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Insectivorous Bat Pollinates Columnar Cactus More Effectively per Visit than Specialized Nectar Bat

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ABSTRACT: Plant-pollinator interactions are great model systems to investigate mutualistic relationships. We compared pollinator effectiveness between facultative and obligate nectar-feeding bats to determine how foraging specialization influences mutualistic interactions in a bat-adapted cactus. We predicted that a specialized nectarivorous bat would deliver more pollen than an opportunistic nectar-feeding bat because of specialized adaptations to nectar feeding that indicate close association with their food plants. Counter to our predictions, the opportunistic *Antrozous pallidus* delivered significantly more pollen grains per visit than the specialized *Leptonycteris yerbabuena*. Higher pollinator effectiveness, based on visitation rates and pollen deposition levels, varied between species by site, and although *A. pallidus* visits flowers much less frequently than *L. yerbabuena* over all sites, it is likely an effective and reliable pollinator of *Pachycereus pringlei* in Baja, Mexico. Our results suggest that morphological adaptations and dietary specialization on nectar do not necessarily confer advantages for pollination over less specialized plant visitors and highlight the reciprocally exploitative nature of mutualisms.

Keywords: bat, cactus, mutualism, pollinator.

Introduction

Quantifying variation in pollinator effectiveness among flower visitors is critical to understanding plant-pollinator mutualisms and the reproductive benefits to plants that different pollinator behaviors provide (Schemske and Horvitz 1984). Pollinators that specialize on floral rewards have often coevolved with the plants they pollinate and are important mutualists (Darwin 1859, 1877; Thompson 1994). These plant-pollinator interactions constitute some of the most spectacular and classic examples of adaptation and are associated with the diversification of plant and

animal lineages (Grimaldi 1999; Kay and Sargent 2009). However, flower-visiting animals may vary from mutualistic to antagonistic, depending on the community context of other visitors and their relative effectiveness at transporting pollen (Thomson 2003). Pollination systems that encompass variable pollinator behaviors, such as pollen delivery and visitation frequency, offer opportunities to study the selective pressures acting on flower-visiting species and the plants they visit (Thompson 2005).

We studied the pollinator effectiveness of two species of bats that differ in their dependence on nectar to determine how foraging specialization influences the contribution of a pollinator to plant reproductive success. Nectar-feeding bats are important pollinators in many tropical habitats; however, their distributions are mostly constrained to tropical and subtropical latitudes and, in the New World, occur within a single family, the Phyllostomidae. The lesser long-nosed bat (*Leptonycteris yerbabuena*) specializes in nectar-feeding and feeds primarily on nectar of columnar cacti and agaves during the spring months in northwestern Mexico (Fleming et al. 1993; Cole and Wilson 2006). The interactions among *L. yerbabuena* and columnar cacti have been well studied in Sonora, Mexico, and *L. yerbabuena* are important pollinators of the cardon (*Pachycereus pringlei*), a columnar cactus adapted for bat pollination (Fleming et al. 2001). On the Baja California peninsula, *P. pringlei* provides the major source of nectar for this species (Fleming et al. 1993). The pallid bat (*Antrozous pallidus*) is a primarily insectivorous bat in the family Vespertilionidae that was recently discovered to visit flowers and drink nectar from *P. pringlei* (Frick et al. 2009). *Antrozous pallidus* represents the first known case of nectarivorous habits in a New World bat outside the Phyllostomidae. Nectar feeding was previously unknown in the family Vespertilionidae, the largest (approximately 318 species) and most widely distributed family of bats. *Antrozous pallidus* drink nectar facultatively and more typ-

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ically glean large arthropods, such as scorpions and crickets, off the ground or plant surfaces (Bell 1982; Hermanson and O'Shea 1983). *Antrozous pallidus* and *L. yerbabuena* co-occur on the southern Baja California peninsula, where their ranges overlap with *P. pringlei*, and both bat species are common visitors to its flowers during the late March to early June flowering season (Frick et al. 2009).

