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Pacific Science, Volume 77, Number 1, January 2023, pp. 1-26 (Article)

Published by University of Hawai'i Press



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Seasonal and Elevational Differences by Sex in Capture Rate of ‘Ōpe‘ape‘a (*Lasiurus semotus*) on Hawai‘i Island¹

Julia P.S. Hoeh,² Aaron A. Aguirre,² Flor A. Calderon,² Sean P. Casler,² Sarah G. Ciarrachi,² Karen N. Courtot,² Kristina M. Montoya-Aiona,² Corinna A. Pinzari,³ and P. Marcos Gorresen^{3,4}

Abstract: The study of nocturnally active bats is difficult even for those species that seasonally congregate. This challenge is particularly acute for ‘ōpe‘ape‘a (Hawaiian hoary bat; *Lasiurus semotus*) because of its solitary foliage-roosting behavior. Yet surveys are essential for conservation and management of this endangered species and only land mammal endemic to the Hawaiian Islands. We surveyed for ‘ōpe‘ape‘a at 23 sites and a range of elevations (33–2,341 m) on Hawai‘i Island from May 2018 to August 2021. We captured 138 unique bats (37 female, 101 male) over 224 mist-netting events. We averaged 16 net-hours per bat capture, with peak captures 30–90 min after sunset. We marked all captured individuals in this study with identifying forearm bands and recaptures represented 7% of total captures (10 of 148). We developed generalized linear mixed models to examine the relationship of nightly bat captures by sex to elevation and time-of-year while accounting for variable sampling effort and repeated sampling in this study. Both males and females were captured at low and high elevations with peak capture rates occurring at approximately 930 m. The capture rate for females was highest during the reproductive season (May to September), whereas it was highest for males during the non-reproductive season (October to April). This study informs future fieldwork with a description of ‘ōpe‘ape‘a capture on Hawai‘i Island by sex, elevation, time-of-year and time-of-night, radio transmitter retention, and recapture frequency.

Keywords: Hawaiian hoary bat, ‘ōpe‘ape‘a, *Lasiurus semotus*, Hawai‘i, mist-net capture

VESPER BATS (FAMILY VESPERTILIONIDAE) are relatively small and primarily nocturnal, making it difficult to evaluate distribution, abundance, and population trends (Carter

et al. 2003). One approach common to bat studies is to observe individuals at known roost locations, such as caves for cave obligate species, or winter hibernacula and maternity roosts for cavity roosting bats (Warren and Witter 2002; Thogmartin et al. 2012; Weller et al. 2014). Foliage roosting, or “tree” bats are more challenging, as they do not aggregate in large groups at roosts, have lower roost fidelity, and perform large-scale seasonal migrations making repeated observations more difficult (Lewis 1995; Cryan and Veilleux 2007; Weller et al. 2016).

Acoustic and visual methods (e.g., ultrasonic acoustic, visible light, night vision, thermal imaging, radar) can quantify behavior, distribution, and to some extent, relative abundance among locations and over time

¹Manuscript accepted 17 January 2023.

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(e.g., Razgour et al. 2010; Rodhouse et al. 2019). However, the type of information produced by these methods is generally limited by not knowing the identity and number of individuals sampled and is potentially biased by social behaviors such as reduced echolocation around conspecifics (Corcoran et al. 2021). Additionally, these methods do not allow for generating metrics important to demographic or population viability assessments (e.g., sex ratio, juvenile ratio, reproductive condition, re-encounter rates).

As a foliage-roosting tree bat with endangered species status, the ‘ōpe‘ape‘a, or Hawaiian hoary bat (*Lasiurus semotus*; Wilson and Mittermeier 2019; Simmons and Cirranello 2021), is particularly challenging to monitor (Gorresen et al. 2017). Acoustic and visual observations demonstrate that ‘ōpe‘ape‘a are distributed across all of the major Hawaiian Islands and elevations up to 3,562 m (Tomich 1986; Bonaccorso et al. 2016), yet population size is currently unknown with threats including collisions with wind turbines and potentially limited habitat and food resources (USFWS 2021). ‘Ōpe‘ape‘a activity varies by geographic location and time-of-year, with greater activity associated with forested locations, insect biomass, and lower elevations during summer months (Jacobs 1994; Menard 2001; Gorresen et al. 2013). Previous specimen collection and capture-release netting surveys have broadened our understanding of reproductive timing, diet, roosting and foraging behaviors, and population genetics (Menard 2001; Todd 2012; Bonaccorso et al. 2015; Bernard and Mautz 2016; Pinzari 2019; Pinzari et al. 2019; Montoya-Aiona et al. 2023). However, gaps remain in our understanding of ‘ōpe‘ape‘a ecological requirements and conservation needs that can be best addressed by efforts that include the capture and tracking of individual bats. Our objective is to provide managers and researchers a perspective on ‘ōpe‘ape‘a captures by sex across time-of-year, elevation, and time-of-night, with considerations for transmitter retention and recapture frequency. Herein we describe bat capture by sex in relation to elevation and time of year

using a model to account for the variable sampling effort and repeated sampling in this study.

MATERIALS AND METHODS

Study Area

We surveyed for ‘ōpe‘ape‘a on Hawai‘i Island from May 2018 to August 2021 at sites ranging from 33 to 2,341 m in elevation and a mean annual rainfall of 430–5,680 mm (Giambelluca et al. 2013). Informed by historical capture data and for logistical reasons, most of our surveys occurred on the northeast (“windward”) side of the island, which typically has a wet season from November to April and intermittent dry periods the remainder of the year. Our netting sites were primarily located in native and non-native forest and mixed agricultural settings including orchards and timber plantations (Figure 1).

We surveyed 23 sites, with a subset of eight sites included in a fixed survey with sampling year-round at repeated intervals between January 2019 and January 2021 (Figure 2). Four fixed sites were located at elevations above 1,000 m (“high elevation”) and four below 1,000 m (“low elevation”). Fixed sites were chosen from locations that offered relatively high levels of bat occurrence and capture success, as determined in previous studies (Gorresen et al. 2008, 2013; Bonaccorso et al. 2015) and from opportunistic surveys and scouting in this study prior to 2019. We surveyed each fixed site at least once per 4-month period (January–April, May–August, September–December), with a survey comprising 1 to 3 netting events (mean 2.5 ± 0.6) depending on capture success (i.e., no capture on first night was followed by additional survey effort), project priorities, weather, and available personnel. We added opportunistic net events at alternate sites or on alternate dates contemporaneous to fixed site surveys, particularly when a bat was not captured during the fixed survey after three netting events. We expanded opportunistic netting surveys from December 2020 to August 2021 to survey a broader geographic area and target reproductive females.

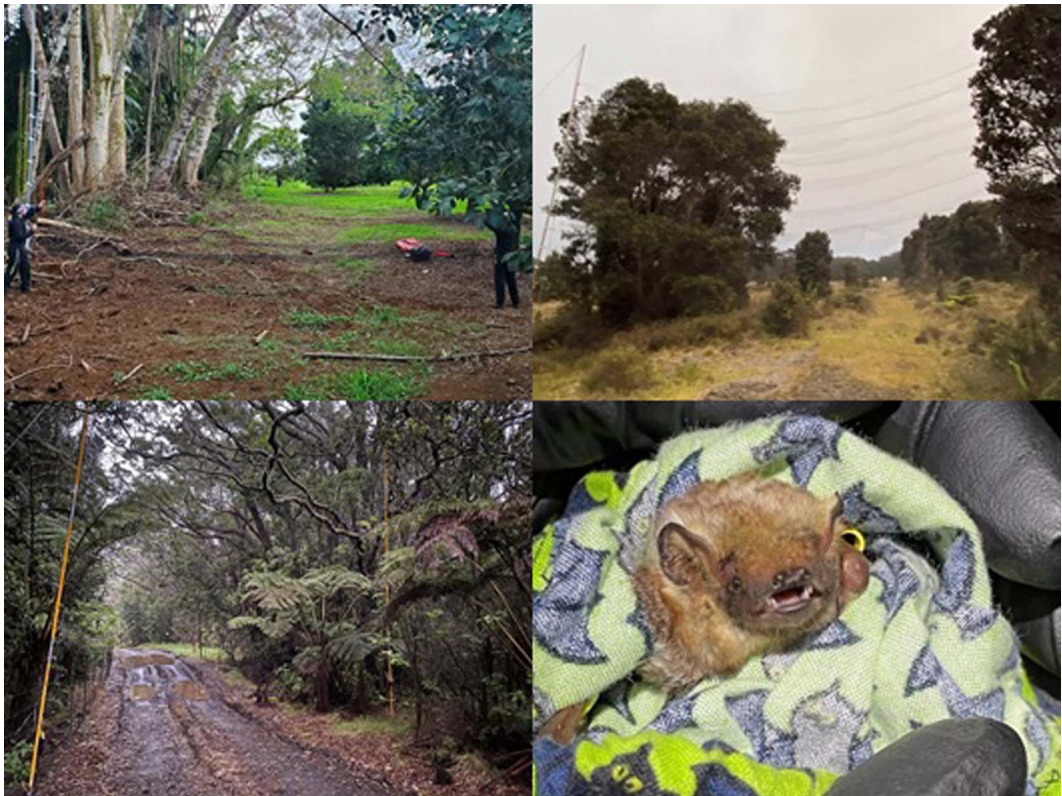


FIGURE 1. Photographs of sites sampled for ‘ōpe‘ape‘a (top left is a low-elevation orchard, top right is a high-elevation native mesic forest, bottom left is a high-elevation native forest) and bat in cloth holding bag after capture on Hawai‘i Island from May 2018 to August 2021.

