FACULTATIVE NECTAR-FEEDING BEHAVIOR IN A GLEANING INSECTIVOROUS BAT (*ANTROZOUS PALLIDUS*)

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Foraging plasticity that includes facultative nectarivory is extremely rare in temperate insectivorous bats. We investigated flower-visiting behavior of pallid bats (*Antrozous pallidus*, Vespertilionidae) to bat-adapted flowers of cardon cacti (*Pachycereus pringlei*) to determine whether pallid bats consume floral nectar or visit flowers to opportunistically glean insects attracted to flowers. In 2007 and 2008, we recorded flower-visiting behavior of bats using infrared videography on 143 cactus-nights across 14 sites in Baja California, Mexico. Pallid bats were regular visitors to cardon flowers and consumed floral nectar by plunging their faces into the corolla to lap pooled nectar. We recorded 1,198 flower visits by *A. pallidus*, which accounted for 10% of visits to flowers by all bats. Pallid bats visited flowers on 57% of cactus-night observations (*n* = 81/143) and 52% (*n* = 28/54) of captured bats had visible pollen loads. Flower-visiting activity by *A. pallidus* was concentrated early in the evening where nectarivorous Mexican lesser long-nosed bats (*Leptonycteris yerbabuenae* [= *curasoae*], Phyllostomidae) were present, but more evenly distributed throughout the night at sites without *L. yerbabuenae*, suggesting potential competitive exclusion among these nocturnal chiropteran pollinators.

Key words: *Antrozous pallidus*, bat pollination, columnar cacti, foraging behavior, *Leptonycteris yerbabuenae*, nectarivory

Behavioral plasticity in foraging may be a key innovation that leads to the evolution of novel diet strategies and speciation. For example, foraging plasticity is hypothesized to have played a role in the adaptive radiation of the diverse neotropical phyllostomid bats (Freeman 2000; Gillette 1975). Most of the wide diversity of diets found in Microchiroptera (including frugivory, nectarivory, sanguinivory, and carnivory) is represented in a single family, Phyllostomidae, and each foraging modality may have evolved only once (Ferrarezzi and Gimenez 1996; Schondube et al. 2001; Wetterer et al. 2000). Almost all other microchiropteran bats, including the carnivorous bats such as megadermatids and nycterids, retain ancestral insectivorous feeding habits, demonstrating a remarkably stable adaptive peak (Freeman 2000).

Bats with nectarivorous and frugivorous foraging strategies likely evolved from insectivorous ancestors that initially gleaned insects from plant surfaces and later evolved to rely on plant-based diets (Gillette 1975). In the Western Hemisphere, there are approximately 38 species of nectarivorous

phyllostomid bats, with species richness peaking at tropical latitudes (Fleming 2005; Simmons 2005). Nectarivorous bats are notably absent in temperate zones, probably because obligate nectar-feeders require year-round availability of flowers (von Helversen and Winter 2003). Some species of phyllostomid bats show varying flexibility and specialization in diet, supplementing nectar diets with insects and pollen (Schondube et al. 2001).

Very few insectivorous bat species are known to supplement diets with nectar, fruit, or other food sources (Ferrarezzi and Gimenez 1996). Outside the Phyllostomidae, there is only a single known species of insectivorous bat with facultative nectarivorous feeding habits (*Mystacina tuberculata*—Arkins et al. 1999). Rarity of diet plasticity in insectivorous bats is puzzling given that omnivory is common in other mammalian taxa (Nowak 1999) and many predominately insectivorous birds include substantial amounts of nectar and fruit in their diets (Wolf and Martínez del Rio 2003; Wolf et al. 2002). Facultative nectar-feeding by insectivorous bats could shed light on the evolution of feeding habits in bats and provide clues about the ecological context for evolution of behavioral plasticity and dietary shifts.

Our research investigated novel flower-visiting behavior of pallid bats (*Antrozous pallidus*, Vespertilionidae) at bat-adapted flowers of the cardon cactus (*Pachycereus pringlei*,

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Cactaceae) in northwestern Mexico. Pallid bats hunt by passive listening and glean large arthropods, such as scorpions or crickets, off the ground or plant surfaces (Bell 1982; Hermanson and O'Shea 1983). Their broad geographic range extends across western North America from central Mexico to southern British Columbia, Canada (Weyandt and Van Den Bussche 2007). In northwestern Mexico, *A. pallidus* is a common resident of Sonoran Desert habitats and occurs sympatrically with nectarivorous Mexican lesser long-nosed bats (*Leptonycteris yerbabuenae*, Phyllostomidae) in habitats dominated by cardon cacti on the Baja California peninsula (Frick et al. 2008a; Hermanson and O'Shea 1983). *L. yerbabuenae* is an important pollinator of *P. pringlei* and other columnar cacti in northwestern Mexico and extensive research has been conducted on this endangered species (see Fleming and Valiente-Banuet [2002] for a review).

