

COMPLEX RESPONSES WITHIN A DESERT BEE GUILD (HYMENOPTERA: APIFORMES) TO URBAN HABITAT FRAGMENTATION

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Abstract. Urbanization within the Tucson Basin of Arizona during the past 50+ years has fragmented the original desert scrub into patches of different sizes and ages. These remnant patches and the surrounding desert are dominated by *Larrea tridentata* (creosote bush), a long-lived shrub whose flowers are visited by >120 native bee species across its range. Twenty-one of these bee species restrict their pollen foraging to *L. tridentata*. To evaluate the response of this bee fauna to fragmentation, we compared species incidence and abundance patterns for the bee guild visiting *L. tridentata* at 59 habitat fragments of known size (0.002–5 ha) and age (up to 70 years), and in adjacent desert.

The 62 bee species caught during this study responded to fragmentation heterogeneously and not in direct relation to their abundance or incidence in undisturbed desert. Few species found outside the city were entirely absent from urban fragments. Species of ground-nesting *L. tridentata* specialists were underrepresented in smaller fragments and less abundant in the smaller and older fragments. In contrast, cavity-nesting bees (including one *L. tridentata* specialist) were overrepresented in the habitat fragments, probably due to enhanced nesting opportunities available in the urban matrix. Small-bodied bee species were no more likely than larger bodied species to be absent from the smaller fragments. The introduced European honey bee, *Apis mellifera*, was a minor faunal element at >90% of the fragments and exerted little if any influence on the response of native bee species to fragmentation. Overall, bee response to urban habitat fragmentation was best predicted by ecological traits associated with nesting and dietary breadth. Had species been treated as individual units in the analyses, or pooled together into one analysis, these response patterns may not have been apparent. Pollination interactions with this floral host are probably not adversely affected in this system because of its longevity and ability to attract diverse pollinators but will demand careful further study to understand.

Key words: *Apiformes*; biodiversity; body size; conservation; habitat fragmentation; matrix effects; nesting biology; oligolecty; pollen specialization.

INTRODUCTION

Fragmentation of uninterrupted landscapes has been implicated in both the genetic impoverishment of populations and diminished taxonomic diversity of communities (Wilcox and Murphy 1985, Kruess and Tscharntke 1994, Turner 1996, Sheffer et al. 1999, Hedrick and Kalinowski 2000). How fragmentation affects interspecific interactions such as plant–pollinator interactions is less understood (Allen-Wardell et al. 1988, Bronstein et al. 1990, Ansett et al. 1997, Kearns et al. 1998, Christian 2001). Case studies have shown flowering plant populations in habitat fragments may be left without the services of reliable pollinators and suffer diminished fruit set (Kevan 1977, Moritz 1984, Jenners-ten 1988, Aizen and Feinsinger 1994a, Yasaka et al. 1994, Ghazoul and McLeish 2001) or reduced out-

crossing (e.g., Sipes and Tepedino 1995, although see Dick 2001, White et al. 2002) and lower genetic diversity (Menges 1991, reviewed in Oostermeijer et al. 1996, Tomimatsu and Ohara 2003). At an extreme, sexual reproduction within populations or species is lost (Warburton et al. 2000), which can restrict individuals to self-compatible genotypes (Washitani 1996).

However, there remains no consensus on how native pollinator communities respond to habitat fragmentation. Studies that have concluded that bee communities decline in species richness and abundance in smaller habitat fragments (Becker et al. 1991, Rathke and Jules 1993, Aizen and Feinsinger 1994a, b, Gathmann et al. 1994) are often difficult to interpret (reviewed in Cane 2001). Some insect-pollinated crops experience reduced pollination in agricultural fields that are more isolated from natural habitats, suggesting that their pollinators rely on undisturbed areas of native vegetation (Kremen et al. 2002, Ricketts et al. 2004). However, in another farm landscape, the diversity of pollinator species

Manuscript received 10 February 2005; revised 18 July 2005; accepted 15 August 2005. Corresponding Editor: M. P. Ayres.

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remained stable after 75 years of progressively more intense agriculture (Marlin and LaBerge 2001). Similarly, forest and scrub fragments of varying sizes have been found to host comparable numbers of species of large orchid bees (Euglossini) (Powell and Powell 1987), hummingbirds (Becker et al. 1991, Stouffer and Bierregaard 1995), and bees, beetles, flies, and butterflies (Donaldson et al. 2002). The array of conclusions mirrors that found in other animal groups (Didham et al. 1998, Krauss et al. 2003, Bonte et al. 2004, Davies et al. 2004, Fernandez-Juricic 2004, Stoner and Joern 2004, Vandergast and Gillespie 2004), and indicates the taxonomic affiliation, ecology, and life history of species in most pollinator communities differ substantially. A further complication occurs when the response of the biota is obscured by differences in the structure and composition of the habitat fragments studied. We minimized these problems in this study by focusing on one group of pollinators that exhibits key ecological differences and uses a single floral resource.

The 20 000 bee species worldwide (Michener 2000) are the primary pollinators of most continental floras (Axelrod 1969) and have nesting and foraging traits that set them apart from other pollinators and from other taxa studied in the context of habitat fragmentation. Females of pollen-provisioning bee species forage around their nest, to which they repeatedly return with pollen and nectar for their offspring. Most bee species nest underground, although some nest aboveground in wood, soft pithy stems, or holes made by wood-boring insects. Social bee species are floral generalists, but many nonsocial (solitary) bees are narrowly restricted in the floral host they use. These specialist, or oligolectic, species consistently forage for pollen at one or only a few plant species or genera (Linsley 1958, Cane and Sipes 2006) and have greater population structure than closely related pollen generalist species (Packer et al. 2005).

The foraging ranges of bees depend largely on their body size (S. S. Greenleaf, N. M. Williams, R. Winfree, and C. Kremen, *unpublished manuscript*) and can range from several square kilometers for larger bodied species (Roubik and Oluja 1983, Walther-Hellwig and Frankl 2000) to perhaps 50 m² for very small-bodied species. Therefore, single fragments may entirely support a population of small bees, support part of a metapopulation of mid-sized bees, or act as a single island of resources for large-bodied bees. Taken together, nesting substrate, diet breadth, and foraging range strongly characterize the habitat requirements bee species have and should predict their response to habitat fragmentation.

We examined how fragmentation of one habitat type affected a diverse set of bee species that we could group by nesting habits, host breadth, and body size. Combining bee species into ecologically relevant groups allowed us to test if ecological and life history features predict how species respond to habitat size and age.