Concurrent netting at nearby locations sometimes occurred when multiple teams were available. From January 2019 to January 2021 netting during fixed surveys was paired with concurrent insect sampling (not detailed in this paper).

In mid-March 2020 we paused bat capture efforts in response to the COVID19 pandemic. Enhanced handling precautions were prudent to minimize the potential for human-to-bat transmission of SARS-CoV-2 (USGS 2020). To achieve this, we developed capture protocols to avoid transmission of SARS-CoV-2 following guidelines issued by the U.S. Geological Survey (USGS), National Wildlife Health Center (USGS 2020), Centers for Disease Control and Prevention (CDC 2021), and the International Union for the Conservation of Nature Bat Specialist Group

(Kingston *et al.* 2021). After careful evaluation of conditions in Hawai‘i, implementation of enhanced fieldwork protocols, acquisition of personal protective equipment, and personnel training in the proper use of N95 respirators, bat captures resumed in early June 2020. Additionally, throughout our field surveys we followed best available decontamination practices for preventing the spread of Rapid ‘Ōhi‘a Death (ROD), an emergent fungal disease affecting the keystone species ‘ōhi‘a lehua (*Metrosideros polymorpha*), a culturally and ecologically important native tree species in Hawai‘i (Roy *et al.* 2020).

Bat Capture Protocol

Mist nets were suspended between poles or from ropes over tree limbs and situated across

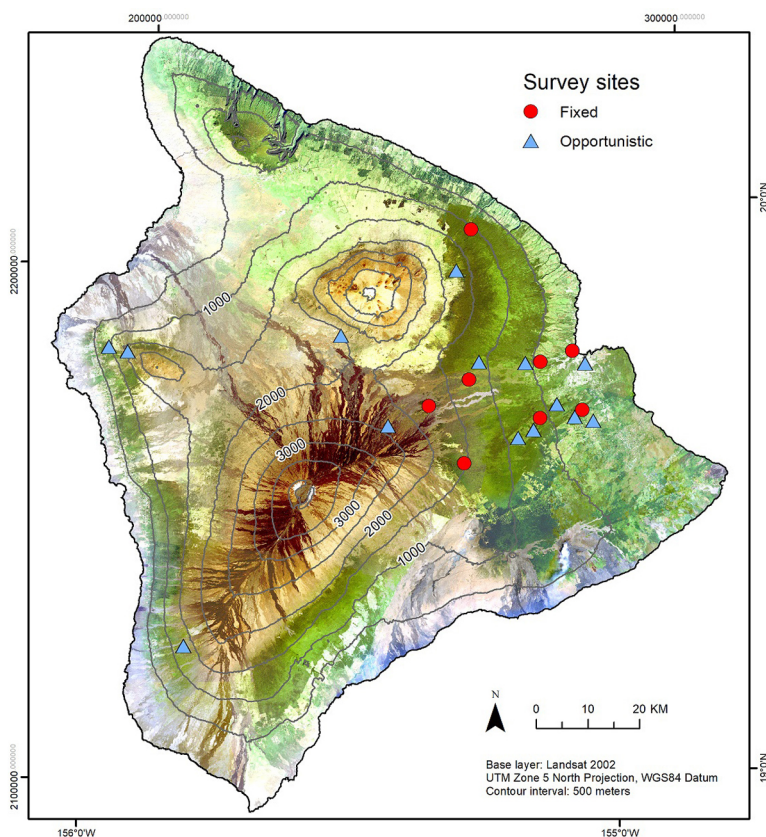


FIGURE 2. Survey sites sampled for 'ōpe'ape'a from May 2018 to August 2021 on Hawai'i Island, Hawai'i. Fixed sites (circles) were surveyed at regular intervals, and opportunistic sites include supplemental surveys at fixed sites and additional locations (triangles). Supporting data on general survey locations are available at <https://doi.org/10.5066/P9G4A2E3>

likely bat flight paths (e.g., forest roads, corridors, and orchard rows). We used nets (38 mm 75 denier/2-ply polyester [Avinet, Portland, Maine, USA]; 28 mm monofilament [Ecotone, Gdynia, Poland]) of lengths 6, 9, 12, or 18 m arranged singly (2.4–2.6 m height) or stacked up to three nets high (7.2–7.8 m [Bat Conservation and Management Triple High Mist Net Pole System, Pennsylvania, USA]). For each netting event (i.e., nightly sample), we set an average of three nets (range 1–5). We typically opened nets within 30 min of sunset and checked every 10 min for 3–5 hr after sunset, excluding periods when nets were closed while

processing captured bats or due to inclement weather.

In scouting new survey sites, we often used full spectrum acoustic recording devices Song Meter SM2BAT+ and Song Meter SM4BAT FS (Wildlife Acoustics, Massachusetts, USA) for several nights prior to netting to help identify locations and periods of the night with relatively higher call activity. At most sites, higher call activity was recorded during our standard netting time (up to 5 hr after sunset). However, at one site we detected a later peak of activity and thus extended netting effort later in the night (up to 8 hr after sunset).

Locally recorded calls from these site scouting efforts were incorporated in our playlist of bat calls. Acoustic playback of bat calls has been shown for some species to attract bats to nets (Hill and Greenaway 2005; Braun De Torrez et al. 2017; Preble et al. 2021), and particularly for hoary bats (Reyes and Szwczak 2022). For ‘Ōpe‘ape‘a capture, acoustic playback has been used on several islands and typically included locally recorded foraging and social calls (Pinzari et al. 2019; H. T. Harvey and Associates 2020). We used acoustic playback by positioning an Ultra-SoundGate Player BL Light (Avisoft Bioacoustics, Glienicke/Nordbahn, Germany) near nets on a tree limb or fence post, with the aim of improving bat captures rather than evaluating the technique. Thus, the calls included in the playlist, delay between calls, and start time of acoustic playback on a given night varied during the study.

Bat Handling Protocol

After removing captured bats from mist nets, we secured them in cloth holding bags for up to 10 min to collect guano samples before recording age, sex, reproductive condition, mass, forearm length, and obtaining additional biological samples. We documented age by observing the degree of epiphyseal-diaphyseal fusion. We classified adults when we observed a fused epiphyseal growth plate and classified juveniles when there was a visible cartilaginous gap (Brunet-Rossinni and Wilkinson 2009). For females, we classified bats as pregnant (P) by abdominal palpation, lactating (L) by swollen mammary glands and little to no fur surrounding nipples, post-lactating (PL) as reduced swelling in mammary glands and fur regrowth, or non-reproductive (NR) as no visible signs of reproductive condition (Racey 1988). For males, we classified bats as having testes descended with visibly enlarged testes or caudae epididymides, or not descended with no visible swelling (Krutzsch 2000; Cryan et al. 2012). We measured the forearm length from elbow to wrist with a caliper. We documented bat mass with a 30-g or 50-g Pesola spring balance. From each capture, we

collected dorsal fur samples, wing tissue biopsy punches (from unique individuals only; not recaptured bats), and guano if available.

Prior to bat release we attached radio transmitters and marked individuals. We trimmed a patch of dorsal fur and affixed very high frequency (VHF) radio transmitters (Model PIP3, transmitter mass 0.63–0.73 g; Biotrak Ltd., Wareham, UK) to bats using surgical glue (Perma-Type Surgical Cement or Torbot Bonding Cement; Carter et al. 2009), allowing up to 10 min for glue to cure with the bat returned to its holding bag. A transmitter was only affixed if less than 5% of bat mass, 12.5–27.5 g. Each bat received a unique color combination of plastic split ring bands (3.1 mm darvic solid color, celluloid striped; Avinet Research Supplies, Portland, Maine, USA), so individuals could be identified if recaptured or resighted at a roost. A 4-mm incision was made in the propatagium to accommodate the band as described in Kunz and Weise (2009). The University of Hawai‘i Institutional Animal Care and Use Committee approved bat capture and handling protocols (IACUC 04-039). We collected biological samples under USFWS Recovery Permit (TE003483) and Hawai‘i Protected Wildlife Permits (WL18-18, WL19-19, and WL19-52).

After bat release, we attempted to track bats to day roosts and document roost use with radio telemetry (Montoya-Aiona et al. 2020). If we successfully located a telemetry signal, we attempted to relocate the bat daily as personnel availability and transmitter retention allowed. We calculated a low and high estimate of transmitter retention days to provide information on the expected duration of telemetry tracking. The low estimate represents the time from capture to the last day we confirmed a signal from the bat. The high estimate represents the time from capture to the day a transmitter was recovered or confirmed dropped and may include some unknown amount of time during which a transmitter was no longer attached to a bat.

