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Michael A. Bogan

Ernest W. Valdez

Elizabeth A. Slauson

POLLINATION ECOLOGY OF AGAVE PALMERI
IN NEW MEXICO, AND
LANDSCAPE USE OF LEPTONYCTERIS NIVALIS
IN RELATION TO AGAVES

by

ANGELA E. ENGLAND

B.S., Zoology, The University of Texas at Austin, 1992

DISSERTATION

Submitted in Partial Fulfillment of the
Requirements for the Degree of

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Biology**

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POLLINATION ECOLOGY OF *AGAVE PALMERI* IN NEW MEXICO, AND LANDSCAPE USE OF

LEPTONYCTERIS NIVALIS IN RELATION TO AGAVES

by

Angela E. England

B.S., ZOOLOGY, THE UNIVERSITY OF TEXAS AT AUSTIN, 1992

PH.D., BIOLOGY, UNIVERSITY OF NEW MEXICO, 2012

ABSTRACT

Where animals spend time can provide important clues to their ecological needs, but this information is very difficult to obtain for small volant animals. The research described in Chapter 1 was an attempt to discern how *L. nivalis* utilize the landscape in relation to the distribution of *Agave havardiana* in Big Bend National Park, Texas. I found that although the landscape use of *Leptonycteris nivalis* is centered on habitat with high concentrations of blooming *A.havardiana*, it is not restricted to those areas, and furthermore adults and juveniles may differ in their behavior. Adult females may remain near food sources in order to replenish energy stores lost to migration and the demands of reproduction, whereas juveniles may feed early in the evening and then undertake occasional far-reaching expeditions, perhaps in order to create a navigational map. If this behavior is widespread among juveniles, it emphasizes the need to carefully assess the

risk of constructing wind-turbine energy facilities not just within agave-rich habitat, but anywhere near the range of this endangered bat species.

The research described in Chapter 2 focused on documenting the importance of flowering agaves as a food resource for the many vertebrate and invertebrate, diurnal and nocturnal visitors. I found that *A. palmeri* was visited by a wide variety of vertebrate and invertebrate visitors, many of which are pollinators of other plants, and that there was considerable variation in visitation rates in space and time – in fact, bats were not even observed at one of the study sites. Increased visitation was associated with larger plant sizes for all visitor types assessed.

In Chapter 3, I explored how the fruit and seed production of *A. palmeri* at these three sites were affected by the plants' morphology, phenology (timing of bloom), prior reproductive success, and the patterns of visitation by different animal guilds. Models indicated that bats were the most effective visitors, because periods with high bat visitation rates also had very high seed. Periods with high bird visitation resulted in many fruits but with poor seed set, possibly indicating that they are responsible for some degree of reproduction, though the exact mechanism is not clear. Floral branch position interacted in a complex manner with prior fruit set, affecting fruit set, seed set, and mean seed mass. Plants with high prior fruit set showed decreased seed set in fruits on late-blooming branches, possibly indicative of resource limitation.

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CHAPTER 1: Introduction

My research on the interaction of nectar-feeding bats and blooming agaves in the southwestern United States began as part of a project conducted by Bat Conservation International with funding support from the U.S. Fish and Wildlife Service via Texas Parks and Wildlife Department. The research described in Chapter 1 was an attempt to discern how *Leptonycteris nivalis* utilize the landscape in relation to the distribution of *Agave havardiana* in Big Bend National Park, Texas. We already knew that the migratory bat *L. nivalis* roosts in Emory Cave during the summer months of at least some years (Brown, 2008; Easterla, 1973), and that the nectar and pollen of *A. havardiana* are the sole known food source for the bats during that period (U.S. Fish and Wildlife Service 1994). Extensive studies on the pollination ecology of *A. havardiana* revealed that when present in the park, *L. nivalis* is the primary pollinator of mountain populations of the agaves, but for lowland populations which bloom before the bats arrive, passerine birds provide backup pollination services (Kuban, 1989). But little was known of how the bats use agave habitat, and how far the bats fly to obtain food. I set out to determine: Where are the agaves found within the park, and do the bats consistently stay in that habitat? Who (age and sex), when (within night and/or within season), where (what parts of the park), and why (day or night roosts, alternate foods, other needs) might they stray from areas where their food resources are abundant, and what does that tell us about their conservation needs?

Subsequently, my efforts moved to southwestern New Mexico, the sole area in the United States where both *L. nivalis* and *L. yerbabuenae* (formerly *L. curasoae yerbabuenae*) are found (Arita and Humphrey, 1988; Hoyt et al., 1994). I assisted with

radio telemetry in 2004 and 2005 led by U.S. Geological Survey biologist Michael A. Bogan (unpublished) which resulted in the discovery of several day and night roosts in the Animas Mountains, and a day roost in the Big Hatchet Mountains seasonally housing thousands of *Leptonycteris* of both species. Telemetry indicated that the bats commuted nightly from the Big Hatchet roost to the Animas Mountains, presumably to feed. There was little evidence that the bats used agaves in the Big Hatchet range, and no indication that they went in other directions (though monitoring elsewhere was limited).

Prior studies on the pollination ecology of *Agave palmeri*, the sole paniculate agave species that blooms while the bats are present, had largely been conducted in southeastern Arizona, where *L. yerbabuenae* occurs but *L. nivalis* does not. Hand-pollination experiments with self pollen of *A. palmeri* indicate self incompatibility (Howell and Roth, 1981; Slauson, 2000), therefore pollinators are considered required for successful reproduction. In Arizona, *A. palmeri* is primarily pollinated by bats, possibly with secondary dependency upon sphinx moths and possibly large bees (Slauson, 2001). But previous studies did not attempt to document how the plant-animal interactions varied in space and time, and what effect such variation might have on overall agave reproduction. Additionally, such studies were generally restricted to floral branches in the center of the inflorescence, despite emerging evidence that a flower's position on the inflorescence often has an influence on reproductive potential (Diggle, 1995; Humphries and Addicot, 2004).

Therefore, in southwestern New Mexico in 2006 I conducted agave-centered research at one site in the southern Animas Mountains (Site "A"), and in 2007 I did the same at one site in the Big Hatchet Mountains (Site "B", approximately 2 km from the

Big Hatchet roost cave), and at one site in the Cedar Mountains (Site "C"). The three sites were situated nearly linearly with Site B in the center, Site A approximately 40 km to the southwest of Site B, and Site C approximately 40 km northeast of Site B. I included all blooming agaves at each site, carefully noting the phenology of floral timing on each plant during each seasonal trip, and included this factor in subsequent analyses.

Although experimental studies can help pinpoint single factors that play limiting roles, they are often conducted under very restricted conditions or on limited sample sizes due to the time necessary to perform manipulations. I was especially interested in how the plants and animals were interacting in their natural habitat, therefore I undertook observational studies hoping to reveal which of the possible contributing factors play discernible roles in the wild. The uncontrolled nature of observational studies makes statistical analysis based on traditional null-hypothesis testing problematic, but a newer method of data analysis has recently gained acceptance in ecological and behavioral fields of biology (Burnham and Anderson, 2002; Stephens et al., 2005; Garamszegi et al., 2009). This "information theoretic" approach is based on simultaneously evaluating the amount of support for competing biologically relevant hypotheses (Burnham and Anderson, 2002; Stephens et al., 2005; Garamszegi et al., 2009).

The research described in Chapter 2 focused on documenting the importance of flowering agaves as a food resource for the many vertebrate and invertebrate, diurnal and nocturnal visitors. Paniculate agaves have been suggested to play a keystone resource (Lundberg and Mobert, 2003) in maintaining populations of desert pollinator species, because they provide copious quantities of nectar and pollen during the early summer dry season (U.S. Fish and Wildlife Service, 1994, 1995; Good-Avila et al., 2006).

Specifically, I asked: How much visitor variation was apparent at different sites, throughout the course of the summer season at each site, and within different parts of the day or night? Did plant characteristics such as size, shape, and bloom stage influence visitation rates? Is there evidence to support the assertion of agaves as a critical resource for any of these animals?

In Chapter 3, I explored how the fruit and seed production of *A. palmeri* at these three sites were affected by the plants' morphology, phenology (timing of bloom), prior reproductive success, and the patterns of visitation by different animal guilds. Could we discern the influence of different visitors? Was there evidence of architectural trends that could indicate shifts between female and male function on early versus late-blooming branches? And was there any evidence that the agave reproductive success went from pollinator limitation to resource limitation?

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CHAPTER 2: Landscape use of adult and juvenile *Leptonycteris nivalis* in Big Bend National Park, Texas

Abstract

Where animals spend time can provide important clues to their ecological needs, but this information is very difficult to obtain for small volant animals. The Mexican long-nosed bat, *Leptonycteris nivalis*, is a nectar-feeding bat that migrates from Mexico into the southwestern United States during summer months. It relies on the nectar and pollen of agave plants for food in the northern part of its range, but little is known of its nightly movements and how it uses the landscape, and almost nothing is known about how these may vary between adults and juveniles.

I undertook radiotelemetry on *Leptonycteris nivalis* in Big Bend National Park, Texas, in 2003. By studying nightly movements, I sought to discover new roosts, analyze use areas, and increase basic biological understanding of this species. Of 25 radiotagged bats, I obtained adequate locations to calculate use areas for 9 bats. The core areas (50% fixed kernels) of juveniles ($\overline{X}$ = 7.64 km^2, *SE* = 2.60, *n* = 4) were larger than those of adults ($\overline{X}$ = 2.08 km^2, *SE* = 0.36, *n* = 5); this difference approached significance (*P* = 0.079). Agave habitat comprised a similar proportion of the core area of both age groups. The home ranges (95% fixed kernels) of juveniles ($\overline{X}$ = 61.90 km^2, *SE* = 19.00, *n* = 4) were significantly larger (*P* = 0.046) than those of adults ($\overline{X}$ = 16.97 km^2, *SE* = 3.90, *n* = 5). There was proportionately twice as much agave habitat in the home ranges of adults as of juveniles. Juveniles were documented making multiple excursions away from the agave-rich areas near their roost, possibly exploring the landscape to build their navigational maps.

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My results suggest that adults and juveniles may use the landscape differently, and juveniles may be at direct risk if wind-energy turbines are sited within proximity of roosts, even if placed in areas without agave populations.

Introduction

Where an animal spends its time can indicate which resources it may be utilizing (Johnston et al. 2005; Marzluff et al. 2004), and provide insight into reproduction, social interactions, foraging, limiting resources, and important habitat components (Lacki et al. 2009; Powell 2000). Additionally, resource needs can vary with age and sex, as exhibited by different patterns of resource use over an animal's lifetime. Habitat use details are often poorly known for endangered species, yet understanding resource needs of individuals is essential for effective conservation efforts. In bats, most spatial-use studies have focused on adult females, leaving the ecological needs of juvenile bats largely unknown (Weller et al. 2009). Because chances of survival are lower for juvenile than adult bats (Frick et al. 2007; Tuttle and Stevenson 1977), identifying crucial habitat components of juveniles may aid recruitment and allow population recovery (Weller et al. 2009).

North American bats are small, nocturnal, highly mobile animals, which makes study of their movement difficult, especially in roadless, rugged terrain. Radiotelemetry is currently the best solution to elucidating patterns of landscape use, even though telemetry for most North American bat species remains technologically constrained solely to transmission of a radio signal (Amelon et al. 2009). By plotting triangulated localities obtained by telemetry, maps can be created to compare landscape use between individuals, and identify potentially important landscape features.

The Mexican long-nosed bat, *Leptonycteris nivalis* (Chiroptera: Phyllostomidae), is federally listed as endangered in the United States and Mexico (U.S. Fish and Wildlife Service 1994). The timing and route of its annual long-distance migration coincide with the availability of food resources (Moreno-Valdez et al. 2000, 2004), which in the northern part of its range are believed to consist solely of the nectar and pollen of blooming agaves. The Recovery Plan (U.S. Fish and Wildlife Service 1994) emphasizes the need for additional basic biological information on the species, including distances travelled nightly to forage, and the distribution and size of foraging areas. This information is needed by land managers to aid conservation efforts. In Big Bend National Park, Texas, adult females and volant young are known to roost in Emory Cave during summer months (Brown 2008; Easterla 1973), but prior to my research, only capture records have provided any information on habitat use within the park.

In this study, I undertook radiotelemetry on *L. nivalis* in Big Bend National Park. By studying nightly movements, I sought to discover new roosts, analyze use areas, and increase basic biological understanding of this species. Because adults and juveniles of closely related *Leptonycteris yerbabuenae* show no difference in summer home range and core use areas (Ober et al. 2005), I predicted that *L. nivalis* would likewise show no difference between age classes. Given that the only documented food source for *L. nivalis* in its northern summer range is the nectar and pollen of paniculate agaves, I also predicted that spatial use of *L. nivalis* would be concentrated in agave-rich areas.

Methods

Study site. -- Research took place in Big Bend National Park (29°20'N, 103°20'W), Brewster County, Texas, an area of approximately 3,200 km^2 within the

Chihuahuan Desert ecoregion. Big Bend National Park is part of 12,000 km^2 of contiguous parks and protected areas along the U.S.-Mexico border. Elevation in the park ranges from 600 m to nearly 2400 m. The Chisos Mountains in the center of the park are part of the northernmost extension of Mexico's Sierra Madre Oriental (Poulos et al. 2009). Vegetation in the study area consists of pine-oak woodlands above 1675 m, shrub woodlands 1370-1675 m, high desert grasslands 915-1525 m, and scrub desert 520-915 m (National Park Service 2005). Research activities occurred mostly in the central part of the park, in the northern half of the Chisos Mountains and the associated foothills and shrub woodlands to the west, north, and east of the Chisos (Fig. 1). Precipitation ranges from 20-30 cm/yr in the scrub desert to >41 cm/yr in the mountains (Poulos et al. 2009). As is typical of the North American monsoon season, the majority of the annual precipitation occurs during the summer (Poulos et al. 2009). In 2003 the 45.7 cm annual precipitation (National Park Service 2005) was above average due to a heavy summer and fall monsoon season (Patrick et al. 2007). High temperatures during the study period averaged 27°C (range 25-29°C), and lows averaged 16.5°C (range 14-18°C; National Oceanic and Atmospheric Administration 2009). The moon phase during the telemetry period went from late 3rd quarter on the night of 25-26 June (rising at 0429 h) to new + 6 days on the night of 5-6 July (setting at 0122 h).

   Study species. -- *Leptonycteris nivalis* is a large glossophagine bat. Females make an annual long-distance migration exceeding 1000 km (Fleming and Eby 2003), from winter mating sites in southern Mexico (Brown 2008; Sanchez and Medellín 2007) to summer post-maternity sites in west Texas (Brown 2008) and southwestern New Mexico (M. A. Bogan, pers. comm.; Hoyt et al. 1994). No night roosts are known in Texas.

Emory Cave in Big Bend National Park is the only documented day roost of *L. nivalis* in

Texas. Emory Cave is considered to be a post-maternity roost, where lactating and post-

lactating adult females arrive with volant young in mid-late June and stay until late July

or early August (Easterla 1973), although recent evidence suggests that Emory Cave may

actually serve as a maternity roost for some individuals (Brown 2008). Adult males are

rarely captured in Big Bend (Easterla 1973).

Havard's agave, *Agave havardiana*, is a semelparous perennial plant with a

paniculate inflorescence and a chiropterophilous pollination syndrome (Kuban 1989;

Slauson 2001). *L. nivalis* is the most efficient pollinator of this agave species, though

white-winged doves (*Zenaida asiatica*) and Scott's orioles (*Icterus parisorum*) may serve

as lower quality pollinators (Kuban 1989). *A. havardiana* is the only known food source

for *L. nivalis* in Texas, and therefore maintenance of agave populations is considered

crucial to conservation efforts (U.S. Fish and Wildlife Service 1994). *A. havardiana* has

a clumped distribution in the piñon-juniper-oak woodlands, sotol grasslands, and scrub

deserts in and around the Chisos Mountains, and there is a great deal of variability in the

number of agaves blooming in any given year (Kuban 1989). The only known

populations of *A. havardiana* within the park are those in and around the Chisos.

Lechuguilla, *Agave lechuguilla*, is also present in the park, but has a spicate (non-

paniculate) inflorescence form that is generally not associated with nectar-feeding bats

(Gentry 1982; Slauson 2001). Pollen from other species of spicate agaves does occur in

the winter diet of *L. nivalis* in central Mexico (Sanchez and Medellín 2007), and closely

related *L. yerbabuenae* has been documented to visit spicate agaves in Hidalgo, Mexico

(Rocha et al. 2005). However, no evidence of bat usage of *A. lechuguilla* has been found

anywhere within its range (Silva-Montellano and Eguiarte 2003). Therefore I did not consider *A. lechuguilla* distribution during this study.

Agave distribution.--To document patches of *A. havardiana* that bats would be expected to use, in 2002 and 2003 my volunteers and I conducted surveys in the main areas of the park where National Park Service (NPS) personnel indicated that agaves were known to bloom in high densities. In 2008 and 2009 we undertook additional surveys in other park areas with suspected agave presence based on telemetry results. Observers hiked to vantage points and scanned the landscape for agave inflorescences. The 5-8 m inflorescences were visible via binoculars from >1 km in optimal lighting. Live blooms displayed green stalks and the bright yellow flowers characteristic of *A. havardiana*; dead stalks from previous years were tan to brown. The position of each blooming agave was estimated using topographic maps and known observer position from handheld Garmin global positioning system units, and subsequently plotted in ArcView 3.1 software.

Additional information on agave distribution was obtained from NPS survey data from annual agave-bloom census reports (1986-2009, except 1988 and 1999 for which no survey maps are on file). For those reports, NPS biologists surveyed the landscape with binoculars from vantage points, and mapped individual blooming plant locations onto 7.5-minute USGS topological maps. Due to time and personnel constraints, the NPS biologists' surveys consistently included only the Green Gulch, Basin, and Lower Oak Canyon areas of the park (Fig. 2). I georeferenced their paper maps into ArcView 3.1 for the purposes of this analysis.

I created a contiguous ArcView coverage to represent agave habitat, using 100-m-radius buffers around all agave location estimates, due to uncertainty of the point locations associated with the survey methods. One ArcView file was created for all 22 years of agave-survey data, and a separate file for the 2003-only data. I considered the 2003 agave area to be a conservative estimate of the amount of agave-rich habitat available to the bats tracked during 2003. As a more liberal estimate of agave habitat, I also analyzed the all-years agave area, in order to include regions that may not have been surveyed in 2003, as well as areas that were surveyed in 2003 but blooms were undetected. Because inflorescences can remain standing for several years after flowering, the dead stalks may serve as a visual cue to resource abundance for nectar-feeding bats (Ober et al. 2005).

Bat capture and handling.-- One 9-m mist net was erected outside the main opening to Emory Cave on the nights of 25 June, 27 June, and 2 July 2003. Each captured *L. nivalis* was aged, sexed, weighed, and positively identified to species using the keys found in Schmidly (1991) and Hoffmeister (1986). Bats with incomplete ossification of the epiphyseal finger joints were classified as juvenile (Anthony 1988). Juvenile bats weighing less than 22 g were not instrumented and were released immediately. All capture and handling was done according to standards of the American Society of Mammalogists (Gannon et al. 2007). Studies were conducted under permits from U.S. Fish and Wildlife Service, Texas Parks and Wildlife Department, and National Park Service.

The 0.69-g BD-2 transmitters from Holohil Systems, Ltd. (Carp, Ontario, Canada), were attached to the backs of 25 *L. nivalis*. The mean body mass of radiotagged

bats was 29.0 g (range 22.5 g – 32.0 g), thus the mass of transmitters represented 2-3% of the bat's body mass, which is below the recommended threshold of 5% load for volant mammals (Gannon et al. 2007). Fur was carefully trimmed from between the scapulae of bats selected for tracking. After trimming, an alcohol-soaked cotton-tipped swab was used to remove oils from the skin and surrounding fur. Once the alcohol had evaporated, Skin Bond ostomy glue (Smith & Nephew, Largo, Florida) was applied to the clipped area and the radio transmitter, and allowed to "cure" for 5 minutes. At that time, the transmitter was put into place, and fur from the surrounding area was combed over any exposed glue. The bat was released, and tracked for 30 sec to ensure it left the immediate area.

Radiotelemetry. -- Bat movements were monitored from remote tracking stations scattered across the landscape at elevated vantage points from 25 June through 5 July 2003. Stations were chosen each night based on height above surrounding terrain, bat activity from previous nights, and 1-3-hr accessibility from established roads and trails. The method of tracking used was similar to that described by Ober et al. (2005). Five-element antennas were mounted atop 2-m tall masts which swiveled on tripod footings. Compasses were attached directly to the masts in order to minimize observer bearing errors (Amelon et al. 2009). Telemetry signals were monitored on Communications Specialists model R-1000, Wildlife Materials model TRS-2000S, and Lotek model STR-1000 receivers.

Global positioning system readings were taken for each telemetry-receiving location, and bearings toward beacons placed at known locations throughout the study area were used to detect and correct any magnetic variation and confirm that equipment

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was functioning properly. The maximum line-of-sight from receiving stations was estimated to be 15 km, although 7-10 km was more typical. No assessment of the accuracy of fixes was undertaken during this study, but subsequent analysis of the same equipment setup revealed that signals had 1-1.5 degree error at a 20-km distance when there was a clear line of sight to a roost (A. E. England, in litt.).

Discontinuous tracking (as defined by Harris et al. 1990) was used to allow concurrent study of a large number of bats. Frequencies for all activated transmitters were scanned throughout the night from 2-7 receiving stations throughout the area. CB radios were used to coordinate data collection between stations. When a signal from a tag was received, that station would communicate the tag number to the other stations, and if no other signal was being tracked all other receivers would switch to the new frequency. Concurrent bearings were recorded for 3 min, based on GPS-system calibrated watches.

GIS analysis. -- Telemetry data were entered into Excel for ease of manipulation, and subsequently imported to Location Of A Signal (LOAS) 4.0 software (Ecological Software Solutions LLC, Hegymagas, Hungary). I computed estimated locations and errors using maximum likelihood estimator with a bearing standard deviation of 5 for all minutes with ≥3 bearings, or the best biangulation for minutes with 2 bearings. Bearing intersections >8 km from receiving stations were excluded, based on the 7-10 km estimate of usual line of sight. Location fixes with associated error estimates of ≥16 km^2 were omitted.

Location estimates were imported into ArcView 3.1 for GIS analysis. Because subsampling to reduce temporal autocorrelation may actually limit the biological

significance of the analysis (Blundell et al. 2001; Cushman et al. 2005; De Solla et al. 1999; Lair 1987; Reynolds and Laundré 1990; Rooney et al. 1998), no correction was made for temporal autocorrelation. Fix locations for each night were compared to receiver locations for that night, and location estimates deemed to be outside the reasonable reception terrain were omitted.

The Animal Movement Extension (Hooge and Eichenlaub 2001) was used to compute the fixed-kernel utilization distributions, using least-squares cross validation to select the bandwidth for smoothing. Fixed-kernel techniques are nonparametric, unbiased, not sensitive to outliers, and robust to autocorrelation (De Solla et al. 1999; Moser and Garton 2007; Powell 2000). The 95% and 50% utilization distribution probabilities were computed for the LOAS data sets for each bat with at least 18 fixes. The 95% contour of the total utility distribution was used as an arbitrary definition of home range (Seaman and Powell 1996; Seaman et al. 1999), and the 50% contour as the core area (Laver and Kelly 2008). To compute the area of agave habitat within the home range and core areas, the agave layers were overlaid onto the home-range and core-area polygons for each bat and agave areas beyond the extent of the bat ranges were omitted.

In order to obtain conservative estimates of flight speeds on round-trip excursions >10 km, minimum distances and times necessary to complete the trips were estimated, using actual LOAS location fixes. To account for positional error in the fixes, locations separated by <3 min and <1 km were examined, and the position nearest other fixes outside the temporal cluster was used for distance calculations.

Statistics. -- All computations were performed using S-PLUS 8.0 for Windows (Tibco Software Inc., Palo Alto, California). Differences were considered significant at *P*

≤ 0.05, and approaching significance at $P \le 0.10$ (reported due to small sample sizes).

Means are reported $\pm$ SE. Traditional t-tests and Wilcoxon tests perform poorly for small

data sets (Motulsky 1999), therefore I used the S+Resample 3.0 library (Insightful Corp.,

Seattle, Washington) to run 2-tailed permutation tests with 10,000 replicates to test for

equality of the means. Permutation tests (i.e. Monte Carlo tests – Gotelli and Ellison

2004) shuffle the original data and randomly reassign the values to the 2 groups without

replacement, then compare the difference in the original observed means to the difference

in the means obtained over many repetitions (Hesterberg et al. 2005; Manly 2007).

Permutation tests are robust to skewed data (Hesterberg et al. 2005), are distribution free,

and are almost as powerful and efficient as the most powerful parametric tests (Good

2006). I compared the size of home range and core areas, the area of agave habitat within

each, and the proportion of agave-rich habitat within each. I tested all variables for

differences of the means between adults and juveniles, and pooled the age groups if no

difference was found.

Results

Agaves. -- *Agave havardiana* is plentiful in Green Gulch and the Basin areas, and

has sparser, scattered populations in the Lower Oak Canyon foothills (Fig. 2). These are

the areas censused during the annual NPS surveys. Agaves are also abundant in some

areas of the southern and eastern Chisos Mountains such as the South Rim, Juniper

Canyon, and Pine Canyon, with some smaller populations scattered elsewhere in the

Chisos and associated foothills (Fig. 2).

The NPS surveys combined with my own surveys resulted in 8062 agave-bloom

locations during the 22 survey years. The all-years data with 100-m radius buffers

resulted in an estimate of 29.77 km^2 of agave-rich habitat within the park (Fig. 2). Using

only buffered locations of agaves known to have bloomed in 2003 resulted in an estimate

of 8.06 km^2 of agave-rich habitat (Fig. 2).

Bats. -- I captured and radiotagged 25 *Leptonycteris nivalis* in late June and early

July 2003, including 18 adult females (9 lactating, 3 postlactating, 6 nonreproductive), 1

adult nonreproductive male, 4 juvenile females, and 2 juvenile males. Telemetry teams

tracked these bats for a total of 317 receiver-hrs during the course of 10 nights. We

obtained 2,606 concurrent bearings, resulting in 514 LOAS location estimates with

associated errors ≤16 km^2. We heard tagged bats from 1 to 10 nights ($\overline{X}$ = 3.9), and

tracked 9 of these for ≥3 nights. Six of the telemetry tags were later found inside the

original roost. I obtained adequate sample sizes to perform kernel analyses on 9 of the 25

bats (Table 1). Due to the small number of males (1 adult, 1 juvenile), they were pooled

for analysis with females (4 adult, 3 juvenile) to test for differences in age classes.

Juveniles had significantly larger home-range areas than adults (Table 1; Fig. 3),

on average 3.6 times larger. The core areas of juveniles were also larger than those of

adults, with the difference approaching significance (Table 1); the pooled mean core area

for all ages was 4.55 km^2 (*SE* = 1.46, *n* = 9). The proportion of total core area to total

home-range area was similar between age groups (Table 1); the mean proportion of core

to home-range area for pooled age groups was 0.13 ± 0.01 *SE.*

Proportion of use area explained by agave distribution. -- There was

proportionately twice as much agave habitat within the home range of adults as within the

home range of juveniles (Table 1), whether the agave habitat area was computed using

the conservative 2003-only data or the all-years agave data. This difference approached

significance for the 2003-only proportion, and was significant for the all-years agave habitat. The proportion of agave habitat within the core area did not differ by age (Table 1) using either the 2003-only or all-years agave data. The pooled mean proportion of agave habitat in the core was 0.30 ($SE = 0.05$, $n = 9$) using the conservative 2003-only data, or 0.65 ($SE = 0.05$, $n = 9$) for all-years agave data.

Areas used by individual bats. -- Laundré and Keller (1984) recommend emphasis on landscape-use patterns, rather than home range sizes, therefore I examined all telemetry results, not just those that contributed to location fixes. This was especially pertinent because on many nights there was only a single observation station within the Basin, generally situated in an area that could receive signals from the direction of Emory Cave as well as overlooking a large agave-rich area. For brevity, dates are given for the beginning of each night (i.e., "27 June" indicates evening twilight (~2130 h) 27 June 2003 to dawn twilight (~0630 h) 28 June 2003).

The 3 juvenile females (Fig. 3a) were heard 5-6 nights, generally using the Basin for at least part of night, presumably foraging on agaves or going to or from Emory Cave. Bat 000 was documented to be present in Green Gulch on one night (an agave-rich area poorly surveyed by our telemetry efforts). Bats 000 and 022 were located in the foothills to the north of Vernon Bailey Peak on 2 nights each, a remote area without known agaves. All 3 of the juvenile females made at least 1 trip outside the agave-rich habitat of the Chisos Mountains. Bat 000 was heard to the northwest of the Chisos on 1 July around 0240 h, and not heard to return until 0550 h later that night. On 5 July, the same bat was heard going from the Bailey foothills (0043 h) to the northwest near Croton Peak (0106 h), outside the park near the Christmas Mountains (0109 h), then back in the Bailey

foothills by 0201 h - a round trip of at least 30 km completed in 78 min. Bat 022 made a flight of ≥25 km in 205 min from the Bailey foothills to the northeast near Paint Gap Hills and back on 29 June. On 30 June, she went from the Bailey foothills (0008 h) to the north near Croton Springs (0014 h - 0024 h), reappeared about 4 km further west (0135 h), and then returned to the Bailey foothills (0148 h), totaling ≥20 km in 140 min. The 3rd juvenile female, Bat 044, made 1 excursion to Croton Peak and back to the Basin on 1 July, a round trip of at least 18 km in 64 min.

The single juvenile male (Bat 832) was heard on 4 nights, including time within the Basin each night (Fig. 3b). He made 1 excursion on 30 June, from in the foothills north of Pulliam Bluff (0428 h), heading north toward Paint Gap (0445 h), then back near Pulliam Bluff (0510 h), a round trip of at least 13 km completed in 102 min. His tag was retrieved within Emory Cave 5 nights after being instrumented.

The single adult male (Bat 710) was heard on 8 nights. His signal was heard from the Basin on 7 nights, and we also documented him in Green Gulch twice during 1 night (Fig. 3b). His signal was located in the Bailey foothills 4 nights, and in fact the signal from his transmitter was first detected from that area (at 2228 h) on 1 of those nights. He seemed to go up and over the Bailey-Pulliam ridge multiple times per night, taking 8-12 min to travel 1 km horizontally with 250 m ascent and descent. This adult male also made several excursions. On 29 June, he went from the Basin (2212 h) to the west over Burro Mesa (2226 h – 2243 h), and then disappeared until 0057 h when he was back in the Bailey foothills, a round trip of ≥27 km in 165 min. On 30 June, he made a trip from the Bailey foothills (0001 h), north toward Paint Gap (0022 h), reappearing in the Bailey foothills by 0156 h, a round trip of at least 15 km in 115 min.

None of the 4 adult females was documented making any long-distance excursions. Bat 740, the single lactating female, was only heard for 2 nights. She apparently did use the Basin, but disappeared both nights for a period of approximately 90 min, presumably to night roost (Fig. 3c). Bat 850, the post-lactating female, was heard in the Basin on all 4 nights we received her signal. On 3 of those nights, she was also heard to the west outside the Basin in the Lower Oak Canyon area, an area with some blooming agaves (Fig. 3c). On 1 night, her signal was also heard from the Bailey foothills. Her transmitter was retrieved within Emory Cave 5 nights after she was tagged. Bat 761, a nonreproductive adult female, was heard on 4 nights, each including some time in the Basin (Fig. 3d). She was also heard briefly in the Green Gulch area on 1 night, but was never heard from any stations outside the Chisos Mountains. The other nonreproductive adult female, Bat 690, was better sampled, with signals received on 10 nights, including time in the Basin on 8 of those nights (Fig. 3d). We had indications that she went up and over the Bailey-Pulliam ridge at least once. She was heard within Green Gulch on 1 night, and within the Bailey foothills on another night. The last 2 nights we heard her signal only from single stations to the west and northwest outside the Chisos.