Nesting attributes and ecological specialization predict how birds (Noss and Csuti 1997, Fernandez-Juricic 2004), spiders (Bonte et al. 2004, Vandergast and Gillespie 2004) and some insects (Den Boer 1979, Stoner and Joern 2004) respond to habitat fragmentation, but have been considered in few previous studies of pollinators (Kotiaho et al. 2005).

To explore the effects of fragmentation on native bees, we systematically sampled and compared the native bee guild of creosote bush (*Larrea tridentata* Moc. and Ses.; Zygophyllaceae) growing in 59 urban habitat fragments in Tucson, Arizona, USA, plus 12 sites in continuous desert outside the city. Number of sites where a species was found (incidence), species richness, and relative abundance were compared. Habitat fragments were classified by their size and age. We also evaluated how the *Larrea* bee fauna responded to urbanization by comparing faunas sampled in the largest recent fragments available to like-sized plots sampled in nearby continuous desert.

We tested four hypotheses for the response of native bees. First, that widespread and abundant bee species in continuous desert would occur most commonly in urban habitat fragments because they were more likely to be original residents of these sites when fragments were first formed, and more likely to repeatedly colonize isolated patches. Incidence and abundance predict occurrence of bird and mammal species at urban fragments (Bolger et al. 1997, Soulé et al. 1988), and in naturally patchy habitats of mountaintops, archipelagos, and desert springs (Atmar and Patterson 1993, Kodric-Brown and Brown 1993), but not for rainforest ground beetles (Didham et al. 1998). In our system, fragmentation involved the dissociation of habitat from continuous desert, changes in habitat size, and alteration of the area around deserts to an urban environment. To determine if urbanization surrounding these desert patches influenced the bee community composition, we compared the bee communities from the largest, most recently fragmented patches to comparably sized plots in the surrounding desert. Use of large, recently fragmented plots allowed us to minimize the chance that observed differences in the samples were due to size and fragment age.

Second, we hypothesized that bee species composition would shift toward large-bodied, broadly dispersing species as fragment size decreased. Very small bee species with limited flight capabilities often nest and forage amid a few individual floral hosts (Bennett and Breed 1985, Neff and Rozen 1995). In contrast, females of large-bodied taxa can venture >2 km from their nests (Rau 1929, Dressler 1982; S. S. Greenleaf, N. M. Williams, R. Winfree, and C. Kremen, *unpublished manuscript*). We reasoned that small-bodied bee species would be periodically extirpated from small habitat fragments because in some years floral resources found there will be limited, and large, more vagile bees would recolonize these fragments as conditions recovered. In

medium-sized fragments, floral resources may be sufficient to maintain populations of small-bodied species. Shifts toward communities of larger bodied bees with increasing isolation occurred at artificial habitat islands in agricultural landscapes (Steffan-Dewenter and Tcharntke 1999). Dispersal ability predicts species occurrence of other insect (Den Boer 1979, Didham et al. 1998, Schultz 1998) and vertebrate groups (Nee and May 1992).

The third hypothesis we tested was that ground-nesting bee species would be more susceptible than cavity-nesting bee species to greater isolation from continuous desert, declining fragment size, and increasing age since isolation. Few solitary bee species have narrowly specific nesting requirements (Michener et al. 1958, Cane 1991), but urbanization often degrades nesting habitat for ground-nesting bees dramatically by transforming vegetation composition and structure (e.g., scrub converted to grass lawns, washes confined to concrete flumes) and altering surface soils through compaction, loss, or burial beneath pavement. Such changes are not as adverse for bee species that nest aboveground in cavities, because cavities in wood and other substrates also occur in the houses, fences, and introduced woody landscape vegetation.

Our final hypothesis was that specialist bee species on *Larrea* floral resources would decline more rapidly than floral generalists in response to urbanization, decreasing fragment size, and greater fragment age. Floral generalists can use alternative flowering species when *Larrea* bloom fails or as stepping stones for fragment recolonization. In contrast, bloom by their floral host must be consistent for specialists to successfully reproduce. Combining these hypotheses, we reasoned that small-bodied, ground-nesting *Larrea* specialists would be most likely to be absent or rare in smaller, older habitat fragments.

MATERIALS AND METHODS

Study area and natural history

The Tucson Basin is centered in the Upper Sonoran vegetation zone (Brown 1994), among the most floristically diverse deserts in the world (Turner et al. 1995). Creosote bush is the dominant woody plant of the basin, sometimes in conjunction with mesquite (*Prosopis velutina*). Rapid urbanization in the Tucson valley over the past 50 years has largely replaced native desert scrub with commercial and residential development. In 1930, Tucson covered just 30 km² and had 45 000 residents; today 750 000 people are spread over 500 km². City growth has dissociated hundreds of fragments of native desert scrub from formerly continuous desert. Most of the larger creosote bushes in these fragments likely grew there before urbanization, given this shrub's slow regeneration (Turner 1990, Bowers et al. 1997). It is likely none were planted. Thus, desert scrub has persisted in undeveloped patches of Tucson, facilitating analyses of habitat fragmentation effects with little

confounding influence from shifting plant composition within these fragments over the past 50–100 years.

Study system

We studied the effects of urban habitat fragmentation on the bee guild associated with creosote bush. The plant is a long-lived shrub, common throughout the Chihuahuan, Sonoran, and Mojave deserts (Turner 1990) that has two disjunct blooming periods (spring and late summer/fall) when rainfall is adequate (Bowers and Dimmit 1994). Across its range, creosote bush flowers attract >120 bee species, one of the richest bee faunas of any plant in North America (Hurd and Linsley 1975, Simpson et al. 1977, Minckley et al. 1999). In the Upper Sonoran Desert, >60 bee species visit flowers of *Larrea* (see *Results*; Minckley et al. 1999). We focused on the spring bee fauna of *Larrea* because all but one of the *Larrea* specialist bee species that occur in the Upper Sonoran Desert are active only in the spring (Hurd and Linsley 1975) and because *Larrea* regularly blooms in Tucson during this season (estimated 90 of past 100 years, Minckley et al. 2000).