Statistical Methods

We used net-hour as our metric of netting effort for each event and calculated it as the

number of mist nets multiplied by the total time nets were open, excluding periods they were closed while processing captured bats or because of sampling interruptions due to inclement weather. Net-hours were used to compare capture rate relative to sunset and as an offset term in capture rate models (described below). We did not include net height or width in this calculation as we selected net size to fit the potential flight corridor as is common with endangered bat species surveying; a larger net area does not necessarily equate to greater net effort (USFWS 2022). However, we also present effort as squared meter net-hour for comparability with previous work (Kunz et al. 2009; H. T. Harvey and Associates 2020).

For evaluating capture rates, we used models to account for the variable sampling effort across sites and repeated visits. We excluded data from opportunistic surveys, as sampling for the fixed survey was designed to explicitly balance effort and make comparable results relative to elevation and time-of-year. Netting locations within and among fixed sites sampled over the study were sometimes located relatively close to one another. We aggregated repeated samples among neighboring locations with hierarchical agglomerative clustering (Legendre and Legendre 2012) and assigned cluster membership to each of the 49 unique netting locations. We performed cluster analysis in R (version 4.1.0; R Core Team 2021) with the package “stats” (Becker et al. 1989), and used the Euclidean method for distance matrix computations, and Ward’s D2 minimum variance method and a cut-tree distance threshold of 2,500 m for hierarchical clustering. The 2,500-m threshold was determined from the observed median distance between capture sites and bat roost locations (Montoya-Aiona et al. 2023), a distance we considered a conservative extent within which our pooled samples at neighboring sites were surveying the same “locally” available bats. From the 49 netting locations we generated 11 clusters, of which 9 had at least one capture at a site that we used for modeling. In this subset, neighboring locations within the same cluster had a mean pairwise distance of 559 m (SD = 411 m).

We examined the relationship of nightly bat captures by sex to elevation and time-of-year with generalized linear mixed models (GLMMs) for the purpose of incorporating random effects and accounting for repeated sampling (Bolker and R Development Core Team 2017). Cluster membership served as a random effect to group repeated measures at proximate net locations. The models included elevation and time-of-year as fixed effects. To improve model convergence, we scaled and centered elevation values using the base “scale” function in R. In addition to its use in models as a linear term, elevation was incorporated as a quadratic term to allow for a non-linear fit to potential seasonal patterns in captures. We incorporated time-of-year as a circular variable by transforming Julian day with a sine and cosine function to allow for modeling counts as a wave-like seasonal pattern (Stolwijk et al. 1999). Alternatively, in an additional set of models we incorporated time-of-year as a categorical variable representing a “reproductive” period (May 1 to September 30) and “non-reproductive” period (October 1 to April 30) (Hoeft et al. 2023). These periods were delimited based on the observed breeding condition and body mass of captured adult bats during this study, and the reproductive period encompassed the pregnancy, lactating, and post-lactating stages. To account for differences among netting efforts in the duration of netting and number of nets set, we included the log of the total nightly duration of net effort as an offset in models, thereby converting counts of predicted captures to a nightly capture rate relative to the mean effort for all fixed site netting events (11:01 net-hours).

We applied Poisson and negative binomial regression to model the count of nightly captures and handle potential over-dispersion in the data (Hilbe 2011). We also accommodated potential under-dispersion by fitting the GLMMs with a generalized Poisson distribution (Brooks et al. 2019). We included zero-inflated Poisson and negative binomial distributions to manage the large number of zero counts in the observed data, from nights with no capture or captures of only one sex.

The five error distribution families are referred herein as NB (negative binomial), P (Poisson), GP (generalized Poisson), ZNB (zero-inflated negative binomial), and ZP (zero-inflated Poisson). GLMMs were run with the R package “glmmTMB” (Brooks *et al.* 2017).

Models were initially fit using maximum likelihood estimates to allow for the comparison of models with different fixed effects (Korner-Nievergelt *et al.* 2015). To investigate the relationship of sex to elevation and time-of-year, model comparisons were applied separately to each of three predictor groupings: (1) elevation-only models; (2) time-of-year-only models; and (3) both elevation and time-of-year models. Two-way interactions (i.e., sex \times elevation; sex \times time-of-year) were included in the former two groups, respectively, and three-way interactions (i.e., sex \times elevation \times time-of-year) were included in the third group. The candidate set of predictor variables totaled to 20 models (Appendix 1 available in the online version of this article) within each of the distribution families, including a null model composed of only the random effect term “cluster,” the offset parameter for net effort and no fixed effects. To compare models within each group we used small-sample-size corrected Akaike information criterion (AICc) via the AICcTab function from the “bbmle” R package (Burnham *et al.* 2011; Bolker and R Development Core Team 2017). Final top-ranked models within each group were examined with post-fitting diagnostics performed with the “DHARMa” R package (Hartig 2020). The final models were re-fit with restricted maximum likelihood (REML) estimates to obtain unbiased coefficients and predictions for the fixed effects (Korner-Nievergelt *et al.* 2015). We used a statistical significance criterion of $P < 0.05$ for all tests.

We examined the potential of acoustic lures to bias capture rate estimation with two-sided Fisher’s exact tests. The tests sought to determine if the proportion of lure use was significantly unequal relative to elevation and time-of-year during sampling at the fixed survey sites, and to compare the effect of lure use on the sex ratio of captures. The test compared the number of nights with and

without lure use between the two elevation categories (i.e., above and below 1,000 m) used to allocate netting effort. We applied a similar test for time-of-year to compare lure use among all 12 months. To evaluate lure effect on sex ratio, we applied a two-sided Fisher’s exact test to compare captures with acoustic playback (captures at the net with acoustic playback and at a different net from the playback speaker) to those without playback (captures before the playback started and on nights without playback).

RESULTS

We conducted 224 mist netting events from May 2018 to August 2021, for a total of 2,409 net-hours of sampling (99,928 m² mist net-hours when including net width and height; Table 1). These efforts resulted in the capture of 138 uniquely identified individuals (37 female, 101 male), of which 10 were recaptured (4 female, 6 male) and an additional 10 were ensnared in nets and escaped, for a total of 158. Sampling required 16 net-hours per bat capture (as averaged across both elevation categories and survey types). Capture rate improved from an average of 20 net-hours per capture in 2018 to 13 net-hours per bat capture by 2021. Net effort per capture was generally lower at both fixed and opportunistic sites above 1,000 m.

We used acoustic playbacks as a lure for some portion of the night for 68% (153 of 224) of the netting events. We captured 62 bats (10 female, 52 male) at the net with acoustic playback, 16 bats (3 females, 13 males) at a different net from the playback speaker, 12 bats (4 female, 8 male) before the playback started, and 58 bats (24 female, 34 male) on nights without playback. A Fisher’s exact test demonstrated a significant difference in the sex ratio of captures with acoustic playback relative to those without (P -value = 0.002, odds ratio = 3.3, 95% confidence interval [CI] = 1.5–7.8).

Considering capture timing relative to sunset across all netting events (fixed and opportunistic), we captured bats from as early as 11 min after sunset to as late as 389 min (~6.5 hr) after sunset with targeted late-night

TABLE 1
Summary of Bats Captured and Netting Effort by Survey Type (Fixed Versus Opportunistic Sampling) and Elevation on Hawai'i Island, Hawai'i, from May 2018 to August 2021

Survey Type – Elevation	No. Bats Captured by Sex (Female, Male)	No. Net Events ^a	Netting Effort (Net-Hours) ^b	Net-Hours Per Bat (hr:min)	Meters ² Net-Hours ^c
Fixed					
Low elevation (<1,000 m)	36 (9, 27)	58	657	18:15	28,452
High elevation (>1,000 m)	55 (19, 36)	64	686	12:28	29,354
Opportunistic					
Low elevation (<1,000 m)	31 (9, 22)	67	701	22:36	28,164
High elevation (>1,000 m)	26 (4, 22)	35	364	14:00	13,959
Total	148 (41, 107)	224	2,408	16:16	99,928

^a Events when multiple crews were surveying on the same night (4 concurrent events).

^b Calculated as number of nets (varying size to fill potential flight corridor) × hours of open net (USFWS 2022).

^c Calculated as net width × net height × hours of open net (Kunz et al. 2009).