Pallid bats covered in pollen or fruit smears have been previously documented in Sonoran Desert habitats, but pollen and smears were thought to result from gleaning moths or other insects at cactus flowers or fruit (Barbour and Davis 1969; Herrera et al. 1993; Howell 1980). Pallid bats lack obvious morphological specializations for nectar-feeding, such as elongated noses and tongues, and thus were suspected to lack the ability to successfully extract nectar from flowers (Herrera et al. 1993). However, in 2005 we observed multiple pallid bats repeatedly visiting cardon flowers and behavior at flowers strongly suggested that these insectivorous bats might be seeking nectar.

This unusual behavior provides an opportunity to investigate a rare chiropteran foraging strategy that could provide insight on the evolution of feeding habits. Our research goals were to determine the extent to which *A. pallidus* nectar-feeds or opportunistically gleans insects at flowers; to assess the geographic and temporal variability in flower-visiting activity by *A. pallidus* on the Baja California peninsula; and to compare patterns of visitation rates of *A. pallidus* and *L. yerbabuenae*, the primary pollinator of the cardon.

MATERIALS AND METHODS

Site description.—Study sites occurred in Sonoran Desert vegetation dominated by columnar cacti (*P. pringlei* and *Stenocereus thurberi*) on the Baja California peninsula and on islands in the Gulf of California in northwestern Mexico (Fig. 1). We collected data from late March to late May in 2007 and 2008, during the flowering season of *P. pringlei* (Fleming et al. 1998, 2001). Geographic range of *P. pringlei* includes roughly three-fourths of the Baja California peninsula, extending northward from the southern tip of the peninsula (Fig. 1). Flowers are large, white, and slightly odiferous, conforming to a chiropterophilous pollination syndrome (Fleming et al. 1994). Individual flowers last for a single night, opening at sunset and closing by the following morning or midday (Fleming et al. 1994). Plants have multiple flowers (range: 1–25) open each night for usually 6–8 weeks during the flowering season (Fleming et al. 1994, 2001).
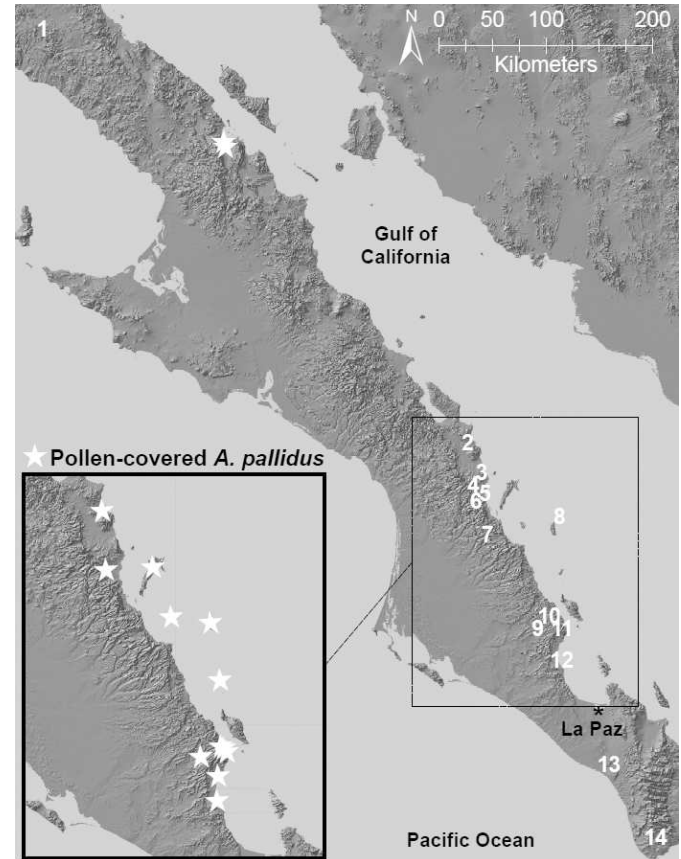

FIG. 1.—Map of study region. Geographic range of cardon (*Pachycereus pringlei*) extends throughout stretch of Baja California peninsula shown and on all gulf islands. Locations of video sampling of flower-visiting activity are labeled 1–14. Stars indicate locations where *Antrozous pallidus* with a visible pollen load was captured.

