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POPULATION TRENDS AND FORAGING BEHAVIOR OF MEXICAN LONG-NOSED BATS (*LEPTONYCTERIS NIVALIS*) IN EMORY CAVE



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I. Project Summary

The Mexican long-nosed bat (MLNB), *Leptonycteris nivalis,* is recognized as endangered by the State of Texas, the United States Fish and Wildlife Service, Mexico and the IUCN (U.S. Fish and Wildlife Service 1994, 2018, 2024a, 2024b). This migratory, nectarivorous species occurs throughout much of Mexico, and a single colony occurs in Texas during the summer months when *Agave havardiana* (their primary nectar source) are blooming in the Chisos Mountains (Kuban 1989). This colony roosts in Mount Emory Cave, in Big Bend National Park (BBNP). Because this migratory species feeds on nectar and specifically is reliant on *Agave* nectar in Texas at the northern extent of its range, conservation efforts are underway to restore agave to the landscape. However, the foraging areas and foraging behaviors have not been identified. The importance is underscored by the fact that the Species Status Assessment completed in 2018 (U.S. Fish and Wildlife Service 2018) identified the main stressors to the MLNB to be loss of food resources and loss of suitable roost sites. Further, these authors identified the main research needs to be focused on the life history of MLNB and specifically the use of foraging grounds and alternate roosts.

To fill some of the knowledge gaps for this species, we used GPS tags on MLNB to identify and characterize foraging areas, foraging behavior, and to reveal alternate roost locations in the area. Understanding how these bats are using the rugged landscape has been difficult to learn by traditional radiotracking because of the difficulty moving through the terrain. Lotek PinPoint VHF transmitters used in this study were able to be remotely downloaded as bats entered or exited the cave. Tags were temporarily glued to 21 bats over 3 weeks. These data revealed their foraging behavior, allowed us to characterize their core use areas, and led to identification of alternate roosts – information that we have not been able to gather before. Bats generally foraged within 8 km of the roost with a few individuals making long distance movements. Overall, MLNB foraged at high elevations in areas with steep slopes, low vegetation height, and a northwest facing aspect. Bats generally foraged within 8 km of the roost although there were a few individuals that exhibited nightly flights more than 100 km from the cave. Adults were found to be significantly more active in the last week of the project compared to the first two weeks. Juveniles exhibited significantly larger home ranges in the last week of tracking compared to the earlier weeks. There were no statistical differences between adults and juveniles in the size of core ranges, their time active each night, and the mean distance flown each night. Remarkably, the longest distance flown by a MLNB in a single night was 295 km. The work associated with this portion of the project is currently being finalized as the thesis of Flor Calderon at Angelo State University for the Master of Science in Biology.

An additional focus of this study was to determine population trends. An accurate roost census is critical to monitoring fluctuations in the colony and understanding, and ultimately protecting, the population of *L. nivalis* in BBNP (U.S. Fish and Wildlife Service 2018). However, their migratory nature makes estimation of the population size very challenging. At the roost site in the Chisos Mountains, emergence censuses were first conducted in 2005 (Ammerman et al. 2009) using thermal imaging video recordings and the cave has censused annually in summer since 2008. To contribute to the understanding of the population trends in this species, we analyzed these long-term census data from the past 18 years to determine population trends at this roost site. These census data were uploaded to the North American Bat Monitoring Program (NABat), which is a continent-wide program to monitor bats at local and

range wide scales to provide reliable, publicly available data to inform resource management decisions and recovery plans (Loeb et al. 2015).

Therefore, in this project, contracted deliverables were met and three large knowledge gaps were addressed:

1. We determined foraging behavior of MLNB roosting at Emory Cave in summer (location, distances traveled, habitat characteristics, and behavior of adults and juveniles)
2. We discovered an alternate day roost location in northern Mexico.
3. We found that despite large annual fluctuations in colony size at Emory Cave (range 294 to 3360 bats), MLNB used this roost each year and there were no significant declines across 16 years.

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II. Overview of Findings

Our first objective was to characterize foraging areas and foraging behavior for Mexican Long-nosed Bats roosting at Emory Cave in summer. Identifying foraging habitat and movement behavior is essential for understanding the ecology of species and guiding conservation strategies. This study focused on *Leptonycteris nivalis* (Mexican long-nosed bat, MLNB), a migratory and nectarivorous bat listed as federally endangered. The population at Emory Cave relies on *Agave havardiana* as a food source in BBNP, Texas, where the only known maternity roost exists in the United States. In summer 2024, we used GPS tracking to identify core foraging areas of 12 adults and 9 juveniles over a three-week period. Foraging areas were observed within the Chisos Mountains and primarily within 8 km of the roost. Sizes of core ranges for MLNB were estimated using 65% local convex hulls which averaged 42.3 ± 94.2 ha for adults and 12.7 ± 15.7 ha for juveniles; however, we found no significant difference in core range size between age groups ($P = 0.94$). Bats generally foraged in high elevation areas with a mean of 1823.4 ± 306.2 m, slope steepness with a mean of 34.3° ± 18.8°, and vegetation height of 1.58 ± 2.41 m. Bats showed a significant preference ($P < 0.001$) for northwest-facing aspects, particularly within a range of 315°– 345°. Bats spent an average of 6.6 ± 1.1 hours active per night, but there was no difference in average nightly active time between age groups ($P = 0.98$). Adults, however, spent significantly more time active per night in the third week ($P = 0.011$). Overall, the mean nightly distance flown was 32.8 ± 26.4 km with no difference ($P = 0.07$) in the distance traveled among age groups or weeks. Additionally, 2 bats spent a day in the Sierra del Carmen Mountains in Coahuila, Mexico, suggesting the use of undiscovered roosts. Maximum flight distances over 295 km and speeds of 84 km/h were recorded, highlighting the high mobility of this migratory species. Understanding how MLNB use the landscape during summer months at this site is crucial for directing land management and agave restoration efforts.

Our second objective was to evaluate population trends for MLNB and contribute long-term census data to the North American Bat Monitoring Program. We consolidated, compiled, and analyzed existing census data for MLNB at Emory Cave collected since 2008 to determine if there were any obvious declines in the number of bats using this roost site in Texas. We used historical thermal video files of nightly emergences of bats from Emory Cave from 2008 to 2023. We manually counted the census videos by slow replay in Research IR Max (FLIR) for those that had not been counted in years past and re-counted video files from 6 nights with discrepancies. The number of bats leaving the cave and entering the cave each minute were recorded separately for MLNB and for the other species in the cave (primarily *Corynorhinus townsendii* and *Myotis thysanodes*). There were no censuses conducted in 2019 or 2020 and in other years censuses were performed between 1 and 6 nights. Most of the videos were recorded in late June or early July when the colony size was expected to be the largest due to the availability of agave, however some censuses were performed in May and August. Nights with technical difficulties with the recordings (battery and/or equipment failures) were not included in this analysis, leaving 35 nights for the analysis of population trends. Colony counts ranged from 5 to 3360 MLNB over all months and years. Analysis of the maximum colony size for each year (14 censuses over 16 years) showed large fluctuations despite being conducted in the first week of July each year. Some of the fluctuations could be due to normal fluctuations in movements of migrating bats resulting in early or late arrival of the bats to this

roost, the number of agave flowering that year to provide a suitable food source near the roost, or environmental conditions (precipitation, wind, moon phase) when the census was conducted. The maximum colony size each year ranged from 294 bats on 3 July 2008 to 3360 bats on 5 July 2021. Based on our results, there was no statistically significant increase or decrease in the colony size at Emory Cave over the 14 years of this study. The mean colony size based on these 14 censuses in July was 2156 MLNB. In addition to manual analyses, we also used a computer-assisted census method called ThruTracker and compared the manual to the automated results. The automated method performed well, with overall 90.8% accuracy (range = 64-99%). These data were published in a Special Issue of *Journal of North American Bat Research* in 2025 (Ammerman et al 2025). After this manuscript was sent for publication, a manual census was conducted in summer of 2024 resulting in a colony size of 1332 bats on 6 July. The combination of these data with all other years resulted in a slight downward trend in population size at Emory Cave that was not significant.

Our third objective was to upload data on foraging behavior and population trends from this project to a public data repository to effectively disseminate these data to state and federal agencies, and conservation organizations. We contributed coordinate data from each of the 21 MLNB tagged at Emory Cave to the public repository called Dryad (https://doi.org/10.5061/dryad.stqjq2cfg). Seven bats (4 adults, 3 volant juveniles) were tagged each week. Tags were programmed to collect location data at intervals of 10 minutes between sunset and sunrise. Data collected from each bat ranged from 2-8 nights and between 37 and 255 total fixes of good quality. A total of 2,652 fixes were collected across all individuals and all weeks. Coordinates within approximately 1km of Emory Peak were removed (approximately 10% of all fixes) to protect the location of this roost site.

We contributed long term census data to the North American Bat Monitoring Program database (NABat). The database is maintained by a partnership among local, state, federal agencies and universities that curate data from acoustic surveys and bat colony counts (https://www.nabatmonitoring.org/). These same data were also uploaded to Dryad (https://doi.org/10.5061/dryad.stqjq2cfg). All colony counts were using the same methods and there were between 2 and 6 colony counts each summer. Video recordings of emerging bats had been collected each year and were used to count the number of MLNB emerging each year. Numbers of non-target species of vespertilionid bats were also reported to NABat.

In addition to contributing the project data to public data repositories (Dryad and NABat), our results on both population trends and foraging behavior were presented to several scientific conferences by Ammerman and Calderón. For example, results were presented at the North American Symposium on Bat Research in October 2023 and 2024, at the Western Bat Working Group meeting in April 2025, and at the Texas Society of Mammalogists meeting in 2024 and 2025.

Management implications and future research needs:

Based on our findings, one management implication of this work involves continued monitoring of Emory Cave using established methods to best track annual trends. Our long-term approach was able to establish that there were major fluctuations in colony size from year to year. Therefore, it is important to maintain monitoring into the future to be able to distinguish between normal fluctuations and real population declines. In addition, the movement and foraging data suggest that directed conservation efforts designed to increase agave resources would be most successful if they were located within 8 km of the cave in areas

at elevations near 1800 m, with steep slopes (between 16 – 52°), low vegetation height (less than 4 m), and a northwest facing aspect. However, because our study took place in late-June through mid-July, there could be seasonal shifts in core use areas at the end of the summer. Therefore, we recommend that when selecting sites for planting agave, some variation in characteristics is encouraged until additional data become available on the shifting needs of MLNB. Additionally, we suggest that future research on the energetic requirements of MLNB in the summer is needed to better address the relationship between numbers of *A. havardiana* and colony size at Emory Cave. We recommend that future research track movement of individuals across the entire summer (when MLNB are present at Emory Cave) and program shorter intervals between fixes to get more information on microhabitat usage. Although our use of a 10 min interval helped to preserve battery life, it limited our ability to discern foraging and roosting behaviors in this highly-mobile species. An additional exciting data gap that arose from this project is the extent to which the newly-discovered alternate roost is used and what role it plays in migration (if any). Investigation and characterization of this roost is needed.

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III. Landscape movements and characteristics of core use areas

The Mexican long-nosed bat, *Leptonycteris nivalis* (Saussure 1860), is a migratory, nectarivorous species that plays a critical role as a pollinator in the ecosystems it inhabits. Listed as endangered by Texas, the United States, Mexico, and the IUCN (USFWS 1994, 2018), this bat species relies heavily on landscapes around key roosting sites for its survival. Only one colony is known to exist in Texas, located at Emory Cave in the Chisos Mountains of Big Bend National Park (BBNP), where it gathers each summer from May to August (Ammerman et al. 2025). This site supports the only known maternity roost for *L. nivalis* in the United States, primarily sheltering lactating females and their volant young. Adult males are rarely captured and generally are not known to migrate as far north as Texas (USFWS 2018). Understanding the movement ecology and foraging behaviors around this cave is crucial for making informed conservation actions to protect this endangered species.

Leptonycteris and *Agave* species have a coevolutionary mutualistic relationship (Gentry 2004; Good-Avila et al. 2006; Rocha et al. 2006). Across the species' range (Fig. 1), *L. nivalis* is estimated to use 49 plant species in its diet, including 27 species within the genus *Agave* as summarized by the USFWS (2018). However, the primary food source for *L. nivalis* in the Big Bend region is *Agave havardiana* (Kuban 1989). As with many other species of Agave, this species is semelparous, flowering once at the end of their life and producing towering inflorescences that serve as critical nectar resources for migrating nectar-feeding bats. In arid and semi-arid landscapes, such plants provide predictable and energetically-rich rewards that influence migration timing and roost site selection in nectar-feeding bats (Fleming et al. 1993, 2009).

This close ecological relationship has driven both morphological and behavioral adaptations in *Leptonycteris*, including long tongues and maneuverable flight that allow them to exploit deep tubular flowers efficiently (Nassar et al. 1997). In return, these bats are highly effective pollinators (Arizaga et al. 2000), especially over long distances, contributing to gene flow between agave populations. The long-distance pollen dispersal performed by these bats helps maintain genetic diversity and population connectivity in agaves, which is vital in fragmented or topographically complex landscapes such as the Chihuahuan Desert.
A nectar corridor, in the case of *L. nivalis,* is considered to be a series of blooming agaves that sustain the bats along their migratory path (Fleming et al. 1993; Moreno-Valdez et al. 2000) and identification and monitoring has become an important approach for conserving this mutualism. Nectar corridors are particularly important in northern Mexico and the southwestern United States, where human development and land-use change have led to agave population declines and fragmentation of suitable foraging habitat (Ammerman et al. 2012; Gómez-Ruiz et al. 2021). Loss of agave due to overharvesting, grazing, fire suppression, and invasive species reduces the availability of nectar during key migration periods (USFWS 2018). In the absence of reliable nectar sources along these corridors, bats may be forced to abandon routes, shift their range, or suffer population-level consequences due to energy deficits. Ensuring the integrity of nectar corridors is therefore essential to the long-term survival of migratory bat species that rely on nectar, such as *L. nivalis*.



Figure 1. *Leptonycteris nivalis* species range map

Agave restoration has become a method of conservation management for *L. nivalis* (Lear et al. 2024). The objective of this approach is to restore nectar corridors by planting native agaves in regions where their populations have declined or where natural recruitment is limited. However, the success of such efforts depends on understanding where bats forage and which landscapes provide the highest foraging value. This requires fine-scale data on foraging behavior and landscape suitability across multiple spatial and temporal scales, which has been addressed to some extent through agave distribution modeling and nectar corridor conservation

(Moreno-Valdez et al. 2000, 2004; Gómez-Ruiz 2015; Gómez-Ruiz and Lacher 2017) as well as observational studies linking bat activity to agave floral patterns (Lear et al. 2024). Without this information, restoration efforts risk missing key foraging zones or failing to align restoration with the ecological needs of the bat species.

The role of agave in supporting bat migration is further complicated by environmental drivers such as elevation, temperature, and precipitation, which influence flowering phenology (Kuban 1989). Kuban documented the flowering phenology of agave in the Chisos Mountains can occur weeks later at higher elevations compared to lower elevation desert scrub, offering a staggered resource that migrating bats can exploit as they move northward. This elevational gradient can potentially sustain nectarivorous bats throughout their summer stay in northern regions, given that agave populations are sufficiently abundant and accessible. However, shifts in climate may disrupt these phenological patterns, creating mismatches between bat arrival times and peak agave blooms (Scott 2004; Buckley and Nabhan 2016; Gómez-Ruiz and Lacher 2019). Agaves are also long-lived and slow to mature, often taking 10–30 years to flower depending on species and environmental conditions (Eguiarte et al. 2000). This lag time presents a significant challenge to restoration, as newly-planted agaves will not immediately support foraging bats. It further highlights the need to protect existing mature agave stands and prioritize restoration in areas already used by foraging bats, ensuring future availability of nectar resources. Understanding fine-scale bat foraging movements is therefore key to selecting optimal planting locations and maintaining the spatial continuity of nectar corridors.

To address these concerns, the U.S. Fish and Wildlife Service developed a recovery plan for *L. nivalis* in 1994, emphasizing the importance of identifying and protecting foraging habitats (USFWS 1994). This plan was later expanded into a more thorough Species Status Assessment report in 2018, providing an updated, comprehensive review of the species (USFWS 2018). Current agave restoration efforts, including those led by Bat Conservation International, focus on preserving these habitats despite limited information on the specific foraging behaviors and spatial requirements of *L. nivalis* (Lear et al. 2024). The Species Recovery Plan emphasizes the urgency of collecting accurate, fine-scale foraging data to better inform agave conservation and management strategies (USFWS 1994).

Although the movements of *L. nivalis* are not well understood, they are generally thought to follow available nectar sources, primarily agave blooms (Moreno-Valdez et al. 2000, 2004; Gómez-Ruiz and Lacher 2017; Burke et al. 2019), and most likely use stopover roosts during migratory movements. While previous studies using radio telemetry have provided valuable insights into the general foraging patterns of *L. nivalis*, these studies lack the fine-scale resolution necessary to pinpoint precise foraging areas (England 2012; Bogan et al. 2017). In 2003, England (2012) radio-tracked *L. nivalis* in BBNP and found that bats commuted up to 30 km per night, and adult home ranges were estimated to have twice as much *A. havardiana* habitat than juveniles. In New Mexico, Bogan et al. (2017) noted similar commuting distances of 30 km to alternate roosts. Despite the valuable information resulting from these studies, inferences on the foraging habitat of *L. nivalis* are still primarily based on niche modeling of habitat suitability of plant species included in their diet (Gómez-Ruiz and Lacher 2017; Burke et al. 2019). A comprehensive understanding of fine-scale foraging patterns is needed to distinguish core foraging areas from potential ones, thereby providing guidance for targeted agave restoration.

This study sought to address these knowledge gaps by using high-resolution GPS tracking to capture the foraging movements of both adult and juvenile (young of the year) *L. nivalis* in the Chisos Mountains region. We hypothesized that both adult and juvenile bats would forage in the Chisos Basin mountain range and its surrounding areas, particularly where *A. havardiana* is historically abundant. Additionally, based on prior telemetry research (England 2012), we expected that juvenile home ranges would be larger than adults, likely due to exploratory behavior of juveniles. Therefore, we hypothesized that there would be significant differences in juveniles and adult behavior regarding home and core range size, duration of activity each night, and the distance flown each night.

METHODS

Study site

Field work occurred in BBNP, Brewster County, Texas. The national park is in the Trans-Pecos region of Texas, which is a part of the greater Chihuahuan Desert Ecoregion. Bats were captured at Emory Cave, the northern-most roost for *L. nivalis*, located at a high elevation (approximately 2160 m) in pine-oak juniper association of the Chisos Mountains (Easterla 1972). This cave was documented to house *L nivalis* in 1937 (Borell and Bryant 1942) but long-term monitoring was not initiated until 2005 (Ammerman et al. 2009, 2025). Through extensive mapping efforts, cavers concluded that there was only one main entrance to this fault cave (Veni 2016). Therefore, bat captures were focused outside the main entrance of the cave. Opportunistic ground truthing of points of interest revealed from GPS tracking data also occurred within the park boundaries. However, not all locations were accessible by trail and were either too distant or located in hazardous terrain (e.g. steep cliffs), which made on-foot observation impractical.

Capture and tagging techniques

Our research team captured *L. nivalis* at Emory Cave and attached GPS tags (n=21) throughout the summer of 2024. There were three consecutive weeks in which a crew captured and tagged bats in the first day of the week (Sunday) and then focused on GPS data retrieval and ground-truthing points of interest during the remaining days. Fieldwork occurred from 22 June to 18 July, during the peak of *L. nivalis* occupancy at Emory Cave (Ammerman et al. 2009, 2025; Adams 2015).

