

EXHIBIT 5

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The Bees of the San Rafael Desert: Implications for the Bee Fauna of the Grand Staircase-Escalante National Monument

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ABSTRACT

■ The Colorado Plateau appears to be a region of rich bee diversity and endemism. A 15-year study of the bee fauna of southeastern Utah's San Rafael Desert, a small portion of the Plateau dominated by sand dunes, recorded 49 genera and 333 species—more genera and nearly as many species as in all of New England. Endemism is very high (one-fourth of the species). Diversity is the result of such factors as floral specialization (at least one-third of the species specialize on plants of the family or generic level), abundant and diverse nesting sites, strong seasonality of solitary species, and the historical contributions of diverse sources. Limited sampling in the Grand Staircase-Escalante National Monument suggests it to be equally diverse, but distinctive; nearly half of the Monument's bees are not present in the San Rafael Desert. ♀

Endemic plants of the Intermountain Region reach their greatest diversity in the Canyonlands section of the Colorado Plateau in southeastern Utah. The high rate of endemism is likely due to the section's age and relatively undisturbed isolation. Mountainous barriers surround the Canyonlands except for two gaps: one in the southeast, between the San Juan and Rio Grande Rivers, and another at the Dixie Corridor, a relatively low-lying area between the Grand Canyon and the Utah Plateau, which connects with the Mojave Desert (Cronquist et al., 1972).

Such isolation and plant endemism likely play a role in fostering the endemism of other taxa

in the Canyonlands. Bees, for example, in their mutualistic association with flowering plants (Roubik, 1989), have exchanged pollination services at flowers for plant resources: all the dietary requisites of bees, such as nectar and pollen, and habitation and nest construction materials for some, are obtained from plants. It is little wonder then that many students of pollination and bee biology have long suspected that bee diversity and speciation is determined, in part, by angiosperm diversity (Neff and Simpson, 1993). For this reason alone, we would expect high endemism among the Canyonlands' bees and a general diversity that reflects that of plants. In addition, the Canyonlands are expected to support a unique and rich bee fauna because it is arid: this large area of southeastern Utah averages but 12.7-20.3 cm of precipitation per year. It is well known that many desert areas are especially rich in endemic bees, probably because the isolation of the area of the monument of bees (e.g.,



fungi) are lower there, and opportunities for specialization on flowers are higher (Michener, 1979).

Prior to 1979, information on bee diversity on the Colorado Plateau was rudimentary. Little survey work had been conducted, and only a handful of species, mostly widespread and common elsewhere, were known from the region. In the summer of 1979, personnel from the USDA Agricultural Research Service Bee Biology and Systematics Lab (BBSL) made their first expedition to the Canyonlands, to the poorly known San Rafael Desert (SRD). The promising results of that expedition led to repeated trips over the next 15 years.

The SRD lies at the heart of the Colorado Plateau. Surrounded by regions of spectacular topography—the San Rafael Swell, Arches National Park, Canyonlands National Park, the Henry Mountains, and Capitol Reef National Park—the SRD presents a contrasting, pedestrian landscape, with only a few scattered buttes and monuments accenting a largely flat terrain. This region, also known as the Green River Desert (Stokes, 1977), ranges in elevation from 1300 to 1800 meters and is marked by extensive sand dunes. Much of the average precipitation (13.3-15.3 cm) comes in late summer and early fall and produces a flora distinctive from that appearing in spring. Summers are hot; average temperatures in July are 27 °C, and many days the maximums exceed 38 °C. The predominant vegetation is galleta three-awned shrubsteppe (Cronquist et al., 1972).

Here we present results of our survey of the bee fauna of the SRD and discuss the implications for other portions of the Colorado Plateau such as the Grand Staircase-Escalante National Monument.

Methods

Collections of bees on the SRD were made as time permitted by various personnel from the BBSL between 1979 and 1993. Most collections were made with insect nets at flowers, but also at nesting and resting spots, while walking through favorable habitat. As a measure of collecting effort, we used the number of collector-days, where a collector-day is a single day's activity by 1 person who captured at least 20 specimens. We tallied 182 collector-days spread across the flight season for bees from April through October, but with collecting effort concentrated in late spring, midsummer, and early fall (Table 1). More than 13,000 specimens were collected as part of trapping studies (Parker and Bohart, 1966), and a few were collected in malaise traps. Specimens were mounted, identified, given unique accession numbers, and entered into a computer database. Specimens are deposited in the U.S. National Pollinating Insects Collection, Logan, Utah.

Results

As anticipated, we found the bee fauna of the SRD to be very rich in bee endemics. We also found it to be very rich in the total number of bee species: 333 species were collected including all of the families and nearly half (41 percent) of the genera known from the United States (Table 2). Except for the well-known honey bee (*Apis mellifera*), which came to the Americas with European colonists early in the 17th century, all are native to North America. The fauna represents 9 percent of the 3,959 species and subspecies known from the continental U.S. in an area of only 0.05 percent of the continental land mass. One-fourth of the species are endemic to the Colorado Plateau and most of these are presently known only from the SRD.