Populations are trioecious, but presence of male plants may vary in relation to densities of *L. yerbabuenae* (Fleming et al. 1998).

Flower visitation activity.—We recorded bat visits to cardon flowers using infrared closed-circuit television cameras extended on 3.6-m tripods and linked to mini–digital video recorders for data compression and storage. We calibrated motion detection sensitivity to ensure that all visits to flowers were recorded. Cameras started recording as flowers opened at sunset until dawn, thereby censusing all nocturnal visits. Flower visits by bats were counted as the number of events observed where a bat's face made contact with a flower. *A. pallidus* and *L. yerbabuenae* were easily distinguishable based on ear and face length, presence of tail membrane, flight pattern, and behavior at flowers. Sphingid moths (Lepidoptera: Sphingidae) also were recorded visiting flowers and predatory attacks by bats on moths were noted if a bat was observed in clear pursuit of a moth.

We recorded nocturnal visits to cactus flowers for 143 cactus-nights at 14 locations along a 900-km transect of the Baja California peninsula, including 14 cacti on Isla Santa Catalina in the Gulf of California (Table 1). Number of sampled cacti varied by location (median: 8; range: 1–24), but

TABLE 1.—Sampling effort, plant characteristics, and mean visitation rates of bats at 14 locations in northwestern Mexico. Data are presented as means with standard errors in parentheses.

| | | | | | | Visits per flower per night | |
Site	No. cacti	No. cactus-nights[a]	No. nights sampled	No. flowers recorded per cactus	Total flowers per cactus	*Antrozous pallidus*	*Leptonycteris yerbabuenae*
1	1	1	1	1.0 (—)	1.0 (—)	23 (—)	0 (—)
2	16	16	4	4.4 (0.43)	8.8 (1.70)	1.41 (0.71)	2.58 (0.91)
3	8	16	4	3.4 (0.75)	7.9 (1.88)	2.89 (1.02)	94.95 (25.25)
4	8	16	4	1.7 (0.33)	2.0 (0.46)	3.24 (1.42)	19.02 (4.49)
5	16	24	6	4.1 (1.08)	6.8 (1.66)	1.05 (0.38)	58.28 (10.21)
6	8	8	2	6.6 (0.50)	11.3 (1.98)	0.86 (0.49)	15.17 (6.38)
7	8	8	2	3.1 (0.90)	5.3 (1.96)	0.14 (0.10)	21.28 (8.59)
8	14	14	5	3.6 (0.34)	8.9 (2.01)	0.29 (0.12)	0 (0)
9	8	9	3	2.3 (0.50)	2.9 (0.56)	15.31 (4.02)	32.35 (6.59)
10	8	8	2	3.0 (0.78)	4.8 (1.06)	11.83 (2.54)	92.29 (12.37)
11	8	8	2	6.1 (0.99)	8.1 (1.36)	1.15 (0.71)	1.20 (0.35)
12	8	8	2	5.5 (0.76)	9.0 (2.04)	1.42 (0.77)	0 (0)
13	3	3	1	1.7 (0.33)	2.0 (0.58)	0 (0)	12.5 (6.93)
14	4	4	1	5.5 (1.66)	13.5 (3.86)	4.95 (1.64)	0 (0)
Totals	118	143	39	—	—	—	—

[a] Includes individual cacti sampled on multiple nights.

we typically sampled 4 cacti per night for 2 nights per location (Table 1). Cacti sampled on the same night were >40 m apart. We resampled 4 cacti at each of 3 locations (sites 3, 4, and 5; Fig. 1) during the early, mid, and late flowering season in 2007 to assess seasonal variability within sites. In cases where a cactus did not have open flowers present during a repeat visit, we used the nearest flowering neighbor.

Plant sex was determined for 82 plants by visual inspection for the presence of ovules and pollen in dissected flowers just after opening on nights when visits were not recorded. We predicted that *A. pallidus* might prefer female flowers if flower size affected a bat's ability to extract nectar, because female flowers have significantly shorter corolla lengths (Fleming et al. 1994). We compared differences in visits by *A. pallidus* according to plant sex and compared geographic variability of visits among 13 sample locations (site RC01 included a single cardon and was excluded from analysis) using nonparametric Kruskal–Wallis analysis of variance (ANOVA) in R (version 2.4.1, R Development Core Team). In all analyses, cacti were considered the sample unit and visits were counted per number of open flowers in the camera view.