Flight speeds.-- There were 7 round-trip excursions of >10 km made by 5 bats, ranging from 13.3 to 30.0 km ($\overline{X}$ = 21.4 km, *SE* = 2.4 km). The estimated flight speeds ranged from 2.0 – 6.4 m/s ($\overline{X}$ = 3.2 m/s, *SE* = 0.6 m/s).

Discussion

Differences in adult versus juvenile landscape use. -- Contrary to my prediction, adults and juvenile *Leptonycteris nivalis* did not have consistently similar landscape-use patterns. The home range and core areas of juveniles were larger than those of adults.

This is in contrast to telemetry results on *L. yerbabuenae* in Arizona, which showed no difference in the home range size of adults versus juveniles (Ober et al. 2005). In my study, agave habitat made up a smaller proportion of the home range of juveniles than adults, but a similar proportion of the core area of both age groups. This also contrasts with Ober et al. (2005) who reported no difference in densities of flowering agaves within the home ranges of adults and juveniles of *L. yerbabuenae* (although Ober et al. (2005) did not measure the density of agaves within core areas). It is possible that juveniles of *L. yerbabuenae* may exhibit different behavior than juvenile *L. nivalis*. However, the mean home-range size of 19.32 ± 2.78 km^2 for *L. yerbabuenae* (Ober et al. 2005) appears to approximate that of adult *L. nivalis* in this study (17.0 ± 3.9 km^2).

The much larger home range of juveniles than adults in my study may have been due to juvenile flights outside of the Chisos Mountains and associated foothills. These quick excursions were made by all 3 of the juvenile females and the 1 juvenile male on 1-2 nights each. The 1 adult male also engaged in similar trips on 2 separate nights. None of the 4 adult females was documented in such an activity. It is possible that the adult females needed to remain close to agave resources to replenish energy lost to costly reproductive activities. Perhaps the juveniles were searching for agaves and foraging habitat, or searching for roosts, but I believe these short excursions may instead have been examples of the juveniles making exploratory trips to learn the landmarks around the Chisos to build their navigational maps. The Ober et al. (2005) study was conducted during August and September, and it is possible that the juveniles had been in the region since mid-July (U.S. Fish and Wildlife Service 1995) and had already explored the area, and therefore were behaving more like the adults.

The details of how bats orient and navigate beyond the range of their echolocation abilities are just becoming known (Holland 2007). No prior information is available for *L. nivalis*, but among other phyllostomid bats, Wilkinson and Fleming (1996) hypothesized that *L. yerbabuenae* uses topographic features to migrate, and *Glossophaga soricina* has been shown to orient by previously learned landmarks and vectors (Winter et al. 2005). Other examples from the Vespertilionidae include *Lasiurus cinereus* migrating with aid from visual landmarks (Cryan and Brown 2007), *Miniopterus schreibersii* using rivers as landmarks for navigation (Serra-Cobo et al. 2000), and *Eptesicus fuscus* using a sunset-calibrated magnetic compass for homing, which may be corrected during the course of the night by using a navigational map (Holland et al. 2006).

It is unknown how important external map signals are for naïve animals in migration, and how navigation develops with age (Alerstam 2006). First year birds have genetically programmed migratory vectors (Berthold 2001), and also use external cues such as geomagnetic coordinates (Alerstam 2006). How and when first-year migratory bats learn about their landscape has been poorly studied to date, largely due to a historical emphasis on the needs of reproductive females (Weller et al. 2009). Although exploration flights may seem energetically costly, the costs of obtaining or maintaining familiarity of the landscape could be offset by fitness benefits (Powell 2000; Stamps 1995). Homing may aid experienced animals to return to previously visited sites (Alerstam 2006). Juveniles will need to be able to find their way to and from roosts and foraging areas all along the many stopovers on their annual migratory pathway during their lifetime (Holland 2007). Although there are no records of the longevity of *L.*

nivalis, in Venezuela *Leptonycteris curasoe* is known to have a lifespan in excess of 10 years in the wild (Martino et al. 2006).

Use of agave-rich areas. -- As predicted, landscape use by *L. nivalis* in Big Bend National Park was concentrated in habitat containing *Agave havardiana*, especially at the core-area level. For both adults and juveniles, agave-rich habitat represented about 30% of the core when computed using the data set of agaves known to have bloomed in 2003, whereas the all-years agave habitat represented about 65% of the core areas of both age groups. Because additional agave habitat was documented subsequent to the 2003 field season, and because some agave blooms may have been undetected due to obscuring vegetation, the all-years agave data set may better represent the foraging area available to the bats. The mean agave-rich proportion of juvenile home ranges was smaller than that of adults.

Use of non-agave areas. -- The use of areas without agaves may be explained by the excursions previously discussed, or to the presence of undocumented night roosts. Night roosts are used for resting, digestion, grooming, protection from weather and predators, as well as for social interactions and information transfer (Kunz and Lumsden 2003). The repeated use of the Bailey foothills area by the 1 adult male, and at least incidental use of the area by 2 of the 4 juvenile females and the 1 postlactating adult female may potentially indicate a night roost in the area. Several exploratory hikes in 2008 and 2009 were unsuccessful in pinpointing the exact location of a roost, but there appeared to be no shortage of possible roosting sites within the rugged landscape.

It is also possible that the bats were foraging in the areas classified as non-agave habitat. *A. havardiana* may have been present but not documented, or the bats could

have been foraging on *A. lechuguilla*. Another possibility is that the bats were foraging on insects in those areas. There is anecdotal evidence from Emory Cave that both insects and pollen are found in guano presumedly from *L. nivalis*, but further dietary studies are needed to confirm this (Brown 2008). Guano pellets recovered from two New Mexico summer roosts used by both *L. nivalis* and *L. yerbabuenae* contained insect remains encased in pollen (M. A. Bogan, pers. comm.). Insect remains have been found in the guano of *L. nivalis* in Mexico in the winter (Sanchez and Medellín 2007), and in the stomach contents of *L. yerbabuenae* in late autumn in Sonora (Hevly 1979) and feces of *L. yerbabuenae* in Arizona (Hinman 2003). Adult and juvenile *L. yerbabuenae* in Arizona show differences in the occurrence of agave pollen and insect remains in fecal samples (Hinman 2003), possibly reflecting differing dietary needs.

Comparisons to other studies. -- There have been 2 telemetry studies previously published on *L. yerbabuenae*. In Sonora, Horner et al. (1998) tracked 4 adult female *L. yerbabuenae* to their foraging areas in columnar-cacti habitat, and used the minimum convex polygon method to estimate a mean foraging area of 1.94 km^2 ($SE = 0.42$ km^2). Despite the differing methods, this is very similar to my core area estimates for adult female *L. nivalis* in agave habitat ($\overline{X} = 2.08$ km^2, $SE = 0.36$ km^2). Ober et al. (2005) used fixed kernel methods to estimate home range and core areas of 21 adult females and 4 juvenile *L. yerbabuenae* in Arizona. They found no difference in adult and juvenile home range or core-use areas. The method I used to compute core area differs from that used by Ober et al. (2005), who used an error polygon cut-off size of 16km^2 for their home range estimates, and an error area of 2km^2 for their core area estimates. My study used the 16km^2 cut off for both estimates, because I was concerned that using more

restrictive criteria would decrease the number of fixes able to be used to compute the core area below a useful level, especially since calculations of inner isopleths (50% kernels, for example) are believed to be more biased by small sample sizes than outer isopleths (Börger et al. 2006). The flight speeds of up to 6.4 m/s in this study fall within the range of those reported for *L. yerbabuenae* (Table 2).

Conservation considerations. -- More studies are needed of the ecology not only of reproductive females, but also of traditionally understudied males and juveniles (Weller et al. 2009). Juvenile bats experience lower survival than adults (Frick et al. 2007; Tuttle and Stevenson 1977), therefore factors that enhance survival of the juvenile age class should aid long-term population recovery. A literature search revealed no formal, telemetry-based, home-range analyses on juvenile bat habitat selection compared to adults. Contradictory anecdotal evidence exists of juvenile bats using the same (Hamilton and Barclay 1998; Racey and Swift 1985) or different (Tuttle 1976) foraging areas than adults.

It is crucial that additional efforts be made to understand the natural history of both adults and juveniles in order to assess the extent of numerous possible threats to conservation (Weller et al. 2009). Anthropogenic impacts from increased illegal activity near the U.S.-Mexico border and associated law-enforcement actions have resulted in increased habitat damage due to foot and off-road vehicle traffic (U.S. Fish and Wildlife Service 2007) and roost disturbances of *L. yerbabuenae* (U.S. Fish and Wildlife Service 2007). Because *Leptonycteris spp.* form large colonies at a limited number of sites, they are considered to be highly sensitive to disturbance at roosts (U.S. Fish and Wildlife Service 1994, 1995). Additionally, the growth of wind-energy facilities as a new form of

alternative energy has resulted in increased mortality to multiple species of migratory bats (Kunz et al. 2007), which may perceive the large structures as landscape-navigational aids (Cryan and Brown 2007). Although no wind-energy facilities have yet been constructed in the United States within the range of *L. nivalis*, there have been proposals for such facilities in southern Arizona that are within the range of *L. yerbabuenae* (U.S. Fish and Wildlife Service 2007), and fatalities of *Leptonycteris spp.* have been reported from wind-energy sites in Mexico (P. M. Cryan, pers. comm.). If *L. nivalis* use landscape features as navigational aids as my research suggests, they may be at particular risk from wind turbines, even if sited in areas away from agave populations.

Another threat comes from potential climate-induced phenological mismatches between the bloom cycle of agaves and the migratory timing of the bats (Robinson et al. 2009; Weller et al. 2009). If the plants bloom at times when the majority of the bats are not present, the plants will experience lower reproductive success, and the bats will miss out on a major food resource, resulting in negative consequences for both agave and bat populations. Increased harvesting of wild agave populations in Mexico for bootleg alcohol production (Burwell 1995) has reduced the availability of food resources along portions of the nectar corridors used by *L. yerbabuenae* (Fleming 1992) and presumably *L. nivalis* during their annual migration, though educational outreach has resulted in planting of agaves in some areas of Mexico (R. A. Medellín, pers. comm.). Many migratory species require an ecologically coherent network of stopover sites along their migration route (Mehlman et al. 2005, Robinson et al. 2009), but so little is known about the migration route and habits of *L. nivalis* (U.S. Fish and Wildlife Service 1994), it is

difficult to predict the impact of changes in food-plant populations at any one site upon the bat populations that use it.

Due to sampling limitations, my estimates almost certainly do not represent the full size of the use area of the bats during their stay in the park. The commute distances recorded here should be viewed as conservative estimates, since I excluded bearing intersections >8 km beyond telemetry stations, due to mountainous terrain. Future telemetry efforts in the area should tag bats throughout the time the bats are present in the park to determine if landscape use changes through time, and include listeners in adjacent protected areas of Texas, Coahuila, and Chihuahua in order to document when bats depart the area, and what direction they go when they leave. Ober et al. (2005) found no difference in landscape use by *L. yerbabuenae* between a high-abundance agave bloom year and a low-abundance year, but multi-year telemetry studies of *L. nivalis* would also be beneficial to confirm if my results were typical.

Additional distributional surveys of agaves would be beneficial to the understanding of this plant's ecology, as well as assisting park personnel in their management of agaves and bats alike. Of particular interest would be determining the extent of any agave stands and location of possible roosts in the rugged, remote foothills to the north of Vernon Bailey Peak. Multiyear studies on agave bloom phenology will be needed to assess any long-term climate-related changes and potential resulting mismatches between the timing of agave blooms and bat migration patterns. On-going annual NPS agave censuses, when combined with recent advances in techniques for roost exit counts at Emory Cave (Ammerman et al. 2009) should result in improved bat-

population estimates, which will provide a clearer idea of how agave bloom numbers influence bat occupancy in the park.

Acknowledgments

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Table 1: Habitat use areas of adult and juvenile *Leptonycteris nivalis* in Big Bend National Park, Texas. Significant differences (at $P \leq 0.05$) are shown in bold. HR = Home Range.

	Adults $n = 5$ $\overline{X} \pm SE$	Juveniles $n = 4$ $\overline{X} \pm SE$	Permutation test of means P
HR Area (km2)	16.97 ± 3.90	61.90 ± 19.00	**0.046**
Core Area (km2)	2.08 ± 0.36	7.64 ± 2.60	0.079
HR Area / Core Area	0.13 ± 0.01	0.12 ± 0.02	0.797
2003 Agave Proportion of HR	0.18 ± 0.03	0.09 ± 0.03	0.068
All-yrs Agave Proportion of HR	0.46 ± 0.05	0.24 ± 0.11	**0.046**
2003 Agave Proportion of Core	0.27 ± 0.07	0.34 ± 0.08	0.471
All-yrs Agave Proportion of Core	0.64 ± 0.06	0.66 ± 0.10	0.818

Table 2: Flight speeds of *Leptonycteris spp.* Demographics: A = adult, J = juvenile; F = female, M = male.

Species	Type of study	Mean flight speed (m/s)	Max flight speed (m/s)	Demographics	Type of flight	Source
L. nivalis	field radiotelemetry	3.2	6.4	3 JF, 1 JM, 1 AM	over land - exploration?	this study
L. yerbabuenae[a]	laboratory flight test	4.8	6.2	2 AF	enclosed corridor	Hayward and Davis 1964
L. yerbabuenae	field radiotelemetry	7.8	--	6 AF	over water commute	Horner et al. 1998
		4.3	--	7 AF	over land commute	Horner et al. 1998
L. yerbabuenae	field radiotelemetry	8.7	--	17 AF	over land commute - w/ respect to ground	Sahley et al. 1993
		8.2	10.3	17 AF	over land commute - w/ respect to wind	Sahley et al. 1993

a = Originally reported as *L. nivalis* but actually *L. yerbabuenae* following taxonomic revision of Wilson and Reeder (2005).

Fig. 1: Study area within Big Bend National Park, Texas. The Chisos Mountains are the large range in the center of the park. Elevation increases with darker gray scale.
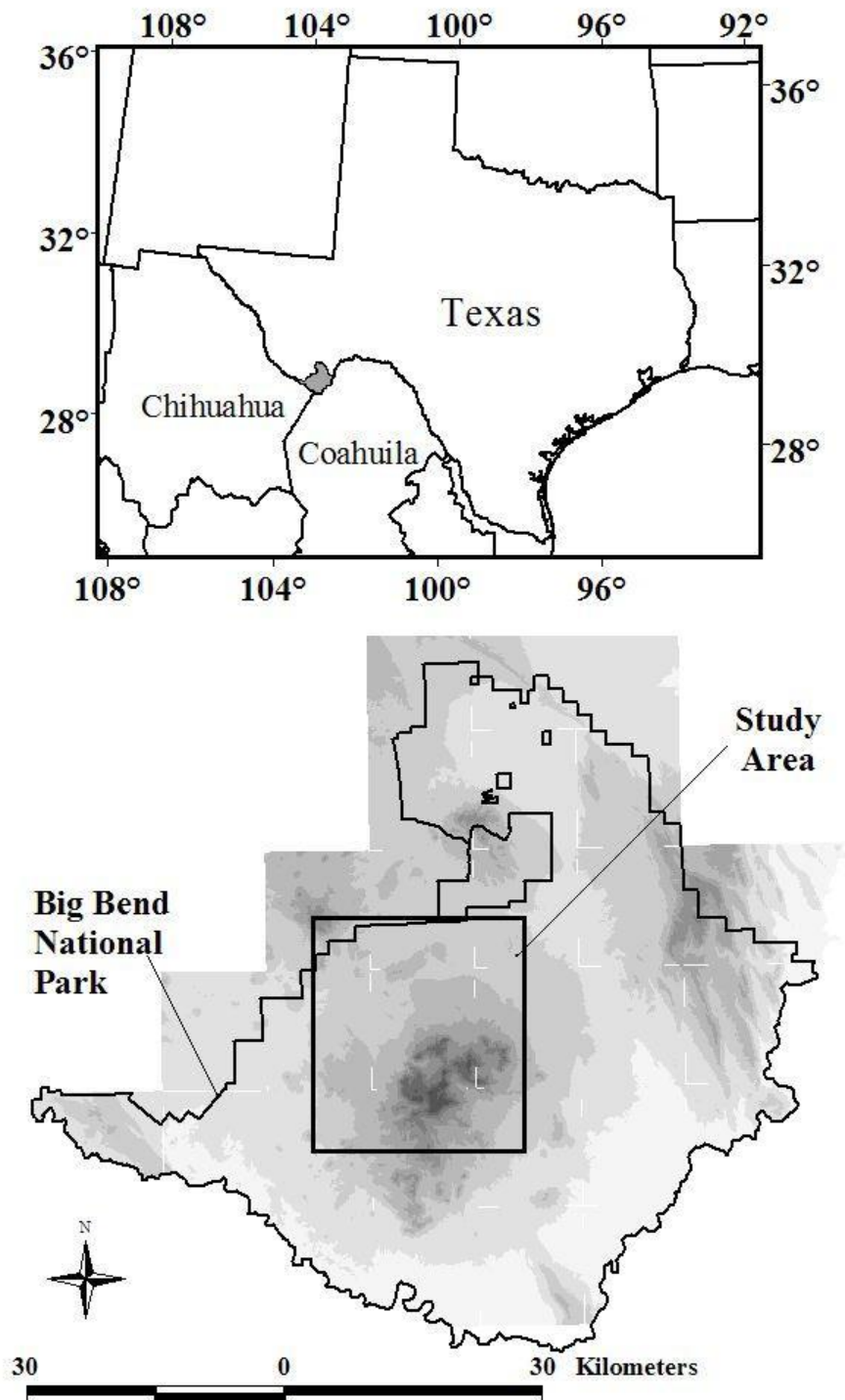
Fig. 2: Distribution of *Agave havardiana* in Big Bend National Park, Texas. Areas shown in white represent 100-m buffers around 700 agave plants known to have bloomed in 2003. Areas in black are 100-m buffers around 8,062 plants that bloomed between 1986 and 2009, representing a more detailed extent of agave-rich habitat within the park.
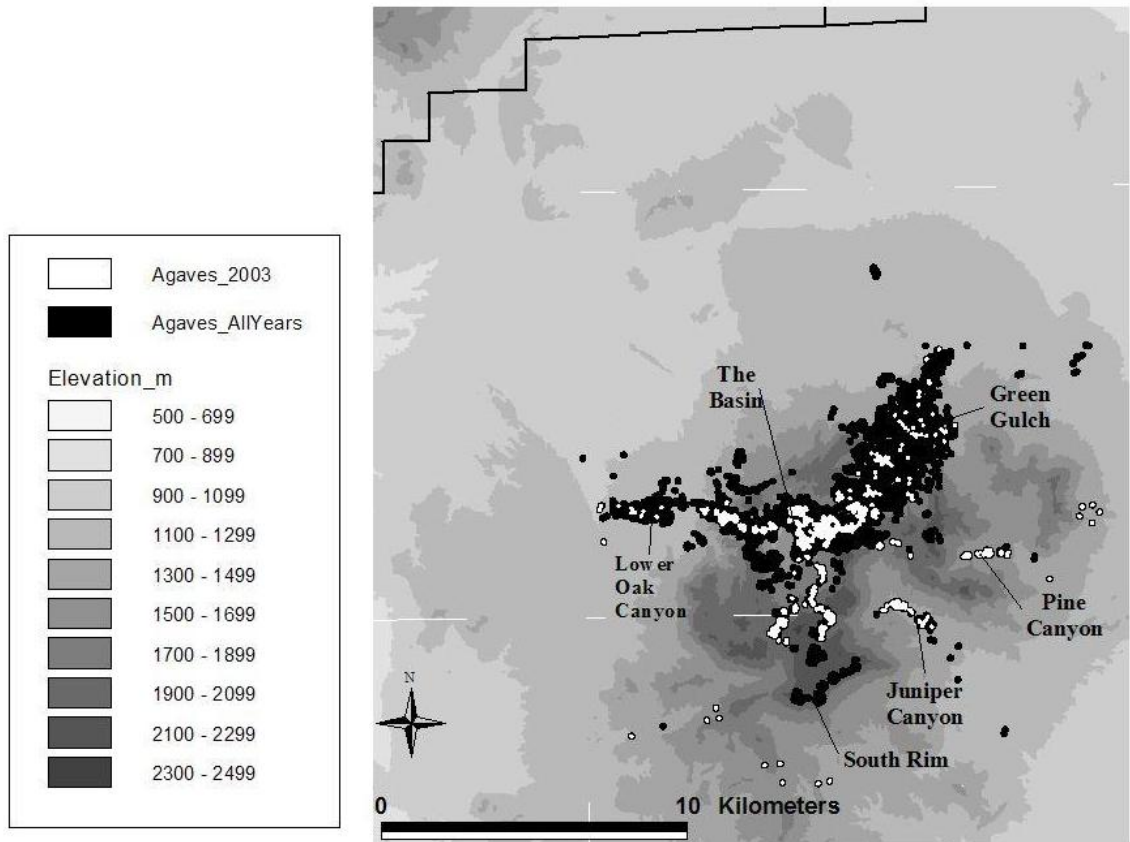
Fig. 3: Home ranges and core areas of 9 *Leptonycteris nivalis* radiotracked in Big Bend National Park in summer 2003. Areas shown are for a) 3 juvenile females (Bat 000, Bat 022, and Bat 044)

FIG. 3b) Home ranges and core areas of 1 adult male (Bat 710) and 1 juvenile male (Bat 832).

FIG. 3c) Home ranges and core areas of 1 lactating adult female (Bat 740) and 1 post-lactating adult female (Bat 850).
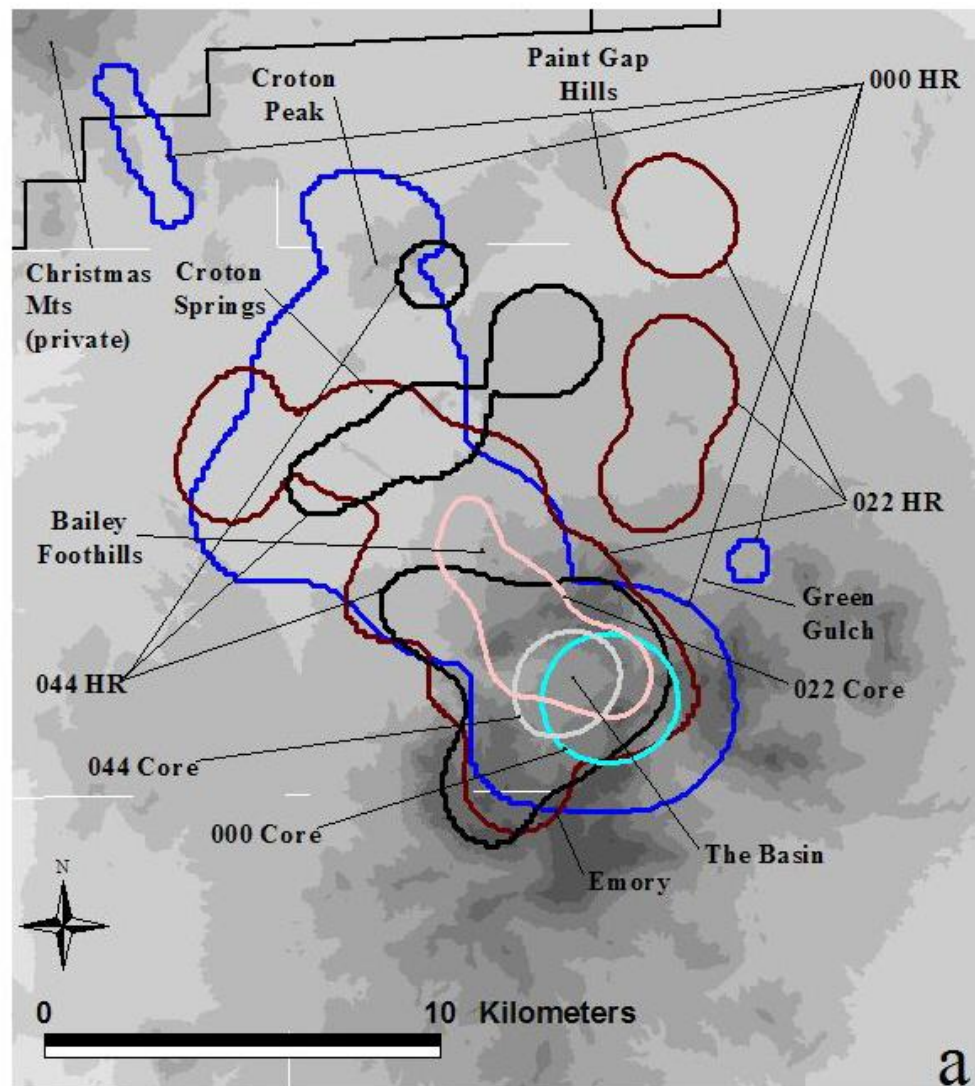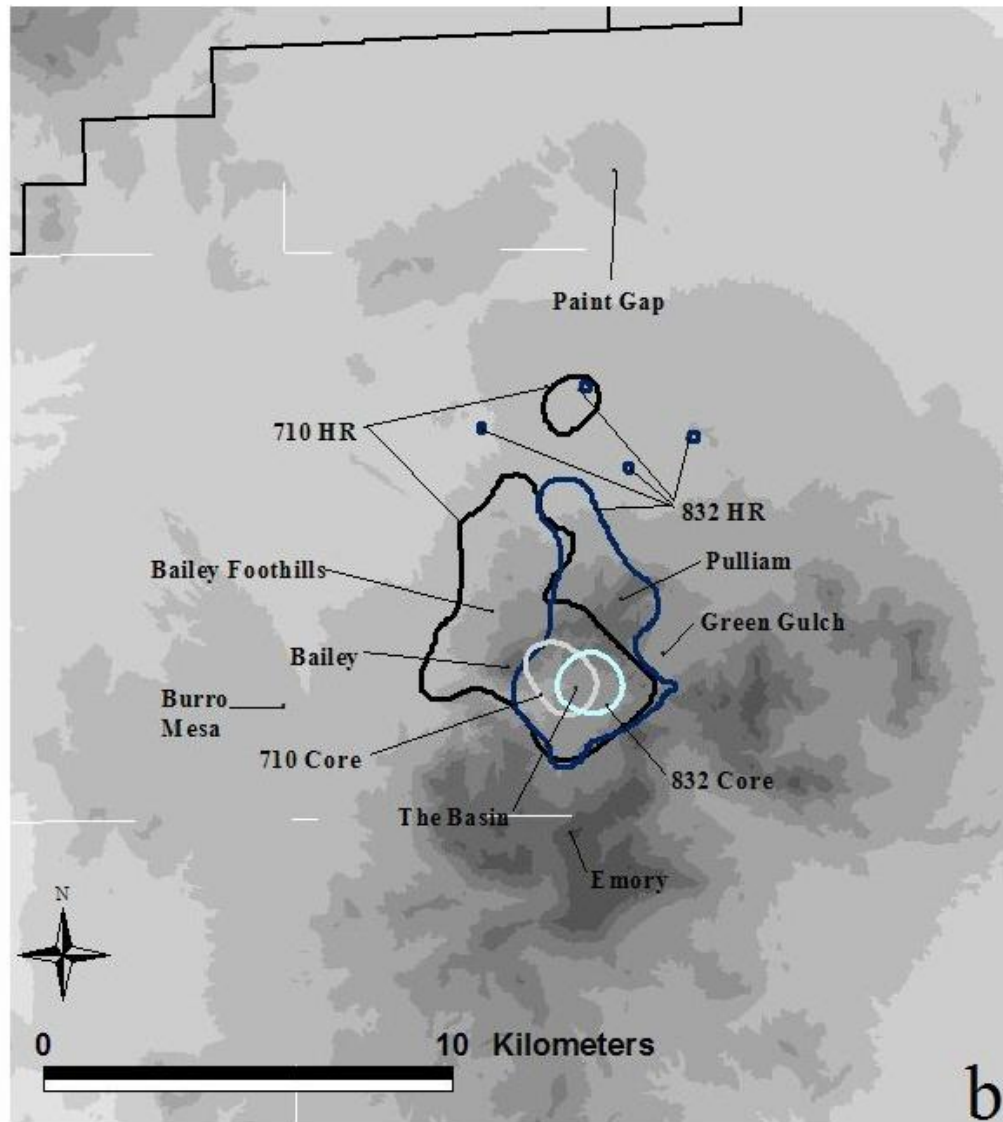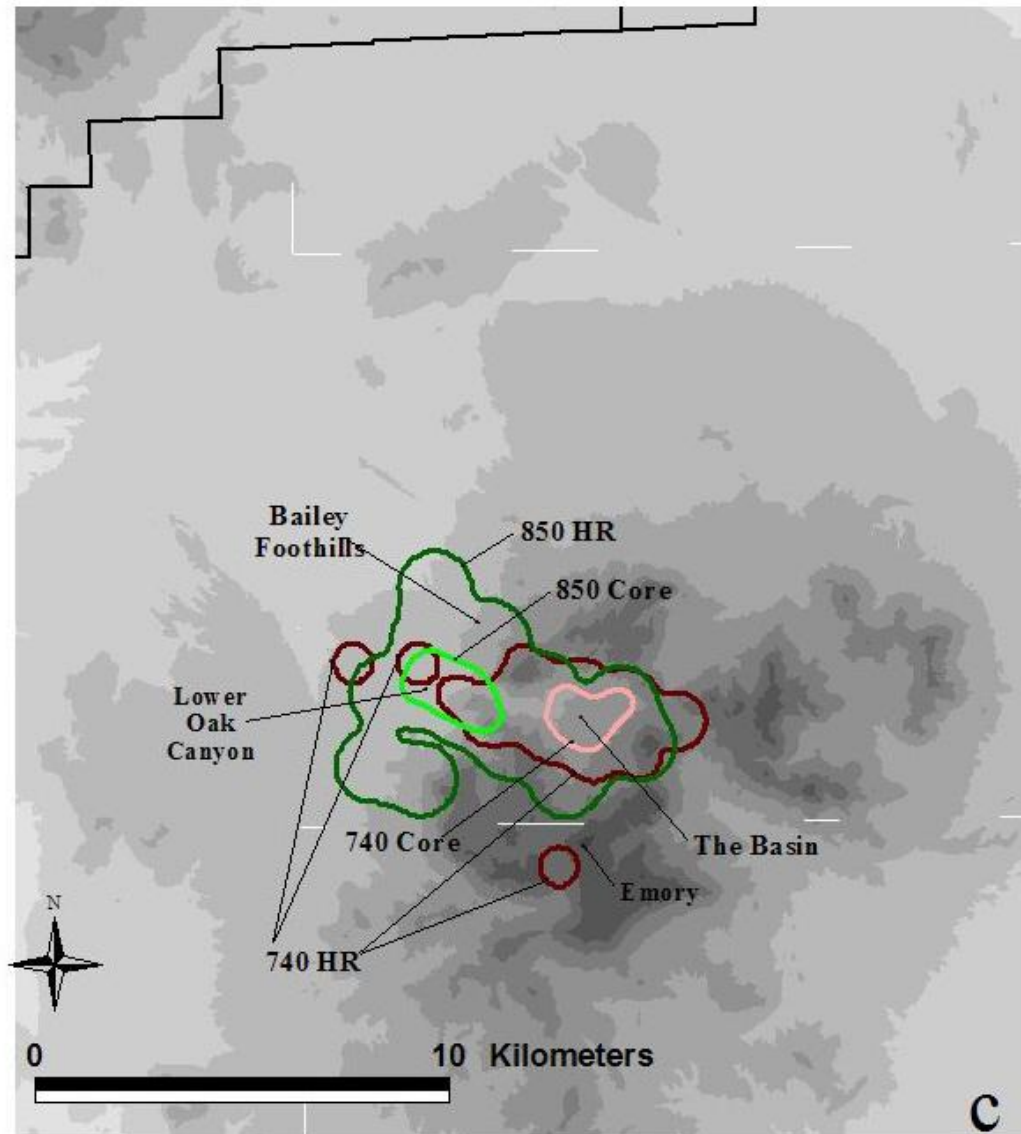
(Figure 3 continued on next page)

FIG. 3d) Home ranges and core areas of 2 nonreproductive adult females (Bat 690 and Bat 761).
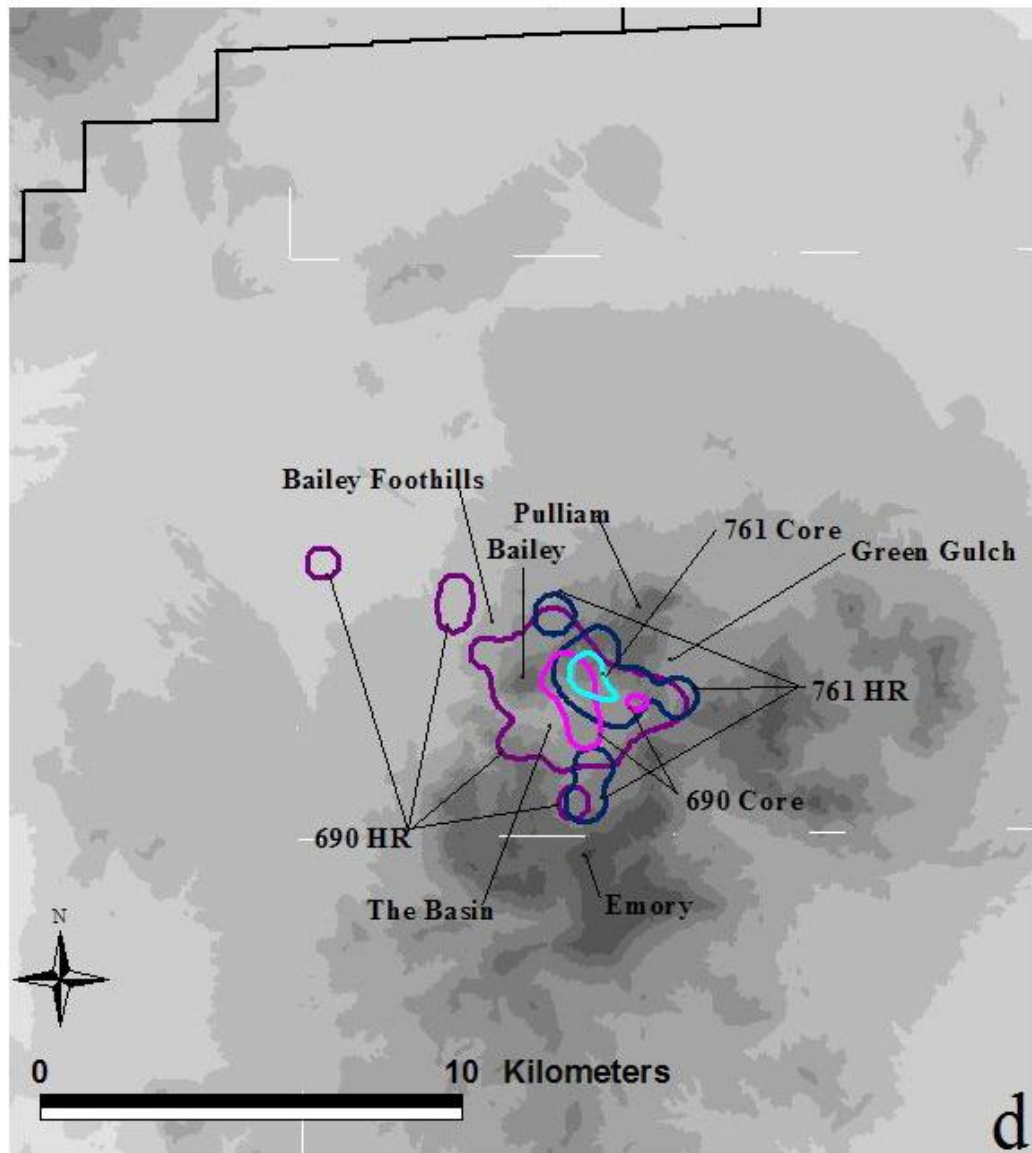
CHAPTER 3 – Animal Visitors to Blooming *Agave palmeri* in New Mexico

ABSTRACT

Premise: In order to assess support for the assertion that blooming agaves provide a keystone food resource for animals in desert ecosystems, I studied the pollination ecology of *Agave palmeri* with a focus on spatiotemporal variation in visitation patterns. My goals were to assess the importance of agaves to the greater pollinator community, and gain insight into what plant traits influence visitation.