All bats were captured using a harp trap positioned adjacent to the main cave entrance (Fig. 2). Personnel included 5 or 6 individuals each night divided into a capture team at the cave entrance and a processing team approximately 30 m away from the cave. Permit restrictions allowed no more than 50 *L. nivalis* to be captured in a night. Therefore, to avoid over-capturing *L. nivalis* and to stay within the one-hour handling time limit, the harp trap was periodically closed by placing a cloth sheet over the trap lines to block the capture of bats.

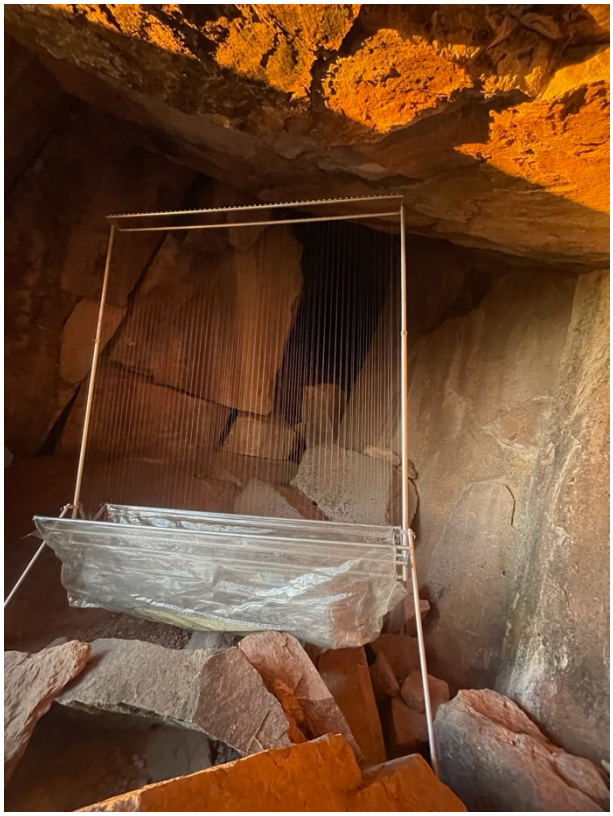


Figure 2. Harp trap set up outside Emory Cave, Chisos Mountains, Big Bend National Park, TX.

Although the impacts of tags on the behavior and body condition of bats are not well studied (Meierhofer et al. 2024), a study that monitored the effects of tag mass on bat species with a mass similar to *L. nivalis* (25–30 g) proposed that it was acceptable to attach tags weighing 5–10% of the body weight for short-term studies (Kelling et al. 2024). O'Mara et al. (2014) suggested that tags weighing less than 5% of the body mass of the bat were ideal and should not exceed 10% if the tags were carried for more than a few days. The GPS tags, PinPoint VHF 40 (Lotek Wireless, Inc., Newmarket, Ontario, Canada), weigh approximately 2.4 g. In accordance with permit conditions, the tags could not exceed 8% of the body mass; therefore, only bats weighing over 30 g were tagged. Based on previous work at the cave (Ammerman LK, [Angelo State University, San Angelo TX], personal communication, [01 May 2024]), approximately 36% of captures were expected to fit the weight criteria of 30 g or greater (20% of adults and 16% of juveniles). We successfully met our tagging quota of 7 bats per week (4 adults and 3 juveniles) and did not exceed the regulated annual capture limit of 200 *L. nivalis*, as detailed in our USFWS endangered species permit. Priority for tag attachment was given to the heaviest bats captured. Pregnant bats were not captured. A previous study at Emory Cave from 2014–2015 studied the seasonality and activity of *L. nivalis* by attaching 79 Passive Integrated Transponders (PIT) tags to individual bats (Adams 2015) and an additional

236 PIT tags were attached in 2017 and 2018 (Ammerman LK, [Angelo State University, San Angelo TX], personal communication, [06 June 2025]), totaling 315 PIT tags deployed prior to this study. The lifespan of this species is unknown; therefore, if time permitted, *L. nivalis* were scanned for PIT tags after capture (approximately 40 bats regardless of age) using a handheld reader (Biomark 601, Biomark, Boise, Idaho) to document any recaptures.

After bats were weighed, they were processed, and tags were attached following general transmitter attachment guidelines (Amelon et al. 2009). Information such as weight, sex, age, forearm length, reproductive status, and general health remarks (ectoparasites, wing injuries, etc.) were recorded. *Leptonycteris nivalis* were considered juveniles based on the gray pelage color and the presence of an epiphyseal gap in the metacarpophalangeal joint when transilluminated; adults were yellowish in coloration and no epiphyseal gap was present and, likely had large, bare lactating or early post-lactating nipples. Given the time of year (early-summer), all juveniles were volant and considered to be the young-of-the-year. If a bat had coloration of a juvenile but a thin or no epiphyseal gap (a "sub-adult") then that bat was considered a juvenile for this study.

GPS tag settings were pre-programmed using PinPoint Host software (Lotek Wireless Inc., Ver. 2.15.20.0) to take latitude-longitude coordinates every 10 min from sunset to sunrise, with an estimated battery lifespan of 3–9 days according to software estimates. The tags were activated just before attachment and tested to ensure they were operational. To attach the GPS tag, each bat had its hair clipped using scissors and/or an electric clipper, then was cleaned with alcohol. GLUture (Zoetis, Inc., Kalamazoo, Michigan), a topical tissue adhesive made of a cyanoacrylate blend, was used to adhere the tag directly to the skin surface on the back between the shoulder blades (Fig. 3). Total handling time for tag attachment averaged 10 min. After the glue dried for a minimum of 2 min, bats were offered a 25% sugar-water solution before release using a disposable pipette. The estimated process from capture to release took approximately 20–25 min. If more than 45 min had passed since their capture and the tagging process had not begun, the bats were released without tag attachment. The bat capture and handling protocols in this study aligned with the guidelines provided by the American Society of Mammalogists (Sikes et al. 2016) and were approved by both the National Park Service and the Angelo State University Institutional Animal Care and Use Committees (#23-202). White nose syndrome decontamination protocols were followed as outlined by the White-nose syndrome disease management working group (www.WhiteNoseSyndrome.org).

Data retrieval

The field crew remotely retrieved GPS data from the tagged bats in flight. The tags transmitted data via VHF (very high frequency) telemetry to the tags' proprietary receiver, PinPoint VHF Commander (Lotek Wireless, Inc., Newmarket, Ontario, Canada). One stationary receiver with an omni-directional antenna (Wildlife Materials, Inc., Murphysboro, IL, USA) was placed outside the cave entrance from 23 June to 18 July 2024. The stationary receiver was programmed to download data for two hours after sunset and again for two hours before sunrise (generally between 0400 to 0600 h), based on the times most likely to detect bats emerging or returning to the roost (Ammerman et al. 2009; Adams 2015). The stationary receiver was secured in a weatherproof case with the omni-directional antenna on top. The case and antenna were secured to a flat surface between boulders with the best positioning to capture

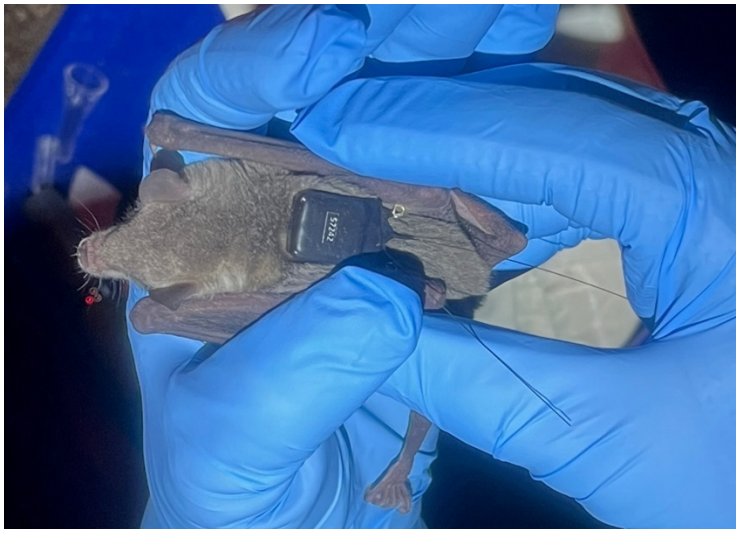


Figure 3. Lotek PinPoint VHF 40 GPS tag attached to juvenile *Leptonycteris nivalis.*

the tag signal as bats enter and exit the cave. The cord to the antenna was inside of a rodent-protective sleeve. The second receiver was carried by team members who hiked within 300 m of the cave and retrieved data using a 5-element Yagi (directional) antenna attached to a 3 m tall telescoping pole for 2 h after sunset. Data from the stationary antenna was downloaded, and batteries were replaced twice a week.

All raw data were uploaded and backed up to a hard drive daily. GPS points collected from tagged bats were uploaded into ArcGIS Pro (ESRI, 2024), where point symbology was modified to visualize intensity of use using a heat map renderer. This allowed for the identification of spatial clusters indicating high-use areas occupied by either single or multiple bats, likely representing potential foraging zones. These focal points were then prioritized for field validation and were noted for presence or absence of blooming *Agave* to confirm that there were foraging resources in the immediate area (generally within 100 m).

The Lotek PinPoint GPS tags recorded location data via satellite "pings" (the moment when a GPS receiver successfully determines its position using satellite signals). Following retrieval, raw data were downloaded and converted into geographic coordinates (longitude, latitude, and altitude) using Lotek PinPoint Host software (version 2.15.20.0; Lotek Wireless Inc.), which required manual input of the deployment location, including geographic coordinates and elevation. All GPS data were recorded in the WGS 84 coordinate system. Altitude values (z-values) provided by the software represented height above the ellipsoid. As vertical movement was not the focus of this study, no transformation to height above ground surface was performed.

Data analysis

GPS data processing–GPS data were consolidated for each tag from both the stationary receiver (omni-directional antenna) and the mobile receiver (5-element Yagi antenna) using Microsoft Excel 365 (Microsoft Corporation 2024). In most cases, both receivers recorded

overlapping data, though occasional location fixes were captured by only one unit. Two GPS points that were clearly erroneous (e.g., extreme outliers with biologically implausible coordinates) were removed prior to analysis.

Subsequently, all time stamps that lacked associated GPS coordinates were excluded, as these likely represented intervals when the bat was not within satellite reception. The remaining dataset was filtered to include only GPS locations with a horizontal dilution of precision (HDOP) value ≤ 20, following recommendations from the tag manufacturer (Lotek Wireless Inc.). HDOP is a measure of satellite geometry and positional accuracy, with lower values indicating greater precision; values >20 can result in location errors exceeding 300 m and are considered unreliable for spatial analysis.

Home and core range estimation–Tracking the movement of individual *L. nivalis* near Emory Cave was essential for identifying home and core ranges, and their associated landscape characteristics. Understanding the size and location of their home and core ranges could guide management and conservation efforts. For both home and core range estimations, all nightly GPS points with HDOP ≤ 20 were included, except for 2 nights during which individuals traveled more than 100 km from the cave, which were excluded to avoid including atypical long-distance excursions in range calculations. To estimate both home and core range of all tagged bats, three methods were compared: minimum convex polygon (MCP; Mohr 1947), kernel density estimation (KDE; Worton 1989), and fixed k local convex hull (LoCoH; Getz et al. 2007). Each method offered unique benefits. MCP, despite being less precise, is widely used and allows for simple comparisons with past and future studies, particularly for coarse data sets where temporal data are limited (Burgman and Fox 2003). KDE provides an accessible estimate of spatial density by clustering GPS points, offering a more detailed picture of habitat use than MCP (Seidel et al. 2018). The LoCoH method uses a polygon method like MCP but arguably is more accurate because it requires a large sample size of GPS points, ensuring a balance between capturing detailed movement patterns and avoiding over-fragmentation in the resulting range estimations (Getz et al. 2007). To calculate k-LoCoH, we used $k = 10$ ($k - 1$ nearest neighbor) which was calculated by taking the average of the square root of the number of GPS points for each individual bat.

Home and core ranges were calculated using the *adehabitatHR* package in R (Calenge 2006), which provides tools for estimating MCPs, KDEs, and LoCoH models. For all three methods, 100, 95, and 90 percent ranges were calculated as home range, while 65 and 50 percent were calculated as core ranges. All three models were visualized side-by-side for comparison following Seidel et al. (2018) and overlayed to actual GPS points. A one-way analysis of variance (ANOVA) was conducted to evaluate differences in range size estimates generated by MCP, KDE, LoCoH methods at 90% and 65% isopleths. Range estimates were log-transformed prior to analysis to meet assumptions of normality and homogeneity of variances.

LoCoH were selected for subsequent analyses because they provided the most conservative and spatially restricted estimates of both home range (90% isopleth) and core use area (65% isopleth). LoCoH also provided a more ecologically meaningful estimate of home range by preserving sharp edges, handling outliers better, and avoiding overestimation issues seen in MCP and KDE (Getz et al. 2007). Following standard practices in home range analysis, we defined the home range using the 90% isopleth and the core range using the 65% isopleth of the k-LoCoH utilization distribution, as these thresholds effectively balance the inclusion of

significant activity areas while minimizing the influence of outliers (Walter et al. 2015; Getz et al. 2007). Additionally, an ANOVA was performed to determine any significant differences between 100%, 95%, and 90% LoCoH home range estimations.

Home and core ranges were compared among individuals across survey weeks and between adults and juveniles. An ANOVA was conducted to assess differences in 90% and 65% local convex hull range sizes between juvenile and adult bats throughout the entire study period and across each of the three weeks within the study period. Home range size was log-transformed to meet normality assumptions, which were verified using Q-Q plots of residuals and Brown-Forsythe test for homogeneity of variance. All ANOVAs were run in the statistics program R (R Core Team 2024).

Nightly flight distance–To estimate nightly flight distances, the processed GPS dataset was uploaded into ArcGIS Pro, where X,Y coordinates were used to generate movement paths. The Points to Line tool was applied to link sequential GPS fixes for each bat within each night, allowing calculation of linear flight distances in km. For each individual, the nightly distance, average nightly distance, and maximum speeds were recorded. Due to the GPS tags being programmed to record fixes at 10-min intervals, the first and last recorded points of the night often did not align exactly with the emergence from or return to Emory Cave. To account for this gap, additional linear measurements were manually taken from Emory Cave to the first GPS fix of the night and from the final GPS fix back to the cave. This assumption is supported by consistent observations of emergence and return behavior (Ammerman et al. 2025), and by the absence of GPS fixes while inside the cave due to lack of satellite reception in this location. Total nightly flight distance was calculated as the sum of all segment distances for each bat per night, including the manual distances to and from the cave. Maximum speed (km/h) was calculated by dividing each distance segment by the 10-min interval between GPS fixes with the longest distance and scaling to hourly rates. Nights representing incomplete activity (e.g., the night of capture or the final night of tag transmission in which the tag battery died while bat was active), where movement data were truncated, were excluded from average nightly distance calculations, as they did not reflect complete activity.

To assess differences in average nightly distance traveled, a series of ANOVAs were conducted in R software. Specifically, we tested for differences between age groups (adult vs. juvenile), across the three sampling weeks, and among age groups across weeks. Assumptions of normality and homogeneity of variance were evaluated using quantile–quantile (Q–Q) plots of residuals and a Brown-Forsythe Test, respectively.

Duration of nightly activity–To quantify duration of nightly activity for each bat, the processed GPS dataset was used to identify the time between the first and last GPS fixes containing valid coordinates for each night. Thus, nightly activity was defined as the interval between the first coordinate fix of the night (post-emergence) and the last coordinate fix before apparent return to the cave, generally at or close to the cave. Time stamps without associated coordinates during the time between cave entry and cave emergence that overlapped with the tags programmed recording time (sunset to sunrise) were assumed to indicate part of day-roosting periods when the individual was within Emory Cave, where satellite signals could not be received.

Because GPS tags were programmed to collect location data at 10-min intervals from sunset to sunrise, there was a maximum of 60 pings per night (~10 h). The number of potential nightly fixes was adjusted to exclude the period before release on the night of capture, since

GPS data collection began immediately upon tag activation, but tagged bats were not released until processing was complete. Nights when bats returned to the cave immediately after handling, as well as the final night of transmission (presumed battery failure or tag dropped), were excluded from average nightly activity calculations, however if they left the cave area (e.g. >500 m) immediately after release, then data from the first night were included in analyses.

For each individual the average time spent 'active' (generally the time spent outside the roost) per night was calculated using nights that reflected a full foraging bout. This included nights where bats may have roosted in alternate day roosts, as long as consistent GPS data were recorded throughout the night. Differences in nightly activity (in min) were analyzed between age groups (adults vs. juveniles) and across weeks using ANOVAs. In addition, battery life was estimated as the duration from the first recorded ping to the final ping across the lifespan of each tag.

Characteristics of foraging habitat–To accurately describe the foraging habitat of *L. nivalis*, this study assessed environmental characteristics within core ranges, including vegetation communities (TPWD 2023) and terrain features such as elevation, slope, aspect, relative ruggedness, and canopy height. Within BBNP, three distinct vegetation communities were generally distinguished by elevation: desert shrubland below 1600 m, grassland between 1600 m and 1850 m, and forest above 1850 m (Skrzypek et al. 2013). To assess habitat use within these zones, GPS points were overlaid on Light Detection and Ranging (LiDAR) data, which was publicly available through the Texas Geographic Information Office (https://geographic.texas.gov/).

LiDAR data were combined into a continuous surface using the Mosaic to New Raster tool in ArcGIS Pro. From this mosaic, a digital elevation model (DEM) was created to derive terrain characteristics using the Surface and Surface Parameters toolboxes. Slope and aspect were calculated with the Slope and Aspect tools respectively, and topographic ruggedness index (TRI) was generated using the Terrain Ruggedness Index tool to quantify terrain complexity.

Differences in elevation between observed core ranges and available habitat were evaluated by comparing values within each core area to those within a corresponding rectangular minimum bounding geometry (MBG) polygon. Elevation data were obtained from a 30-m resolution DEM, and summary statistics (mean, standard deviation, and range) were calculated using the Zonal Statistics tool in ArcGIS Pro. The number of 30-m raster cells within each zone was used as the sample size. A Welch's two-sample t-test was applied to compare mean elevation values between observed and expected areas, accounting for unequal variances and large sample sizes.

Aspect values of the landscape (expressed in degrees from 0° to 360°) were extracted from DEMs and used to characterize the terrain within core foraging areas of *L. nivalis*. To visually analyze the general landscape, values were reclassified using the Reclassify tool in ArcGIS Pro to distinguish north-facing slopes (0–67.5° and 292.5–360°) from non-north-facing slopes (67.5–292.5°). To visualize the directional distribution of aspect within core areas compared to the rectangular minimum bounding geometry of the landscape surrounding the core foraging area, rose diagrams were generated using the circular package in R software (Agostinelli and Lund 2017). To statistically assess differences in directional use, a Watson–Wheeler (Zar 2010). test for homogeneity of angles, which does not assume normally

distributed data, was performed to compare aspect distributions between the core foraging areas and the available landscape.

To further assess terrain heterogeneity, the Focal Statistics tool was applied to slope and TRI layers using the Variety statistic, which calculated the number of unique neighboring values within the neighborhood of each raster cell. A canopy (vegetation) height model was produced by subtracting the DEM from the first-return digital surface model using the Raster Calculator tool, providing vegetation height above ground level. The CHM was then filtered to exclude values exceeding 15 m, as vegetation taller than this threshold is unlikely to occur in the region. *Pinus cembroides* (pinyon pines) Zuccarini, 1832, one of the tallest native species in the area, typically reaches heights of 10 m according to the United States National Herbarium (1963).