Feeding behavior at flowers.—Behavior of pallid bats at selected flowers was recorded on high-definition mini–digital videotapes using a Sony HDV Handycam Nightshot Camera (Sony Corp., New York, New York) fitted with external infrared illuminator. High-resolution video was not included in estimates of nightly visitation rates to flowers because high-definition tapes recorded only approximately 1 h of flower-visiting activity. High-resolution imagery was used for close-up recordings of bats at flowers to describe behavior. To determine whether pallid bats consumed nectar, we cut openings into the side of cardon flowers to reveal the nectary and recorded feeding behavior inside the corolla by free-flying (noncaptive) bats (Supporting Information, Video S1 and Video S2, available

online at http://dx.doi.org/10.1644/09-MAMM-A-001.s1 and http://dx.doi.org/10.1644/09-MAMM-A-001.s2).

Presence of cactus pollen on pallid bats.—Mist-net sampling of bats was conducted at 28 locations on the Baja California peninsula and on islands in the Gulf of California as part of this and previous research from 2005 to 2008 (Frick et al. 2008a, 2008b; Fig. 1). Mist nets were placed to maximize captures in dry arroyos, desert scrub habitats, or over ephemeral freshwater pools. We opened mist nets at sunset and monitored them at least every 15 min for 4 h. Captured bats were identified to species, age, sex, and reproductive status (Anthony 1988; Racey 1988). Animals were handled in accordance with guidelines approved by the American Society of Mammalogists (Gannon et al. 2007) and were approved by Animal Care and Use Committees at Oregon State University and the University of Florida. Presence of pollen on pallid bats was noted before captured bats were placed in a cloth holding bag so that pollen was not rubbed off before processing and release of the animals. Pollen loads were scored as light, medium, or heavy dusting on dorsal and ventral torso, ears, face, and wings. Pollen was visually identified based on color and texture.

RESULTS

Flower-visiting behavior of *A. pallidus* is strikingly different from behavior of nectarivorous *L. yerbabuenae*, which hovers and extracts nectar with a long, specialized tongue (Horner et al. 1998; Supporting Information, Video S1). *A. pallidus* lands on a flower and plunges its head and upper torso into the corolla while grasping the rim with its wings and feet (Fig. 2). Video recordings of flowers with openings cut in the corolla revealed that *A. pallidus* laps at pooled nectar in the base of the corolla (Supporting Information, Video S2).
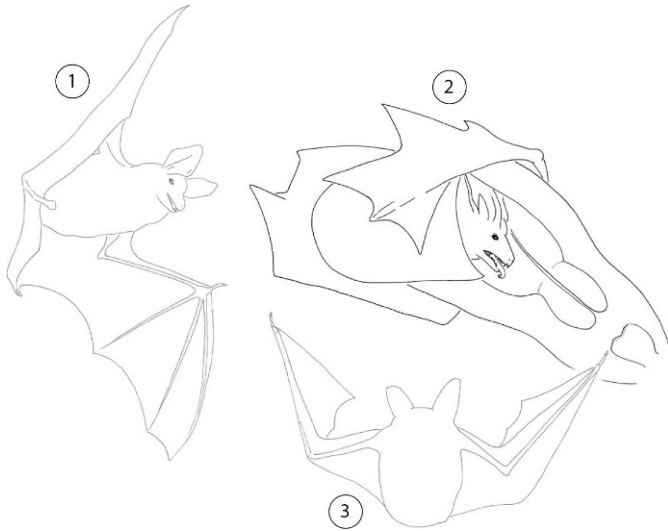
F<small>IG</small>. 2.—Nectar-feeding behavior of *Antrozous pallidus* at cardon flowers. 1) Approach phase; 2) feeding phase with head well inside corolla; and 3) withdrawal phase.

Pallid bats routinely consumed floral nectar from cactus flowers on the Baja California peninsula. We recorded 1,198 visits to cardon flowers by *A. pallidus* (10% of all bat visits) and 10,858 visits by *L. yerbabuenae* (90% of all bat visits). These totals include repeat visits to flowers by an unknown number of individuals. We recorded visits by *A. pallidus* on 57% of sampled cactus-nights ($n = 143$) and recorded visits by *L. yerbabuena* on 76% of cactus-nights. We recorded 29 events of *A. pallidus* chasing or capturing sphingid moths at flowers. Interactions with moths made up only 2% of video observations. Observations of predatory attacks by *A. pallidus* on moths included pallid bats trapping sphingid moths inside flowers, but the vast majority (98%) of flower-visiting activity was consistent with nectar-feeding behavior.

