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The floral hosts and distribution of a supposed creosote bush specialist, *Colletes stephensi* Timberlake (Hymenoptera: Colletidae)

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Abstract. *Colletes stephensi* Timberlake is thought to be a narrow oligolege of creosote bush, *Larrea tridentata* (DC.) Coville (Zygophyllaceae) with limited distribution in the Sonoran Desert of the western United States. Based on appraisal of museum specimens and field surveys from 1999 to 2001 on 21 sand dunes, we found *C. stephensi* to be a much more widely distributed psammophile of the Sonoran, Mojave, and Great Basin Deserts that utilizes two unrelated plant pollen sources, *Larrea* Cav. and *Psoralea* Rydb. (Fabaceae). The geologic history of the region suggests a potential host shift from the more ancient occupant, *Psoralea*, to the Neogene colonizer, *Larrea*.

INTRODUCTION

Many insects, from herbivores (Bernays & Chapman, 1994) to flower visitors (Wcislo & Cane, 1996) display host plant specialization. Bees are commonly presented as being flower constant, *i.e.*, collecting pollen from a select subset of many available and potentially valuable pollen sources (Chittka *et al.*, 1999), individuals of a species, but not the species as a whole, consistently visiting a single flower species. In contrast some species exhibit a narrow dietary breadth. These are often referred to as oligolectic (specialist) bees, defined in Linsley (1958) as species in which “individual members throughout the range of the population, and in the presence of other pollen sources, consistently and regularly collect pollen from a single plant species or a group of related plant species, turning to other sources, if at all, only in the face of a local absence of the pollen.” More recently, the concept of oligolecty has been refined by Cane & Sipes

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(2006) to accommodate bee species that consistently utilize a few unrelated plant genera (eclectic oligolecty) while those utilizing a single plant genus are termed narrowly oligolectic. Among bee pollinators, the specialist habit is thought to be especially common in xeric communities such as the hot deserts of the American Southwest.

Larrea tridentata (DC.) Coville (Zygophyllaceae), a shrub common in America's hot deserts, provides resources for many species of desert bees, 22 of which are presumed narrowly oligolectic on its pollen (Hurd & Linsley, 1975). Few other plants support such a large number of specialists. Because of this, the guild of *Larrea* bees has been used in several studies of oligolecty among desert solitary bees (Hurd & Linsley, 1975; Minckley *et al.*, 1999, 2000; Cane *et al.*, 2005, 2006). The solitary bee, *Colletes stephensi* Timberlake, has consistently been included in this guild of specialists.

Colletes stephensi is an uncommon bee. Unknown at the time of the revision of North American *Colletes* Latreille (Stephen, 1954), it was subsequently described (Timberlake, 1958) for a species found in large numbers on *Larrea* Cav. and at adjacent nest sites in the spring of 1958 on small sand dunes located 18 miles (29 km) west of Blythe, near Hopkins Well, Riverside County, California. The only other location known at the time of the original description was to the west, near Indio in California's Coachella Valley (Timberlake, 1958). Hurd & Powell (1958) studied the nesting biology at the Hopkins Well site. They found the species to be crepuscular and to nest gregariously at depths up to, and sometimes exceeding, 130 cm in the sand and underlying clay pack. Cell provisions taken from excavated nests were composed wholly of *Larrea* pollen.

Colletes stephensi has long remained an enigmatic bee. No additional populations were found in two subsequent intensive studies. Dawn to dusk surveys of the bees of creosote bush conducted across the Mojave, Sonoran, and Chihuahuan Deserts of North America from 1972 through 1974 (Hurd & Linsley, 1975) failed to detect it beyond the original Hopkins Well site. A subsequent, similarly broad sampling effort across these three deserts in 1993–1995 (Minckley *et al.*, 1999) also found it only at Hopkins Well. Based on what was known, *C. stephensi* has been widely regarded as a *Larrea* oligolecte (Hurd & Linsley, 1975; Simpson *et al.*, 1977; Hurd, 1979; Moldenke, 1979; Minckley *et al.*, 1999, 2000).

Evidence suggesting that *C. stephensi* might not be a creosote specialist, nor endemic to the hot deserts was hidden in a single entry within a checklist of the aculeate Hymenoptera of Sand Mountain (Rust *et al.*, 1983, as *C. "stephani"*), an isolated sand dune system in the Great Basin cold desert 160 km north of the most northerly limit of *Larrea*, and begged the question whether additional populations existed in the intervening region. Here we present the results of a focused exploration of the distribution and plant hosts of *C. stephensi*.

MATERIAL AND METHODS

Bee collections with major holdings from the western deserts were searched for unidentified material of *C. stephensi*. Of twelve collections visited, specimens were found in the following five collections (curators in parentheses): DVNP, Death Valley National Park, Furnace Creek, California (B. Davenport); BBSL, U.S. National Pollinating Insects Collection, USDA-ARS Bee Biology and Systematic Laboratory, Logan, Utah; WFBM, W.F. Barr Entomological Collection, University of Idaho, Moscow, Idaho (F. Merikel); CSCA, California State Collection of Arthropods, Sacramento, California (C. Bellamy, M. Wasbauer); CAS, California Academy of Sciences, San Francisco, California (V. Lee, W. Pulawski).

Table 1. Dunes sampled, ordered from north to south. Italicized site names indicate collection sites where *Colletes stepheni* Timberlake was not found. GrBsn/Moj = Great Basin/Mojave transition zone.