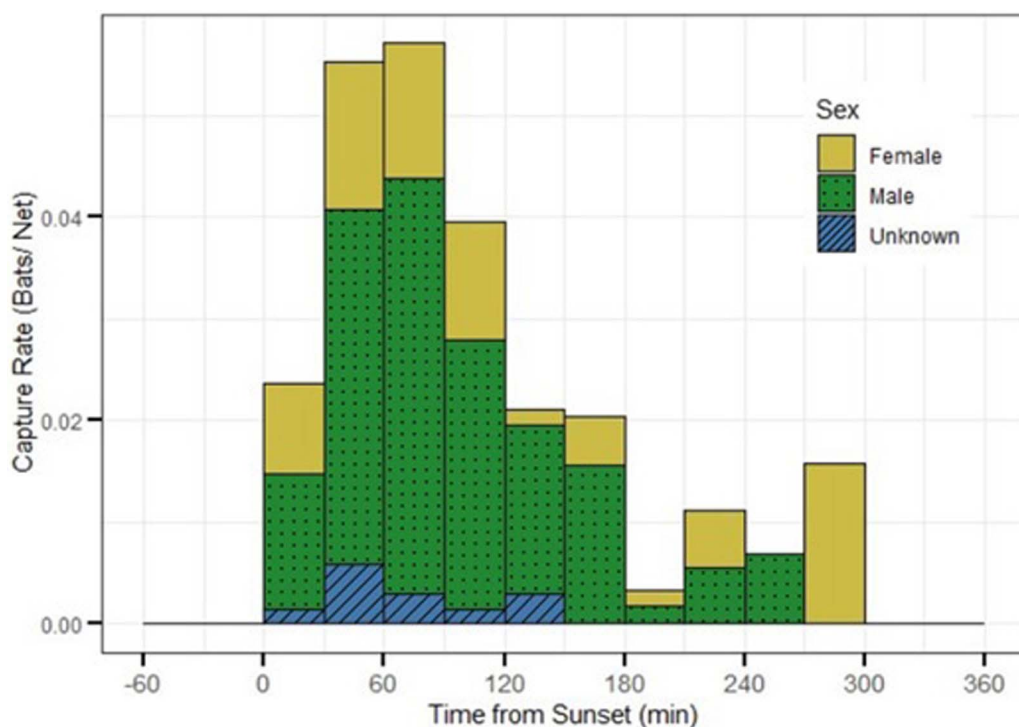


FIGURE 3. Capture rate (number of bats captured/net) and sex of bats relative to sunset (0 min) as adjusted for netting effort on Hawai‘i Island, Hawai‘i, for all netting events from May 2018 to August 2021. “Unknown” were bats ensnared in nets and escaped before handling.

netting (Appendix 2, Figure 1). Ninety-eight percent of our netting effort occurred from 30 min before to 300 min (5 hr) after sunset (Appendix 2, Figure 2). Excluding targeted netting efforts, we observed the highest capture rates from 30 to 90 min after sunset (Figure 3).

Of the total 148 captured bats, we affixed 131 with radio transmitters and attempted to relocate 127 on subsequent days of tracking. Radio signals were not detected for 36 bats (6 female, 30 male). Of the 91 bats (32 female, 59 male) that were detected, we calculated a low and high estimate of transmitter retention days as described in the methods. For 15 bats, the low estimate coincides with the end of tracking effort. We were able to calculate a high estimate for only 30 bats, as we were often unable to confirm a dropped transmitter. Generally, males retained transmitters

longer than females (Figure 4), with a mean low estimate of 9 ± 6 days for males and 6 ± 4 days for females, and a mean high estimate 12 ± 7 days for males and 9 ± 7 days for females. In Figure 4, we present only the more conservative low estimate of transmitter retention with the observed maximum of 25 days for males and 17 days for females.

Over the 2,408 net-hours during both fixed and opportunistic netting events, we recaptured 9 bats, with one individual recaptured twice (totaling 10 recaptures), for an average of 241 net-hours per recapture. All bats were recaptured at the same site as their initial capture, with recaptures occurring 6–654 days after the first capture (Table 2). The weight of individual bats did not substantially change between captures, except for a female captured the first time while lactating and then recaptured a year later while pregnant (mean

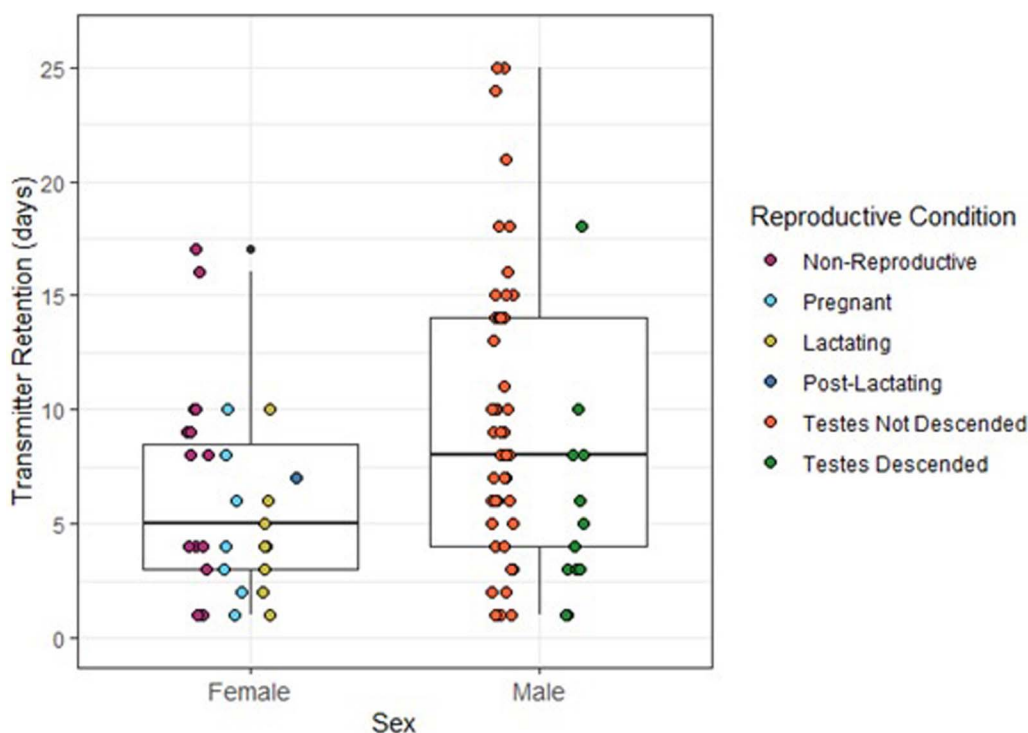


FIGURE 4. Estimate of radio transmitter retention time (days) for bats captured on Hawai'i Island, Hawai'i, from May 2018 to August 2021. Transmitter retention estimate ($n = 93$) represents the time from capture to the last day a signal was confirmed from the bat. Box plot depicts minimum, first quartile, median, third quartile, maximum, and outliers (as black points). Reproductive conditions are presented, but not discussed as the sparse number of observations among categories limits interpretation.

difference excluding pregnant female, female = 0.0 g, male = 0.5 g; Table 2).

Capture rate models evaluated sampling from fixed surveys only, which required almost 15 net-hours per bat (1,343 net-hours, 91 bats captured; Table 1). The top-ranked capture rate models included those from both the elevation-only and the time-of-year-only sets of candidate models (Appendix 3). Models that combined both elevation and time-of-year terms did not yield results with significant coefficients for both elevation and time-of-year parameters and are not addressed further (Appendix 4).

The elevation-only model with the greatest weight (model E5; Appendices 3 and 4) included elevation both as a quadratic term and as an interaction with sex, indicating that capture rate as a function of elevation differed

between male and female bats and exhibited a unimodal distribution. The maximum mean capture rate for both sexes peaked at 930 m (Figure 5). The capture rate at this elevation was 0.95 (standard error [SE] = 0.47) for females and 0.83 (SE = 0.23) for males given the mean netting effort for all fixed survey events (11:02 net-hours). Males demonstrated a higher overall capture rate than females at both lower and higher elevations. The Fisher's exact test of the consistency of lure use above and below 1,000 m elevation was not significant ($P = 0.558$) and did not demonstrate unequal use at this coarse scale. Due to our assumptions surrounding the ability to capture bats at high elevations, we deployed acoustic playback as a lure during fixed netting surveys at our highest elevation sites (consisting primarily of open-low stature forest

TABLE 2
Recaptured Bats on Hawai‘i Island, Hawai‘i, from May 2018 to August 2021

Sex	Initial capture (Repro. Cond.) ^a	Subsequent Capture (Repro. Cond.)	Days Since Initial Capture	Mass (g) Initial/Subsequent
Female	Jul-2018 (PL)	May-2019 (NR)	300	19.5/19.5
Male	Dec-2018 (ND)	Feb-2019 (ND)	50	15.8/15.0
Male	Mar-2019 (ND)	Feb-2020 (ND)	331	16.0/16.0
Male	Mar-2019 (ND)	Jul-2019 (ND)	118	15.5/17.5
Female	Jul-2019 (L)	Jul-2019 (L)	6	19.5/19.5
Female	Jul-2019 (NR)	Jun-2020 (L)	335	20.5/20.5
Male	Feb-2019 (ND)	Nov-2020 (ND)	654	15.0/15.0
Male	Sep-2019 (TD)	Sep-2020 (ND)	358	13.5/15.0
(as above)	(as above)	Dec-2020 (ND)	468	13.5/14.0
Female	Aug-2020 (L)	June-2021 (P)	300	20.0/24.5

^a Reproductive conditions: non-reproductive (NR), pregnant (P), lactating (L), and post-lactating (PL) for females; and testes not descended (ND) or testes descended (TD) for males. All bats were classified as adult.