Methods: I conducted repeated observations on 182 plants at three sites, and used an information-theoretic approach to select among competing explanatory models and evaluate the relative contribution of spatiotemporal, morphological, and phenological factors influencing visitation rates.

Key Results: There was considerable spatiotemporal variation in visitation rates for all visitor guilds. The primary presumed pollinators, nectar-feeding bats, were only present during mid and late summer at one site, late summer at a second site, and were not observed at a third site. Models indicated that increased visitation rates of birds, bees, and sphinx moths were correlated with increased plant size and the number of flowers blooming.

Conclusions: The broad array of animals observed at blooming *Agave palmeri* supports the assertion that it is an important food resource for many desert-dwelling vertebrates and invertebrates. This species serves as a sequential mutualist to other plants in this desert community by maintaining pollinator populations during periods of restricted resource availability, and provides stopover habitat for migratory pollinators including hummingbirds and nectar-feeding bats. By protecting agaves, conservationists may aid

not only local pollinator populations and their associated host plants, but also have far-reaching benefits to pollinator-linked ecosystems across the continent.

INTRODUCTION

Plant-pollinator interactions change over multiple temporal and spatial scales (Rocha et al., 2005; Elzinga et al., 2007; Burkle and Alarcón, 2011; Dunnell and Travers, 2011), but relatively few studies (e.g., Herrera, 1988; Horwitz and Schemske, 1990; Price et al., 2005; Artz et al., 2010) have attempted to document both spatial and temporal patterns of floral visitation. Abiotic factors such as topography, substrate, and weather may contribute to environmental variability and lead to an ephemeral mosaic of floral resources (Jackson, 1966; Fleming, 1992; Bowers and Dimmitt, 1994; Alarcón et al., 2008b); this heterogeneity can subsequently influence flower visitation rates in space and time (Eckhart, 1992; Figueroa-Castro and Cano-Santana, 2004). For example, nomadic animal populations wander seasonally to follow patchy resources (Des Granges, 1978; Holbrook et al., 2002), while migratory pollinators track temporally reliable resources across the landscape, resulting in predictable annual migration patterns (Feinsinger, 1976; Fleming, 1992; Robinson et al. 2009). Meanwhile, on a daily scale, "traplining" animals may first visit plants nearest their roost, nest, or colony then move away, resulting in a repeated temporal pattern of stops at plants along their spatial route (Linhart and Mendenhall, 1978; Des Granges, 1978; Proctor et al., 1996); such paths are expected to shift as floral resources change over time (Feinsinger, 1976; Neuweiler, 2000). The visitation rate of pollinators is influenced by various plant traits, and when geographically varying assemblages of pollinators select for alternate plant phenotypes, a mosaic of plant populations will result with traits shaped by these interactions (Thompson, 1997; Gómez

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and Zamora, 1999; Silva-Montellano and Eguiarte, 2003). These varying plant-animal

interactions affect plant reproduction (Moeller, 2006; Marshall et al., 2010) as well as the

survival and reproduction of the animals involved (Waser et al., 1996; Nabhan, 2004;

Hegland et al., 2009), thus an understanding of this variability is crucial for conservation

planning (Allen-Wardell et al., 1998; Burkle and Alarcón, 2011).

Because blooming plants and their flower visitors form a complex set of

interactions (Kearns et al., 1998; Dalsgaard et al., 2008), the roles each species plays in

others' natural histories may be overlooked if we neglect to consider them, or if we only

examine a narrow snapshot of space or time (Waser et al., 1996; Price et al., 2005). For

any given flower, some animals transfer more conspecific pollen per visit than others due

to morphological and behavioral traits (Inouye et al., 1994); however, if the most efficient

pollinator is only a rare or unpredictable visitor, more frequent pollen transfers from less

effective vectors may actually result in higher overall seed set (Sahli and Conner, 2007).

In actuality, some visitors exploit the pollination interaction by consuming nectar and/or

pollen while transferring no conspecific pollen (Inouye, 1980; Bronstein, 2001), which

decreases the number of legitimate pollinator visits and thereby negatively influences the

plant's reproduction (Maloof and Inouye, 2000; Irwin et al., 2001; Irwin and Maloof,

2002). Yet within a community, one plant's pollen or nectar thief may be another plant's

primary pollinator (Irwin and Maloof, 2002). And while flowering plants may compete

for pollinator services when pollinators are scarce, the plants may be considered

sequential mutualists if their bloom seasons are staggered in a manner that maintains

pollinator populations throughout the year (Waser and Real, 1979; Rocha et al., 2005;

Alarcón et al., 2008a). Plants and animals that provide resources or services at times

when availability is otherwise restricted may be considered keystone components of ecosystem stability (Power et al., 1996; Lundberg and Moberg, 2003), and be especially important in the face of disturbance or environmental uncertainty (Lundberg and Moberg, 2003).

One such proposed keystone interaction is the mutualistic relationship between paniculate agaves and nectar-feeding bats (U.S. Fish and Wildlife Service, 1994, 1995; Good-Avila et al., 2006). In the paniculate form, umbellate clusters of flowers are held away from the center stalk of the inflorescence upon lateral branches, presumably facilitating visits from larger-bodied vertebrate visitors (Gentry, 1982; Slauson, 2001). Among the variety of animals that provide pollination services to these plants, bats of the genus *Leptonycteris* are considered to have co-evolved as the primary pollinators, providing highly efficient pollen transfer, in large quantities, from long distances (Gentry, 1982; Slauson, 2001; Rocha et al., 2006). However, the presence and abundance of migratory taxa such as *Leptonycteris* can be unpredictable within seasons (Scott, 2004; Ober et al., 2005; Ammerman et al., 2009) and between years (Easterla, 1973; Cockrum, 1991; Molina-Freaner et al., 2003). In instances when the agaves cannot rely on bats to transfer pollen between individuals, other floral visitors may be crucial to ensure successful reproduction (Kuban, 1989; Slauson, 2000; Rocha et al., 2006); this may be particularly relevant in areas near or beyond the edge of nectar-feeding bats' ranges (Fulton, 1983; Slauson, 2000; Fleming et al, 2001). Thus, many agave species have floral traits that are evolutionarily generalized enough to allow pollination by other species such as birds and large-bodied insects (Slauson, 2001; Molina-Freaner et al., 2003; Rocha et al., 2006). The agave pollination system is considered to be a "leaky"

mutualism with nectar-feeding bats, because in the process of providing copious amounts of nectar and pollen to entice large-bodied visitors, the agaves benefit not only legitimate pollinators, but also nectar and pollen thieves (Proctor et al., 1996; Rocha et al., 2006). In fact, the abundant floral rewards serve as a crucial food resource for many animal species for at least a few weeks of the summer dry season (Kuban et al., 1983; Baltosser, 1989; Lange and Scott, 2001; Riffell et al., 2008), thereby playing a keystone role in maintaining desert pollinator communities (Rocha et al., 2005; Riffell et al., 2008). Paniculate agaves are seasonally prominent components of the diet of the federally endangered nectar-feeding bats *Leptonycteris yerbabuenae* and *L. nivalis*, and in fact constitute the sole known food source in parts of their ranges (Fleming et al., 1993; U.S. Fish and Wildlife Service, 1994, 1995; Moreno-Valdez et al., 2004). These bats act as pollinators and seed dispersers of columnar cacti and a variety of other plants along their migratory routes from southern Mexico to the southwestern United States (Fleming et al., 1993; Rojas-Martinez et al., 1999; Valiente-Banuet, 2002; Stoner et al., 2003). Nectar-feeding bats and other large pollinators provide crucial components of ecosystem stability in their role as "mobile links" that allow the persistence of multiple plant species upon which many other species depend (Lundberg and Moberg, 2003).

Agave palmeri is among the best studied of the paniculate agaves, particularly in Arizona (Howell, 1972; Schaffer and Schaffer, 1977; Howell and Roth, 1981; Slauson, 2000; Hinman, 2003; Ober and Steidl, 2004), however its distribution also extends into Sonora, Chihuahua, and New Mexico (Gentry, 1982). The only prior publications on *A. palmeri* outside Arizona were a study on floral responses to fire (Slauson, 2002), and a bat-visitation study (Scott, 2004). The southwestern corner of New Mexico provides a

unique study area because three species of migratory nectar-feeding bats (*Leptonycteris yerbabuenae*, *L. nivalis*, and *Choeronycteris mexicana*) co-occur during the mid-to-late summer in the sole known area of sympatry in their northern distributions (Arita and Humphrey, 1988; Hoyt et al., 1994). In this area, populations of *A. palmeri* are found both within and beyond the known range of these bats (Gentry, 1982). *Agave palmeri* relies almost exclusively on animal-mediated pollen transfer for successful reproduction (Slauson, 2000). Although prior publications (Martinez del Rio and Eguiarte, 1987; Kuban, 1989; Slauson, 2000; Rocha et al., 2005; Riffell et al., 2008) have found temporal or spatial variation in populations of animals that visit paniculate agaves, no previous studies have documented how the animal visitation patterns to *A. palmeri* may change within the course of a bloom season and the degree to which those patterns vary among sites.

In order to characterize the nature of the leaky agave-pollination system in areas near the edge of the bats' distributions I studied the pollination ecology of *A. palmeri* in southwestern New Mexico with a focus on how patterns change through time and space. My goals were to assess the importance of the plants to the greater pollinator community, and to gain insight into what factors influence visitation. My specific questions were: 1) What animals visit blooming *A. palmeri* in New Mexico? 2) Are the visitation rates of different guilds affected by plant size, inflorescence morphology, bloom phenology, and/or other organisms? 3) Do the visitation rates of different guilds vary among seasons and sites, and throughout the course of the agave bloom sequence? Rather than taking a manipulative experimental approach on a more limited sample size, I conducted repeated observations on a large number of plants at three widely separated sites, and used an

information-theoretic approach (Burnham and Anderson, 2002) to select among competing explanatory models and evaluate the relative contribution of spatiotemporal, morphological, and phenological attributes influencing visitation rates of various visitor guilds (Agrawal et al., 2007). When several candidate models had similar support, I used model averaging to provide robust parameter estimates. I tested for the influence of plant size and inflorescence shape, as well as bloom phenology, because different relative positions on the plant's inflorescence had varying numbers of flowers. In models of moth visitation rates, I also included bat visitation rate as a potential explanatory factor, to evaluate if there was any evidence that moth activity decreases with increasing bat activity. Temporal visitation patterns were assessed within day and night, and within season. I also compared spatial patterns among the three study sites to determine if there were differences in visitor patterns possibly related to ecoregion or proximity to bat roosts.

METHODS

Plant natural history—*Agave palmeri* stores water and nutrients in a basal rosette for an estimated 20-40 years before reaching reproductive maturity (Gentry, 1982; Slauson, 2001, 2002). The single 2-8 m tall paniculate inflorescence produces a striking visual display that is discernable from a distance (Howell, 1979; Slauson 2002), with an average of 1500-2200 protandrous flowers over the course of the flowering season (Slauson, 2000). Each individual flower is capable of producing 2.5 ml of nectar over the course of six days (Slauson, 2000, 2002; Riffell et al., 2008). Unlike some agaves, *A. palmeri* rarely reproduces vegetatively, and is typically self incompatible (Howell and

Roth, 1981; Gentry, 1982; Slauson, 2000). Successful reproduction therefore depends on attracting high-quality pollinators to the single reproductive event (Slauson, 2001).

This species displays traits typically associated with pollination by nectar-feeding bats, including nocturnal peaks of nectar production, anther dehiscence, and stigma receptivity (Schaffer and Schaffer, 1977; Howell and Roth, 1981; Slauson, 2000; Hinman, 2003), as well as strongly scented compounds that may attract visitors from a distance (Knudsen and Tollstein, 1995; Raguso, 2004; Alarcón et al., 2008a). The flowers remain open during the day with large amounts of nectar and pollen, and stigmas are receptive for several days, which allows for some diurnal pollination (Slauson, 2000). Flowering proceeds upward along the inflorescence's many branches over a roughly 3-6 wk period in summer (Slauson, 2001), and is asynchronous within populations (Ober et al., 2005). This phenology variation allows for temporal changes in visitor patterns over the course of the bloom season, as well as opportunities for pollen exchange with different mates when visitors shift foraging areas as new individuals become reproductively available (Ober et al., 2005). In Arizona, its important pollinators include *L. yerbabuenae,* sphinx moths, and carpenter bees, but it is also visited by noctuid moths, bumble bees, honey bees, wasps, flies, hummingbirds, orioles, and tanagers (Slauson, 2000; Lange and Scott, 2001; Bronstein et al., 2009). The bloom season of *A. palmeri* in southwestern New Mexico coincides loosely with the presence of nectar-feeding bats (Gentry, 1982; Hoyt et al., 1994). Populations of *A. palmeri* are scattered, with a 20-30 km separation between suitable agave habitats in this basin-and-range landscape (Gentry, 1982). Seed dispersal events of that distance are likely extremely rare; however, *Leptonycteris* routinely commute that far during the course of their evening feeding

activities (Horner et al., 1998; England, 2012a), potentially providing opportunities for pollen-mediated gene flow between isolated populations (Slauson, 2000).

   Study area—Fieldwork was conducted in July and August of 2006 and 2007 at three sites in Hidalgo and Luna counties of southwestern New Mexico, U.S.A. (**Fig. 1, Table 1**). In 2006, a single site was monitored in the southern Animas Mountains (Site A: 108°43' W, 31°23' N, NAD 1927, elevation 1625 m) located on the Diamond A Ranch (a.k.a. Gray Ranch), private property owned and managed by the Animas Foundation. In 2007, two sites on U.S. Bureau of Land Management (BLM) property were monitored. Site B (108°24' W, 31°39' N, 1625 m) was located near the northwestern boundary of the Big Hatchet Wilderness Study Area, whereas Site C (108°09' W, 31°57' N, 1575 m) was located just outside the boundary of the Cedar Mountains Wilderness Study Area. The three sites were situated approximately linearly, with Site A about 40 km southwest of Site B, and Site C about 40 km northeast of Site B. Site B is 2 km north of a major day roost of both *L. yerbabuenae* and *L. nivalis* (M. A. Bogan, U.S. Geological Survey, Albuquerque, New Mexico, unpublished manuscript). Sites A and B are located in the Madrean Archipelago ecoregion (Griffith et al., 2006), whereas Site C is within the Chihuahuan Desert ecoregion (Griffith et al., 2006). Sites A and C were mostly open grasslands with rarely occurring *Quercus* and *Juniperus*, while Site B was open woodland with *Pinus, Quercus*, *Juniperus*, and *Fouqueria* as common elements. All three sites are managed for cattle grazing, though cattle were not present on the sites during the study periods.

   Sites were selected in early July (2006, Site A) or late June (2007, Sites B and C) with relatively high densities of blooming agave plants compared to the surrounding

habitat. Observations at Site A took place 2006 Jul 14-15, Jul 26-29, and Aug 12-14; Site B visits occurred 2007 Jul 5-8, Jul 26-27, and Aug 11-12; and Site C visits occurred 2007 Jul 12-15, Jul 21, and Aug 9-10 (**Table 1**). Trip lengths varied depending on weather conditions and availability of volunteers.

Climate of the American Southwest is semi-arid and warm (Sheppard et al., 2002). Roughly half of the area's 28 cm of annual precipitation falls during the North American monsoon season of July to September (Sheppard et al., 2002). However, the interaction of local topology, the El Niño Southern Oscillation, and other longer-phase climate cycles results in extremely high variability in temperature and precipitation across the landscape at daily, seasonal, and multiyear scales (Sheppard et al., 2002). Unfortunately, minimal detailed weather information is available for this sparsely populated region, and the remote nature of the study sites and the possibility of theft or vandalism of unattended technology (U.S. Fish and Wildlife Service, 2007) made gathering on-site weather conditions during the entire season implausible, therefore local-level temperature and precipitation data were not collected.

Plant morphometrics and phenology—To document variation in rosette characteristics, for all blooming agaves within each site (78, 58, and 46 agaves at Sites A, B, and C, respectively), I recorded the rosette height and diameter in centimeters. I assumed that rosette volume would be linearly correlated with the dry mass of the plant (McLaughlin, 1993), so I calculated rosette volume using the rosette as a half sphere (0.5 x 4/3 x π x height x (diameter/2)^2) to provide an estimate of the stored resources available for reproduction in these semelparous plants (Aker, 1982).

I documented differences in inflorescences by measuring inflorescence height at the end of the study period to the nearest half meter (measured from ground to tip), and counted the number of branches on the entire inflorescence. Branches were easy to differentiate along the majority of the inflorescence where they emerged semi-perpendicularly from the axis, but for approximately the top 15% of the inflorescence, I considered a branch to be a contiguous clump of flowers that would allow large insects to crawl from one flower to another without traversing supporting pedicels or branches.

Morphometric variables were not normally distributed even after transformation, therefore nonparametric tests were used. Results were considered significant at $\alpha = 0.05$ for all analyses. Differences among sites in rosette volume, inflorescence height, and number of branches were tested using SAS software version 9.2's PROC NPAR1WAY's Kruskal-Wallis tests (SAS Institute Inc., 2008a), while least-squares mean differences were checked using PROC GLM's LSMEANS statement and the Tukey-Kramer adjustment for multiple comparisons (SAS Institute Inc., 2008a). I tested correlation of rosette volume, inflorescence height, and number of branches using PROC CORR SPEARMAN (SAS Institute Inc., 2008a). Because there was considerable correlation between morphometric traits (see Results), principal component analysis (PCA) was conducted using PROC PRINCOMP (SAS Institute Inc., 2008a) to capture variation between plants and produce a smaller number of uncorrelated variables for subsequent analyses (Gotelli and Ellison, 2004).

To assess the phenological variation within and among sites, each site was visited three times during the focal summer (**Table 1**). During the early-summer trip to Site A, data were collected slightly differently than for subsequent sampling periods, so those

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data were excluded from formal analyses. During each trip, I counted the number of branches blooming on surveyed agaves, and recorded each blooming branch's location on the inflorescence relative to other branches, following the sequential upward pattern of blooms. To calculate the plant's proportional bloom stage for each trip, I divided the location of the median branch blooming by the total number of branches on the inflorescence (e.g., if branches 2-4 out of 20 were blooming, the plant's proportional bloom stage would be $3/20 = 0.15$). The bloom stage was used to classify which quarter of the inflorescence was most active during that trip, with bloom stage of 0.01-0.25 being classified as 1st quarter, etc. PROC MEANS (SAS Institute Inc., 2008a) was used to compute the mean bloom stage among all plants blooming each trip.

I returned to each site in late September or early October of the same year. From each studied agave, I collected 1-2 of the branches that had been observed during each of the three summer visits ($N = 412$ branches from 164 plants). Collected branches were stored in individual paper bags, labeled with plant and branch number, allowed to dry, and then the number of flowers was counted from the persistent pedicels. In order to estimate the quantity of resources available to visitors during different phenological phases, I modeled the number of flowers per collected branch for each quarter of inflorescence. I hypothesized that this could be predicted by a combination of phenological, spatial, and morphological factors, so I prepared an a priori set of six ANCOVA models including the quarter of inflorescence within which the branch occurred, with various combinations of Principal Components 1 and 2 (PC1, PC2), and site (**Appendix Table A1**).

Information-theoretic modeling—To evaluate the support for considered models,

I used an information-theoretic approach (Burnham and Anderson, 2002; Stephens et al.,

2005; Garamszegi et al., 2009). Under this framework, the recommended maximum

number of models to consider should be less than the sample size (Burnham et al., 2011),

though I further restricted my model set using a rule-of-thumb of less than one predictor

variable per ten subjects (Grueber et al., 2011). I created generalized linear models using

PROC GENMOD (SAS Institute Inc., 2008a), with a Poisson probability distribution, a

log link function, and a scale parameter set to deviance to correct for overdispersion of

the count data. Observations from each plant were expected to be correlated, so models

were fitted using generalized estimating equations, with plant as the repeated subject.

The correlation structure was chosen that produced the smallest Quasi-likelihood

Information Criteria (QIC) values for null and single-variable models (Pan, 2001). QIC

goodness-of-fit statistics are a modification to Akaike's Information Criteria (AIC) scores

to allow model selection among generalized estimating equations (Pan, 2001). The

approximated QICu adds a penalty to the quasi-likelihood for the number of parameters

used in a model (Pan, 2001; SAS Institute Inc., 2008b); the model with the smallest QICu

score ($QICu_{min}$) is preferred. For each competing model, I calculated QICu differences

($\Delta QICu = QICu - QICu_{min}$), and then ranked all candidate models based on strength of

evidence as represented by QICu weight (Pan, 2001; Anderson, 2008). A model weight

is the probability that the given model is the most parsimonious, best fit for the data from

the candidate set (Anderson, 2008). I considered the best-ranked model to be definitive

relative to other candidates if the QICu weight was > 0.95, otherwise I included the top-

ranked models in the 95% confidence set such that the cumulative sum of their QICu

weights was just ≥ 0.95 (Burnham and Anderson, 2002). Model weights in the confidence set were then renormalized to sum to 1 for subsequent analyses (Anderson, 2008).

Multi-model inference was used to estimate model-averaged parameters for each of the predictor variables in the 95% confidence set, by weighting the estimate for each parameter by the summed weight of the models it appeared in; when the term did not appear, the parameter estimate of 0 was utilized (Burnham and Anderson, 2002). I used the LSMEANS and DIFF options of GENMOD (SAS Institute Inc., 2008a) as a post-hoc test for least-squares differences between class variables. Least-squares mean and standard error estimates were computed in log scale, but transformed for presentation (Grueber et al., 2011); reported standard errors are therefore not symmetrical around the mean. I also model averaged the weights of each predictor variable, in order to quantify the relative importance of each term to the global set of considered variables (Burnham and Anderson, 2002).

Insect capture—In order to document the identity of insect visitors to agave blooms, during each trip I collected insects over both day and night periods. One yellow Japanese Beetle Trap and one blue Asian Ladybug Trap (SpringStar LLC, Woodinville, Washington, USA) were filled with soapy water and hung from branches of one blooming agave plant each visit, approximately 4-6 m above ground. Traps were changed at dusk and dawn to differentiate nocturnal versus diurnal visitor guilds. Only one diurnal and one nocturnal trap were set during most trips in order to not deplete the visitor populations; however, on several occasions equipment malfunctions or poor weather resulted in low capture numbers so an additional day or night was sampled.

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Captured insects were rinsed with distilled water and stored in 70% ethanol for transport, then pinned for identification. Thrips, leafhoppers, and mosquitoes were not analyzed as I considered them incapable of moving pollen between plants due to their small body sizes (Slauson, 2000). Moths were identified by E. Metzler of Michigan State University, bees by K. Wright of the University of New Mexico's Museum of Southwestern Biology (MSB), and all other insects by D. Lightfoot (MSB). Specimens were deposited in the MSB. Over the three sites, I totaled 203.5 diurnal and 197 nocturnal trap-hours (Table 1).

Visitor observation—Diurnal visitors to all blooming agaves within each study site were censused using a point-count method (Sutherland, 2006), following routes between plants chosen haphazardly by different observers. Birds and insects were identified with Nikon 7x35 binoculars from seated positions 10-15 m away from the focal plant. Each daytime observation period was classified by 2-hr period of the day (the sunrise-to-sunset day length was very near 14 hrs total for all trips). The emphasis was on periods of expected peak activity (0600-1100 and 1700-2000 daily), but some observations extended through the afternoon when temperatures allowed. My goal was to observe each plant for 10 min, though a few observation periods had only 8 or 9 min; for these, I divided the sum by 8/10 or 9/10 to give a standardized rate of visitors per 10-min observation period, rounded to the nearest integer for analysis. During each minute, observers estimated the number of each of the following types of insects: carpenter bees, bumble bees, "medium" bees and flies (honey bee or house fly sized, approximately 2 cm long), "small" bees and flies (sweat bee sized, approximately < 1 cm long), wasps, butterflies, and other insects. The small bees and flies category was recorded in 2007

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(Sites B and C) only. Each minute we also estimated the number of birds observed in direct contact with floral reproductive structures. The identity and behavior of birds documented visiting any blooming agave (not just during the observation periods) were noted to the best of the observers' ability, but identifications from non-focal plants were not included in visitation-rate calculations. Bird visits were often fleeting and at a distance away from the focal plants, sometimes hindering identification. It was also difficult to count the number of visitors per minute during periods of high activity, and when insects were hidden within the flower clusters.

Video imagery of diurnal visitors was recorded in 2006 (Site A, $N = 2$ plants), using a Sony DCR-TRV9 camcorder, with Standard Play setting and optical zoom from 8-15 m away. Tapes were able to record for 60 min each. Daytime filming took place when there was no precipitation or strong wind in the area, between dawn (approximately 06:20, 06:25, and 06:35 MDT on the three trips) and dusk (20:25, 20:15, 20:05, respectively). Focal plants were chosen based on ease of access, and typically we left the video setup focused upon a single agave rather than losing time by moving the camera between different plants across the rugged landscape. Analysis (not shown) of filmed versus live observations revealed no significant differences in visitation rates, so in 2007 I discontinued daytime filming in order to increase the number of different plants observed in person.

Video imagery of nocturnal visitors to one (2006) or two (2007) agave plants per trip ($N = 13$ plants) was recorded using the Nightshot feature on Sony DCR-TRV9 and DCR-HC52 camcorders. Supplemental infrared lighting was supplied by IR6 Lamps (Wildlife Engineering, Tucson, Arizona, USA). Recording was done using the Standard

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Play setting with optical zoom from 8-15 m away. Nocturnal recording took place when there was no precipitation in the area, between the end of civil twilight (about 20:50 MDT during early-summer trips and 20:30 in late-summer trips) and roughly midnight, involving usually two to three 60-min tapes per night. Filmed agaves were chosen based on ease of access, and cameras remained trained on the same plants throughout each night's filming.

Subsequent analysis of videos was aided by Sony Vegas Movie Studio 8.0 software (Sony Creative Software, Middleton, Wisconsin, USA), which allowed the videos to be slowed during playback when necessary. Videos were broken into observation periods of 10 min (a few 8 or 9-min periods were converted to 10-min rates, as described above). Diurnal videos were analyzed in the same manner as the binocular counts described previously. For each minute of nocturnal video, I counted the number of bat visits, and estimated the number of sphinx moths and other moths. Bats were identified as nectar feeders or not, based on size and characteristic flight style at branches. Due to limitations of the imagery, it was impossible to determine if bats made actual contact with stigmas, so a "visit" was defined to be any pass within 1 m of a blooming branch (Arizaga et al., 2000); bat-visitation rates therefore may have been somewhat inflated. Sphinx moths of all sizes displayed a distinctive hovering and bobbing motion that other moths did not. Sphinx moths were larger and more reliably counted than the other moths when video quality was poor, resulting in more sphinx-moth than other-moth observation periods.

My team of eight volunteers and I logged a total of 593 diurnal binocular observation periods across the 3 sites (Table 1). I also recorded and analyzed a total of

114 diurnal video observation periods at Site A (2006 only), and 226 nocturnal observation periods (all sites). This resulted in 6984 min of diurnal data from 178 plants, and 2051 min of nocturnal data from 13 plants.

Information-theoretic modeling of visitation rates—For each diurnal visitor category (birds, carpenter bees, bumble bees, medium bees and flies, and small bees and flies), the total number of visits per 10-min observation period was summed. I omitted records from 2-hr periods having < 9 observations per trip, resulting in 640 bird, 553 carpenter bee, 553 bumble bee, 598 medium bee and fly, and 281 small bee and fly records for analysis. Wasps, butterflies, and other diurnal insects visited at very low rates and were therefore not included in modeling efforts. Based on previous pollinator-behavior studies, I hypothesized that diurnal visitation rates could be explained by some combination of spatiotemporal, plant-morphological, and plant-phenological characteristics. I therefore prepared a series of 13 a priori ANCOVA models (Appendix A2), all containing the predictor variables site, season within site, and 2-hr period of day, along with various combinations of PC1, PC2, number of blooming branches, and quarter of inflorescence in which the median blooming branch's position fell. In some of the candidate models I included the interaction term between number of branches and quarter of inflorescence as a proxy for the total number of flowers in bloom, because branches in the first and last quarter of the inflorescence had fewer flowers than those in the central quarters.

