical-point-drying for preparing small (or large) flies. *Fly Times* 11:10.
- [CCRFC] CLARK COUNTY REGIONAL FLOOD CONTROL DISTRICT. 2015. Rainfall data. Regional Flood Control District, Las Vegas, NV; [accessed 29 May 2015]. <http://www.ccrfcd.org/raingauges.htm>
- COLE, F.R. 1969. The flies of western North America. University of California Press, Berkeley, CA.
- DAFNI, A. 1992. Pollination ecology: a practical approach. IRL Press at Oxford University Press, Oxford, England, United Kingdom.
- [DRI] DESERT RESEARCH INSTITUTE. 2015. Cooperative climatological data summaries. Western Regional Climate Center, Reno, NV; [accessed 29 May 2015]. <http://www.wrcc.dri.edu/climatedata/climsum>
- FAEGRI, K., P.E. KALAND, AND K. KRZYWINSKI. 1989. Textbook of pollen analysis. 4th edition. John Wiley & Sons, New York, NY.
- FOOTE, R.H., F.L. BLANC, AND A.L. NORRBOOM. 1993. Handbook of the fruit flies (Diptera: Tephritidae) of America north of Mexico. Comstock Publishing Associates, Ithaca, NY.
- GLAZNER, J.T., B. DEVLIN, AND N.C. ELLSTRAND. 1988. Biochemical and morphological evidence for host race evolution in desert mistletoe, *Phoradendron californicum* (Viscaceae). *Plant Systematics and Evolution* 161:13–21.
- GOEDEN, R.D., AND D.W. RICKER. 1986. Phytophagous insect fauna of the desert shrub *Hymenoclea salsola* in southern California. *Annals of the Entomological Society of America* 79:39–47.
- GOEDEN, R.D., AND J.A. TEERINK. 1998. Life history and description of immature stages of *Trupanea pseudovicina* Hering (Diptera: Tephritidae) on *Porophyllum gracile* Benth in southern California. *Proceedings of the Entomological Society of Washington* 100:361–372.
- HADLEY, A. 2013. CombineZP. [Accessed 29 May 2015]. <http://www.hadleyweb.pwp.blueyonder.co.uk>
- HAWKSWORTH, F.G., AND D. WIENS. 2002. Viscaceae, mistletoe family. Pages 513–514 in B.G. Baldwin, S. Boyd, B.J. Ertter, R.W. Patterson, T.J. Rosatti, and D.H. Wilken, editors, *The Jepson Desert Manual*. University of California Press, Berkeley, CA.
- HUCKETT, H.C. 1987. 104. Anthomyiidae. Pages 1099–1114 in J.F. McAlpine, editor, *Manual of Nearctic Diptera*. Volume 2. Agriculture Canada Monograph No. 28, Canadian Government Publishing Centre, Quebec, Canada.
- HUCKETT, H.C., AND J.R. VOCKEROTH. 1987. 105. Muscidae. Pages 1115–1131 in J.F. McAlpine, editor, *Manual of Nearctic Diptera*. Volume 2. Agriculture Canada Monograph No. 28, Canadian Government Publishing Centre, Quebec, Canada.
- KUIJT, J. 1969. The biology of parasitic flowering plants. University of California Press, Berkeley, CA.
- KUIJT, J. 2003. Monograph of *Phoradendron* (Viscaceae). *Systematic Botany Monographs* 66:1–643.
- LARSON, D.L. 1996. Seed dispersal by specialist versus generalist foragers: the plant's perspective. *Oikos* 76:113–120.
- MICHENER, C.D. 2000. The bees of the world. Johns Hopkins University Press, Baltimore, MD.
- MIRANDA, G.F.G., A.D. YOUNG, M.M. LOCKE, S.A. MARSHALL, J.H. SKEVINGTON, AND F.C. THOMPSON. 2013. Key to the genera of Nearctic Syrphidae. *Canadian Journal of Arthropod Identification* 23:1–351.
- NETER, J., M.H. KUTNER, C.J. NACHTSHEIM, AND W. WASSERMAN. 1996. Applied linear statistical models. 4th edition. WCD McGraw-Hill, Boston, MA.

- OVERTON, J.MCC. 1997. Host specialization and partial reproductive isolation in desert mistletoe (*Phoradendron californicum*). *Southwestern Naturalist* 42:201–209.
- SHEWELL, G.E. 1987a. 106, Calliphoridae. Pages 1133–1145 in J.F. McAlpine, editor, *Manual of Nearctic Diptera*. Volume 2. Agriculture Canada Monograph No. 28, Canadian Government Publishing Centre, Quebec, Canada.
- SHEWELL, G.E. 1987b. 108, Sarcophagidae. Pages 1159–1186 in J.F. McAlpine, editor, *Manual of Nearctic Diptera*. Volume 2. Agriculture Canada Monograph No. 28, Canadian Government Publishing Centre, Quebec, Canada.
- TRELEASE, W. 1916. The genus *Phoradendron*: a monographic revision. University of Illinois, Urbana, IL.
- TRIPLEHORN, C.A., AND N.F. JOHNSON. 2005. Borror and DeLong's introduction to the study of insects. 7th edition. Thomson Brooks/Cole, Belmont, CA.
- VOCKEROTH, J.R., AND F.C. THOMPSON. 1987. 52, Syrphidae. Pages 713–743 in J.F. McAlpine, editor, *Manual of Nearctic Diptera*. Volume 2. Agriculture Canada Monograph No. 28, Canadian Government Publishing Centre, Quebec, Canada.
- WHITTAKER, P.L. 1984. The insect fauna of mistletoe (*Phoradendron tomentosum*, Loranthaceae) in southern Texas. *Southwestern Naturalist* 29:435–444.

Received 10 June 2015

Accepted 4 November 2015