Site name	Site location (decimal lat/long)	Drainage System	State	Desert
<i>Bruneau Dunes</i>	42.8984 -115.6953	Snake River Plain	ID	Great Basin
<i>Winnemucca Dunes</i>	41.1051 -117.7008	Desert Valley	NV	Great Basin
Sand Mountain	39.3086 -118.3961	Carson Sink	NV	Great Basin
Thorne Dunes	38.55206 -118.47342	Gabbs Valley	NV	Great Basin
Crescent Dunes	38.23481 -117.32839	Big Smokey Valley	NV	Great Basin
Marble Canyon Dunes	37.15067 -117.83073	Eureka Valley	CA	GrBsn/Moj
Eureka Dunes	37.0983 -117.67407	Eureka Valley	CA	GrBsn/Moj
Saline Dunes	36.76729 -117.86249	Saline Valley	CA	Mojave
Panamint Dunes	36.45777 -117.45271	Panamint Valley	CA	Mojave
Stovepipe Wells Dunes	36.61163 -117.13418	Death Valley	CA	Mojave
<i>Big Dune</i>	36.6497 -116.5833	Amargosa Valley	NV	Mojave
Ibex Dunes	35.69757 -116.36764	Death Valley	CA	Mojave
Buckwheat Wash Dunes	35.78196 -116.46102	Death Valley	CA	Mojave
<i>Dumont Dunes</i>	35.6943 -116.2097	Amargosa Valley	CA	Mojave
<i>China Lake Dunes</i>	35.7747 -117.4271	Indian Wells Valley	CA	Mojave
Kelso Dunes	34.89647 -115.72889	Mojave River	CA	Mojave
<i>Topoc Dunes</i>	34.72921 -114.49828	Colorado River	CA	Mojave
Hopkins Well Dunes	33.60565 -114.99783	Chuckwalla Valley	CA	Sonoran
Algodones Dunes	32.95555 -115.04825	Sand Hills	CA	Sonoran

Label data was captured for all specimens found and localities were subsequently georeferenced. Using this larger set of known locations, which suggested restriction to dunes, a set of dunes was selected that included dunes within the known range, and those north and south of their respective known limits in the Great Basin and western Sonoran Desert. Because one aspect of the study was to determine plant hosts, more intense sampling effort was focused on sand dunes in the region around the interface of the Mojave and Great Basin Deserts, which coincides with the boundary of *Larrea*, Death Valley and the Lahontan Drainage Systems. Sampling occurred during the springs of 1999–2001, each season beginning in early March in Death Valley, and extending to mid June in Great Basin localities. A total of 21 sand dunes were sampled (Table 1). In locations where populations of *C. stepheni* were expected, but not initially found (e.g., Dumont Dunes, Big Dune, and China Lake Dune), multiple collections were attempted during at least two of the three collecting seasons. Specimens were collected by one or more collectors with an insect net at flowers and at nesting sites when such sites were located. Bee collections were also frequently made 5–8 km from the dunes to determine if the association of this species with dunes is obligatory. All floral associations were recorded. Most specimens were collected directly into 100% EtOH or acetone to preserve genetic material. Where possible, additional voucher specimens were preserved dry and pinned, and pollen slides were made from the pol-

len loads of these specimens. Unfortunately, because the initial focus of the study was a phylogeographic analysis based on molecular data, not investigation of the floral relationships of *C. stephensi*, few female specimens with pollen loads were collected. None of the pinned females from the Great Basin and transition zone populations in Eureka Valley, California bear pollen loads. Pollen types were identified for all pollen loads and when there was more than one type of pollen present on a slide, a count of 100 pollen grains was made. Pollen identifications were verified by comparison with pollen taken from plants. Bee specimens from the field study are deposited in BBSL and DVNP.

RESULTS

Colletes stephensi was found to be much more widely distributed than previously thought. A total of 133 specimens of *C. stephensi* were found in collections, representing eight new locality records; all were on dunes. Field studies documented *C. stephensi* on 13 of the 21 dunes surveyed (see below).

