Survey Methods for Monitoring Bat Populations
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Using Passive Integrated Transponder (PIT) Tags to Monitor and Research Bats: Applications, Benefits, and Limitations

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Abstract - Worldwide declines of bat populations underscore the value of developing and refining survey tools to assess and monitor population statuses and dynamics. Passive integrated transponder (PIT) tags can be an effective marking technique, facilitating the monitoring of individual bats at roost sites by using radio frequency (RFID) readers and antennas. We detail 5 ongoing studies, discuss the rationale for our study designs, and offer recommendations for monitoring and researching bats with PIT tags that are broadly applicable across species and locations. Using data from RFID readers, we show how population parameters can be precisely estimated across space and time, while improving our understanding of bat ecology and vulnerability to threats. We discuss PIT-tag loss as a potential limitation that varies across species, sex, and season, present minimum loss rates from 2 studies, and describe consequences and techniques to ameliorate this issue. Overall, integrating PIT tags with autonomous RFID readers and antennas provides a powerful survey method for monitoring, researching, and conserving bat populations.

Introduction

As bat populations worldwide are decreasing at unprecedented rates (Frick et al. 2020), the development and refinement of survey methods is important to track demographic parameters and advance our understanding of ecology. Monitoring bat populations is critical for making effective conservation decisions, yet standard survey techniques (e.g., acoustics, captures, and emergence counts) have limitations in the precision and scale of data they can provide (Kunz 2004). While particularly useful for monitoring spatial and temporal occupancy of species, and establishing baselines at local scales to inform conservation needs (Myers et al. 2024), these methods give little insight into individual-level processes essential for understanding population dynamics. Individually marking bats enables the collection of long-term data on movement patterns, roosting behavior, feeding strategies, reproductive phenology, and other metrics of conservation importance. These individual-based data are crucial for precisely estimating abundance and survival rates, and for inferring the vulnerability of populations to environmental disturbances, such as disease, climate change, habitat loss, and wind-energy development (Weller et al. 2009).

Marking and repeatedly resighting marked bats throughout their lives permits the use of robust analytical techniques capable of identifying critical populations or regions in need of attention. Through improving the accuracy and precision of methods to estimate demo-

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graphic parameters, vulnerable bat populations requiring conservation action can be identified, and managers can directly evaluate the degree that ongoing conservation actions are benefiting populations (O'Shea et al. 2003, Runge 2011). An increased understanding of bat ecology generated from these strategies can also lead to the development of more informed management approaches, as we can synthesize data about the bat's specific behaviors, social structures, foraging strategies, disease dynamics, and phenology of migrations, reproduction, and hibernation (Weller et al. 2009).

Mark-recapture and mark-resight techniques (McClintock and White 2012) are 2 of the most effective methods for identifying environmental and individual factors affecting bat populations at local scales (Frick et al. 2010, Maslo et al. 2015). For decades, the primary method to mark bats has been attaching metal forearm bands engraved with unique characters, enabling identification upon recapture and assessment of survival, longevity, distribution, and roost use (Ellison 2008). However, this technique has several challenges: improper application can lead to injury, irritation, and altered behaviors; identifying characters can become obscured by damage or tissue overgrowth; and bands can be lost (Baker et al. 2001, O'Shea et al. 2004, Zambelli et al. 2009). While these occurrences are well documented (Ellison 2008, O'Shea et al. 2004), their negative effect on population parameter estimates is poorly understood, as it is difficult to quantify the degree of information lost when bat health is impaired, or marks are compromised (Mellado et al. 2022).

To mitigate these challenges, researchers needing to mark various wildlife species have subcutaneously implanted passive integrated transponder (PIT) tags, which are small (usually 9–12-mm long and 2 mm in diameter), lightweight (<0.1 g), uniquely coded microchips (Kunz and Weise 2009). PIT tags are considered passive because they do not contain batteries, remaining dormant until activated by electromagnetic fields emitted from nearby radio frequency identification (RFID) antennas. This benefit allows PIT tags to operate throughout the lifespan of a tagged animal and provides researchers a unique opportunity to install autonomous long-term monitoring systems that collect data continuously. Initially used to identify bats in laboratory conditions (Barnard 1989), PIT tags have since become valuable tools in studies of bat population and ecology (Ellison et al. 2007b, Kerth and Reckardt 2003, O'Shea et al. 2004). Although injecting PIT tags is an invasive procedure, there is no evidence that it causes significant or prolonged injury, alters behavior, or negatively affects survival, reproduction, or body condition (O'Shea et al. 2011, Rigby et al. 2012, van Harten et al. 2019). Since bats sometimes exhibit trap-avoidance (Berry et al. 2004), using PIT-tag-reading antennas instead of physically recapturing marked individuals can improve detection probability, making RFID technology uniquely valuable for mark-recapture studies (Ellison et al. 2007a, van Harten et al. 2022b). Because capture effort is no longer required to re-encounter tagged bats with RFID readers and antennas, large amounts of data can be collected without disturbance, greatly increasing the precision of population parameter estimates, such as apparent survival, recruitment, and population growth rates (Ellison et al. 2007a).

Our objective was to review 5 ongoing bat studies employing various methodologies to showcase the utility of PIT tags in supporting investigations and monitoring efforts across diverse species, research questions, and study areas. To demonstrate the utility of PIT tags with automated RFID readers and antennas, we offer a comprehensive overview of projects optimizing their use, each including relevant data, along with guidance and insights for designing effective RFID studies. In addition to the merits of this technique, we present key limitations, such as PIT-tag loss, by describing minimum rates of loss observed in 2 of our studies. We then discuss how tag loss and other factors may affect population parameter estimates across different species, sexes, and seasons, and address ways to ameliorate potential biases, both before and after data collection. Overall, our collective studies demonstrate how integrating PIT-tagging with autonomous RFID monitoring provides a powerful approach for evaluating bat populations and advancing ecological understanding, while minimizing disturbance.