Geographic and temporal variability of flower visits.—Pallid bats visited cardon flowers throughout the geographic range of *P. pringlei* on the Baja California peninsula (Fig. 1). Mean number of visits by *A. pallidus* per flower per night was 3.17 ± 0.51 *SE* ($n = 143$ cactus-nights), but visitation rate varied significantly with location (Kruskal–Wallis ANOVA; $\chi^2 = 44.63$, *d.f.* = 12, $P < 0.0001$; Fig. 3). Highest levels of flower-visiting by *A. pallidus* occurred at 2 sites in the Sierra de la Giganta (sites 9 and 10; Fig. 1), where the mean number of visits per flower per night was 15.3 and 11.8, respectively (Fig. 3). The only location where we failed to record activity of *A. pallidus* at flowers was at a site on the Pacific Coast where we sampled only 3 cacti for a single night during which there was heavy coastal fog (site 13; Fig. 1).

Most flower-visits by *A. pallidus* (67%) occurred in the 2 h following sunset (2000–2200 h) when flowers had just opened (Fig. 4). However, the proportion of visits by hour of night differed according to whether *L. yerbabuenae* was recorded at a site (Pearson's $\chi^2 = 199.83$, *d.f.* = 8, $P < 0.00005$). In locations where *L. yerbabuenae* was not recorded, activity of *A. pallidus* was not concentrated during the early evening

hours and was more similar to the temporal pattern of visits by *L. yerbabuenae* (Fig. 4).

Contrary to our prediction that *A. pallidus* may prefer smaller flowers on female plants, there was no significant difference among visitation rates according to plant sex (Kruskal–Wallis ANOVA; $\chi^2 = 0.95$, *d.f.* = 2, $P = 0.62$).

Pollen loads on bats.—Fifty-two percent of *A. pallidus* ($n = 54$) from 20 locations on Baja California and gulf islands had pollen visible on their bodies at the time of capture (Fig. 1). Pollen was usually present over the entire face and ears and often extended to mid-torso on both the ventral and dorsal sides. Pollen loads ranged from light dusting to a heavy covering of pollen on skin and fur.

DISCUSSION

Pallid bats in Sonoran Desert habitats display unusual plasticity in their foraging behavior and are the 1st known example of an insectivorous bat with facultative nectarivorous habits in northern temperate regions. Nectar-feeding behavior appears to be widespread on the Baja California peninsula as roughly one-half of pallid bats captured in the region had visible pollen loads and flowers were visited at almost all locations sampled (Fig. 1). Pallid bats may have initially learned about floral nectar by predatory pursuit of sphingid moths or other insects attracted to flowers, but examination of our data demonstrates that pallid bats now visit flowers primarily to drink floral nectar.

Behavior of pallid bats provides a compelling living example of the food source duality model of evolution of phytophagous foraging habits in bats, which suggests that plant-based diets evolved from insectivorous bats specialized for gleaning insects from plant surfaces (Freeman 2000; Gillette 1975). As a dramatic example, 1 of the 29 moth attacks recorded during our study was of a pallid bat trapping a sphingid moth inside a cardon flower (the moth ultimately escaped from the flower and eluded the bat). However, most visits (98%) show a ''grasp and plunge'' foraging behavior where a pallid bat alights on a flower and grasps the rim of the corolla with its wings and feet while plunging its face into the corolla to lap nectar from the nectary (Fig. 2).