Table 1. San Rafael Desert collecting effort by half month (number collector-days*).

Apr	May	June	July	Aug	Sept	Oct	Total
early							
3	14	27	31	40	15	1	182
late							
7	16	2			25	1	

* Collector-day = One person's activity for 1 day with a minimum of 20 specimens collected.



Table 2. The bee fauna of the San Rafael Desert.

Family	Subfamily	Genus	Species	Number of:					
				New Species	Endemics	Hot Desert Disjuncts	Great Plains Disjuncts		
Colletidae	Colletinae	<i>Colletes</i>	13	1	1	3	1		
	Hylaeinae	<i>Hylaeus</i>	7	3	3				
Halictidae	Rophitinae	<i>Dufourea</i>	2	1	1	1			
	Nominae	<i>Nomia</i>	3			1	1		
	Halictinae	<i>Agapostemon</i>	4						
		<i>Dialictus</i>	22						
		<i>Evyloeus</i>	5					1	
		<i>Halictus</i>	4					1	
		<i>Isotiglossum</i>	1						
		<i>Sphexodes</i>	7						
	Andrenidae	Andreninae	<i>Ancylandrena</i>	1			1	1	
			<i>Andrena</i>	25	3	6	4	3	
Panurginae		<i>Callopsis</i>	5	1	1	2	1		
		<i>Heterosarus</i>	2	1	1				
		<i>Panurginus</i>	1		1				
			<i>Perdita</i>	56	24	36	8	1	
Melittidae		Dasypodinae	<i>Hesperapis</i>	4	2	2			
Megachilidae		Lithurginae	<i>Lithurge</i>	1					
		Megachilinae	<i>Anthichellum</i>	1					
			<i>Anthidium</i>	8	1		3		
	<i>Dianthidium</i>		6			2			
	<i>Diaxys</i>		4	1	1	1			
	<i>Stelis</i>		6	1	1	2			
	<i>Coelioxys</i>		5						
	<i>Megachile</i>		17		1	1	1		
	<i>Atoposmia</i>		2	1	1	1			
	<i>Ashmeactella</i>		13	1	1	5			
	<i>Hoplitis</i>		5		2	2			
	<i>Osmia</i>		14	2		5	1		
	Apidae		Nomadinae	<i>Epeolus</i>	1				
				<i>Holcopastus</i>	1				1
<i>Neolarva</i>		7		2	4		1		
<i>Nomada</i>		12		1	1		2		
<i>Triepoelus</i>		8					1		
Xylocopinae		<i>Ceratina</i>	2						
		<i>Xylocopa</i>	1						
Apinae		<i>Anthophora</i>	14	1	1	1	1		
		<i>Habropoda</i>	2			1			
		<i>Diadasia</i>	4						
		<i>Melissodes</i>	14			1	1		
		<i>Svastra</i>	3			1			
		<i>Synhalicta</i>	6			2	1		
		<i>Exomalopsis</i>	2		2				
		<i>Xeromelecta</i>	1						
		<i>Melecta</i>	3	1	1	1			
		<i>Zacospia</i>	1						
		<i>Apis</i>	1						
	<i>Bombus</i>	3							
Total			333	48	68	50	21		



The bees of the SRD are diverse in size (they range in length from 3 to 25 mm), aspect (they vary in color from those that are black with fuzzy light hair, to those with red or yellow markings on the body, to others that are entirely red, blonde, or bright metallic blue or green), and lifestyle (solitary, social, and cleptoparasitic). Unlike the perennial honey bee, which lives in hives containing a queen with many workers, females of the vast majority of our native bees live solitary adult lives of short duration (only a few weeks per year): queens and workers are absent. Our relatively few social species include all of the bumblebees (*Bombus*) and an unknown fraction of the Halictinae in the genera *Halictus*, *Dialictus*, and *Eurylaeus*. Also, unlike honey bees, most native bees do not make honey (bumblebees are the only exception). And, while honey bees collect pollen from a wide array of flower species, many native bees restrict pollen collection to a single family or genus of plants. Twelve genera (17 percent of the species) are cleptoparasites, cuckoo bees who collect no pollen, but whose offspring mature in the usurped cells of other pollen- and nectar-collecting bees. Just as many pollen-collecting bees have specialized foraging habits, most cleptoparasites attack nests of a single host genus.

As might be expected, the numbers of individuals and species collected were positively related to collecting effort. When collecting effort and bee species collected were graphed in temporal sequence, beginning with the first collection in August 1979 and ending with the last collection in April 1993, there was a strong relationship between cumulative

effort and cumulative unique species recorded ($R^2 = 0.96$, $P < 0.0001$, Figure 1). Noteworthy is the absence of any obvious approach to an asymptote: an undetermined number of species remain to be collected. Those times most likely to yield additional, unrecorded species are April, October, the last half of June, and the first halves of July and August (Table 1) because collecting efforts during these periods have thus far been light.