Benefits of PIT-tagging for Estimating Apparent Annual Survival

To illustrate the benefits of PIT-tagging bats for monitoring efforts and studies of population dynamics, we analyzed 8 years of mark-recapture data from 2 maternity colonies of PIT-tagged *Myotis lucifugus* (Le Conte) (Little Brown Myotis) in northwestern Colorado (Schorr and Siemers 2021). Our objective was to compare the performance between physical recaptures and detections of tagged bats by RFID equipment. Although we could have selected any population parameter of conservation interest to compare these techniques, we used apparent survival and reported associated recapture probabilities and variability estimates. Physical recaptures occurred when PIT-tagged bats were caught in nets on subsequent nights. We used these recaptures as a proxy for other marking methods, such as banding, that require animals to be physically present to identify marks. However, we recognize that our rates of physical recapture could differ from rates based on recaptures of banded bats, as PIT tags may be lost at different rates than other marks (see below). Nevertheless, RFID-reader recaptures (detections) demonstrate the benefit of passively scanning animals without requiring subsequent physical recaptures.

Our study was conducted at 2 maternity roosts, 42 km apart in the Yampa Valley of northwest Colorado — the Rehder House (herein called "Ranch House") and Carpenter Barn (herein called "Old Barn"). Using mist nets and harp traps, we captured bats biannually in June and August 2014–2018, then annually in July 2019–2022. Captures were not conducted in August 2017 at the Ranch House, nor at either location in 2020 due to COVID-19 restrictions. Captured bats were marked with a 9-by-2 mm low-frequency (134.2 kHz) PIT tag (HPT, Biomark, Inc., Boise, ID), inserted subcutaneously below (i.e., inferior to) the scapulae, with injection sites sealed using a biomedical adhesive (Vetbond Tissue Adhesive, 3M Science, St. Paul, MN) to increase tag retention and prevent infection.

Beginning in 2015, PIT-tagged bats were detected with a 7.6-m-long cord antenna attached to an RFID reader (IS1001, Biomark, Inc.) at each roost (for specific configurations see Schorr and Siemers 2021). For this analysis, we only used data from adult females, because this demographic comprised most (78%) captures during the study (Schorr and Siemers 2021). We constructed separate encounter histories for PIT-tag detections and physical recaptures, based on yearly encounters from 2015 to 2022. These data were analyzed using a Cormack-Jolly-Seber model in the RMark package (v. 3.0.0) within R (R Core Team 2023; v. 4.3.2), to estimate apparent survival (φ) and capture probability (p). We compared competing models and selected the most parsimonious, using Akaike's information criterion (AIC_c weight; w) for small samples (Burnham and Anderson 2002). Models were constructed by first modeling p, while keeping φ time (year) dependent. Once the best set of models of p were identified, we used those models of p to model φ. We ran 7 models for p and φ using the best model of p (Table 1).

We implanted PIT tags in 800 Little Brown Myotis at Old Barn and 715 at Ranch House (1515 total). Of those, we recaptured 15.7% using mist nets and harp traps, with no single individual caught more than 3 times (Fig. 1). In contrast, 64% and 75% of PIT-tagged individuals were detected more than once by antennas attached to RFID readers at Old Barn and Ranch House, respectively, with 8% of the 2015 cohort detected every year throughout the study (Fig. 1). The roosts appeared to host distinct, closed colonies, as shown by analyses indicating the absence of movement between them and colonies different φ stressors.

The most parsimonious model for both recapture types included a location (ranch) * time (year) interaction for *p*, with an AIC_c > 98%. All φ models were built using a *p* (ranch * time) parameterization. For physical recaptures, the top model of apparent survival included φ (time) (54.8% *w*) and φ (location) (35.3% *w*), with the remaining models receiving little support (*w* < 1%). For RFID reader recaptures, the top model of apparent survival was φ (location * time) (99.9% *w*). The last estimates of φ and *p* are not presented as they were time-dependent and, thus, confounded in the Cormack-Jolly-Seber model (Lebreton et al. 1992; Fig. 2).

Table 1. Parameterization of apparent survival and capture probability for capture-mark-recapture analysis of PIT-tagged adult female Little Brown Myotis physically captured and detected by RFID readers from 2015 to 2022.

Parameter	Constraints	Symbol
capture probability (*p*)	constant	.
apparent survival (*φ*)	time	t
	trend over time	T
	location	ranch
	location + time	ranch + t
	location * time	ranch * t
	location + trend	ranch + T
	location * trend	ranch * T

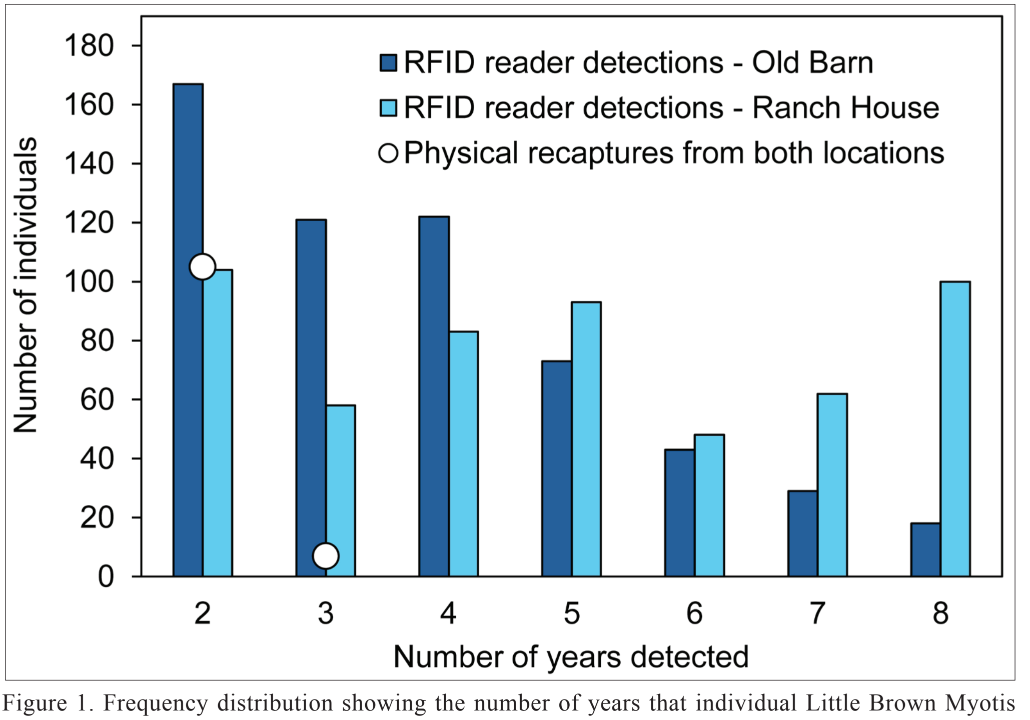

Figure 1. Frequency distribution showing the number of years that individual Little Brown Myotis were detected by RFID readers (bars) or physically recaptured (circles) from 2015 to 2022. The bats were tagged at 2 summer roosts: Old Barn (*n* = 800) and Ranch House (*n* = 715).