Cactophily (opportunistic or obligatory reliance on cactus nectar or fruit) has independently evolved multiple times in phyllostomids, and 17 phyllostomid species visit cacti at least occasionally (Simmons and Wetterer 2002). Evolutionary dietary shifts to opportunistic cactophily may be common among nectarivorous or frugivorous phyllostomids whose geographic ranges overlap those of chiropterophilous columnar cacti (Simmons and Wetterer 2002). Facultative nectar-feeding by pallid bats demonstrates convergent evolution of cactophilic habits and supports the hypothesis of Simmons and Wetterer (2002) that cactophily can arise as independently evolved population-level phenomena. The ecological opportunity for a shift to nectar-feeding from another foraging modality may be facilitated by chiropterophilous cactus flowers that are large, white, and nocturnal and thus suited for bat visits.
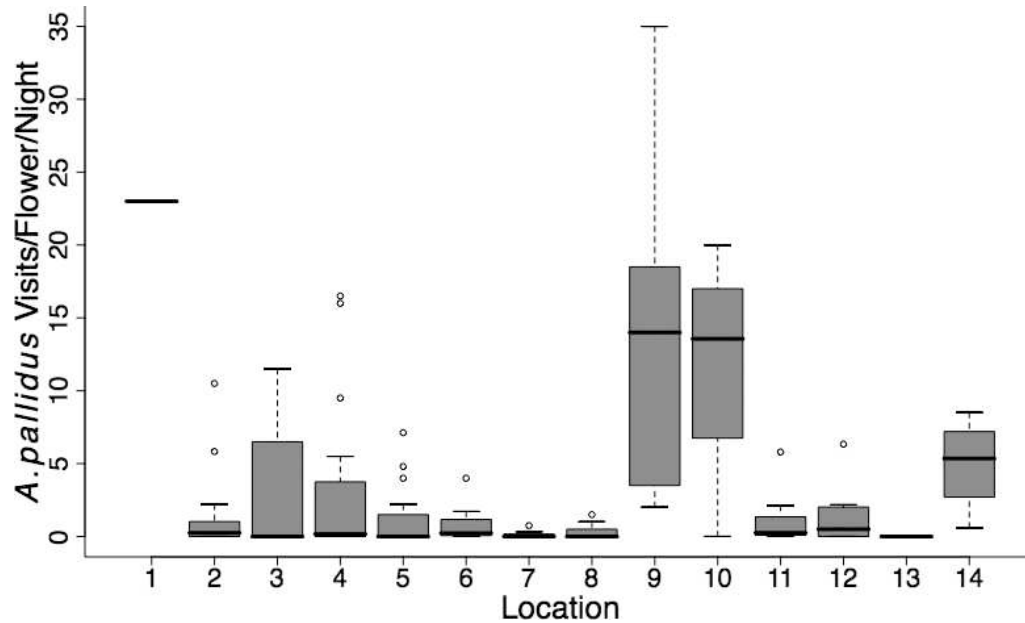
F<small>IG</small>. 3.—Flower visitation rate by *Antrozous pallidus* at 14 locations in northwestern Mexico.

Examination of our data raises interesting questions about foraging trade-offs between search and handling time for large protein-rich prey like sphingid moths and widely available (although seasonally limited) carbohydrate-rich nectar. Moth activity at cardon flowers was highly variable across sites in 2007 and apparently was absent (or at least never recorded) at all sites in 2008, suggesting that moths may be unreliable or unpredictable prey at cactus flowers. In contrast, cardon nectar is a prolific resource across the Baja California peninsula from late March to early June. Although a given flower is only open for 1 night, plants generally have multiple flowers open each night over a flowering season of 6–8 weeks, making floral nectar a spatially and temporally predictable resource (Fleming et al. 2001).

Diets of pallid bats vary regionally based on prey availability and individual foraging behavior (Johnston and Fenton 2001). In addition to nectar and sphingid moths, terrestrial arthropods (scorpions) are likely components in diets of pallid bats in our study region (Hermanson and O'Shea 1983). Flexibility to forage for both arthropods (including nectar-seeking moths) and nectar may increase overall foraging success and fitness of individuals in a resource-variable landscape (Parrish 2000). Ground-gleaning and behaviorally flexible predatory bats tend to have significantly larger brains, which may help explain the ability of *A. pallidus* to exploit a novel food source (Ratcliffe et al. 2006). Predominately insectivorous birds, including white-winged doves (*Zenaida asiatica*) and several species of woodpeckers, regularly consume columnar cacti nectar in Sonoran Desert habitats (Wolf and Martínez del Rio 2003).

Cactus nectar and fruit in xeric desert landscapes provide vital sources of water to some species (Wolf et al. 2002). Pallid bats may drink nectar not only for energy rewards but also for hydration, because free-standing water is a limited resource in desert habitats. If pallid bats primarily drink nectar for hydration, we might expect rates of flower visitation by *A.*

pallidus to be higher in areas more distant from sources of freshwater. Examination of our data shows no relationship between proximity of freshwater and flower-visiting activity by pallid bats. In fact, flower-visiting activity by *A. pallidus* was highest in the Sierra de la Giganta (sites 9 and 10; Fig. 1) in areas in close proximity to permanent freshwater. A simple relationship between visitation rates and proximity to freshwater could be obscured by other factors that may covary with both visitation rates and water availability, such as local population abundance. Given that we have no estimates of relative abundance across our study sites nor information about how abundance relates to flower-visiting activity, we cannot rule out that cactus nectar may be important for hydration in desert populations of pallid bats without further physiological research.