The co-occurrence of facultative and obligate nectar-feeding bats visiting the same floral resource provides an opportunity to investigate how morphological, behavioral, and dietary specialization on floral resources may affect mutualistic interactions. *Leptonycteris yerbabuena* are highly specialized for nectar feeding and have elongated tongues and faces (fig. 1A). In contrast, *A. pallidus* lack obvious morphological specializations for nectar feeding and instead have large ears and blunt faces associated with arthropod gleaning (Herrera et al. 1993; fig. 1B). We hypothesized that *L. yerbabuena*, an obligate nectar feeder, would be a more effective pollinator than *A. pallidus*, a facultative nectar feeder, given that the specialized morphology of *L. yerbabuena* for flower visiting is indicative of high dependence on nectar and would suggest close association with their food plants. To measure pollinator effectiveness per visit, we compared stigma pollen loads per visit for each species. We also hypothesized that stigma pollen loads per visit could vary depending on when a visit occurs during the night. Pollen deposition may be lower earlier in the evening, before a buildup of pollen accumulates during foraging. Therefore, we compared the association of timing of visit with pollen deposition by each species to determine whether this was an important component of pollinator effectiveness.

Pollinator effectiveness is a measure of the efficiency by which a pollen vector delivers compatible pollen to receptive stigmas that ultimately benefits plant fitness in terms of fruit and seed set (Inouye et al. 1994). Factors such as visitation rates, pollen deposition to stigmas per visit, and pollen loss from active or passive removal influence the effectiveness of pollinators (Inouye et al. 1994; Thomson 2003). The pollinator "milieu" and spatiotemporal variation in pollinator performance can determine whether pollinators serve as mutualists or functional parasites that preclude pollen transfer by more effective visitors (Thomson 2003). *Leptonycteris yerbabuena* are migratory throughout most of northwestern Mexico and may be unreliable as pollinators if visitation rates vary greatly in space and time (Fleming et al. 2001). In contrast, *A. pallidus* are resident species throughout most of Baja California but in general have much lower visitation rates than *L. yerbabuena* (Frick et al. 2009). We combined visitation rates with stigma pollen loads per visit to compare differences in the mean probability of effectiveness of each species across 14 sites visited in 2007–2008 (Frick et al.

2009). We predicted that high visitation rates by *L. yerbabuena* would result in higher effectiveness overall but that *A. pallidus* may function as an effective pollinator in areas where *L. yerbabuena* were absent.

Material and Methods

Study System

Study sites were located in Sonoran Desert vegetation in areas dominated by *Pachycereus pringlei* near Loreto and in the Sierra de la Giganta in Baja California Sur, Mexico (sites 2–6, 9, and 10; Frick et al. 2009). The large, white flowers of *P. pringlei* are open for a single night, opening at sunset and closing the following morning or midday (Fleming et al. 1994). Plants have multiple flowers open each night for approximately 6–8 weeks from late March to early June (Fleming et al. 1994, 2001). Flowers are visited by a variety of bird species and diurnal insects during morning hours, but the majority of pollination occurs from nocturnal bat visits (Fleming et al. 2001). *Leptonycteris yerbabuena* and *Antrozous pallidus* are the only two bat species that regularly occur and visit *P. pringlei* flowers in our study area (Frick et al. 2008, 2009). *Pachycereus pringlei* are trioecious, and there is no significant difference in floral rewards (nectar production) among the sexes, although flower size is generally smaller in female plants than in hermaphroditic and male plants (Fleming et al. 1994, 1998a).

Data Collection

We collected 89 stigmas from female *P. pringlei* flowers after observing a single visit from a bat to a flower ($n = 56$ by *A. pallidus*; $n = 33$ by *L. yerbabuena*) during the period April 10 to May 10, 2011. Flowers were observed using trained observers and infrared closed circuit television (CCTV) cameras attached to miniature digital video recorders (DVRs) from shortly before flowers open (approximately 2000 hours) until all flowers were visited or 0100 hours. *Antrozous pallidus* (13–29 g) and *L. yerbabuena* (23–29 g) are easily distinguishable on the basis of flower-visiting behavior and visible morphological characteristics (Frick et al. 2009). Stigmas were immediately fixed and preserved in fuchsin jelly on a microscope slide for later identification and quantification of pollen (Kearns and Inouye 1993). We sampled female flowers to ensure that pollen deposited on stigmas was delivered by visiting bats. Preserved stigmas were examined under a microscope ($\times 5$ magnification), and pollen grains were identified and counted.

