Origins and ecological consequences of pollen specialization among desert bees

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An understanding of the evolutionary origins of insect foraging specialization is often hindered by a poor biogeographical and palaeoecological record. The historical biogeography (20 000 years before present to the present) of the desert-limited plant, creosote bush (*Larrea tridentata*), is remarkably complete. This history coupled with the distribution pattern of its bee fauna suggests pollen specialization for creosote bush pollen has evolved repeatedly among bees in the Lower Sonoran and Mojave deserts. In these highly xeric, floristically depauperate environments, species of specialist bees surpass generalist bees in diversity, biomass and abundance. The ability of specialist bees to facultatively remain in diapause through resource-poor years and to emerge synchronously with host plant bloom in resource-rich years probably explains their ecological dominance and persistence in these areas. Repeated origins of pollen specialization to one host plant where bloom occurs least predictably is a counter-example to prevailing theories that postulate such traits originate where the plant grows best and blooms most reliably. Host-plant synchronization, a paucity of alternative floral hosts, or flowering attributes of creosote bush alone or in concert may account for the diversity of bee specialists that depend on this plant instead of nutritional factors or chemical coevolution between floral rewards and the pollinators they have evolved to attract.

Keywords: biogeography; foraging; insect–plant interactions; environmental variation

1. INTRODUCTION

Host specialization is widespread among herbivorous insects yet the selective advantage leading to the evolutionary origin of foraging specializations remains unclear. Competing hypotheses can be grouped into those that involve reciprocal evolution of the host and consumer (e.g. the arms race hypotheses (Ehrlich & Raven 1964)), and those that involve unilateral evolution by the consumer in response to host attributes such as resource quality and/or abundance or its spatio-temporal predictability (Bernays & Chapman 1994; Strong *et al.* 1984). These hypotheses are not mutually exclusive, yet a serious impediment to evaluating their relative importance is the lack of phylogenetic and historical information on the ecology and distribution of insects and their plant hosts. The historic distribution and spread of creosote bush (*Larrea tridentata*) is unusually complete (Betancourt *et al.* 1994) and its flowers are visited by a phylogenetically diverse specialist bee fauna (Hurd & Linsley 1975). This system therefore provides a unique opportunity to examine both the long-term history and the present-day ecology of a plant–animal mutualism. In this study we examine the historical ecology associated with repeated origins of specialization by bees to creosote bush.

Bees (series Apiformes, superfamily Apoidea) are a diverse insect group of 20 000 species that depend on plant pollen as a source of protein. Species range in their degree of pollen specificity from those that visit many plant species for pollen (polylecty), to others that restrict their foraging to one (monolecty) or a few (oligolecty)

closely related plant species (Linsley 1958; Wcislo & Cane 1996). More than 120 bee species have been collected at *L. tridentata* flowers (Hurd & Linsley 1975; Minckley *et al.* 1999; Simpson *et al.* 1977), second only to sunflower (*Helianthus annuus*) (Hurd *et al.* 1980), and 21 species are pollen specialists of *L. tridentata* while the rest are generalists. Most of the specialist species appear to be monoleges that visit only *Larrea*, although females of several species have been reported at alternative pollen host species and may prove to be oligoleges. Other than the introduced honeybee (*Apis mellifera*) and the few species of *Lasioglossum* in the subgenus *Dialictus* which are social, the *Larrea* bee fauna are solitary species that build nests in natural cavities or excavate tunnels in the ground or plant stems.

The creosote bush is a dominant element of the flora in the three warm North American deserts, the Chihuahuan, Sonoran and Mojave (Turner *et al.* 1995). Flowering by the creosote bush is triggered by rainfall events of > 12 mm, one of the lowest rainfall thresholds reported for any New World desert perennial (Bowers & Dimmitt 1994), and a profusion of nectar and pollen-bearing flowers are produced (Simpson 1977).