The polygons created by calculating the core ranges (65% LoCoH) for individual bats were combined into a single shapefile using the Dissolve tool in ArcGIS Pro to create a unified representation of all core foraging areas. This layer was then overlaid onto the LiDAR-derived terrain and vegetation rasters. The Zonal Statistics as Table tool was used to extract summary statistics (mean, minimum, maximum, range, and standard deviation) for each environmental variable (elevation, slope, aspect, topographic ruggedness index, and canopy height) within the defined core areas.

Potential undocumented roosts–Locating undocumented roost sites would have significant conservation benefits by identifying alternative shelters that could reduce pressure on the single known roost at Emory Cave in the northeastern extent of their geographic range. A previous PIT tag study indicated gaps in nightly detections at Emory Cave, suggesting the possibility of alternate day roosts nearby (Adams 2015). We visually analyzed nightly movement patterns of each bat to identify the use of potential night roosts and alternative day roosts. If the tagged bats day roosted elsewhere and then returned to Emory Cave on the following nights, then we were able to retrieve alternate roost site coordinates if the tag was still functional because GPS data retrieval was focused only on Emory Cave.

RESULTS

Capture and tagging

A total of 190 bats from 5 species were captured during three capture events over a three-week period in June–July 2024 at Emory Cave (Table 1). We captured 82 *L. nivalis* and 108 bats from 4 non-target species. A total of 21 *L. nivalis* (12 adults, 9 juveniles) were successfully tagged (7 bats per week) during these capture events (Table 2). The mean body mass of bats that were tagged was 31 g (range: 30–35 g), and mean tag weight represented 7.7% of body weight (range: 6.9–8.0%). All adult *L. nivalis* that were captured were females, their reproductive status was either lactating or non-reproductive. Among the 9 juveniles that were tagged, 4 were females and 5 were males, all non-reproductive. No PIT tags from previous studies were detected on any *L. nivalis*. No bat was injured during capture or processing and all were released successfully.

Table 1. Count of species captured by date at Emory Cave, Chisos Mountains, Big Bend National Park, TX. All capture dates took place in summer 2024.

Species	**23-June**	**30-June**	**7-July**	**Total**
Leptonycteris nivalis	8	19	55	82
Corynorhinus townsendii	5	18	30	53
Eptesicus fuscus	0	1	1	2
Myotis ciliolabrum	0	1	11	12
Myotis thysanodes	19	15	7	41
Total	**32**	**54**	**104**	**190**

Data retrieval

Location data were retrieved using both the 5 element Yagi and omni-directional antennas. Most data were collected from the 5 element Yagi antenna because the stationary omni-directional antenna and receiver had technical difficulties the first week. Data from the 5-element Yagi was collected approximately 300 m from the cave but was at times collected at lower elevation in the Chisos Basin parking area approximately 3 km from the cave. This lower elevation method was only used when hiking near the cave was not feasible, and it was not preferred because of the potential of being out of range of some bats. We relied on the stationary omni-directional antenna for the days no one was available to collect data (generally 1-2 days a week) and to collect data in the mornings 2 h before sunrise.

We recorded a total of 2,674 GPS points across all individuals. After removing 2 extreme outliers and all GPS data with a HDOP >20, there were 2,652 GPS locations that were used for analysis (Fig. 4). These coordinate data have been deposited in Dryad (https://doi.org/10.5061/dryad.stqjq2cfg). GPS locations divided by bats captured in each week and sorted by age are displayed for geographic reference (Fig 5-7). Tags recorded locations for a total of 95 nights (75 nights if partial nights are excluded). Tag life ranged from 2-8 nights and at least 1 full night of GPS data was recorded for each tag. There were 6 tags (2 tags in week 1, 3 tags in week 2, and 1 tag in week 3) that only transmitted for 2 nights. The average battery life for the 15 tags that stayed on past 3 days was 4 days, 16 h, and 20 min.

Table 2. Capture data and GPS tag information for *Leptonycteris nivalis* at Emory Cave, Chisos Mountains, Big Bend National Park, TX. Capture dates for week one, two, and three were 23 June 2024, 30 June 2024, and 7 July 2024, respectively.

Week	Tag Number	Weight (g)	Age	Sex	Reproductive Status
1	57222	32.0	Juvenile	Female	Non-reproductive
1	57223	30.0	Juvenile	Female	Non-reproductive
1	57224	30.0	Adult	Female	Lactating
1	57225	30.0	Adult	Female	Non-reproductive
1	57226	31.0	Adult	Female	Lactating
1	57227	30.0	Adult	Female	Non-reproductive
1	57228	30.0	Subadult	Female	Non-reproductive
2	57229	33.3	Juvenile	Male	Non-reproductive
2	57230	31.3	Juvenile	Male	Non-reproductive
2	57231	33.3	Subadult	Male	Non-reproductive
2	57232	31.3	Adult	Female	Lactating
2	57233	30.3	Adult	Female	Lactating
2	57234	30.3	Adult	Female	Lactating
2	57235	31.3	Adult	Female	Lactating
3	57236	31.0	Juvenile	Female	Non-reproductive
3	57237	30.0	Adult	Female	Lactating
3	57238	31.0	Adult	Female	Non-reproductive
3	57239	31.0	Adult	Female	Lactating
3	57240	30.5	Adult	Female	Lactating
3	57241	35.0	Juvenile	Male	Non-reproductive
3	57242	31.0	Juvenile	Male	Non-reproductive

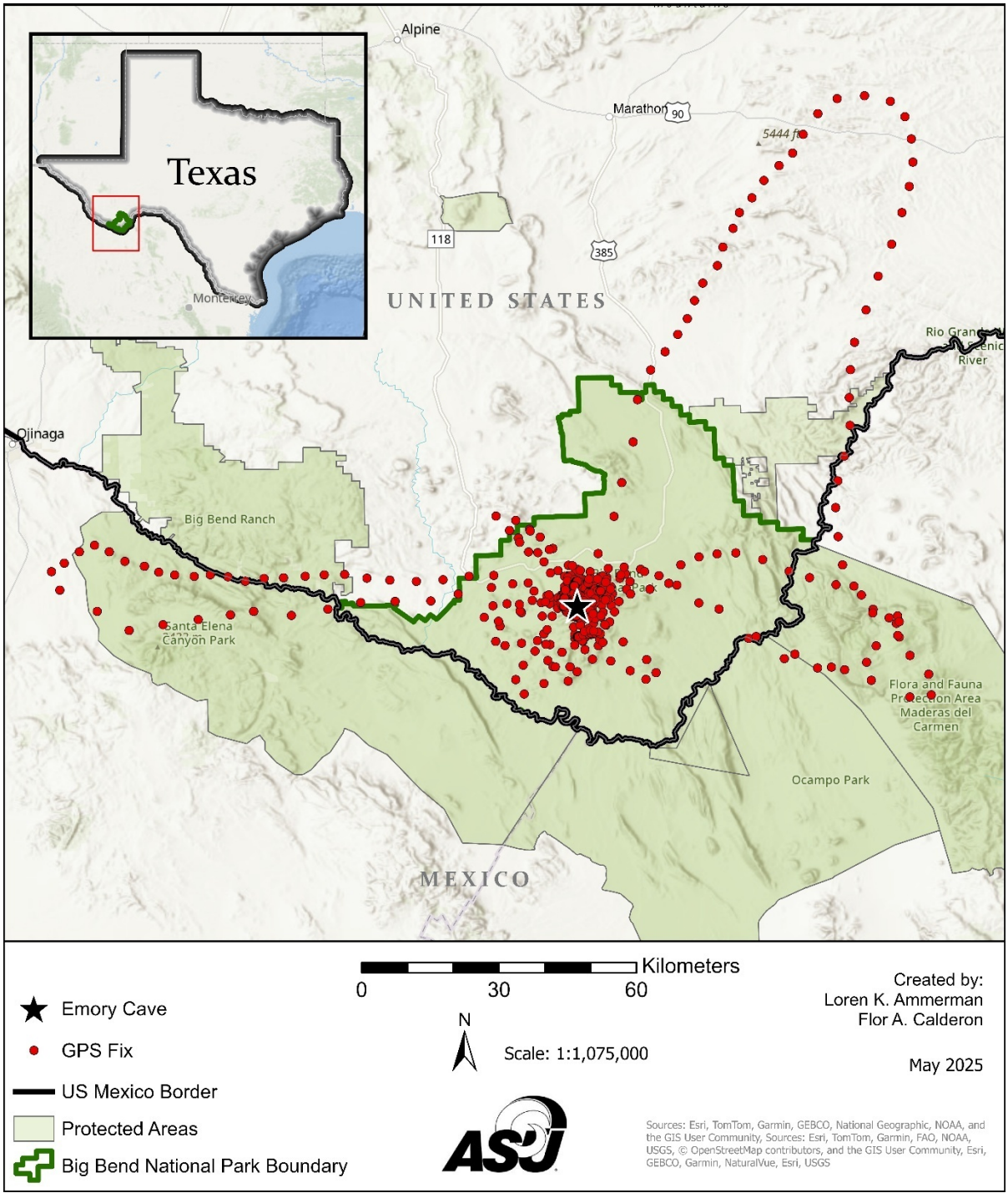


Figure 4. GPS locations (fixes) of all *Leptonycteris nivalis* captured in summer 2024 at Emory Cave, Chisos Mountains, Big Bend National Park, TX.

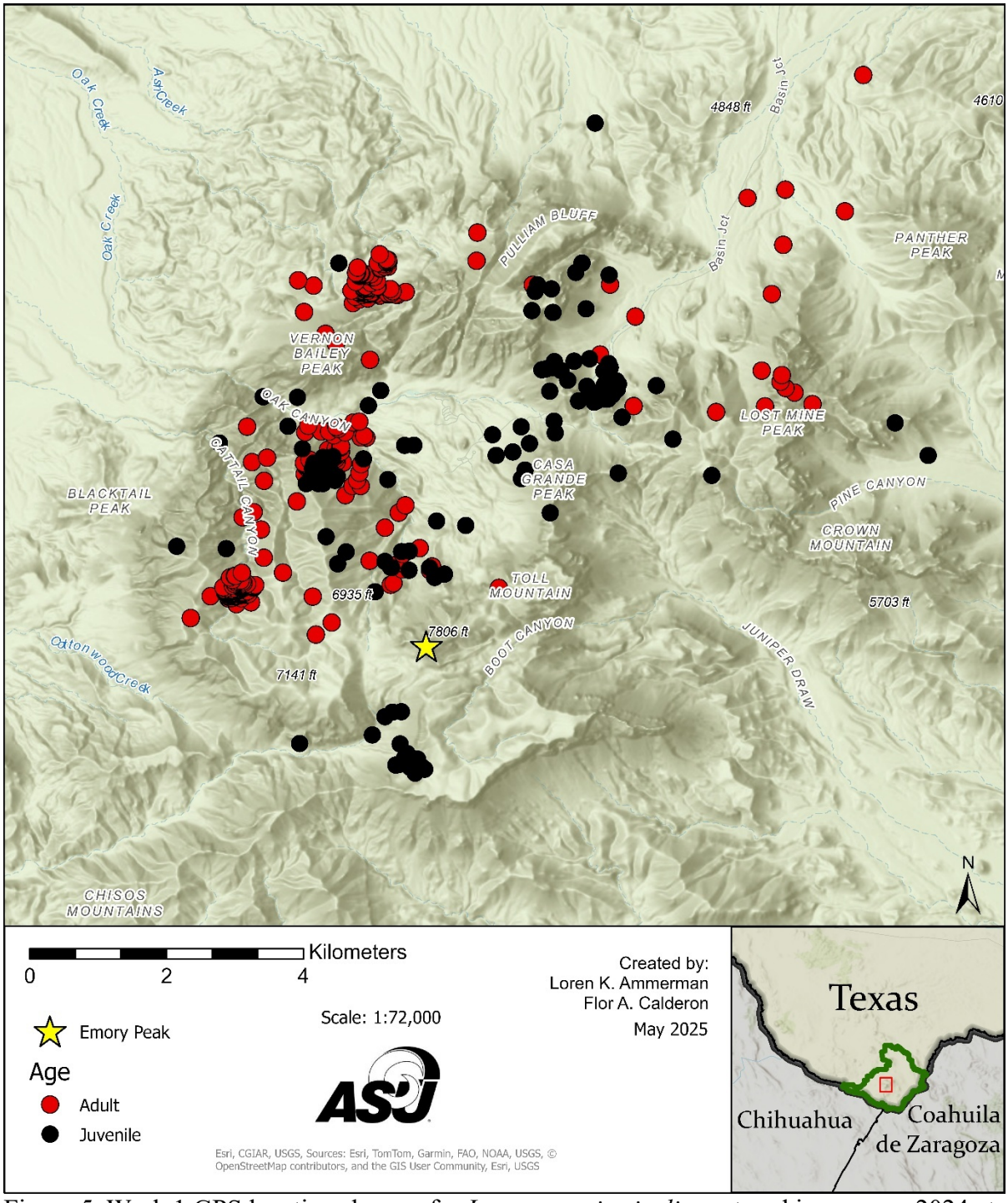


Figure 5. Week 1 GPS locations by age for *Leptonycteris nivalis* captured in summer 2024 at Emory Cave, Chisos Mountains, Big Bend National Park, TX. GPS points were buffered to exclude points within 1 km of Emory Peak and do not include points for flights over 50 km from Emory Peak.

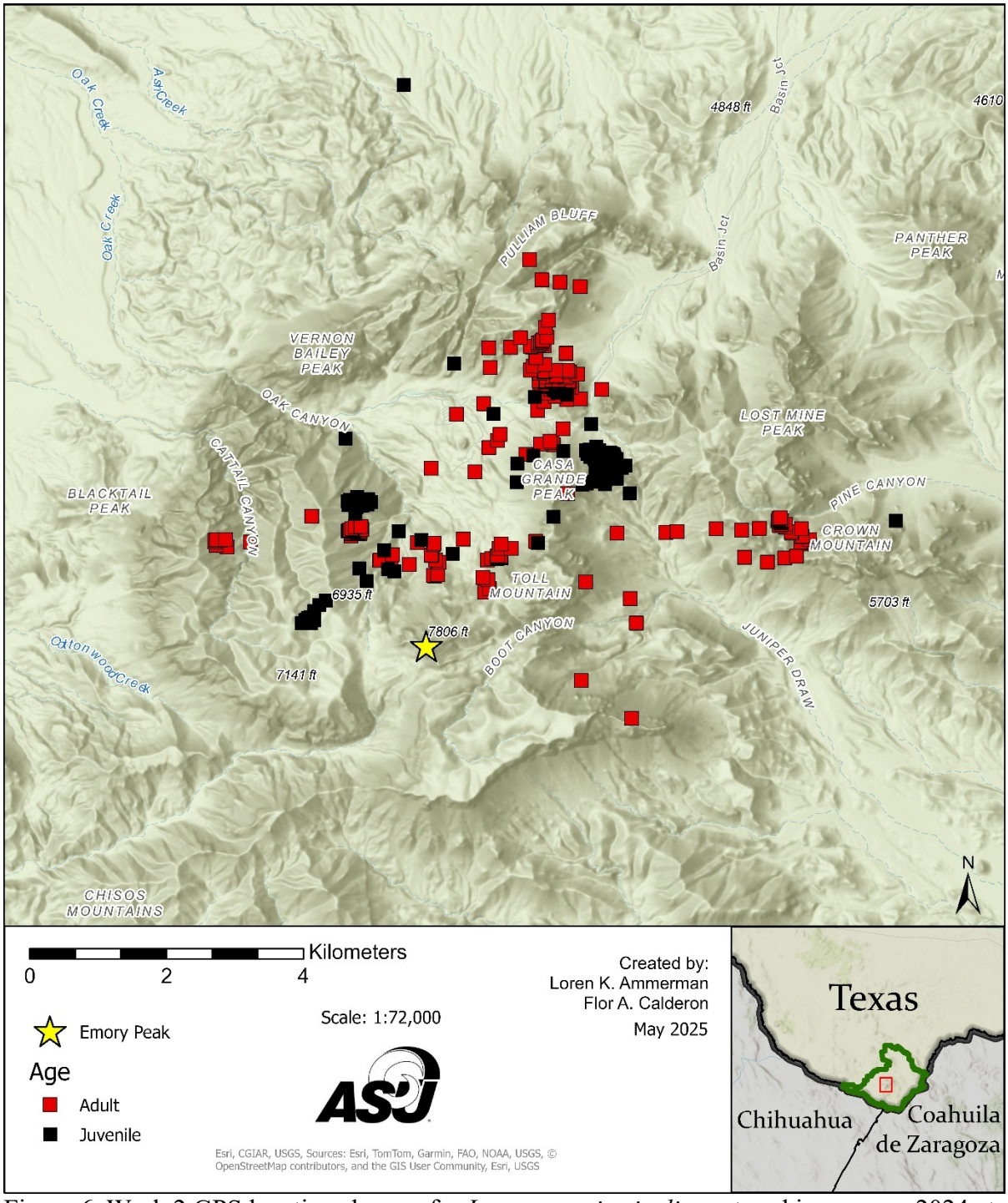


Figure 6. Week 2 GPS locations by age for *Leptonycteris nivalis* captured in summer 2024 at Emory Cave, Chisos Mountains, Big Bend National Park, TX. GPS points were buffered to exclude points within 1 km of Emory Peak and do not include points for flights over 50 km from Emory Peak.

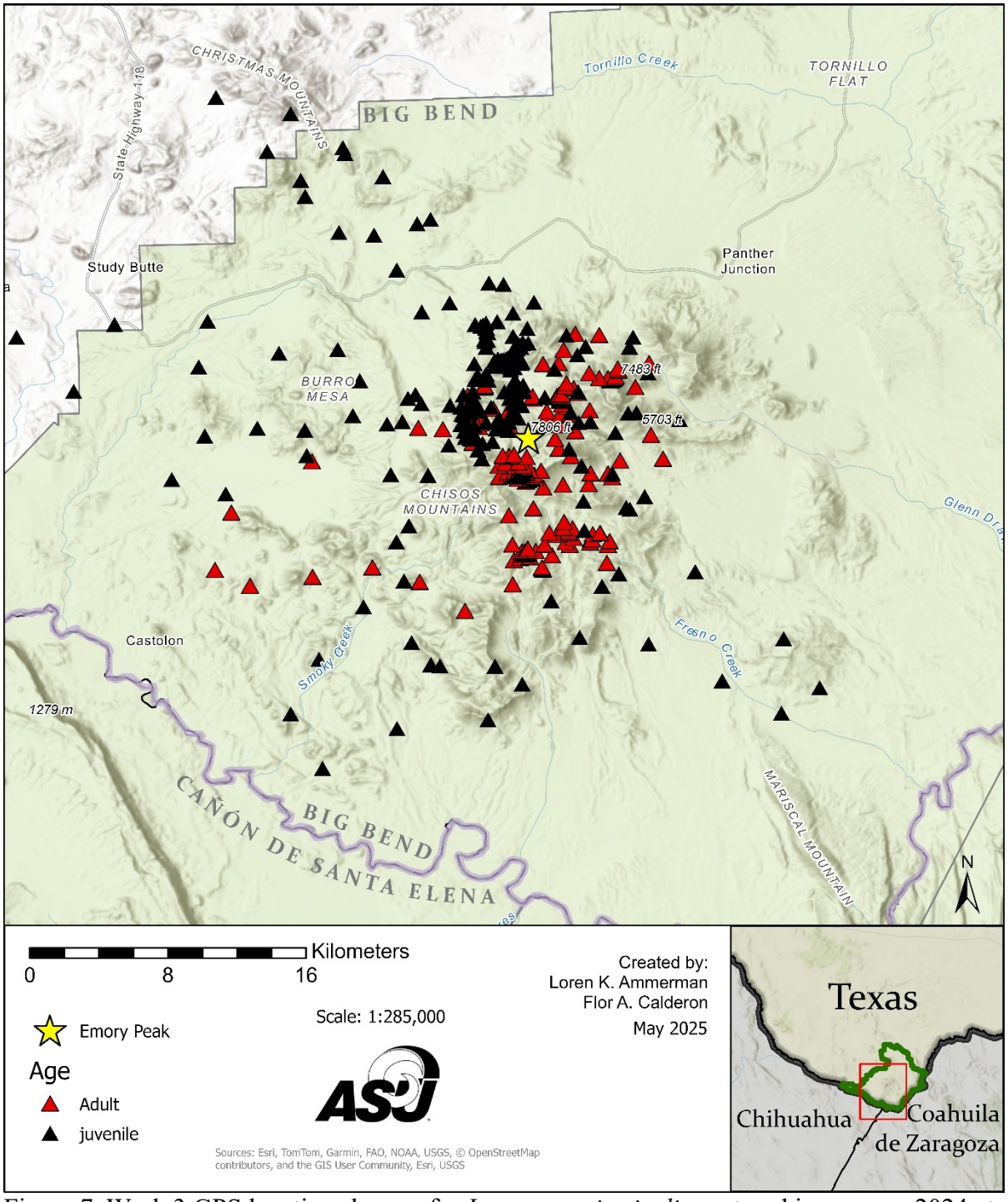


Figure 7. Week 3 GPS locations by age for *Leptonycteris nivalis* captured in summer 2024 at Emory Cave, Chisos Mountains, Big Bend National Park, TX. GPS points were buffered to exclude points within 1 km of Emory Peak and do not include points for flights over 50 km from Emory Peak.