To estimate visitation rates, we used data on the number of visits by bats to 731 flowers from 143 cacti observed at 14 sites in Baja California Sur from April through May in



Figure 1: A, The lesser long-nosed bat (*Leptonycteris yerbabuena*), a nectar-feeding specialist, visiting a cardon (*Pachycereus pringlei*) flower. *Leptonycteris yerbabuena* is highly adapted to nectar feeding, having an elongated face and tongue and hovering ability. B, The pallid bat (*Antrozous pallidus*), a facultative nectar-feeding bat, heavily doused in cardon pollen (yellow dusting on ears and face). *Antrozous pallidus* lacks any special morphological adaptations for nectar feeding and has large ears, a blunt nose, and large teeth, which are typical for a bat that eats large arthropods.

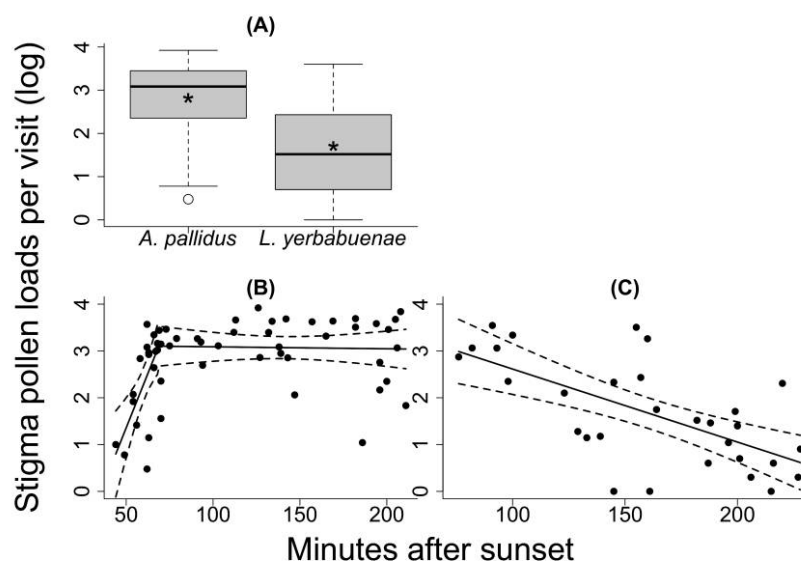


Figure 2: A, Stigma pollen loads per visit to cardon (*Pachycereus pringlei*) were significantly greater by facultative nectar-feeding *Antrozous pallidus* than by nectar specialist *Leptonycteris yerbabuena*. The bold horizontal line of the box-and-whisker plot displays the median and the asterisk indicates the mean stigma loads per visit (log). Relationships between stigma loads per visit and timing of pollinator visits show different patterns for each species. B, For *A. pallidus*, a piecewise regression model with a threshold value of 69 min past sunset suggests that pollen deposition increases during the first part of the night and then remains constant ($F = 8.637$ on 3 and 50 df, $R^2 = 0.34$). C, In contrast, for *L. yerbabuena* the median stigma pollen loads per visit decreased by 88% (95% confidence interval: 76%–94%) in each hour past sunset ($F = 20.2$ on 1 and 28 df, $R^2 = 0.42$). Dashed lines represent 95% confidence intervals around the regression lines.

2007 and 2008, as reported in Frick et al. (2009). Visits were censused using infrared CCTV cameras attached to mini-DVRs from 2000 to 0900 hours and counted as the number of events observed where a bat's face made contact with a flower. We took a random sample of one visit by each species from 20 different cacti ($n = 20$ visits per species) and counted the number of frames from when a bat's face first made contact with the flower to when a bat removed its head from the corolla to measure visit duration.