Bats were only present at certain sites on certain dates, presumably due to the timing of their migration (Cockrum, 1991), so bat visitation rates were assessed only for nights when bats were present at a site. This limited the number of bat observation

periods to 49 records. Therefore, only three a priori models were fitted for bat visitation

rates, including the effects site, season within site, 1-hr period of night (beginning 30-min

after sunset to allow full darkness to fall), and the interaction between site and hour in

case visitors had to travel to the agave patches from site-specific distances (Appendix

A3). Phenological and morphological terms were not included because of the limited

number of agaves observed during nights bats were present.

Sphinx-moth observation periods ($N = 183$) were assessed with 13 a priori

models, (Appendix A4) including the terms site, season within site, 1-hr period of night,

and various combinations of PC1, PC2, and the interaction of hour with site. Certain

candidate models also included the number of bat passes during the moth-observation

period, because some moths reduce their flight activity when they detect ultrasonic bat

calls (Roeder, 1962; Roeder and Treat, 1970; Faure et al., 1990; Ratcliffe et al., 2008).

Phenological traits had insufficient variation to evaluate importance, so were not included

in modeling.

Other-moth observation periods ($N = 146$) were assessed with 5 a priori models

(Appendix A5) including the terms site, season within site, 1-hr period of night, and

combinations of the interaction between hour and site, and/or the number of bat passes.

Because other moths were recorded at fewer plants than sphinx moths were, phenological

and morphological terms were not modeled.

Each diurnal and nocturnal visitor category was modeled with a Poisson response,

using a log link function. Generalized estimating equations were computed with PROC

GENMOD (SAS Institute Inc., 2008a), with plant as the repeated subject. QICu, ΔQICu,

and QICu weights were computed as previously described to determine the strength of

evidence for each considered model. When no single best model was found, model averaging based on the 95% confidence set was used to estimate parameters and evaluate the importance of predictor variables.

RESULTS

Plant morphometrics and phenology—Among the agaves that bloomed during study years, all three sites differed significantly in rosette volume, being smallest at Site A and largest at Site C (Kruskal-Wallis χ^2 = 85.27, df = 2, P < 0.0001; Fig. 2a). Likewise, mean inflorescence height increased from Site A to Site B to Site C (Kruskal-Wallis χ^2 = 72.48, df = 2, P < 0.001, Fig. 2b). The mean number of branches per inflorescence differed significantly by site (χ^2 = 31.58, df = 2, P < 0.0001), and was similar between Site A and B (least squares means: P = 0.9995), both of which had fewer branches than plants at Site C (both P < 0.0001; Fig. 2c). Rosette volume was strongly correlated with inflorescence height (Spearman r_s = 0.74, P < 0.0001) and moderately strongly with the number of branches (Spearman r_s = 0.61, P < 0.0001). Inflorescence height was moderately correlated with the number of branches (Spearman r_s = 0.45, P < 0.0001). This pattern held true within Sites A and B, but at Site C the inflorescence height was not significantly correlated with the number of branches (Spearman r_s = 0.06, P = 0.7109).

Principal Component 1 (PC1) explained 70% of the variation in the morphological variables, and consisted of variable loadings of 0.62 rosette volume, 0.56 inflorescence height, and 0.55 number of branches; PC1 is hereafter interpreted as the overall plant size. PC2 explained an additional 19% of the variation among individuals, and consisted of 0.73 number of branches, -0.68 inflorescence height, and -0.04 rosette

volume; PC2 is hereafter referred to as display shape, representing a tradeoff between horizontal and vertical attributes of the inflorescence. PC3 explained the final 11% of the morphological variation between plants, consisting of -0.79 rosette volume, 0.47 inflorescence height, and 0.40 number of branches. PC3 was not used in subsequent analyses, in order to reduce the number of variables analyzed.

The mean number of flowers per branch varied by site and inflorescence quarter. Agaves at Site A had fewer mean flowers per branch than plants at Site B or C (Fig. 3a). The mean number of flowers per branch was significantly higher for branches in the central two quarters of the inflorescence than the bottom or top quarters (Fig. 3b). The differences between the first and last quarter, and the second and third quarters, both approached significance ($P = 0.0584$ and $P = 0.0558$, respectively). The selected best model for the number of flowers per branch contained the terms site, plant size, and quarter of inflorescence.

The mean bloom stage progressed within each site during the summer season. During the early trips, approximately 80% of the plants had bloom stages in the 1st or 2nd quarter of the inflorescence, while during the late trips over 80% of the plants were in the 3rd or 4th quarter, and over 40% were in the final quarter of the inflorescence.

Insect capture—During the summers of 2006 and 2007, I captured and identified 64 insect species in 40 genera of 24 families. Sampling was not equal between all trips; therefore results are presented as capture rates per trap hour. Rates of > 0.1 capture per trap hour were considered "relatively high" and included four species of noctuid moths, nine species of bees, and two families of flies (Table 2).

Diurnal capture rates were highest for small bees, were moderate for flies and medium bees, and were low for large bees (Table 2). The most abundant bee species overall in diurnal traps was *Lasioglossum microlepoides*, which had relatively high rates at all three sites, and was present during all trips. The second highest overall capture rate was for the undescribed morphotype *Lasioglossum sp.* 2, which was never captured at Site A (2006), but was found in relatively high numbers at Sites B and C (both 2007). The third highest overall bee capture rate was for *Apis mellifera*, which were trapped at high rates at Site A, but were infrequently captured at the other two sites. Although carpenter bees (*Xylacopa californica*) and bumble bees *(Bombus sonorous)* were frequently observed, they were captured at rates of < 0.1 / trap hour. Sarcophagid flies were captured at relatively high rates in diurnal traps at Sites B and C. Tachinid flies were captured at slightly lower rates overall, though were more abundant in traps than sarcophagids at Site C.

Nocturnal captures were predominantly moths, of which 94% were Noctuidae, 5% Pyralidae, and 1% Sphingidae. Moth capture rates and species diversity were highest at Site B during the late summer trip, where four noctuid moth species were captured at relatively high rates (Table 2). Only one noctuid moth species (*Striacosta albicosta*) was trapped in relatively high rates at Site A, also during the late summer. No moths were captured at Site C on either of the 2 nights sampled. Sphinx moths were observed at all sites, though only *Hyles lineata* was captured, once each at Sites A and B.

Diurnal visitor observations—Examination of the 95% confidence set of models for diurnal visitors (Table 3) revealed that in addition to the terms that were included for all models (site, season within site, and period of day), the predictor variables of plant

size and number of branches blooming were consistently important influences on the number of diurnal visitors (Table 4). Model selection for diurnal visitors had difficulty resolving whether models with both plant size and display shape performed better than models with only plant size (Table 3); the exception was for small bees and flies, which showed influence by plant size but not display shape. Display shape showed the highest relative importance (0.95) for carpenter bees; for all other diurnal visitors it had cumulative weights < 0.40 (Table 4). The quarter of inflorescence in bloom was supported as an important diurnal-visitor predictor variable, with a weight of 1.0 for all visitor guilds except carpenter bees (0.71). The interaction term between number of branches blooming and quarter of inflorescence (a proxy for the total number of flowers in bloom) was an important predictor for diurnal visitors, though potentially less for carpenter bees and bumble bees than other guilds (Table 4).

Birds—Eight species of birds were observed in contact with open flowers on focal agaves; of these, rufous hummingbirds were most common (Table 5). Two additional species, *Zenaida asiatica* (white-winged dove) and *Corvus sp.* (one of three species of ravens and crows potentially present in the study area), were observed at open flowers on non-focal plants. Rufous hummingbirds were present at Site A in very large numbers during the mid-summer trip, and in lower numbers during the late-summer trip (Table 5). At Site B, rufous hummingbirds were not observed until the late-summer trip, while Site C had low observation rates of rufous hummingbirds during all visits. Black-chinned hummingbirds were observed in low numbers at Site A during the mid-summer trip. Unidentified hummingbirds (possibly female or juvenile black-chinned hummingbirds) were also present during the late-summer trip to Site B and all trips to Site C. Aggressive

territorial behavior was displayed by rufous hummingbirds when bird densities were high, whereas black-chinned hummingbirds were not observed to defend agaves, though they did attempt feeding visits to defended inflorescences. All hummingbirds appeared to avoid contact with pollen-bearing structures unless bumped by wind or chased by other hummingbirds.

The overall bird visitation rate was highest at Site A, intermediate at Site B, and lowest at Site C (Table 6; all pair-wise differences $P < 0.005$). Seasonally, bird visits were highest during the mid-summer trip at Site A, moderate during the late-summer trips to Sites A and B, highly variable in the middle-summer trip to Site B, and low during the early trip to Site B and all trips to Site C (Table 7). There were slight peaks at dawn, mid-afternoon, and dusk (Table 8). Bird visits were highest to inflorescences in the second quarter of bloom, and lowest to those in the fourth quarter (Table 9). The log number of bird visits increased with increasing plant size ($P < 0.01$)

Carpenter bees—Carpenter bee visitation rates were significantly higher at Site B than at Sites A and C (Table 6). Carpenter bees visited agaves at moderately low rates during all trips except the late-summer trip to Site A when they were rarely observed, and the late-summer trip to Site B when they were abundant (Table 7). Carpenter bees were most frequent visitors during the middle of the day, and were lowest during the late afternoon (Table 8). There were no significant differences between rates of carpenter bee visits to different quarters of the inflorescence (Table 9). The log number of carpenter bee visits increased with number of branches blooming ($P < 0.01$). Display shape was present in the top three carpenter bee models, having a variable weight of 0.95, and when present it was statistically significant ($P < 0.05$), thus suggesting that higher carpenter bee

visitation was associated with tall, few-branched displays than with short, many-branched displays.

Bumble bees—Bumble bee visitation rates were slightly lower at Site A, though this was not significant (Table 6). Bumble bees were abundant at agaves during the late-summer 2007 trips to Site B and Site C, but were observed at significantly lower rates during all other trips (Table 7). There was a peak in bumble bee visits during the 7th 2-hr period of the day (approximately 12:30 to 14:30 local time; Table 8). Bumble bee visits were highest to plants in the second quarter of their bloom phenology, and lowest during the distal quarter (Table 9).

Medium bees and flies—The visitation rate of medium bees and flies was slightly but not significantly lower at Site B than at Sites A and C (Table 6). There was not a consistent seasonal pattern of medium bees and flies visitation at the different sites (Table 7). Activity was highest near dawn, dropped steadily during the morning, was low most of the afternoon, and had a mild resurgence before sundown (Table 8). More visits were recorded to inflorescences in the central two quarters than the first and last quarters of their bloom phenology (Table 9). The log number of medium flies and bees visiting increased significantly with plant size ($P < 0.01$) and with the number of branches blooming ($P < 0.05$).

Small bees and flies—The visitation rate of small bees and flies was lower at Site B than Site C, but this was not significant (Table 6; $P = 0.0923$). Small bees and flies visited agaves at low rates during the early-summer trip to Site B, but at higher, fairly consistent rates during the mid- and late-summer trips to Site B and all trips to site C (Table 7). The 2-hr period immediately after dawn had lower small bee and fly visitation

rates than mid- and late-morning or pre-sunset periods (Table 8), though mid-afternoon sampling was inadequate to characterize rates during those times. Small bees and flies occurred at highest rates at plants blooming in the second quarter of their inflorescence, while lowest rates were associated with the third and fourth quarters (Table 9). The log number of visits from small bees and flies increased significantly with plant size (P = 0.0045).

Nocturnal visitor observations—

Bats—The top model for bat visitation included site, season within site, hour, and the interaction of site and hour (Table 10). Bats were not observed at Site C, and were only observed at Site B during the late-summer trip. Bats visited agaves at higher rates at site A than site B ($P < 0.0001$; Table 6), with intermediate rates during the mid-summer trip to Site A, high rates during late summer trip to Site A, and low rates during the late-summer trip to Site B (all pairwise differences $P < 0.0001$; Table 7). The hour and site terms interacted such that bat visits increased with hour at Site A, but decreased with hour at Site B (Fig. 4).

Sphinx moths—In addition to site, season, and hour, the confidence set of models for sphinx moth visitation rates also included plant size in all selected models (Table 10), but not the interaction of hour and site. There was limited evidence supporting bat visitation rate as a predictor of sphinx-moth visitation rate (Table 4). Sphinx moths were least frequent visitors at Site A, intermediate at Site B, and most frequent at Site C (Table 6). Seasonally, sphinx moths were most abundant in late-summer trips to Sites B and C, though particularly variable during the late-summer trip to Site B (Table 7). Sphinx

visitation rates were lowest during the second hour of the night (Table 11). The log

number of sphinx moth visits increased with overall plant size ($P < 0.001$).

   Other moths—The best model for other moths included site, season, hour, the

interaction of site and hour, and concurrent bat rates (Table 10). Non-sphinx moths

visited agaves at highest rates at Site A, intermediate at Site B, and lowest at Site C

(Table 6). Seasonally, other-moth visitation was very high in late summer at Site B, high

in mid-summer at Site A, medium-high in late summer at Site A, and lower during other

trips (Table 7). Other moth visitation was highest during the first hour of night (Table

11), though this pattern was potentially complicated at Site B where bat activity was

highest during the early part of the night (Fig. 4). The log number of non-sphinx moth

visits decreased as the number of bat passes increased ($P < 0.0001$).

DISCUSSION

   Plant morphometrics—Plant size (PC1) accounted for 70% of the variation

between plants. Because agaves store water, energy, and nutrients in their rosette, a

larger rosette size may allow the individual to produce an inflorescence that is taller, has

more branches, and/or more flowers capable of producing larger quantities of rewards or

olfactory signals (Aker, 1982; Silva-Montellano and Eguiarte, 2003; Rocha et al., 2005).

Larger floral displays may improve detectability and serve as advertisement to attract

high-quality pollinators that move pollen longer distances, resulting in greater genotypic

variability of offspring, increased fruit and seed set, and improved germination rates and

seedling viability (Schaffer and Schaffer, 1979; Waser, 1983; Huxman and Loik, 1997;

Donnelly et al., 1998; Winter and von Helversen, 2001; Ornelas et al., 2002; Rocha et al.,

2005). *Agave palmeri* at Site C had substantially larger rosettes, more branches, and

taller inflorescences than those at other sites. Although this could have been due to abiotic microclimate factors, geographically variable selection by various pollinator guilds for different morphological traits may have contributed. Agave populations in the Cedar Mountains are near the edge of the known range of nectar-feeding bats, and the bats were not observed there. This could result in distinct agave morphometric profiles if alternative pollinators select for different characters than bats do. I lacked enough observations on different plants to evaluate the effect of plant size on bat visitation, but in southeastern Arizona, visitation rates of *L. yerbabuenae* were not explained by inflorescence height of *A. palmeri* (Ober and Steidl, 2004). In contrast, plant size was an important predictor variable in top models for all presumed backup pollinators, such that increasing plant size was associated with increased visitation rates; this effect was statistically significant for birds, medium bees and flies, and sphinx moths.

Display shape (PC2) explained an additional 19% of the variation between plants, and was present as a predictor variable in all visitor guilds assessed, though its effect was most strongly supported in carpenter bee visitation rates, such that more visits were associated with taller, few-branched displays than with shorter, many-branched displays. This lends support to prior studies that found orioles, carpenter bees, and bumble bees preferred taller agave inflorescences (Schaffer and Schaffer, 1977, 1979; Ornelas et al., 2002).

Plants with positive values of PC3 had relatively larger displays and smaller rosettes, while negative PC3 plants had less display and larger rosettes; PC3 thus represented the tradeoff of resource spent on display infrastructure, compared to the amount saved for fruit and seed development, and could perhaps be thought of as the

advertizing budget. Although beyond the scope of my studies, it would be interesting to see if PC3 affected visitation rates, nectar or pollen production, flower or ovule number, or fruit or seed set.

Plant phenology—Inflorescence quarter and its interaction with the number of branches blooming were present in top models predicting diurnal visitation rates (though I was unable to assess its impact on nocturnal visitors). Branches in the proximal and distal quarters of the inflorescence have fewer flowers than those in the center half, therefore early and late branches likely have smaller reward quantities available for visitors. Nectar quantity and quality may also decline in the distal portion of the inflorescence due to resource limitation (Slauson, 2002) or architectural effects (Diggle, 1997). For these reasons, it is important that researchers document agave phenology in order to be able to estimate the floral resources available to visitors at any particular location and time. The inflorescence-quarter method satisfies the recommendation to use mean or peak flowering dates of plant populations as indicators of variation in flowering dates over time (Miller-Rushing and Inouye, 2009), and is fast and easy to visually estimate even at a distance. Asynchrony of plant blooming can also affect pollen movement distances, potentially leading to spatiotemporal variation in plant mating patterns (Elzinga et al., 2007).

Insect capture—The broad array of insects captured supports the importance of blooming agaves as a food source for desert invertebrates; however, not all the insects captured should be assumed to be legitimate pollinators of *A. palmeri*. Some may have been acting as nectar or pollen thieves (Inouye, 1980; Bronstein, 2001), while some may have been visiting in search of mating opportunities or oviposition sites (Thompson and

Pellmyr, 1992; Riffell et al., 2008; Seagraves et al., 2008). Likewise, trapping rates should not be assumed to represent floral visitation frequencies, because weather conditions such as temperature, precipitation, or wind may have affected capture success (Ausden and Drake, 2006; Brown and McNeil, 2009). Additionally, a trap size bias may have been present, as the traps used are designed to capture insects about 1.0-1.5 cm long. More types of insects were observed than were trapped, especially those of medium-to-large body sizes such as wasps, carpenter and bumble bees, and sphinx moths, which had body sizes that were near or larger than the size of the trap opening. Although only one species of sphinx moth was captured in traps, there were several instances of video showing small, medium, and large sized moths that displayed sphinx-style hovering behavior. At least 30 species of sphinx moths may be present in the area (Tuttle, 2007; Opler et al., 2011), and at least eight of these have been reported to feed at agaves (Tuttle, 2007; Alarcón et al., 2008a). Other flying insects were observed on nocturnal video from all three trips to Site B that were likely adult antlions (Neuroptera: Myrmeleontidae), some of which eat nectar (Milne and Milne, 1995); however, they were never captured, and did not occur often enough to analyze statistically.

Bat visits—Bat passes were assumed to be from *Leptonycteris*, though the similar body sizes and distance from camera to subject made identification to species impossible. A third species of nectar-feeding bat (*C. mexicana*) occurs in the study area during the mid-to-late summer (Arita, 1991; Hoyt et al., 1994), but is rarely encountered, and is not known from the Big Hatchet or Cedar ranges (Cryan and Bogan, 2003), whereas there are multiple roosts in southwestern New Mexico housing *L. yerbabuenae* and *L. nivalis* in numbers seasonally reaching thousands of individuals (M. A. Bogan, U.S. Geological

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Survey, Albuquerque, New Mexico, unpublished manuscript). All bat visits showed a similar behavior of swooping up to the branch, stalling briefly, and then swooping down and away, which has been described (Kuban, 1989) as typical foraging behavior for *Leptonycteris*. Although some insectivorous bats previously have been documented carrying agave pollen either from facultatively foraging on nectar or gleaning insects from agave panicles (Kuban, 1989; Herrera et al., 1993; Hinman, 2003; Frick et al., 2009), no such instances were observed on > 2000 min of nocturnal video.

The video footage showed multiple instances of several bats approaching blooming branches from roughly the same trajectory in rapid succession (2006 Jul 28, Aug 13 and 14; 2007 Aug 11), as described by Horner et al. (1998) and Hinman (2003). In some instances, one of the bats subjectively appeared clumsy in its approach and feeding. I believe this was likely to have been instances of mother and her young feeding. This seasonal timing is consistent with the reproduction and development of *L. yerbabuenae* in Arizona, where young are born in June and begin flying about a month later (Cockrum, 1991). Late-summer capture data from southeastern Arizona reveal that post-reproductive females are often found in the company of subadult or young adult bats (Hinman, 2003). During this period, *A. palmeri* is likely a critical food resource necessary for rapidly growing juveniles and females recovering from the energy demands of pregnancy and lactation to refuel before their autumn migration south (Cockrum, 1991).

Nectar-feeding bats such as *Leptonycteris* are considered to be high-quality pollinators of agaves. Their visits generally involve direct contact with reproductive structures (i.e., 100% of visits result in stigma contact; Slauson, 2000), and their fur

captures and holds pollen effectively (Howell and Hodgkin, 1976; Muchhala and

Thomson, 2010). This ability to transfer large quantities of pollen may ensure adequate

amounts of pollen to fertilize many ovules, and allow for multi-sire competition for

access to ovules (Fleming et al., 2009). Because *A. palmeri* is believed to be the primary

food source for *Leptonycteris* in New Mexico (Hevly, 1979; Howell, 1979), the pollen

loads they carry should be largely uncontaminated by non-conspecific pollen. Pollen

load on the fur of captured *L. yerbabuenae* increases thoughout the night (Hinman, 2003).

Leptonycteris are highly mobile, flying distances up to 100 km nightly (Horner et al.,

1998; Ober et al., 2005; England, 2012a), and are therefore capable of aiding plant gene

flow by visiting fragmented or low-density populations across the landscape (Horner et

al., 1998; von Helversen and Winter, 2003). This combination of characteristics makes

them more likely to be highly efficient long-distance pollen vectors for *A. palmeri* than

many territorial birds and insects (Fleming and Sosa, 1994).

Bat visitation patterns varied in time and space. For the first three hours of the

night, I observed decreasing bat visitation rates at Site B, and increasing visitation rates at

Site A. This is consistent with bats foraging early near the Big Hatchet roost and then

commuting to agave-rich areas in the Animas, as has been inferred from radio telemetry

results (M. A. Bogan, U.S. Geological Survey, Albuquerque, New Mexico, unpublished

manuscript). This accords with prior findings that visits of *L. yerbabuenae* to *A. palmeri*

within 4 km of a known roost were highest within the first few hours of night, and then

declined between midnight and sunrise (Ober and Steidl, 2004). Nectar-feeding bats

were not observed at Site C, but because my sampling was limited to the first two-to-

three hours of full darkness, the bats may have escaped detection if they arrived after

recording ceased. However, *Leptonycteris* are capable of covering the 40-km distance from the Big Hatchets roost to Site C in about an hour (Sahley et al., 1993; Horner et al., 1998; England, 2012a), so whether the bats used the area in 2007 or not is unknown. *L. yerbabuenae* have been captured and observed at hummingbird feeders over 100 km north of the Big Hatchet roost and 80 km northwest of Site C (M. A. Ramsey, Bureau of Land Management, Silver City, New Mexico, unpublished data). Therefore, based on the highly mobile nature of these bats and the observed density of agaves in the Cedar Mountains, I believe it is possible that nectar-feeding bats may visit the area, at least in some years.

There was also seasonal and inter-annual variation in bat visitation. Although bats were present at Site A in mid and late summer in 2006, they were not observed at Site B until late summer in 2007. Previous years' New Mexico roost counts indicate variation in the timing of occupancy, but that *Leptonycteris* spp. were generally in the area in large numbers from late July through early September (M. A. Bogan, U.S. Geological Survey, Albuquerque, New Mexico, unpublished manuscript). Colony sizes of *Leptonycteris* are correlated with the density of agave and columnar cactus blooms in the surrounding landscape (Fleming et al., 2001; Moreno-Valdez et al., 2004). When food resources grow scarce, bats may abandon roosts or migrate out of an area (Fleming, 1992, 2004; Horner et al., 1998; Ober et al., 2005); this appears to have happened in southeastern Arizona in 2006, when agaves bloomed at very low densities (U.S. Fish and Wildlife Service, 2007).

Moth visits—In Arizona populations of *A. palmeri*, 18% of sphinx moth visits resulted in stigma contact (Slauson, 2000); it is therefore likely that sphinx moths served

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as important pollination agents of *A. palmeri* during periods such as late summer 2007

when they were abundant. At least eight species of sphinx moths feed at agaves in the

southwestern United States (Tuttle, 2007; Alarcon et al., 2008a). Recent studies have

shown that adult female *Manduca sexta* subsidized their diet heavily with nectar of *A.*

palmeri (Alarcón et al., 2010) and consistently carried high pollen loads from *A. palmeri*

even when captured at *Datura wrightii*, their preferred oviposition host plants (Riffell et

al., 2008). In fact, before *Datura* bloom, *A. palmeri* constitutes > 90% of the pollen load

carried by this species (Riffell et al., 2008). Populations of *A. palmeri* are patchily

distributed in habitats often several kilometers distant from *Datura* (Bronstein et al.,

2009; Alarcón et al., 2010), and pollen movement in excess of 12 km has been estimated

for some sphinx moths (Stockhouse, 1976).

Video analysis showed multiple instances of bats chasing sphinx moths (2006 Jul

28, Aug 13; 2007 Aug 11), but it is not known if these actions were aggressive or

predatory in nature, as the end of the pursuit was outside the camera's field of view.

Models did not reveal a decrease in sphinx moth activity due to increased bat activity,

even though some species of sphinx moths are sensitive to bat echolocation calls (Roeder

and Treat, 1970). Possibly the larger size of sphinx moths would make their capture and

handling by *Leptonycteris* more difficult than for smaller moths, however the larger body

size might lead bats to view sphinx moths as competitors for floral resources. Aggressive

behavior by *Leptonycteris* at agaves against floral competitor *Choeronycteris mexicana*

has been previously documented (Arias-Cóyotl et al., 2006).

The "other moths" visitor category was composed of moths generally smaller than

sphinx moths, and if capture proportions were representative of species present, most

were probably noctuid moths. These moths generally avoided contact with anthers and stigmas (Slauson, 2000; pers. obs.), and thus were not likely to have contributed substantially to pollination of *A. palmeri*. At least some species may have contributed negatively to the reproductive success of the agaves if they were searching for oviposition sites among the floral tissues (Thompson and Pellmyr, 1992; Seagraves et al., 2008; England, 2012c).

The highly significant decrease in non-sphinx moth visitation with increasing bat visitation could indicate selective pressure for the moths to detect and avoid *Leptonycteris.* Some moths are known to respond to the calls of insectivorous bats by executing evasive maneuvers and reducing flight activity (Roeder, 1962; Faure et al., 1990; Windmill et al., 2006; Ratcliffe et al., 2008). This study lends indirect support to the growing body of evidence that insects may contribute to the diet of nectar-feeding bats at least some of the time (Hoffmeister and Goodpaster, 1954; Hevly, 1979; Cockrum, 1991; Hinman, 2003; Stoner et al., 2003; Sanchez and Medellín, 2007; Brown, 2008).

Bird visits—Birds may also serve as pollinators of *A. palmeri*. I observed house finches and Scott's orioles, which have been suggested as potential pollinators of *A. deserti* (Fulton, 1983) and *A. havardiana* (Kuban, 1989), respectively. Orioles may have been more abundant at study sites than numbers would otherwise indicate, because they are easily startled by human movement (Anthony, 1892). Orioles made regular contact with floral reproductive structures when they thrust their head into the branch to drink nectar while perched either directly atop the flowers or on the branch's peduncle, and are known to carry agave pollen (Martinez del Rio and Eguiarte, 1987; Kuban, 1989; Ornelas

et al., 2002).   Although the observed ladder-backed woodpeckers and other chiefly

insectivorous birds might have been foraging among the agave blooms for insect prey

(Lowther, 2001) or using the flowers as moisture sources (Gentry, 1978), they could

nonetheless have accidentally transferred pollen between plants.

The high number of agave visits by rufous hummingbirds during the mid-summer

trip to Site A may have been a migratory wave of these long-distance travelers, timed to

coincide with nectar availability of *A. palmeri* at stopover sites along a migration corridor

(Kodric-Brown and Brown, 1978).   Anthony (1892) recorded such a wave at *A. palmeri*

in the Apache Hills, midway between the Big Hatchet and Cedar Mountains.   It is not

clear why no seasonal peak in rufous hummingbird numbers was observed at Site C;

perhaps a migratory wave occurred between visits to the site.

Throughout the day, bird visitation rates exhibited relatively even rates,

suggesting that agaves in this area supply abundant rewards (Sutherland et al., 1982)

which are crucial for refueling during migratory stopovers (Calder, 2004).   Hummingbird

territoriality is common when the surrounding habitat is open and bird-to-agave densities

are high (Kuban et al., 1983; Martinez del Rio and Eguiarte, 1987), such as observed at

Site A in mid- and late-summer.   This behavior during peak migratory periods could

increase the possibility of pollen transfer via unintended collisions with floral structures,

thereby benefiting the agaves to which they otherwise would provide little pollination

service (Slauson, 2000).

Bee and fly visits—The late-summer abundance of carpenter bees at Site B and

bumble bees at Sites B and C may have contributed valuable backup pollination services

at those times.   In southeastern Arizona, carpenter bees made stigma contact with *A.*

palmeri in 7% of visits, whereas bumblebees made contact in 1% of visits (Slauson, 2000). When provisioning their nests inside dead flowering stalks of *Yucca*, *Dasylirion*, and *Agave* species including *A. palmeri* (Waring and Smith, 1987; Scott et al., 1993), female carpenter bees commonly specialize on one to two flower species with high nectar and pollen rewards (Smith and Whitford, 1978; Scott et al., 1993). This behavior should result in relatively pure pollen loads. Carpenter bees may forage 6 km from their nests (Pasquet et al., 2008), potentially allowing movement of agave pollen at least within mountain ranges. Likewise, bumblebees are capable of homing almost 10 km, and have been documented foraging over 4 km from their nests (Goulson and Stout, 2001). Pollen carryover from flower to flower on large bees may be considerable, commonly moving 7-8 flowers from the original source, but in at least one case has been documented 54 flowers later (Willson, 1983).

Although honeybees have been documented foraging > 9 km from their hive (Beekman and Ratnieks, 2000), medium and small bees and flies were not expected to be important pollen vectors for *A. palmeri* because of their tendency to forage within the same inflorescence. Additionally, their small size allows them to avoid contacting stigmas (Slauson, 2000), though my observations were not designed to confirm this. The large number of visits from these guilds does emphasize the abundance of pollen and nectar remaining after the presumed nocturnal peaks of production, as well as the importance of the agaves to these smaller pollinators of other desert plants.

Conservation implications—Understanding the complex interactions of plants and animals at multiple scales helps us predict the effects of possible perturbations such as climate change upon the many species present (Field et al., 2007; Enquist and Gori,

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2008; Robinson et al., 2009; Robles and Enquist, 2010; Burkle and Alarcón, 2011).

Although climate models vary, most predict warming temperatures, changes in the amount and variation of precipitation, and increased frequency of extreme events such as heat waves, droughts, and associated wildfires (Easterling et al., 2000a; Parmesan et al., 2000; Field et al., 2007). Warming trends in the southwestern United States have exceeded global average changes by nearly 50% (Gutzler and Garfin, 2006), and compared to the previous 30 year period, from 1991-2005, the Animas, Big Hatchet, and Cedar Mountains experienced mean temperature increases of 1.1, 0.9, and 1.0°C and decreased precipitation of 9, 3, and 2%, respectively (Enquist and Gori, 2008). Models also predict that within the next century, southwestern North America will transition to a more arid climate (Seager et al., 2012). Unusual timing and amounts of precipitation may alter the initiation and duration of flowering in some desert plants (Bowers and Dimmitt, 1994), and thereby contribute to the decline or extirpation of dependent pollinator populations (Harrison, 2000; McLaughlin et al., 2002; Alarcón et al., 2008b). During drought years, high-quality floral patches such as agaves may be especially critical to pollinators (Russell et al., 1994), when other flowers bloom in lower densities or for shorter periods (Calder, 2004; Alarcón et al., 2008b). Unlike many plants, the number of agaves blooming during any one year is not believed to be influenced by current-year precipitation, as inflorescence bolting is triggered 1-2 yrs before the summer in which flowers occur (Nobel, 1987, 1992). However, because moist soil conditions are required for agave photosynthesis and growth, prolonged multi-year droughts will likely reduce seedling establishment and the number of agaves blooming (Nobel, 1992), with subsequent impacts on pollinator species.