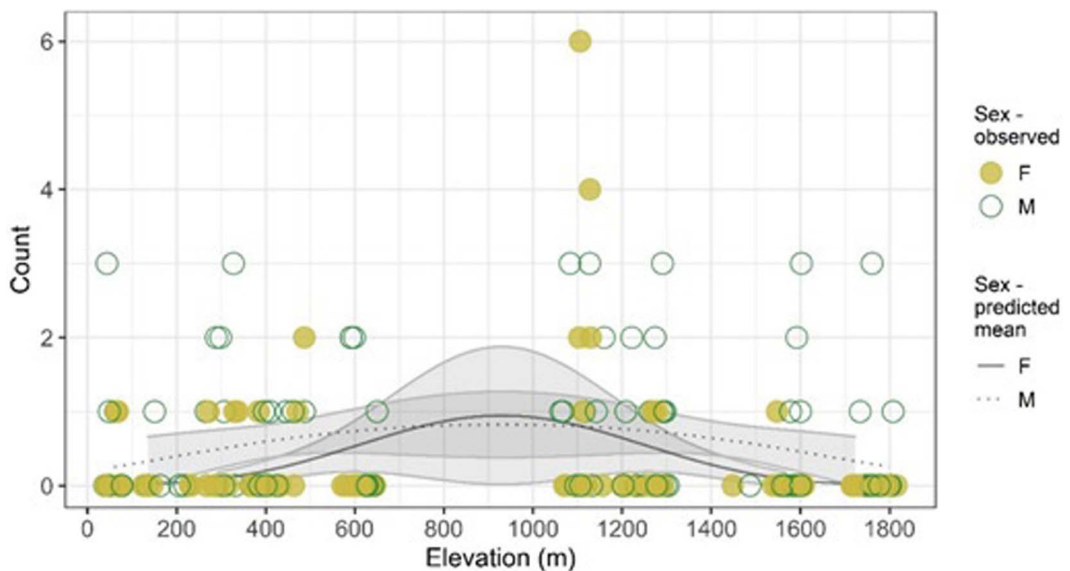


FIGURE 5. Observed bat captures and predicted capture rates by sex (count adjusted for effort; mean and 95% CI) relative to elevation for captures at fixed sites on Hawai‘i Island, Hawai‘i, from January 2019 to January 2021.

and grassland). The reliance on lure use in these areas may have biased our capture rate as modeled for higher elevations.

The time-of-year model with the greatest weight (model T2; Appendices 3 and 4) included the categorical predictor for reproductive period and indicated a seasonal relationship that differed significantly

between males and female bats, particularly for the non-reproductive period (October 1 to April 30). Given the mean effort for all fixed surveys (11:02 net-hours), the capture rate for females was 0.61 (SE = 0.19) during the reproductive period and 0.17 (SE = 0.09) during the non-reproductive period. Conversely, there was not a strong seasonal pattern

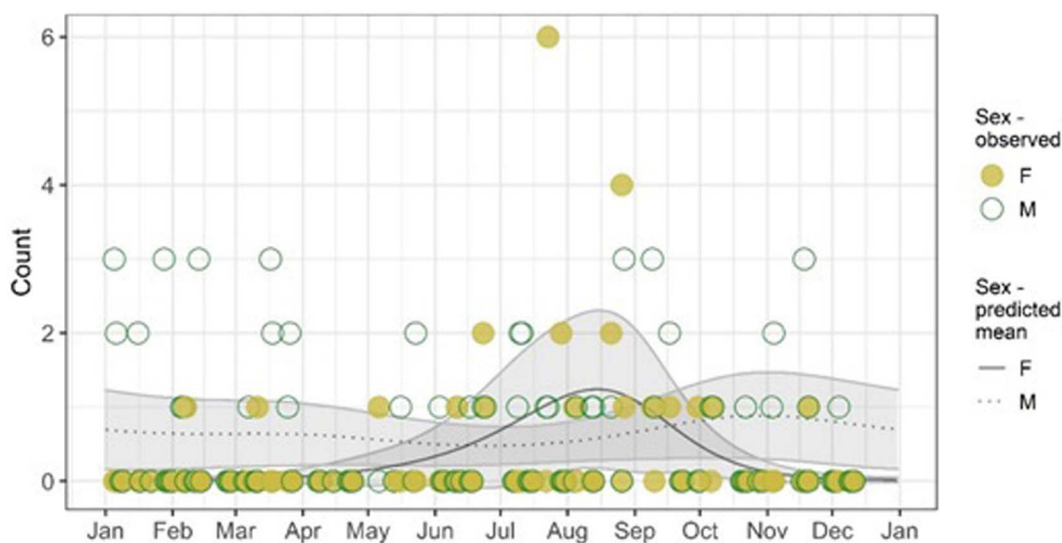


FIGURE 6. Observed bat captures and predicted capture rates by sex (count adjusted for effort; mean and 95% CI) relative to time-of-year for captures at fixed sites on Hawai'i Island, Hawai'i, from January 2019 to January 2021.

to male captures by reproductive period, as the capture rate for males was 0.71 (SE = 0.16) and 0.57 (SE = 0.15) for the same respective periods.

The second ranked model (model T3; Appendices 3 and 4), which described time-of-year as a continuous variable, provided a more nuanced depiction of capture rate relative to time and demonstrated a significant interaction with sex (Figure 6). The capture rate for females peaked in mid-August at a mean of 1.24 (SE = 0.54), trailing off markedly by mid-October, with few captures until May. In contrast, male bats exhibited the opposite pattern with the lowest capture rate at the end of June (mean = 0.48, SE = 0.13) and the highest at the end of October (mean = 0.88, SE = 0.30). The Fisher's exact test of the temporal consistency of playback use over the survey period, as assessed with one-month bins, was not significant ($P = 0.202$) and demonstrated no evidence that its use was unequal over time or contributed to a bias in modeled captures by month.

DISCUSSION

Our 3-year period of fieldwork determined that bat capture required an average of

16 net-hours of netting over a period of 2 to 3 nights, a result that may inform the expected level of effort needed in the planning of similar studies. In general, identifying productive sites across years and seasons can improve monitoring efficacy and assessment of local population trends (Weller and Lee 2007; Green et al. 2020). Scouting and targeting effort towards potentially productive sites, as determined through our efforts and previous work (Gorresen et al. 2008, 2013; Bonaccorso et al. 2015), markedly improved capture rates during the study. Scouting included the use of acoustic recording, night-vision, and thermal observations at several potential net locations within a site to compare bat activity. We targeted net effort by revisiting sites and placing nets in corridors with previous captures. Consequently, capture rate improved from an average of 20 net-hours per capture in 2018 to 13 net-hours per bat capture by 2021. 'Ōpe'ape'a surveys at new sites may require greater netting effort than expended in this study (e.g., see USFWS 2022 guidelines that prescribe substantial survey effort to assess *Myotis sodalis* and *M. septentrionalis* presence at a new location) and capture success at a given site may vary among months.

We used acoustic lures for at least a portion of the night during most net events and were able to capture bats at nets located near the playback source. We determined that the sex ratio of females to males significantly differed with playback, with greater capture of males relative to females when playback was in use. However, we used acoustic playback with the aim of improving bat captures rather than evaluating the technique. Thus, our assumptions about a site influenced playback use; for example, we used the lure for most netting events at our highest elevation sites, and often delayed use of the lure until an hour after sunset or deployed it if we had no captures. We cannot effectively evaluate these influences on the sex ratio of captures. Additional research would be beneficial to evaluate how the capture rate and potential for sex biases are affected by the context of the call recording (e.g., echolocation, social, feeding buzzes), source of the call (e.g., locally recorded calls, synthesized calls), and reproductive period when calls are recorded or broadcast. Although it appears that ‘ōpe‘ape‘a are lured to acoustic playbacks, particularly with playback of locally recorded calls (Pinzari *et al.* 2019; H. T. Harvey and Associates 2020), to date no standardized studies have evaluated lure efficacy for this species. A study of the effects of acoustic playback on the capture of hoary bats (*L. cinereus*) in California demonstrated that it was capable of luring individuals to nets, although female captures were too few to evaluate effectiveness by sex (Reyes and Szewczak 2022). Similarly, Preble *et al.* (2021) determined acoustic playback on Okinawa Island in Japan was effective at luring *Myotis* bats and markedly increasing capture rates, but with a probable male bias. As such, although lure use may benefit capture-dependent studies in which objectives are not complicated by the potential sex bias, further investigation on the use and effects of acoustic playback to lure ‘ōpe‘ape‘a to nets would be beneficial to understand potential biases (e.g., female bat avoidance, seasonal effects, capture rate).

We observed relatively higher capture rates from 30 to 90 min after sunset, a result compatible with documented higher acoustic

activity by ‘ōpe‘ape‘a during the first 2 hr of the night (Menard 2001; Todd 2012; Gorresen *et al.* 2013, 2020) and early night activity patterns described for other species (Maier 1992; Catto *et al.* 1995). Location-specific activity patterns in ‘ōpe‘ape‘a are known from visual observations (Jacobs 1994). Although our study focused netting on the first 3 to 5 hr of the night, we noted mid-night acoustic activity in recordings made at one sampling location. In response to these recordings, we adjusted sampling timing at that site and successfully captured ‘ōpe‘ape‘a 6 hr after sunset (Appendix 2, Figure 1). Acquiring acoustic samples for several nights prior to initial net surveys could be used to help determine locations with relatively higher bat vocal activity and timing of occurrence.