To discern the pattern of seasonal occurrence of bee species, we divided each month into early (days 1-15) and late (days 16 ff.) periods, and tabulated the number of species recorded (Figure 2). Because of uneven collecting effort, the results are intended for illustration only

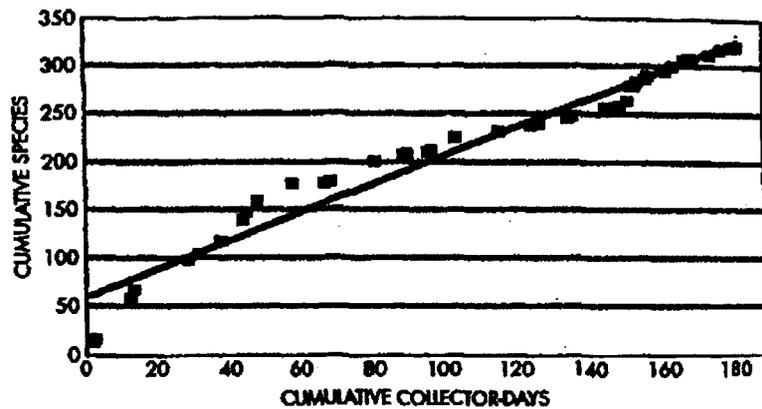


Figure 1. Cumulative number of unique bee species collected from 1979 to 1993 versus cumulative collecting effort. A collector-day is defined as a single day's activity by 1 person who captured at least 20 specimens. The relation is described by the equation: $y = 1.48x + 59.66$. ($R^2 = 0.96$, $P < 0.0001$).

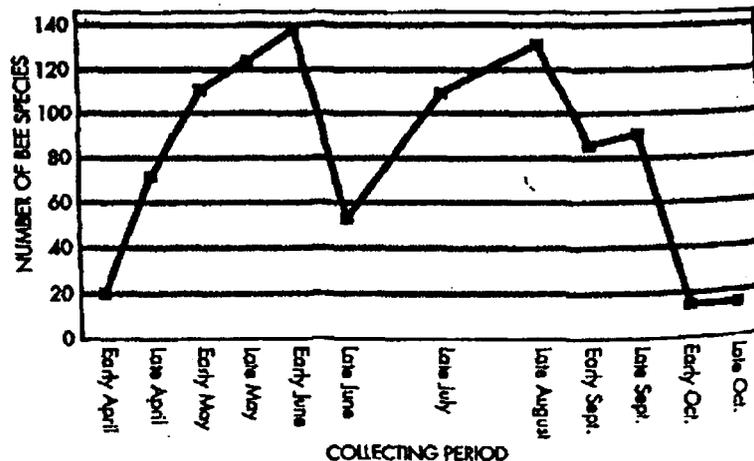


Figure 2. Number of bee species recorded by half month (early = 1-15, late = 16 ff.). No collections were made in early July or early August.



and should be examined with Table 1 in mind. Indeed, there were highly significant correlations between collecting effort and the two dependent variables individuals collected per half month ($R^2 = 0.91$, $P < 0.0001$) and species collected per half month ($R^2 = 0.71$, $P < 0.001$). As might be surmised, there was also a significant relation between the number of individuals and number of species collected by half month ($R^2 = 0.86$, $P < 0.0001$).

Despite the influence of collecting effort, the data can be used to make several points of interest. First, large numbers of species can be in flight at any given time: we recorded roughly 130 species in 2-week periods in both early June and late August (Figure 2). Second, like some other arid areas, e.g., shortgrass prairie (Tepedino and Stanton, 1980), the bee fauna of the SRD seems organized into two primary peaks, one in spring that culminates sometime in May or June, and another in August. For the most part, all families react in approximately the same manner throughout the bee flight season (Figure 3). While these are also times of peak collecting effort, other times of heavy collecting (late July, late September) do not yield as many species. Thus, the bimodality seems a real phenomenon though the troughs are likely to be less deep when sampling is complete.

The seasonal turnover in the composition of the four major bee families can also be seen through the use of similarity indices (Figure 4). We used Sorenson's Presence-Absence Index (Southwood, 1978) to compare the similarity of the bee fauna of each month with that of subsequent months. (Sorenson's Index is given by: $2A/(B + C)$ where A is the number of species shared between two samples, here months, and B and C are the number of species recorded in each sample being compared.) From the graphs, it is clear that the longer the time between sampling periods, the lower the similarity in the fauna. This is especially true for bees in the Megachilidae, the leafcutting bee family, which generally have the lowest similarity values. Turnover in this family may be great because many species have very selective flower-visiting habits: such species likely cease their adult activity as soon as their preferred floral resources finish blooming. Conversely, the lowest turnover is displayed by the family Halictidae, which is likely to have many primitively social species. Species displaying social behavior use a diversity of flowering plants and fly for longer periods. Thus, they are a more predictable component of the fauna.