2. METHODS

Samples were made during the spring bloom of *L. tridentata* (mid-March to late-May) in 1993, 1994 or 1995. Localities of the sample sites and bee species composition from each site are described fully in Minckley *et al.* (1999). At all but three sites, bees were collected using a stratified random sampling protocol. One-hectare plots were divided into 100 overlapping 2.5 m-wide parallel strip quadrats (= belt transects). For each sampling period, each of two collectors began at a randomly selected *x*, *y* coordinate and walked for 20 min along the strip quadrat
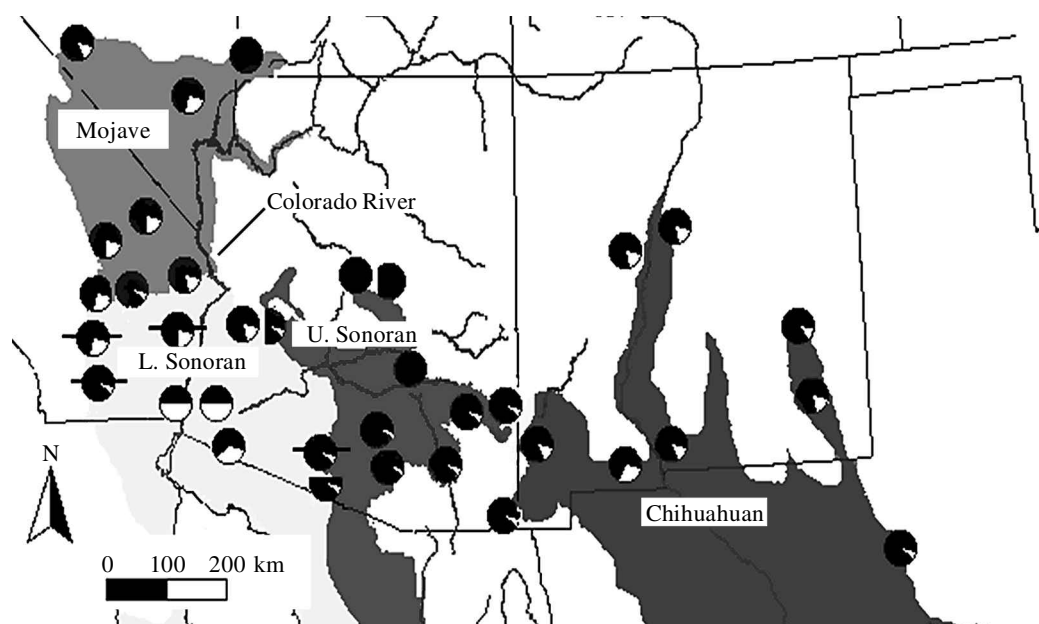
Figure 1. Map of western North America showing the warm deserts and 40 sampling localities (pie diagrams) used in this study. Pie diagrams with horizontal bars signify two sites. Black areas of pie diagrams are estimates of the proportion of years that *L. tridentata* bloomed during spring based on precipitation data from the weather station nearest to each sampling locality.

netting any bee that foraged on *Larrea* flowers. Sampling periods began every 30 min from the beginning of bee activity in the morning (06.30–08.00) for 6 h. Species accumulation curves from samples taken both in 1993 by us and from data of Hurd & Linsley (1975) showed that a morning to midday census yielded more than 85–95% of all taxa represented in an all day census (R. L. Minckley and J. H. Cane, unpublished data). For the analyses presented in this study, all samples represent the combined collections of two collectors during one day's survey. Some ($n = 3$) collections were also included from sites where bees were collected haphazardly. Samples from sites within 20 km radius of each other were pooled. The 40 sites range from 25 to 1450 km apart, nine are in the Chihuahuan desert, eight are in the Mojave desert, 13 are in the Lower Sonoran desert and ten are in the Upper Sonoran desert.