Ground-truthing of suspected foraging areas

Based on GPS heat map analysis, we identified 23 areas of interest as potential foraging grounds (Fig. 8). Of these, 15 were successfully ground-truthed during field surveys. Generally, these areas were inspected within 7 days from the date the bat(s) occupied the area. All 15 ground-truthed locations had blooming *A. havardiana* present, and in many cases, these areas were within or adjacent to visible cliffs or rocky outcrops higher in elevation than the focal areas. These confirmed locations are represented by black-filled diamonds in Fig. 8. The remaining 8 areas, represented by hollow diamonds, could not be accessed due to logistical constraints, and their status remains unverified.

Selection of estimated range method

LoCoH provided the most conservative estimates overall of both home and core range, while KDE produced the largest range estimates (Appendix I). Side-by-side visual comparisons of the three methods that were calculated (LoCoH, KDE, and MCP), overlaid with GPS locations, revealed that LoCoH estimates more closely matched observed GPS point distributions. Specifically, the 90% LoCoH isopleth excluded broad unused areas often encompassed by KDE and MCP, while still capturing the full extent of nightly movements. For core areas, the 65% LoCoH isopleths provided the most conservative estimates that coincided most closely with GPS clusters, offering ecologically meaningful delineations of frequently used areas. There was a significant effect of estimation method on range size at the 90% isopleth ($F_{2,60} = 7.352$, $P = 0.0014$). Post hoc comparisons using Tukey's HSD revealed that LoCoH estimates were significantly smaller than KDE ($P_{adj} < 0.001$) but did not significantly differ from MCP ($P_{adj} > 0.10$). No significant difference was detected between MCP and KDE ($P_{adj} > 0.10$). The difference between the three methods of estimation at 65% isopleth is even more apparent ($F_{2,60} = 22.55$, $P < 0.001$). Post hoc comparisons using Tukey's HSD indicated that all three methods differed significantly from one another ($P_{adj} < 0.05$). Based on these findings, LoCoH was selected for all subsequent analyses of home range and foraging areas because of the conservative range estimates and better spatial alignment with actual GPS data. In the sections that follow, 'home range' refers to the 90% local convex hull, and 'core range' or 'foraging area' refers to the 65% local convex hull (Fig. 9 and Fig. 10).

Home range and core range estimates

Home range estimates were highly variable across individuals (903.7 ± 1,572.2 ha), with values ranging from 0.78 ha to 5,326.99 ha (Appendix I). The distribution was strongly right-skewed, therefore the median and interquartile range (72.9 ha; IQR = 15.4–626.0 ha) provided a more representative measure of central tendency. Core range estimates were also right-skewed but more concentrated than home range estimates. The mean core range was 29.6 ± 72.2 ha, with individual values ranging from 0.08 ha to 309.8 ha. The median was 4.4 ha (IQR = 1.0–13.7 ha), indicating that most individuals used relatively small, spatially restricted areas for foraging activity.

Adults versus juveniles–We found no significant difference in home range size between adults and juveniles ($F_{1,19} = 1.24$, $P = 0.28$), indicating that both age groups occupied similarly sized home ranges. Although not statistically different, juveniles tended to exhibit larger home ranges than adults. The adult home range size mean was 700.5 ± 1,433.9 ha, with values

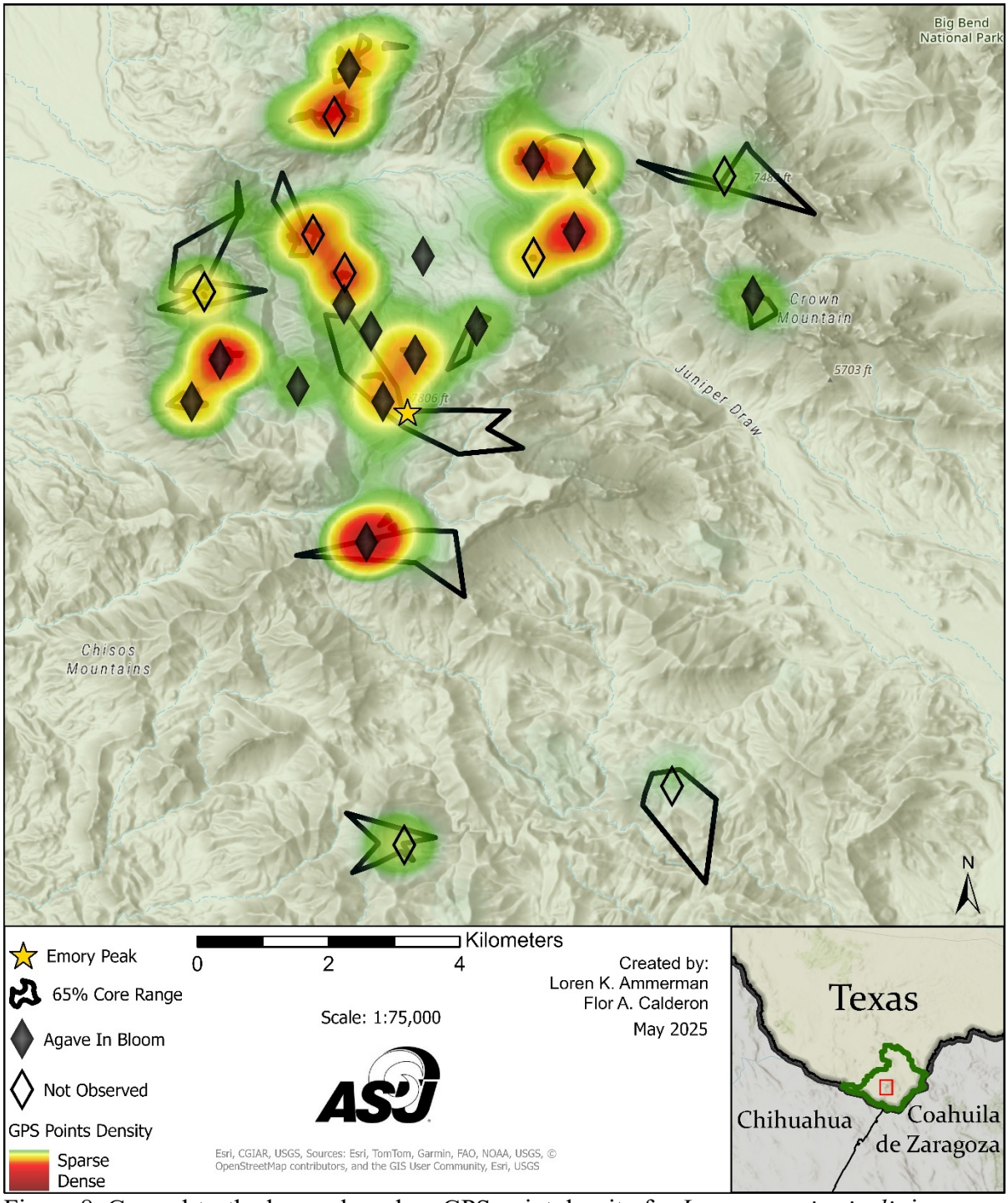


Figure 8. Ground-truthed areas based on GPS point density for *Leptonycteris nivalis* in summer 2024, Big Bend National Park, TX. Black diamonds represent areas that were visually confirmed to have blooming agave. Hollow diamonds represent areas that were points of interest that were not observed in-person. GPS point Density is overlayed on polygons representing the 65% core change.

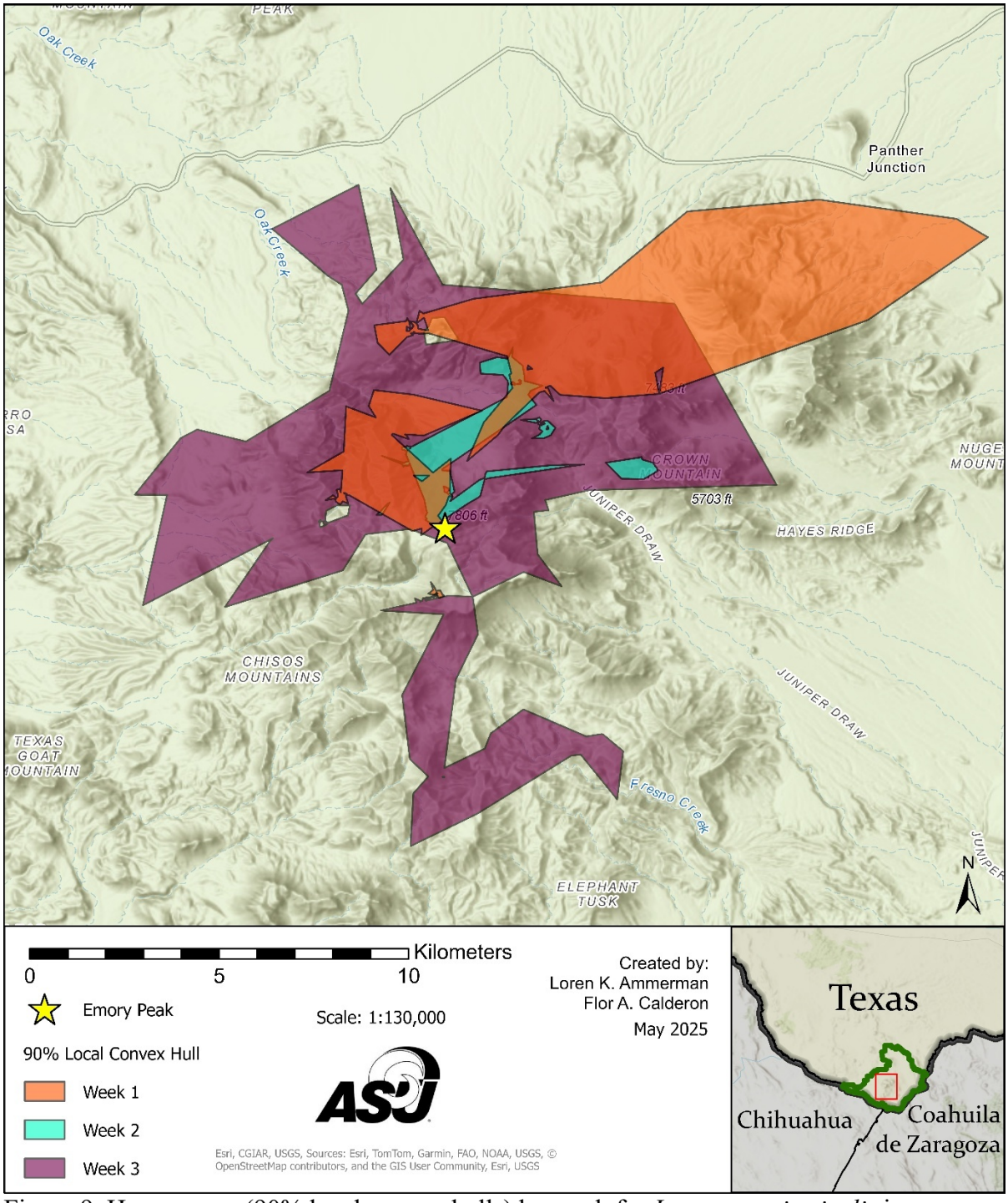


Figure 9. Home range (90% local convex hulls) by week for *Leptonycteris nivalis* in summer 2024, Big Bend National Park, TX.

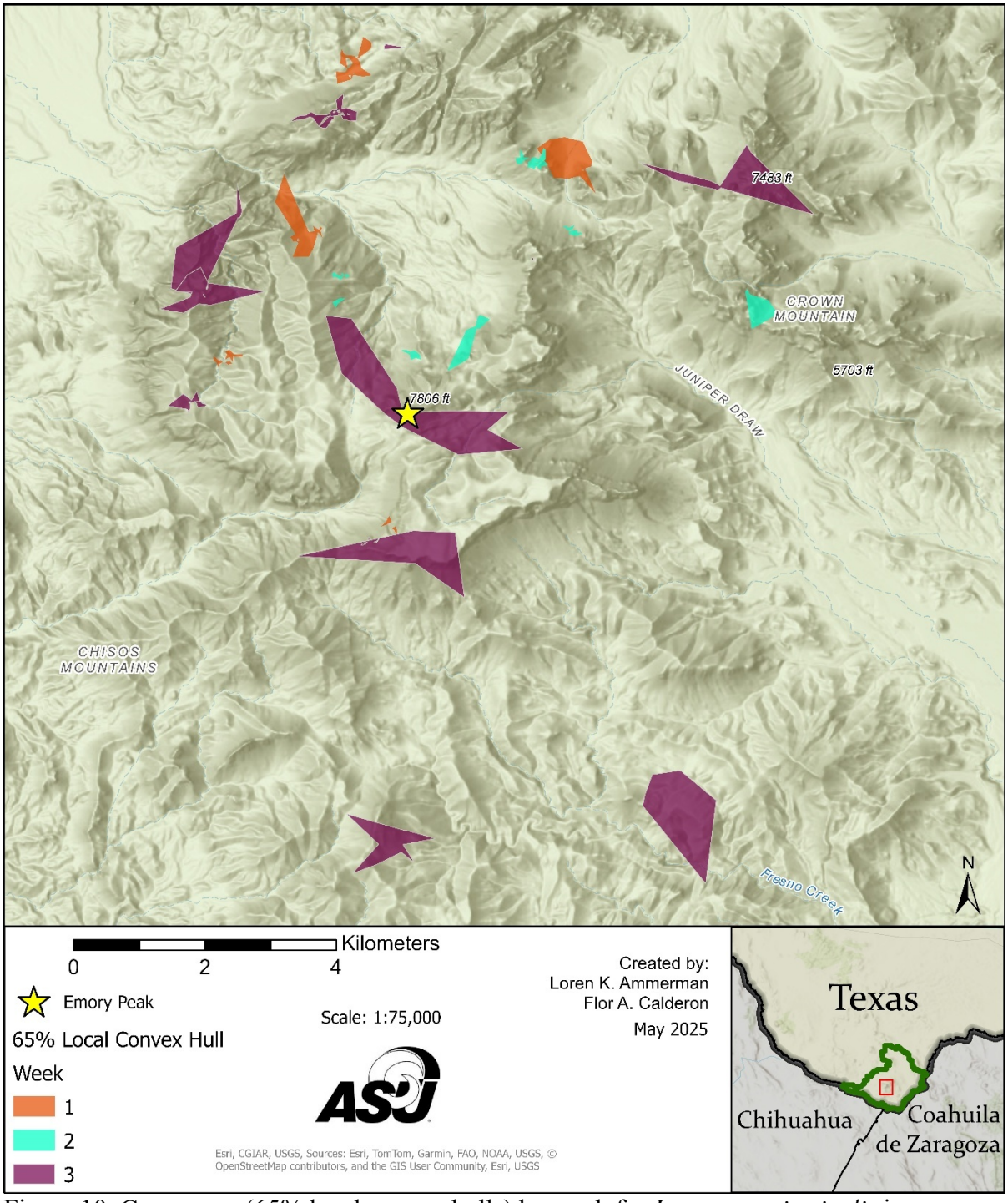


Figure 10. Core range (65% local convex hulls) by week for *Leptonycteris nivalis* in summer 2024, Big Bend National Park, TX.

ranging from 0.78 ha to 4,013.7 ha. The median was 44.1 ha (IQR = 17.7–219.3 ha). The mean juvenile home range size was 1,174.7 ± 1,791.1 ha, with values ranging from 4.01 ha to 5,326.99 ha. The median was 302.9 ha (IQR = 15.4–1,727.5 ha), indicating that some juveniles used notably larger home ranges than adults.

Similarly, we found no significant difference in core range size between adults and juveniles ($F_{1,19} = 0.006$, $P = 0.94$), suggesting comparable core use areas. However, adults tended to have larger and more variable core ranges. Adult core range size averaged 42.3 ± 94.2 ha, with values ranging from 0.08 ha to 309.8 ha. The median was 3.3 ha (IQR = 1.1–12.7 ha). In contrast, juvenile core ranges averaged 12.7 ± 15.7 ha, with values ranging from 0.21 ha to 39.0 ha. The median was 5.3 ha (IQR = 1.0–25.7 ha), indicating that juveniles generally occupied slightly larger core areas than adults.

All individuals across weeks–Home and core range sizes did not differ significantly across the three weeks of the study when comparing all individuals. Figures 5–7 show the GPS locations of bats by age and the week they were captured. Although not statistically significant, differences in home range size across the three-week study period suggest temporal variation in spatial use patterns ($F_{2,18} = 1.07$, $P = 0.36$). However, these apparent differences may be influenced by uneven sample sizes (the number of GPS locations recorded per tag) across weeks and the relatively small number of individuals tracked. Mean home range size increased from week 1 (676.3 ± 1478.9 ha) to week 3 (1954.6 ± 1975.5 ha), with week 2 exhibiting the smallest mean (80.3 ± 100.0 ha). However, the median home range was 23.2 ha in week 1 (IQR = 17.2–326.4 ha), 46.3 ha in week 2 (IQR = 28.6–78.3 ha), and 1727.5 ha in week 3 (IQR = 315.5–2997.9 ha), indicating substantial increase during the third week.

A similar trend of increasing size was observed for core ranges. Mean core range increased from 11.2 ± 13.8 ha in week 1 and 4.5 ± 5.1 ha in week 2 to 73.2 ± 117.5 ha in week 3. The median core range was 1.5 ha in week 1 (IQR = 1.1–19.7 ha), 2.1 ha in week 2 (IQR = 0.8–7.7 ha), and 7.1 ha in week 3 (IQR = 2.8–94.8 ha), again highlighting the increased variability during the final week of tracking. Although these differences were not statistically significant ($F_{2,18} = 0.71$, $P = 0.51$), the larger and more dispersed values observed in week 3 suggest more variable or extensive foraging behavior during that period.