Climate change could also affect the abundance and timing of the visitor population peaks if nectar-feeding bats or birds change the timing or routes of their migrations (Hill et al., 1998; Robinson et al., 2009), or if sphinx moths or large bees mature and emerge earlier or later in the summer (Kameyama and Kudo, 2009; Alarcón et al., 2010). Further timing mismatches may occur if the agave phenology shifts in a different temporal manner than that of its pollinators; this could result in lower plant reproductive success and in the animals missing out on a major food resource (Memmott et al., 2007; Robinson et al., 2009; Weller et al., 2009). There could also be changes in the bloom timing of other flower species that may be sequentially necessary to maintain pollinator populations throughout the year or along migratory routes (Miller-Rushing and Inouye, 2009; Aldridge et al., 2011).

Agaves may be especially challenged to keep pace with rapidly changing environmental conditions, given their extremely long generation times, infrequent episodic nature of seedling establishment, and limited seed-dispersal ability (Nobel, 1987, 1992; Alley et al., 2003; Rice and Emery, 2003). Animal and plant distributions tend to be moving poleward and upward in elevation in response to increased warming (Kullman, 2001; Walther et al., 2002; Parmesan, 2006; Forister et al., 2010), with local population extirpations at the lower edges of their range (Pounds et al., 1999; Parmesan, 2006; Miller-Rushing and Inouye, 2009). The mobile nature of nectar-feeding bats may provide a rescue for the agaves from effects of climate-induced disruptions (Fleming et al., 2009), because even relatively rare visits from high-quality pollen dispersers may be disproportionately important for aiding gene flow between isolated habitat fragments (Waser, 1979; Ellstrand, 1992; Proctor et al., 1996; Fleming et al., 2009). Agave

populations with higher genetic variation should have a better capacity to adapt to changing environmental conditions and escape extirpation or extinction (Lundberg and Moberg, 2003; Rice and Emery, 2003).

The wide variety of insects captured and birds identified support the assertion that *A. palmeri* in this region may be a keystone food resource for many desert-dwelling animals, especially during the seasonal pre-monsoon drought when few other plants bloom (Baltosser, 1989; Lange and Scott, 2001; Rocha et al., 2005; Riffell et al., 2008; Alarcón et al., 2010). *Agave palmeri* may therefore be seen as a sequential mutualist to other plants in this desert community by maintaining populations of their resident pollinators during this period of restricted resource availability (Waser and Real, 1979; Nabhan, 2004; Alarcón et al., 2008b, 2010). It also provides critical stopover feeding habitat for migratory pollinators including hummingbirds and bats (Mehlman et al., 2005). In addition to food, the stalks of agave inflorescences also provide nesting habitat for carpenter bees (Waring and Smith, 1987; Scott et al., 1993), ladder-backed woodpeckers (Lowther, 2001), and Scott's orioles (Flood, 2002), and the rosettes provide protective nest sites for a variety of rodents (Gentry, 1982).

Agave population declines could negatively impact both resident and migratory pollinators. Pollinator declines are a growing source of global concern (Allen-Wardell et al., 1998; Kearns et al., 1998; Potts et al., 2010), as pollination is considered a critical ecosystem service (Kearns et al., 1998), due to the role of pollinators as "mobile links" that ecologically connect diverse plant and animal communities (Lundberg and Moberg, 2003; Fontaine et al., 2006). Community-level cascades of population decline and extinction of plants and their pollinators have been documented in some areas

(Biesmeijer et al., 2006; Anderson et al., 2011). Populations of migratory rufous hummingbirds seem to be declining (Committee on the Status of Pollinators, 2007), and many resident bee species have shown recent population declines and range contractions (Watanabe, 2008; Ratnieks and Carreck, 2010; Singh et al., 2010; Cameron et al., 2011), but population trends of other pollinators are poorly known (Allen-Wardell et al., 1998; Tuttle, 2007). Larger migratory pollinators such as nectar-feeding bats, hummingbirds, and orioles seasonally follow "nectar trails" of progressively blooming plants from tropical Mexico into the southwestern U.S. (Fleming et al., 1993; Rising and Williams, 1999; Flood, 2002; Molina-Freaner and Eguiarte, 2003; Fleming, 2004; Nabhan, 2004), and even, in the case of some hummingbird species, western Canada (Healy and Calder, 2006). These vertebrates all require an ecologically coherent network of stopover sites along their long-distance migration routes in order to replenish body condition for the next stage on their journeys (Russell et al., 1994; Calder, 2004; Mehlman et al. 2005; Huntley et al., 2006; Robinson et al. 2009). The migratory timing, routes, and stopover feeding ecology of these species are poorly known (Holland and Wikelski, 2009), making it difficult to predict what impact floral resource declines at any one site may have (Calder, 2004; Nabhan, 2004). By protecting both agaves and the nectar-feeding bats, conservationists may aid not only local pollinator populations and their associated hosts, but also have far-reaching benefits to ecosystems serviced by both resident and migratory pollinators across the continent.

ACKNOWLEDGEMENTS

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TABLE 1: Sampling during three trips each to three sites in southwestern New Mexico. E = early, I = intermediate, L = late summer. Observation periods were standardized to 10-min intervals.

Location	Animas Mountains			Big Hatchet Mountains			Cedar Mountains			
Site	A			B			C			
Season	E	I	L	E	I	L	E	I	L	
Dates	Jul 14-15	Jul 26-28	Aug 12-14	Jul 5-8	Jul 26-27	Aug 11-12	Jul 12-15	Jul 21	Aug 9-10	
Year	2006			2007						TOTAL
Agaves blooming	58	72	65	53	43	19	37	34	40	**182**
Insect trap hours										
day	15	24	38.5	26	16	15	28.5	15	25.5	**203.5**
night	18	35	54.5	17	18	17.5	16.5	0	20	**196.5**
Observation periods										
day binocular	0	182	60	80	25	38	115	36	57	**593**
day video	4	51	59	0	0	0	0	0	0	**114**
night video	5	12	25	50	23	23	41	0	47	**226**

TABLE 2: Insects captured at three sites in southwestern New Mexico. Only taxa captured with site rates ≥ 0.10 individuals / trap hr are shown. Species with numbers are undescribed morphotypes.

			Site: A 2006				Site: B 2007				Site: C 2007				Total Rate
		Month:	Jul	Jul	Aug	Site Rate	Jul	Jul	Aug	Site Rate	Jul	Jul	Aug	Site Rate	
		Dates:	14-15	27-28	13-14		6-7	26-27	11-12		13-14	21	9-10		
		day hrs:	15	24	38.5	**77.5**	26	16	15	**57**	28.5	15	25.5	**69**	**203.5**
		night hrs:	18	35	54.5	**107.5**	17	18	17.5	**52.5**	16.5	0	20	**36.5**	**196.5**
Order	**Family**	**Genus species**													
Lepidoptera															
	Noctuidae	*Acontia quadirplega*	0.06	0	0	**0.01**	0	0	0.74	**0.25**	0	-	0	**0**	0.07
	Noctuidae	*Catabenoides terminellus*	0.06	0	0	**0.01**	0	0	1.83	**0.61**	0	-	0	**0**	0.17
	Noctuidae	*Paectes ambrostolella*	0.06	0	0	**0.01**	0	0	0.57	**0.19**	0	-	0	**0**	0.06
	Noctuidae	*Striacosta albicosta*	0	0	0.29	**0.15**	0	0	0.34	**0.11**	0	-	0	**0**	0.11
Hymenoptera															
	Andrenidae	*Perdita* sp. 1	0	0	0	**0**	0	0.44	0.07	**0.14**	0	0.07	0.08	**0.04**	0.05
	Apidae	*Apis mellifera*	0.87	0.46	0	**0.31**	0.04	0	0	**0.02**	0.04	0	0	**0.01**	0.13
	Halictidae	*Agapostemon angelicus*	0	0	0	**0**	0.31	0	0	**0.14**	0	0	0	**0**	0.04
	Halictidae	*Lasioglossum aff. Pervarum*	0	0	0	**0**	0.08	0	0.20	**0.09**	0.14	0.13	0.04	**0.10**	0.06
	Halictidae	*Lasioglossum comulum*	0	0	0.03	**0.01**	0.12	0.13	0.13	**0.12**	0.25	0.07	0.12	**0.16**	0.09
	Halictidae	*Lasioglossum microlepoides*	0.20	0.04	0.31	**0.21**	0.88	1	2.87	**1.44**	0.32	0.27	0.55	**0.39**	0.61
	Halictidae	*Lasioglossum* sp. 1	0	0	0	**0**	0.15	0.81	0.27	**0.37**	0	0	0	**0**	0.10
	Halictidae	*Lasioglossum* sp. 2	0	0	0	**0**	0.23	1.69	0.73	**0.77**	0.67	1.60	0.31	**0.74**	0.47
	Halictidae	*Lasioglossum* sp. 3	0	0	0	**0**	0	0.44	0.33	**0.21**	0	0	0	**0**	0.06
Diptera															
	Sarcophagidae	unk.	0.13	0	0.08	**0.06**	0.50	0.06	1.40	**0.61**	0.46	0.27	0.08	**0.28**	0.29
	Tachinidae	unk.	0	0	0.05	**0.03**	0.04	0.125	0.47	**0.18**	0.53	0	0.31	**0.33**	0.17

TABLE 3: Ranking of generalized linear models predicting the effects of spatiotemporal, morphological, and phenologic variables on the diurnal visitation rates to *Agave palmeri* at three sites in southwestern New Mexico, 2006 and 2007. Models with the smallest QICu are preferred. Only models in the 95% model confidence set are presented.

QICu	ΔQICu	*w*	*K*	Model
Birds (N = 640)				
165.5	0	0.61	29	Site + Season(Site) + Period + Number Blooming + Quarter + Number Blooming x Quarter + Size
166.4	0.9	0.39	30	Site + Season(Site) + Period + Number Blooming + Quarter + Number Blooming x Quarter + Size + Shape
Carpenter Bees (N = 553)				
251.4	0	0.36	30	Site + Season(Site) + Period + Number Blooming + Quarter + Number Blooming x Quarter + Size + Shape
252.0	0.6	0.27	22	Site + Season(Site) + Period + Number Blooming + Size + Shape
252.0	0.6	0.27	26	Site + Season(Site) + Period + Number Blooming + Quarter + Size + Shape
255.6	4.1	0.05	29	Site + Season(Site) + Period + Number Blooming + Quarter + Number Blooming x Quarter + Size
Bumble Bees (N = 553)				
309.3	0	0.45	29	Site + Season(Site) + Period + Number Blooming + Quarter + Number Blooming x Quarter + Size
310.6	1.3	0.23	30	Site + Season(Site) + Period + Number Blooming + Quarter + Number Blooming x Quarter + Size + Shape
311.0	1.7	0.19	25	Site + Season(Site) + Period + Number Blooming + Quarter + Size
312.2	2.9	0.10	26	Site + Season(Site) + Period + Number Blooming + Quarter + Size + Shape
Medium Bees and Flies (N = 598)				
-3935.9	0	0.87	29	Site + Season(Site) + Period + Number Blooming + Quarter + Number Blooming x Quarter + Size
-3932.1	3.8	0.13	30	Site + Season(Site) + Period + Number Blooming + Quarter + Number Blooming x Quarter + Size + Shape
Small Bees and Flies (N = 281)				
-1976.4	0	0.99	29	Site + Season(Site) + Period + Number Blooming + Quarter + Number Blooming x Quarter + Size

QICu = approximated Quasi-likelihood Information Critera.

ΔQICu = difference between QICu values of the given model and the model with the minimum QICu value.

w = QICu weight, the probability that the given model is the best model for the data.

K = number of estimated parameters in model.

N = number of observation periods

Period = 2-hr period of day, starting at sunrise

Number Blooming = number of branches blooming

Quarter = quarter of inflorescence in which the median blooming branch occurred

Number Blooming x Quarter = interaction term used as proxy for number of flowers blooming

Size = Principal Component 1, overall plant size

Shape = Principal Component 2, display shape: trade-off of vertical and horizontal attributes of inflorescence

TABLE 4: Relative importance of predictor variables in the 95% confidence set of models of visitation rates to *Agave palmeri*. Values of 1 suggest the term is an important predictor, while 0 indicates no evidence of support for importance. Bold font indicates variables that were included in all tested models (term assumed to be important based on prior studies). A dash indicates that the term was not included in modeling efforts.

Diurnal Visitors	Site	Season (Site)	Period	Size	Shape	Number Blooming	Quarter	Number Blooming x Quarter
Birds	**1**	**1**	**1**	1	0.39	1	1	1
Carpenter bees	**1**	**1**	**1**	1	0.95	1	0.71	0.43
Bumble bees	**1**	**1**	**1**	1	0.35	1	1	0.70
Medium bees and flies	**1**	**1**	**1**	1	0.13	1	1	1
Small bees and flies	**1**	**1**	**1**	1	0	1	1	1

Visitor	Site	Season (Site)	Hour	Hour X Site	Size	Shape	Bats
Bats	1	1	1	1	-	-	-
Sphinx moths	1	1	1	0	1	0.84	0.11
Other moths	1	1	1	1	-	-	1

TABLE 5: Presence-rate of birds visiting blooming *Agave palmeri* during each site trip: number of 10-min observation periods that each species made contact with open agave flowers on focal plants / number of observation periods per trip.

		Site:	A		B			C		
		Year:	2006		2007					
		Month:	Jul	Aug	Jul		Aug	Jul	Aug	
		Dates:	26-28	12-14	5-8	26-27	11-12	12-15	21	9-10
Family	**Genus species**	**common name**								
Trochilidae	*Selasphorus rufus*	rufous hummingbird	0.65	0.43	0	0	0.24	0.03	0.08	0.05
	Archilochus alexandri	black-chinned hummingbird	0.07	0	0	0	0	0	0	0
	hummingbird sp.	unidentified hummingbird	0.09	0	0	0	0.13	0.01	0.03	0.02
Picidae	*Picoides scalaris*	ladder-backed woodpecker	0	0	0	0	0	0.01	0	0
Troglodytidae	*Campylorhynchus brunneicapillus*	cactus wren	0	0	0	0	0	0.01	0	0
Icteridae	*Icterus parisorum*	Scott's oriole	0.03	0	0.01	0	0	0	0.03	0
	Icterus bullockii	Bullock's oriole	0.01	0	0	0	0	0	0	0
	Icterus sp.	unidentified oriole	0	0.02	0	0	0	0	0	0
	Sturnella sp.	unidentified meadowlark	0	0	0	0	0	0	0	0.02
Fringillidae	*Carpodacus mexicanus*	house finch	0	0	0.03	0.04	0	0.01	0	0
unk.	unk.	unidentified bird	0	0	0.03	0	0	0	0	0
		TOTALS	0.84	0.45	0.06	0.04	0.37	0.06	0.14	0.09

TABLE 6: Mean (in bold) ± SE number of visits per 10-min observation period to inflorescences of *Agave palmeri* at 3 sites in southwestern New Mexico by diurnal and nocturnal visitors. Rates were computed in logarithmic scale but were back-transformed for presentation, thus standard errors are asymmetrical around the means. Values that share the same lower case letter within a row are not significantly different ($P > 0.05$, after Tukey-Kramer correction for multiple comparisons).

Site	A	B	C
Year	**2006**	**2007**	**2007**
Diurnal			
Birds	**2.05** [a]	**0.55** [b]	**0.09** [c]
	+0.29, -0.26	+0.28, -0.19	+0.04, -0.03
Carpenter bees	**0.18** [a]	**1.35** [b]	**0.49** [a]
	+0.09, -0.06	+0.36, -0.28	+0.14, -0.11
Bumble bees	**0.08** [a]	**0.25** [a]	**0.25** [a]
	+0.07, -0.04	+0.14, -0.09	+0.15, -0.09
Medium bees & flies	**10.09** [a]	**8.44** [a]	**10.44** [a]
	+1.66, -1.43	+1.65, -1.38	+1.23, -1.10
Small bees & flies	-	**15.94** [a]	**22.41** [a]
	-	+3.14, -2.62	+1.46, -1.37
Nocturnal			
Bats	**56.15** [a]	**21.33** [b]	-
	+0.00, -0.00	+1.09, -1.04	-
Sphinx moths	**0.41** [ab]	**0.51** [a]	**2.00** [b]
	+0.22, -0.14	+0.15, -0.12	+0.70, -0.52
Other moths	**40.74** [a]	**15.84** [b]	**10.25** [c]
	+1.46, -1.41	+1.77, -1.59	+1.24, -1.10

TABLE 7: Seasonal pattern of mean (in bold) ± SE number of visits per 10-min observation period to inflorescences of *Agave palmeri* by diurnal and nocturnal visitors. Values within a row that share the same lower case letter are not significantly different.

Visitor type	Site	A		B			C		
	Year	2006		2007			2007		
	Dates	7/26 - 7/28	8/12 - 8/14	7/5 - 7/8	7/26 - 7/27	8/11 - 8/12	7/12 - 7/15	7/21	8/9 - 8/10
Diurnal	Birds								
		3.25 a	**1.3** bc	**0.25** b	**0.51** ab	**1.35** bc	**0.11** b	**0.06** b	**0.10** b
		+0.50, -0.43	+0.22, -0.19	+0.15, -0.09	+0.88, -0.32	+0.40, -0.31	+0.09, -0.05	+0.06, -0.03	+0.07, -0.04
	Carpenter bees								
		0.42 a	**0.08** b	**0.66** a	**0.75** a	**5.81** c	**0.38** ab	**0.59** a	**0.56** a
		+0.14, -0.11	+0.09, -0.04	+0.23, -0.17	+0.38, -0.25	+3.02, -1.98	+0.14, -0.10	+0.26, -0.18	+0.18, -0.14
	Bumble bees								
		0.05 a	**0.11** a	**0.06** a	**0.08** a	**3.20** b	**0.09** a	**0.09** a	**1.93** b
		+0.03, -0.02	+0.18, -0.07	+0.05, -0.03	+0.15, -0.05	+2.07, -1.26	+0.06, -0.03	+0.18, -0.06	+0.94, -0.63
	Medium bees & flies								
		14.81 a	**6.88** b	**8.74** b	**8.05** abc	**8.54** bc	**13.43** ac	**11.81** ac	**7.18** b
		+1.80, -1.61	+1.64, -1.32	+1.00, -0.89	+5.48, -3.26	+2.71, -2.06	+1.87, -1.64	+1.87, -1.62	+1.13, -0.97
	Small bees & flies								
		-	-	**7.72** a	**27.41** b	**19.15** b	**23.47** b	**20.34** b	**23.55** b
		-	-	+1.62, -1.34	+10.63, -7.66	+6.21, -4.69	+2.78, -2.48	+2.65, -2.34	+2.74, -2.45
Nocturnal	Bats								
		44.16 a	**77.41** b	-	-	**21.33** c	-	-	-
		+0.00, -0.00	+0.00, -0.00	-	-	+0.11, -0.11	-	-	-
	Sphinx moths								
		0.19 a	**0.90** b	**0.07** a	**0.33** ab	**5.94** c	**0.45** ab	-	**8.77** c
		+0.10, -0.07	+0.49, -0.32	+0.11, -0.04	+0.28, -0.15	+1.63, -1.28	+0.38, -0.21	-	+0.43, -0.41
	Other moths								
		46.81 a	**35.45** b	**3.98** c	**8.64** d	**115.70** e	**6.61** d	-	**15.89** f
		+0.99, -0.97	+1.78, -1.69	+0.10, -0.10	+1.43, -1.23	+28.90, -23.13	+0.59, -0.54	-	+3.27, -2.71

TABLE 8: Mean (in bold) ± SE diurnal visitation rates to inflorescences of *Agave palmeri* during 2-hr periods of day, starting at sunrise (approximately 06:30 MDT). Values within a row that share the same lower case letter are not significantly different.

Approximate time	06:30-08:30	08:30-10:30	10:30-12:30	12:30-14:30	14:30-16:30	16:30-18:30	18:30-20:30
Period of day	1	3	5	7	9	11	13
Birds							
	0.81 ab	**0.36** b	**0.38** ab	**0.29** b	**0.59** ab	**0.37** b	**0.62** a
	+0.84, -0.41	+0.10, -0.08	+0.13, -0.10	+0.08, -0.06	+0.32, -0.21	+0.09, -0.07	+0.15, -0.12
Carpenter bees							
	0.63 cd	**2.01** ab	**0.84** abc	**2.17** a	**0.64** bcd	**0.04** e	**0.26** d
	+0.63, -0.17	+0.56, -0.44	+0.22, -0.18	+1.27, -0.80	+0.36, -0.23	+0.03, -0.02	+0.12, -0.08
Bumble bees							
	0.28 bc	**0.21** bc	**0.06** bd	**1.45** a	**0.30** bc	**0.08** bcd	**0.03** d
	+0.16, -0.10	+0.10, -0.07	+0.04, -0.02	+1.13, -0.64	+0.26, -0.14	+0.06, -0.04	+0.03, -0.02
Medium bees & flies							
	27.57 a	**18.20** b	**12.48** c	**5.49** d	**3.85** d	**4.21** d	**13.64** ab
	+3.56, -3.15	+1.98, -1.79	+1.66, -1.47	+0.84, -0.73	+0.76, -0.64	+0.77, -0.65	+2.49, -2.11
Small bees & flies							
	12.36 a	**23.10** b	**21.79** b	-	-	-	**20.50** b
	+2.14, -1.83	+2.53, -2.28	+2.69, -2.39	-	-	-	+2.54, -2.26

TABLE 9: Mean (in bold font) ± SE diurnal visitation rates to inflorescences of *Agave palmeri* during four phenological stages of their bloom sequence. Branches on the inflorescences bloom sequentially upward, so inflorescence quarter 1 is lowest and first, while quarter 4 is highest and last. Rates were computed in logarithmic scale but were back-transformed for presentation.

Quarter	1	2	3	4
Birds	0.49 [ab]	0.60 [a]	0.45 [ab]	0.34 [b]
	+0.15, -0.11	+0.13, -0.11	+0.09, -0.08	+0.07, -0.06
Carpenter bees	0.57 [a]	0.73 [a]	0.67 [a]	0.52 [a]
	+0.40, -0.24	+0.41, -0.26	+0.37, -0.24	+0.34, -0.20
Bumble bees	0.21 [ab]	0.45 [a]	0.19 [ab]	0.05 [b]
	+0.16, -0.09	+0.19, -0.13	+0.07, -0.05	+0.05, -0.03
Medium bees & flies	7.87 [bcd]	12.76 [ab]	10.59 [abc]	8.04 [cd]
	+1.63, -1.35	+1.76, -1.55	+0.89, -0.82	+1.10, -0.97
Small bees & flies	20.83 [ab]	25.15 [a]	16.76 [b]	14.52 [b]
	+4.19, -3.49	+3.37, -2.97	+1.81, -1.63	+2.94, -2.45

TABLE 10: Ranking of generalized linear models predicting the effects of spatiotemporal and interspecies interactions on the nocturnal visitation rates to *Agave palmeri* at three sites in southwestern New Mexico, 2006 and 2007. Models with the smallest QICu are preferred. Only models in the 95% model confidence set are presented. Bat data were only analyzed for nights when bats were present at site, moth data were for all nights.

QICu	ΔQICu	*w*	*K*	Model
Bats (N = 49)				
-608.5	0.0	1.00	15	Site + Season(Site) + Hour + Hour x Site
Sphinx Moths (N = 183)				
-305.9	0.0	0.70	16	Site + Season(Site) + Hour + Size + Shape
-302.9	3.0	0.16	15	Site + Season(Site) + Hour + Size
-302.2	3.7	0.11	17	Site + Season(Site) + Hour + Size + Shape + Bats
Other Moths (N = 146)				
-2535.5	0.0	1.00	24	Site + Season(Site) + Hour + Hour x Site + Bats

QICu = approximated Quasilikihood Information Critera.
ΔQICu = difference between QICu values of the tested model and the model with the minimum QICu value.
w = QICu weight, the probability that the given model is the best model for the data. *K* = number of estimated parameters in model.
N = number of observation periods

Hour = 1-hr period of night, beginning 30-min after sunset (to exclude twilight).
Size = Principal Component 1, overall plant size
Shape = Principal Component 2, display shape: trade-off of vertical and horizontal attributes of inflorescence
Bats = number of bat passes during moth observation period.

TABLE 11: Mean (in bold) ± SE nocturnal visitation rates to inflorescences of *Agave palmeri* during 1-hr periods of day, starting at sunrise. Values within a row that share the same lower case letter are not significantly different.

Hour of night	1	2	3
Bats			
	41.60 [a]	**37.33** [ab]	**26.69** [b]
	+0.12, -0.12	+5.36, -4.69	+1.17, -1.60
Sphinx moths			
	0.99 [a]	**0.47** [b]	**0.90** [a]
	+0.14, -0.12	+0.09, -0.08	+0.11, -0.10
Other moths			
	24.90 [a]	**16.05** [b]	**16.56** [b]
	+2.51, -2.28	+1.20, -1.12	+1.17, -1.09

Fig. 1: Map of study area. Letters represent study sites: Site A: Animas Mountains, B: Big Hatchet Mountains, C: Cedar Mountains. Stars are approximate locations of nearby known roosts of nectar-feeding bats. Polygon represents approximate distributional extent of *Agave palmeri*, based on Gentry (1982). Map by T. Lorraine McInnes.
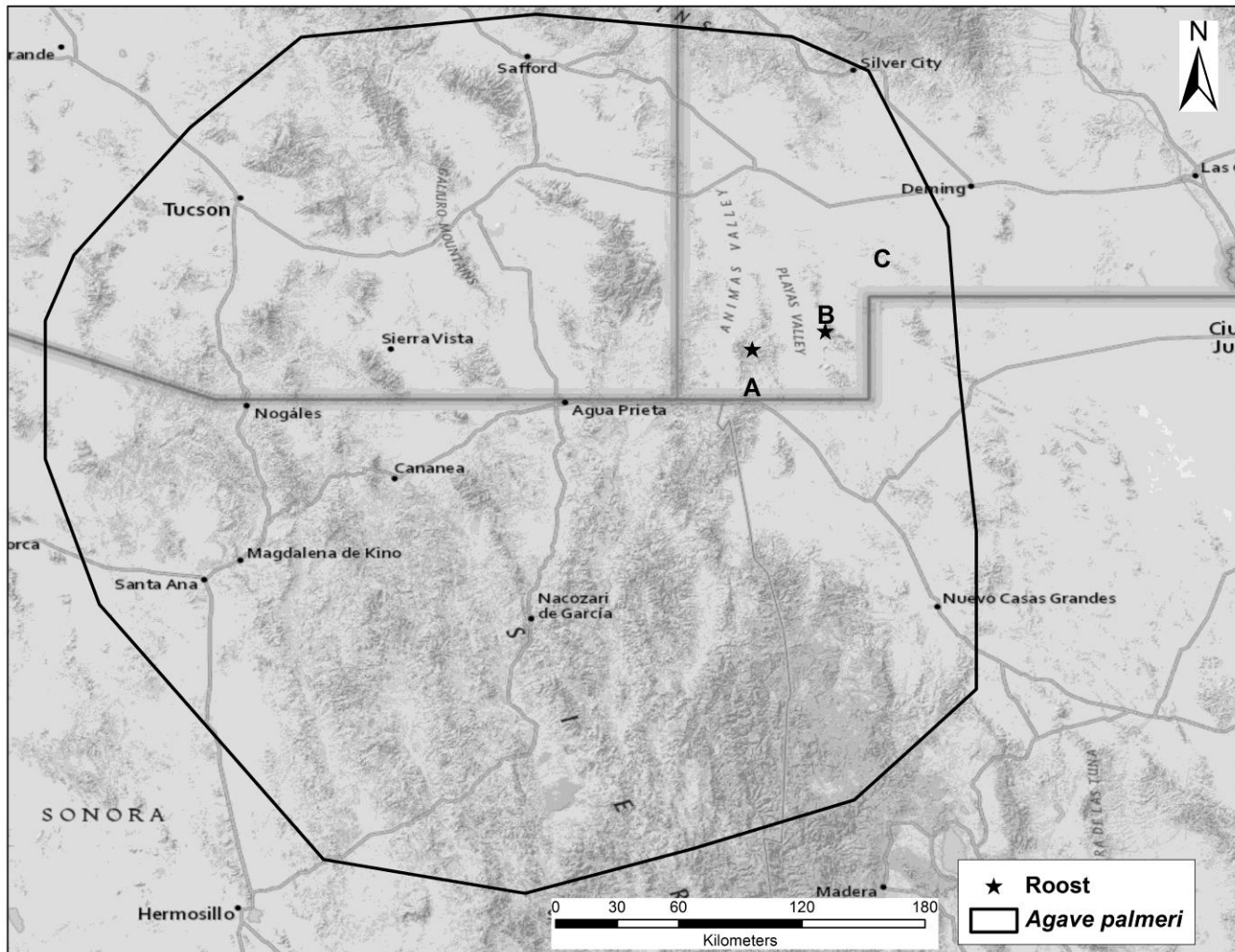
Fig. 2: Morphological measurements of blooming *Agave palmeri* at three sites in southwestern New Mexico. Lower-case letters indicate significant pairwise differences, *: *P* = 0.0503.
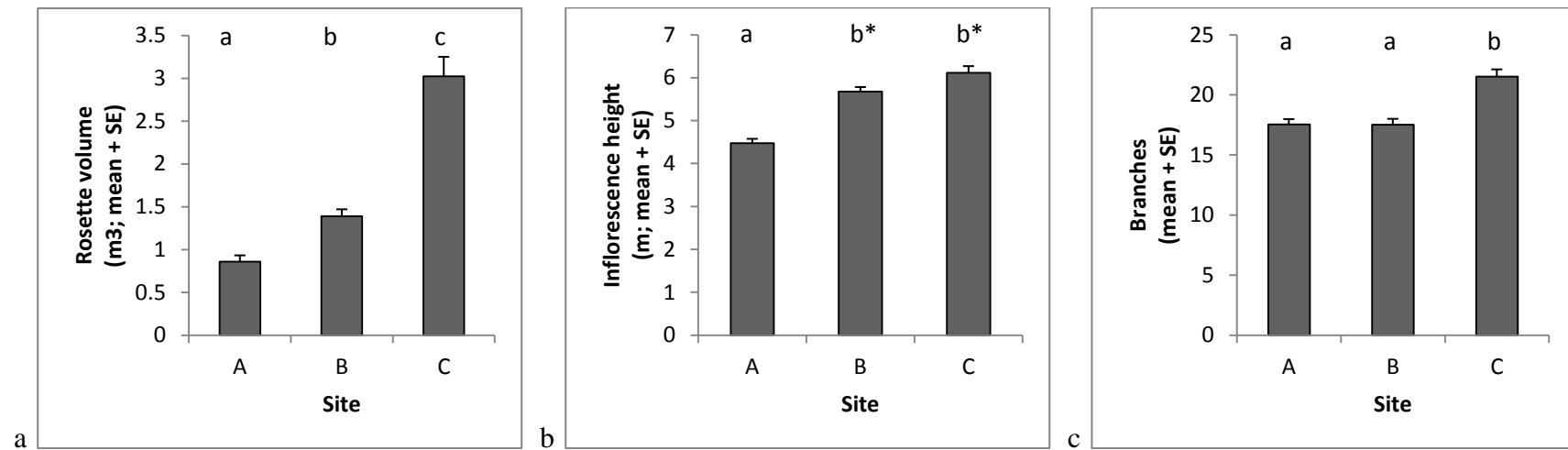
Fig. 3: Number of flowers per branch of *Agave palmeri* by a) study site, and b) quarter of inflorescence in which branch occurred. Branches bloom sequentially upward along the inflorescence, with the earliest blooms in Quarter 1, the last blooms in Quarter 4. Lower-case letters indicate significant pairwise differences, after Tukey-Kramer correction. * = least-squares mean difference between Quarter 1 and Quarter 4: $P = 0.0584$. ** = least-squares mean difference between Quarter 2 and Quarter 3: $P = 0.0558$.