The bee species associated with *Larrea* are ecologically diverse. Floral specificity ranges from species that are broad floral generalists for pollen (polyleges) to specialist species (oligoleges) that collect pollen (and even nesting materials) exclusively from *Larrea* (Hurd and Linsley 1975, Cane 1996). Body lengths range from 4 to 17 mm, among the smallest and largest bees in North America. Most of these species nest in the ground, but some burrow into wood or pith (*Xylocopa*, *Hylaues*, some *Megachile*) or co-opt preexisting cavities (above and/or below ground; *Ashmeadiella*, *Hoplitis*, some *Megachile*). This combination of attributes (e.g., ground-nesting and cavity-nesting *Larrea* specialists, small and large body sizes among floral generalists and specialists, and others) in the *Larrea* bee fauna makes this group unusually well suited to study fragmentation effects.

We sampled bees at 59 desert fragments during the spring bloom in 1997 and 1998. Fragments ranged in size from single bushes (0.002 ha) to >5 ha (Table 1), and were located from 1 to >10 km from continuous desert from which they had been dissociated for as many as 70 years (Appendix A). We grouped fragments into size and age classes to compare *Larrea* bee faunas. Dimensions of each fragment were measured on-site and mapped using Geographic Information System (GIS) coordinates from the fragment center. The years since fragment isolation from continuous desert were determined from historical aerial photographs made in 1924, 1941–1947, 1964, 1971, and 1995 available at the Arizona Historical Society (Tucson) and in Glinski (1996). We designated patches of *Larrea* as fragments once they appeared bounded by development on all sides.

Bee samples were also made at 12 sites in the desert outside Tucson. Most of these sites were not pristine

TABLE 1. Spatial dimensions of desert fragments sampled for bees in the Tucson Basin, Arizona, USA.

Fragment dimensions†	Area class name	No. fragments
≥1 ha	hectare+	10
400 m ² –0.2 ha	medium	13
5 bushes‡–399 m ²	small	13
1–4 bushes‡	tiny	11

† The lower limit for each size class is one-fifth the size of the next larger size class.

‡ From our measurements of shrub densities at larger fragments, each bush is spaced on 20 m², so four shrubs occupy ~80 m².

(grazing, fire exclusion, or past farming history nearby) but all consisted of five or more contiguous hectares of *Larrea* with additional adjoining desert habitat.

Floral phenology

Bees are entirely dependent on pollen and nectar for food, suggesting floral abundance should profoundly influence the *Larrea* bee fauna. We assessed *Larrea* bloom stage at each fragment by counting buds, flowers, and fruits (including withered blooms) of the apical 30 cm of the topmost branch of up to 10 randomly chosen *Larrea* shrubs. Fruit number was then divided by the sum of buds, flowers, and fruits for each site and averaged for all plants at the site to yield an index of bloom phenology. We also counted the blooming and nonblooming bushes along the transects to estimate the proportion of bushes in bloom per site. We then compared fragments sampled in 1997 to those sampled in 1998 for bloom phenology, flower counts, and the proportion of bushes in bloom at each fragment. Blooming phenology was about seven days more advanced in 1997 than 1998; in both years, we sampled during the latter half of flowering (75% vs. 54% of total bloom) when species dependent on *Larrea* bloom should have been active. Most bushes at sites were in bloom each year ($72 \pm 26\%$, 1997; $98 \pm 2\%$, 1998).

Faunal composition and ecology

Sampling.—Bee species composition and abundance at flowering creosote bush were based on observation and net samples from flowers. A few large species could be reliably identified in flight (e.g., *Trachusa larreae* or species of *Xylocopa*); these were counted in situ with occasional vouchers. All other bees were collected, pinned, and identified to species or morphospecies. All pinned material is deposited at the Pollinating Insect Museum, USDA-ARS Bee Biology and Systematics Laboratory, Utah State University, Logan, Utah, USA.

The 1000-fold range in fragment sizes necessitated alternative sampling protocols. Larger fragments (hectare+ and large classes) were subsampled along 2 m wide parallel strip quadrats (belt transects) by 1–2 collectors. Strip quadrats were sampled in random order, beginning at random starting points (Minckley et al. 1999). Smaller fragments (medium and small

classes) were subdivided into several quadrats of equal size for random sampling (with replacement); every bush of tiny fragments was visited during each timed sampling period. All quadrats were sampled twice hourly for 20 min, commencing with the onset of bee activity (0800 MST) and continuing until 1300 MST. Tiny fragments were sampled for less time per half hour, but all collecting periods were timed for standardization. This time period was chosen because a previous study showed that few additional bee species or new individuals were added by further collecting (Minckley et al. 1999). For each sampling period, a collector slowly moved along a transect or through a quadrat, netting bees individually as they visited *Larrea* flowers. Collectors counted bushes along the sample route. “Incidence” of bee species was defined as the proportion of fragments or sites occupied. “Abundance” was defined as the total number of individuals sampled per person-hour of collecting.

Ecological groupings.—We classified bee species according to dietary breadths (*Larrea* specialist or floral generalist), nesting habits (subterranean or above-ground cavity), and body size (small or large) to evaluate how ecological traits of this bee guild determined their responses to urbanization per se, fragmentation from continuous desert, fragment size, and fragment age. We consider body size to be a surrogate for dispersal ability. Body sizes were estimated by measuring the shortest distance between an individual’s wing bases (intertegular span) which correlates well with dry mass (Cane 1987). Bees were grouped into two body size classes: small bees comprised the genera *Perdita*, *Hylaeus*, *Hesperapis*, *Ceratina*, and the red and green morphospecies of *Lasioglossum* (subgenus *Dialictus*), all of whose intertegular spans were <1.36 mm (estimated 5 mg dry mass). All remaining bee species were classified as large. Both size classes include *Larrea* specialists, floral generalists, and species that nest either in underground or in aboveground cavities (Appendix B).

Dietary breadth and nesting habit were determined for most species by reference to previous studies (Hurd and Linsley 1975, Krombein et al. 1979, Minckley et al. 1999, 2000). Nesting habits of bee species for which published records were not available were inferred if all other members of the same genus or subgenus used the same nesting substrate (e.g., all nest in the ground). Only two species represented by two individuals remained ambiguous for their nesting habits and were excluded from analyses. Because honey bees are not native and are often managed in hives, they were excluded from statistical analyses.

Analyses

Continuous desert–fragment comparisons.—The shift in bee species composition from continuous desert to urban fragments was examined by comparison of incidence of the bee faunas of all 59 urban fragments to 1-ha sites outside of Tucson using a goodness-of-fit

TABLE 2. Fragment size and the numbers of ground-nesting bee species sampled at flowering creosote bush in 59 habitat fragments.