Adults across weeks– Among adults, no statistically significant difference in home range size was detected across the three-week study period ($F_{2,9} = 0.006$, $P = 0.10$), suggesting consistent spatial use throughout the tracking period. Mean home range sizes for weeks 1, 2, and 3 were 1016.8 ± 1997.9 ha, 61.2 ± 20.3 ha, and 1023.4 ± 1652.0 ha, respectively. Despite large standard deviations indicating individual variability, particularly in weeks 1 and 3, these differences were not statistically meaningful.

Core range estimates among adults also showed no significant difference across weeks ($F_{2,5} = 0.93$, $P = 0.45$), although variance in core range size differed significantly between groups ($P < 0.001$), prompting the use of a Welch's ANOVA. Mean core range sizes increased across weeks, from 4.2 ± 6.3 ha in week 1, to 7.5 ± 5.0 ha in week 2, and 115.2 ± 147.8 ha in week 3. The high variance in week 3 suggests that those individuals in the latter part the season had expanded core use areas considerably compared to the individuals earlier in the season, despite the lack of a statistically significant trend.

Juveniles across weeks– Juvenile home range size varied across weeks, although it is important to note that statistical power was limited due to a small sample size (n = 3 per week, n = 9 total). We found differences in juvenile home range size across the three weeks ($F_{2,6} =$

6.09, $P = 0.036$). Tukey's post hoc test revealed that home ranges were significantly larger in week 3 compared to week 2 ($P_{adj} = 0.033$), while no significant difference was observed between weeks 1 and 2 $P_{adj} = 0.57$) or weeks 1 and 3 ($P_{adj} = 0.12$). Mean home range sizes increased across weeks, from 222.3 ± 181.8 ha in week 1, to 105.7 ± 166.4 ha in week 2, and 3196.1 ± 1888.9 ha in week 3, indicating substantial expansion of space use during the final week.

In contrast, core range size did not differ significantly across weeks among juveniles ($F_{2,6} = 1.57$, $P = 0.28$). Mean core range sizes were 20.4 ± 16.9 ha in week 1, 0.6 ± 0.4 ha in week 2, and 17.1 ± 19.0 ha in week 3. Although these values suggest reduced core use in week 2, high individual variability, particularly in week 3, may have masked potential differences.

Nightly flight distance

To investigate whether bats nightly foraging effort differed, average nightly distance flown was analyzed across individuals, age classes, and weeks. There was a total of 75 tracking nights with coordinates recorded the entire night (from cave emergence to re-entry); of those 33 were from juveniles and 42 were adults (Table 3). Overall, the mean nightly distance flown was 32.5 ± 26.4 km, with individual values ranging from 8.11 km to 100.07 km. The median nightly distance was 20.0 km (IQR = 15.3–42.4 km), indicating moderate but variable travel distances among individuals. Juveniles exhibited higher average nightly distances than adults (juvenile mean = 44.7 ± 33.7 km; adult mean = 23.4 ± 15.6 km), although this difference was not statistically significant ($F_{1,19} = 3.62$, $P = 0.07$). These results suggest a possible trend toward longer nightly movements in juveniles. While these data show an upward trend in nightly distance flown across weeks for all bats, there was no significant variation ($F_{2,18} = 0.62$, $P = 0.55$), with mean weekly distances of 26.4 ± 19.0 km (week 1), 30.1 ± 31.0 km (week 2), and 41.7 ± 29.2 km (week 3). Similarly, adult nightly distances did not vary significantly by week ($F_{2,9} = 0.13$, $P = 0.88$), with consistent means of 25.6 ± 22.8 km (week 1), 20.2 ± 2.9 km (week 2), and 25.6 ± 18.3 km (week 3). Juveniles showed an upward trend across weeks (27.4 ± 17.4 km [week 1], 43.3 ± 49.1 km [week 2], and 63.3 ± 29.0 km [week 3]), but this was not statistically significant ($F_{2,6} = 0.81$, $P = 0.49$) and likely due to variation in individuals and a small sample size (n = 3 juveniles per week).

In general, bats roosting at Emory Cave did not undertake long-distance nightly flights (>100 km), although a few individuals did exhibit such movements. The longest recorded flight was made by a juvenile male who traveled 295 km in a single night (Table 3). This individual departed the Emory Cave region, flew northward beyond the town of Marathon, Texas, then reversed course and ultimately day-roosted in the Sierra del Carmen Mountains of Coahuila, Mexico, before returning to Emory Cave the following night. The second longest flight was by a juvenile female, who traveled 251 km in one night, traveling westward, past Santa Elena Canyon Park, Mexico and retuned to Emory Cave. An adult female also exhibited a notable long-distance movement, traveling 121 km in a night and roosted in the Sierra del Carmen before returning the next night. This same adult female achieved the highest recorded flight speed of the study at 84 km/h, possibly aided by a favorable tailwind during her return flight eastward to Emory Cave. Although wind assistance is a plausible explanation, weather data for the region were not available to confirm this interpretation. Notably, the juvenile male that undertook the longest single-night flight (295 km) also reached the second-highest recorded speed at 65.7 km/h while traveling through the same general area.

Table 3. Summary of nightly distance traveled and flight speeds by adults and juveniles for tracked *Leptonycteris nivalis* captured in the summer 2024 at Emory Cave, Chisos Mountains, Big Bend National Park, TX. Summarized are the average distance traveled per night, maximum single-night distance, average speed, and maximum recorded speed. In bold are the three longest distances flown in a night, and the fastest juvenile and adult bat.

Age	Capture week	Tag ID	No. of full nights	Average distance per night (km)	Furthest distance (km)	Average speed* (km/h)	Max. speed (km/h)
Adult	1	57224	5	8.11	9.52	2.93	15.5
Adult	1	57225	1	19.96	19.96	1.51	17.39
Adult	1	57226	7	53.77	**121.23**	2.87	**84.02**
Adult	1	57227	4	15.42	20.30	6.91	26.5
Adult	2	57232	6	17.82	23.27	13.16	27.4
Adult	2	57233	3	18.91	26.52	2.90	15.7
Adult	2	57234	2	19.87	33.87	3.19	21.1
Adult	2	57235	2	24.37	25.82	3.23	32.4
Adult	3	57237	2	8.41	9.65	11.20	18.8
Adult	3	57238	3	44.05	78.61	1.14	39.2
Adult	3	57239	2	38.61	45.93	8.22	38.6
Adult	3	57240	5	11.35	17.72	5.17	21.8
			average	23.39	36.03	5.20	29.87
Juvenile	1	57222	1	41.50	41.50	8.50	38.27
Juvenile	1	57223	4	8.49	14.88	2.93	11.6
Juvenile	1	57228	4	32.90	40.70	6.18	35.1
Juvenile	2	57229	1	14.61	14.61	2.14	14.22
Juvenile	2	57230	5	15.28	22.28	2.35	24.5
Juvenile	2	57231	4	100.07	**295.01**	13.16	**65.7**
Juvenile	3	57236	4	96.41	**251.20**	11.20	58.4
Juvenile	3	57241	5	50.99	90.25	5.93	32.4
Juvenile	3	57242	5	42.38	87.37	5.11	42.2
			average	44.74	95.31	6.39	35.82
Average — all bats				32.54	61.44	5.71	32.42

*Average nightly distances likely reflect periods of inactivity or roosting away from the cave and may underestimate total flight effort.

Duration of nightly activity

The same tracking nights that were used to calculate average distance were used to calculate nightly activity time (n=75; Table 4). Across all individuals and nights, bats spent an average of 6.6 ± 1.1 h active per night. There was no significant difference in average time active between adults (6.58 ± 0.89 h) and juveniles (6.57 ± 1.31 h; $F_{1,19} = 0.00$, $P = 0.98$), suggesting broadly similar activity patterns across age classes.

When comparing time active across the three sampling weeks, we found a significant difference ($F_{2,18} = 7.87$, $P = 0.035$). Bats were active for an average of 5.81 ± 1.03 h in week 1, 6.40 ± 0.78 h in week 2, and 7.52 ± 0.91 h in week 3. Tukey's post hoc test revealed that bats in week 3 spent significantly more time active than those in week 1 ($P_{adj} = 0.0029$) and week 2 ($P_{adj} = 0.048$), while weeks 1 and 2 did not differ significantly ($P_{adj} = 0.40$). These results suggest increased nightly foraging time later in the summer.

Among adults only, nightly time active also differed significantly across weeks ($F_{2,9} = 7.65$, $P = 0.011$). Adult bats were active for 6.08 ± 0.66 h in week 1, 6.13 ± 0.78 h in week 2, and 7.54 ± 0.22 h in week 3. Adults in week 3 spent significantly more time active than those in week 1 ($P_{adj} = 0.0018$) and week 2 ($P_{adj} = 0.022$), while weeks 1 and 2 did not differ ($P_{adj} = 0.99$).

In contrast, juvenile nightly active time did not differ significantly by week ($F_{2,6} = 2.54$, $P = 0.16$). However, mean active time increased from 5.47 ± 1.92 h in week 1, to 6.76 ± 0.09 h in week 2, and 7.49 ± 0.11 h in week 3. While not statistically significant, this trend suggests that juvenile bats may have increased duration of nightly activity over time. These comparisons should be interpreted cautiously due to small sample sizes (n = 3 juveniles per week).

Two individuals were confirmed to night roost at alternate locations, and one non-reproductive adult (tag number 57238) returned to Emory Cave on 2 separate occasions to night roost for up to 2 h based on gaps in GPS location data near the cave. It is possible that a few other bats may have night roosted at Emory Cave as well, but this could not be confirmed due to sparse GPS coverage and short visit durations. Lastly, tag battery life (Table 4) over all tags was 3 days, 15 h and 12 min, but if only calculated with tags that were active for 2 days or more, the average battery life was 4 days, 16 h, and 20 min.

Characteristics of foraging habitat

Core ranges encompassed 22 vegetation communities as identified through TPWD Landscape Ecology Program (TPWD 2023). The most prevalent vegetation type was juniper woodland (32.7%), followed by deciduous chaparral (13.6%) and cliff and outcrop habitats (11.8%) (Table 5).

Elevation– The mean elevation within the core range for all *L. nivalis* was 1,823.6 ± 306.2 m, with a range of 1,250 m (Fig. 11). The minimum and maximum elevations were 1,121 m and 2,371 m, respectively. The mean for expected areas (MBG) was 1,684.0 ± 252.7 m. Elevation ranged from 1,121.3 to 2,387.3 m in MBG zones. A Welch's two-sample t-test indicated a statistically significant difference in mean elevation between the observed core areas and the expected MBG ($t = -1103.7$, $P < 0.001$). The effect size was moderate (Cohen's d = 0.54), suggesting that bats foraged in moderately higher-elevation terrain than expected based on the available landscape. These values suggest that bats primarily foraged in the upper half of the available elevation gradient in BBNP, where elevation ranges from 550 m to 2,387 m.

Table 4. Summary of nightly activity duration, number of GPS points with recorded coordinates per bat and GPS tag battery lifespan traveled by adults and juveniles for tracked *Leptonycteris nivalis* captured in the summer 2024 at Emory Cave, Chisos Mountains, Big Bend National Park, TX.

Age	Capture week	Tag ID	No. of GPS points	No. of full nights	Average tag battery life (dd:hh:mm)	Average time active (hh:mm)
Adult	1	57224	155	5	04:23:50	5:23
Adult	1	57225	55	1	01:01:29	6:10
Adult	1	57226	231	7	07:06:59	6:56
Adult	1	57227	99	4	04:23:50	5:49
Adult	2	57232	184	6	05:06:40	6:11
Adult	2	57233	117	3	03:00:00	7:10
Adult	2	57234	43	2	01:05:40	5:50
Adult	2	57235	37	2	01:03:59	5:19
Adult	3	57237	73	2	01:07:30	7:24
Adult	3	57238	137	3	03:04:19	7:40
Adult	3	57239	67	2	02:23:29	7:19
Adult	3	57240	255	5	05:21:00	7:47
Juvenile	1	57222	50	1	01:00:50	6:00
Juvenile	1	57223	73	4	05:01:20	3:20
Juvenile	1	57228	139	4	04:19:39	7:04
Juvenile	2	57229	41	1	00:06:50	6:50
Juvenile	2	57230	185	5	04:05:30	6:39
Juvenile	2	57231	165	4	03:07:40	6:47
Juvenile	3	57236	154	4	04:02:10	7:37
Juvenile	3	57241	235	5	05:03:50	7:27
Juvenile	3	57242	179	5	05:22:49	7:24
Total Average					**03:15:12**	**6:34**

Table 5. Proportion of vegetation communities in core range of *Leptonycteris nivalis.*

Common Name (Trans-Pecos)	**Proportion**
Pinyon - Juniper Woodland	32.69
Deciduous Chaparral	13.64
Cliff and Outcrop	11.82
Pinyon - Juniper Shrubland	10.15
Hill and Foothill Grassland	8.10
Mixed Desert Shrubland	6.32
Succulent Desert Scrub	2.93
Mountain Grassland	2.35
Gray Oak Savanna and Woodland	1.64
Mixed Oak Savanna and Woodland	1.59
Montane Mesic and Canyon Pine - Juniper Forest	1.48
Evergreen Chaparral	1.30
Montane Mesic and Canyon Hardwood - Pine - Juniper Forest	0.93
Lower Montane Riparian Shrubland	0.89
High Mountain Conifer Forest and Woodland	0.82
Montane Mesic and Canyon Hardwood Forest	0.64
Montane Mesic and Canyon Shrubland	0.64
Montane Mesic and Canyon Evergreen Shrubland	0.53
Desert Wash Shrubland	0.49
Juniper Savanna and Woodland	0.46
Mountain Evergreen Oak - Pine Shrubland	0.34
Lower Montane Riparian Woodland	0.26

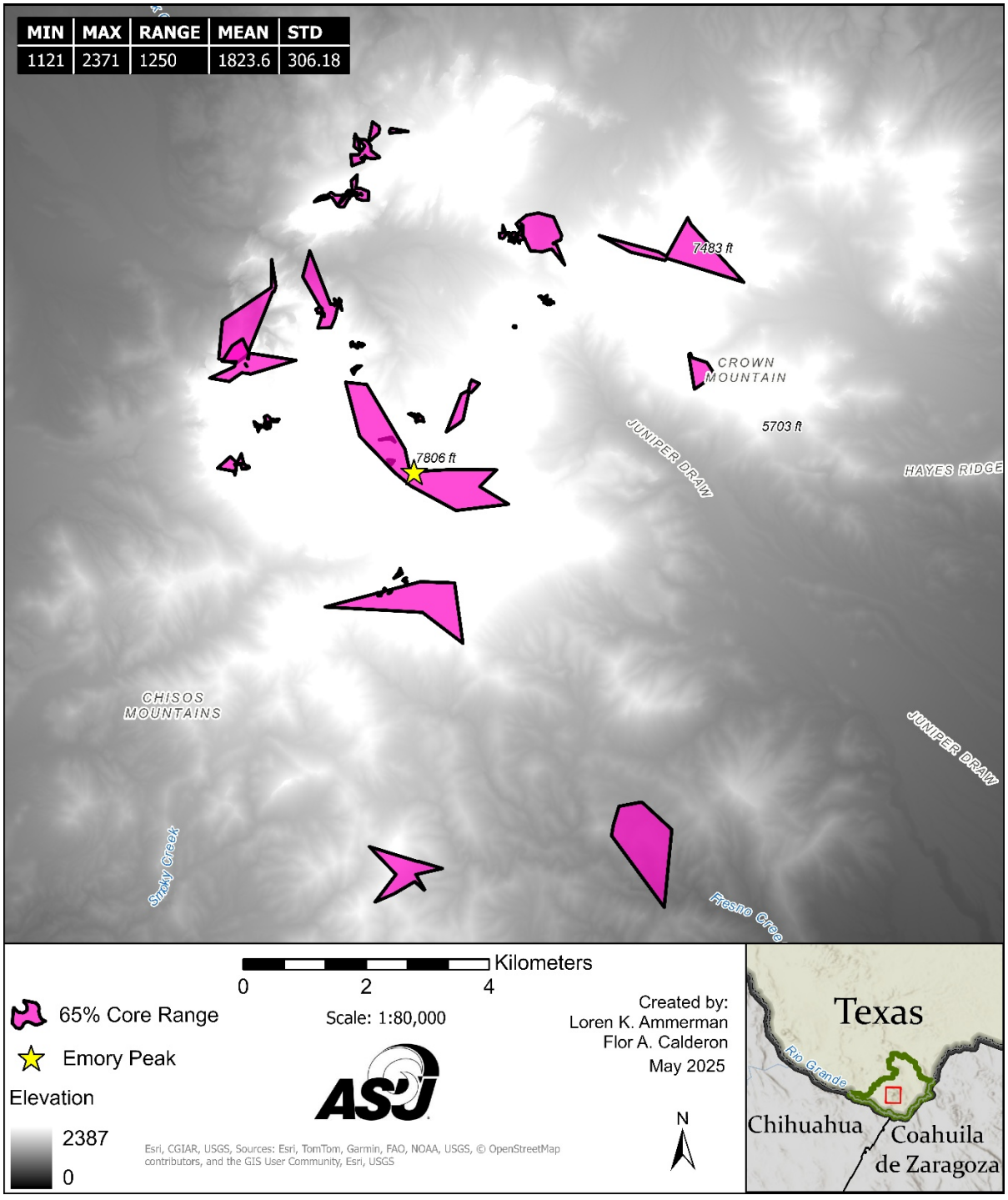


Figure 11. Elevational gradient of *Leptonycteris nivalis* core ranges and surrounding area of the Chisos Mountains, Big Bend National Park. Values in table are representative of the area within the 65% core ranges during the summer of 2024.

Slope and topography– Core ranges were topographically complex. Observed core range slopes were significantly steeper than those derived from the MBG of the core range. The mean slope of observed core ranges was 34.13° ± 18.55°, compared to 30.06° ± 13.90° for the MBG-derived expectations. A Welch's two-sample t-test confirmed a statistically significant difference between the observed core areas and the expected MBG ($t = –552.3$, $P < 0.001$). Although statistically significant due to large sample sizes, the effect size was small to moderate (Cohen's d = 0.30), indicating that observed core range areas were associated with modestly steeper terrain. The range of the slope within the core range spanned from 0° to 89°, indicating use of a wide variety of terrain from flat areas to very steep slopes (Fig. 12). The TRI averaged 5.81 ± 1.84 on a scale of 1–9, also reflecting the rough terrain of the presumed foraging areas, including canyons, ridgelines, and steep mountain slopes (Fig. 13).

Aspect– The Watson–Wheeler test revealed a significant difference in aspect use between the landscape and the core foraging areas ($W_2 = 562401$, $P < 0.001$). Visual inspection of rose plots (Fig.14 and 15) indicated that *L. nivalis* disproportionately used north-facing slopes, with a strong preference for northwest-facing aspects, particularly within the 315°–345° range. These findings indicate non-random aspect selection, with a pronounced preference for north-facing slopes.

Canopy height– To estimate vertical vegetation structure, canopy height was extracted from LiDAR data. After excluding all values greater than 15 m (to eliminate outliers or overstory trees unlikely to represent agave-dominated habitat), the mean canopy height within core ranges was 1.58 ± 2.41 m (Fig. 16). All statistical tests from this study have been summarized in Appendix II.

Potential undocumented roosts

Analysis of GPS movement patterns revealed the use of 2 potential undocumented roost sites outside of Emory Cave. Two bats exhibited directional movements consistent with commuting behavior (both to and from these roosts) rather than localized foraging. These movements led to day roosting in areas located approximately 60 km southeast of Emory Cave, within the Maderas del Carmen Flora and Fauna Protected Area in the Sierra del Carmen Mountains of Coahuila, Mexico (Fig. 17; Roost A: 29.2203°N, 102.6825°W, 1410 m; Roost B: 29.0922°N, 102.6179°W, 2483 m). These coordinates represent the estimated center point for each roost within a 2 km radius of uncertainty.