It would be instructive to compare the phenology of the bee fauna with that of flowering angiosperms of the SRD. The bimodally distributed bee fauna may track, albeit roughly, a bimodal distribution of plant flowering diversity (Tepedino and Stanton, 1980). Others (e.g., Kochmer and Handel, 1986) have described plant communities that display bimodal flowering patterns. Unfortunately, we have been unable to locate such data for the SRD. The only list of plants of the area known to us includes all of the San Rafael Swell, but little of the SRD (Harris, 1983).

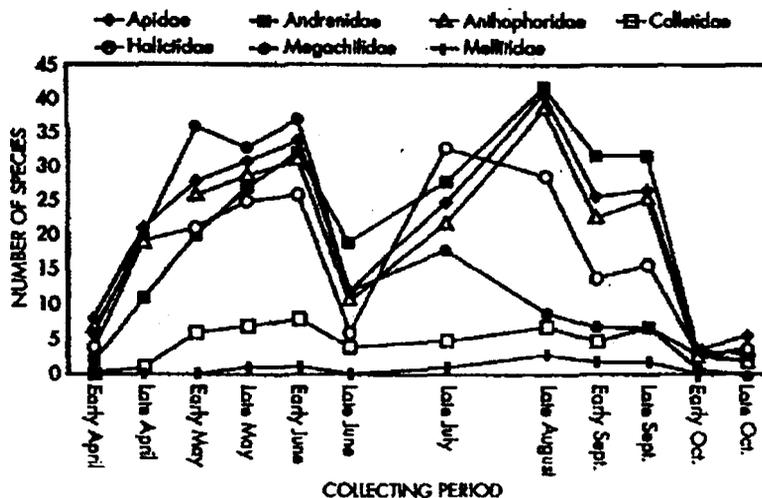


Figure 3. Number of bee species recorded in each family by half month (early = 1-15, late = 16 ff.). No collections were made in early July or early August.