Mark-recapture studies can provide valuable information into long-distance movements (Glass 1982), demographic rates (Frick *et al.* 2010), and longevity of bats (Podlutzky *et al.* 2005). However, these studies are challenging because radio transmitter retention is relatively short (e.g., a maximum of 25 days in our study) and efficient methods for tracking small volant animals over long periods and long distances are not well developed (Cryan and Diehl 2009). Moreover, plastic split-ring bands degrade with environmental exposure (Anderson 1980) and plastic band retention on bats has not been well studied, a knowledge gap that may hamper its use in mark-recapture studies. Recaptures accounted for a relatively small proportion (7%) of all captures and required an average of 241 net-hours per recaptured bat. All bat recaptures occurred at the same location as the initial netting site, potentially indicating site fidelity. Although we sampled some sites at which bats had been captured and banded from 2004 to 2015 (primarily ending in 2011; Todd 2012; Bonaccorso *et al.* 2015), we did not recapture any individuals banded prior to the start of our study in 2018. Our longest time between recaptures was 654 days for a bat originally captured as an adult, providing a first step toward determining the life span of ‘ōpe‘ape‘a, as estimates currently rely on related species (USFWS 2021). The low rate of ‘ōpe‘ape‘a recapture evident in our study

provides insight into the difficulty of mark-recapture studies in Hawai'i. However, demographic and longevity data for 'ōpe'ape'a could be expected to improve with long-term mist-net monitoring, use of genetic methods (Oyler-McCance et al. 2018; Wright et al. 2021; Van Harten et al. 2022), or persistent marking techniques such as passive integrated transponder (PIT) tags.

We captured both male and female 'ōpe'ape'a across much of the elevation gradient sampled but observed moderately higher capture rates for both sexes around 1,000 m. Relatively high numbers of captures (≥ 5 bats per netting event) occurred only in tall-stature native forest, a land-cover type associated with higher 'ōpe'ape'a occupancy (Gorresen et al. 2013), but largely restricted to elevations $\geq 1,000$ m (Jacobi et al. 2017). Of our eight fixed survey sites, three high elevation sites had net events with ≥ 4 bats captured, whereas this occurred at only one low elevation site. Netting at our highest elevation opportunistic sampling sites (1,800–2,341 m) included limited netting effort and resulted in no captures. Although 'ōpe'ape'a occur above 1,800 m (Bonaccorso et al. 2016), bat capture at these very high elevations could be hampered by the open terrain and low-stature vegetation, which lack flight corridors between trees that in turn facilitate mist-netting. Bat capture on Maui was accomplished in open terrain at high elevations when netting at ponds (Pinzari et al. 2019). Water sources of this type were not readily available at our sites but could be a consideration in open terrain. To increase capture probability, double- or triple-high net sets may be used in closed vegetation within canopy gaps that form potential bat flight paths.

'Ōpe'ape'a were captured throughout the year in our study area. The mean capture rate for females was higher in the summer months (June to October) and peaked in mid-August, a span coincident with parturition and lactation, and the period when pups become volant but may not yet be weaned and fully independent (Koehler and Barclay 2000). Reproductive female bats generally have

greater energy needs and are foraging more actively than at other times of year (Barclay 1989), and thus may be more available and susceptible to capture in flight during this period. In the winter and spring, female hoary bats may use torpor to prolong sperm storage after mating or delay parturition for more favorable conditions (Willis et al. 2006), potentially making them relatively less available than males for capture. In contrast to females, the capture rate of male 'ōpe'ape'a in our study was relatively uniform throughout much of the year but increased slightly towards the end of October, a probable mating period during which males may be more available and susceptible to capture in flight while searching for mating opportunities. These results align with previous acoustic surveys of 'ōpe'ape'a throughout an annual cycle showing echolocation detections increasing through the summer and peaking in fall (Menard 2001; Gorresen et al. 2013). As with other tree bats, movement patterns and timing are likely sex dependent (Cryan 2003; Jonasson and Guglielmo 2016), and our study results indicate that 'ōpe'ape'a distribution and activity differs seasonally by sex. An important caveat to the above is that differential responses by male and female bats to acoustic playback (e.g., Preble et al. 2021) complicate our ability to make inferences about 'ōpe'ape'a capture rates in relation to phenology.

Our study is the largest effort to date involving 'ōpe'ape'a capture. The results presented herein provide key information on how 'ōpe'ape'a capture varies by sex over time and elevation for Hawai'i Island, and the challenges posed by the short-lived retention of radio transmitters and infrequent recapture of individuals. Multi-year standardized capture and tracking of bats provide opportunities to better examine patterns of distribution, abundance, and define demographic metrics for assessing population viability. Incorporating standardized mist-netting efforts in survey guidelines and future research, as has been done for other rare North American bat species (USFWS 2022), can broaden our knowledge of this cryptic species.

DISCLAIMER

Any use of trade, product, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the U.S. Government.

SUPPLEMENTARY DATA

Supporting data are available at <https://doi.org/10.5066/P9G4A2E3> (Hoeh *et al.* 2023).

ACKNOWLEDGMENTS

We acknowledge that our field work took place across many ahupua‘a, in the moku of Hāmākua, Hilo, Ka‘ū, and Kona, on the mokupuni of Hawai‘i, which are the ancestral and traditional lands of the Native Hawaiian people. We thank F. Bonaccorso for development of ideas for this work, acquiring funding, and for years of dedicated research on the ‘ōpe‘ape‘a that built a foundation for this project. This work could not have been done without the help of many people in the field; we thank T. Black, A. Canady, H. Davies, R. Davis, A. Durham, J. Dickey, C. Farrar, D. Gross, M. Holden, C. Holliday, E. Lancaster, V. Mavusana, A. Mendez-Bye, B. Miles, R. Peck, R. Seward, C. Snook, G. Solomon, J. Tupu, and T. Zinn. This research was supported by funding from: Kaheawa Wind Power II, LLC (Agreement Number 17WSTAAZB005541); State of Hawaii, Department of Land and Natural Resources, Division of Forestry and Wildlife (Collaborative Agreement Number 19ZBCCOLL04-DOFKC); and U.S. Geological Survey, Pacific Island Ecosystems Research Center. For land and special use access we thank: Hawai‘i Department of Land and Natural Resources, Division of Forestry and Wildlife—Forest Reserve System, Natural Area Reserve System, and Land Division; USDA Forest Service—Hawai‘i Experimental Tropical Forest; The Nature Conservancy; USFWS—Hakalau Forest National Wildlife Refuge; Department of Hawaiian Home

Lands; County of Hawai‘i—Department of Water Supply; and many private landowners. We thank T. Menard and two anonymous reviewers for comments that improved this manuscript.

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APPENDIX 1

Candidate Set of ‘ōpe‘ape‘a, or Hawaiian Hoary Bat (*Lasiurus semotus*) Capture Rate Models for Three Predictor Type Groupings: (1) Elevation-Only Models (“E”); (2) Time-of-Year-Only Models (“T”); and (3) Both Elevation and Time-of-Year Models (“B”)

Model	Predictor Variables	Type
0	cluster+effort	Null
1	sex+cluster+effort	Sex only
E1	sex+elev+cluster+effort	Elevation
E2	sex+elev+elev ² +cluster+effort	Elevation
E3	sex+elev ² +cluster+effort	Elevation
E4	sex+elev+sex*elev+cluster+effort	Elevation
E5	sex+elev ² +sex*elev ² +cluster+effort	Elevation
E6	sex+elev+elev ² +sex*elev+sex*elev ² +cluster+effort	Elevation
T1	sex+jd.sin+jd.cos+cluster+effort	Time-of-year
T2	sex+repro+cluster+effort	Time-of-year
T3	sex+jd.sin+jd.cos+sex*jd.sin+sex*jd.cos+cluster+effort	Time-of-year
B1	sex+jd.sin+jd.cos+elev+cluster+effort	Both
B2	sex+jd.sin+jd.cos+elev ² +cluster+effort	Both
B3	sex+jd.sin+jd.cos+elev+elev ² +cluster+effort	Both
B4	sex+repro+elev+cluster+effort	Both
B5	sex+repro+elev ² +cluster+effort	Both
B6	sex+repro+elev+elev ² +cluster+effort	Both
B7	sex+jd.sin+jd.cos+elev+sex*jd.sin+sex*jd.cos+sex*elev+sex*jday*elev+cluster+effort	Both
B8	sex+repro+elev+sex*repro+sex*elev+sex*repro*elev+cluster+effort	Both
B9	sex+repro+elev+elev ² +sex*repro+sex*elev+sex*elev ² +sex*repro*elev ² +cluster+effort	Both

The candidate set also includes a null model with no predictors (model 0), and a model with only bat sex as a predictor (model 1). Variables include the sex of bat captures (“sex”), elevation as a linear (“elev”) and quadratic term (“elev²”), and time-of-year as either sine-cosine values of Julian day (“jd.sin”, “jd.cos”) or reproductive season (“repro”). The term “cluster” is the random effects parameter that identifies groups of neighboring netting locations. The variable “effort” is an offset term for adjusting the predicted number of captures by netting effort.