Most bees were collected and pinned for later identification. Those species that could be identified on the wing (honeybees, *Xylocopa californica arizonensis*, *X. varipuncta* and *Bombus pensylvanicus sonorus*) were tallied from visual counts alone.

We identified 94% out of the 4803 specimens collected to the level of species. Most of the unnamed specimens were designated as morphospecies. *Agapostemon angelicus* and *A. texanus* were pooled into one taxon because females of these species are indistinguishable (Roberts 1972). Members of the genus *Lasioglossum* subgenus *Dialictus* were separated into two morphospecies based on the coloration of their abdomens (red or green). Excluded from our analyses were undescribed species (nine species, 15 individuals) and honey bees (*Apis mellifera*). We were not able to associate reliably sexes of undescribed species. *Apis* was excluded because it is not native to North America. Vouchers of all material are deposited at the Auburn University Entomological Museum (Auburn University), Snow Entomological Museum (University of Kansas) and the Bee Biology and Systematics Laboratory (Utah State University).

Estimates of the proportion of years that *L. tridentata* bloomed during spring were made based on precipitation data from the weather station nearest to each sampling locality. Stations ranged in the number of continuous years with data from 48 to 110 years. Single rainfall amounts of 12–25 mm during the winter months trigger bloom in *L. tridentata* the following spring (Bowers & Dimmitt 1994). Using these rainfall amounts as surrogate estimates for bloom, the number of winters when no winter month (October to March) exceeded 12 mm of rain was calculated. One site in the Mojave desert was omitted because the nearest weather station was at a substantially higher elevation than the sample site.

Distributions of specialist and generalist bee species that visit creosote bushes were made by consulting primary taxonomic works on each of the species (Hurd & Linsley 1975; Krombein *et al.* 1979), our database of label information from specimens in five United States museums with large holdings of North American desert bees (see Minckley *et al.* 1999), and our own samples.

3. RESULTS

Spring bloom by *L. tridentata* is least frequent at sites in the Lower Sonoran and Mojave deserts and most frequent in the Upper Sonoran desert (figure 1). The frequency of bloom corresponds closely with bloom predictability. The same areas where we estimated spring bloom occurred least frequently are where Davidowitz (2000) found interannual precipitation to be most unpredictable.

Our samples yielded 20 out of the 21 species of creosote bush pollen specialists (table 1) and the greatest number of *L. tridentata* pollen specialists occurred in those areas where *L. tridentata* bloomed least frequently. Four distributional patterns are represented among these specialist bees (table 2a): (i) Lower Sonoran and Mojave deserts ($n = 8$ species); (ii) Lower Sonoran, Upper Sonoran and Mojave deserts ($n = 7$ species); (iii) all desert regions ($n = 5$ species); and (iv) Chihuahuan desert ($n = 1$ species). Notably, endemism among the *L. tridentata* oligoleges is almost entirely restricted to the Lower Sonoran desert or

Table 1. *List of bee species that are specialists of* L. tridentata *pollen and the desert regions where they occur*

(C, Chihuahuan; M, Mojave; LS, Lower Sonoran; US, Upper Sonoran.)

	region
Colletidae	
Colletes clypeonitens	C, M, LS, US
C. covilleae	M, LS, US
C. larreae	M, LS, US
C. stepheni	M, LS
Andrenidae	
Ancylandrena larreae	M, LS, US
Megandrena enceliae	M, LS, US
Calliopsis foleyi	M, LS
C. larreae	M, LS
Perdita covilleae	M, LS, US
P. eremica	M, LS
P. flavipes	M, LS
P. larreae	C, M, LS, US
P. lateralis	M, LS, US
P. punctulata	M, LS, US
P. semicaerulea	C
P. turgiceps	M, LS
Melittidae	
Hesperapis arida	M, LS
H. larreae	C, M, LS, US
Megachilidae	
Trachusa larreae	C, M, LS, US
Hoplitis biscutellae	C, M, LS, US
Apidae	
Habropoda pallida	M, LS

the Lower Sonoran and Mojave deserts, whereas only one creosote bush specialist (*Perdita semicaerulea*) occurs solely in the Chihuahuan desert and none in the Upper Sonoran desert.