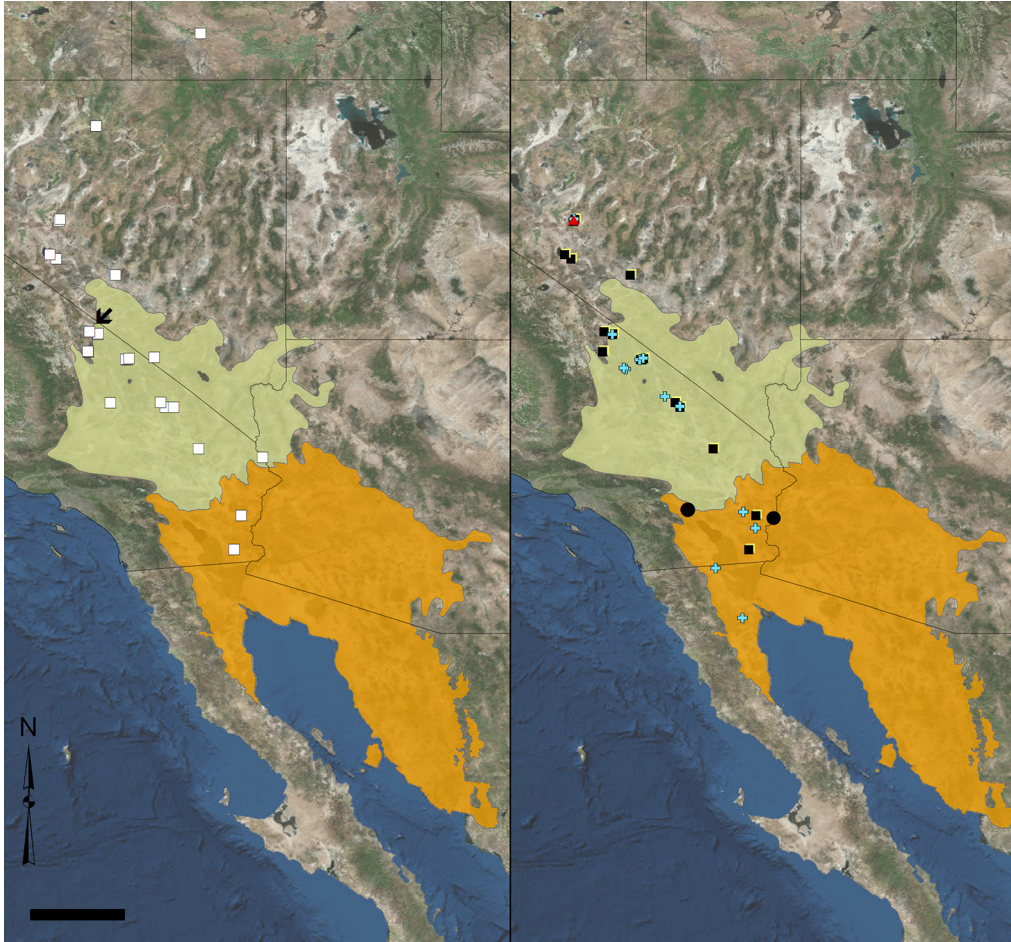
In contrast to this species' presumed geographical center in the Sonoran Desert (Fig. 1; Hurd & Linsley, 1975), this study shows that *C. stephensi* is commonly found on sand dunes in the eastern Mojave Desert as well as in the southwestern Great Basin Desert. Previously undiscovered populations in the Mojave Desert include Kelso Dunes, Stovepipe Wells Dunes, Buckwheat Wash Dunes, Panamint Dunes, and Saline Valley Dunes. Eureka Valley Dunes and Marble Canyon Dunes (also in Eureka Valley) represent new populations in the Great Basin/Mojave transition zone. Our findings verify the existence of the Sand Mountain population reported by Rust *et al.* (1983), and provide evidence of two additional Great Basin populations (Thorne Dune and Crescent Dune). Sand Mountain may represent the northern limit for *C. stephensi*. Collections made at Winnemucca Dunes and Bruneau Dunes, approximately 230 and 480 km north of Sand Mountain, respectively, failed to detect *C. stephensi*. Abundant bloom from diverse flowering plants was present at both these localities, but the absence of *Psorothamnus* Rydb. (Fabaceae), an apparent preferred plant host, was notable. Mojave Desert dunes where *C. stephensi* is apparently absent are: Big Dune, Dumont Dune, China Lake Dunes, and Topoc Dune.

This study confirms *C. stephensi* as an obligate psammophile. Collections made 5–8 km from sand dunes yielded no specimens of *C. stephensi*, supporting the species' assumed restriction to sandy substrates.

Colletes stephensi was commonly found in association with *L. tridentata* in the Sonoran Desert and most of the Mojave Desert. In contrast, all Great Basin and Eureka Valley collections of *C. stephensi* were taken on the fabaceous shrub *Psorothamnus polydenius* var. *polydenius* (Torrey ex S. Watson) Rydberg. This may not seem surprising for the three Great Basin localities since the dominant blooming shrub in all was *Psorothamnus* and *Larrea* were absent. But on the dunes in Eureka Valley, located in the Great Basin/Mojave transition zone, both *Larrea* and *Psorothamnus* were found blooming.

Curiously, despite the fact that *Larrea* are the dominant flowering shrub in the Eureka Valley, *C. stephensi* showed a definite preference for *Psorothamnus*. Focused collecting efforts on *Larrea* at the Eureka Dunes were largely futile. Only a lone male of *C. stephensi* was seen or collected at or near abundant blooming bushes of *Larrea* at this location. Instead, numerous males and females were observed patrolling and presumably foraging on a single blooming bush of *Psorothamnus* located no more than 30 m from the nearest blooming bush of *Larrea*. Collecting on the nearby Marble Canyon

Figure 1. Distribution of *Colletes stepheni* Timberlake. Left: Dunes sampled, arrow indicates Eureka Valley. Right: Known localities for *C. stepheni*. Black circles indicate distribution of *C. stepheni* when described (Timberlake, 1958); red triangle, documented Great Basin record (Rust *et al.*, 1983); blue plus signs, museum records; black squares, dunes sampled in present study where *C. stepheni* was detected. The hot deserts whose distribution coincides with that of *Larrea tridentata* (DC.) Coville are indicated by green (Mojave Desert) and orange (Sonoran Desert). Black bar = 500 km. World Imagery Source: Esri, DigitalGlobe, GeoEye, i-cubed, USDA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community.



Dunes produced similar results. Both *Psorothamnus* and *Larrea* in full flower were more abundant at this location and in closer proximity (<20 m) to one another. Despite focused collection efforts on both potential hosts, male and female *C. stepheni* were collected only on *Psorothamnus*. Unfortunately, because no female voucher specimens bearing pollen loads were collected from either Eureka Valley population, pollen loads from these populations could not be analyzed to confirm pollen preferences in this transitional location.