Some (e.g., Linsley, 1958) have suggested that the

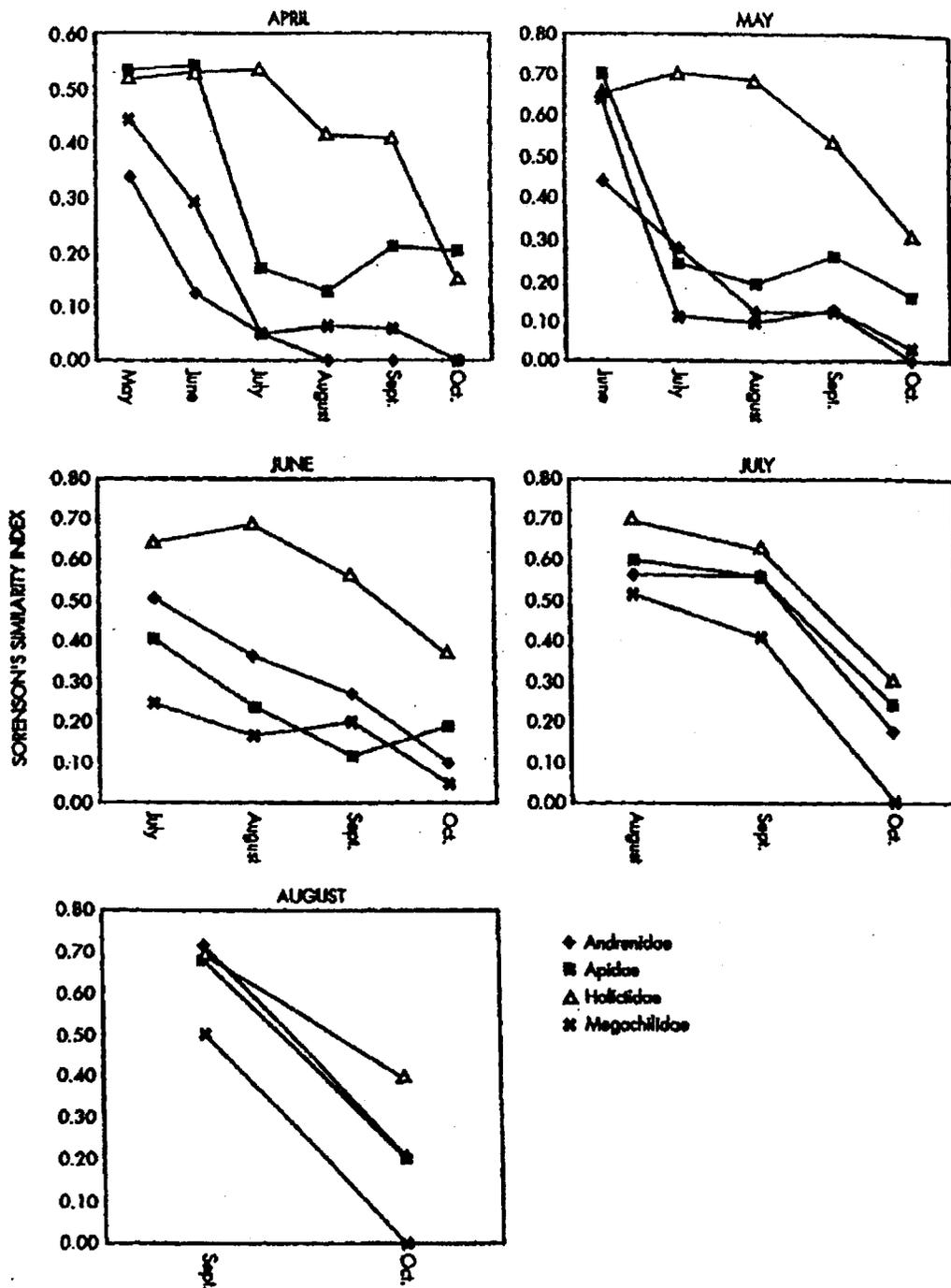


Figure 4. Change in similarity of bee fauna with time for the four most important families. Each graph represents the similarity between the month of note and succeeding months. To calculate similarity, Sorenson's Presence-Absence Index was used.

emergence of adult bees from diapause or quiescence in arid regions is triggered by precipitation: bee species richness might be correlated with precipitation because of the

connection between plant flowering and available moisture. We examined average monthly precipitation data from the two closest weather stations in Hanksville and Green River

(about 80 km apart). Precipitation is highly correlated between the sites (Spearman's rho = 0.96) and the totals differ by only 11 mm. Like the pattern of bee species richness, precipitation is bimodal in the SRD: about 25 percent falls between March and May, and 37 percent falls between August and October. We compared bee species richness using the number of unique bee species collected each month with monthly precipitation. Because we were unsure of the lag between precipitation and bee emergence we conducted correlations for the months April to September [we eliminated October because collecting effort was very low (Table 1)] using several estimates of precipitation: monthly, sum of previous 3 or 4 months, and previous 6-month estimates in two ways— including and excluding the precipitation in the bee sampling month. Only in the latter case did we obtain significant results ($R^2 = 0.61$, $P < 0.05$), and then the relationship was inverse rather than positive. Thus, we were unable to relate bee species richness to precipitation in any simple way.

Preston (1948, 1962) advanced the theory that species abundance distributions of taxa in diverse collections should fit a lognormal distribution. This was thought to be a property of species-rich assemblages where species abundances were governed by numerous independent factors compounded multiplicatively (Whittaker, 1972). Certainly, native bees in the SRD fit this description. Their species abundances do not, however, fit a lognormal curve ($\chi^2 = 87.1$, $P < 0.001$). The curve deviates from the expected values, particularly in the region of uncommon species (Figure 5). There are

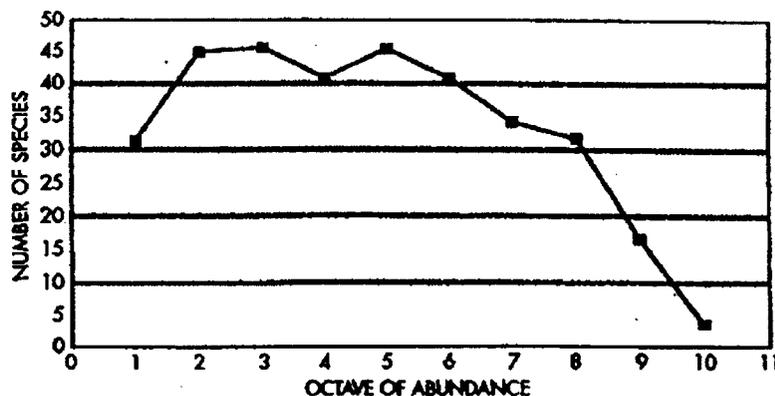


Figure 5. Species abundance data for the entire collection fitted to a lognormal distribution. Each octave of abundance is double the previous one; i.e., Octave 1 = 0-1 individuals/species, Octave 2 = 1-2, Octave 3 = 2-4, etc. The collection does not fit a lognormal distribution ($\chi^2 = 87.1$, $P < 0.001$). See Ludwig and Reynolds (1988) for further details.

fewer uncommon species and more common ones than expected. Whether additional collecting during the time periods that are under-represented will bring the curve closer to log-normality remains to be seen.

How diverse is the SRD compared to other known bee faunas? Such a comparison is hampered first by the paucity of complete local or regional faunas, and second by disparities in geographic size, location, context, and sampling intensity. For example, lower diversity is expected on islands, both physical (Channel Islands) and habitat (Sand Mountain and Blow Sand Mountain) (Michener, 1979). One could also argue that the largely sandy substrates with extensive exposed sandy regions characteristic of the SRD represent a habitat island, as they are surrounded by regions largely devoid of sand. However, the SRD bee fauna is in no sense depauperate. Indeed, it compares favorably with the six other western local faunas available, and with a regional count for New England (Table 3).

Table 3. Diversity of nearctic bee faunas.