Furthermore, the historical distribution of bees that specialize on *L. tridentata* was probably more strongly associated with the low desert along the Colorado River than we observe today. The area presently occupied by the Upper Sonoran desert was predominately oak woodland and substantially cooler and wetter until 3000–4000 years before present (yr BP) (Betancourt *et al*. 1994). In contrast, where the Colorado River crosses the present-day Lower Sonoran and Mojave deserts is an area of unusual long-term climatic and elevational stability in western North America. Tectonic and stratigraphic evidence places the Colorado River approximately in its present-day position beginning in the early Cenozoic, emptying into the Pacific Ocean prior to the formation of the Gulf of California (Dokka & Ross 1995; Howard 1996). Persistent low elevation along the palaeo-Colorado river and dry inshore air currents off the Pacific Ocean suggest that arid conditions have been continuous, at least locally, in this region (Axelrod 1979). This interpretation is consistent with more recent data (<20 000 yr BP) from pack rat middens in this area that establish the presence of xeric-adapted vegetation characteristic of the Sonoran desert scrub since at least the Quaternary (Betancourt *et al*. 1994). Prevailing views are that the ranges of desert

vegetation, including the creosote bush, expanded recently from low areas along the Colorado River into the present-day Upper Sonoran desert. The seven *L. tridentata* specialist bee species that currently occur in the Lower Sonoran, Mojave and Upper Sonoran desert regions probably dispersed along with their host plant, and previously were restricted to the low desert areas along the Colorado River, e.g. parts of the present-day Lower Sonoran and Mojave deserts. In total, at least 15 out of the 21 *L. tridentata* specialist bee species seem to have been historically restricted to the Lower Sonoran and Mojave deserts (table 2*b*). The 21 bee species that specialize on *L. tridentata* represent nine genera and five out of the seven bee families that occur in North America. Based on current hypotheses of bee phylogeny (Alexander & Michener 1995; Roig-Alsina & Michener 1993), the 15 species of *L. tridentata* specialists represent at least nine independent evolutionary shifts to the use of *L. tridentata* as a sole pollen resource.

To test if the age of the desert areas explained the distributional pattern found among bee species that are *Larrea* specialists, we compared their distributions with those of 64 desert-restricted generalist bee species that also visit *Larrea*. Besides also being limited to arid areas, these generalist species share all features of bee biology exhibited by the specialist species (e.g. nesting habit, body size and edaphic preferences), except specialization for *Larrea* pollen. We found that the modern-day distribution pattern of generalist species was even more than it was for specialist species across areas and endemic generalist bee species occurred in all of the desert regions, not predominately in the Lower Sonoran and Mojave desert as was observed for specialists (table 2*a*). Inferred palaeo-distributions of bee species were more skewed. When species distributions were pooled into larger categories based on the historical extent of these areas, the high endemism in desert areas along the Colorado River (e.g. the present-day Lower Sonoran and Mojave deserts) of specialist bee species on the creosote bush was not evident among generalist bee species (table 2*b*). Comparable levels of endemism should be observed in both specialist and generalist bee groups if speciation was simply related to the age of these desert areas. In addition, age of the Chihuahuan and Sonoran deserts are thought to be similar (Betancourt *et al*. 1994) and based on chromosomal data *Larrea* first colonized North America in the Chihuahuan desert and subsequently spread to the other North American deserts (Hunziker *et al*. 1977). However, only one bee species that is a *Larrea* pollen specialist is known to be endemic in the Chihuahuan desert. Therefore, the strikingly different patterns of distribution among specialist and generalist bee species suggest age of areas does not explain the pattern of specialist bees and suggests the importance of specialization for persistence in these strongly variable desert environments.