a

b
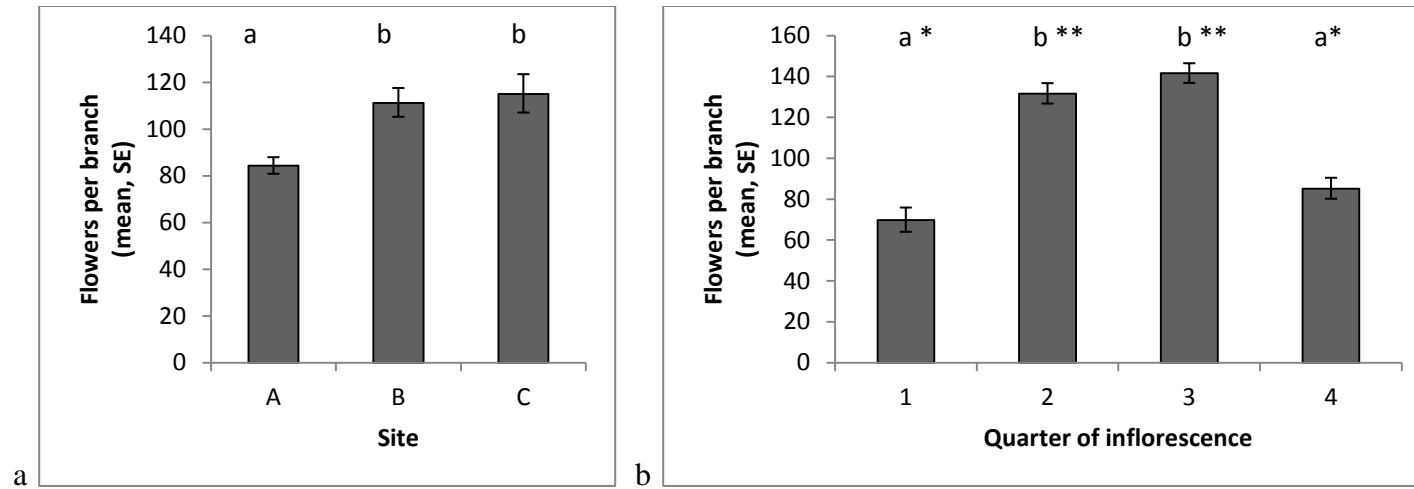
Fig. 4: Hour site interaction
Hourly variation of visitation rates to blooming *Agave palmeri* at three sites in southwestern New Mexico by a) bats, b) moths other than sphinx moths.   Data were recorded for the first three hours of night, beginning 30 min after sunset to exclude twilight. Bat data shown are only for nights bats were present at a site.
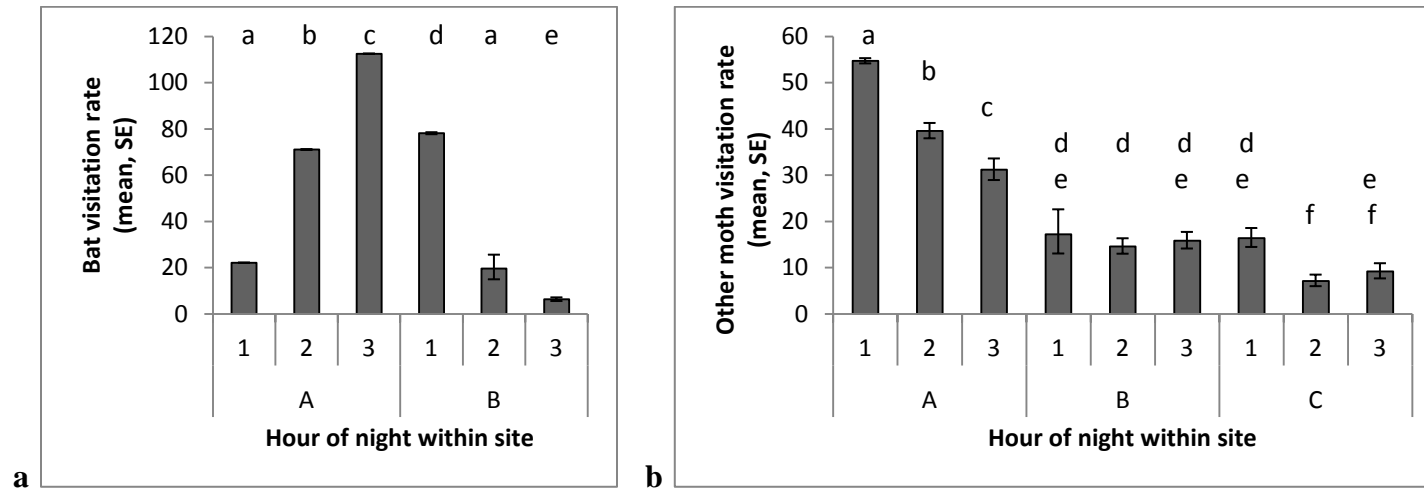
APPENDIX A1: Set of 7 a priori models predicting the effects of spatial, morphological, and phenological variables on the number of flowers per branch of *Agave palmeri* at three sites in southwestern New Mexico.

		spatial	morphological		phenological
i	*K*	Site	Size	Shape	Umbel Quarter
1	1				
2	10	Site	Size	Shape	Umbel Quarter
3	9	Site	Size		Umbel Quarter
4	8	Site			Umbel Quarter
5	7		Size	Shape	Umbel Quarter
6	6		Size		Umbel Quarter
7	5				Umbel Quarter

i = model number
K = number of parameters
Size = Principal Component 1, overall plant size
Shape = Principal Component 2, display shape: trade-off of vertical and horizontal attributes of inflorescence
Quarter = quarter of inflorescence within which the modeled branch's location occurred. Branches bloomed sequentially upward, and branches in the lower $1/4^{th}$ and upper $1/4^{th}$ of the inflorescence had fewer flowers than those near the center.

APPENDIX A2: Set of 13 a priori models used to evaluate the effects of spatiotemporal, morphological, and phenological variables on the visitation rates of diurnal visitors (birds, carpenter bees, bumble bees, medium bees and flies, and small bees and flies) to *Agave palmeri* at three sites in southwestern New Mexico in 2006 and 2007.

i	K	spatiotemporal			morphological		phenological		
		Site	Season (Site)	Period	Size	Shape	Number Blooming	Quarter	Number Blooming x Quarter
1	1								
2	28	Site	Season (Site)	Period			Number Blooming	Quarter	Number Blooming x Quarter
3	24	Site	Season (Site)	Period			Number Blooming	Quarter	
4	23	Site	Season (Site)	Period				Quarter	
5	20	Site	Season (Site)	Period			Number Blooming		
6	29	Site	Season (Site)	Period	Size		Number Blooming	Quarter	Number Blooming x Quarter
7	25	Site	Season (Site)	Period	Size		Number Blooming	Quarter	
8	24	Site	Season (Site)	Period	Size			Quarter	
9	21	Site	Season (Site)	Period	Size		Number Blooming		
10	30	Site	Season (Site)	Period	Size	Shape	Number Blooming	Quarter	Number Blooming x Quarter
11	26	Site	Season (Site)	Period	Size	Shape	Number Blooming	Quarter	
12	25	Site	Season (Site)	Period	Size	Shape		Quarter	
13	22	Site	Season (Site)	Period	Size	Shape	Number Blooming		

i = model number

K = number of parameters

Period = 2-hr period of day, starting at sunrise

Size = Principal Component 1, overall plant size

Shape = Principal Component 2, display shape: trade-off of vertical and horizontal attributes of inflorescence

Number Blooming = number of branches blooming

Quarter = quarter of inflorescence in which the median blooming branch occurred

Number Blooming x Quarter = interaction term used as proxy for number of flowers blooming

APPENDIX A3: Set of 3 a priori models used to evaluate the effects of spatiotemporal variables on the visitation rates of nectar-feeding bats to *Agave palmeri* at two sites in southwestern New Mexico, 2006 and 2007. Data were only analyzed for nights when bats were present.

i	*K*	Site	Season (Site)	Hour	Hour x Site
			spatiotemporal		
1	1				
2	15	Site	Season (Site)	Hour	Hour x Site
3	9	Site	Season (Site)	Hour	

i = model number
K = number of parameters
Hour = 1-hr period of night, starting 30 min after sunset

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APPENDIX A4: Set of 13 a priori models used to evaluate the effects of spatiotemporal, morphological, and ecological variables on the visitation rates of nocturnal sphinx moths to *Agave palmeri* at three sites in southwestern New Mexico in 2006 and 2007.

i	*K*	spatiotemporal				morphological		ecological
		Site	Season (Site)	Hour	Hour x Site	Size	Shape	Bats
1	1							
2	24	Site	Season (Site)	Hour	Hour x Site			Bats
3	15	Site	Season (Site)	Hour				Bats
4	23	Site	Season (Site)	Hour	Hour x Site			
5	14	Site	Season (Site)	Hour				
6	25	Site	Season (Site)	Hour	Hour x Site	Size		Bats
7	16	Site	Season (Site)	Hour		Size		Bats
8	24	Site	Season (Site)	Hour	Hour x Site	Size		
9	15	Site	Season (Site)	Hour		Size		
10	26	Site	Season (Site)	Hour	Hour x Site	Size	Shape	Bats
11	17	Site	Season (Site)	Hour		Size	Shape	Bats
12	25	Site	Season (Site)	Hour	Hour x Site	Size	Shape	
13	16	Site	Season (Site)	Hour		Size	Shape	

i = model number
K = number of parameters
Hour = 1-hr period of night, starting 30 min after sunset
Size = Principal Component 1, overall plant size
Shape = Principal Component 2, display shape: trade-off of vertical and horizontal attributes of inflorescence
Bats = number of bat passes during moth observation period

APPENDIX A5: Set of 5 a priori models used to evaluate the effects of spatiotemporal, morphological, and ecological variables on the visitation rates of non-sphinx moths to *Agave palmeri* at three sites in southwestern New Mexico in 2006 and 2007.

i	K	Site	Season (Site)	Hour	Hour x Site	Bats
			spatiotemporal			**ecological**
1	1					
2	24	Site	Season (Site)	Hour	Hour x Site	Bats
3	15	Site	Season (Site)	Hour		Bats
4	23	Site	Season (Site)	Hour	Hour x Site	
5	14	Site	Season (Site)	Hour		

i = model number
K = number of parameters
Hour = 1-hr period of night, starting 30 min after sunset
Bats = number of bat passes during moth observation period

CHAPTER 4 - Factors affecting female reproductive success of *Agave palmeri* in southwestern New Mexico

ABSTRACT

Premise: The reproduction of semelparous agaves is believed to be limited by pollinator availability, yet to what extent bat visitation rates interact with limitations imposed by plant morphology, phenology, other visitation rates, and the activity of seed predators has not been studied.

Methods: I conducted repeated observations on 182 *Agave palmeri* at three sites, and used an information-theoretic approach to evaluate the relative contribution of morphology, potential-pollinator visitation rates, and prior reproductive success on the potential and realized reproduction.

Key Results: Models indicated that flower and ovule numbers were affected by plant size, shape, and phenology, however plant size and display shape had no discernible effect on reproductive success. High bat visitation rates were associated with low fruit set but high seed set, whereas bird visitation showed the opposite pattern. Seed set decreased in fruits on late branches of plants with high prior reproductive success. The observation period with highest fruit and seed set also experienced high rates of infestation by caterpillars and weevils, but these two seed predators selected for opposite morphometric traits.

Conclusions: A spatiotemporal mosaic of pollination and seed predation appears to be present in this system, such that fluctuating numbers and activities of mutualists and antagonists may be interacting in a manner that preserves a variety of agave phenotypes across different populations, as is consistent with the geographic mosaic theory of

coevolution. When present, bats were the most effective pollinators, yet high bird visitation did increase fruit set even though those fruits had relatively few seeds. Agaves receive vital pollination services from both migratory nectar-feeding bats and birds, and in return are vital stopover feeding resources for these species, therefore continued persistence of both agaves and their pollinator populations will likely be aided by conservation efforts for both.

INTRODUCTION

Both intrinsic and extrinsic factors affect successful plant reproduction. Intrinsic plant morphological features include plant size, inflorescence architecture, flower number and size, ovule number, and seed size (Stephenson, 1981; Diggle, 1995), though the phenotypic expression of each may be influenced by environmental conditions such as resource availability, temperature, or herbivory (Diggle, 1995). Intrinsic patterns of resource allocation may therefore reveal past directional selection for those traits. For example, if flowers at certain inflorescence positions have relatively high ovule number, it could indicate an evolutionary history of high pollen receipt in that region of the inflorescence (Burd et al., 2009), and potentially a predisposition for high fruit set in that region (Ashman and Hitchens, 2000). Meanwhile, extrinsic factors such as temporal and spatial fluctuations in the synchrony of mates, availability and behavior of pollinators and activity of seed predators may also combine to influence the ultimate patterns of reproductive success (Heithaus et al., 1982; Huth and Pellmyr, 1997; Humphries and Addicott, 2004).

The interplay of factors is not only apparent among plants, but also within the phenotypically plastic responses of individuals (Stephenson, 1981; Diggle, 1997; Gómez

and Zamora, 2006). A plant's early fruits may act as resource sinks, pre-empting development of later flowers or causing selective abortion of later fruits (Aker, 1982; Diggle, 1995; Humphries and Addicott, 2004). Early reproductive success can also lead to later changes in visitor-reward production and seed provisioning (Sutherland, 1987; Diggle, 1995). Some plants abort early fruits with high seed parasite loads, in favor of gambling on later reproductive success (McIntosh, 2002; Thompson and Cunningham, 2002). Even within a branch or fruit, architectural constraints may combine with pollination success to pull additional resources to a well-fertilized fruit (Stephenson, 1981), or alternatively to cause seeds within a fruit compete for limited resources (Silvertown and Charlesworth, 2001; Fenner and Thompson, 2005; Wesselingh, 2007). Disentangling the influences of the complex array of intrinsic and extrinsic factors that affect plant reproductive effort and success is difficult, because in nature, these factors rarely act in isolation (Heithaus et al., 1982; Pellmyr and Thompson, 1996; Agrawal et al., 2007).

Studying semelparous plants provides insights about the patterns influencing reproduction, because their entire resource pool is devoted to a single "big bang" reproductive effort, with no resources saved for future parental survival or reproduction. This strategy may allow the production of larger floral displays which serve as advertisement to attract high-quality pollinators that move pollen longer distances, resulting in greater genotypic variability of offspring, increased fruit and seed set, and improved germination rates and seedling viability (Schaffer and Schaffer, 1979; Waser, 1983; Huxman and Loik, 1997; Donnelly et al., 1998; Winter and von Helversen, 2001; Ornelas et al., 2002; Rocha et al., 2005). Tall inflorescences are also thought to facilitate

wind-mediated seed dispersal (Aarssen, 1995). Large plant size may also allow

production of a massive cohort of seeds, which may reduce the probability that all seeds

are eaten by seed predators (Silvertown, 1980; Bonal et al., 2007). However, seed

predators may actually prefer larger inflorescences or correlated traits, thereby exerting

selective pressure against the same characters that benefit the plant when preferred by

pollinators (Fenner and Thompson, 2005; Klips et al., 2005; Lay et al., 2011). On an

evolutionary scale, the amount of any directional selection by a single mutualist or

antagonist species may fluctuate if its presence and abundance varies geographically or

temporally (Petterson, 1994; Waser et al., 1996; Gómez and Zamora, 2006).

There is considerable evidence that the pollinators of semelparous agaves have

selected for large floral displays (Gentry, 1982). Agaves are considered to have

coevolved with nectar-feeding bats of the genus *Leptonycteris*, which provide the plants

with highly efficient pollen transfer, in large quantities, from long distances (Gentry,

1982; Slauson, 2001; Rocha et al., 2006). However, many agave species have floral traits

that are evolutionarily generalized enough to allow some pollination by other species

such as birds and large-bodied insects (Kuban, 1989; Slauson, 2000, 2001; Rocha et al.,

2006). At a site in central Mexico, nectar-feeding bats were found to be the primary

pollinators of 4 semelparous agave species, and fruit set and seed number were correlated

with inflorescence height in 3 out of the 4 species (Rocha et al., 2005). Studies of *Agave*

havardiana revealed that *L. nivalis* preferentially visited taller inflorescences and

branches with many flowers, resulting in higher fruit set on large plants, and more seeds

per fruit on many-flowered branches (Kuban, 1989). However, Ober and Steidl (2004)

found that visitation rates of *L. yerbabuenae* were not explained by inflorescence height

of *A. palmeri*, but rather with the relative position of blooming branches upon the inflorescence, and therefore the number of available flowers. In another study, pollen-carrying orioles visited taller *A. marmota* before visiting shorter inflorescences (Ornelas et al., 2002). Likewise, Schaffer and Schaffer (1977) found that the bumble bee *Bombus sonorous* preferred taller inflorescences on *A. schottii*. Elsewhere in the Agavaceae, compared to an iteroparous variety, individuals of the semelparous *Yucca whipplei* var. *whipplei* produce larger inflorescences with more flowers and more seed-bearing fruits, with seeds that are 1.5 times more viable and germinate twice as quickly (Huxman and Loik, 1997). Yet the relative importance of morphology, phenology, and visitation rates of potential pollinators upon the overall female reproductive success of agaves has not been evaluated.

In order to assess factors affecting female reproductive success, I studied the pollination ecology of *Agave palmeri* in southwestern New Mexico with a focus on how patterns of potential and realized reproduction change through the course of the flowering season and across sites. Prior research on the reproductive ecology of *A. palmeri* generally involved experimental manipulations on a few branches in the center of the inflorescence of a small number of plants, once per site and year (Howell and Roth, 1981; Slauson, 2000, 2002; Hinman, 2003). However, because the dynamics of pollination and resource allocation occurs at different scales within plants, pollination experiments restricted to a subset of a plant's flowers can lead to erroneous conclusions about overall pollinator and resource limitation (Knight et al., 2006; Wesselingh, 2007). My goals were to use repeated observations on a larger number of plants in three populations to evaluate the evidence for intrinsic and extrinsic factors previously hypothesized to be

important to the female reproductive success of these plants (Agrawal et al., 2007).

Using an information-theoretic approach (Burnham and Anderson, 2002) to select among

competing explanatory models and evaluate the relative contribution of various factors, I

assessed patterns at the scales of plants, branches, fruits, and seeds. My specific

questions were:

1) How do morphological traits affect female reproductive potential, specifically the

number of flowers per branch and the number of ovules per fruit?

2) Do plant morphology, visitation rates of potential pollinators, and/or prior plant

reproductive experience affect reproductive success in the form of fruit set and seed

set?

3) Does mean seed mass per fruit change with seed set, and are patterns of per-seed

investment affected by the same factors as fruit set and/or seed set?

4) What factors influence seed predation, and how does it vary among seasons and

sites?

METHODS

Plant natural history—*Agave palmeri* Engelm. (Agavaceae: Ditepalae) stores

water and nutrients in a basal rosette for an estimated 20-40 years before reaching

reproductive maturity (Gentry, 1982; Slauson, 2001, 2002). The vegetative growth of *A.*

palmeri is poorly known, but *A. deserti*, a xeriphytic Sonoran Desert species, has been

relatively well studied. Photosynthesis in *A. deserti* occurs only during periods when soil

moisture is adequate to avoid water loss; therefore growth is limited to periods following

rainfall (Nobel, 1987). The rosette size of *A. deserti* at reproductive maturity varies, but

bolting is triggered by the number of wet days two years previous to the bloom summer

(Nobel, 1987). Seeds are immediately viable (Freeman, 1975) though can remain capable of germination up to 15 yrs later (L.A. Slauson, pers. comm.). Seedling establishment represents the most vulnerable phase of the agave life cycle, is generally timed to coincide with moist soil conditions (Nobel, 1992; Arizaga and Ezcurra, 2002; Slauson, 2002; Figueredo et al., 2011), and benefits from the presence of nurse plants (Nobel, 1987, 1992). Gusty winds associated with thunderstorms could additionally increase dispersal distances of the lightweight seeds (Aarssen, 1995; Nathan et al., 2002).

The single 2-8 m tall paniculate inflorescence produces a striking visual display that is discernible from a distance (Howell, 1979; Slauson 2002), with an average of 1500-2200 protandrous flowers over the course of the flowering season (Slauson, 2000). Unlike some agaves, *A. palmeri* rarely reproduces vegetatively, and is typically self incompatible (Howell and Roth, 1981; Gentry, 1982; Slauson, 2000, 2002). Successful reproduction therefore depends on attracting high-quality pollinators to the single reproductive event (Slauson, 2001). This species displays traits typically associated with pollination by nectar-feeding bats, including nocturnal peaks of nectar production, anther dehiscence, and stigma receptivity (Schaffer and Schaffer, 1977; Howell and Roth, 1981; Slauson, 2000; Hinman, 2003), as well as strongly scented compounds that may attract visitors from a distance (Knudsen and Tollstein, 1995; Raguso, 2004; Alarcón et al., 2008). The flowers remain open during the day with large amounts of nectar and pollen, and stigmas are receptive for several days, which allows for some diurnal pollination (Slauson, 2000). Flowering proceeds upward along the inflorescence's many branches over a roughly 3-6 week period in summer (Slauson, 2001), and is asynchronous within populations (Howell, 1979; Ober et al., 2005). This phenological variation allows for

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temporal changes in visitor patterns over the course of the extended bloom season (Bustamante and Búrquez, 2008), as well as opportunities for pollen exchange with different mates when visitors shift foraging areas as new individuals become reproductively available (Ober et al., 2005).

The southwestern corner of New Mexico provides a unique study area because three species of migratory nectar-feeding bats (*L. yerbabuenae*, *L. nivalis*, and *Choeronycteris mexicana*) co-occur during the mid-to-late summer in the sole known area of sympatry in their northern distributions (Arita and Humphrey, 1988; Hoyt et al., 1994). In this area, widely scattered populations of *A. palmeri* are found both within and beyond the known range of these bats (Gentry, 1982), and the bloom season of *A. palmeri* coincides loosely with the presence of the nectar-feeding bats, though their arrival to the area varies considerably between years (Fleming et al., 1993; Slauson, 2000). Adult *Leptonycteris* have individual home range areas of approximately 17-19 km^2 (Ober et al., 2005; England, 2012a), and routinely commute distances up to 100 km nightly (Horner et al., 1998; U.S. Fish and Wildlife Service, 2007; M. A. Bogan, U.S. Geological Survey, Albuquerque, New Mexico, unpublished manuscript), providing opportunities for long-distance gene flow between widely scattered plant populations (Horner et al., 1998; von Helversen and Winter, 2003). Nectar-feeding bats are assumed to be the primary pollinators (Gentry, 1982; Hoyt et al., 1994), as they make contact with stigmas in 100% of visits (Slauson, 2000). However, the presence and abundance of migratory taxa such as *Leptonycteris* can be unpredictable within seasons (Scott, 2004; Ober et al., 2005; Ammerman et al., 2009) and between years (Easterla, 1973; Cockrum, 1991; Molina-Freaner et al., 2003), especially near the edges of the bats' ranges (Fulton, 1983; Slauson,

2000). A variety of other floral visitors have been documented (Slauson, 2000; Lange and Scott, 2001; Bronstein et al., 2009; England 2012b), with per-visit stigma contact rates of 18% by white-lined sphinx moths, 7% by carpenter bees, 1% by bumble bees, and < 1% by hummingbirds (Slauson, 2000).

   Study area—Fieldwork was conducted in 2006 and 2007 at three sites in Hidalgo and Luna counties of southwestern New Mexico, U.S.A. For map and detailed study site descriptions, see England (2012b). Sites A, B, and C were situated approximately linearly, with Site A about 40 km southwest of Site B, and Site C about 40 km northeast of Site B. Site B is 2 km to the north of a major day roost of both *L. yerbabuenae* and *L. nivalis* (M. A. Bogan, U.S. Geological Survey, Albuquerque, New Mexico, unpublished manuscript).

   Plant morphometrics and phenology—I documented variation in plant morphology by recording the rosette height and diameter, inflorescence height, and number of inflorescence branches for all blooming agaves within each site (78, 58, and 46 agaves at Sites A, B, and C, respectively).   To assess the phenological variation within and among sites, each site was visited three times during the focal summer (England, 2012b). During trips, each blooming branch's location on the inflorescence was recorded relative to other branches, following the sequential upward pattern of blooms. Each branch's relative position on the inflorescence was calculated by dividing the location of the branch by the total number of branches on the inflorescence, such that the 3rd branch upward out of 20 had a position of 0.15 (Humphries and Addicott, 2004). Agave floral visitors were also documented during these trips (patterns described in England, 2012b).

I returned to each site in late September or early October of the same year. For every branch of each studied agave, I estimated a per-branch fruit-set category where High, Medium, and Low subjectively appeared to have > 70%, 30-70%, and 5- 30% of the umbel surface covered in fruits, or category Zero had 0 or 1 fruit. I then collected a subset of the branches that had been observed during each of the summer trips ($N = 412$ branches from 164 plants). In 2006, for 39 of the observed individuals, I gathered the two branches from each visit period that were in the middle of the range of branches blooming that visit (Site A: 194 branches from 39 plants), and for the other 38 of the sampled plants I gathered one branch from any visit ($N = 38$ branches from 38 plants). For 2007, from each plant one branch from each summer visit period was collected (Site B: 89 branches from 48 plants; Site C: 108 branches from 46 plants). Collected branches were stored in individual paper bags, labeled with plant and branch number, and allowed to dry. For each focal branch, the total numbers of fruits and flowers (from persistent pedicels) were counted. Each branch's fruit set was computed as the number of mature fruits / number of flowers.

The dehiscent stage of each fruit was categorized as "closed" if no seeds came loose after several gentle shakes, "open" if some seeds shook loose, or "spilled" if it was judged that the fruit was so open that the seeds were completely gone or could have easily been intermingled with other fruits of the same branch within the paper bag. A random sample of up to 6 open and 6 closed fruits from each sampled branch was individually labeled and retained for subsequent analyses. If all fruits on a branch were spilled, then up to 6 were retained for volume measurements and ovule counts. For each

retained fruit ($N = 2235$), I measured the length and width of the fruit the nearest 0.1 mm, from which I later computed the fruit volume using the volume of a cylinder.

Seeds were then removed from the fruit. Any seeds showing insect damage were discarded; no attempt was made to count the number of damaged seeds because many were entirely consumed, and therefore any count would have been incomplete. The type (generally adult weevil or Lepidopteran larvae, sometimes eclosed adult moth) and number of any seed predators were recorded, and representative specimens were retained for identification. Moths were identified by E. Metzler of Michigan State University, and weevils by D. Lightfoot of the University of New Mexico's Museum of Southwestern Biology (MSB). Insect specimens were deposited in the MSB. Fertile seeds (black (Gentry, 1982)) were sorted from unfertilized ovules (beige), and counted for all retained closed fruits and a subset of open fruits, and the total mass of all seeds per fruit was determined to the nearest 0.1 mg ($N = 141,525$ seeds from 1209 fruits on 210 branches of 105 plants). For each fruit, the total fertile seed mass was divided by the number of fertile seeds, to give a mean seed mass.

On a subset of fruits, the number of ovule scars was counted along one row of the fruit using a dissecting microscope, and then multiplied by the number of rows to give an estimate of the total number of ovules per fruit. In 2006 only a few fruits were haphazardly chosen for ovule counts (Site A: $N = 47$ closed, 11 open fruits), but ovule counts were done routinely for fruits from 2007 for branches having at least 3 closed, open, or spilled fruits (Site B: $N = 84$ closed, 152 open, 31 spilled; Site C: $N = 75$ closed, 191 open, 60 spilled fruits). Each fruit's seed set was computed as the number of fertile seeds / number of ovules. Seed set, seed number, and total seed mass per fruit were

underestimates for open fruits; and in fruits with some seeds eaten these values should be viewed as post-predation values.

Data analysis—Data were analyzed using SAS software, version 9.3 (SAS Institute Inc., 2010). Because rosette volume was correlated with inflorescence height and number of branches ($r_s = 0.74$ and $r_s = 0.61$, respectively, (England 2012b)), principal component analysis (PCA) was conducted using PROC PRINCOMP (SAS Institute Inc., 2010) to capture variation between plants and produce a smaller number of uncorrelated variables for subsequent analyses (Gotelli and Ellison, 2004). Principal components analysis of plant traits revealed that Principal Component 1 (PC1) and Principal Component 2 (PC2) explained 89% of morphological variation between the plants (Table 1). PC1 explained 70% of the variation, and consisted of variable loadings of 0.62 rosette volume, 0.56 inflorescence height, and 0.55 number of umbels; PC1 is hereafter referred to as "plant size." PC2 explained an additional 19% of the variation among individuals, and consisted of 0.73 number of umbels, -0.68 inflorescence height, and -0.04 rosette volume. PC2 represented a tradeoff between horizontal and vertical attributes of the inflorescence, such that plants having negative values of PC2 were relatively taller with fewer branches, while positive values represented shorter, many-branched individuals. PC2 is hereafter referred to as "display shape."

To evaluate factors affecting pre-pollination patterns at a gross scale, I hypothesized that the number of flowers per branch (*N*= 442 branches from 163 plants) could be predicted by a combination of morphological and phenological factors. Scatter plots of branch position within inflorescence by the number of flowers per branch showed improved regression line fit with a quadratic equation applied to the natural log

of the number of flowers per branch (quadratic: $R^2 = 0.2996$), so in addition to main

effects, a branch-position-squared (position^2) term was included in modeling efforts. I

prepared an a priori set of 3 regression models (Appendix 1), all of which included

branch position and branch position^2, with various combinations of the terms plant size

and display shape. The null (intercept-only) model was also routinely included in

modeling efforts (Mundry, 2011) though not numbered among the competing candidate

models. Because count data are not expected to fit a normal distribution, PROC

GENMOD (SAS Institute Inc., 2010) was used with a Poisson probability distribution, a

log link function, independent correlation type, and plant as the repeated subject.

I applied an information-theoretic approach (Burnham and Anderson, 2002;

Stephens et al., 2005; Garamszegi et al., 2009) to evaluate the support for candidate

models (for flower number and all subsequently discussed modeling efforts). Under this

framework, the recommended maximum number of models to consider should be less

than the sample size (Burnham et al., 2011). Observations from each plant were expected

to be correlated, so generalized linear models were fitted using generalized estimating

equations via PROC GENMOD. The correlation structure was chosen that produced the

smallest Quasi-likelihood Information Criteria (QIC) values for null and single-variable

models (Pan, 2001). QIC goodness-of-fit statistics are a modification to Akaike's

Information Criteria (AIC) scores to allow model selection among generalized estimating

equations (Pan, 2001). The approximated QICu adds a penalty to the quasi-likelihood for

the number of parameters used in a model (Pan, 2001; SAS Institute Inc., 2011); the

model with the smallest QICu score (QICu$_{min}$) is preferred. For each competing model, I

calculated QICu differences (ΔQICu = QICu − QICu$_{min}$), and then ranked all candidate

models based on strength of evidence as represented by QICu weight (Pan, 2001; Anderson, 2008). A model weight is the probability that the given model is the most parsimonious, best fit for the data from the candidate set (Anderson, 2008).

I considered the best-ranked model to be definitive relative to other candidates if the QICu weight was > 0.95, otherwise I included the top-ranked models in the 95% confidence set such that the cumulative sum of their QICu weights was just ≥ 0.95 (Burnham and Anderson, 2002). Model weights in the confidence set were then renormalized to sum to 1 (Anderson, 2008). Multi-model inference was used to estimate model-averaged parameters for each of the predictor variables in the 95% confidence set, by weighting the estimate for each parameter by the summed weight of the confidence set of models it appeared in; when the term did not appear, the parameter estimate of 0 was utilized (Burnham and Anderson, 2002). Parameter estimates were computed in log scale, but transformed for presentation (Grueber et al., 2011); reported means are presented with 95% confidence limits. When models were averaged, the resulting parameter estimates were considered statistically significant if their 95% confidence limits did not span 0.