Fragment size class	Species of <i>Larrea</i> specialists					Species of <i>Larrea</i> generalists			
	4	3	2	1	0	7–8	5–6	3–4	1–2
Hectare+	3	3	1	2	1	4	3	1	2
Large	1	3	2	3	3	3	4	5	0
Medium	0	1	1	5	6	3	4	3	3
Small	0	0	2	2	9	1	4	6	2
Tiny	0	0	0	2	8	1	2	6	2

test (two habitats $\times$ 62 species). To further control for effects of sampling protocol or fragment size, age, and isolation, and to focus specifically on the effects due to urban transformation of the habitat matrix surrounding these fragments, we compared the bee faunas found at *Larrea* of 12 large (>0.75 ha), recently isolated fragments with 12 like-sized plots in outlying desert scrub. All but one of these fragments had been separated from continuous desert in the preceding 27 years, and all but one was <2 km from continuous desert. Differences in richness and abundance of bees were compared with *t* tests or Mann-Whitney *U* tests.

Ecological attributes of bees and fragment size.—To test if body size, nesting habit, or foraging specialization influenced how bee species respond to fragmentation, numbers of species represented in each of these ecological functional groups within a fragment was regressed against fragment size. To evaluate foraging specialization as a factor, we used just ground-nesting species, because only one cavity-nesting species, *Ho. biscutellae*, is a *Larrea* specialist. We used separate logistic regressions (Allison 1999) for each type of functional group. Logistic regression accommodated the considerable number of zero values (species absence) and allowed for greater insight into the structure of such ordinal data than a contingency analysis. Convergence criteria were met, and the proportional odds assumption accepted in this and subsequent logistic regressions unless otherwise noted. The Wald test was the appropriate overall statistical test in this and the other logistic analyses, given our sample sizes. The proportional odds model was satisfactory for most comparisons; the remainder satisfied these criteria once incidence values were pooled in pairs (thus, 1–2 species, 3–4 species, and so on) or else when a normit distribution rather than proportional odds model was adopted.

Abundance, or bees caught per hour of sampling, was also compared among fragment size-classes using ANOVA followed by an a posteriori multiple range test (Ryan-Einot-Gabriel-Welch). $\log_{10}$ transformation corrected data skew and heterogeneous variances. Bias can arise when a few numerically dominant species per fragment mask the greater rarity of most species in the smaller fragment classes (Tilman and Lehman 2001). To avoid this bias, we just compared “small” with “hectare+” fragment size classes for their proportional

representation of individuals of the most common bee species, and for the three most common bee species in each fragment size class. Abundance of the cavity-nesting *Larrea* specialist, *Ho. biscutellae*, also was evaluated as a percentage of all native bees caught in each fragment. Fragments were grouped by size class and the arcsine-transformed percentages for *Ho. biscutellae* tested by ANOVA followed by the Ryan-Einot-Gabriel-Welch a posteriori test.

Specialization and fragment age.—We compared responses of ground-nesting specialist and generalist bees to fragmentation over time by testing differences in incidence and abundance between the two groups as a function of fragment age. We limited comparisons to fragments of “medium” and “large” size-classes because so few of the “tiny” or small fragments hosted ground-nesting *Larrea* specialists (Table 2), and we were able to find younger fragments to sample only in the hectare+ size class. Fragments were grouped into two age classes: 14 younger fragments (formed by 1971 or later) and 11 older fragments (formed before 1964). This division provided a clear temporal break and balanced sample sizes. Four species of *Larrea* specialists were present in this subset of fragments: *Ancylandrena larreae*, *H. larreae*, *P. punctulata*, and *T. larreae*. To test for differences in species incidence, for each bee species we calculated the difference between the fractions of young vs. old sites occupied. We then compared difference scores between specialists and generalists using the Wilcoxon two-sample test. To test if age of fragment equally influenced the abundance of *Larrea* specialists and floral generalists, we compared their proportional abundances from the same set of young and old fragments again using a Wilcoxon two-sample test.

RESULTS

During 158 h of collecting, 2512 individuals representing 62 native bee species in 31 genera were sampled while visiting flowers of 7683 creosote bushes growing in 59 urban habitat fragments (Appendix B). Only 12 bee species were morphospecies (228 individuals) that could be assigned to a genus but no described species. Honey bees visited *Larrea* flowers at most fragments (42 of 59), but they comprised $<25\%$ of the total bees sampled at 53 of 59 fragments (median 5% of a fragment's bee fauna).

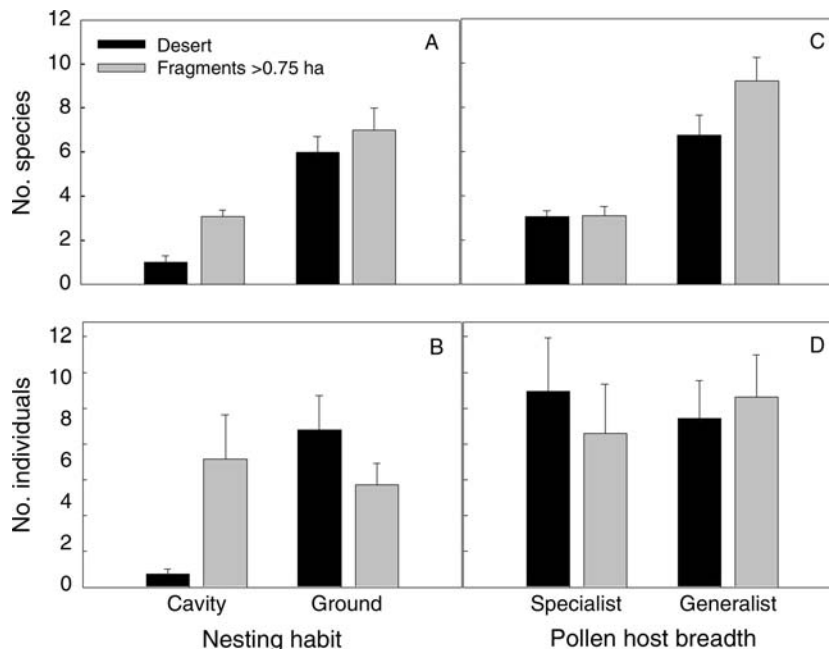


FIG. 1. Effect of the urban matrix on bee species composition (mean + SE) in desert fragments. Fragments >0.75 ha are compared with 1-ha plots in continuous desert for species richness (A, C) and abundance (B, D), contrasting species that differ in nesting habits (A, B) and foraging predilection (C, D).