Stable isotope studies have revealed the ecological importance of columnar cacti for nutrients and water to desert animal communities (Wolf and Martínez del Rio 2003). Herrera et al. (1993) analyzed carbon stable isotopes to determine carbon composition of pallid bats in relation to columnar cacti and agave populations (crassulacean acid metabolism [CAM]–based carbon) in Sonoran Desert habitats. Their results suggested that delta ^{13}C values from pallid bats were more representative of CAM-based sources than other sympatric insectivorous bat species and tissue samples from 4 bats collected on the Baja California peninsula had the highest (most CAM-like) ^{13}C values (Herrera et al. 1993). We hypothesize that *P. pringlei* is likely an important source of nutrition for pallid bats in Baja California and perhaps in other desert regions with columnar cacti. Research using stable isotopes is underway to determine seasonal variability and relative importance of nectar versus arthropods as nutritional resources for desert populations of pallid bats.

Pallid bats may serve an important role in the reproductive dynamics of cardon populations. Visual inspection of stigmas
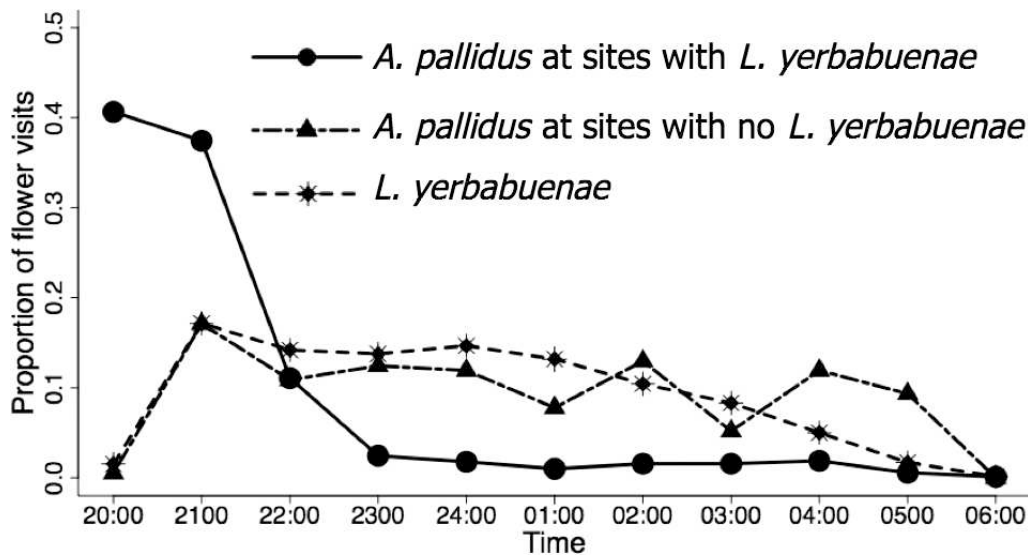
Fig. 4.—Temporal patterns of flower visitations by *Antrozous pallidus*: A) at sites with *Leptonycteris yerbabuenae* present (*n* = 903 visits to 86 cacti at 10 sites); B) at sites with no recorded visits by *L. yerbabuenae* (*n* = 193 visits to 27 cacti at 4 sites); and C) temporal pattern of flower visits by *L. yerbabuenae* for comparison (*n* = 10,261 visits to 86 cacti at 10 sites).

exposed to visits by pallid bats showed generous deposition of pollen on stigma lobes, suggesting that pallid bats are legitimate pollinators of cardon. Visits by pallid bats comprised roughly 10% of all bat visits recorded at cardon flowers, and 67% of all visits occurred in the first 2 h after flowers opened and before most flower-visiting activity by *L. yerbabuenae* at sites with both species (Fig. 4). In 4 locations, pallid bats were the only nocturnal visitors during our sampling efforts (Table 1). Timing of visits by pallid bats and geographic variability in visitations suggest that pallid bats are likely important pollinators of cardon.

Differences in seasonal and nightly movement patterns of pallid bats and Mexican lesser long-nosed bats could have consequences for gene flow among cardon populations. The pallid bat is a resident species, whereas Mexican lesser long-nosed bats are seasonal migrants that follow blooming agaves and columnar cacti along the Baja California peninsula and may cross the Gulf of California to mainland Mexico (Fleming et al. 1993; Morales-Garza et al. 2007). In addition to long-distance migratory movements, *L. yerbabuenae* can commute 30 km to foraging areas from a maternity roost in a given night (Horner et al. 1998). In contrast, home ranges of *A. pallidus* are likely considerably smaller (<10 km diameter). Pollination by pallid bats could result in more localized gene flow, particularly for insular populations where pallid bats are island residents and *L. yerbabuenae* may be absent or unreliable visitors (Frick et al. 2008a).