A juvenile male (tag number 57231), tagged during the second week of the study, flew north then returned south on the night of 2 July 2024 and day-roosted within the region designated as Circle A in Figure 17. A second bat, an adult female (tag number 57226), made an excursion to the same region on the night of 29 June 2024. She night-roosted for approximately 2 hours in Circle A before continuing an additional 16 km south to day-roost in Circle B. After emergence the following night, each of these bats made directed flights from these roosts back toward the Emory Cave foraging area, further supporting the interpretation of commuting behavior. These locations may represent alternative day roosts, stopover sites, or migratory staging areas. Their apparent use by tagged individuals suggests that a small proportion of the Emory Cave population intermittently rely on roosts outside of the protected cave system.

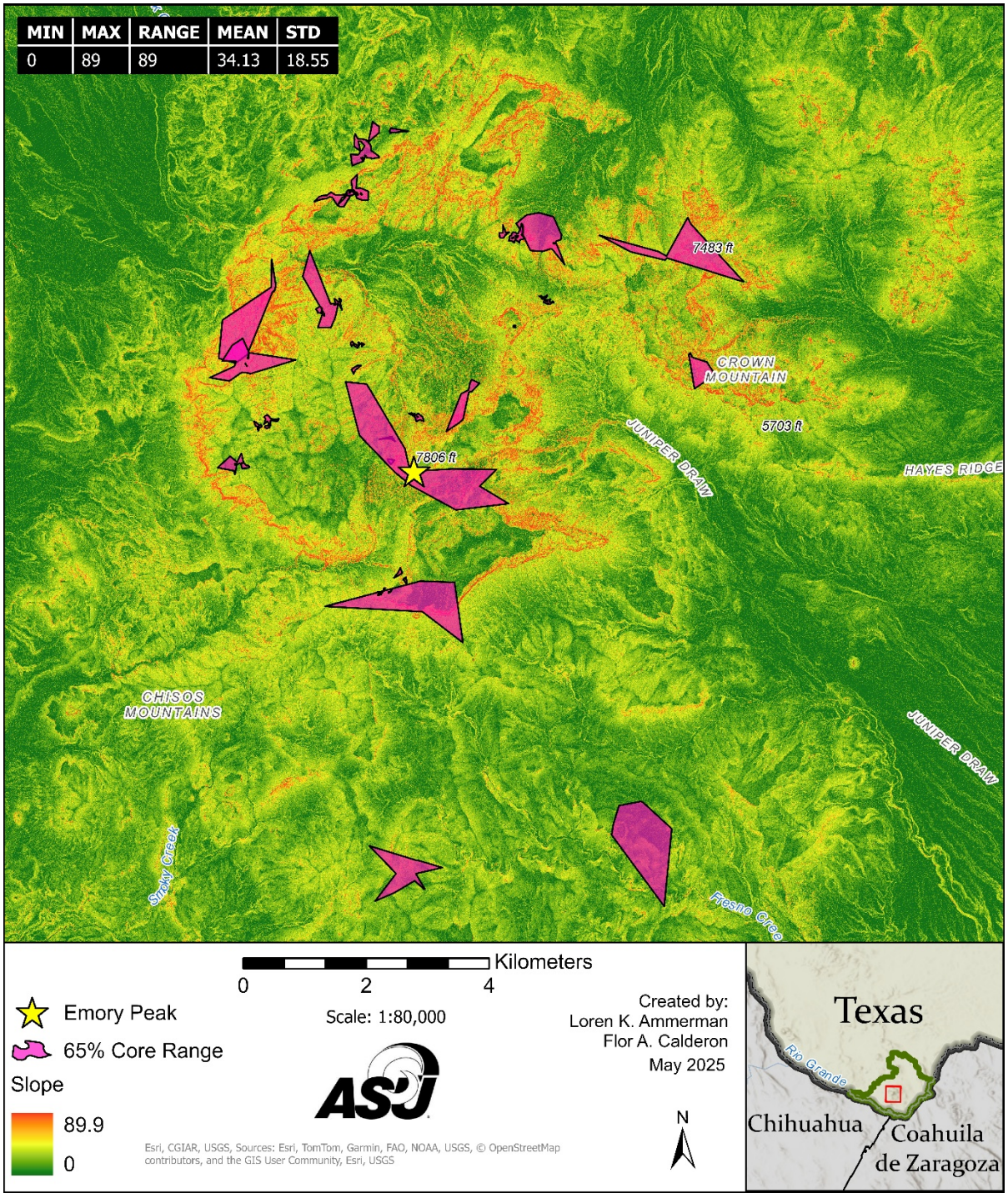


Figure 12. Slope of *Leptonycteris nivalis* core ranges and surrounding area of the Chisos Mountains, Big Bend National Park. Values in table are representative of the area within the 65% core ranges during the summer of 2024.

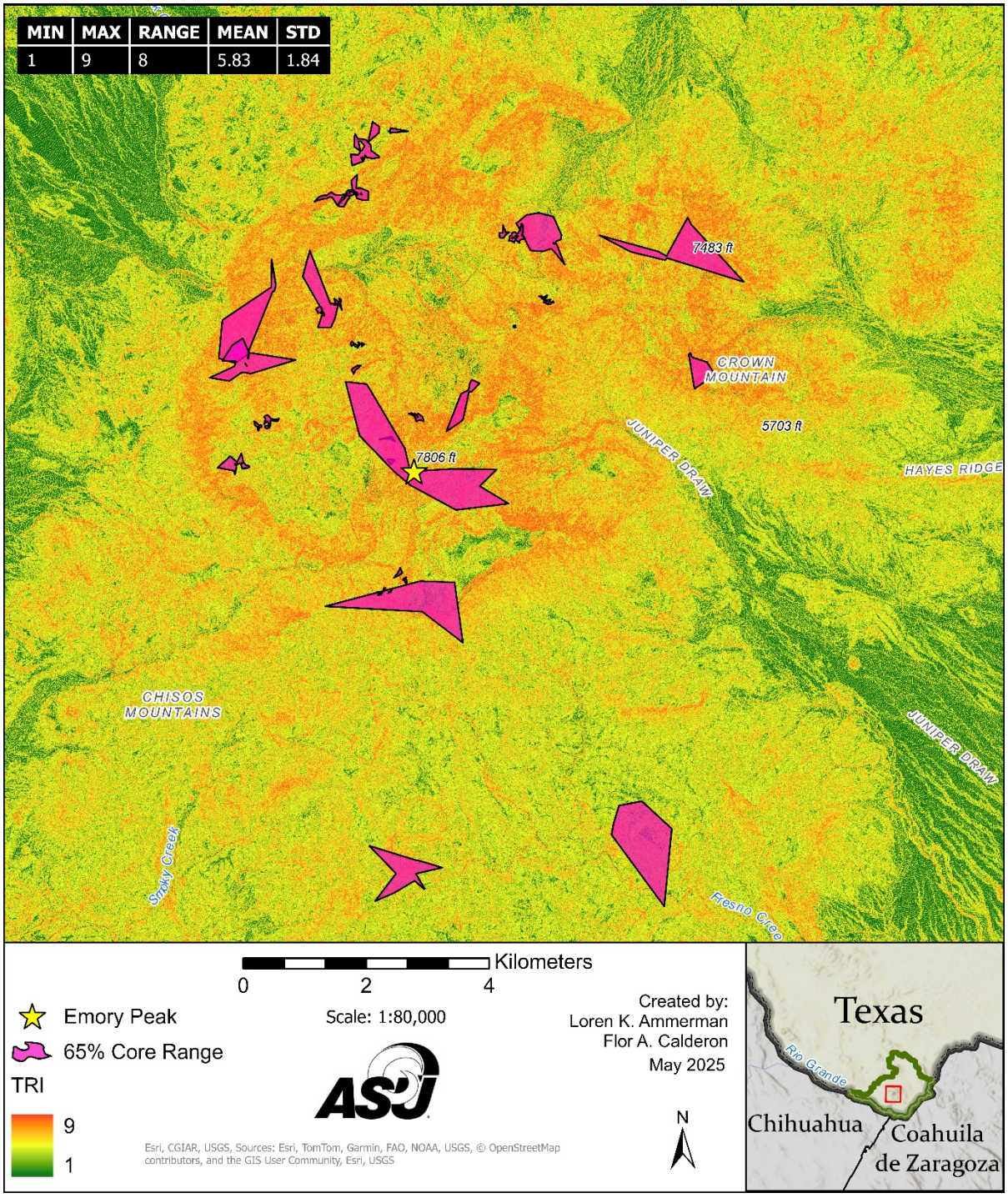


Figure 13. Topographic ruggedness of *Leptonycteris nivalis* core ranges and surrounding area of the Chisos Mountains, Big Bend National Park. Values in table are representative of the area within the 65% core ranges during the summer of 2024.

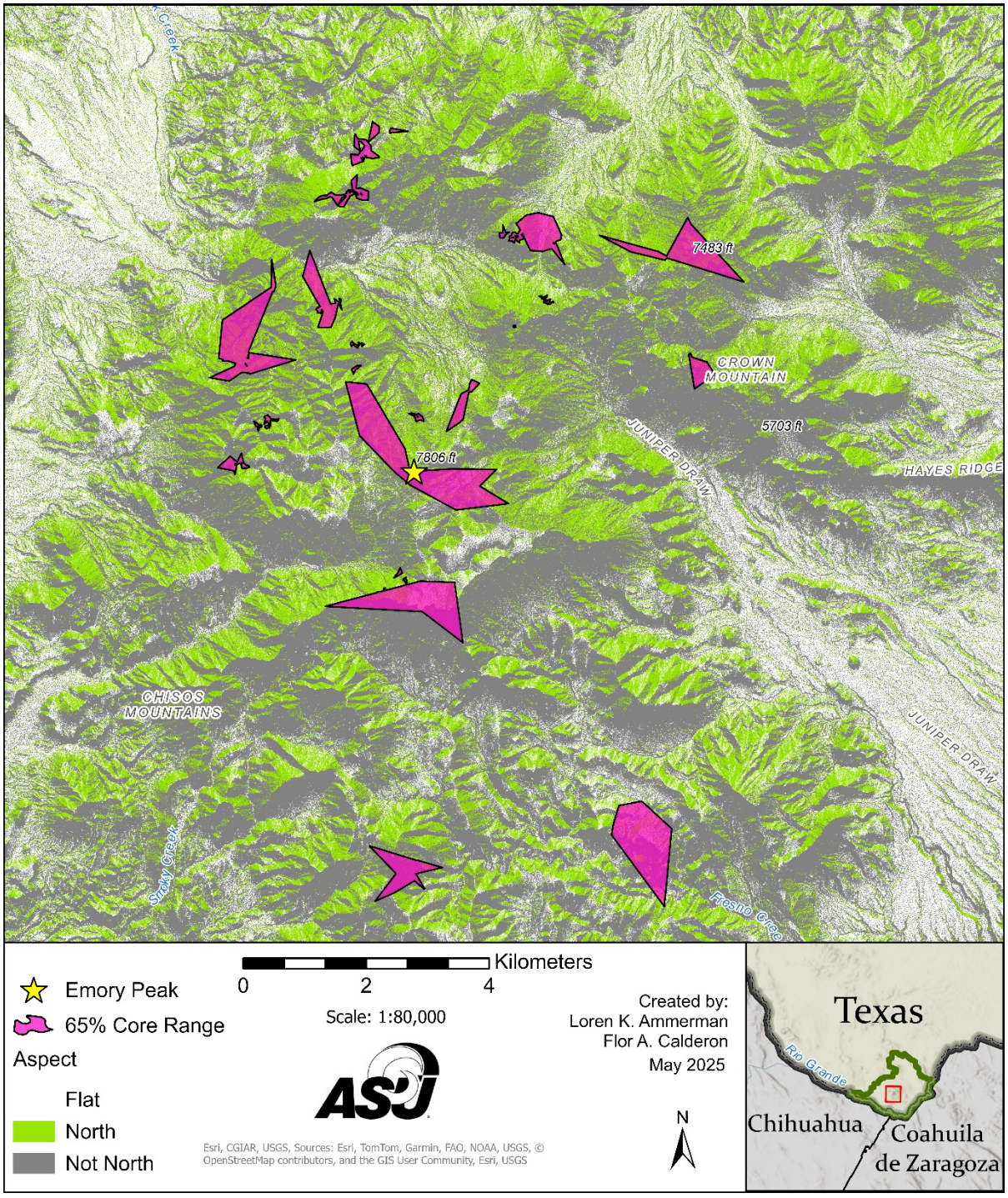


Figure 14. Aspect of *Leptonycteris nivalis* core ranges and surrounding area of the Chisos Mountains, Big Bend National Park. The values on the map represent north-facing slopes (0–67.5° and 292.5–360°), non-north-facing slopes (67.5–292.5°) and flat terrain within the map view.

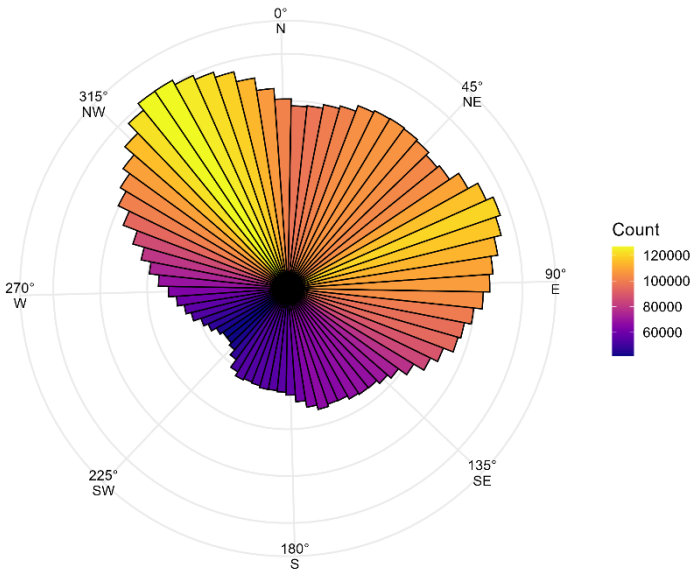


Figure 15. Aspect preferences of *Leptonycteris nivalis* within core ranges of the Chisos Mountains, Big Bend National Park. The count is the number of cells within each raster with the same aspect degree.

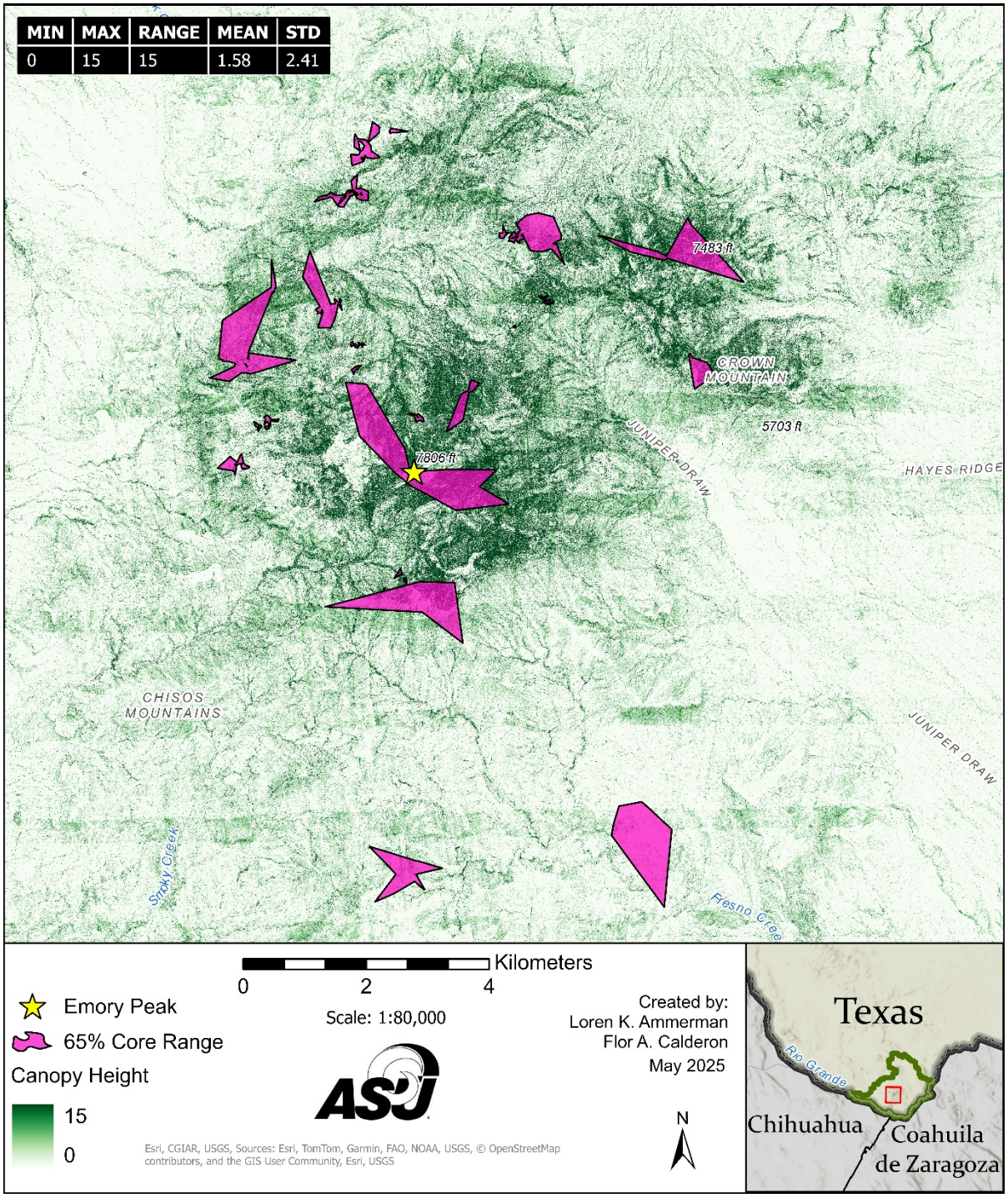


Figure 16. Canopy height of *Leptonycteris nivalis* core ranges and surrounding area of the Chisos Mountains, Big Bend National Park. Values in table are representative of the area within the 65% core ranges during the summer of 2024

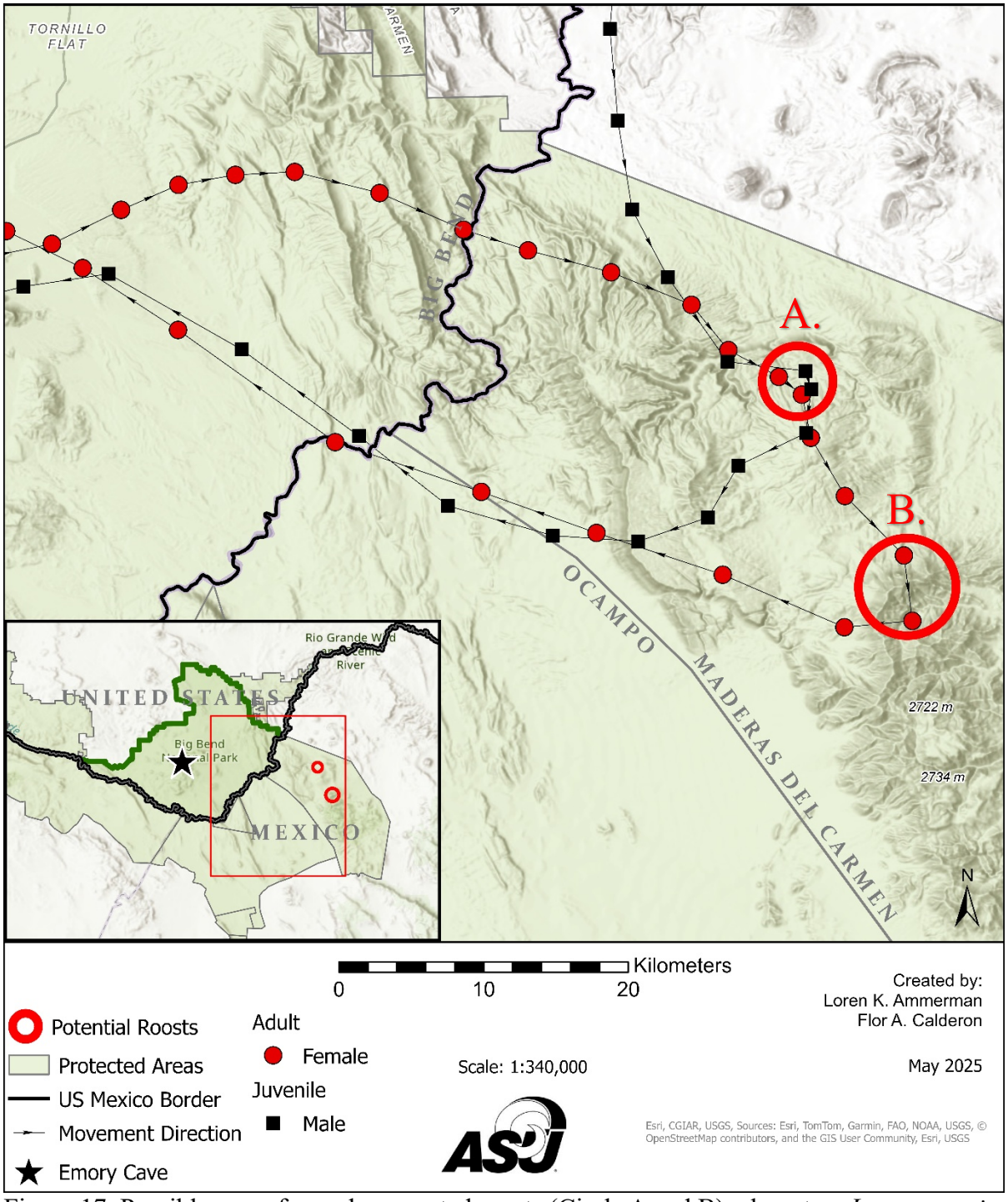


Figure 17. Possible areas for undocumented roosts (Circle A and B) where two *Leptonycteris nivalis* day roosted in the Maderas del Carmen Flora and Fauna Protected Area, Coahuila, Mexico in the summer of 2024. Roost locations are estimated to be within the circled regions.