The ecological consequences of host plant synchrony are indicated by the present-day patterns of species richness, abundance and biomass of the specialist and generalist bees in these desert areas. Using our samples, we compared the specialist with the generalist bee fauna of *L. tridentata* at sites in the Upper Sonoran, Lower Sonoran and Chihuahuan desert areas north of the United States–Mexico border, and throughout the

Table 2. (*a*) *Modern and* (*b*) *inferred palaeodistributions of bee species that are* L. tridentata *pollen specialists and generalists that visit* L. tridentata

(Number in dashed lines indicates number of species. Species in the generalist category are restricted to those that visit plants in addition to creosote bushes for pollen and have distributions largely limited to the deserts. Parasitic species and species that are oligoleges of other plants, but occasionally visit creosote bushes for nectar, were excluded. Palaeodistributions are based on the premise that the creosote bush has dispersed into the present-day Upper Sonoran desert in the past 3000–4000 years and bee species have spread along with their floral host. The modern distribution of the single generalist species limited to the modern Upper Sonoran desert was omitted in (*b*) because its past distribution could not be determined. Dotted lines indicate species ranges are disjunct, perhaps because of sampling error. Palaeodistributions across all desert regions for generalist and specialist bee species were significantly different ($\chi^2 = 28$, d.f. $= 5$, $p < 0.001$).)

(*a*) modern distribution

bee species	Mojave	Lower Sonoran	Upper Sonoran	Chihuahuan
specialist	|------------ 8 ------------------------------------|		
		---------- 7 --------------------------------------		
		---------- 5 --	
				|---------- 1 ----------|
generalist	|-----------2 ----------|		
		|--------- 1 ----------|	
			|--------- 1 ----------|
				|---------- 2 ----------|
		---------- 5 ------------------------------------		
		|---------- 6 ----------------------------------|	
			|---------- 2 --|
		|---------- 7 ----------------------------------|	
			---------- 13 --	
		---------- 3 ------------------------------------........................--	
		--------- 23 --	

(*b*) inferred palaeodistribution

bee species	Mojave	Sonoran	Chihuahuan
specialist		|---------- 15 ------------------------------------|	
		---------- 5 --	
			|---------- 1 ----------|
generalist	|----------- 2 ----------|	
		|---------- 7 ----------|	
			|---------- 4 ----------|
	|---------- 9 ------------------------------------|	
		|---------- 15 ------------------------------------|	
		---------- 26 --	

Mojave desert (figure 1). Numbers of specialist species were smallest in the Chihuahuan desert and greatest in the Lower Sonoran and Mojave deserts (figure 2*a*). The low species richness of specialist bees in the Chihuahuan desert was paralleled by the fewest numbers of specialist individuals per site (figure 2*b*) and the least specialist bee biomass per site (figure 2*c*) of any desert region. In contrast, for generalists, the average number of species, individuals and biomass were least in the Lower Sonoran desert and greatest in the Upper Sonoran desert (figure 2*a*–*c*). Numbers of generalist bee species, individuals and their average biomass at sites in the Upper Sonoran desert were greater than sites in all other desert areas. Annual precipitation in the Upper Sonoran desert is the greatest of any desert area in the world (MacMahon 1979). The influence of precipitation on plant diversity and flowering presumably translates into comparable ecological responses among the spring-active bee faunas (Herrera 1988; Viejo & Templado 1986). Our data suggest

that, for bees at the creosote bush, this response consists largely of an increase in individuals and biomass of generalist species.