At a finer scale, I also assessed ovule patterns. I was concerned that there could be fundamental within-branch differences between closed and open fruits, therefore I compared the number of ovules between 3 closed and 3 open fruits from 28 branches of 24 plants, using PROC GLM (SAS Institute Inc., 2010) to perform a type III repeated-measures ANOVA with branch as the repeated subject, and dehiscent class, site, and the interactions between site, dehiscence, and fruit as independent variables. To evaluate factors affecting potential reproductive capacity at a fine scale, I hypothesized that the

number of ovules per closed fruit ($N = 206$ fruits from 97 branches on 57 plants) could be predicted from a combination of phenological and morphological factors, thus I tested 8 models containing the predictors branch position, branch position^2, plant size, and display shape (Appendix 2). I used PROC GENMOD with a Poisson distribution, a log link function, and exchangeable correlation type, with branch nested within plant as the repeated subject.

A one-way ANOVA (PROC GLM) was used to compare field-estimated fruit set category with actual fruit set of focal (collected) branches. To estimate how successful the reproductive efforts of each plant had already been prior to blooming of focal branches, I averaged the fruit set for all previous branches, and used the resulting "prior fruit set" variable in subsequent modeling.

I posited that patterns of fruit production ($N = 408$ branches on 163 plants) would be related not only to the morphological and phenological factors relevant to flower and ovule patterns, but also to variation in pollinator visitation rates. Although not strictly count data per se, percent fruit set could be viewed as the number of successful fruits per 100 flowers, so PROC GENMOD was used to model floral success as percent fruit set with the Poisson distribution, a log link, exchangeable correlation, scale set to deviance to correct for over-dispersion, and plant as the repeated subject. I created an a priori set of 24 models with the categorical season-within-site factor to account for overall visitation differences between sampling periods as well as any unmeasured environmental variation, and various combinations of plant size, display shape, branch position, branch position^2, mean prior fruit set of all branches that bloomed before the focal branches, and the interaction of prior fruit set with branch position (Appendix 3). From the resulting

95% confidence set of models, I obtained least-squares mean estimates of fruit set for each season within site. Because I also wished to learn which combination of visitors were most influential, the plant factors present in the top two season-site models were retained to create a new set of candidate models with various combinations of one, two, and three of the mean per-trip visitation rates (England, 2012b) of floral-visitor guilds that could potentially have affected pollination success: bats, sphinx moths, birds, carpenter bees, and bumble bees (Slauson, 2000). This resulted in a total of 48 candidate visitor models (Appendix 4). The same methods were used to analyze percent seed set per fruit seed ($N = 203$ fruits from 95 branches on 57 plants), except with branch nested within plant as the repeated subject (Appendix 3, 4).

The relationship between mean seed mass and seed set within closed, uneaten fruits ($N = 203$) was examined using PROC CORR (SAS Institute Inc., 2010) with the Spearman option. I hypothesized that morphology, phenology, and pollination could also affect mean seed mass per fruit ($N = 834$ fruits, 193 branches, 99 plants). Masses were not normally distributed, nor did they fit the gamma distribution, so I compared QIC values for single-variable models using gamma distribution with logarithmic and inverse links, as well as Poisson distribution with a logarithmic link. Poisson models yielded considerably lower QIC values than gamma models, so the Poisson distribution was used for model comparisons, with a log link and exchangeable correlation. The same a priori set of 24 plant with season-site models (Appendix 3) and 48 plant with visitor models (Appendix 4) were used as described for fruit set above.

In order to discern potential influences upon the pattern of seed predation, I once again used PROC GENMOD with the Poisson distribution, a log link, and exchangeable

correlation to model the number of caterpillars per fruit, and weevils per fruit (both $N =$ 1131 closed fruits, 209 branches, 105 plants). Candidate models ($N = 23$) included the potential predictor terms of plant size, display shape, branch position and branch position^2, number of seeds per fruit, mass of all seeds within the fruit, and/or fruit volume (Appendix 5). Recall that in eaten fruits, rather than being true approximations of pollination success, the seed number and total seed mass per fruit were underestimates because eaten seeds were discarded without counting; therefore these values could be viewed as post-predation rates. Models failed to converge when season within site was used, so PROC MEANS (SAS Institute Inc., 2010) was used to obtain per-trip mean predation rates.

RESULTS

1) How do morphological traits affect the number of flowers per branch, and the number of ovules per fruit?—The single model that best predicted the number of flowers per branch included plant size ($P < 0.0001$), display shape ($P = 0.0037$), and branch position and branch position^2 (both $P < 0.0001$, Table 2). Generally, the mean number of flowers per branch peaked in branches located in the middle of the inflorescence, and increased with overall plant size. Tall, few-branched displays had more flowers per branch than short, many-branched displays.

Repeated-measures ANOVA revealed that the number of ovules per fruit was significantly greater in open fruits ($\overline{X} = 454$, SD = 88.5) than closed ones ($\overline{X} = 433$, SD = 81.4) from the same branch ($F = 607.55$, df = 2, $P < 0.0001$), but site and interaction effects were not statistically significant predictors (all $P > 0.10$). Because of this inherent difference in ovule number and related terms (seed set, seed mass), and because open

fruits had potentially lost an unknown number of seeds, subsequent analyses therefore considered closed fruits only, as a conservative measure of actual reproduction.

The single model (Table 2) that best predicted the number of ovules per closed fruit included plant size, display shape, branch position and branch position^2; of these terms, only size had a statistically significant effect ($P = 0.0047$). The mean number of ovules per closed uneaten fruit declined with increasing overall plant size. Tall, few-branched displays tended to have more ovules per fruit than short, many-branched displays, though this effect was not statistically significant ($P = 0.16$). The quadratic influence of branch position was such that ovule number per fruit was relatively stable on branches in the lower 80% of the inflorescence, and then declined somewhat on later branches, though this effect was not significant (branch position $P = 0.38$, branch position^2 $P = 0.16$).

2) Do plant morphology, visitation rates, and/or prior plant reproduction affect fruit set and seed set? — Field-estimated fruit set category corresponded significantly to actual fruit set on sampled branches ($R^2 = 0.69$, $P < 0.0001$, Fig. 1). The top season-site model revealed that fruit set was highest during the midsummer trips to Sites A and B, intermediate in late summer at Site B, and lowest during all other all trips (Fig. 2). The visitor models (Table 3) that best predicted fruit set per branch included branch position and branch position^2, prior fruit set and its interaction with branch position, bats, birds, and carpenter bees; of these, prior fruit set, bats, birds, and carpenter bees were statistically significant terms. Fruit set decreased significantly with increasing bat visitation rate (Fig. 3a), and increased with increasing bird visitation (Fig. 3b) and

carpenter bee visitation (Fig. 3c). Fruit set increased with branch position and prior fruit set.

Seed set per closed uneaten fruit was highest during all trips to Site A and the late summer trip to Site B, and lowest during the early and mid summer trips to Site B and all trips at Site C (Fig. 4). The top visitor model for seed set (Table 3) included branch position and branch position^2, prior fruit set, the interaction of branch position with prior fruit set, and bat and bird visitation rates. Prior fruit set and the interaction of prior fruit set with branch position were statistically significant ($P = 0.0062$, $P = 0.0017$ respectively), as were bats ($P < 0.0001$) and birds ($P = 0.0017$). Seed set increased with bat visitation rate (Fig. 5a) but decreased with bird visits (Fig. 5b), the opposite pattern seen in fruit set for these two visitors. The interplay of branch position, branch position^2, and prior fruit set and its interaction with branch position resulted in a complex pattern of mean seed set, such that seed set generally was greatest on early (low) branches with high prior fruit set, and to a lesser extent on late branches when prior fruit set was low.

3) Does mean seed mass change with seed set, and is seed mass affected by the same factors as fruit set and/or seed set? —The mean mass per seed was negatively correlated with the number of seeds in closed uneaten fruits ($r_s = -0.25$, $P = 0.0003$). The single model (Table 3) that best explained mean seed mass included the predictors of plant size, display shape, branch position and branch position^2, prior fruit set and its interaction with branch position, and visitation rates of bats, birds, and carpenter bees. Of these, statistically significant terms included display shape ($P = 0.0061$), prior fruit set ($P = 0.016$) and its interaction with branch position ($P = 0.0086$), and the visitation rates of bats ($P < 0.0001$), birds ($P < 0.0001$), and carpenter bees ($P = 0.0009$). Heavier seeds

were associated with tall, few-branched displays. Mean seed mass per fruit decreased with bat visitation rate (Fig. 6a), and increased with bird and carpenter bee visitation rates (Figs. 6b, 6c). Once again, the interplay of branch position, branch position^2, and prior fruit set and its interaction with branch position resulted in a complex pattern for mean seed mass, showing generally the opposite pattern of their influence on seed set. Heavier seeds were associated with early branches when prior fruit set was low, and with late branches with high prior fruit set.

4) What factors influence seed predation, and how does it vary among seasons and sites? — The abundance of seed predators varied between sites and seasons. Site A had caterpillars in closed fruits during all sample periods, at low rates in early summer, moderate rates in midsummer, and high rates in late summer (Fig. 7). Caterpillars were never observed in closed fruits from Site B, and only were observed at low rates in late summer at Site C. The best model (Table 4) explaining the number of caterpillars per closed fruit contained the terms plant size ($P = 0.0085$), display shape ($P = 0.023$), branch position ($P = 0.014$) and branch position^2 ($P = 0.0036$), and fruit volume ($P < 0.0001$). The mean number of caterpillars per closed fruit decreased with increasing plant size, was higher in short, many-branched displays, increased on branches toward the middle of the display, and increased with fruit volume. Adult moths found emerged from fruits with caterpillar infestation did not match any of the moths captured in floral traps during summer trips, thus their identification is pending. Parasitoid wasps (identification also pending) were found associated with one of the mid-summer and nine of the late-summer caterpillar-occupied fruits from Site A.

The number of weevils per closed fruit was highest in midsummer at Site A, with lower numbers at Site A in early and late summer fruits (Fig. 7); no weevils were observed in any of the closed fruits from Sites B or C. Weevils were identified as *Scyphophorus acupunctatus* (Coleoptera: Curculionidae). The 95% confidence set of models included four of the 23 considered models, all of which contained branch position and branch position^2, and some combinations of plant size, display shape, and either total mass of all seeds per fruit, or seed number per fruit (Table 4). Of these, the total seed mass appeared in the highest-weighted three models (summed model weight = 0.97) and was consistently significant ($P < 0.01$), while seed count ($P = 0.020$) only appeared in the lowest-weighted model (model weight = 0.03). Closed fruits with a higher total seed mass were associated with more weevils.

DISCUSSION

A spatiotemporal mosaic of pollination and seed predation appears to be present in this system, such that fluctuating numbers and activities of mutualists and antagonists may be interacting in a manner that preserves phenotypic variety across different populations, as is consistent with the geographic mosaic theory of coevolution (Thompson, 1997; Gómez and Zamora, 1999; Thompson and Cunningham, 2002; Silva-Montellano and Eguiarte, 2003). Site A had the highest fruit and seed set, but also the highest seed predation rate. At Site B, over half the agaves had completed blooming before the primary pollinators (bats) arrived. Site C had no obvious pollinators to assist long-distance gene flow, yet had low seed predation rates and a relatively high rate of fruit set, and non-zero seed set.

1) How do morphological factors affect female reproductive potential? — All of the morphological factors considered affected reproductive potential at gross and fine scales. Not surprisingly, larger plants had more flowers per branch, and branches in the middle of the inflorescence had more flowers. Taller displays with fewer branches had more flowers per branch than shorter displays with more branches.

On a fine scale, the factor most strongly affecting ovule number was plant size, but contrary to expectation, larger plants had fewer ovules per fruit than small plants, perhaps because they divided them into more flowers and branches. This strategy could be a mechanism to expand the period of seed production throughout a longer bloom period, thus allowing for temporal changes in visitor patterns over the course of the bloom season, and opportunities for pollen exchange with different mates as new individuals become reproductively available (Ober et al., 2005). A longer reproductive period could also exceed the peak activity period of seed predators (English-Loeb and Karban, 1992). Although not statistically significant, branch position did occur in the top model predicting ovule number per fruit, such that the number of ovules per fruit decreased somewhat on more distal floral branches; this accords with the pattern of decreasing ovule number with increasingly distal floral positions in 15 liliaceous species (Thomson, 1989).

2) Do plant morphology and phenology interact with visitation rates and/or the plant's prior reproductive experience to affect reproductive success? —Branch position and branch position[2] affected fruit set, such that fruit set was relatively constant in the lower half of the inflorescence, and then increased moderately on branches in the more distal portions of the inflorescence. This finding is not consistent with a prior study on *A.*

mckelveyana that found fruit set to be very low in the first 35-40% of branch positions, and then to sharply increase on central and distal branches (Sutherland, 1987). Flowers on the lower branches of *A. mckelveyana* had a high proportion of nectar secretion during the pollen-presentation phase of flowering, thus suggesting that flowers on early branches of *A. mckelveyana* primarily act as pollen donors to other agaves rather than in a maternal role (Sutherland, 1987). Intrinsic architectural patterns of fruit set, seed set, seed mass, and flower mass are more widely studied in *Yucca* species, and have been found to be quite variable between and within species (Aker and Udovick, 1981; Huth and Pellmyr, 1997; Humphries and Addicott, 2004), yet per plant, the overall fruit set is generally believed to be resource limited in most agave and yucca species (Sutherland, 1987; Huth and Pellmyr, 1997; Slauson 2000).

The mean amount of fruit set on earlier branches positively affected fruit set on sampled branches. Nectar-feeding bats, hummingbirds, sphinx moths, and large bees have been shown to visit previously rewarding plants in a trapline manner (Linhart and Mendenhall, 1977; Des Granges, 1978; Proctor et al., 1996), so it is possible that certain plants offered intrinsically higher quality or quantity of nutritional rewards for their effective pollinators, and the animals visited those plants preferentially. Larger *A. palmeri* were associated with increased bird and sphinx moth visitation rates (England, 2012b); whereas taller, few-branched displays were associated with increased carpenter bee visitation rates compared to shorter, many-branched ones (England, 2012b). However, Ober and Steidl (2004) found that visitation rates of *L. yerbabuenae* were not explained by inflorescence height.

Seed set showed a complicated response to the interaction of branch position and prior fruit set. Positive seed set on low branches with high prior fruit set could be simply a side effect of the autocorrelation of proximate branches, because sequential branches tend to have some flowers open concurrently, and thus will experience temporal overlap in pollination regimes (Gentry, 1982; Slauson, 2001). The positive seed set observed for late-blooming branches when prior fruit set was low could potentially have been a mechanism to use up remaining resources, perhaps via a release from selfing restrictions, as gene expression may also vary with flower position upon inflorescence (Barrett and Harder, 1992; Diggle, 1995). The lower seed set observed on late branches of high prior fruit set plants could have been due to resource depletion (Huth and Pellmyr, 1997; Pellmyr and Thompson, 1996; Humphries and Addicott, 2004). This is in accord with evidence that later-blooming flowers of *A. palmeri* may have reduced nectar volume and concentration (Slauson, 2002).

Modeling efforts for visitors selected bats, birds, and carpenter bees as the three most influential on agave female reproductive success, whereas sphinx moths and bumble bees were not among the top three most influential visitors for any trait examined. The models most strongly supported the role of bats as the most effective pollinators (Fleming and Sosa, 2004), as high bat visitation rates were associated with high seed set. The low fruit set per branch associated with high bat-activity periods may have been due to selective abortion for sparsely filled fruits that would have been allowed to mature on less pollinated branches. Bats are known to carry large pollen loads, and make contact with floral tissues in 100% of visits (Slauson, 2000), and thus are considered to be very efficient pollen vectors when present. They also routinely commute distances of 20-30

km during the course of their nightly feeding activities (Horner et al., 1998; England, 2012b), thus potentially providing opportunities for pollen exchange between geographically isolated agave populations.

Bird visits were associated with the production of many fruits but low seed set per fruit. The most frequent bird visits were from hummingbirds (England, 2012b) which tend to avoid floral contact (Slauson, 2000; England, 2012b); however, when hummingbird densities were high, territorial aggression (Martinez del Rio and Eguiarte, 1987; Kuban, 1989; England, 2012b) could have resulted in inadvertent pollen transfer that potentially could account for more fruits with fewer seeds. Visits from orioles and other perching birds that do make floral contact (Fulton, 1983; Martinez del Rio and Eguiarte, 1987; Kuban, 1989; Ornelas et al., 2002) may have been more efficient, but were relatively rare (England, 2012b), as also observed in Arizona (Slauson, 1996).

Carpenter bee visits affected fruit set but not seed set in this study. Carpenter bee visits in Arizona populations of *A. palmeri* resulted in stigma contact rates of 7% (Slauson, 2000). Female carpenter bees commonly specialize on one to two flower species with high nectar and pollen rewards (Smith and Whitford, 1978; Scott et al., 1993), so their pollen loads should be relatively pure. Carpenter bees may forage 6 km from their nests (Pasquet et al., 2008), potentially allowing movement of agave pollen at least within mountain ranges, and on a smaller scale, pollen carryover from flower to flower on large bees may be considerable, commonly moving 7-8 flowers from the original source, but in at least one case has been documented 54 flowers later (Willson, 1983). Although some species **of** sphinx moths carry large quantities of agave pollen (Riffell et al., 2008), and in Arizona approximately 18% of sphinx visits resulted in

stigma contact of *A. palmeri* (Slauson, 2000), the results from the present study found sphinx moths to be less influential than carpenter bees. Experimental studies would be required to elucidate to what degree large bees and sphinx moths are exploiting the floral rewards but providing no net pollination services.

During periods when bats and birds were either absent or present in low numbers, fruit set (Fig. 3) and seed set (Fig. 5) were relatively low. This was the case at Site B in early summer when birds were present at low numbers but presumably before the migratory bats had arrived (Cockrum, 1991); blooming branches achieved approximately 5-7% seed set and 12% fruit set. At Site C, where bats were never observed and birds were relatively scarce, blooming branches achieved 8-9% seed set and 17-19% fruit set during each of the sample periods. The increased rates at Site C could be due to a generalization of floral traits to allow pollination by one or more of the other visitor types (Slauson, 2000; Fleming et al., 2001; Bustamante et al., 2010) or an increased rate of selfing (Fulton, 1983); floral traits of this population have not been examined.

Both fruit set and seed set are useful metrics to understanding patterns of reproduction, but it is important to recall that fruit production is only a gross measure of reproductive success. Fruit set is much more rapid to assess in the field, and due to the persistent nature of agave fruits, fruit set estimates can still be made several years later. However, a fruit with only a few good seeds appears much the same as a fruit with much higher seed set. Ultimately it is the number of seeds produced that is most important to establishment of the next generation. Unfortunately, compared to fruit set, seed set is much more time consuming to quantify in the field, and harvesting entire branches for later study depletes the seed bank unless propagules are returned to their source after

processing. Additionally, due to the natural dehiscence of the fruits, there is a rather short temporal window in which to collect accurate seed-set data, and even unopened fruits may contain insects that will foul the actual census of seeds that were originally fertilized. Although Howell and Roth (1981) indicated that the pigmentation stripes on inner fruit walls corresponded to the number of fertile seeds produced, as had been found by Slauson (1996), this was not reliable in my populations.

   3) Does mean seed mass per fruit change with seed set, and are patterns of per-seed investment affected by the same factors as fruit set and/or seed set? —The negative correlation between seed mass and seed set per fruit suggests that seeds might be competing for a limited per-fruit supply of resources (Fenner and Thompson, 2005; Wesselingh, 2007), rather than being able to pull additional resources based on fertilization success (Stephenson, 1981). This could be due to an anatomical constraint (Diggle 1995), since display shape was a statistically significant predictor of seed mass. Compared to short, many-branched displays, those plants having tall, few-branched displays had more flowers per branch and heavier seeds, which could be indicative of a higher per-fruit capacity to nourish seed development.

   Visitor-influenced trends in mean seed mass mirrored those of fruit set rather than seed set, in particular carpenter bee visits increased both mass and fruit set though had no influence on seed set. As expected from the negative correlation of seed set with seed mass, because bats increased seed set and birds decreased seed set, these two had opposite effects on seed mass: bats decreased seed mass whereas bird visits increased mass. This pattern is similar to a pattern observed in *Silene alba*, where moth visits

increased seed set yet decreased seed mass, and bee visits decreased seed set but increased seed mass (Young, 2002).

4) What factors influence seed predation, and how does it vary among seasons and sites? —The number of caterpillars per mature fruit decreased with increasing plant size, and was lower in tall, many-branched displays; these traits were associated with more flowers per branch. The antagonistic action of caterpillars may have thus resulted in directional selection for bigger plants with taller inflorescences, at least when they were abundant, such as mid and late summer at Site A. On the other hand, weevils were most strongly positively associated with the total mass of all seeds within the fruit, such that fruits with a higher total seed mass had more weevils. Plant size and display shape showed weaker potential influences on weevil infestation rates, but in the opposite direction of caterpillar selection: increasing plant size had a slight (but not statistically significant) positive influence on weevil numbers; display shape appeared only in the third best model (model weight 0.05), indicating very weak support for its influence on weevil number. Previous reports of weevil impacts upon agaves have focused on damage to the rosette and base of the flowering stalk, caused by weevils and associated fungi and bacteria (Waring and Smith, 1986). This appears to be the first documentation of weevils directly consuming agave seeds.

Like pollinators, the number of seed predators per mature fruit exhibited fluctuating spatiotemporal patterns, with the highest caterpillar infestation rates at Site A in mid and late summer, and highest weevil infestation rates in midsummer at Site A. The higher number of seed predators at Site A (2006) than at Sites B and C (both 2007) could have been due to inter-annual variation, or a spatial trend. Other studies have

found seed predation to vary within and between years and sites (e.g. English-Loeb and Karban, 1992; Huth and Pellmyr, 1997). Such variation can lead to fluctuating selection against whichever plant traits are associated with seed predator selection (Klips et al., 2005). In cases where seed predation exhibits temporal peaks within a year, the plant may benefit from an extended bloom season exceeding the activity span of seed predators (Pettersson, 1991; English-Loeb and Karban, 1992; McIntosh, 2002; Lacey et al., 2003; Tarayre et al., 2007), and benefit from the presence of those visitors such as birds and carpenter bees that increase fruit set, even when they have no or slightly negative impacts on seed set.

Evidence for selection?—Increased plant size did not show significant direct effects on fruit set or seed set, though larger plants receive more bird and sphinx moth visits (England, 2012b). Bird visits lowered seed set but increased fruit set and seed mass; this effect spreads out seed production among a greater number of fruits, possibly allowing seeds to escape predation and to garner greater provisioning apiece. Increased carpenter bee visitation rates were associated with increased fruit set, but had a weaker impact on mean seed mass than birds. Because bat visitation rate was the only extrinsic factor associated with increased seed set, the results of this study support those of prior experimental studies that found bats to be primary pollinators of *A. palmeri*; unfortunately due to sample size limitations, I was unable to assess whether plant size or display shape influence bat visits (England, 2012b). Plant display shape affected reproductive potential in the form of flower and ovule numbers, but did not emerge as having direct effects on fruit set or seed set. Taller, many-branched displays had more

flowers per branch, more ovules per fruit, and heavier mean mass per seed, as well as increased carpenter bee visitation rates (England, 2012b).

Higher numbers of lepidopteran larvae were associated with smaller plants, and with short, many-branched displays; both these traits tended to have fewer flowers per branch. However, caterpillar infestation was highest in fruits of centrally positioned branches, which had more fruits than early or late branches. This implies that the number of flowers per branch may not have been the main criterion for oviposition site. The antagonistic action of the caterpillars against small plants and those with relatively short displays may indicate natural selection for increased plant size and display height.

Evidence for limitations?—Prior studies on agave reproduction have found conflicting patterns, in part because experiments were conducted on different scales. On a per-branch level, fruit set and seed set of *A. palmeri* are considered pollinator limited (Slauson, 2000), but when similar experiments were performed on a whole-plant level in *A. mckelveyana*, fruit set was found to be limited by resources (Sutherland, 1987). In this study, on a per-branch scale, the large increases in fruit set and seed set when bats and birds were present, at least at Sites A and B, suggest that pollinator limitation is present. Additionally, within fruits, the tradeoff of seed number versus per-seed mass suggests the existence of "plumbing" constraints that limited nutrient supplies to each fruit (Diggle, 1995), and may demonstrate the transition at the fruit scale from a pollinator-limited to resource-limited reproductive state (Wesselingh, 2007). On a whole-plant scale, prior fruit set positively influenced subsequent fruit and seed set, such that individuals with high maternal success rates remained successful. Toward the end of high-success plants models indicated a decline in seed set, possibly indicative of resource depletion (Aker,

1982; Diggle, 1995; Humphries and Addicott, 2004). It would be interesting to see if nectar quality or quantity also declined in late flowers on successful plants.

Implications—Agaves may be especially challenged to keep pace with rapidly changing environmental conditions, given their extremely long generation times, infrequent episodic nature of seedling establishment, and limited seed-dispersal ability (Nobel, 1987, 1992; Alley et al., 2003; Rice and Emery, 2003; Ghazoul, 2005). Although climate models vary, most predict warming temperatures, changes in the timing, amount, and variation of precipitation, and increased frequency of extreme events such as heat waves, droughts, and associated wildfires (Easterling et al., 2000a; Parmesan et al., 2000; Field et al., 2007). Temperature increases and precipitation decreases have already been recorded in this area (Gutzler and Garfin, 2006; Enquist and Gori, 2008), while 2011 and 2012 have seen the largest fires in recorded Arizona and New Mexico histories (National Interagency Coordination Center, 2012; NOAA National Climatic Data Center, 2012). In response to increased warming, animal and plant distributions tend to be moving poleward and upward in elevation (Walther et al., 2002; Parmesan, 2006; Forister et al., 2010), with local population extirpations at the lower edges of their range (Pounds et al., 1999; Parmesan, 2006; Miller-Rushing and Inouye, 2009). Thus, habitat suitability in areas where *A. palmeri* currently exists may be questionable in as little as 2-3 generations in the future (Peterson et al., 2002).

Human activities are directly reducing agave population sizes and eroding genetic variability. Wild agaves are harvested for ornamental landscape sales in the United States (pers. obs.) and for the production of alcoholic beverages in Mexico (Burwell, 1995; Sánchez-Teyer et al., 2009). Likewise, the conversion of native vegetation to

exotic invasive buffelgrass and lovegrass for cattle ranching in northern Mexico has

contributed to fragmentation of agave habitat (Sánchez-Teyer et al., 2009), and

potentially changed wildfire regimes (Burquez-Montijo et al., 2002); little information is

available on the long-term survival, reproduction, or distribution responses of agaves to

fire (U.S. Fish and Wildlife Service, 2007). Increased grazing and the intentional burning

of communal rangelands also reduce soil moisture and alter the availability of nurse

plants needed for agave seedling establishment, and lead to increased trampling of young

agaves by livestock (Burwell, 1995). Livestock and wildlife grazing upon on elongating

agave inflorescences also reduces the number of agaves reaching reproductive maturity,

especially in drought periods (Widmer, 2002; U.S. Fish and Wildlife Service, 2007).

The mobile nature of nectar-feeding bats may provide a rescue for the agaves

from effects of anthropogenic and climatic disruptions (Fleming et al., 2009). Even

relatively rare visits from high-quality pollen dispersers may be disproportionately

important for aiding gene flow between isolated habitat fragments (Proctor et al., 1996;

Fleming et al., 2009). Agave populations with higher genetic variation may have a better

capacity to adapt to changing environmental conditions and escape extirpation or

extinction (Rice and Emery, 2003).

Pollinators will likely be affected by climate change, potentially altering

migration routes or timing in response to resource availability (Hill et al., 1998; Robinson

et al., 2009). Changing environmental cues could result in mismatched timing of life

history events with resource availability (Robinson et al., 2009; Weller et al., 2009).

However, the degree to which this is already taking place is unknown because little is

known about the basic ecology and life history of the organisms. If agaves bloom at

times when the most of their pollinators are not present, then the plants will experience

lower reproductive success, and their visitors will miss out on a major food resource,

resulting in negative consequences for both agave and pollinator populations (Memmott

et al., 2007; Robinson et al. 2009; Weller et al. 2009). Many migratory species require an

ecologically coherent network of stopover sites along their migration route (Russell et al.,

1994; Mehlman et al., 2005, Robinson et al., 2009), but so little is known about the

migration route and habits of nectar-feeding bats (U.S. Fish and Wildlife Service, 1994,

1995), it is difficult to predict the impact of changes in food-plant populations at any one

site upon the bat populations that use it.

By protecting both agaves and nectar-feeding bats, conservationists may aid not

only local pollinator populations and their associated hosts, but also have far-reaching

benefits to ecosystems serviced by migratory pollinators across the continent. *Agave

palmeri* plays a keystone role in maintaining pollinator communities of the Chihuahuan

Desert by providing copious quantities of nectar and pollen when these resources are

otherwise scarce during the pre-monsoon dry season (U.S. Fish and Wildlife Service,

1994, 1995; Good-Avila et al., 2006; England, 2012b). Specifically, *A. palmeri*

seasonally serves as the sole known food source for two species of endangered migratory

nectar-feeding bats (Fleming et al., 1993; U.S. Fish and Wildlife Service, 1994, 1995).

These bats' highly mobile nature provides gene flow between isolated populations of

agaves and columnar cacti in northern Mexico and the southwestern United States

(Fleming et al., 1993; Rojas-Mártinez et al., 1999; Molina-Freaner and Eguiarte, 2003;

Stoner et al., 2003). Persistence of populations of *A. palmeri* is therefore of critical

conservation concern to the stability of desert ecosystems. Nectar-feeding bats and other

large pollinators provide crucial components of ecosystem stability in their role as "mobile links" that allow the persistence of multiple plant species upon which many other species depend (Lundberg and Moberg, 2003). Understanding the complex interactions of plants and animals at multiple scales helps us predict the effects of possible perturbations such as climate change upon the many species present (Field et al., 2007; Enquist and Gori, 2008; Robinson et al., 2009; Robles and Enquist, 2010; Burkle and Alarcón, 2011).

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Table 1. Principal components explaining variation between plants.