All other specimens of *C. stepheni* collected in this study were taken at *L. tridentata* or at nesting sites. Despite the presence of species of *Psorothamnus* on some Mojave and Sonoran Desert sand dunes (*e.g.*, Kelso Dunes, Algodones Dunes), no *C. stepheni* were collected on this potential alternate host. *Psorothamnus* were not specifically tar-

geted in these locations, however, as *C. stephensi*'s association with *Psorothamnus* was not known at the time of sampling.

Nine pollen slides were made from the pollen loads of bees from four populations in the Mojave and Sonoran Deserts. All were exclusively composed of pollen of *L. tridentata* with the exception of a single pollen load taken from a bee from the Hopkins Well Dune population. It consisted of two pollen types: *Larrea* represented at least 65% of the load, the other pollen type, likely a legume, was present at ~35%.

Collection data from this study combined with published records of *C. stephensi* suggest a distribution in the western portions of the deserts of the Southwest extending from Sand Mountain, Churchill County, Nevada in the north to northern Baja California, Mexico (Fig. 1). There are no known populations in the Chihuahuan Desert and the eastern portion of the Sonoran Desert, nor in the more xeric parts of cismontane California.

New records based on museum specimens: **MEXICO, Baja California:** 1♂, Mexicali, 23.9 km W, at km 23.9 on Mexican Hwy 2, 13 Apr 1979, D.B. Weissmann (CAS); 1♂, Sierra Pinta Dunes, 16 May 1979, D.B. Weissmann (CAS). **USA, California, Inyo Co.:** 1♀, Eureka Valley Dunes, 4 Jun 1979, D. Giuliani (CSCA); 1♂, Panamint Dunes, 27 Apr 1974 (BBSL); 1♂, Panamint Valley, the dunes east, 27 Apr 1974, E.L. Sleeper (CAS); 1♂, Stovepipe Wells, 4 mi E, sand dunes, 11 Apr 1966, D.L. Coates, R.E. Morel (BBSL); 2♂♂, Stovepipe Wells, 4 mi E, sand dunes, 11 Apr 1966, D.L. Coates, R.E. Morel (WFBM); 1♂, 7♀♀, Stovepipe Wells, Death Valley, 24 Apr 1964, A.R. Gittins (WFBM); 1♂, 3♀♀, Stovepipe Wells, Death Valley, 24 Apr 1964, A.R. Gittins (BBSL); 1♂, 2♀♀, Stovepipe Wells, Death Valley, 24 Apr 1964, W.F. Barr, *Larrea tridentata* (WFBM); 1♀, Stovepipe Wells, Death Valley, 24 Apr 1964, W.F. Barr, *Larrea tridentata* (BBSL). **Riverside Co.:** 1♂, Palen Dunes, 27 Apr 1978, A. Hardy (CSCA); 1♂, Palen Dunes, 27 Apr 1978, F.G. Andrews, A.R. Hardy (BBSL); 1♂, Palen Dunes, 28 Apr 1974 (CSCA). **San Bernardino Co.:** 53♂♂, Ibex Dune, 4 Apr 1982, J.B. Knight, R.W. Rust (BBSL); 51♂♂, 1♀, Ibex Dune, 4 Apr 1982, R.W. Rust, *Larrea tridentata* (BBSL).

Records of bees collected during surveys (collection events without numbers of males and females are collections where specimens were destroyed for molecular work): **USA, California, Imperial Co.:** Glamis Dunes, 7 Apr 2000, R. Andrus, *Larrea tridentata* (BBSL). **Inyo Co.:** 2♂♂, Cottonwood Cyn., 11.96 mi ENE, 29 Mar 2005, R. Andrus, *Larrea tridentata* (BBSL); 1♂, Eureka Dunes, N end, 8 May 2000, T.L. Griswold, *Larrea tridentata* (BBSL); 4♂♂, Marble Canyon Dunes, NE side, 9 May 2000, J. Janjic, *Psorothamnus polydenius* (BBSL); 2♂♂, Marble Canyon Dunes, NE side, 9 May 2000, R. Andrus, *Psorothamnus polydenius* (DVNP); 4♂♂, Marble Canyon Dunes, NE side, 9 May 2000, R. Andrus, *Psorothamnus polydenius* (BBSL); 2♂♂, Marble Canyon Dunes, NE side, 9 May 2000, R. Andrus, no floral record (BBSL); 1♂, Marble Canyon Dunes, NE side, 10 May 2000, T.L. Griswold, *Psorothamnus polydenius* (DVNP); 4♂♂, 1♀, Marble Canyon Dunes, NE side, 10 May 2000, T.L. Griswold, *Psorothamnus polydenius* (BBSL); Panamint Dunes, 26 Apr 1999, R. Andrus, *Larrea tridentata*; Saline Dunes, 12 Apr 2000 R. Andrus, *Larrea tridentata*; Saline Dunes, 7 May 1999, R. Andrus, *Larrea tridentata*; 2♀♀, Saline Dunes, W margin, 11 Apr 2000, R. Andrus, *Larrea tridentata* (DVNP); 2♀♀, Saline Dunes, W margin, 11 Apr 2000, R. Andrus, *Larrea tridentata* (BBSL); 1♂, Stovepipe Main Dunes, 15 Mar 1999, R. Andrus (DVNP); 5♂♂, Stovepipe Main Dunes, 15 Mar 1999, R. Andrus (BBSL); 1♂, Stovepipe Main Dunes, 29 Mar 1999, R. Andrus, W. Apperson (DVNP); 4♂♂, Stovepipe Main Dunes, 29 Mar 1999, R. Andrus, W. Apperson (BBSL); 3♂♂, Stovepipe Main Dunes, 29 Mar 1999, R. Andrus, *Larrea tridentata* (BBSL); 2♂♂, Stovepipe Main Dunes, 29 Mar 1999, R. Andrus, *Larrea tridentata* (DVNP);