Flower visitations by pallid bats were concentrated in early evening before arrival of *L. yerbabuenae* at sites where both species were recorded but were more evenly distributed throughout the night at sites without *L. yerbabuenae* (Fig. 4). Observations of interspecific interactions at flowers reveal potential aggressive behavior, although similar behavior between conspecifics of *L. yerbabuenae* also was recorded

and we were cautious to definitively classify recordings of inter- and intraspecific chasing behavior as social versus aggressive interactions. The strong contrast in timing of visits suggests that processes such as competitive exclusion or negative interspecific interactions may influence foraging behavior.

Flower-visiting activity by pallid bats was variable among sample locations, but ubiquitous across a large geographical area (Figs. 1 and 2). Our data and observations suggest that there is a background level of flower-visiting activity by *A. pallidus* throughout the Baja California peninsula that is punctuated by hotspots or spikes in activity on particular nights or sites. Repeat sampling at 3 locations in 2007 suggests that visitation rate is variable across the flowering season within sites; some of the observed geographic variability could be due to this temporal variability, because sites were not sampled simultaneously. Variability in flower-visiting activity could be related to either differences in population densities of *A. pallidus*, spatial or temporal variation in reliance on nectar in individual's diets, or a combination of these factors.

Whether flower-visiting behavior by *A. pallidus* extends to other parts of its geographic range is unknown. In similar habitats in Sonora, Mexico, researchers have captured *A. pallidus* dusted with cactus and agave pollen (Herrera et al. 1993), but flower-visiting activity by *A. pallidus* appears less common in this region because years of intensive research by Fleming and colleagues on nocturnal pollinators of columnar cacti did not document a phenomenon similar to what we report here (T. H. Fleming, University of Miami [emeritus], pers. comm.). Future research is needed on the broadscale variability of flower-visiting behavior of *A. pallidus* in other ecological contexts, which may influence foraging opportunities and behavior.

Foraging plasticity to include nectar or fruit in an insectivorous diet has been rarely observed in bats, yet is common in birds and other mammalian groups. Availability

of bat-adapted flowers may have provided a novel eco-
logical opportunity to *A. pallidus* to shift toward a more
generalized diet. For bats, gleaning insects from plant sur-
faces may be the innovation that allows behavioral shifts to
increase dietary breadth (Gillette 1975). Facultative nectar-
feeding behavior of *A. pallidus* supports this food source
duality model of evolution of feeding strategies and highlights
the potential role of behavioral flexibility in evolution of
dietary strategies.

RESUMEN

La plasticidad de forrajeo incluyendo a los nectarívoros
facultativos es rara en murciélagos insectívoros templados. En
este trabajo investigamos el comportamiento del murciélago
pálido (*Antrozous pallidus*, Vespertilionidae) que visita flores
de cardón adaptadas para el consumo de murciélagos
(*Pachycereus pringlei*, Cactaceae). Intentamos determinar si
el murciélago pálido consume el néctar floral o si visita las
flores en forma oportunista consumiendo los insectos atraídos
por las flores. En el 2007 y 2008, documentamos el
comportamiento de murciélagos visitando flores usando un
sistema de video infrarrojo durante 143 cactus/noche en 14
sitios de Baja California, México. Los murciélagos palidos
visitan en forma regular las flores de cactus y consume el néctar
floral insertando su cara en el interior de la corola para lamer el
néctar acumulado en la flor. En total registramos 1198 flores
visitadas por *A. pallidus*, correspondiendo al 10% de las visitas
de todos los murciélagos. Los murciélagos pálidos visitaron
flores en el 57% de las observaciones nocturnas ($n = 81/143$) y
en el 52% de las capturas ($n = 28/54$) se observó la presencia de
polen. *A. pallidus* concentro la actividad de visitar flores
temprano en el atardecer, cuando *Leptonycteris yerbabuenae* ($=$
curasoae) estaba presente y de manera igualmente distribuida
durante la noche cuando *L. yerbabuenae* no esta presente. Esto
suguiere exclusión competitiva potencial entre quirópteros
polinizadores nocturnos.

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SUPPORTING INFORMATION

VIDEO S1.—Nectar extraction by *Leptonycteris yerbabuenae* at cardon flower with opening in corolla. Found at DOI: 10.1644/09-MAMM-A-001.sl (2920 KB WMV).

VIDEO S2.—Nectar-feeding behavior of *Antrozous pallidus* at cardon flower with opening in corolla. Found at DOI: 10.1644/09-MAMM-A-001.s2 (5595 KB WMV).