Physical recapture data yielded model-averaged estimates of *p* ranging from 0.009 (*SE* = 0.005) to 0.05 (0.02) at Old Barn and 0.016 (0.007) to 0.260 (0.008) at Ranch House. Apparent survival from physical recaptures varied from 0.59 (0.40) to 0.89 (0.09). RFID reader redetection data yielded model-averaged estimates of *p* ranging from 0.73 (0.03) to 0.90 (0.02) at Old Barn and 0.88 (0.02) to 0.97 (0.01) at Ranch House. Apparent survival from PIT-tag recaptures varied from 0.67 (0.03) to 0.86 (0.03).

As expected, estimates of *p* from PIT-tag detections were dramatically higher than those from physical recaptures, providing much more precise estimates of φ ($SE_{\text{PIT tags}}$ ~0.03 vs. SE_{Physical} ~0.15). The lack of precision in physical-recapture-based φ makes assessing trends difficult, as indicated by the wide standard errors for physical-recapture-based φ (Fig. 2). The added precision of φ estimates from RFID-reader recaptures demonstrate parabolic or

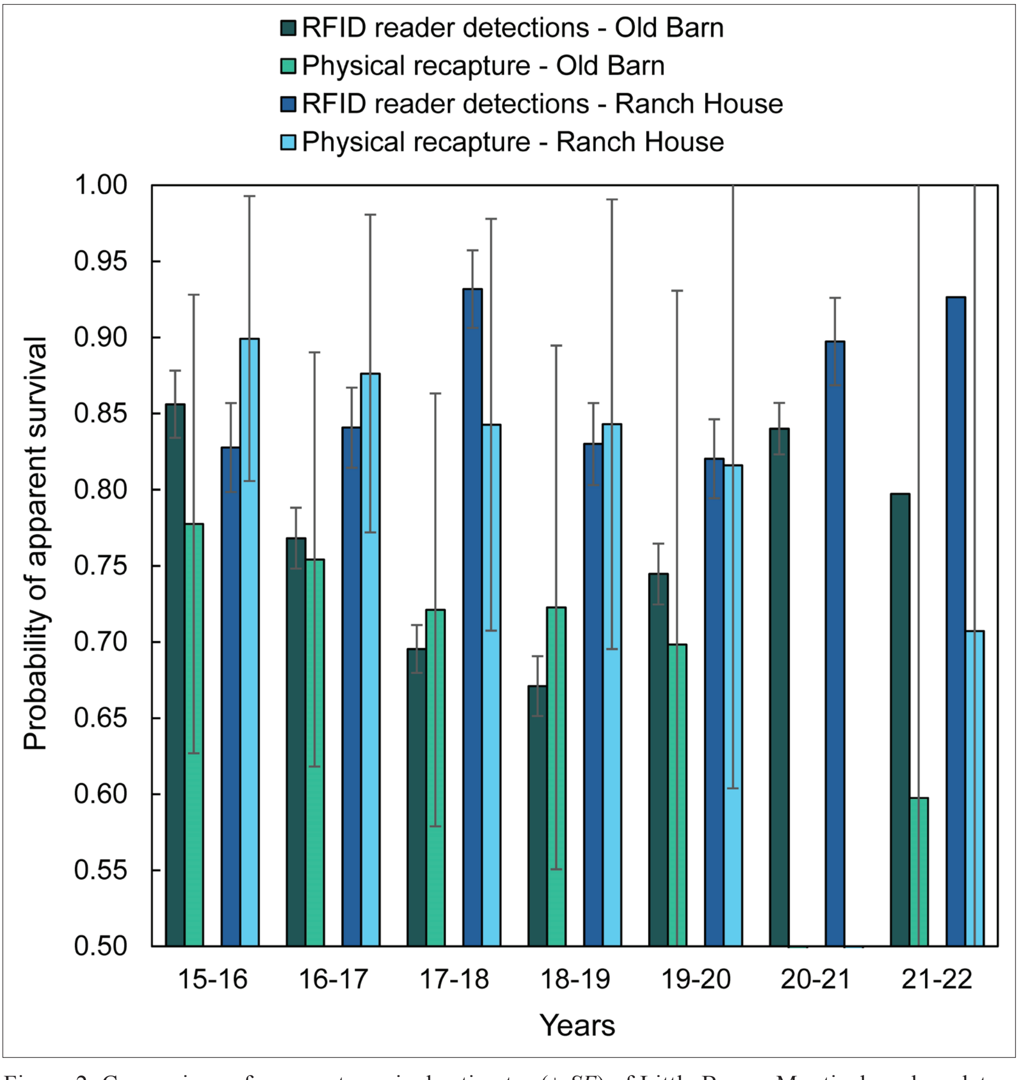

Figure 2. Comparison of apparent survival estimates (± *SE*) of Little Brown Myotis, based on detections by an RFID reader (dark shades with relatively smaller *SE*) and physical recaptures (light shades with relatively larger *SE*) at 2 summer roosts, Yampa Valley, Colorado (2015–2022). Standard error was not calculated for the final year of PIT-tag data.

cubic patterns to φ (Fig. 2), suggesting the ability to detect different influences underlying φ patterns at each roost. Besides improving our ability to assess demographic parameters precisely, the use of RFID equipment also prevented a break in our long-term dataset by providing recapture data to estimate yearly survival in 2020, despite COVID-19 restrictions preventing physical captures. From the implementation of this monitoring program, we have established robust baseline estimates of survival and abundance before populations experienced exposure to the fungus that causes white-nose syndrome, providing us a method to evaluate how our populations may respond to that disease, should it spread to our RFID-monitored colonies (Schorr and Siemers 2021).

The use of RFID equipment in studies of *Eptesicus fuscus* (Palisot de Beauvois) (Big Brown Bats) yielded similar results, doubling *p* and likewise improving precision of φ estimates (Ellison et al. 2007a). This increase in the precision of *p* and φ can be attributed to the ability of RFID readers and antennas to record an enormous amount of data continuously, as highlighted by van Harten et al.'s (2019) work with *Miniopterus orianae bassanii* (Cardinal and Christidis) (Southern Bent-wing Bats), for which 97% of 3000 PIT-tagged bats were redetected at least once across 1.6 million detections. These data enabled robust assessments of *p* and φ, which are currently being used to identify and incorporate physiological, seasonal, and environmental stressors into conservation strategies for this endangered species (van Harten et al. 2022b).