Only in the Lower Sonoran desert, where the creosote bush blooms least frequently, were more specialist species sampled per site than generalist species (figure 3*a*). This disparity was accentuated because fewer generalist species occurred on *L. tridentata* in the Lower Sonoran desert than in any other desert region (figure 2*a*). The ratio of specialist to generalist individuals, and specialist to generalist biomass at each site show a pattern similar to that observed for numbers of species (figure 3*b*). Overall, both measures are skewed toward specialists, except for biomass in the Chihuahuan desert. Most extreme are sites in the Lower Sonoran desert which were biased tenfold toward specialist bee species in comparison with sites in the Upper Sonoran desert (figure 3*b*). Sites in the Mojave desert were of intermediate values.
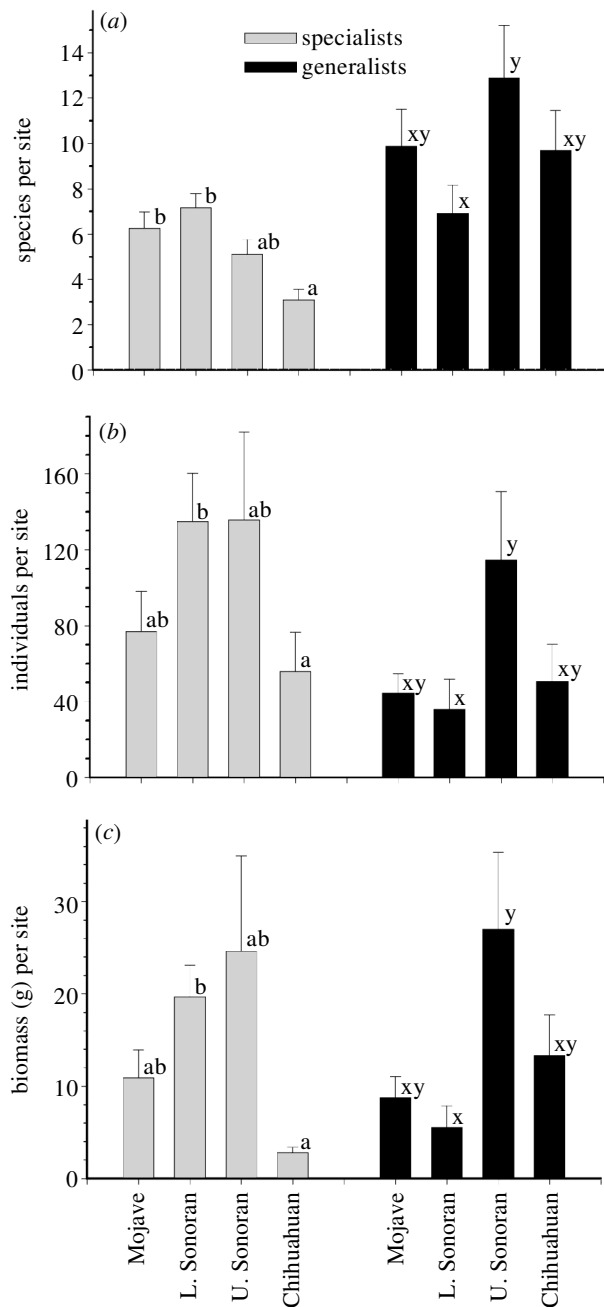
Figure 2. (*a*) Mean number of specialist and generalist bee species per site, (*b*) mean number of specialist and generalist individuals per site, and (*c*) mean estimated biomass of specialist and generalist bee species per site, in each of the four desert regions. All comparisons used a Kruskal–Wallis one-way ANOVA and pairwise comparisons were made using Dunn's method. Letters ab and xy above bars represent different analyses. Different letters above bars within an analysis indicate significant differences.