1♀, Stovepipe Main Dunes, 25 Apr 1999, R. Andrus, T.L. Griswold, *Larrea tridentata* (DVNP); 1♀, Stovepipe Main Dunes, 25 Apr 1999, R. Andrus, T.L. Griswold, *Larrea tridentata* (BBSL); 18♂♂, 2♀♀, Stovepipe Wells Sand Dunes, 29 Mar 2002, R. Andrus, *Larrea tridentata* (BBSL); 1♂, Stovepipe West Dunes, 31 Mar 1999, R. Andrus, W. Apperson, *Larrea tridentata* (BBSL). **Riverside Co.:** 4♂♂, 2♀♀, Wiley Well exit off Hwy 10, 18 mi W Blythe, 7 Apr 2001, R. Andrus, E. Pilgrim, *Larrea tridentata* (BBSL). **San Bernardino Co.:** Buckwheat Wash Dunes, 10 Apr 2000, R. Andrus; Ibex Dunes, 17 Mar 2000, R. Andrus, *Larrea tridentata*; Kelso Dunes, 1 May 2000, R. Andrus, *Larrea tridentata*. **Nevada, Churchill Co.:** 6♂♂, 1♀, Sand Mountain Dunes, 6 Jun 2000, R. Andrus, *Psorothamnus polydenius* (BBSL). **Mineral Co.:** 1♂, 4♀♀, Thorne Dunes, 7 Jun 2000, R. Andrus, *Psorothamnus polydenius* (BBSL). **Nye Co.:** Crescent Dunes, 7 Jun 2000, R. Andrus, *Psorothamnus polydenius* (BBSL).

DISCUSSION

Recent collections confirm that the range of *C. stephensi* extends far beyond the range of its purported host, *L. tridentata* (Fig. 1), necessitating a reevaluation of the status of *C. stephensi* as one of its specialists. Those populations located outside the range of *Larrea* necessarily utilize an alternate host plant, apparently the unrelated shrub *Psorothamnus*. *Colletes stephensi*, therefore, cannot be categorized as an oligolege according to the accepted definition (Linsley, 1958). *Colletes stephensi* does, however, appear to possess specific host-use habits that differ according to geographic location. Exactly which floral resources are utilized by different populations and individuals in different locations, and under the changing interannual climatic conditions, is not entirely understood. Conflicting observations made concerning floral preferences in the Eureka Valley transition zone exemplify the persisting uncertainties. Our observations indicate a definite preference for *Psorothamnus* among bees foraging on the dunes in this location. Observations made during a study of pollinators of *Larrea* indicated otherwise (Jim Cane, pers. comm.). Specimens of *C. stephensi* were observed and collected on *Larrea* at a location only 1.6–3.2 km from Eureka Dune. (It should be noted that the *Larrea* observation was during a study focused on *Larrea*; other plants, including *Psorothamnus*, were not sampled.) Because no pollen loads were procured in either of these studies, it remains unknown whether or not individual bees at this location collect pollen from both hosts.

The dual hosts of *C. stephensi* contrast sharply in several aspects of their natural history. *Psorothamnus* are an ancient North American lineage, whose members are largely highly modified xerophytes of the Sonoran, Mojave, and Chihuahuan Deserts, and desert basins of the Colorado Plateau and Great Basin (Barneby, 1977). *Psorothamnus*, along with the two other members of the daleoid clade, *Dalea* Linnaeus and *Marina* Liebmann (McMahon, 2005), are well visited by a diversity of bees. Whether *Psorothamnus* (alone or including other clade members) support a specialist bee fauna comparable in size to that of *Larrea* is unknown; there has not been the rigorous sampling such as that conducted on *Larrea* and there are no published accounts. Specimen records from the U.S. National Pollinating Insects Collection suggest that multiple species of bees spanning eight bee genera specialize on *Psorothamnus* (sometimes including the closely related plant genus *Dalea*), including three species of *Colletes* of the *daleae* species group, to which *C. stephensi* presumably belongs (Timberlake, 1958). In contrast, *Larrea* are an amphitropical genus of South American origin. The oldest documented record of *L. tridentata* is dated to 18,700 ybp (years before present; Felger *et al.*, 2012),

but suggested dates for its appearance on the North American landscape range from ~30,000 ybp (Betancourt *et al.*, 1994) to 1.5–8.4 million years before present (Hunter *et al.*, 2001; Lia *et al.*, 2001), with most recent estimates placing arrival in the Pleistocene or late Pliocene [0.42–3.36 mya (million years ago); Laport *et al.*, 2012]. However, the expansion of *Larrea* to be virtually coextensive with the present Sonoran, Mojave, and Chihuahuan Deserts (MacMahon, 1988) likely is recent. These hot deserts were absent 18,000 ybp, attaining their modern limits by 6,000 ybp (Thomson & Anderson, 2000). Chronosequences from packrat middens demonstrate that colonization by *L. tridentata* in the Sonoran Desert is recent, mostly ranging from 12,500 ybp to as recent as 3,400 ybp (Van Devender, 1990). Colonization appears later in the Mojave Desert with ages ranging from 8,200 ybp to 5,500 ybp (Spaulding, 1990). Sometime during its existence in North America *Larrea* acquired some 21 bee oligoleges (excluding *C. stephensi*) representing nine genera including four of *C. stephensi*'s congeners (*C. larreae* Timberlake, *C. salicicola* Cockerell, *C. clypeonitens* Swenk, *C. covilleae* Timberlake). No member of this guild of specialists occurs on any of *L. tridentata*'s South American congeners or on any other member of the Zygophyllaceae (Hurd & Linsley, 1975). This large and novel guild of specialist bees is thought to reflect at least nine (Roig-Alsina & Michener, 1993; Alexander & Michener, 1995; Wcislo & Cane, 1996), and perhaps as many as 13–16 (Minckley *et al.*, 1999), independent evolutionary shifts from ancestral hosts since the advent of *Larrea* on this continent. It is possible that *C. stephensi*'s use of *Larrea* across much of its distribution represents a similar shift from an ancestral host, presumably the North American endemic, *Psorothamnus*. In that context it is of note that the majority of the species of *Colletes* in the *daleae* species group appear to specialize on Fabaceae, principally *Psorothamnus*, *Dalea*, and *Prosopis* Linnaeus (Moldenke, 1979; Griswold, pers. obs.), though in the absence of a phylogeny it is only suggestive.