	Genera	Species
San Rafael Desert, Utah	49	333
Curlew Valley, Idaho/Utah (Bohart and Knowlton, 1973)*	43	340
Mojave National Preserve, California (Griswold, unpub.)	58	305
Channel Islands, California (Ruel et al., 1985)	36	154

*Augmented by postpublication records.



The SRD has a higher generic diversity than all except the two mainland California sites and greater species richness than all sites but Curlew Valley. There are nearly as many species as in all of New England.

Discussion

What might account for the high diversity and endemism of the SRD bees? Both biological and historical factors likely play a role: floral specialization, an abundance of favorable nesting sites, strong seasonality, and historic contributions from a variety of faunal sources.

Floral Specialization

Bees visit flowers for both nectar and pollen. They frequently visit a variety of flowers for the nectar needed to fuel their own activities. Some bees also have catholic tastes for pollen, the primary source of food (often mixed with nectar) for their offspring. Other bees are much more discriminating in their choice of pollen sources, restricting their collections to a single family or genus of plants. Accurate determination of pollen specialization requires either analysis of pollen loads carried by bees in their "pollen brushes" or of nest cell provisions. We have not conducted such a study, but specialization can be inferred from observations on visitation. Where females consistently restrict their floral visits to particular plant taxa in the presence of other flowering plants at different sites and dates, pollen specialization is likely. Flower visitation records from the SRD suggest that at least one-third of the bees are specialists at least at the family level, with most specializing at the generic level (Table 4). The estimated incidence

of specialization is probably an underestimate given our limited data on visitation. Regrettably, floral visitation was not assessed during the early years of this study.

Some patterns are apparent among specialists. Members of the family Andrenidae (*Andrena*, *Calliopsis*, *Perdita*) are disproportionately abundant among specialist bees. *Perdita*, in particular, accounts for 26 percent of known specialists. By contrast, the Halictidae are poorly represented. All known specialists are solitary bees, as would be expected, given the short

Table 4. Floral specialization in San Rafael Desert bees.

Plant	Bee Genera (Number of species, no number = 1 species, specializing)
Asteraceae	<i>Perdita</i> (7), <i>Calliopsis</i> , <i>Anthophora</i> , <i>Esoneolopis</i> , <i>Melissodes</i> (9), <i>Svastra</i> , <i>Colletes</i> (4), <i>Ashmeadiella</i> , <i>Dianthidium</i> (4), <i>Megachile</i> (3), <i>Osmia</i> , <i>Hesperapis</i>
<i>Chrysothamnus</i>	<i>Andrena</i> , <i>Perdita</i> , <i>Anthophora</i> , <i>Melissodes</i> (2)
<i>Encelia</i>	<i>Atoposmia</i>
<i>Helianthus</i>	<i>Andrena</i> (2), <i>Perdita</i> (2), <i>Diadasia</i> , <i>Svastra</i> (2), <i>Hesperapis</i>
<i>Malacothrix</i>	<i>Calliopsis</i> , <i>Dufourea</i>
<i>Stephanomeria</i>	<i>Perdita</i>
<i>Wyethia</i>	<i>Perdita</i>
Boraginaceae	
<i>Cryptantha</i>	<i>Hoplitis</i> (2)
<i>Tiquilia</i>	<i>Perdita</i> (2)
Brassicaceae	<i>Andrena</i> (2)
<i>Lepidium</i>	<i>Calliopsis</i> , <i>Perdita</i>
<i>Stanleya</i>	<i>Perdita</i> (2)
Cactaceae	
<i>Opuntia</i>	<i>Diadasia</i> , <i>Ashmeadiella</i> , <i>Lithurge</i>
Capparidaceae	
<i>Cleome</i>	<i>Perdita</i> (2)
Euphorbiaceae	
<i>Euphorbia</i>	<i>Perdita</i>
Fabaceae	<i>Anthidium</i> (2), <i>Hoplitis</i> , <i>Osmia</i> (5), <i>Anthophora</i>
<i>Dalea</i> & <i>Psoralea</i>	<i>Colletes</i> , <i>Ashmeadiella</i>
<i>Lote</i>	<i>Ashmeadiella</i> (2)
<i>Psilostemon</i>	<i>Perdita</i> , <i>Colletes</i>
Hydrophyllaceae	
<i>Phacelia</i>	<i>Anthidium</i>
Loasaceae	
<i>Mentzelia</i>	<i>Perdita</i> (2)
Molvaceae	
Sphaeraleae	<i>Andrena</i> , <i>Calliopsis</i> , <i>Perdita</i> (4), <i>Diadasia</i> (2), <i>Colletes</i> , <i>Megachile</i> (2), <i>Hesperapis</i>
Onagraceae	
<i>Camissonia</i>	<i>Dufourea</i>
<i>Oenothera</i>	<i>Andrena</i> (2), <i>Anthophora</i> , <i>Synhalicta</i> , <i>Sphexodogastera</i> (3)
Papaveraceae	
<i>Argemone</i>	<i>Perdita</i>
Polemoniaceae	
<i>Gilia</i>	<i>Perdita</i> (2)
Scrophulariaceae	
<i>Cordylanthus</i>	<i>Anthidium</i>
<i>Parthenon</i>	<i>Atoposmia</i>



bloom period of most flowering plants. Small- to medium-sized bees (3-10 mm body length) are better represented than are large bees.