Predictive value of species incidence and abundance

Data from the largest, more recently isolated fragments suggested some bee species responded positively to urbanization (Fig. 1A, B). The number of cavity-nesting species was threefold greater on average in these fragments than from similar-sized plots in the continuous desert (3.1 ± 0.9 species in fragments vs. 1.0 ± 1.0 species in desert, $U_{10,12} = 166$, $P < 0.001$). Cavity-nesting species were also 10-fold more populous on average in the fragments than in the continuous desert plots (17.9 ± 19.5 individuals in fragments vs. 1.8 ± 2.4 individuals in desert, $U_{10,12} = 168$, $P < 0.001$). In contrast, the number of ground-nesting species and their abundance did not differ between fragments and like-sized plots in continuous desert (richness, $t_{10,12} = 0.821$, $P = 0.33$; abundance, $t_{10,12} = -1.294$, $P = 0.21$).

Incidence of bee species visiting *Larrea* growing in the desert scrub outside of Tucson was a poor predictor of species occurrence at *Larrea* growing in urban fragments ($\chi^2_{58} = 1613$, $P < 0.0001$; Fig. 2). Several native bee species found visiting *Larrea* at outlying sites in the basin were absent entirely from urban fragments. These include a large-bodied ground-nesting polylectic species (*Eucera venusta*), as well as both a large (*Megandrena enceliae*) and several very small-bodied *Larrea* pollen specialists (four spp. *Perdita*, especially *P. lateralis*). Some species found at most sites in continuous desert were infrequent in fragments (*Colletes salicicola* and *Trachusa larreae*). Other species common in continuous desert, were also common in habitat fragments (*C. lousiae*; Fig. 2). Finally, other bee species increased

markedly in abundance and incidence in fragments, including the cavity-nesting *Larrea* specialist, *Hoplitis biscutellae*, and a ground-nesting generalist, *Anthophora californica* (Fig. 2, Appendix B).

Native bees were more numerous at *Larrea* shrubs growing in smaller fragments ($F_{4,55} = 5.27$, $P = 0.001$, Fig. 3). Bees in each fragment were numerically dominated by a few species; the single most common species at each fragment accounted for 37% and 43% of all individuals in hectare+ and small fragments, respectively. The three most abundant species in each fragment accounted for 60% of the individuals in hectare+ fragments and 72% of individuals in the small size class of fragments.

Bee body size and fragment size

Smaller fragments hosted fewer bee species at *Larrea*, but contrary to our expectation, small-bodied bee species were well represented. Fragments of medium, small and tiny sizes hosted significantly fewer species of both smaller (Wald $\chi^2_4 = 12.22$, $P = 0.016$) and larger bodied bees (Wald $\chi^2_4 = 19.6$, $P = 0.0006$). Both size classes of bees appeared to lose species at nearly equivalent rates in progressively smaller fragments (Fig. 4). Bees of smaller body size were significantly less abundant at flowering *Larrea* in fragments of medium and smaller size (Wald $\chi^2_4 = 13.3$, $P = 0.01$).

Nesting specificity and fragmentation

Consistent with our prediction of greater nest site availability in this urban matrix, the cavity-nesting guild

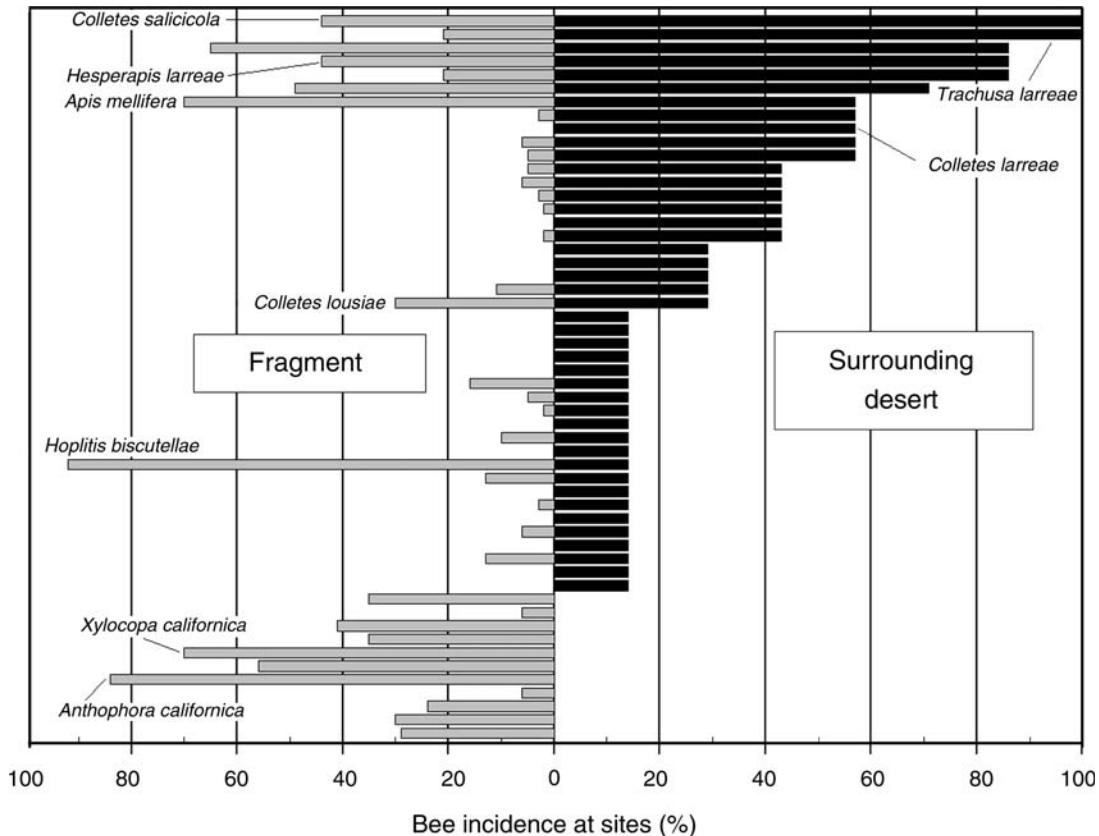


FIG. 2. Patterns of individual species incidences among the bee guild sampled at flowering creosote bush in the Tucson Basin, comparing faunas in desert outside Tucson with those at the pool of 59 habitat fragments in the city.