Larrea possess many distinctive attributes that make them incredibly well suited to extreme desert environments and an especially reliable floral resource. This reliability, even in extreme conditions, may have facilitated numerous evolutionary host-shifting events. *Larrea* require a minimum of only 12 mm of annual rainfall to bloom each spring (Bowers & Dimmitt, 1994), and has been observed to withstand 12+ months of complete drought (D. Guiliani, pers. comm.). They reproduce vegetatively as well as asexually, with clones persisting for thousands of years, and can grow on diverse substrates ranging from sand dunes to rocky soils (Simpson *et al.*, 1977). As a result, they are the most common and widespread shrub throughout the warm deserts of the Southwest (MacMahon, 1988). During extended periods of hot, dry weather, such as experienced during the altithermal phase (7,000–4,500 ybp) when mean temperatures were several degrees hotter than now (Antevs, 1948; Houghton, 1976; Woodcock, 1986), it is conceivable that *Larrea* continued to bloom regularly on the dunes, while many other bee hosts, including *Psorothamnus*, failed to do so. During this time, a switch to the use of pollen of *Larrea* may have been imperative to the survival of many bees, including *C. stephensi*. The overlap in the habitat requirements and bloom phenology of plants of *Larrea* and *Psorothamnus* may have facilitated such a switch.

Assuming *Psorothamnus* are the ancestral host, their apparent maintenance as the preferred host among members of *C. stephensi*'s northern populations is a matter of interest. Thorp's (1969) fragmentation hypothesis states "if periodic local extinction occurs during years when the preferred pollen source is absent, disjunct populations may be created, leading to geographic speciation." It is possible that *C. stephensi* experienced disruptive selection as certain populations or subpopulations began to switch to *Larrea* as pollen source. During subsequent dry periods, those geographically in-

intermediate populations may have gone extinct, creating disjunct Great Basin and Mojave Desert populations. The movement of sands, previously representing continuous habitat along rivers and lake shores, would have expedited this process. As the rivers and lakes dried up, their sands were blown into distinct and often isolated sand dunes resulting in the natural fragmentation of suitable habitat, further restricting gene flow between populations. *Colletes stepheni* mtDNA COI sequence data indicates that such a gene flow restriction does exist between Great Basin and Mojave Desert populations (Nelson, unpubl. data), supporting this hypothetical explanation.

Although rarely addressed, it is possible that the oligolectic nature of some desert specialists represents the novel evolution of the specialist habit within formerly generalist clades or species. It has frequently been noted that specialist bees are more abundant in xeric communities than in tropical and many mesic temperate ecosystems (Michener, 1954; Michener, 1979; Moldenke, 1979; Wcislo & Cane, 1996). The consistency of this trend suggests that evolutionary pressures selecting for specialist lifestyle characteristics are stronger in desert communities than in mesic temperate or tropical communities. During the Pleistocene (1.6 mya to 10,000 ybp) a temperate climate prevailed throughout most of the American Southwest. What is now a dry and sparsely vegetated desert was then green and flush with water. Undoubtedly, the selective forces active during this period were different from those of today. Perhaps the abundance of specialists in this area is a relatively recent occurrence, evolved under modern selective pressures unique to desert ecosystems. If *C. stepheni*'s floral preferences were more general during the Pleistocene, it is possible that as selective pressures gradually changed in response to desertification, specific preferences for *Larrea* and *Psoralea* evolved independently in disjunct regions of this bee's distribution.

Establishing the true nature of floral host preferences for *C. stepheni* and testing the hypotheses presented here would include a rigorous appraisal of *C. stepheni*'s floral host preferences throughout its range, including examination of pollen loads. The Eureka Valley, and similar transition-zone locations with *C. stepheni* populations provide the perfect natural laboratories for focused host choice tests that would be key in clarifying the nature of evolutionary mechanisms responsible for the distribution and host use patterns of *C. stepheni*.

One additional possibility needs to be addressed: that the bees using *Psoralea* in the Great Basin and the bees using *Larrea* in the Mojave Desert actually represent two species that were recently diverged or are in the process of diverging. If this is the case, Eureka Valley populations potentially represent a hybrid or sympatric zone. This appears unlikely. Analysis of multiple populations from both the Mojave and Great Basin Deserts using nuclear genes failed to detect any difference (Wilson *et al.*, 2009).