Causes of specialization are difficult to ascertain. Floral characteristics may play a part. Restrictive floral morphologies (Boraginaceae, Fabaceae, *Gilia*, Scrophulariaceae), odd pollen morphologies (*Opuntia*, *Oenothera*), and atypical timing of pollen presentation (*Mentzelia*, *Oenothera*, *Argemone*, *Stephanomeria*) may be important. Most specialists on plants with distinctive flowering times have flight activity patterns timed to synchronize with pollen presentation. Examples include dawn flight of *Andrena linsleyana* on *Oenothera*, early morning activity of *Perdita moabensis* on *Stephanomeria*, and late afternoon flights of *Perdita multiflorae* and *P. holoxantha* coinciding with the blooming of *Mentzelia*.

Specialization on abundant floral resources might be expected. Many of the plants listed in Table 4 are widespread and abundant; others, such as *Camissonia*, *Penstemon*, and *Argemone*, are localized in small populations. Some abundant components of the SRD flora that are attractive to bees, *Astragalus* (Fabaceae), *Poliomentha* (Lamiaceae) and *Eriogonum* (Polygonaceae), appear to lack specialists.

Nesting

Bees are known to nest in a variety of substrates and environments. Nests may be excavated in the soil, vertical banks, sandstone cliffs, pithy stems, or wood. Other bees construct exposed nests of resin or resin and pebbles. Nesting biologies of a handful of species from the SRD have been published (Parker, 1984, 1986, Parker and Griswold, 1982, Parker et al., 1986); biological information on a few others remains

unpublished, including the results of trap-nesting studies. The nesting biologies of the vast majority of SRD bees remain unknown. Based on available data from the SRD and studies conducted elsewhere, patterns of nesting can be inferred for the SRD bees (Table 5).

Most bees excavate their nests in the soil. Tunnels are constructed leading to one or more cells, ellipsoids excavated in the soil and often lined with glandular secretions. Each cell is the birthing place for a single offspring. An egg is laid on the provision, the pollen and nectar mass, which provides the nutrients needed for the developing larva. Following egg laying, the female seals the cell and has no further interaction with her offspring. Many species nest shallowly, less than 10 cm below the surface. Others nest much deeper. An excavated nest of *Andrena haynesi* descended to a depth of almost 3 meters (Parker and Griswold, 1982), representing the greatest depth recorded for any temperate zone bee.

Most bees are solitary nesters, constructing and provisioning their nests without the assistance of other bees. These nests may be aggregated, however. Sandy substrates seem to be particularly attractive to many ground nesting bees and dense aggregations have often been observed on dunes and dune margins. In a few instances, multiple females use a common nest entrance, but are assumed to provision

Table 5. Nesting strategies of San Rafael Desert bees.

Excavators	Ground	Colletidae: <i>Colletes</i> Halictidae Andrenidae Melittidae Megachilidae: <i>Anthidium</i> (some), <i>Osmia</i> (few), <i>Megachile</i> (some) Apidae (most)
	Vertical banks	Colletidae: <i>Hylaeus</i> (some) Apidae: <i>Anthophora</i> , <i>Exomalopsis</i>
	Stems & wood	Megachilidae: <i>Lithurge</i> , <i>Hoplitis</i> Apidae: <i>Ceratina</i> , <i>Xylocopa</i>
Ranters	Wood cavity	Colletidae: <i>Hylaeus</i> (most) Megachilidae (most)
	Soil cavity	Megachilidae (some)
	Cracks in rocks	Megachilidae: <i>Alaposmia</i> , <i>Ashmeadiella</i> (some)
Builders	Surface of stones & stems	Megachilidae: <i>Anthidiellum</i> , <i>Dianthidium</i> (most)



independently. A nest of *Perdita multifloras*, with at least 23 females, was excavated on a dune margin (Griswold and Parker, unpub.). While the majority of SRD bees appear to prefer sandy substrates, other soils are also utilized. Dense aggregations of *Diadasia* have been observed along seldom-used dirt tracks in hard-packed clay soils. One species of *Anthidium* excavates very shallow nests in friable soils (Griswold, unpub.).

Seasonality

At least as colonies, groups of social bees are long-lived. Honey bees are perennial; nests of *Bombus* and some halictids are active throughout the blooming season. By contrast, the adult lives of most solitary bees are short, on the order of a few weeks at most. They generally have but one generation per year, and thus are, for the most part, seasonally restricted. This results in a marked change in the composition of the fauna which is manifested in bimodality (Figure 4). *Andrena* (8 percent of spring fauna) and Megachilinae (26 percent) are best represented early in the season. During the summer and fall, *Perdita* and *Melissodes* dominate (30 percent of summer-fall fauna). The presence of both spring and summer-fall floras that differ in familial composition may increase bee diversity by effectively increasing the portion of the year with adequate but different floral resources.