Poor representation of generalist bees at sites in the Lower Sonoran desert probably was not because this area is depauperate for generalist bee species. Using distributions of the same 64 pollen-generalist bee species discussed above, the pool of species for each region was as follows: Lower Sonoran ($n = 57$), Chihuahuan ($n = 45$), Upper Sonoran ($n = 44$) and Mojave ($n = 37$). Although these data are poor estimates of the absolute differences among desert regions, they provide no indication that
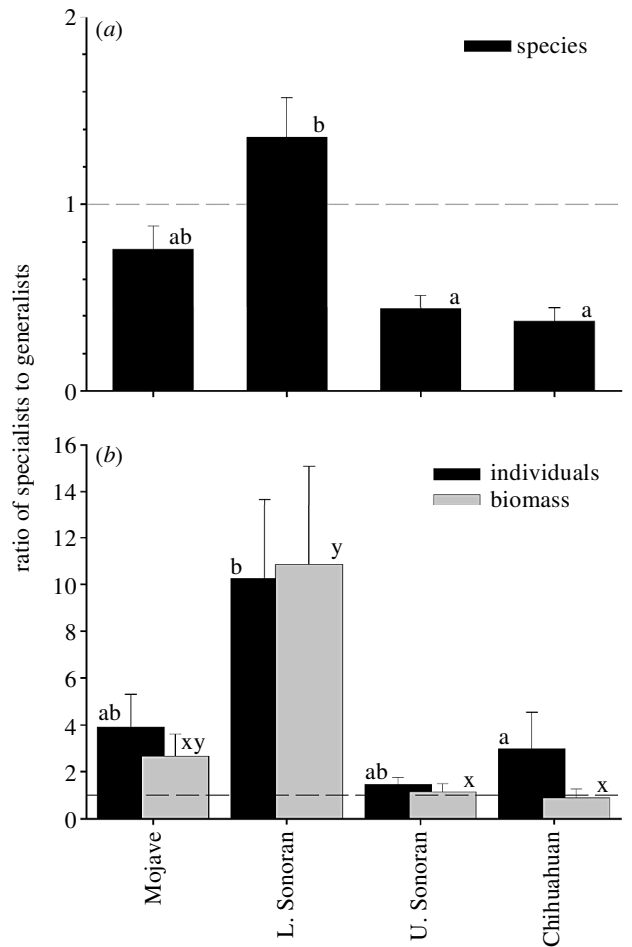

Figure 3. (*a*) Ratio of specialist to generalist species at sites in each of four desert regions ((Σ specialist/generalist species)/ number of sites). (*b*) Average ratio of numbers of specialist and generalist individuals at sites and average biomass of specialist and generalist species expressed as a ratio of specialists to generalist bee species. Different letters above bars within categories indicate significant differences.

species richness in the Lower Sonoran desert is lower for generalist bees than in other desert regions. Therefore, in the Lower Sonoran desert generalist bee species are likely to have more patchy distributions and be less abundant than in other desert regions. The low incidence and rarity of generalist species in our samples from the Lower Sonoran desert may result from unpredictability of bloom and a depauperate flora in the Lower Sonoran desert, which act as a filter on persistence of populations of the generalist bee species found there.

4. DISCUSSION

Why are creosote bush specialists more species-rich and abundant where their host plant blooms least predictably? Annual precipitation at sites in the Lower Sonoran and Mojave deserts is least and occurs most unpredictably between-years of any North American desert (Frank & Inouye 1994; Davidowitz 2000). In such environments, an important advantage of pollen specialization would be reliable synchrony with the floral host. Some species of solitary bees (Danforth 1999, and references therein), including two *L. tridentata* specialists (Rust 1980, 1988),

remain in diapause during drought years and emerge in those years when their host plant blooms. Evidently the bees that visit *L. tridentata* are able to time their flight season quite precisely with bloom of their host plant. By adopting emergence cues that are either the same as those used by the plant or that reliably signal bloom, specialist bees effectively make bloom by *Larrea* a predictable event in an unpredictable environment (see also Danforth 1999). Presumably generalist bees in these environments are not as well synchronized to the available floral hosts and become extirpated.