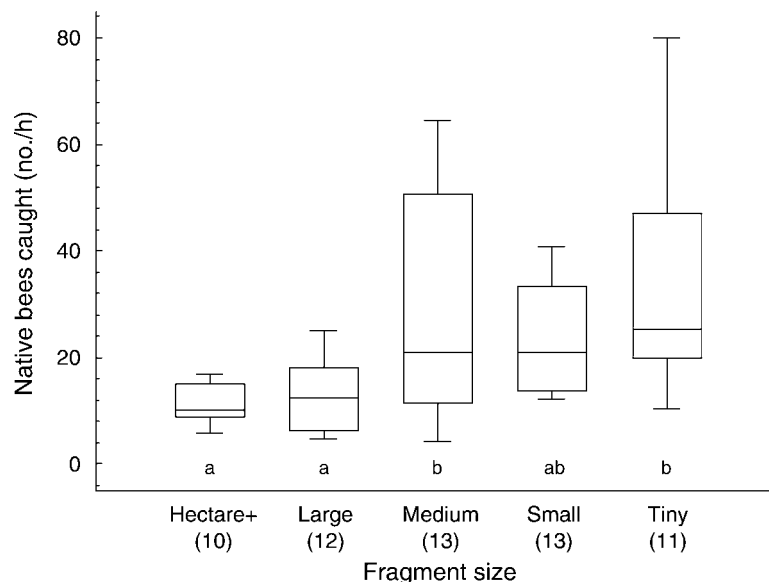


FIG. 3. Bee densities estimated by number of individuals caught per hour in 59 habitat fragments grouped into five size categories. Boxes extend from the 25% (lower edge) to the 75% (upper edge) quartiles, with median observation indicated by the line inside. Bars outside each box extend from the 5% to 95% percentiles. Numbers of fragments in each size category are given in parentheses at the bottom. Size classes subtended by a different letter are significantly different by a posteriori comparison ($P \leq 0.05$).

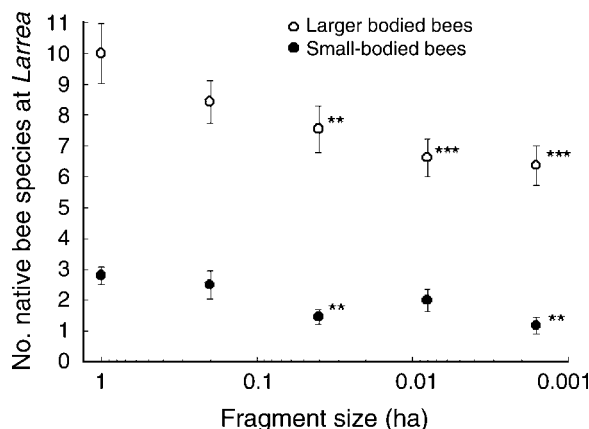


FIG. 4. Number of bee species sampled (mean $\pm$ SE) of large- and small-bodied bees in each fragment size class. Note the log scale.

was represented by more species and its species were more abundant in large fragments within the urban matrix than in like-sized fragments in continuous desert (Fig. 1A, B). In addition, the numbers of species of cavity-nesting floral generalists remained constant across fragment size classes (Wald $X^2_4 = 0.66$, $P = 0.96$), which would be expected if nesting opportunities for these species occur in the size-constant matrix and not the size-variable fragments. *Ho. biscutellae*, the sole cavity-nesting *Larrea* specialist, increased fivefold in its proportional abundance among native species in the five fragment size classes ($F_{4,55} = 3.37$, $P < 0.015$; a posteriori test, small $\geq$ medium = tiny = large $\geq$ hectare). In contrast to cavity-nesting species, ground-nesting bee species declined in smaller fragments, due primarily to a strong negative response by *Larrea*

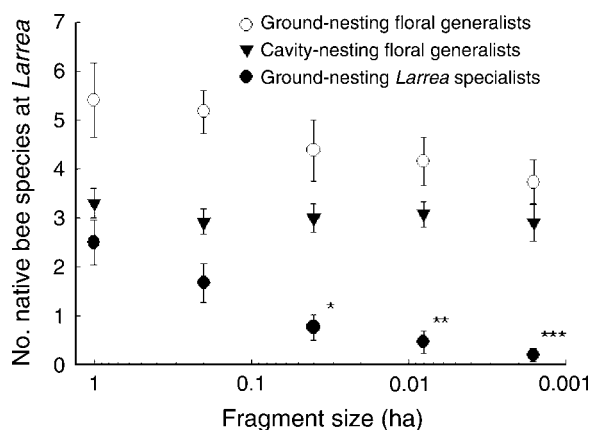


FIG. 5. Number of bee species sampled (mean $\pm$ SE) of different functional groups at flowering creosote bush across fragment size classes. The asterisks denote significant differences (* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$) in species of ground-nesting *Larrea* specialists, comparing smaller size classes with the “hectare+” size class using logistic regression. Note the log scale.

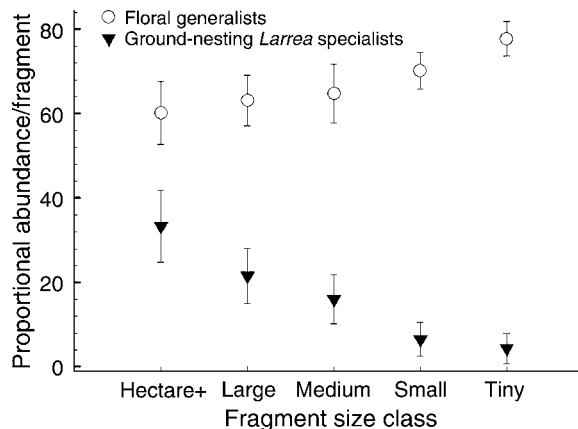


FIG. 6. Proportional abundances (mean $\pm$ SE) of bees sampled at flowering creosote bushes, comparing ground-nesting floral generalists and ground-nesting *Larrea* specialists.

specialist species (Fig. 5; generalist bee species, Wald $X^2_4 = 4.81$, $P = 0.31$; *Larrea* specialists, Wald $X^2_4 = 21.8$, $P = 0.0002$).

Floral specialization and fragmentation

Differences in diet breadth and nesting biology together predicted the response of bee species to habitat size. Habitat fragments 0.75 ha or larger were not different than continuous desert sites in abundance or number of ground-nesting species that were either floral generalists or *Larrea* specialists (Fig. 1C, D). However, in progressively smaller fragment sizes, declines in species sampled and abundance of ground-nesting floral generalists was weak and insignificant, yet was strong and significant for ground-nesting *Larrea* specialists (see *Results: Nesting specificity*; Figs. 5 and 6). *Larrea* specialists that nest underground were typically absent from tiny fragments (Fig. 5), a pattern opposite to that of the cavity-nesting *Larrea* specialist, *Ho. biscutellae*.