Faunal Affinities

The SRD fauna is remarkable for its high rate of endemism. Fully one-fourth of the species are endemic. A handful of these have been described (Parker, 1983, 1985, Griswold and Parker, 1988, 1998, Griswold, 1993, Thorp, 1987); the majority remain unnamed. A number of these species may be more broadly distributed across parts of the Colorado Plateau, but they are unlikely to be present outside this region. Some endemics seem to be replaced in other parts of the Colorado Plateau by sibling endemics. An example is two recently described *Argemone* specialists, *Perdita ute*, presently known only from the SRD, and its sibling *Perdita angollata*, from the southern part of the Plateau in northern Arizona.

The remainder of the fauna shows the influence of diverse source areas. One-fourth of the fauna represents disjuncts either from the hot deserts to the southwest (17 percent) or from the Great Plains and east (7 percent). Most of the remaining species are restricted to the west: widespread in the western United States (21 percent), southwestern including non-desert areas (12 percent), Intermountain Region (7 percent), northwestern (2 percent), and Intermountain to Great Plains (2 percent). Eight percent are transcontinental. Widespread species tend to be social and/or generalists.

The predominant influence of combinations from warmer-weather sources is evident when the fauna is viewed in terms of taxonomic constituents. Genera with apparent desert origins (*Perdita*, *Ashmeadiella*) or higher diversities in xeric regions (*Dialictus*, *Anthophora*, *Melissodes*) predominate, while the contribution of genera of mesic origins (*Andrena*, *Lastoglossum*, *Osmia*, *Bombus*) is limited. For example, numbers of *Osmia* species at mesic sites range from 20 to 34 (Barthell et al. 1997), compared to the 14 recorded from the SRD.

Implications for Other Parts of the Colorado Plateau

Data from other parts of the Colorado Plateau are fragmentary at best. They do hint of diverse faunas across the region. Higher altitude "islands" such as the La Sal, Henry, Mountains, Abajo Mountains, Navajo Mountain, and the San Francisco Mountains might be expected to have distinctive faunas with affinities to Rocky Mountain faunas. What little data there is suggests this to be true. Insular montane components not found in the SRD include *Andrena* (20 species), *Osmia* (16), *Bombus* (5), *Colletes* (3), *Hyleaus* (2), *Megachile* (2), *Anthidium* (2), *Lastoglossum* (2), and *Anthophora* (1). Most of these represent southern outposts of primarily northern species. For example, *Osmia penstemonis* is widespread at higher elevation, mesic sites across the northwest ranging south along the mountains of California, Utah, and Colorado. What is at least a distinctive morph of this



species was recently discovered above treeline in the San Francisco Mountains. One exception to this pattern of northern "mainland" source areas is *Osmia juxta*, which occurs in Pacific states from British Columbia to California and appears to have colonized higher altitude areas of Arizona and New Mexico from the west; it does not occur in northern Utah or the northern Rocky Mountains. *Andrena coconina*, known only from the San Francisco Mountains, hints at an insular endemic fauna waiting to be discovered. When the upper elevations of the San Rafael Swell have been surveyed, they likely will be added to the list of insular regions. Among the handful of records from the Swell are representatives of *Bombus huntii* and several montane *Osmia*.

Bees of the Grand Staircase-Escalante National Monument

Even regions with elevations comparable to that of the SRD likely have dissimilar faunas. An example is the region encompassed by the Grand Staircase-Escalante National Monument (GSENM). There has been extremely limited sampling of the bees of the Monument: 15 collector-days, 20 localities, and less than 1,000 specimens (182, 95, and greater than 13,000 respectively for the SRD). Further, the localities are not representative of the Monument's diversity; almost all are located along the northwest boundary of the monument between Henrieville and Boulder. Nor are collections comprehensive seasonally. The only major collections are in late May, early June, and late summer (late July to late August). There are no spring collections.

Despite these limitations, the GSENM shows signs of comparable diversity and a distinctive bee fauna. There are presently 152 species known from this region, nearly half (46 percent) the number known from the SRD. Several of these represent northern extensions of species previously believed to be restricted to Arizona, New Mexico, and Texas (*Andrena pecosana*, *Trachusa cordaticeps*, *Megachile rossi*, *Heriades timberlakei*, *Hoplitis incanescens*). Thirteen undescribed species are so far recog-

nized in the genera *Hylaeus*, *Perdita*, *Stelis*, *Hoplitis*, *Osmia*, and *Megachile*. Perhaps most significant is the large proportion of the known fauna that is not shared with the SRD. Two genera (*Heriades* and *Trachusa*) and 41 percent of the Monument's bees are not present in the SRD. We suspect at least two causes: faunal components restricted to habitats not present in the SRD (i.e., pinyon-juniper), and an infusion of austral elements from source areas in Arizona. Given the greater habitat diversity and size of the GSENM, we would expect a larger fauna than that of the SRD when the Monument has been adequately surveyed.

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