DISCUSSION

This study provides the first use of GPS tracking methods to investigate landscape use and foraging of *L. nivalis* in the Chisos Mountains of BBNP, presenting quantitative estimates of home and core ranges for *L. nivalis*, which revealed substantial individual and temporal variability in space use. Despite this variability, our findings support the view that agave resources within the park are sufficient to sustain the seasonal population of *L. nivalis* at Emory Cave during early to mid-summer because all core ranges were within 8 km radius of the cave. The consistent annual return of this species to the Chisos Mountains (Ammerman et al. 2025) and our results showing repeated use of relatively localized foraging areas suggest that the nectar resources available within the park provide reliable and predictable food to support lactating females and newly-volant, young-of-the-year juveniles.

Prior to this study, there was little understanding of how *L. nivalis* used the Chisos Mountains landscape. Consistent with findings of our study, England's (2012) telemetry study observed *L. nivalis* to center their foraging activity where agave was more abundant in the Chisos Mountains. England also observed juveniles moving a long distance from Emory Cave but were unable to track the details of their flights due to the restrictions of telemetry. A historic capture record from the Chinati Mountains in 1969 (Mollhagen 1973) and subsequent speculation has suggested that bats using Emory Cave might range far beyond BBNP, potentially traveling to the Chinati Mountains or even to northern Mexico to forage where agave distribution models indicate the presence of suitable nectar resources (Gómez-Ruiz and Lacher 2017). However, the scale and patterns of movement we observed, particularly the concentration of GPS locations within the park boundary and the recurrence of core areas near agave patches, suggest that *L. nivalis* is able to meet its energetic needs without extensive nightly travel.

Although no significant differences in home or core range sizes were detected between age classes, juveniles in the final week of tracking exhibited significantly larger home ranges than juveniles in earlier weeks. This result could reflect the dispersal behavior of the young-of-the-year, which begin exploring a broader area as they develop greater flight capability and gain independence from their mothers. While adult space use remained relatively consistent across the three-week period, juvenile movements were highly variable by the end of the study, suggesting that their foraging behavior may be exploratory (Schabacker et al. 2024) as summer progresses. It remains unclear whether these exploratory movements are important as a precursor to migratory departure from the Chisos.

Ultimately, our data suggest that the Chisos Mountains provide essential habitat to support *L. nivalis* during a key reproductive window. However, the pronounced variability in home range size, especially among juveniles, stresses the importance of understanding how spatial use shifts later in the season as flowering agaves begin to set fruit. Future research using longer-duration tags or collaborative tracking at a regional scale could help clarify movement along hypothesized nectar corridors to other foraging and roost areas, such as towards New Mexico or northern Mexico, once the local bloom subsides.

Landscape characteristics of the foraging range

The foraging behavior of *L. nivalis* in BBNP was strongly influenced by the mountainous terrain and vegetation structure of the region. Overall, tagged individuals concentrated their activity in the higher elevations available in the park, with core foraging

areas greatly overlapping the Sotol-Grassland association in which *A. havardiana* is most abundant and in which the timing of blooms overlaps most with *L. nivalis* presence (Kuban 1989). These mid to higher elevations are consistent with the known distribution of *A. havardiana* in BBNP, the primary nectar source during summer months, although few *A. havardiana* do occur in the low elevation desert scrub association (Kuban 1989; England 2012). The Chisos Mountains, where these foraging ranges occur, is considered a sky island. Therefore, the region is geographically isolated from other mountain ranges with suitable conditions for agave, which may further concentrate foraging activity in this area.

Foraging occurred predominantly on steep canyon slopes and rugged mountain sides (Fig. 10), with bats frequently appearing to commute along ridgelines between foraging patches. Although the resolution of the GPS data (10-min intervals) introduced some spatio-temporal uncertainty, especially in distinguishing between foraging and night-roosting behaviors, certain patterns emerged. In particular, many locations interpreted as foraging points were in close proximity to steep cliff faces and rocky outcrops, suggesting possible use of short-term night roosts situated just above foraging sites. Given the suspected association of *L. nivalis* with cliff roosts in this study, these high-elevation rocky zones may serve dual purposes as both feeding grounds and resting areas during extended nightly movements.

Aspect analysis revealed a non-random distribution of habitat use, with a clear selection for north and especially northwest-facing slopes within core areas (Fig. 14 and 15). Kuban (1989) reported that agaves in the Sotol-Grassland association, *A. havardiana*, were especially numerous on north and north-west facing slopes in his study. These aspects may provide cooler, wetter microclimates that support delayed flowering of agave or may help reduce thermal stress if *L. nivalis* use them for night roosting habitat, but more research on this is needed to better understand this pattern.

Vegetation structure across core foraging areas was generally low, with an average canopy height of approximately 1.6 m, consistent with pinyon-juniper woodlands, shrublands and grasslands that characterize much of the Chisos (Powell 1998). These open-canopy conditions likely facilitate maneuverability for nectar-feeding bats and increase visibility of flowering agaves on the landscape.

Together, these patterns suggest that *L. nivalis* selected foraging habitat based on a combination of elevation, slope, aspect, and vegetation structure that maximize resource availability and energetic efficiency. However, fine-scale behaviors of the bats including movement within single foraging areas or night roosting near foraging areas were not distinguishable because of the discrete time setting chosen for the tag (10 min intervals) and the error in GPS location accuracy which was variable for each point (Supplemental Data in Dryad; https://doi.org/10.5061/dryad.stqjq2cfg). Future work that incorporates finer-resolution tracking and environmental data could help more clearly distinguish between foraging and roosting microhabitats and refine our understanding of habitat selection mechanisms in this endangered migratory bat.

Movement behavior

Patterns in nightly flight distances and time spent active offer insight into the nightly foraging behavior of *L. nivalis* during the study period. While nightly flight distances did not differ significantly across weeks or age groups, adult bats spent significantly more time active in the third week. This increase in active time may reflect reduced time spent nursing pups and

a shift from lactation to post-lactation, allowing adult females to be away from the roost longer. Juvenile bats, though not statistically different, showed a similar upward trend in both nightly distance traveled and time active over the three weeks. This pattern may indicate developmental progression as volant juveniles matured into subadults, expanding their spatial use and foraging durations with increased flight capability and experience. Ontogenetic development likely plays a role, as juveniles in other bat species have been shown to gradually increase their activity levels and movement ranges with age (Buchler 1980). Social learning might also contribute, with young bats learning effective foraging strategies and routes by observing adult conspecifics or through independent exploration (Wright et al. 2011; Goldshtein et al. 2022). The increase in both duration of activity and distance traveled by juveniles in the final week suggests that even within a brief summer season at Emory Cave, individual development can influence spatial behavior, potentially impacting how the population tracks and utilizes shifting nectar resources like *Agave*. The increased activity and spatial coverage observed in week 3 could therefore reflect a combination of physiological maturation, growing independence from lactation, and environmental factors such as reduced nectar availability later in the flowering season (Kuban 1989) or increased competition as an influx of bats arrive at Emory Cave generally around the end of the first week in July (Ammerman et al. 2025).

Patterns of large-scale movement revealed notable long-distance excursions and speeds by both juvenile and adult *L. nivalis*, showcasing the remarkable mobility of the species and potential for landscape-scale habitat use (Fig. 18; Table 3). While long-distance excursions over 100 km were uncommon during the three-week study period (represented by 14% of tagged bats), they underscore the capacity of *L. nivalis* to make extensive flights across the landscape, potentially linking resource patches or alternate roosts over large spatial scales. These flight distances are similar to those of their congener, *Leptonycteris yerbabuenae,* which have been recorded traveling up to approximately 189 km between roosts (Laverty et al. 2025) and making round trip flights of approximately 100 km for foraging (Medellín et al. 2018). Additionally, these long-distance movements did not occur within 24 hours of tag attachment, therefore it is unlikely the tagging events influenced this behavior. On average, nightly flight distances were 32.5 km (± 26.4 km), consistent with previous studies reporting average distances up to 30 km per night (England 2012; Bogan et al. 2017). Nearly a third of the tagged bats (29%) made nightly flights over 60 km, and juveniles were twice as likely as adults to make those longer trips (2:1 ratio; Table 3). These findings reinforce the understanding that *L. nivalis* requires broad landscapes and well-connected foraging and roosting habitats to support its migratory and energetic needs.

Two tagged bats (a juvenile male and an adult female) exhibited long, directed flights consistent with commuting rather than foraging (Fig. 17), followed by day roosting within the Sierra del Carmen Mountains in Coahuila, Mexico, approximately 60 km southeast of Emory Cave. The female also night-roosted in-transit, indicating potential use of multiple roost locations during a single journey. Based on patterns of PIT tag detection, Adams (2015) suspected that there were alternate roosts in the region and the movements in our study imply the presence of undocumented roosts within the Maderas del Carmen Flora and Fauna Protected Area. The location of these undocumented roosts corresponds with *Agave* migratory corridor previously modeled (Gómez-Ruiz and Lacher 2017; Burke et al. 2019). Although our

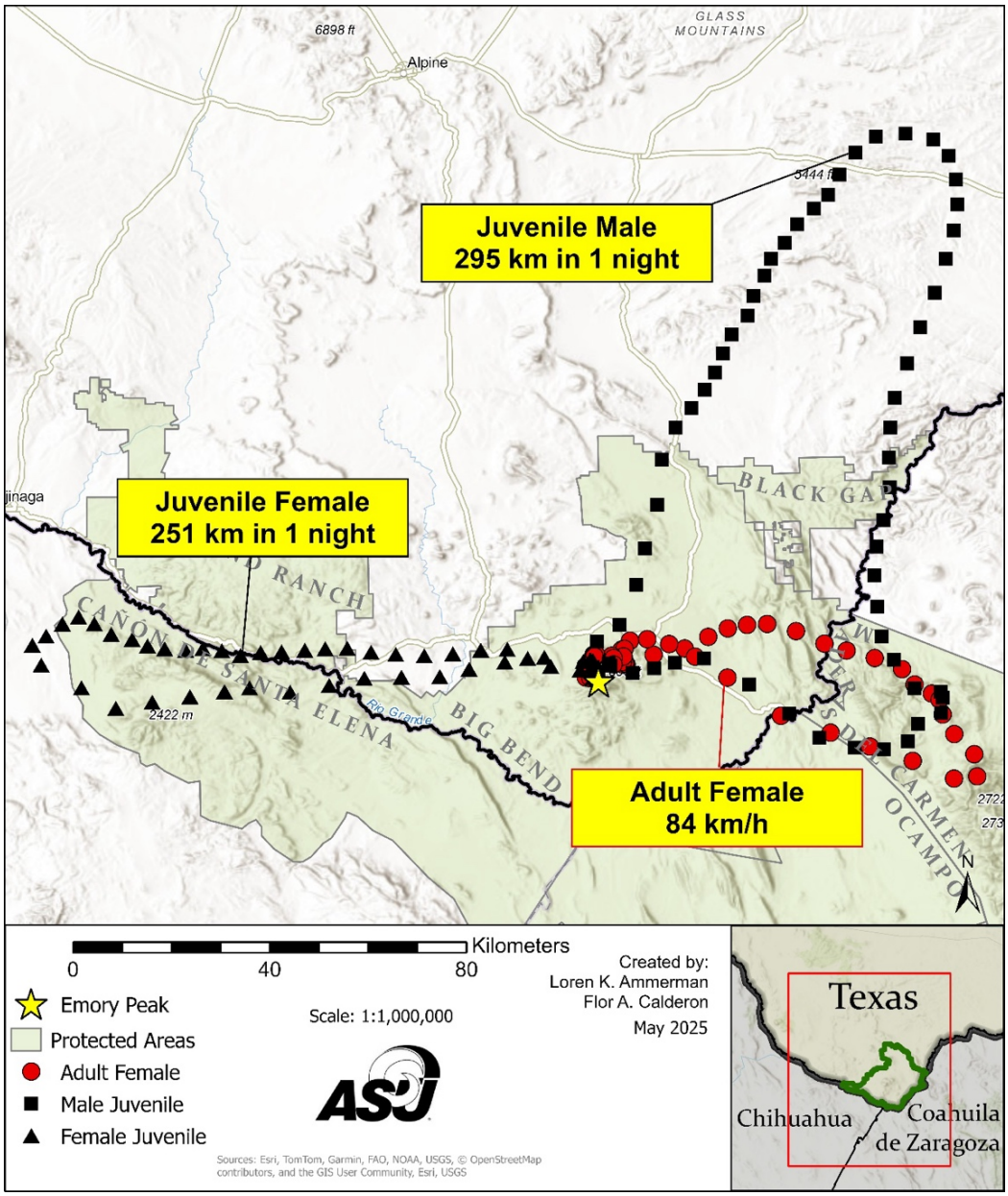


Figure 18. Notable movements of *Leptonycteris nivalis* captured in summer 2024 at Emory Cave, Chisos Mountains, Big Bend National Park, TX. GPS locations include the top 3 longest distances traveled from Emory Cave in one night and the fastest speed recorded for an individual.

GPS data could not resolve their precise locations, we have identified a 2 km radius region for further roost exploration (Fig. 17). Identifying and protecting these undocumented roosts is a critical conservation priority. According to the U.S. Fish and Wildlife Service (1994) recovery plan for *L. nivalis*, protection of roosting sites is central to the long-term survival of the species. Furthermore, the area between Emory Cave and the nearest known roost to the south, El Rosillo Cave (USFWS 2018), which is located approximately 400 km south, likely includes important migratory stopover sites. Bats undertaking such long-distance flights almost certainly require intermediate roosts for rest and thermoregulation as seen in other bats such as *Lasionycteris noctivagans* (McGuire et al. 2012), especially during seasonal movements between Mexico and the southwestern United States. These sites could function as temporary stopovers or alternate shelters used opportunistically during migration and may even be maternity roosts. Notably, return flights toward the Emory Cave region from these areas showed overlapping travel paths by individual bats, suggesting the existence of established movement corridors between the Sierra del Carmens and the Chisos Mountains. Future work should aim to clarify the locations, structure, and occupancy patterns of these undocumented roosts to guide transboundary conservation efforts.

Capture and tagging.– The species composition at Emory Cave during the study period aligned with expectations based on previous survey efforts (Adams 2015; Pourshoushtari and Ammerman 2021; Ammerman et al. 2025). The consistent presence of *L. nivalis* and four sympatric species indicates the ecological importance of this roost and supports continued monitoring. We encountered no difficulty in locating and capturing *L. nivalis* individuals that met our tagging criteria and allowed us to maintain transmitter weights below the 10% body mass guideline commonly recommended as the upper limit for tags on bats for short-term studies (Aldridge and Brigham 1988; O'Mara et al. 2014). While six tagged bats stopped transmitting after the first night, likely due to tag detachment, mortality, battery failure, or long-distance dispersal, 71% of individuals (15 out of 21) provided location data for more than two nights. This suggests that under favorable conditions, sufficient sample sizes of both adult and juvenile *L. nivalis* can be ethically tagged for transmitter-based studies. Notably, no previously PIT tagged individuals were recaptured, which may be attributed to the species' unknown average lifespan and our limited sample size. The absence of recaptures from previous studies could also reflect natural mortality, tag loss, or emigration patterns.

Data retrieval.– Our data retrieval strategy proved largely effective, yielding high-resolution GPS data from all tagged *L. nivalis* individuals. Despite some early technical issues with the stationary omni-directional antenna, the use of a 5-element Yagi antenna allowed consistent recovery of GPS fixes, facilitated by the central place foraging behavior of this species (Ober et al. 2005; Rainho and Palmeirim 2011). Like other phyllostomid bats, *L. nivalis* reliably returns to a day roost after nightly foraging, which enabled routine detection and download of location data in proximity to the cave. The total dataset of 2,652 filtered GPS locations across 95 tracking nights demonstrated the suitability of Lotek PinPoint GPS-VHF tags for this species, especially when coupled with strategic field-based remote data downloading. Although several tags recorded only brief durations of activity (2–3 days), most tags performed within the manufacturer’s expectation regarding lifespan given the programmed duty cycle. These results illustrate the importance of combining mobile and stationary download methods to maximize data recovery, particularly in topographically complex landscapes where line-of-sight signal reception may be hindered.

Ground-truthing of suspected foraging areas.– All verified sites of high bat activity contained blooming *A. havardiana*, the known dietary specialization of *L. nivalis* in their summer range in Texas (Kuban 1989). The relative daily nectar production modeled for latitudes of the Big Bend region peak during mid-July and agave have been documented to potentially be flowering from April to November (Moreno-Valdez et al. 2000). Notably, each confirmed foraging site was within visual range of rocky outcrops, which likely serve as suitable night roosts. Although these rocky features were not inspected closely, their proximity suggests that this landscape structure may play a dual role in providing both foraging areas and night roosting areas during active hours. The eight unverified sites likely contain similar habitat characteristics but were inaccessible due to terrain or time constraints. Future research should consider incorporating drone-based surveys with techniques using automatic image processing and machine learning to detect agaves (Flores et al. 2021; López-Alfaro et al. 2023). This approach could increase the efficiency of detection of flowering agave and aid in mapping potential night roosting substrates in the rugged terrain of this region.