Estimating Abundance and Describing Roosting Behaviors with PIT Tags

While the previous case study demonstrated the benefits of using automated RFID systems to estimate survival, obtaining data that effectively addresses research questions requires careful antenna placement and study design, based on research and monitoring priorities and how bats use a site. To estimate abundance, roost fidelity, social interactions, and seasonal phenology of Little Brown Myotis in Yellowstone National Park, Wyoming, we subcutaneously implanted 384 female bats with 12-by-2.15 mm high-frequency (13.56 MHz) PIT tags (HID Global, Granges-Paccot, Switzerland) (Waag et al. 2021, 2022). Injection sites were sealed with surgical adhesive (Vetbond Tissue Adhesive) and lightly coated with a cornstarch "baby" powder that was non-scented and talc-free; this application allowed bats to be instantly released without waiting for the adhesive to dry, which reduced handling time and injury risk from bats adhering to themselves or other surfaces.

To study how bats occupying the same roost form social relationships and interact with each other, 5 readers (HDX Multi-antenna Reader, Oregon RFID, Portland, OR) were installed at maternity roosts in Mammoth Hot Springs and Lamar Valley, 37 km apart. On ceilings within these roosts, 32 antennas (24 at Mammoth Hot Springs and 8 at Lamar Valley) were installed, enabling the construction of intraroost networks based on the proximity and frequency of interactions between bats (see Waag et al. 2021 for specific configurations). We also placed 3 antennas (2 at Mammoth Hot Springs and 1 at Lamar Valley) over entrances to create cohabitation networks using the arrival and departure of bats to each roost. Intraroost and cohabitation networks were overlaid to provide detailed observations of roostmate preference, interactions, and relationship change over time.

To our knowledge, this was the first wildlife study to use automated high-frequency readers. Developing these readers with Oregon RFID was essential for ensuring the detection of all tagged bats present near ceiling antennas, as high-frequency systems possess advanced anti-collision algorithms to ensure hundreds of PIT tags can be read simultaneously by a single antenna without interference. At this time, available low-frequency systems possess simpler or no anti-collision capabilities, and some tags (often the largest or closest to an antenna) may block other tags from being recorded (Klair et al. 2010). Although, as low-frequency readers can scan for tags multiple times per second, this limitation may not be an issue if tagged bats are moving through an antenna's field or are present in small numbers. While high-frequency RFID offered necessary advantages for our study, low-frequency systems remain highly valuable due to their high-frequency systems in detection range, signal penetration through materials, susceptibility to interference, and cost-effectiveness.

At both Yellowstone roosts, we compared cohabitation and intraroost networks, showing that roost cohabitation, which is commonly used as a measure of social relationship strength in bats, did not reflect the proximity or frequency of interactions within the roost due to social or environmental factors (e.g., size, structure, and individual preferences) (Waag et al. 2021). The substantial differences in these 2 networks contrast with findings from other studies (Patriquin et al. 2010, Sunga et al. 2024, Wilkinson et al. 2019) and suggest that social network analyses based solely on cohabitation because they can obscure true social structures and dynamics, and may provide misleading results. Our study design highlights the utility of using PIT tags with automated readers to examine associations of bats at finer time scales than daily cohabitation allows, providing insights into social structures that may be overlooked by traditional methods (Waag et al. 2021).

Although passive detection of PIT-tagged bats can provide valuable data on survival, movements, and roost use, this approach alone often lacks the resolution needed to calculate an accurate estimate of abundance. One of the most common methods used to monitor colony sizes involves periodically recording the number of bats that emerge at dusk throughout the maternity season. However, since bats asynchronously switch roosts, these emergence counts only capture a portion of the bats using the roost that happen to leave at dusk on any given night, rather than the total number of bats using the roost throughout the season (Barclay et al. 2024, Kerth 2008, Waag et al. 2022). Performing emergence counts outside RFID-monitored roosts provided estimates that approximated the roost fidelity of PIT-tagged bats occupying the roost, rather than estimates of the summer population size itself (Fig. 3). However, through our emergence counts, we obtained valuable data on the exact number of bats, both with and without PIT tags that passed through antennas at roost entrances. This information enabled us to derive precise population size estimates, increase the precision of other population parameters, and more fully capture the dynamics of the entire colony throughout the year (Waag et al. 2022).

Our abundance estimates were created using the immigration-emigration logit-normal mark-resight estimator (McClintock and White 2012). Models were built in Program MARK (White and Burnham 1999), with 1 primary sampling interval (the maternity season) composed of secondary occasions (emergence counts). We found this analysis to be well suited because it accounts for imperfect detection to produce estimates of the superpopulation, which in our study represented the total number of adult females (marked and unmarked) using each RFID-monitored roost during the maternity season. Only adult females were included in analyses, because data collection occurred before young became volant and males do not occupy these roosts (Johnson et al. 2017).

At Mammoth Hot Springs, emergence counts performed in 2017 and 2018 ranged from 59 to 498 bats (= 214 ± 23 *SE*), while estimated population sizes at the roost during the maternity season were substantially higher in both 2017 (847 ± 60 bats, 95% CI = 749–987) and 2018 (836 ± 67 bats, 722–989). For the Lamar Valley roost in 2018, emergence counts ranged from 27 to 172 bats (= 56 ± 13), while the population estimate was 208 ± 6 bats (198–222). The development of this long-term monitoring system provides Yellowstone Park with a tool to detect, in real-time, if measures of abundance, roost fidelity, and seasonal phenology deviate from these baseline estimates, potentially serving as an early warning system for conservation intervention.

Monitoring Movements, Activity, Population Status, and Phenology

While the previous case study demonstrated how PIT tags and RFID readers can collect data to estimate local abundance, roost fidelity, seasonal phenology, and behavioral interactions at individual roosts, RFID monitoring also allows for the study of the behavior, ecology, and population status across the entire range of a species. Since 2013, we have marked 4000 *Leptonycteris yerbabuenae* Martínez and Villa-R (Lesser Long-nosed Bats) at roosts with 12.5-by-2.03 and 8-by-1.4 mm PIT tags using an applicator gun (Biomark, Inc.), sealing insertion sites with a surgical adhesive (Vetbond Tissue Adhesive). The smaller tags were used by collaborators in the beginning of the study, before we switched to larger tags to increase detection range. This study involves monitoring 7 maternity roosts, 4 late-summer transitional roosts (where females and volant young stage before traveling south), and 1 bachelor roost, through the installation of RFID readers (IS1001, Biomark, Inc.) and 5–25 m flexible cord antennas (Biomark, Inc.) over roost entrances. These RFID-monitored caves and mines, some containing aggregations of tens of thousands of bats, are located throughout southern Arizona, New Mexico, and western Mexico, including Baja California. See Laverty et al. (2025), Frick et al. (2018), and Rivera-Villanueva et al. (2024) for additional details concerning this study.