APPENDIX 2

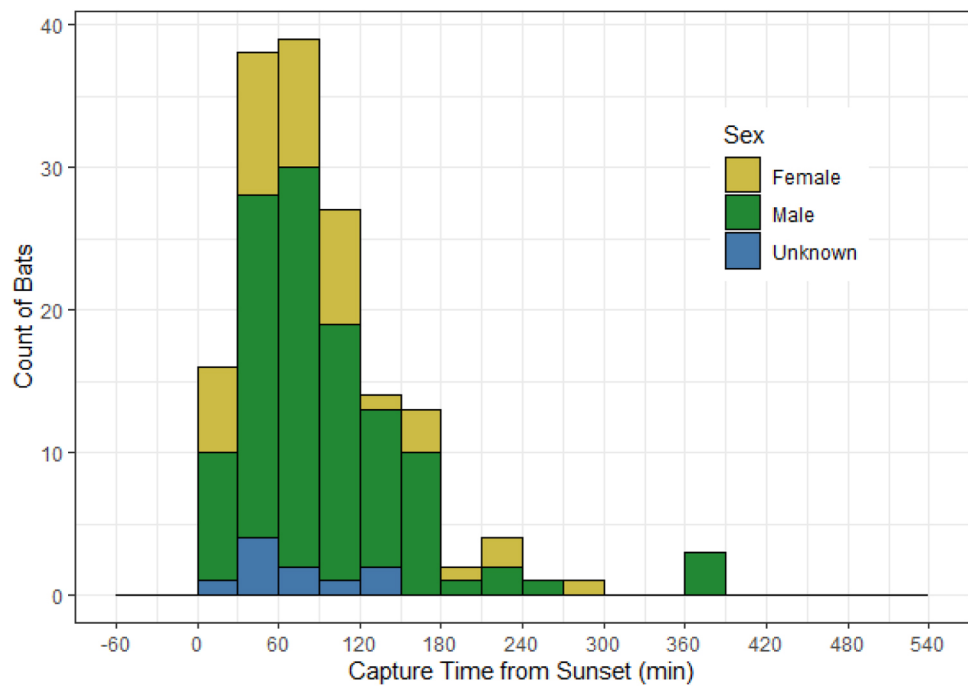


FIGURE 1. Bat captures relative to sunset (0 min) on Hawai'i Island, Hawai'i, from May 2018 to August 2021.

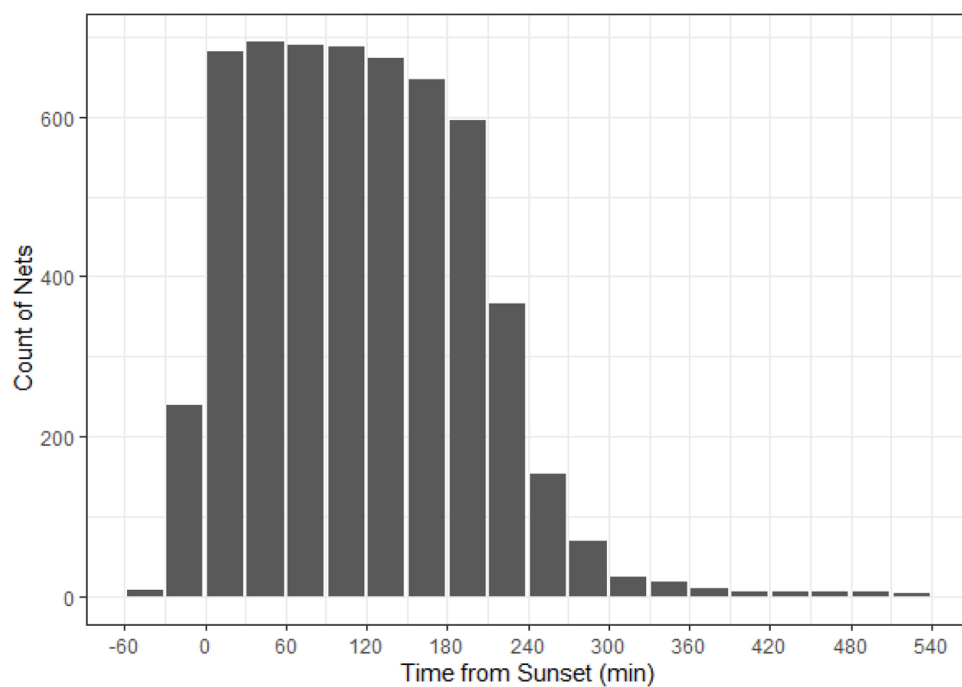


FIGURE 2. Netting effort (number of mist nets open) relative to sunset (0 min) for bat mist netting on Hawai'i Island, Hawai'i, from May 2018 to August 2021.

APPENDIX 3

Model Ranking for Each of Three Predictor Type Groupings: (1) Elevation-Only Models (“E”); (2) Time-of-Year-Only Models (“T”); and (3) Models with Both Elevation and Time-of-Year Parameters (“B”)

Elevation-Only Models						
Model	LogLik	AICc	ΔLogLik	ΔAICc	DF	Weight
E5.ZNB	−186.7	394.3	44.7	0.0	10	0.33
E5.ZP	−188.6	396.1	42.7	1.8	9	0.14
E6.ZNB	−183.4	396.7	47.9	2.4	14	0.10
1.ZNB	−192.2	396.8	39.1	2.5	6	0.09
E1.ZNB	−190.1	396.9	41.2	2.6	8	0.09
E3.ZNB	−188.2	397.5	43.1	3.2	10	0.07
E2.ZNB	−190.4	397.5	40.9	3.2	8	0.07
E6.ZP	−185.4	398.4	45.9	4.1	13	0.04
E4.ZNB	−189.1	399.2	42.2	4.9	10	0.03
E2.ZP	−193.3	401.2	38.0	6.9	7	0.01
1.ZP	−195.6	401.5	35.7	7.2	5	0.01
E3.ZP	−191.9	402.5	39.5	8.2	9	<0.01
E1.ZP	−194.2	402.9	37.1	8.6	7	<0.01
E2.GP	−197.1	404.4	34.2	10.1	5	<0.01
0.ZNB	−198.2	404.5	33.2	10.2	4	<0.01
E3.GP	−196.4	405.1	35.0	10.8	6	<0.01
E4.Z	−193.2	405.2	38.1	10.9	9	<0.01
E5.NB	−196.5	405.4	34.8	11.1	6	<0.01
1.G	−198.7	405.6	32.6	11.3	4	<0.01
E5.GP	−196.9	406.2	34.4	11.9	6	<0.01
E1.GP	−198.1	406.6	33.2	12.3	5	<0.01
E2.NB	−198.3	406.8	33.0	12.5	5	<0.01
1.NB	−199.8	407.7	31.5	13.4	4	<0.01
E6.NB	−195.7	408.0	35.6	13.7	8	<0.01
E6.GP	−195.8	408.3	35.5	14.0	8	<0.01
E4.GP	−198.0	408.3	33.3	14.0	6	<0.01
E3.NB	−198.2	408.7	33.1	14.4	6	<0.01
E1.NB	−199.7	409.6	31.6	15.3	5	<0.01
0.ZP	−201.9	409.9	29.4	15.6	3	<0.01
E4.NB	−199.5	411.4	31.8	17.1	6	<0.01
0.NB	−203.9	414.0	27.4	19.7	3	<0.01
0.GP	−204.9	415.9	26.4	21.6	3	<0.01
E5.P	−219.9	450.0	11.4	55.7	5	<0.01
E6.P	−218.9	452.3	12.4	58.0	7	<0.01
E2.P	−222.4	453.0	8.9	58.7	4	<0.01
E3.P	−222.0	454.3	9.3	60.0	5	<0.01
1.P	−224.4	454.9	6.9	60.6	3	<0.01
E1.P	−224.1	456.3	7.2	62.0	4	<0.01
E4.P	−224.0	458.4	7.3	64.1	5	<0.01
0.P	−231.3	466.7	0.0	72.4	2	<0.01

Time-of-Year-Only Models						
Model	LogLik	AICc	Δ LogLik	Δ AICc	DF	Weight
T2.ZNB	-186.7	390.0	44.6	0.0	8	0.33
T3.ZNB	-180.3	390.5	51.0	0.5	14	0.26
T3.ZP	-181.9	391.4	49.4	1.4	13	0.16
T1.ZNB	-185.3	391.5	46.1	1.5	10	0.16
T1.ZP	-188.0	394.8	43.3	4.8	9	0.03
T2.ZP	-190.5	395.5	40.8	5.4	7	0.02
1.ZNB	-192.2	396.8	39.1	6.8	6	0.01
T3.NB	-191.0	398.5	40.4	8.5	8	<0.01
T3.GP	-191.2	399.0	40.1	9.0	8	<0.01
T2.GP	-194.7	399.7	36.6	9.7	5	<0.01
T1.GP	-194.0	400.3	37.3	10.3	6	<0.01
1.ZP	-195.6	401.5	35.7	11.5	5	<0.01
T2.NB	-197.0	404.2	34.4	14.2	5	<0.01
0.ZNB	-198.2	404.5	33.2	14.5	4	<0.01
1.GP	-198.7	405.6	32.6	15.5	4	<0.01
T1.NB	-197.0	406.5	34.3	16.4	6	<0.01
1.NB	-199.8	407.7	31.5	17.7	4	<0.01
0.ZP	-201.9	409.9	29.4	19.9	3	<0.01
0.NB	-203.9	414.0	27.4	24.0	3	<0.01
0.GP	-204.9	415.9	26.4	25.9	3	<0.01
T3.P	-208.3	431.1	23.0	41.1	7	<0.01
T2.P	-218.4	445.0	12.9	55.0	4	<0.01
T1.P	-218.2	446.6	13.1	56.6	5	<0.01
1.P	-224.4	454.9	6.9	64.9	3	<0.01
0.P	-231.3	466.7	0.0	76.7	2	<0.01