Data Analysis

We compared per visit pollinator effectiveness using stigma pollen loads per visit by *L. yerbabuena* and *A. pallidus* with a mixed-effects model, with species as a categorical explanatory variable and site location ($n = 5$) as a random effect (Zuur et al. 2009). We log transformed the response variable of number of pollen grains deposited per visit to conform to assumptions of normality. We fit a simple linear regression model to assess the relationship between time of visit and the logarithm of pollen deposited by *L. yerbabuena* and fit a piecewise regression model to describe the nonlinear relationship between time of visit and the logarithm of pollen deposited by *A. pallidus*. We com-

pared duration of visits to flowers by each species with Welch's two-sample t -test.

We estimated the per flower probability of effectiveness for each bat species by combining visitation rates to individual flowers with the distribution of stigma loads per visit. Because a flower is open only for a single night and the number of visits to a flower is censused per night, we estimated the expected amount of pollen delivered during the entirety of a flower's life span. For each flower, we multiplied the number of visits from each species by 10,000 random draws from a negative binomial distribution, with shape parameters (size, mean) estimated from samples of pollen loads per visit for that species. We calculated the mean probability of effectiveness as the percentage of iterations of this sampling that exceeded minimum known values of seed set in *P. pringlei* (922 seeds per fruit; Fleming et al. 2001). We performed comparisons of pollinator effectiveness probabilities between species using nonparametric Wilcoxon rank-sum tests at 14 sites across the Baja California peninsula (Frick et al. 2009). All analyses were conducted in R (ver. 2.12.1; R Core Development Team).

Results

The amount of pollen deposited per visit by *Antrozous pallidus* and *Leptonycteris yerbabuena* was significantly

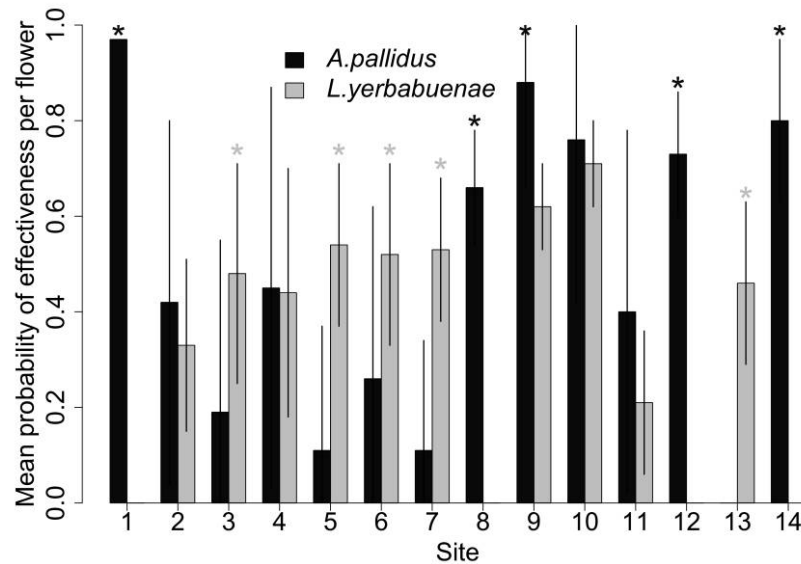


Figure 3: Comparisons of mean probability of effectiveness per flower for *Antrozous pallidus* and *Leptonycteris yerbabuenae* at 14 sites on the Baja California peninsula. Bars represent standard deviations from the mean, and asterisks indicate statistically significant differences in pairwise comparisons using nonparametric *t*-tests at $P < .01$. Specific site locations and visitation rates by species are reported in Frick et al. (2009).

different ($t = -4.01$, $df = 83$, $P < .0001$). Contrary to our hypothesis, *A. pallidus* deposited 8.1 (95% confidence interval [CI]: 2.9–22.9) times more pollen grains per visit than *L. yerbabuenae* (fig. 2A). The estimate of the standard deviation for the random effect of site location ($SD = 0.33$) indicated little influence of spatial locality on differences among species; therefore, we present data pooled from all sites (fig. 2A). *Antrozous pallidus* delivered on average 609 (95% CI: 224–1,622) grains per visit, compared with 75 (95% CI: 10–564) grains per visit by *L. yerbabuenae*. Duration of visits was significantly longer in *A. pallidus* (mean = 0.52 s; $SE = 1.28$) than in *L. yerbabuenae* (mean = 0.37 s; $SE = 0.95$), which is consistent with differences in flower-visiting strategies (landing on flowers versus hovering; $t = 2.88$, $df = 34.98$, $P < .007$).