Given the substantial distance between the northernmost and southernmost roost (~1630 km), this study has the potential to detect a range of movements in Lesser Long-nosed Bats, including migration, long-distance within-season movements, and variations in phenology across populations. This wide geographic coverage (both in distance and number of RFID-

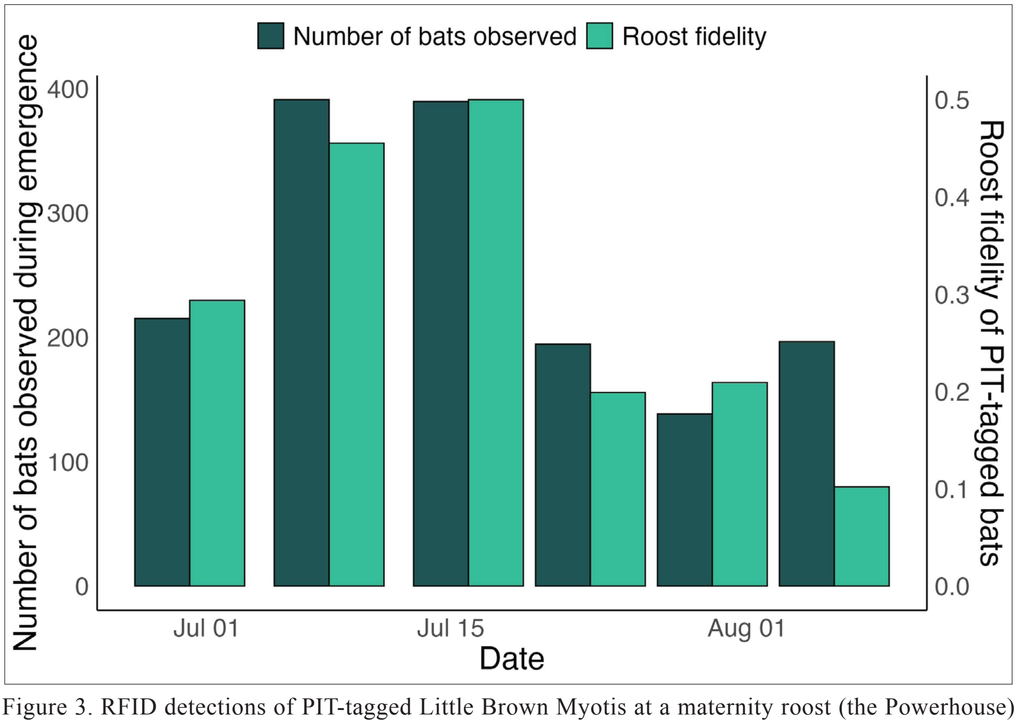

Figure 3. RFID detections of PIT-tagged Little Brown Myotis at a maternity roost (the Powerhouse) in Yellowstone National Park help explain fluctuations in nightly emergence counts. Emergence count and roost fidelity values are averages of data collected between consecutive dates shown during 2017.

monitored sites) is vital for measuring range shifts and monitoring how climate change affects population metrics and ecological dynamics. As nectarivores that must seek available food sources continually to compensate for the low energetic gain from nectar (Kelm et al. 2011), Lesser Long-nosed Bats follow migration corridors during the spring and summer bloom of paniculate agave and columnar cacti (Rojas-Martínez et al. 1999). Using PIT-tag detections from bats marked during different seasons, Frick et al. (2018) discerned that most bats occupying a roost in mid-winter were likely migrants, rather than year-round residents.

In addition to metrics described in our previous case studies, RFID readers recorded seasonal occupancy, migratory patterns, reproductive phenology, and long-distance movements. Collectively, these data recorded across the network of RFID readers enabled researchers to make inferences about the dynamics and statuses of Lesser Long-nosed Bat populations. As nearly one-third of the maternity sites reported in Frick et al. (2018) have since been destroyed, PIT-tagging provides a valuable method to complement population monitoring and aid efforts to inform conservation actions (Frick et al. 2018, Laverty et al. 2025, Rivera-Villanueva et al. 2024).

Although seasonal ecology and behaviors of Lesser Long-nosed Bats in some areas are well-known (e.g., sections of mainland Mexico and southwestern U.S.), population threats and resilience due to varying resource requirements may differ across the species' range (Channell and Lomolino 2000). For example, daily detections at an RFID-monitored roost on Isla Carmen, in Baja California Sur, show that bats consistently leave the cave for about 2 weeks in mid-June each year, coinciding with the shift in food availability from cactus nectar to cactus fruit and the time when young-of-the-year become fully volant (Frick et al. 2018, Rivera-Villanueva et al. 2024). The reason for this temporary exodus and return remains unknown, but it may be related to the maternal guidance hypothesis, which proposes that offspring develop their spatial memory through social learning, as mothers guide pups to known roost sites and foraging areas (Stumpf et al. 2017, van Harten et al. 2022a). As these habitats are at high risk of environmental modification from land practices and climate change (Zamora-Gutierrez et al. 2018), researching the effects of seasonal nectar and fruit availability on movements and populations will be valuable for estimating Lesser Long-nosed Bat vulnerability throughout their range (Vargas-Contreras et al. 2009). As more sites are equipped with RFID readers and antennas, the ability to monitor population status improves, as does our understanding of Lesser Long-nosed Bat ecology across space and time, both of which can inform conservation efforts as they relate to climate and land use changes.