Conservation Implications

Understanding the natural history of endangered species is fundamental for effective conservation and management. For *L. nivalis*, these findings contribute essential information on spatial ecology, nightly behavior, and landscape use, with several actionable implications for current and future conservation efforts. One of the most immediate applications of this research is informing habitat restoration initiatives. Based on core ranges estimated from GPS data and habitat associations observed in this study, agave restoration efforts should prioritize north-facing slopes (ideally oriented between 315° and 350°) at elevations near 1800 m, especially locations that contain steep, rocky cliffs within 1 km. Focusing agave restoration in these areas is likely to have the most successful ecological impact and can enhance both nectar availability and roost accessibility across the migratory range. Likewise, the results can help prioritize regions for agave population monitoring, particularly in areas shown in this study to be repeatedly used by foraging bats. Focusing vegetation surveys in these zones can help assess the availability of nectar resources and identify potential gaps in agave distribution that may affect bat foraging efficiency.

This study also emphasizes the ecological significance of *L. nivalis* as a long-distance pollinator. The documented nightly movements (some exceeding 250 km) highlight the potential of these bats to facilitate gene flow among widely dispersed agave populations. Protecting and enhancing habitat connectivity is therefore essential to maintaining this mutualistic interaction, particularly in the face of habitat fragmentation and climate change (Gómez-Ruiz et al. 2022; Trejo-Salazar et al. 2023).

Finally, these results raise important questions for future research. The presence of potential undocumented roosts in northern Coahuila and the extraordinary range of nightly movements suggest that *L. nivalis* may use a network of migratory stopover sites that have yet to be identified. Post-summer movements, seasonal shifts in habitat use, and the complete migration route from Mexico to the southwestern United States remain largely unresolved (USFWS 2018). Continued tracking studies, especially those spanning multiple seasons are essential to fill these knowledge gaps and inform species recovery efforts (USFWS 2018).

This study was subject to several limitations, particularly related to data collection using GPS tags. The Lotek PinPoint VHF transmitters had limited battery life, which required

programming trade-offs between spatial resolution and temporal coverage. Tags were set to record locations every 10 min, which extended battery life to increase the number of nights tracked, thus increasing the likelihood of detecting movements to nearby alternative roosts. However, this setting reduced the ability to detect fine-scale behaviors, such as short foraging trips or quick roost shifts. Additionally, the inherent spatial uncertainty of GPS data, especially at small scales, made it difficult to determine whether a bat remained stationary or moved short distances (e.g., <10 m). This level of positional error, combined with uncertainty in vertical accuracy, made it challenging to confidently distinguish foraging locations from nearby night roosting sites, particularly in steep, rocky areas where these behaviors may occur in close proximity and GPS satellite signal is more likely to be obstructed.

The GPS transmitters used in this study reported vertical position (z-values) as height above the WGS 84 ellipsoid. However, accurately determining height above ground level (AGL) from these values proved problematic. A commonly recommended approach is to subtract DEM values from the ellipsoidal heights to approximate AGL (Péron et al. 2020). This method, however, often produced negative values and inconsistent results, likely due to horizontal GPS error combined with the spatial resolution limits of available elevation data. While some studies improve vertical accuracy by incorporating barometric pressure sensors (Péron et al. 2020; Lato et al. 2022; Pineda 2023), that option was not available with our devices in order to keep the tag weight below 2.5 g. Determining the height AGL at which the bats were flying would provide more insight into understanding bat behavior, as bats can actively use topography and nocturnal updrafts to gain altitude, enhance flight efficiency, and access distant foraging areas (O'Mara et al. 2021). However, due to the unreliability of the derived elevation values, z-values were excluded from all analyses.

Lastly, this study represents just a single field season and may not capture broader inter-annual variation in bat behavior or agave flowering phenology. While we successfully identified foraging areas and possible night roosts in the Chisos Mountains region, a more comprehensive understanding of *L. nivalis* habitat use would benefit from long-term monitoring and repeated sampling across years. Future work incorporating landscape-scale agave surveys would also provide critical context for interpreting movement patterns and better inform conservation efforts.

Overall, this research underscores the importance of fine-scale movement data in guiding conservation effort for wide-ranging, migratory pollinators like *L. nivalis*. By identifying key foraging areas in the Chisos Mountains and patterns of nightly activity, these findings provide critical insight into the ecological needs of this endangered species. This information can help prioritize conservation strategies, such as targeted agave planting, focused monitoring, and international coordination, allowing conservationists to direct resources to the areas most vital for recovering *L. nivalis* populations and the ecosystems that support them.

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IV. Population trends of *Leptonycteris nivalis* at Emory Cave

Management strategies for bats require accurate knowledge of population size to determine population trends. However, the migratory nature of Mexican Long-nosed Bats (MLNB, *Leptonycteris nivalis*) makes estimation of the population size very challenging. Since 2008, the colony that occupies Emory Cave in the summer has been recorded with a thermal video camera as they emerge in the evening. Although the annual census results are reported to permitting agencies, there had not been a comprehensive analysis of population trends using these data.

We consolidated, compiled, and analyzed existing census data for MLNB Emory Cave collected since 2008 to determine if there were any obvious declines in the number of bats using this roost site in Texas. We consolidated all historical thermal video files of nightly emergences from Emory Cave from 2008 to 2023 and organized them into a spreadsheet for a total of 39 video files. During this process we also saved back-ups of every video file. Nights where there were technical difficulties with the camera were not included in this analysis (4 nights), leaving 35 nights for the analysis of population trends.

We used 4 models of thermal infrared cameras (FLIR Systems, Boston, MA) over the span of 16 years. Frame rates and resolution differed among models. We used a 45° wide-angle lens in most years and recorded emergences directly to a laptop computer instead of an internal memory card. We manually counted the census videos by slow replay in Research IR Max (FLIR) for those that had not been counted in years past and re-counted video files from 6 nights with discrepancies. The number of bats leaving the cave and entering the cave each minute were recorded separately for MLNB and for the other species in the cave (primarily *Corynorhinus townsendii* and *Myotis thysanodes*). There were no censuses conducted in 2019 or 2020 and in other years censuses were performed between 1 and 6 nights. Most of the videos were recorded in late June or early July when the colony size was expected to be the largest due to the availability of agave, however some censuses were performed in May and August. Nights with technical difficulties with the recordings (battery and/or equipment failures) were not included in this analysis, leaving 35 nights for the analysis of population trends.

Colony counts ranged from 5 to 3360 MLNB over all months and years. Analysis of the maximum colony size for each year (14 censuses over 16 years) showed large fluctuations despite being conducted in the first week of July each year. Some of the fluctuations could be due to normal fluctuations in movements of migrating bats resulting in early or late arrival of the bats to this roost, the number of *Agave* flowering that year to provide a suitable food source near the roost, or environmental conditions (precipitation, wind, moon phase) when the census was conducted. The lowest colony size was documented to be 294 on 3 July 2008 and the highest was 3360 5 July 2021. There were only 4 nights that the colony size was greater than 3000 bats (in 2009, 2012 and 2021). Based on our results, there was no obvious increase or decrease in the colony size at Emory Cave over the 14 years of this study. The mean colony size based on these 14 censuses in July was 2156 MLNB. In addition to manual analyses, we also used a computer-assisted census method called ThruTracker and compared the manual to the automated results. The automated method performed well, with overall 90.8% accuracy (range = 64-99%). These data were analyzed in more detail and were

published in a Special Issue of *Journal of North American Bat Research* in 2025 (Appendix III).

After this manuscript was sent for publication, a manual census was conducted in summer of 2024 using the same methodology resulting in a colony size of 1332 bats on 6 July 2024 (Fig. 19). With the additional information from this additional census year, the mean colony size across all the years that have been surveyed has decreased to 2101 individual MLNB compared to the published value of 2156 MLNB and the regression shows a slight decrease in colony size (Fig. 20).

To meet data sharing requirements, we created a project in the North American Bat Monitoring Program's (NABat) website (https://www.nabatmonitoring.org/) and submitted our census data from GRTS cell ID 109135. Users of this portal can request access to these emergence count data from 2008-2024. Note that the coordinates for the roost location contains a suitable amount of error to obscure the exact location of the cave. A Microsoft Excel spreadsheet of the data submitted to NABat is also available on Dryad (https://doi.org/10.5061/dryad.stqjq2cfg).

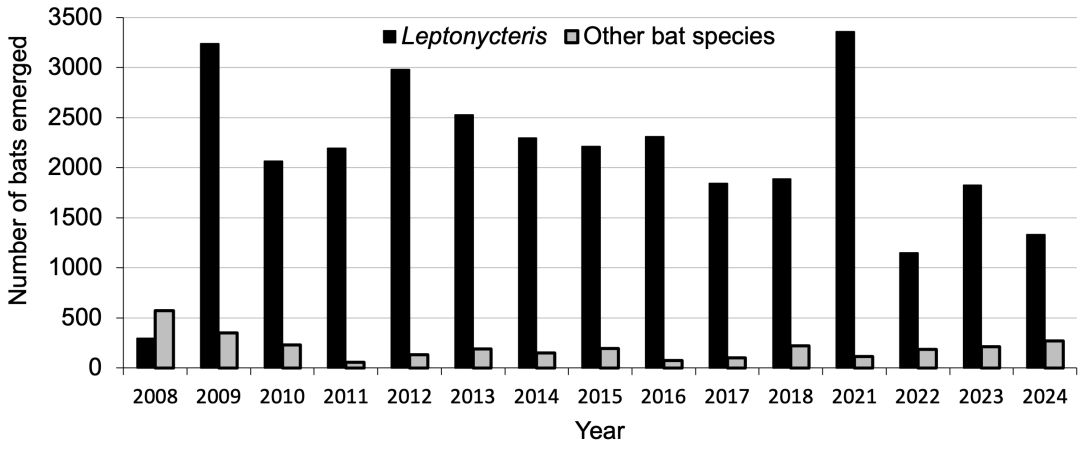


Figure 19. Annual census results for bats emerging from Emory Cave, Big Bend National Park in early July using thermal imaging techniques. Note that there was no census in 2019 and 2020. Other bat species include *Corynorhinus townsendii* and *Myotis thysanodes*.

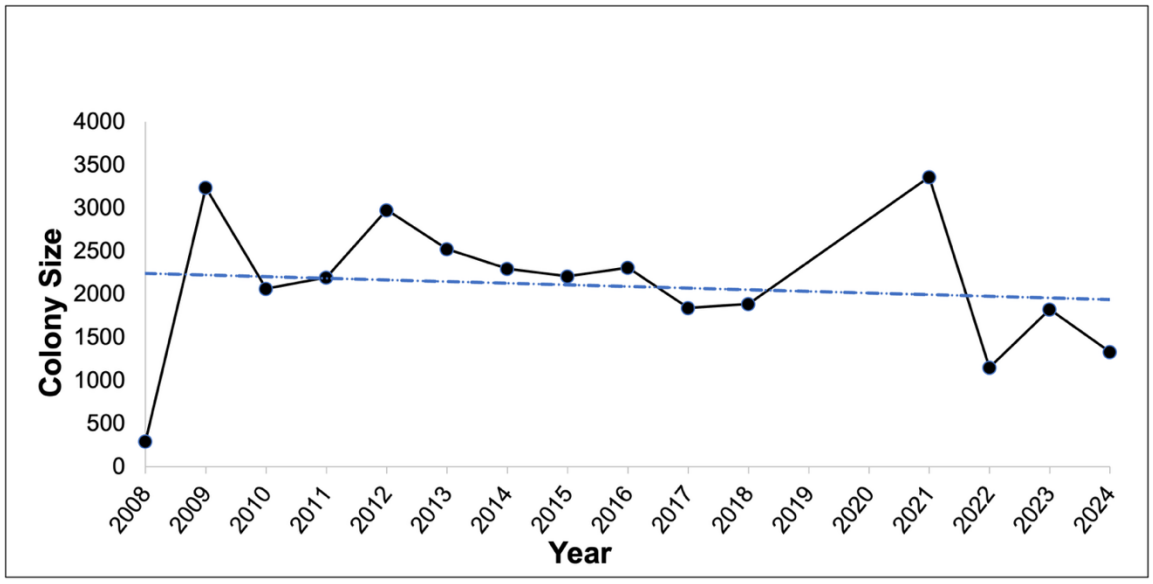


Figure 20. Population trend for *L. nivalis* at Emory Cave from 2008-2024. The single highest manual count in July of each year was reported. The blue dashed line is regression line with $r^2 = 0.0154$.

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VI. Appendices

APPENDIX I

Estimates of home range (100%, 95%, and 90%) and core range (65% and 50%) sizes in hectares for *Leptonycteris nivalis*, calculated using Minimum Convex Polygons (MCP), Kernel Density Estimation (KDE), and Local Convex Hulls (LoCoH). Estimates are based on filtered GPS data excluding locations with HDOP ≥ 20 and individual movements exceeding 100 km.

Tag ID	MCP 100	MCP 95	MCP 90	MCP 65	MCP 50	KDE 100	KDE 95	KDE 90	KDE 65	KDE 50	LoCoH 100	LoCoH 95	LoCoH 90	LoCoH 65	LoCoH 50
57222	2325.25	1265.12	669.08	46.38	44.87	4399.71	4399.71	2823.90	857.82	494.63	1445.53	911.59	349.79	25.71	2.83
57223	115.87	104.71	103.48	53.87	50.76	444.60	444.60	344.39	151.96	87.75	45.66	29.45	14.04	1.49	0.69
57224	290.04	280.87	221.46	9.24	8.89	488.30	488.30	344.65	103.95	61.23	46.02	26.75	10.12	1.12	0.54
57225	276.52	155.53	46.08	7.00	6.97	378.11	378.11	237.45	74.62	43.37	57.67	57.67	20.29	0.85	0.26
57226	111616.16	65233.39	7696.11	5480.88	3853.87	139878.34	139878.34	69901.51	18998.03	11271.19	65232.12	19217.79	4013.70	13.67	3.21
57227	278.69	183.62	179.84	49.51	29.51	655.47	655.47	495.67	176.04	94.88	113.62	54.39	23.22	1.17	0.38
57228	2836.70	1888.65	1321.29	87.93	74.11	2507.26	2507.26	1723.75	425.48	227.64	1283.67	742.40	302.93	34.06	1.49
57229	169.96	158.19	112.16	93.87	85.85	624.33	624.33	506.54	245.08	153.42	36.17	36.17	4.01	0.51	0.51
57230	636.98	312.51	29.55	9.31	5.29	352.03	352.03	181.85	49.01	27.80	299.93	148.51	15.44	1.03	0.40
57231	58841.90	24008.28	1249.23	1234.54	1226.57	95040.11	95040.11	51606.63	15303.49	9103.04	40395.23	17347.30	297.69	0.21	0.10
57232	766.15	649.29	313.35	15.39	11.96	786.20	786.20	496.98	121.13	66.04	348.91	182.42	83.67	4.43	1.05
57233	410.36	260.56	111.28	74.04	40.57	514.72	514.72	378.95	145.17	78.38	110.49	71.58	41.83	2.13	0.59
57234	847.84	743.41	178.70	25.34	9.45	1698.73	1698.73	1262.34	434.58	257.58	185.96	72.91	72.91	10.97	2.19
57235	444.63	341.25	307.84	99.90	36.74	3069.60	1932.15	1129.55	33.03	388.80	46.32	46.32	46.32	12.37	0.62
57236	13852.63	6143.80	2587.84	641.96	602.61	485752.17	485752.17	372412.60	107255.11	1827.77	8444.33	5249.05	1727.46	5.25	1.08
57237	104.12	5.33	1.70	0.83	0.79	119.66	119.66	72.37	26.59	16.55	4.07	4.07	0.78	0.08	0.04
57238	21017.00	12179.76	7836.88	3731.43	2980.87	24028.37	24028.37	15970.54	6658.82	4373.73	8463.89	5460.57	3461.95	309.80	36.75
57239	5719.88	5223.05	4981.57	4324.91	2990.51	13537.21	13537.21	10846.09	5068.40	3175.83	2692.52	1076.21	626.01	150.70	16.27
57240	496.06	81.73	11.72	2.21	1.51	94.84	94.84	41.23	10.49	4.78	259.84	58.82	4.95	0.41	0.11
57241	50577.23	29117.87	6678.13	130.95	126.07	27148.38	27148.38	11636.41	2296.77	1190.47	21381.39	10033.29	2533.77	38.99	1.36
57242	36757.55	26008.47	9369.01	393.62	25.16	27829.85	27829.85	14359.29	2545.75	1325.15	20263.22	14667.98	5326.99	7.06	1.27

APPENDIX II

Summary of statistical test results regarding home range sizes and characteristics, nightly distance, and nightly duration of activity of *L. nivalis* from Emory Cave. Values in bold were statistically significant.

Analysis	Comparison	Test	Test statistic	df	P-value
Home Range Size	Adults vs Juveniles	ANOVA	1.24	1,19	0.28
Home Range Size	Across weeks: All bats	ANOVA	1.07	2,18	0.36
Home Range Size	Across weeks: Adults	ANOVA	0.006	2,9	1.00
Home Range Size	Across weeks: Juveniles	ANOVA	6.09	2,6	**0.036**
Core Range Size	Adults vs Juveniles	ANOVA	0.006	1,19	0.94
Core Range Size	Across weeks: All bats	ANOVA	0.71	2,18	0.51
Core Range Size	Across weeks: Adults	Welch's ANOVA	0.93	2,5	0.45
Core Range Size	Across weeks: Juveniles	ANOVA	1.57	2,6	0.28
Nightly Distance	Adults vs Juveniles	ANOVA	3.62	1,19	0.07
Nightly Distance	Across weeks: All bats	ANOVA	0.62	2,18	0.55
Nightly Distance	Across weeks: Adults	ANOVA	0.13	2,9	0.88
Nightly Distance	Across weeks: Juveniles	ANOVA	0.81	2,6	0.49
Nightly Activity	Adults vs Juveniles	ANOVA	0	1,19	0.98
Nightly Activity	Across weeks: All bats	ANOVA	7.87	2,18	**0.035**
Nightly Activity	Across weeks: Adults	ANOVA	7.65	2,9	**0.011**
Nightly Activity	Across weeks: Juveniles	ANOVA	2.54	2,6	0.16
Home Range Method	MCP vs KDE vs LoCoH	ANOVA	7.35	2,60	**0.0014**
Core Range Method	MCP vs KDE vs LoCoH	ANOVA	22.55	2,60	**0.001**
Landscape: Elevation	Observed vs Expected	Welch's t-test	-1103	na	**< 0.001**
Landscape: Slope	Observed vs Expected	Welch's t-test	-552.3	na	**< 0.001**
Landscape: TRI	Observed vs Expected	Welch's t-test	525.86	na	**< 0.001**
Landscape: Canopy Height	Observed vs Expected	Welch's t-test	727.04	na	**< 0.001**
Landscape: Aspect	Observed vs Expected	Watson-Wheeler test	562401	2	**< 0.001**

APPENDIX III

Publication in *Journal of North American Bat Research* over population trends of *Leptonycteris nivalis* at Emory Cave from 2008 to 2023

The following published article was facilitated by funding from this grant. The citation is:

> Ammerman, L. K., A. E. Loehn, F.A. Calderon, R. D. Pourshoushtari, E. R. Adams, and M. T. Dixon. (2025). **Long-term monitoring of endangered Mexican Long-nosed Bats (*Leptonycteris nivalis*) and a test of an automated census approach**. *Journal of North American Bat Research*, Special Issue 1 (2024): 11–29.

Link to this paper: https://www.eaglehill.us/NABRonline/access-pages/spec01/002-Ammerman-accesspage.shtml