For *A. pallidus*, the association between timing of visit and pollen deposition matched our hypothesis that stigma pollen loads per visit are lower earlier in the evening before a buildup of pollen occurs on a bat and then remain constant during the rest of the night (fig. 2B). Piecewise regression estimated a threshold value of 69 min past sunset ($F = 8.637$ on 3 and 50 df , $R^2 = 0.34$), suggesting that after roughly the first hour after sunset, the relationship between time of visit and pollen deposition changed. In the first 68 min after sunset, the median stigma pollen load per visit experienced a 10-fold increase ($\log_{10}(y) =$

$-3.293599 + 0.093009x$; $P < .001$), with scant pollen deposition levels at sunset increasing to 1,074 (95% CI: 315–3,657) grains at 68 min after sunset. After those initial 69 min, there was no significant linear relationship between timing of visit and pollen deposition during the nocturnal sampling period, which ended around 2400 hours ($\log_{10}(y) = 3.1313622 - 0.0004231x$; $P > .1$; fig. 2B).

In contrast, there was a significant negative linear relationship between the number of minutes after sunset and the amount of pollen deposited during a single visit by *L. yerbabuenae* ($R^2 = 0.42$, $df = 28$, $P < .001$; $\log_{10}(y) = 4.173753 - 0.015605x$; $P > .001$; fig. 2C). The median number of pollen grains deposited by *L. yerbabuenae* decreased by 88% (95% CI: 76%–94%) in each hour increase after sunset (fig. 2C).

Comparisons of the probability of effectiveness per flower revealed that *A. pallidus* had significantly higher mean probabilities of effectiveness than *L. yerbabuenae* at 5 of 14 sites ($P < .01$); an additional 4 of 14 sites showed higher mean effectiveness, but differences were statistically insignificant ($P > .10$). At 4 of the 5 sites at which *A. pallidus* significantly outperformed *L. yerbabuenae*, we did not record any visits by *L. yerbabuenae*, whereas *A. pallidus* was observed at all but one site. Probabilities of effectiveness were significantly higher for *L. yerbabuenae* at 5 of 14 sites (fig. 3).



Video 1: Still photograph from a video (video 1, available online) showing a flower visit by *Leptonycteris yerbabuena*.

Discussion

Flower-visiting behaviors of *Leptonycteris yerbabuena* and *Antrozous pallidus* differ considerably, which may contribute to the observed differences in pollen delivery per visit. Being highly adapted for nectar extraction, *L. yerbabuena* hover while extracting nectar from the nectary with a specialized long tongue (fig. 1A; video 1, available online). The stigma in *Pachycereus pringlei* extends toward the lip of the corolla and generally rubs on top of the head of a visiting *L. yerbabuena*. Anthers with copious pollen line the corolla interior in hermaphroditic and male plants and deposit pollen on the face and head of a visiting bat. Lacking morphological specializations for flower visiting, such as an elongated face or tongue, *A. pallidus* land on flowers and plunge their face and upper torso into the corolla to reach the nectary at the bottom of the corolla (Frick et al. 2009; video 2, available online). This behavioral mechanism to compensate for a lack of morphological adaptation for nectar extraction results in longer visit durations and substantial buildup of pollen on the ears, face, and torso of *A. pallidus* (fig. 1B).

Why *A. pallidus* successfully deliver more pollen grains per visit may also be linked to differences in dietary needs and grooming behavior. Nectarivorous bats are physiologically stressed for sources of protein in their diet, and pollen serves as an important source of protein and nitrogen (Howell 1974). *Leptonycteris yerbabuena* groom pollen from fur by autogrooming at night and day roosts as well as in flight (Howell and Hodgkin 1976; Fleming et al. 1998b). Pollen is known to be an important dietary component for this species in other parts of Mexico (Stoner et al. 2003).