Assessing PIT-tag Loss at Lesser Long-nosed Bat Roosts

While PIT tags generally remain securely implanted throughout a bat's lifetime, tags may be expelled through the skin (Fig. 4), due to healing and physiological processes or the immune system recognizing the tag as a foreign object (Siemers and Neubaum 2018). Given the range of morphologies, ecologies, and behaviors observed within Chiroptera (e.g., varying skin thickness, roosting strategies, and grooming practices), it is important to investigate how tag loss varies across species and life stages (e.g., adult vs. juvenile). Rates of tag retention can also differ dramatically between sexes, due to sex-specific mating strategies (e.g., pugnacity or production of mating secretions) that can increase tag loss (Laverty and Stoner 2022). Assessing tag loss is critical, because studies unable to estimate this metric will likely produce skewed demographic data, underestimating survival and abundance by an unknown margin. Understanding the frequency and timing of tag loss enables these metrics to be incorporated into population models, improving accuracy and precision (Arnason and Mills 1981, Kendall et al. 2006, O'Shea et al. 2004, Touzalin et al. 2023). By identifying species, sexes, behaviors, or life stages associated with higher rates of tag loss, protocols and tagging techniques (e.g., implantation locations, tag types, and tag sizes) can be refined to enhance rates of tag retention.

To investigate loss of PIT tags in the Lesser Long-nosed Bat, we visited 2 RFID-monitored roosts (Isla Carmen and Chivato) in Baja California Sur, Mexico, during December 2016, January 2017, and December 2017, when bats were absent (see Frick et al. 2018, for roost specifics). We scanned roost floors for expelled tags using a hand-held reader to provide insights into tag retention rates, as well as the quantity and timing of loss. From 64 discovered tags, initially injected into bats between April 2013 and April 2016, minimum tag loss was calculated to be 16.1% for males (27/168 bats) and 7.4% for females (37/502) (Fig. 5). RFID reader detection histories of individuals showed that males (n = 27) retained tags for at least 45–635 days (median = 300 days), whereas females (n = 21) retained tags for 0–956 days (median = 702 days).

This higher rate of tag loss by males could be partially attributed to "dorsal patches", areas of specialized sebaceous glands that sexually active males develop around their scapulae during the mating season (Laverty and Stoner 2022). These patches, likely produced to influence mate attraction, may cause tags to be ejected as males secrete sebum, an oily substance, and repetitively smear body fluids over the area using their feet (Laverty and Stoner 2022). This higher loss rate could also be influenced by a smaller male sample size, due to captures occurring at maternity and mating roosts. Other studies on the sister species, *Leptonycteris curasoae* (Miller) (Curaçaoan Long-nosed Bat), revealed that males with dorsal patches had significantly lower body mass and poorer body condition than males with enlarged testes but no patch (Muñoz-Romo and Kunz 2009). This suggests that the energetic cost of developing these patches could be an additional factor of tag loss. Current

Figure 4. Female Lesser Long-nosed Bat, captured about 1 year after tagging, with PIT tag partly extruded from skin. Photo by Winifred F. Frick.

research studies are further examining the seasonal timing of tag loss in males, but until more conclusive findings are available, tagging males with active dorsal patches may not be worthwhile, due to an elevated risk of tag loss (Laverty and Stoner 2022).

Estimating and Ameliorating Rates of PIT-tag Loss

PIT-tag loss has also been reported by Neubaum et al. (2005), the first study to use PIT tags to research population biology in bats. During periodic captures of Big Brown Bats roosting in buildings, Neubaum et al. (2005) sporadically encountered bats with tags protruding from their skin, where healing processes, such as scabbing, had prevented tags from being completely shed. Our study design, which enabled periodic physical captures of previously tagged bats allowed researchers the opportunity to reinsert tags and seal any wounds before most tags were ejected, increasing retention rates (Ellison et al. 2007b).

To investigate demographic and ecological questions, such as seasonal roost use, movements, site fidelity, and survival, Siemers and Neubaum (2018) tagged *Corynorhinus townsendii* (Cooper) (Townsend's Big-eared Bat) with 12-by-2.25 mm PIT tags (Avid Identification Systems, Inc., Norco, CA) at a maternity colony of >1000 individuals using an abandoned mine in central Colorado. During 2011 and 2014–2016, 840 bats were tagged—256 males and 584 females, including 116 juveniles. Two circular antennas (Avid

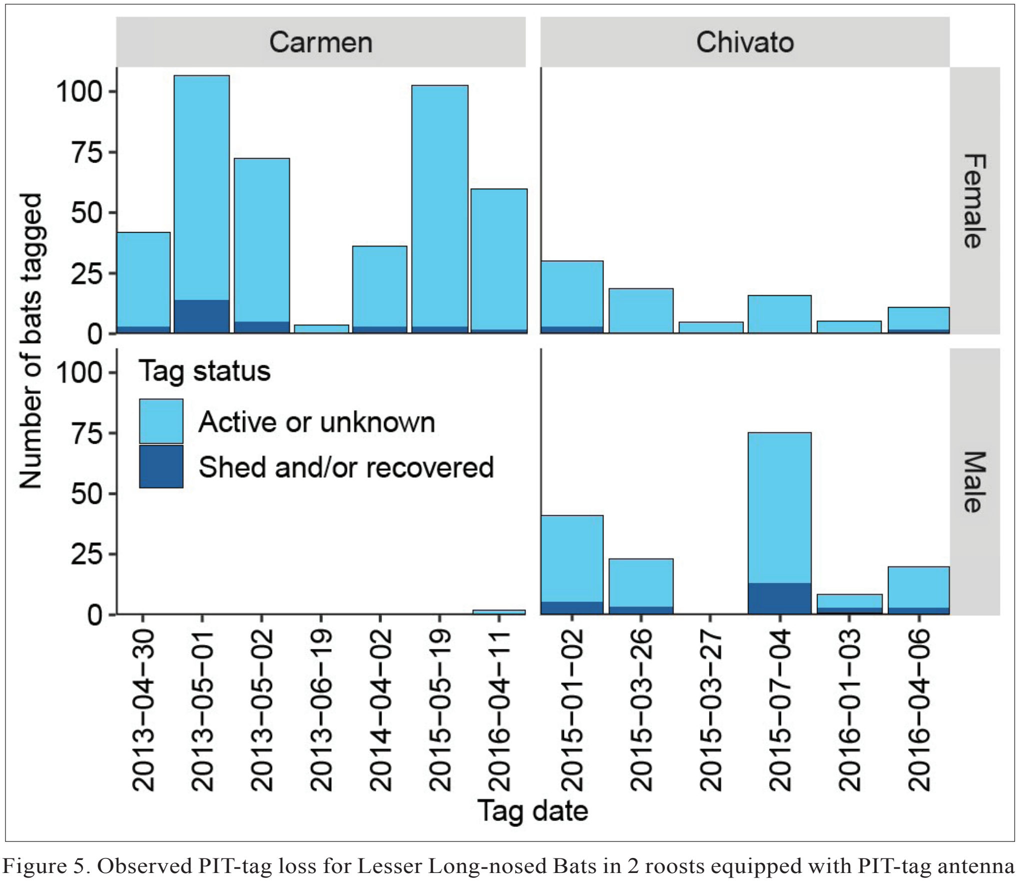

Figure 5. Observed PIT-tag loss for Lesser Long-nosed Bats in 2 roosts equipped with PIT-tag antenna systems in Baja California Sur. The number of tags with unknown or presumably active status (light blue) are compared to shed tags that were detected from roost floors (dark blue), for each sex, tagging location, and tag date prior to 2017.