The response of *Larrea* specialists to fragment age was similar to their response to fragment size. The oldest fragments were significantly depauperate in ground-nesting bees that were *Larrea* specialists (Wald $X^2_2 = 6.68$, $P = 0.035$; Fig. 7). The most ubiquitous ground-nesting *Larrea* specialist in Tucson, *Hesperapis larreae* (Fig. 2, Appendix B) occupied slightly more of the older than the younger fragments. However, the other three ground-nesting *Larrea* specialists were more often absent from older fragments, which was also true for 12 of 19 ground-nesting generalist bee species. On average, the ratio of ground-nesting floral generalists to specialists were comparable in older and younger fragments. Abundance followed a similar pattern. Older fragments had fewer individuals of each of the four species of ground-nesting *Larrea* specialists than did younger fragments, but their decline was only marginally greater than the decline in abundance of 20 species

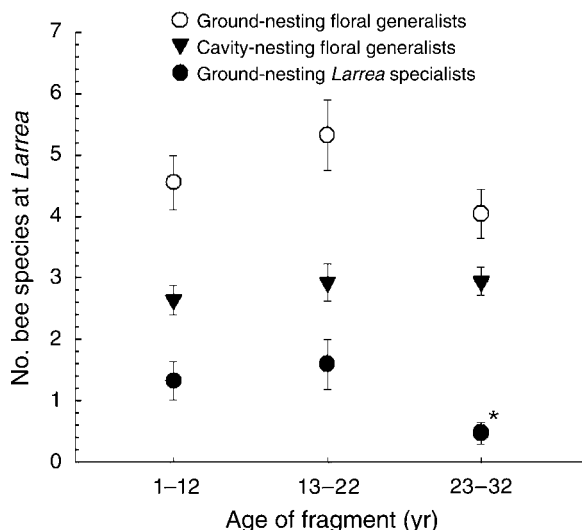


FIG. 7. Number of bee species (mean $\pm$ SE) captured at flowering creosote bush across three fragment age classes. The asterisk denotes a significant difference ($P \leq 0.05$) by logistic regression, comparing numbers of ground-nesting *Larrea* specialists in the oldest and youngest fragment age classes.

of ground-nesting floral generalists ($Z_{4,20} = -2.71$, $P = 0.04$, Wilcoxon test).

DISCUSSION

Mechanisms of fragmentation-induced extirpation

Habitat fragmentation can result in the local extirpation and extinction of species by a number of mechanisms acting alone or in combination. Such mechanisms include invasion by exotic competitors or predators, reduced immigration, disturbance in the surrounding matrix, edge effects, changes in community structure, and reduced population sizes (Turner 1996). Exotic competitors or predators, and reduced immigration can be reasonably dismissed for the *Larrea*-bee system. The honey bee (*A. mellifera*) was the only exotic bee species in our study, and was either rare or absent at >90% of the fragments and probably ecologically inconsequential (Butz-Huryn 1997, Cane 2003, Minkley et al. 2003). Red imported fire ants (*Solenopsis invicta*) and Argentine ants (*Linepithema humile*) or other exotic predatory ants that impact native bees elsewhere in North America and Hawaii (Porter and Savignano 1990, Cole et al. 1992) do not occur in Tucson.

We found that the smallest sized fragments were unusually poor in ground-nesting pollen specialist species but not for ground-nesting species that were small-bodied and presumably did not disperse far (Fig. 4). Immigration rates, which are often related to distance to source populations and species vagility (MacArthur and Wilson 1967), do not explain this pattern easily. Pollen specialist species represent a range of body sizes, and the smallest sized desert fragments

that we sampled were poor in ground-nesting specialist bee species regardless of how close they were to large fragments (data not shown). Possibly, extirpation rates of pollen specialist bee species is unusually increased in small fragments, a finding consistent with the genetic study of specialist and generalist bees by Packer et al. (2005). Small-bodied bees may maintain viable population sizes in small fragments because individuals require less pollen and nectar to successfully reproduce, which buffers them against local extinction from fragments during low resource availability, and diminishes the reliance of population viability on repeat colonization.

We hypothesize that the decline of the *Larrea* specialist, ground-nesting bee fauna over the short term (i.e., the 40–70 years over which most fragments studied herein were formed) is most closely associated with decreased availability of *Larrea* floral resources in fragments and alteration of the surrounding matrix. The importance of *Larrea* resources is indicated by the pronounced decline of most specialist bee species relative to generalists. Specialist bee species should be more sensitive to diminished resources on creosote bush because this is their sole host for pollen and their primary host for nectar. Smaller fragments support fewer bushes and so provide less floral resource, which at some threshold cannot support a resident bee population. Above that threshold, small bee populations may have adequate food, but are prone to extirpation because of stochastic effects. Generalist bee species use native and introduced floral species in addition to *Larrea* that may occur in fragments and the surrounding urban matrix. The larger resource base these alternative resources provide to generalist bees should enhance the chances their populations would persist. Interactions among fragmentation and food resource availability have not been investigated for bees, but have been shown to increase species occurrence of the wood decomposing insect fauna after logging (Davies 2002), and of stem boring insects (Collinge et al. 2001). Other studies have related lower food availability in fragments to fewer bird species (Fernandez-Juricic 2002, Herzog et al. 2003) and increased propensity for them to disperse (Boudjemadi et al. 1999, Sutherland et al. 2000). The relationship of floral resource availability to fragment size means a theoretical minimum area of *Larrea* that would maintain persistent populations of specialist bees could be calculated if better estimates of viable bee population size were available. How reliant bee populations in desert fragments are on immigration and emigration remains an open question.

We did not examine how the urban matrix surrounding the desert fragments affected bee dispersal, mortality, and habitat use as done by others (Ricketts 2001, Schultz and Crone 2001), but we infer that the effect of the urban matrix posed a substantial barrier to some bee species and offered an ecological opportunity for others. For ground-nesting species that were floral specialists of *Larrea*, the urban matrix probably limited recoloniza-

tion of isolated sites after populations were extirpated because their food resources were increasingly isolated. We favor this hypothesis over one that concerns loss of nest sites because Tucson landscapes are mostly planted with xeric-adapted vegetation and maintain property with exposed soil favorable for nesting. Consistent with this resource isolation hypothesis was our finding that floral generalist, ground-nesting bee species did not respond strongly to decreasing fragment size. The intervening matrix offered some resources to generalist species and so posed less resistance to dispersal among desert fragments for them.