Principal Components	Eigenvalue	Proportion of variance explained	Cumulative variance explained	weight Rosette volume	weight Inflorescence height	weight Number of branches
PC1	2.11	0.70	0.70	0.62	0.56	0.55
PC2	0.57	0.19	0.89	-0.04	-0.68	0.73
PC3	0.32	0.11	1.00	-0.79	0.47	0.40

Table 2. Top models predicting the number of flowers per branch, and ovules per closed uneaten fruit. Top row contains parameter estimate means; next row 95% confidence limits. Increasing values of PC2 (display shape) indicate more branches but shorter inflorescence height.

	model weight (w95)	Intercept	**Morphology**		**Phenology**	
			PC1 Plant Size	PC2 Display Shape	Branch Position	Branch Position^2
Per branch						
ln(Flower #)	1.00	**3.48**	**0.23**	**-0.11**	**5.36**	**-4.83**
		3.26, 3.70	0.19, 0.26	-0.18, -0.04	4.62, 6.11	-5.48, -4.18
Per closed uneaten fruit						
ln(Ovule #)	1.00	**6.10**	**-0.03**	**-0.03**	0.28	-0.39
		5.93, 6.26	-0.05, -0.01	-0.08, 0.01	-0.35, 0.92	-0.93, 0.15

Table 3. The 95% confidence set of models predicting mean fruit set per branch, mean seed set per closed uneaten fruit, and mean seed mass per closed uneaten fruit. Top row contains parameter mean estimates; next row represents 95% confidence limits. Final row of fruit set models represents the model-averaged parameter estimates. W95 = model weight within 95% confidence set of models. Increasing values of PC2 (display shape) indicate more branches but shorter inflorescence height.

model weight (w95)	intercept	Morphology		Phenology		Resource depletion		Visitation rates				
		PC1 Plant Size	PC2 Display Shape	Branch Position	Branch Position^2	Prior Fruit Set	Position X Prior Fruit Set	Bat Rate	Sphinx Moth Rate	Bird Rate	Carpenter Bee Rate	Bumble Bee Rate
ln (% Fruit set) per branch												
0.89	**1.75**	**0**	**0**	**0.39**	**0.65**	**3.32**	**0**	**-0.02**	**0**	**0.68**	**0.13**	**0**
	1.09, 2.40	0, 0	0, 0	-1.53, 2.31	-0.90, 2.20	2.57, 4.06	0, 0	-0.03, -0.01	0, 0	0.49, 0.88	0.04, 0.23	0, 0
0.11	**1.63**	**0**	**0**	**0.64**	**0.66**	**3.86**	**-1.19**	**-0.02**	**0**	**0.67**	**0.14**	**0**
	0.86, 2.40	0, 0	0, 0	-1.42, 2.70	-0.83, 2.16	1.84, 5.89	-4.47, 2.08	-0.03, -0.01	0, 0	4.78, 0.87	0.05, 0.22	0, 0
1.00	**1.74**	**0**	**0**	**0.42**	**0.65**	**3.38**	**-0.14**	**-0.02**	**0**	**0.68**	**0.13**	**0**
	1.07, 2.40	0, 0	0, 0	-1.51, 2.44	-0.89, 2.30	2.49, 4.27	-0.51, 0.24	-0.02, -0.01	0, 0	0.49, 0.87	0.04, 0.23	0, 0
ln (% Seed set) per closed uneaten fruit												
1.00	**1.51**	**0**	**0**	**0.48**	**1.49**	**5.45**	**-11.51**	**0.04**	**0**	**-0.46**	**0**	**0**
	0.46, 2.55	0, 0	0, 0	-2.17, 3.12	-0.70, 3.69	1.55, 9.36	-18.70, -4.31	0.03, 0.06	0, 0	-0.74, -0.17	0, 0	0, 0
ln (mean seed mass) per closed uneaten fruit												
1.00	1.97	**-0.01**	**-0.10**	**-0.75**	**0.33**	**-0.75**	**1.90**	**-0.02**	**0**	**0.41**	**0.07**	**0**
	1.74, 2.20	-0.05, 0.02	-0.17, -0.03	-1.58, 0.08	-0.39, 1.06	-1.36, -0.14	0.51, 3.29	-0.03, -0.02	0, 0	0.30, 0.52	0.03, 0.11	0, 0

Table 4. The 95% confidence set of models predicting the number of caterpillars and weevils per closed fruit. Top row contains parameter estimates; next row represents parameter 95% confidence limits. Bottom row of weevil models represents the model-averaged parameter estimates. W95 = model weight within confidence set. Increasing values of PC2 (display shape) represent more branches but shorter inflorescence height. Seed Count and Total Seed Mass are underestimates of each in eaten fruits.

| model weight (w95) | intercept | Morphology | | Phenology | | Food availability | | |
		PC1 Plant Size	PC2 Display Shape	Branch Position	Branch Position^2	Seed Count	Total Seed Mass	Fruit Volume
In (Caterpillar #) per closed fruit								
1.00	**-7.49**	**-0.51**	**0.75**	**18.82**	**-16.51**	**0**	**0**	**0.00**
	-12.30, -2.68	-0.88, -0.13	0.10, 1.40	3.84, 33.80	-27.63, -5.39	0, 0	0, 0	0.00, 0.00
In (Weevil #) per closed fruit								
0.66	**-4.01**	**0**	**0**	**5.89**	**-5.73**	**0**	**0.00**	**0**
	-8.20, 0.17	0, 0	0, 0	-8.70, 20.49	-17.40, 5.94	0, 0	0.00, 0.00	0, 0
0.26	**-4.02**	**0.09**	**0**	**6.04**	**-5.88**	**0**	**0.00**	**0**
	-8.29, 0.24	-0.24, 0.41	0, 0	-8.94, 21.01	-174.87, 6.11	0, 0	0.00, 0.00	0, 0
0.05	**-4.01**	**0.08**	**-0.20**	**6.06**	**-5.95**	**0**	**0.00**	**0**
	-8.25, 0.23	-0.26, 0.42	-0.74, 0.33	-8.79, 20.92	-17.83, 5.94	0, 0	0.00, 0.00	0, 0
0.03	**-3.92**	**0**	**0**	**5.78**	**-5.72**	**0.00**	**0**	**0**
	-8.09, 0.24	0, 0	0, 0	-8.80, 20.34	-17.45, 6.01	0.00, 0.00	0, 0	0, 0
1.00	**-4.02**	**0.03**	**-0.01**	**5.94**	**-5.78**	**0.00**	**0.00**	**0**
	-8.23, 0.19	-0.07, 0.13	-0.03, 0.02	-8.78, 20.66	-17.56, 5.99	0.00, 0.00	0.00, 0.00	0, 0

Fig. 1. Actual percent fruit set per branch for each field-estimated fruit set class (zero, low (L), medium (M), high (H)). All pairwise differences were statistically significant ($P < 0.0001$).
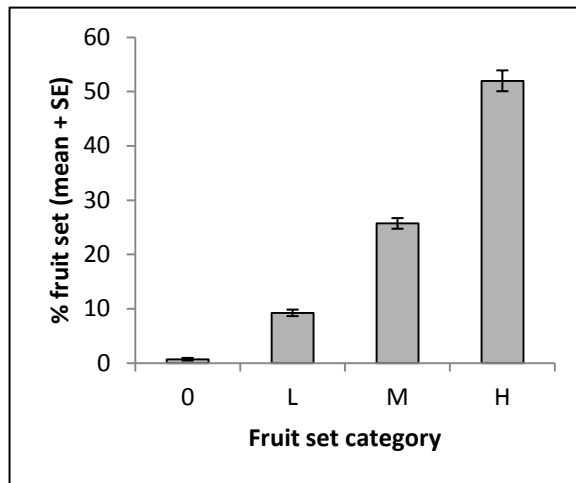
Fig. 2. Percent fruit set on branches that bloomed during early (E), intermediate (I), and late (L) summer trips to Sites A, B, and C. Least-squares means estimates with different lower-case letters indicate significant ($P < 0.05$) differences between trips.
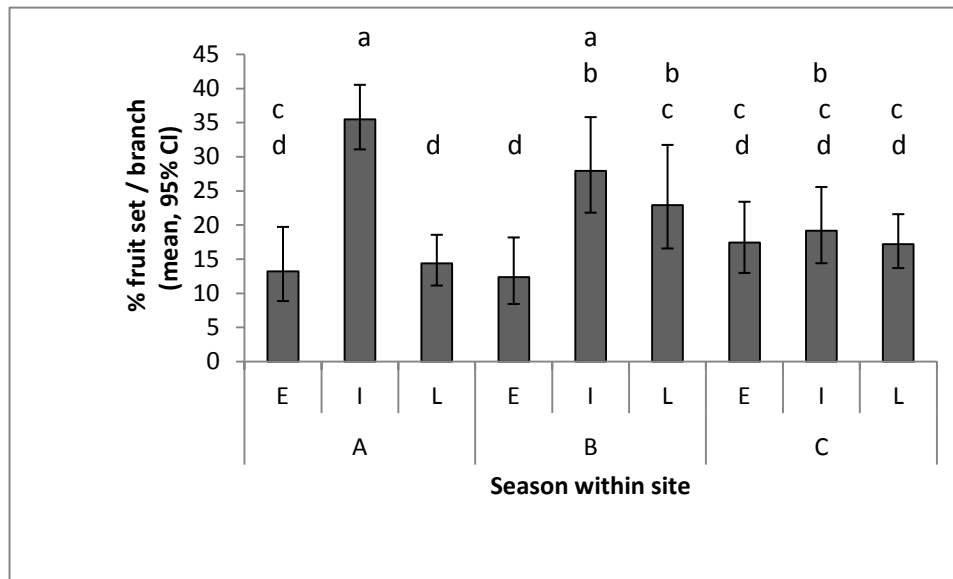
Fig. 3. Percent fruit set as predicted by a) bat visitation rate ($P < 0.0001$), b) bird visitation rate ($P < 0.0001$), and c) carpenter bee visitation rate ($P = 0.0030$).
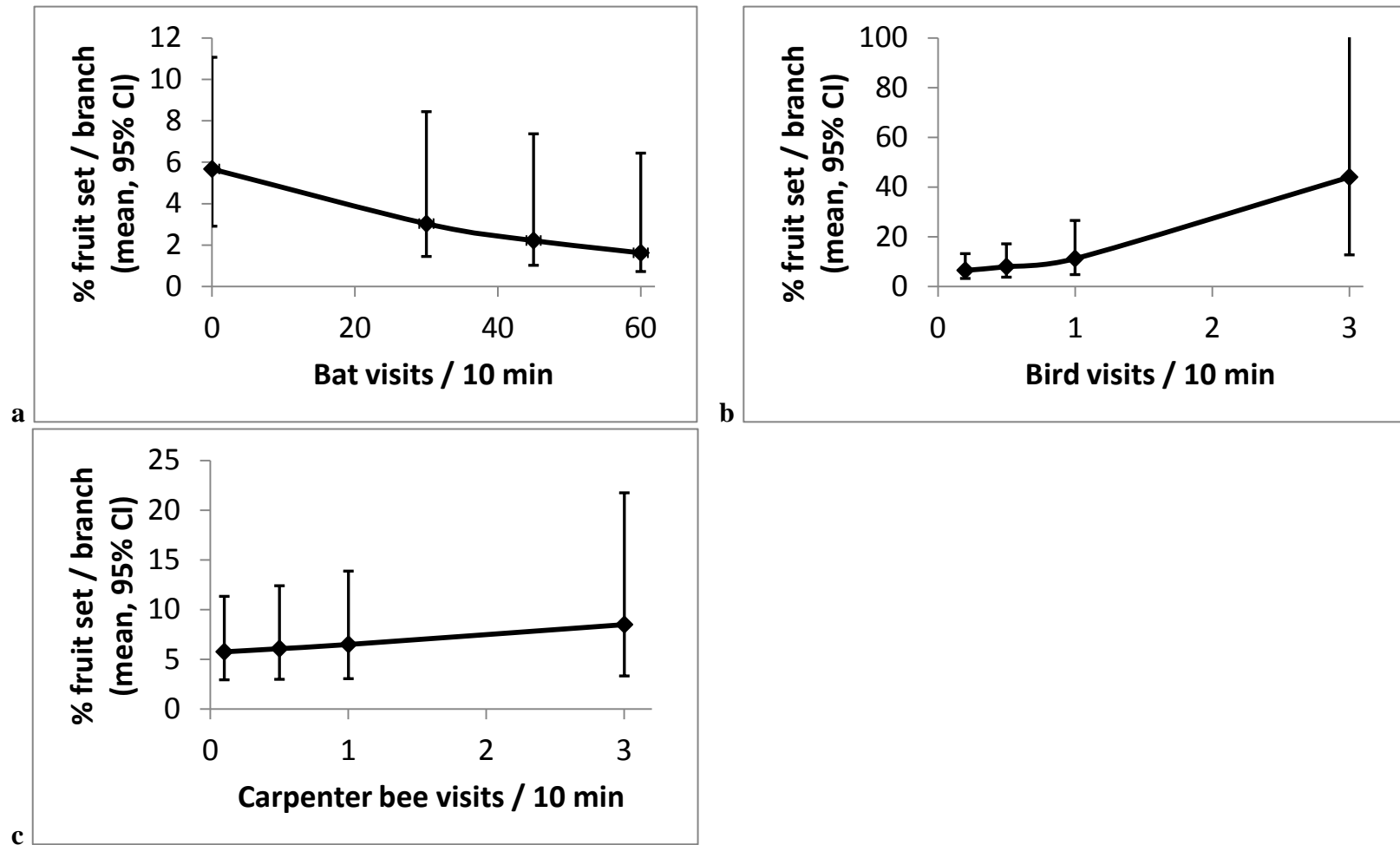
Fig. 4. Percent seed set per fruit on branches that bloomed during early, intermediate, and late summer trips to Sites A, B, and C. Least-squares means estimates with different lower-case letters indicate significant ($P < 0.05$) differences between trips.
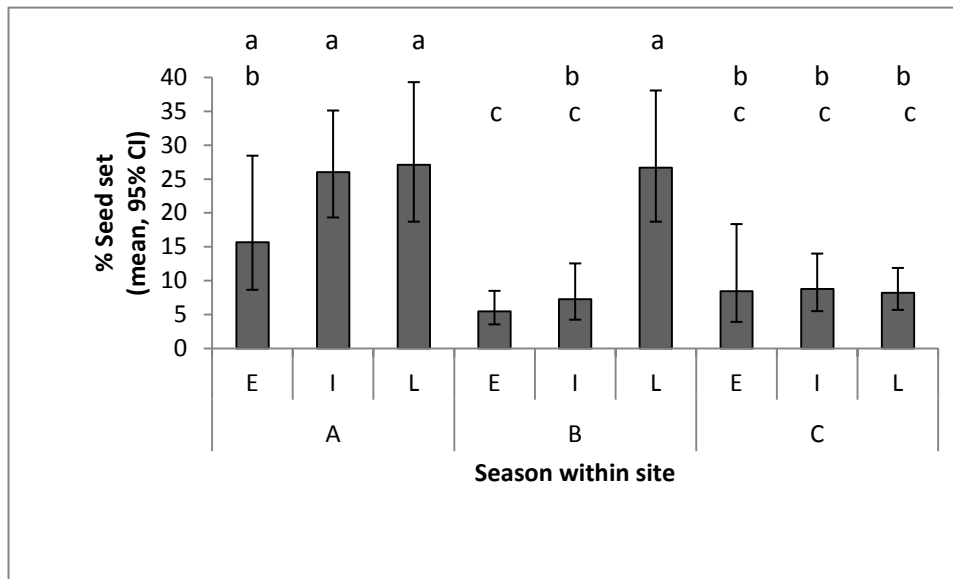
Fig. 5. Model-averaged percent seed set as predicted by a) bat visitation rate ($P < 0.0001$), and b) bird visitation rate ($P < 0.01$).
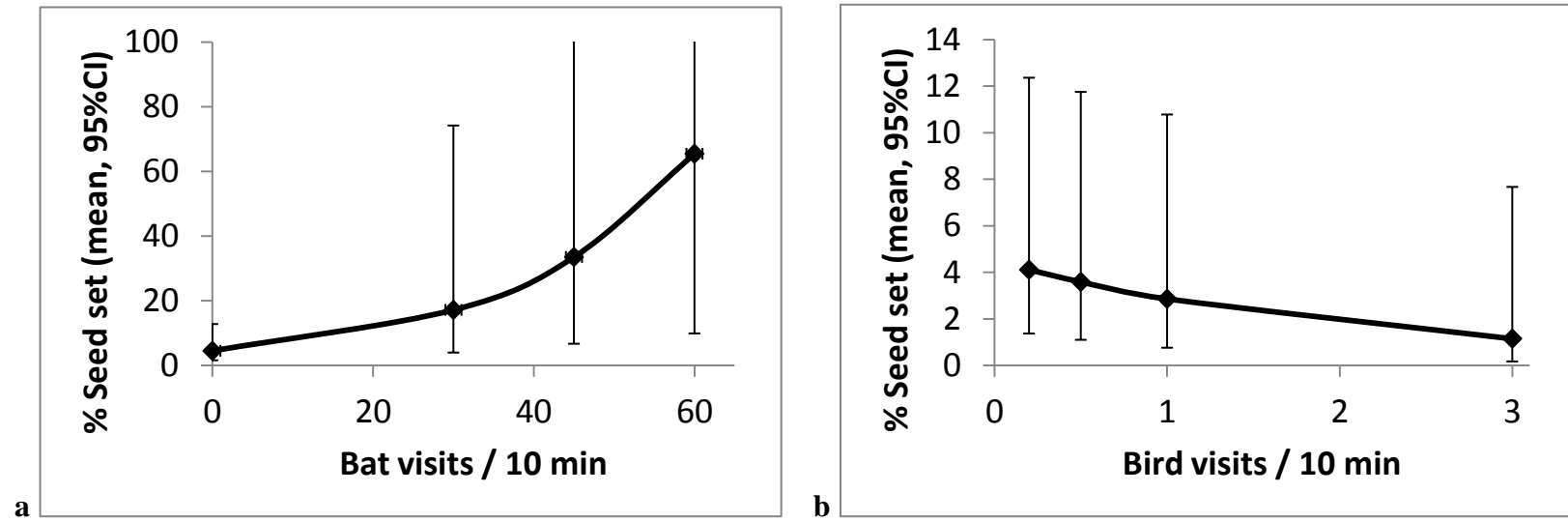
Fig. 6. Mass per seed, as predicted by a) bat visitation rate ($P < 0.0001$), b) bird visitation rate ($P < 0.0001$), and c) carpenter bee visitation rate ($P = 0.0020$).
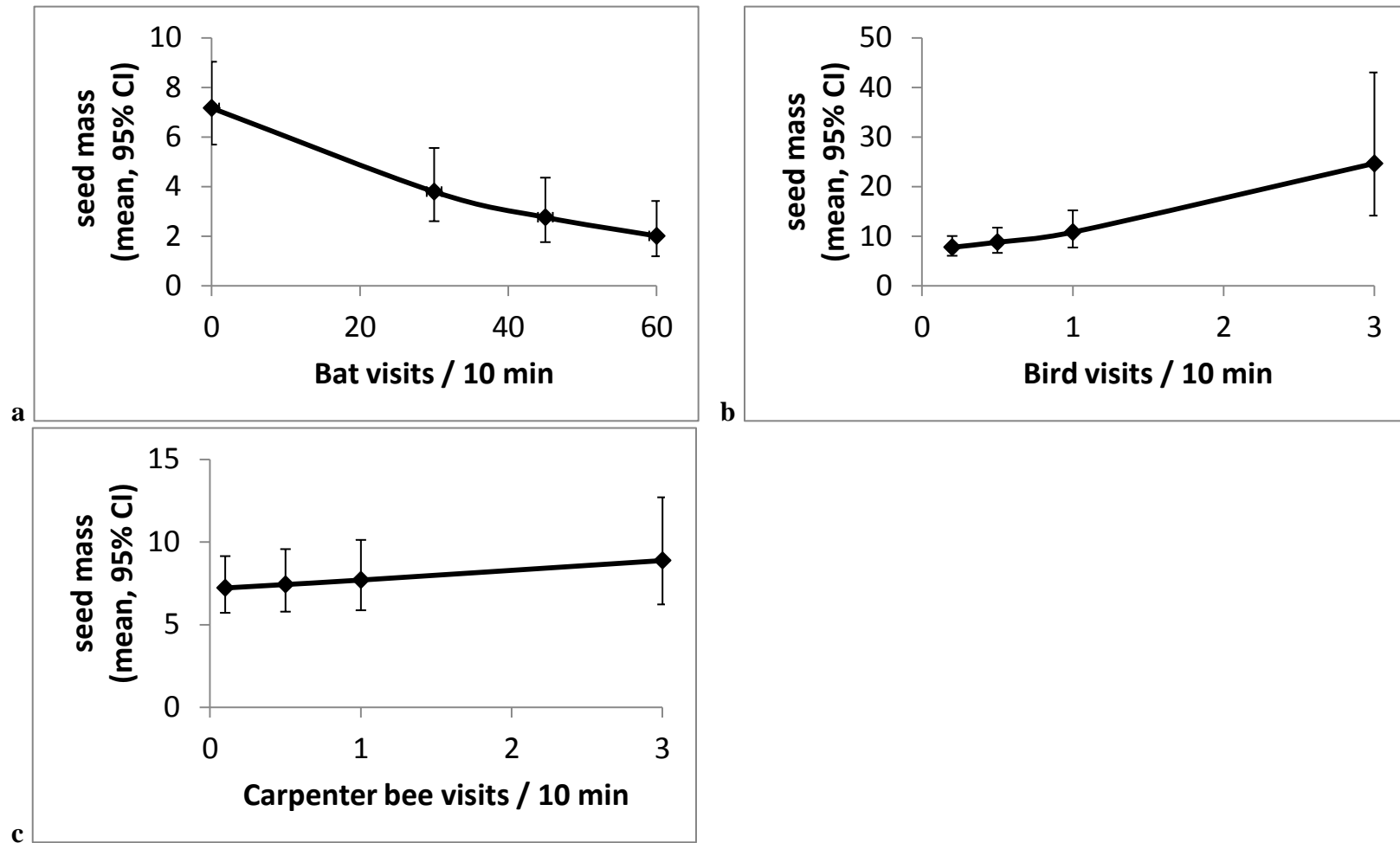
Fig. 7. Number of caterpillars and weevils per fruit during early (E), intermediate (I), and late (L) summer trips to Sites A, B, and C.
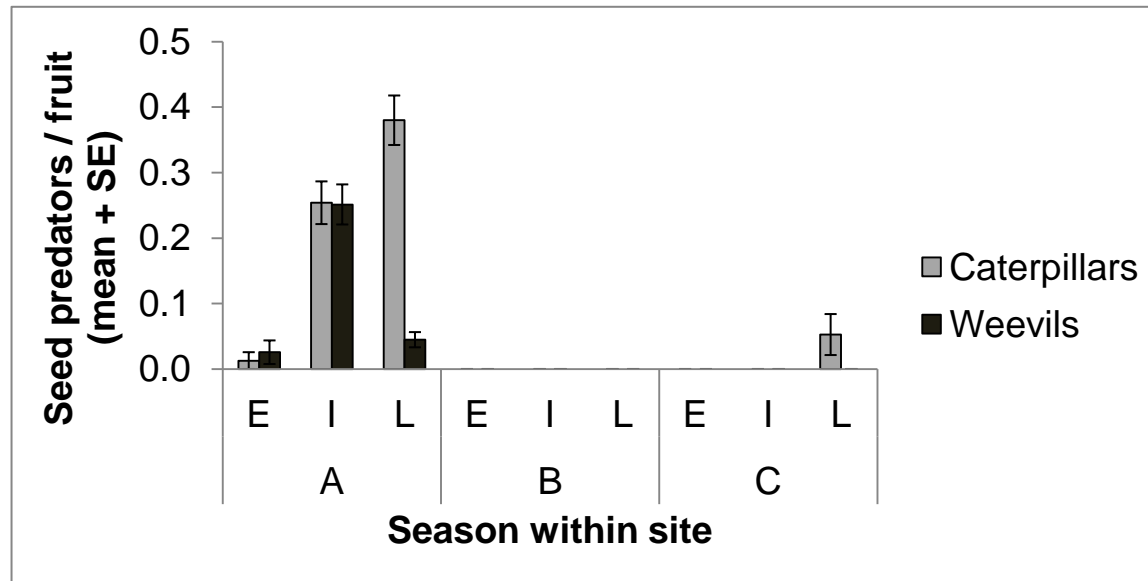
APPENDIX 1. Candidate models assessing factors influencing the log number of flowers per branch ($N = 442$ branches on 163 plants).

i	Morphology		Phenology	
	PC1 Plant Size	**PC2 Display Shape**	**Branch Position**	**Branch Position^2**
0				
1	Size	Shape	Position	Position^2
2	Size		Position	Position^2
3			Position	Position^2

APPENDIX 2. Candidate models assessing factors influencing the log number of ovules per fruit ($N = 206$ closed fruits from 97 branches on 57 plants).

	Morphology		Phenology	
	PC1 Plant Size	PC2 Display Shape	Branch Position	Branch Position^2
i				
0				
1	Size	Shape		
2	Size			
3	Size	Shape	Position	
4	Size		Position	
5			Position	
6	Size	Shape	Position	Position^2
7	Size		Position	Position^2
8			Position	Position^2

APPENDIX 3. Candidate models assessing plant factors influencing site-specific seasonal log percent fruit set per branch ($N = 442$ branches on 163 plants), log percent seed set per fruit ($N = 203$ closed fruits from 95 branches on 57 plants), and log mean seed mass ($N = 834$ closed fruits from 193 branches on 99 plants).

i	Morphology PC1 Plant Size	Morphology PC2 Display Shape	Phenology Branch Position	Phenology Branch Position^2	Resource depletion Prior Fruit Set	Resource depletion Position X Prior Fruit Set	Bat Rate	Sphinx Rate	Bird Rate	Carpenter Bee Rate	Bumble Bee Rate	Season (Site)
0												
1	Size	Shape										Season (Site)
2	Size											Season (Site)
3												Season (Site)
4	Size	Shape	Position									Season (Site)
5	Size		Position									Season (Site)
6			Position									Season (Site)
7	Size	Shape	Position	Position^2								Season (Site)
8	Size		Position	Position^2								Season (Site)
9			Position	Position^2								Season (Site)
10	Size	Shape			PriorFS							Season (Site)
11	Size				PriorFS							Season (Site)
12					PriorFS							Season (Site)
13	Size	Shape	Position		PriorFS							Season (Site)
14	Size		Position		PriorFS							Season (Site)
15			Position		PriorFS							Season (Site)
16	Size	Shape	Position	Position^2	PriorFS							Season (Site)
17	Size		Position	Position^2	PriorFS							Season (Site)
18			Position	Position^2	PriorFS							Season (Site)
19	Size	Shape	Position		PriorFS	PositionXPriorFS						Season (Site)
20	Size		Position		PriorFS	PositionXPriorFS						Season (Site)
21			Position		PriorFS	PositionXPriorFS						Season (Site)
22	Size	Shape	Position	Position^2	PriorFS	PositionXPriorFS						Season (Site)
23	Size		Position	Position^2	PriorFS	PositionXPriorFS						Season (Site)
24			Position	Position^2	PriorFS	PositionXPriorFS						Season (Site)

APPENDIX 4. Candidate models to assess the visitation rates most responsible for the log percent fruit set per branch ($N = 442$ branches on 163 plants), log percent seed set per fruit ($N = 203$ closed fruits from 95 branches on 57 plants), and log mean seed mass ($N = 834$ closed fruits from 193 branches on 99 plants).

i	Morphology		Phenology		Resource depletion		Visitation rates during each Season within Site					Season
	PC1 Plant Size	PC2 Display Shape	Branch Position	Branch Position²	Prior FS	Position X PriorFS	Bat Rate	Sphinx Rate	Bird Rate	Carpenter Bee Rate	Bumble Bee Rate	(Site)
0												
1	plant terms from top two Season(Site) models											
2												
3							Bats					
4							Bats					
5								Sphinx				
6								Sphinx				
7									Birds			
8									Birds			
9										Carpenters		
10										Carpenters		
11											Bumbles	
12											Bumbles	
13							Bats	Sphinx				
14							Bats	Sphinx				
15							Bats		Birds			
16							Bats		Birds			
17							Bats			Carpenters		
18							Bats			Carpenters		
19							Bats				Bumbles	
20							Bats				Bumbles	
21								Sphinx	Birds			
22								Sphinx	Birds			

(continued on next page)

APPENDIX 4, continued.

i	Morphology		Phenology		Resource depletion		Visitation rates during each Season within Site					
	PC1 Plant Size	PC2 Display Shape	Branch Position	Branch Position^2	Prior FS	Position X PriorFS	Bat Rate	Sphinx Rate	Bird Rate	Carpenter Bee Rate	Bumble Bee Rate	Season (Site)
23	*plant terms from top two Season(Site) models*							Sphinx		Carpenters		
24								Sphinx		Carpenters		
25								Sphinx			Bumbles	
26								Sphinx			Bumbles	
27									Birds	Carpenters		
28									Birds	Carpenters		
29									Birds		Bumbles	
30									Birds		Bumbles	
31							Bats	Sphinx	Birds			
32							Bats	Sphinx	Birds			
33							Bats	Sphinx		Carpenters		
34							Bats	Sphinx		Carpenters		
35							Bats	Sphinx			Bumbles	
36							Bats	Sphinx			Bumbles	
37							Bats		Birds	Carpenters		
38							Bats		Birds	Carpenters		
39							Bats		Birds		Bumbles	
40							Bats		Birds		Bumbles	
41							Bats			Carpenters	Bumbles	
42							Bats			Carpenters	Bumbles	
43								Sphinx	Birds	Carpenters		
44								Sphinx	Birds	Carpenters		
45								Sphinx	Birds		Bumbles	
46								Sphinx	Birds		Bumbles	
47									Birds	Carpenters	Bumbles	
48									Birds	Carpenters	Bumbles	

APPENDIX 5. Candidate models assessing factors influencing the log number of caterpillars per fruit, and the log number of weevils per fruit (both $N = 1131$ closed fruits from 209 branches on 105 plants).

i	Morphology PC1 Plant Size	Morphology PC2 Display Shape	Phenology Branch Position	Phenology Branch Position^2	Food availability Seed Count	Food availability Total Seed Mass	Food availability Fruit Volume
0							
1	Size	Shape					
2	Size						
3	Size	Shape	Position	Position^2			
4	Size		Position	Position^2			
5			Position	Position^2			
6	Size	Shape			Seeds		
7	Size				Seeds		
8					Seeds		
9	Size	Shape	Position	Position^2	Seeds		
10	Size		Position	Position^2	Seeds		
11			Position	Position^2	Seeds		
12	Size	Shape				Mass	
13	Size					Mass	
14						Mass	
15	Size	Shape	Position	Position^2		Mass	
16	Size		Position	Position^2		Mass	
17			Position	Position^2		Mass	
18	Size	Shape					Volume
19	Size						Volume
20							Volume
21	Size	Shape	Position	Position^2			Volume
22	Size		Position	Position^2			Volume
23			Position	Position^2			Volume

CHAPTER 5 - CONCLUSION

The research described in Chapter 1 was an attempt to discern how *L. nivalis* utilize the landscape in relation to the distribution of *Agave havardiana* in Big Bend National Park, Texas. I found that although the landscape use of *Leptonycteris nivalis* is centered on habitat with high concentrations of blooming *Agave havardiana*, it is not restricted to those areas, and furthermore adults and juveniles may differ in their behavior. Adult females may remain near food sources in order to replenish energy stores lost to migration and the demands of reproduction, whereas juveniles may feed early in the evening and then undertake occasional far-reaching expeditions, perhaps in order to create a navigational map. If this behavior is widespread among juveniles, it emphasizes the need to carefully assess the risk of constructing wind-turbine energy facilities not just within agave-rich habitat, but anywhere near the range of this endangered bat species.

The research described in Chapter 2 focused on documenting the importance of flowering agaves as a food resource for the many vertebrate and invertebrate, diurnal and nocturnal visitors. I found that *A. palmeri* was visited by a wide variety of vertebrate and invertebrate visitors, many of which are pollinators of other plants, and that there was considerable variation in visitation rates in space and time – in fact, bats were not even observed at one of the study sites. Increased visitation was associated with larger plant sizes for all visitor types assessed.

In Chapter 3, I explored how the fruit and seed production of *A. palmeri* at these three sites were affected by the plants' morphology, phenology (timing of bloom), prior reproductive success, and the patterns of visitation by different animal guilds. Models

indicated that bats were the most effective visitors, because periods with high bat

visitation rates also had very high seed. Periods with high bird visitation resulted in

many fruits but with poor seed set, possibly indicating that they are responsible for some

degree of reproduction, though the exact mechanism is not clear. Floral branch position

interacted in a complex manner with prior fruit set, affecting fruit set, seed set, and mean

seed mass. Plants with high prior fruit set showed decreased seed set in fruits on late-

blooming branches, possibly indicative of resource limitation.

The difficulty of working in rugged, remote areas near the U.S.-Mexico border

has intensified in the past decade due to political unrest in the region (U.S. Fish and

Wildlife Service, 2007). Negotiating the traditional maze of federal, state, and private

owners and managers and associated grazing leases has been increasingly complicated by

the necessity to coordinate research activities with the U.S. Border Patrol in order to

ensure safety of researchers. Several federally managed sites, including several

important *L. yerbabuenae* roost caves, have been closed to all biological research and

monitoring activities because researchers have been fired upon (U.S. Fish and Wildlife

Service, 2007). On both sides of the border, illegal activity and associated surveillance

and law enforcement have resulted in habitat damage from foot and off-road vehicle

traffic and the creation of new roads (U.S. Fish and Wildlife Service 2007). The research

presented here is likely the last of its kind that will take place until the political climate

improves dramatically. This is especially troubling, given the model projections for

climate change predicted throughout the next century, the slow reproductive rate of

agaves which limits how quickly populations can evolve in the face of habitat change,

and the keystone interdependence of the bats upon the agaves for their sole known food

source for much of the summer, and the dependence of the agaves upon the bats for gene flow between isolated populations, and seed set in general.

Literature Cited

U.S. Fish and Wildlife Service. 2007. Lesser long-nosed bat 5-year review: summary and evaluation. Arizona Ecological Services Field Office, U.S. Fish and Wildlife Service, Tucson, Arizona, USA.