Identification Systems, Inc.) connected to an RFID reader (IS1001, Biomark, Inc.) were initially installed at the entrance, before being replaced by a single antenna that was 0.6-by-0.6 m (Biomark, Inc.). Metal from a gate blocking the mine entrance initially obstructed the antenna's magnetic field, necessitating adjustments. We rectified the interference by hanging the antenna in front of the gate on a wooden frame with vinyl rope, as in Britzke et al. (2014), to address this common constraint. Further optimization was achieved using a tuning box to maximize tag detection and ensure that metal was no longer reducing detection distances. Disturbance from capturing and tagging bats, installing monitoring equipment, and gating entrances to prevent human access did not reduce bat use of the roost (Siemers and Neubaum 2018).

To estimate tag loss, we searched the mine on 3 occasions when the colony was absent, recovering 135 tags (16% of marked individuals). Discovered tag loss was considerably higher in females at 19.3% (113/584 bats), compared to 8.6% (22/256) in males. As bats may have lost additional PIT tags that were not recovered, actual loss rates are likely higher. The lower tag loss in males may be explained by their lower site fidelity, increasing the probability that tags were shed while bats were outside the mine (Siemers and Neubaum 2018). We saw no difference in tag loss by juvenile females (16%, 8/50) compared to adult females (19.7%, 105/534), or juvenile males (9.1%, 6/66) compared to adult males (8.4%, 16/190) (Siemers and Neubaum 2018). However, minimum tag-retention lengths varied significantly across sex and age groups ($F_{3,114} = 53.42$, $P < 0.001$), with juvenile females retaining tags for at least 65 days on average, followed by adult males (56 days), adult females (44 days), and juvenile males (10 days).

Similar to our study of Lesser-long Nosed Bats, the very low rate of tag loss in the initial weeks post-implantation suggests that tags are shed after injection sites have fully healed, indicating that improper sealing is not the primary cause. However, it remains possible that some tags were lodged in the injection site soon after implantation and became more prone to later loss. While some personnel were trained to implant PIT tags during the study, the extended durations before tags were ejected also suggested that level of experience was not a significant predictor of tag retention. To assess the potential for increased tag loss in Townsend's Big-eared Bats due to their anatomy, we investigated morphological characteristics, such as dermal thickness at implant locations, by opportunistically measuring tissue collected from carcasses of Townsend's Big-eared Bats and Big Brown Bats. However, findings were inconclusive, with high variability in dermal thickness, both within and between species. Further efforts to assess dermal thickness in bats using larger sample sizes may help determine which species or sex could be more vulnerable to tag loss.

For species like Townsend's Big-eared Bats that may experience tag loss long after implantation, investigating new implant locations or testing smaller PIT tags may be worthwhile. Numerous studies across various taxa have found that smaller tags generally result in lower rates of loss (Buhlmann and Tuberville 1998, Larsen et al. 2013, Ward et al. 2015), but more data are needed to examine the effect of tag size on loss rates for specific species. When designing a PIT-tag study, biologists must consider how detection rates could be affected by smaller tag sizes, because smaller tags generally have lower detection distances. For example, maximum detection distance with a Biomark 25-cm antenna and 12-mm PIT tags is 31 cm, but when using 9-mm tags detection distance is 23 cm, a 25% decrease.

Although sufficient data regarding PIT-tag loss is currently unavailable from our featured case studies involving Little Brown Myotis, tag loss in this species is believed to be relatively low, at least in captive studies (T. Rocke, USGS National Wildlife Health Center, Madison, WI, unpubl. data). To understand tag loss better in this species, we are double-marking Little Brown Myotis with both PIT tags and metal forearm bands. At a maternity roost in Ohio, a high-frequency reader (HDX Multiple Antenna Reader, Oregon RFID) powers antennas to detect double-marked bats entering and exiting the roost, enabling the monitoring of population size, survival, and seasonal fidelity. Through regular captures at the roost, the quantity and timing of PIT tag or band loss could be incorporated into analyses to improve the accuracy and precision of population parameter estimates and guide model selection (O'Shea et al. 2004, Touzalin et al. 2023).

Double-marking bats or incorporating genetic identification with PIT tags are 2 methods to estimate tag loss and characterize how loss rates vary across species, sex, and season (Rigby et al. 2012). Reporting estimated rates of loss can guide other researchers attempting to account for tag loss in their own studies. While capture-mark-recapture models, such as the Cormack-Jolly-Seber, allow the violation of the assumption that tags are retained and recognized, overparameterization can lead to challenges in interpretation if tag loss data are insufficient (Cai et al. 2021).

Discussion

The case studies presented here highlight the utility of PIT tags and RFID readers to advance our understanding across various aspects of bat ecology, through the autonomous collection of extensive datasets, with minimal disturbance or trap-avoidance bias. Even without automated RFID readers, manually scanning PIT tags is an invaluable technique for detecting captured individuals and tracking seasonal movements of bats in ceiling clusters within hibernacula and sensitive maternity roosts, where reading ID numbers on bands would cause disruption. Across multiple species, including Lesser Long-nosed Bats, Little Brown Myotis, Southern Bent-wing Bats, and Townsend's Big-eared Bats, recapture probabilities of PIT-tag detections at RFID readers are dramatically higher compared to probabilities based on physical recaptures (Frick et al. 2018, Siemers and Neubaum 2018, Schorr and Siemers 2021, van Harten et al. 2019, Waag et al. 2022). These recapture probabilities allow more precise estimates of population parameters, such as apparent survival (Ellison et al. 2007a), which otherwise may not be possible.