The urban matrix appears to offer greater nesting opportunities for bee species that excavate or co-opt holes aboveground and nested in cavities (*Xylocopa*, *Hoplitis*, *Hylaeus*, *Ceratina*, some *Megachile*). Both species number and abundance of cavity-nesting species increased in fragments relative to continuous desert (Figs. 1 and 2), and they composed a greater proportion of the fragment fauna as fragment size decreased. The only *Larrea* specialist species that nested in cavities, *Ho. biscutellae*, was widespread and common in habitat fragments and invariably rare in outlying desert. Nesting substrate may be a limiting resource for cavity-nesting bees in undisturbed desert either because trees are relatively uncommon or wood riddled with cavities made by boring insects are often exposed and exceed the thermal tolerance of most bee larvae. Fencing, homes, and shade trees in urban areas may, in contrast, provide many suitable nest sites. Other studies document a similar response of cavity-nesting bees in disturbed habitats. Cavity nesters increased more than ground nesters in remnant meadows surrounded by German farmland (Tscharnke et al. 1998 and references therein). In fragments of subtropical dry forest in Argentina, several cavity-nesters (*Xylocopa ordinaria*, *Chrysaeris* spp.) also increased in abundance in fragments where decreases had been expected (Aizen and Feinsinger 1994a; Appendix). Nesting habits of bees may be particularly valuable for predicting how native bee faunas respond to habitat fragmentation in urban and possibly other settings. A decline in bee and wasp diversity was attributed to nesting substrate loss in a British heathland by Archer (1989).

Species-specific responses vs. ecological functional groups

The patterns of incidence and abundance of spring bees at *Larrea* in urban habitat fragments were not predictable from their local or regional incidence or abundance, contrary to some theoretical expectations that propose these factors should predict their occurrence in fragmented habitats (Bolger et al. 1997). For example, *Trachusa larreae* and *Hesperapis larreae* were the two most abundant and widespread *Larrea* specialists in the Tucson Basin and across the southwestern United States (Minckley et al. 1999, Cane et al. 2005); however, the former declined sharply in fragments, and the latter remained a dominant component of fragment

faunas (Fig. 2). Similarly, one ground-nesting species of floral generalist, *Lasioglossum sisymbrii*, was both widespread and common at *Larrea* in the Tucson Basin, but rare in the fragments, and another, *A. californica*, was rare and infrequent at *Larrea* everywhere but in Tucson's urban fragments (Fig. 2, Appendix B; Minckley et al. 1999). Didham et al. (1998) suggest that one reason for such incongruity between continuous and fragmented habitats may be that naturally rare species are adapted to rarity and persist more easily than common widespread species when habitats are perturbed. This hypothesis did not consistently predict how the *Larrea* bee community responded to urban fragmentation. Only when we combined species into ecologically functional groups was it evident that fragmentation and declining habitat area increased extirpation of ground-nesting specialist species, little affected ground-nesting floral generalist species, and dramatically increased cavity-nesting species in urban fragments. This was possible because the bee fauna that use *Larrea* is a diverse species group with considerable ecological and life history variation. These response patterns may not have been apparent if species were treated as individual units of analysis, or all species were pooled into one analysis.

Generalization and conservation implications

Incomplete sampling of rare species adds uncertainty for faunal samples (Gotelli and Colwell 2001), and many bee species are rare in all bee communities studied (Minckley et al. 1999, Williams et al. 2001). Rare species may thus have been present in this study, but were not collected. However, our overall conclusions are based on a sampling protocol where effort increased as fragment size declined. Sampling was therefore biased such that it provided conservative tests of our hypotheses. We are therefore confident in detecting strong shifts in incidence or abundance of bee species that were common at *Larrea* before or after fragmentation, but hesitate to interpret decreasing incidences of any bee species that were probably already rare at *Larrea* before fragmentation.

Extrapolation of our results to other bee faunas experiencing habitat fragmentation should be considered carefully and incorporate knowledge of floral host ecology, nesting requirements, and historical land use. Not only is creosote bush a dominant perennial shrub native to the Sonoran desert, it also blooms more reliably than any other co-occurring annual and perennial plant species studied to date (Bowers and Dimmitt 1994). For floral hosts that are not so common, dependable, or widespread, future studies could find these hosts are less able to support their bee faunas in comparably fragmented habitats. The bee community we studied was ecologically diverse. If, for example, the study was of a community composed of only generalist bee species, host use redundancy either could be sufficient to maintain adequate reproduction by the

host plant species and for the number of pollinator species to not decline (Mommott et al. 2005), or result in subtle changes only detectable by evaluating interaction webs (Vasquez and Simberloff 2002). The increase of cavity-nesting bees in Tucson reflects the importance of nesting substrates to bee diversity in desert scrub environments. In contrast, cavity-nesting bees or other species dependent on forested habitats may decline when urban areas expand into natural forest. Historical land use patterns around growing metropolitan areas also influence the later impacts of urban habitat fragmentation. Tucson has expanded mostly into intact desert where a rich diversity of native bees occurs. However, bee faunas in urban areas that are expanding into space previously dominated by agriculture (e.g., Phoenix, Arizona) may already be depauperate in species (e.g., Kremen et al. 2002).

In need of further study is how fragmentation effects on the bee fauna that visits *Larrea* translate to changes in gene flow and reproductive success among *Larrea* and co-occurring flowering plant species. For example, there is no reason to believe specialist bees of *Larrea* will invariably prove to be more important than generalists as pollinators of *Larrea* (Minckley and Roulston 2006), or that greater seed set is achieved by cavity-nesting than by ground-nesting species. This study therefore provides a solid baseline for unraveling the complex interactions that make up these pollination mutualisms, but does not answer these still interesting questions.

ACKNOWLEDGMENTS

This study benefited from discussions with Jerome Rozen, Jr., Peter Marchand, Charles Michener, and Rob Brooks. Barbara Minckley provided considerable logistical support. Useful revisions were provided by Justin Schmidt, Jordi Bosch, Rae Winfree, and anonymous reviewers of this and an earlier draft. Research support was provided by the Joint Program on Terrestrial Ecology and Global Change, administered through NSF grant IBN-9652599.

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APPENDIX A

Location of all habitat fragments and six of the 12 continuous desert sites in the study (*Ecological Archives* A016-027-A1).

APPENDIX B

Species of bees sampled at *Larrea* habitat fragments in Tucson, including total counts of individuals, and each species' dietary and nesting habits (*Ecological Archives* A016-027-A2).