Grooming behavior to consume pollen may account for

the observed pattern of pollen loads delivered by *L. yerbabuena* declining throughout the night (fig. 2B). The pattern of pollen deposition for *A. pallidus* matched our expectations that pollen loads would build up early in the evening and then maintain a relatively constant supply of pollen delivery during the night (fig. 2A). *Antrozous pallidus* has less incentive to aggressively groom and consume pollen because its insectivorous diet is not deprived of nitrogen. The results presented here are suggestive of this potential “grooming” mechanism but require further observation and testing to determine whether pollen grooming by *L. yerbabuena* contributes to changes in pollen deposition during the night and overall lower deposition levels compared with *A. pallidus*.

Leptonycteris yerbabuena must visit flowers of *P. pringlei* between 80 and 100 times a night to fulfill energy demands (Horner et al. 1998). High visitation rates can compensate for low stigma loads per visit in determining the effectiveness of a given pollinator (Thomson 2003). Visitation rates by *L. yerbabuena* were sufficiently high in most years in areas near Loreto, Baja California Sur, to suggest functioning as an effective pollinator (fig. 3). However, considerable spatiotemporal variation in visitation rates have been documented in Sonora, Mexico (Fleming et al. 2001), and in other study locations in Baja (Frick et al. 2009), suggesting that spatiotemporal variation in visitation by this species may affect its reliability as a pollinator (Fleming et al. 2001). Although visitation rates of *A. pallidus* are considerably lower than those of *L. yerbabuena* (Frick et al. 2009), high stigma loads per visit by *A. pallidus* compensate for low visitation rates in many areas, suggesting that this opportunistic flower visitor is an effective pollinator despite low visitation rates.



Video 2: Still photograph from a video (video 2, available online) showing a flower visit by *Antrozous pallidus*.

Our results highlight the reciprocally exploitative nature of mutualistic interactions, in which the interactors often have significant conflicts of interest (Thompson 1982; Herre et al. 1999). Overall, we demonstrate that *A. pallidus*, an opportunistic nectar-feeding bat lacking morphological adaptations for nectar extraction, delivers significantly more pollen per visit than a highly adapted nectar-feeding specialist and is an effective pollinator despite low visitation rates characteristic of opportunistic nectar feeding. Although we were unable to directly measure differences in plant fitness, our results show that morphological adaptations and dietary specialization in pollinators may not necessarily benefit the plants they visit (Thomson 2003). The narrow face, long tongue, and hovering capability of *L. yerbabuena* likely evolved to maximize its effectiveness at foraging for nectar and only facilitate seed set in *P. pringlei* incidentally. In the presence of an evolutionarily naive interactor such as *A. pallidus*, *L. yerbabuena* may even function as a conditional parasite, similar to pollen-grooming bees in the presence of hummingbirds (sensu Thomson 2003). Likewise, *P. pringlei* may be under selection for more generalization in its pollination system because of the variable effectiveness of *L. yerbabuena* (due to both unreliable visitation and low pollen delivery), similarly to many ancestrally bat-adapted columnar cacti that show generalized pollination toward birds at their northern latitudinal range limit (Fleming et al. 2001).

Although much attention has been paid to invaders of mutualisms that exploit the benefits offered by one partner while delivering fewer benefits in return (especially in the context of species invasions; e.g., Traveset and Richardson 2006), less is known about situations in which a coevolved mutualism can be invaded by a less antagonistic interactor, in this case a primarily insectivorous bat. Future work will aim to determine the costs and benefits of the interaction to both bat species.

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The lesser long-nosed bat, seen here visiting a cardon flower, exhibits specialized morphology and behavior for extracting nectar from flowers, such as an elongated face and hovering capabilities. Nevertheless, we find it is a less effective pollinator on a per-visit basis than the typically insectivorous pallid bat, which grasps the flower and plunges its blunt face deeply inside to access the nectar. Photograph by Winifred F. Frick.