For now, eclectic oligolecty, the term coined by Cane & Sipes (2006) for those whose host preferences are limited to only a few, but unrelated, plant genera would seem appropriate for *C. stepheni*. Evidence suggests *C. stepheni* is not the only bee incorrectly assigned as a member of *Larrea*'s specialist guild of pollinators. *Megandrena enceliae* (Cockerell) and *Habropoda pallida* (Timberlake), both purported *Larrea* specialists (Hurd & Linsley 1975), appear to use alternate hosts under normal environmental conditions. Pollen samples taken from *M. enceliae* collected on *Arctomecon* Torr. & Frém (Papaveraceae), clearly showed that pollen of *Arctomecon* was collected by individuals of this species in Clark County, Nevada (Hickerson, 1998). Likewise, pollen samples taken from some specimens of *H. pallida* proved to be composed exclusively of pollen from *Oenothera* Linnaeus (Onagraceae) (Nelson, unpubl. data).

This study points to the value of reviewing the status of “oligolectic” bees and highlights the need for researchers to continue to reassess assumptions concerning habits and distribution. The presumed oligolectic nature of a bee assumes constraints on its range and floral hosts. The incorrect assignment of oligolecty necessarily hinders our ability to investigate the evolutionary origins of diet breadth and its function in modern ecosystems. Robust assignments to oligolecty will be based upon studies that pair collections on the purported host with systematic collections on associated flowering plants and sample adjacent regions beyond the boundary of the putative host. Examination of pollen loads, and a continued effort to search for presumed oligolectes in locations and on flowers where they are not expected, will be helpful in avoiding the misapplication of oligolecty.

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REFERENCES

- Alexander, B.A., & C.D. Michener. 1995. Phylogenetic studies of the families of short-tongued bees (Hymenoptera: Apoidea). *University of Kansas Science Bulletin* 55(11): 377–424.
- Antevs, E. 1948. Climatic changes and pre-white man in the Great Basin, with emphasis on glacial and postglacial times. *Bulletin of the University of Utah* 38(20): 168–191.
- Barneby, R.C. 1977. Daleae Imagines, an illustrated revision of *Errazurizia* Philippi, *Psorothamnus* Rydberg, *Marina* Liebmann, and *Dalea* Lucanus emend. Barneby, including all species of Leguminosae tribe Amorphaeae Borissova ever referred to *Dalea*. *Memoirs of the New York Botanical Garden* 27: 1–894.
- Bernays, E.A., & R.F. Chapman. 1994. *Host Plant Selection by Phytophagous Insects*. Chapman & Hall; New York, NY; xiii+312 pp.
- Betancourt, J.L., T.R. Van Devender, & P.S. Martin, eds. 1994. *Packrat Middens: The Last 40,000 Years of Biotic Change*. University of Arizona Press; Tucson, AZ; vii+469 pp.
- Bowers, J.E., & M.A. Dimmitt. 1994. Flowering phenology of six woody plants in the northern Sonoran Desert. *Bulletin of the Torrey Botanical Club* 121(3): 215–229.
- Cane, J.H., R.L. Minckley, L.J. Kervin, & T.H. Roulston. 2005. Temporally persistent patterns of incidence and abundance in a pollinator guild at annual and decadal scales: The bees of *Larrea tridentata*. *Biological Journal of the Linnean Society* 85(3): 319–329.
- Cane, J.H., R.L. Minckley, L.J. Kervin, T.H. Roulston, & N.M. Williams. 2006. Complex responses within a desert bee guild (Hymenoptera: Apiformes) to urban habitat fragmentation. *Ecological Applications* 16(2): 632–644.
- Cane, J.H., & S. Sipes. 2006. Characterizing floral specialization by bees: Analytical methods and a revised lexicon for oligolecty. In: Waser, N.M., & J. Ollerton (Eds.), *Plant-Pollinator Interactions: From Specialization to Generalization*: 99–122. The University of Chicago Press; Chicago, IL; xii+445 pp.
- Chittka, L., J.D. Thomson, & N.M. Waser. 1999. Flower constancy, insect psychology, and plant evolution. *Naturwissenschaften* 86(8): 361–377.
- Felger, R.S., T.R. Van Devender, B. Broyles, & J. Malusa. 2012. Flora of Tinajas Altas, Arizona—A century of botanical forays and forty thousand years of *Neotoma* chronicles. *Journal of the Botanical Research Institute of Texas* 6(1): 157–257.