Elevation and Time-of-Year Models						
Model	LogLik	AICc	Δ LogLik	Δ AICc	DF	Weight
B5.ZNB	-185.0	391.0	46.3	0.0	10	0.34
B2.ZNB	-183.9	393.1	47.4	2.2	12	0.11
B7.ZNB	-167.2	393.1	64.1	2.2	26	0.11
B4.ZNB	-186.3	393.5	45.0	2.6	10	0.09
B7.ZP	-169.1	394.5	62.2	3.5	25	0.06
B6.ZNB	-184.6	394.6	46.7	3.6	12	0.06
B1.ZNB	-184.8	395.0	46.5	4.0	12	0.05
B5.ZP	-188.4	395.7	42.9	4.7	9	0.03
B2.ZP	-186.4	396.1	44.9	5.1	11	0.03
1.ZNB	-192.2	396.8	39.1	5.9	6	0.02
B3.ZNB	-183.5	396.9	47.8	5.9	14	0.02
B5.GP	-192.9	398.1	38.4	7.2	6	0.01
B8.ZP	-180.7	398.2	50.6	7.2	17	0.01
B1.ZP	-187.5	398.2	43.8	7.2	11	0.01
B7.NB	-184.3	398.4	47.1	7.5	14	0.01
B4.ZP	-189.9	398.7	41.4	7.7	9	0.01
B6.GP	-192.2	398.8	39.2	7.8	7	0.01
B6.ZP	-187.9	398.9	43.5	7.9	11	<0.01
B2.GP	-192.5	399.5	38.8	8.5	7	<0.01
B3.ZP	-186.0	399.6	45.3	8.6	13	<0.01
B7.GP	-184.9	399.6	46.5	8.6	14	<0.01

APPENDIX 3

Elevation and Time-of-Year Models						
Model	LogLik	AICc	Δ LogLik	Δ AICc	DF	Weight
B3.GP	-191.6	399.8	39.7	8.9	8	<0.01
B9.NB	-187.5	400.3	43.9	9.3	12	<0.01
B4.GP	-194.2	400.7	37.1	9.8	6	<0.01
B9.GP	-187.8	401.0	43.5	10.0	12	<0.01
B1.GP	-193.3	401.0	38.1	10.0	7	<0.01
B8.GP	-190.1	401.2	41.2	10.2	10	<0.01
1.ZP	-195.6	401.5	35.7	10.5	5	<0.01
B8.NB	-190.8	402.6	40.5	11.6	10	<0.01
B5.NB	-195.8	403.9	35.6	12.9	6	<0.01
0.ZNB	-198.2	404.5	33.2	13.5	4	<0.01
1.GP	-198.7	405.6	32.6	14.6	4	<0.01
B6.NB	-195.7	405.9	35.6	14.9	7	<0.01
B4.NB	-196.9	406.2	34.4	15.2	6	<0.01
B2.NB	-196.0	406.5	35.3	15.5	7	<0.01
1.NB	-199.8	407.7	31.5	16.8	4	<0.01
B9.ZP	-180.9	408.2	50.4	17.2	21	<0.01
B1.NB	-197.0	408.5	34.3	17.5	7	<0.01
B3.NB	-195.9	408.5	35.4	17.6	8	<0.01
0.ZP	-201.9	409.9	29.4	18.9	3	<0.01
0.NB	-203.9	414.0	27.4	23.0	3	<0.01
0.GP	-204.9	415.9	26.4	24.9	3	<0.01
B7.P	-197.5	422.6	33.9	31.6	13	<0.01
B9.P	-202.6	428.4	28.7	37.5	11	<0.01
B8.P	-209.2	437.2	22.1	46.2	9	<0.01
B5.P	-216.4	443.0	14.9	52.1	5	<0.01
B6.P	-216.0	444.4	15.3	53.4	6	<0.01
B2.P	-216.5	445.3	14.8	54.4	6	<0.01
B4.P	-218.1	446.4	13.2	55.4	5	<0.01
B3.P	-216.0	446.4	15.3	55.5	7	<0.01
B1.P	-217.7	447.8	13.6	56.8	6	<0.01
1.P	-224.4	454.9	6.9	64.0	3	<0.01
0.P	-231.3	466.7	0.0	75.7	2	<0.01
B8.ZNB ^a	NA	NA	NA	NA	18	NA
B9.ZNB ^a	NA	NA	NA	NA	22	NA

The candidate set also includes a null model with no predictors (model 0), and a model with only bat sex as a predictor (model 1). The model names indicate the respective negative binomial ("NB"), Poisson ("P"), generalized Poisson ("GP"), zero-inflated negative binomial ("ZNB"), and zero-inflated Poisson ("ZP") error distribution families. See Appendix 1 for description of model variables.

^aModels did not converge.

APPENDIX 4

Summary for Selected Top-Ranked Models (see Appendix 3), Including Coefficient Estimates, Standard Errors (SE), Associated Wald's z -score and Significance Level P for Count And Zero-Inflated Components of Fixed and Random Effect Terms (Including Intercept Standard Deviation [SD])

Model E5.ZNB – Elevation						
Effect	Component	Term	Estimate	SE	z	P
Fixed	Count	intercept	−5.410	0.581	−9.300	0.000
Fixed	Count	sexM	−1.020	0.546	−1.860	0.062
Fixed	Count	elev ²	−1.750	0.602	−2.900	0.004
Fixed	Count	sexM × elev ²	1.700	0.620	2.750	0.006
Fixed	Zero-inflated	intercept	−5.180	0.584	−8.860	0.000
Fixed	Zero-inflated	sexM	−2.240	0.849	−2.640	0.008
Fixed	Zero-inflated	elev ²	−0.915	0.948	−0.965	0.334
Fixed	Zero-inflated	sexM × elev ²	1.570	1.060	1.480	0.140
Random	Count	intercept SD	0.498	–	–	–
Model T2.ZNB – Time-of-Year (Categorical)						
Effect	Component	Term	Estimate	SE	z	P
Fixed	Count	intercept	−6.310	0.578	−10.900	0.000
Fixed	Count	sexM	−0.200	0.433	−0.462	0.644
Fixed	Count	repro	−0.368	0.380	−0.968	0.333
Fixed	Zero-inflated	intercept	−4.280	0.619	−6.920	0.000
Fixed	Zero-inflated	sexM	−2.300	0.706	−3.260	0.001
Fixed	Zero-inflated	repro	−2.190	0.808	−2.710	0.007
Random	Count	intercept SD	0.650	–	–	–
Model T3.ZNB – Time-of-Year (Continuous)						
Effect	Component	Term	Estimate	SE	z	P
Fixed	Count	intercept	−8.008	0.548	−14.610	0.000
Fixed	Count	sexM	1.545	0.553	2.796	0.005
Fixed	Count	jd.sin	−0.894	0.562	−1.591	0.112
Fixed	Count	jd.cos	−2.251	0.559	−4.026	0.000
Fixed	Count	sexM × jd.sin	0.852	0.637	1.337	0.181
Fixed	Count	sexM × jd.cos	2.918	0.630	4.630	0.000
Fixed	Zero-inflated	intercept	−7.545	2.028	−3.722	0.000
Fixed	Zero-inflated	sexM	0.467	2.083	0.224	0.823
Fixed	Zero-inflated	jd.sin	0.528	0.981	0.538	0.591
Fixed	Zero-inflated	jd.cos	−2.376	2.305	−1.031	0.303
Fixed	Zero-inflated	sexM × jd.sin	−0.207	1.120	−0.185	0.853
Fixed	Zero-inflated	sexM × jd.cos	3.830	2.433	1.574	0.115
Random	Count	intercept SD	0.432	–	–	–
Model B5.ZNB – Combined Elevation and Time-of-Year						
Effect	Component	Term	Estimate	SE	z	P
Fixed	Count	intercept	−5.758	0.637	−9.035	0.000
Fixed	Count	sexM	−0.186	0.432	−0.431	0.667
Fixed	Count	repro	−0.403	0.379	−1.063	0.288
Fixed	Count	elev ²	−0.515	0.376	−1.372	0.170
Fixed	Zero-inflated	intercept	−4.459	0.710	−6.278	0.000
Fixed	Zero-inflated	sexM	−2.268	0.699	−3.242	0.001
Fixed	Zero-inflated	repro	−2.186	0.825	−2.651	0.008
Fixed	Zero-inflated	elev ²	0.197	0.439	0.450	0.653
Random	Count	intercept SD	0.585	–	–	–