In our roost-specific studies, we strategically positioned antennas to quantify metrics such as abundance, fidelity, survival rates, and social association patterns (Siemers and Neubaum 2018, Schorr and Siemers 2021, Waag et al. 2021, 2022). In contrast, our regional networks of RFID-monitored roosts enabled inferences of broad-scale distributions, migratory timing, food availability, and impacts of climate change for wide-ranging species, like the Lesser Long-nosed Bat (Frick et al. 2018). While these 5 studies showcase examples of how we leveraged PIT tags, it is important to recognize that study designs similar to ours can be used to explore a wide range of research questions and demographic parameters. For instance, data from PIT tags can be used to infer reproductive status and parturition dates (Fontaine et al. 2024).

In our research, PIT tags and RFID readers were applied to populations with high roost fidelity and large stable aggregations. Although there is clearly an inherent benefit in selecting species amenable to capture and redetection that are also using roosts suitable for antenna installation, this can unintentionally lead to an opportunism bias, if studies are prioritizing precision and feasibility over variety of species and roosting strategies. Due to this bias, some of the most robust bat population metrics in the literature have been derived from populations that use or benefit from anthropogenic infrastructure (e.g., buildings, mines, and bridges), where population estimates may be inflated in correlation with habitat quality

(Johnson et al. 2019, Lausen and Barclay 2006). While these studies have advanced our understanding of bat demographics and ecology, and further research in human-influenced habitats remains crucial, we must carefully consider how our interpretation of these data shapes our broad perception of bat population dynamics and health.

The same methodologies discussed throughout our paper can be used to study bat populations with lower roost fidelity or fission-fusion relationships across a large number of bat colonies, as seen in our Lesser Long-nosed Bat study. Temporarily deploying RFID readers and antennas can also be a particularly effective strategy when researching such populations; for example, Ružinská et al. (2022) examined patterns of swarming behavior and frequent roost-switching of *Myotis daubentonii* (Kuhl) (Daubenton's Myotis) using a network of tree roosts.

PIT tags integrated with RFID readers offer clear advantages over mark-recapture techniques requiring physical bat handling, but tag loss, if not properly accounted for, can potentially bias demographic estimates (Arnason and Mills 1981). Scanning roosts with handheld RFID readers could be additionally advantageous, because the discovery of ejected tags, which remain functional on the landscape near indefinitely, can reveal valuable insights into roost usage and movement dynamics that may otherwise go undetected. Across the case studies, minimum rate of PIT-tag loss varies across species, sex, and season, with rates of at least 7.4% in female and 16.1% in male Lesser Long-nosed Bats, and 19.3% in female and 8.6% in male Townsend's Big-eared Bats. Tag loss appears high in these 2 species compared to other bats. For example, tag loss in Big Brown Bats was 1.6% (O'Shea et al. 2004), and double-marked *Chalinolobus gouldii* (Gray) (Gould's Wattled Bats) experienced a 2.7% tag loss (van Harten et al. 2021). However, other species have even higher loss rates, such as Daubenton's Myotis, for which 41% of adult females (n = 23) and 33% of adult males (n = 14) lost PIT tags over a span of 3 years (Rigby et al. 2012). Although a lack of adhesive over the injection site may have contributed to this high loss rate, over a quarter of these losses occurred >1 year after injection.

Improving our understanding of how tag retention varies taxonomically enables appropriate correction factors to be applied in population models, mitigating potential impacts on demographic parameters. Systematically quantifying factors like species-specific skin thickness, aggressive behaviors, roosting ecology, and sex-based physiological changes could guide the development of new practices to increase long-term tag retention. Additionally, testing alternative sizes, types, or implantation locations for PIT tags may reveal options for enhancing retention, particularly for species like Lesser Long-nosed Bats and Townsend's Big-eared Bats that seem more prone to expelling tags (Siemers and Neubaum 2018, Laverty and Stoner 2022). Even when following PIT-tagging protocols (Rigby et al. 2012, Wimsatt et al. 2005), the experience level of personnel performing injections may also influence tag retention for some species.

Since tag loss is a known issue, analytical techniques to estimate tag loss empirically have been developed. Double-marking, through combining PIT tags with wing bands, genetic fingerprinting, or permanent marks, such as tattoos (Markotter et al. 2023), is a valuable method to estimate tag loss. Based on sample sizes and observed loss rates of tags, the proportion of the population that studies will need to mark for realized loss to be estimated will vary; however, this too can be estimated (Laake et al. 2014). Statistical approaches such as the Jolly-Seber model with tag loss or Hidden Markov models can then incorporate these loss estimates to provide demographic parameters (Cowen and Schwarz 2006).

Although our case studies demonstrate the value of PIT tags and RFID monitoring, there are opportunities for further enhancement of this technique through improving the ease of collaboration and data access. Currently, a national PIT-tag database for North American bats does not exist for contributors to store and share information, and there is little standardization for data collection and reporting. The utility of PIT tags can be improved through the development of a collective database that allows users to submit PIT-tag data and accompanying metadata, increasing the amount and quality of information available to make inferences across spatial, taxonomic, and institutional boundaries (Reichert et al. 2021). Collaborative projects, such as the USGS Bird Banding Laboratory (Smith 2013), Motus Wildlife Tracking System (Taylor et al. 2017), and North American Bat Monitoring Program (Loeb et al. 2015, Reichert et al. 2021) are effective examples of how local data can be combined to increase the spatial scales of research and monitoring efforts. By integrating contributions from studies tagging various species throughout different regions, we can gain a more comprehensive picture of bat distributions, seasonal ecology, and potential range shifts over time. In addition, this aggregated dataset can reveal new insights about PIT-tag loss, detection of infrequent dispersals to distant roost sites (Bullen and Reiffer 2019), within-season movements, migratory connectivity, and gene flow that may not be possible with other techniques. As environmental conditions change (Locatelli et al. 2019), an accessible record of historic data could be immensely valuable for directing bat conservation and management, by improving our ability to interpret and forecast population fluctuations and behavior.

In summary, our case studies demonstrate that PIT-tagging combined with RFID monitoring provides a precise, flexible, and minimally invasive approach for studying bat population dynamics across diverse taxa and spatial scales, especially when addressing limitations such as tag loss. Continued sharing of best practices, methodological refinements, and collaborative data efforts through accessible PIT-tag databases can further advance the potential capabilities of this method. Overall, using PIT tags with RFID readers provides a powerful tool to advance our ecological understanding while continually evaluating population status, both which are critical for effective and timely conservation and management actions.

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