- Hickerson, L.L. 1998. *The reproductive ecology, demography, and population structure of *Arctomecon californica* Torrey and Fremont (Papaveraceae) in fragmented and unfragmented habitat*. MA Thesis, Utah State University; Logan, UT; viii+93 pp.
- Houghton, S.G. 1976. *A Trace of Desert Waters: The Great Basin Story*. A.H. Clark Company; Glendale, CA; 287 pp.
- Hunter, K.L., J.L. Betancourt, B.R. Riddle, T.R. Van Devender, K.L. Cole, & W.G. Spaulding. 2001. Ploidy race distributions since the Last Glacial Maximum in the North American desert shrub, *Larrea tridentata*. *Global Ecology and Biogeography* 10(5): 521–533.
- Hurd, P.D., Jr. 1979. Superfamily Apoidea. In: Krombein, K.V., P.D. Hurd, Jr., D.R. Smith, & B.D. Burks (Eds.), *Catalog of Hymenoptera in America North of Mexico, Volume 2: Apocrita (Aculeata)*: 1741–2209. Smithsonian Institution Press; Washington, D.C.; 1199–2209 pp.
- Hurd, P.D., Jr., & E.G. Linsley. 1975. The principal *Larrea* bees of the southwestern United States (Hymenoptera: Apoidea). *Smithsonian Contributions to Zoology* 193: 1–74.
- Hurd, P.D., Jr., & J.A. Powell. 1958. Observations on the nesting habits of *Colletes stepheni* Timberlake. *Pan-Pacific Entomologist* 34(3): 147–153.
- Laport, R.G., R.L. Minckley, & J. Ramsey. 2012. Phylogeny and cytogeography of the North American creosote bush (*Larrea tridentata*, Zygophyllaceae). *Systematic Botany* 37(1): 153–164.
- Lia, V.V., V.A. Confalonieri, C.I. Comas, & J.H. Hunziker. 2001. Molecular phylogeny of *Larrea* and its allies (Zygophyllaceae): Reticulate evolution and the probable time of creosote bush arrival to North America. *Molecular Phylogenetics and Evolution* 21(2): 309–320.
- Linsley, E.G. 1958. The ecology of solitary bees. *Hilgardia* 27(19): 543–599.
- MacMahon, J.A. 1988. Warm deserts. In: Barbour, M.G., & M.D. Billings (Eds.), *North American Terrestrial Vegetation*: 232–264. Cambridge University Press; New York, NY; x+434 pp.
- McMahon, M.M. 2005. Phylogenetic relationships and floral evolution in the papilionoid legume clade Amorphaeae. *Brittonia* 57(4): 397–411.
- Michener, C.D. 1954. Bees of Panamá. *Bulletin of the American Museum of Natural History* 104(1): 1–176.
- Michener, C.D. 1979. Biogeography of the bees. *Annals of the Missouri Botanical Garden* 66(3): 277–347.
- Minckley, R.L., J.H. Cane, & L. Kervin. 2000. Origins and ecological consequences of pollen specialization among desert bees. *Proceedings of the Royal Society of London, Series B, Biological Sciences* 267(1440): 265–271.
- Minckley, R.L., J.H. Cane, L. Kervin, & T.H. Roulston. 1999. Spatial predictability and resource specialization of bees (Hymenoptera: Apoidea) at a superabundant, widespread resource. *Biological Journal of the Linnean Society* 67(1): 119–147.
- Moldenke, A.R. 1979. Host-plant coevolution and the diversity of bees in relation to the flora of North America. *Phytologia* 43(4): 357–419.
- Roig-Alsina, A., & C.D. Michener. 1993. Studies of the phylogeny and classification of long-tongued bees (Hymenoptera: Apoidea). *University of Kansas Science Bulletin* 55(4): 123–162.
- Rust, R.W., L.M. Hanks, & R.C. Bechtel. 1983. Aculeata Hymenoptera of Sand Mountain and Blow Sand Mountains, Nevada. *Great Basin Naturalist* 43(3): 403–408.
- Simpson, B.B., J.L. Neff, & A.R. Moldenke. 1977. Reproductive systems of *Larrea*. In: Mabry, T.J., J.H. Hunziker, & D.R. DiFeo, Jr. (Eds.), *Creosote Bush: Biology and Chemistry of Larrea in New World Deserts*: 92–114. Dowden, Hutchinson, & Ross; Stroudsburg, PA; xvi+284 pp.
- Spaulding, W.G. 1990. Vegetational and climatic development of the Mojave Desert: The last glacial maximum to the present. In: Betancourt, J.L., T.R. Van Devender, & P.S. Martin (Eds.), *Packrat Middens: The Last 40,000 Years of Biotic Change*: 166–199. University of Arizona Press; Tucson, AZ; vii+469 pp.
- Stephen, W.P. 1954. A revision of the bee genus *Colletes* in America North of Mexico (Hymenoptera, Colletidae). *University of Kansas Science Bulletin* 36, Part 1(6): 149–527.
- Thompson, R.S., & K.H. Anderson. 2000. Biomes of western North America at 18,000, 6000 and 0 ¹⁴C yr BP reconstructed from pollen and packrat midden data. *Journal of Biogeography* 27(3): 255–284.

- Timberlake, P.H. 1958. A new species of the genus *Colletes* from the Colorado Desert of California (Hymenoptera: Apoidea). *Pan-Pacific Entomologist* 34(3): 143–145.
- Thorp, R.W. 1969. Systematics and ecology of bees of the subgenus *Diandrena* (Hymenoptera: Andrenidae). *University of California Publications in Entomology* 52: 1–146.
- Van Devender, T.R. 1990. Late Quaternary vegetation and climate of the Sonoran Desert, United States and Mexico. In: Betancourt, J.L., T.R. Van Devender, & P.S. Martin (Eds.), *Packrat Middens: The Last 40,000 Years of Biotic Change*: 166–199. University of Arizona Press; Tucson, AZ; vii+469 pp.
- Wcislo, W.T., & J.H. Cane. 1996. Floral resource utilization by solitary bees (Hymenoptera: Apoidea) and exploitation of their stored foods by natural enemies. *Annual Review of Entomology* 41: 257–286.
- Wilson, J.S., J.P. Pitts, & C. von Dohlen. 2009. Lack of variation in nuclear genes among isolated populations of the sand dune restricted bee *Colletes stephensi* (Hymenoptera: Colletidae). *Journal of the Kansas Entomological Society* 82(4): 316–320.
- Woodcock, D. 1986. The late Pleistocene of Death Valley: A climatic reconstruction based on macrofossil data. *Palaeogeography, Palaeoclimatology, Palaeoecology* 57(2–4): 273–283.



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