The specialist bee fauna represents a number of independent origins of pollen specialization among the bees that visit *Larrea,* yet undoubtedly not all have followed the same route to specialization. Most species in the genera *Perdita* and *Calliopsis* are oligolectic suggesting the ancestors of the *Larrea* specialists in these groups were pollen specialists of plant species other than *Larrea*. In these cases the evolutionary novelty would be the shift to creosote bush pollen and not specialization *per se*. Other genera, such as *Colletes* and *Hoplitis*, consist of numerous generalist species and ancestors of some *Larrea* specialists in these groups might have been floral generalists. Regardless of the evolutionary pathway taken, the exceptional diversity of pollen specialist bees that use *Larrea* pollen suggests there is a strong selective advantage for bees to the floral resources of this plant.

Host synchrony has been shown to affect the fitness of individuals in other ecological relationships (Dixon 1976; Fisher 1984; Powell & Mackie 1966) and has been implicated in large-scale patterns of species diversity of some insect groups (Gess 1992; Janzen 1981; Wilson 1985), including cleptoparasitic (cuckoo) bees (Wcislo 1987). Bee species diversity is lowest in the tropics and peaks around the Mediterranean Sea in the eastern hemisphere and in the highly seasonal temperate deserts of western North America (Michener 1979) where this study occurred. Although pollen specialists also occurs on plants found in more mesic environments (Minckley *et al.* 1994), species of pollen specialist bees are also most numerous where bee species richness is greatest, which has led to speculation that pollen specialization contributes importantly to this biogeographical pattern (Linsley 1958; Michener 1974).

General expectations regarding the origins of foraging specializations in insects predict specialization is favoured where host plants grow best and occur most reliably (Lawton & Strong 1981; Leigh 1975; MacArthur 1972). Instead, we have found that the evolution of pollen specialization is favoured where seasonal bloom is temporally least predictable. If modern-day climatic conditions are comparable with those that existed when pollen specialization to *Larrea* evolved, our findings show some selective factors that have been rarely considered in studies of insect host specialization may be involved in the origins of pollen specialization in bees. One hypothesis is that unpredictable bloom between years has invoked strong selection on bees to coordinate the cessation of diapause and subsequent adult activity for periods when floral resources are available. For the spring-active bees that use *L. tridentata* this is especially true because the creosote bush blooms in response to such low rainfall that in some years it may be the only plant in flower. Therefore, in these environments synchronization with

the host plant is the sole factor involved in the evolution of specialization. The presence of abundant, alternative floral hosts when the creosote bush flowers may also play a strong role in specialization. If few other plant species, or plant species that are uncommon, flower coincidentally with the creosote bush, bee species which are active synchronously with the bloom period of *Larrea* may specialize on the most common host. This could explain the different patterns of endemism of creosote specialist bee species among the Lower Sonoran–Mojave and Chihuahuan deserts. The Chihuahuan desert is higher in elevation than all the Lower Sonoran and the area of the Mojave desert along the Colorado River, and annual precipitation for the last 10 000 years has been summer-dominated in the Chihuahuan desert and winter-dominated in the Sonoran desert (Betancourt *et al.* 1994; Turner *et al.* 1995). One or both of these features of the Chihuahuan desert may mean that other bee-suitable plant species are in flower when *Larrea* blooms while in the Lower Sonoran and Mojave deserts such alternative floral resources are not available. Under these circumstances, the cost to bees of ignoring other resources outweighs the benefit of specializing on one host when alternative floral resources are available.

Finally, the highly diverse specialist bee fauna associated with *Larrea* may be primarily related to the unusually low rainfall amounts which initiate flower production by this plant (Bowers & Dimmitt 1994). In this desert ecosystem the floral resources of the creosote bush may present bees with an unusually predictable resource. Comparative studies of the bee faunas visiting deep-rooted perennial plant species which rely on ground water and annuals or shallow-rooted perennial plant species that rely on rainfall could be revealing tests of this latter hypothesis. These theories are not exclusive and deserve further attention. Notably, however, a feature common to each hypothesis is that it obviates the need to explain the origin and maintenance of pollen specializations in bees by proposing nutritional or other foraging benefits to bees, or chemical coevolution between floral rewards and the pollinators they have evolved to attract.

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