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HAWAIIAN HOARY BAT OCCUPANCY AT KALOKO-HONOKŌHAU NATIONAL HISTORICAL PARK

Corinna Pinzari¹, Frank Bonaccorso², and Kristina Montoya-Aiona²

¹Hawai'i Cooperative Studies Unit, University of Hawai'i at Hilo, Kilauea Field Station,
P.O. Box 44, Hawai'i National Park, HI 96718

²U.S. Geological Survey, Pacific Island Ecosystems Research Center, Kilauea Field Station,
P.O. Box 44, Hawai'i National Park, HI 96718

Hawai'i Cooperative Studies Unit
University of Hawai'i at Hilo
200 W. Kawili St.
Hilo, HI 96720
(808) 933-0706

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TABLE OF CONTENTS

List of Tables	i
List of Figures	i
Abstract.....	1
Introduction.....	1
Methods	2
Study Area	2
Bat Detection and Recording Equipment.....	2
Data Analysis.....	5
Characteristics of Hawaiian Hoary Bat Calls	7
Results	8
Acoustic Detections of Bats.....	8
Timing of Nightly Bat Activity.....	9
Bat Call Activity Relative to Reproductive Seasons.....	9
Foraging and Group Activity	9
Habitat Use	11
Discussion	11
Acknowledgements	12
Literature Cited	13
Appendix: Terminology	15

LIST OF TABLES

Table 1. Recording stations at Kaloko-Honokōhau National Historical Park	4
Table 2. SD1 records of call events and pulses.....	8
Table 3. SM2 records of call events and total pulses	9

LIST OF FIGURES

Figure 1. Map of bat-monitoring stations and park boundaries at Kaloko-Honokōhau National Historical Park.....	3
Figure 2. Habitat and vegetation around the four acoustic recording stations.....	4
Figure 3. Anabat Hi-Mic microphone unit and SM-USX microphone unit.	5
Figure 4. Typical search-phase pulses in a call event..	6
Figure 5. Search-phase pulses followed by a feeding buzz in a single call event	6
Figure 6. Search-phase pulses produced by two bats.....	7

Figure 7. Mean bat detectability for recording stations using pooled SD1 recorders and single SM2 recorders.....	8
Figure 8. Timing of nightly bat call events.....	10
Figure 9. Mean detectability of bats during reproductive and non-reproductive periods.....	10

ABSTRACT

Hawaiian hoary bat (*Lasiurus cinereus semotus*) vocalizations were recorded using Anabat SD1 and Song Meter SM2Bat ultrasonic recorders at four monitoring stations in Kaloko-Honokōhau National Historical Park on the island of Hawai'i. We hypothesize that echolocation call events are more numerous during the reproductive season of this bat. Bat detectors recorded from 1700 to 0730 hrs on a total of 42 nights between October 2011 and September 2012. Peak activity occurred between 1800 and 2000 hrs, although in May a secondary peak occurred between 0100 and 0300 hrs. Detectability proportions (0 to 1.0) were calculated using the software program PRESENCE (v4.2) and reported for each seven day recording session which was repeated on a bimonthly schedule. Hawaiian hoary bats were present in four of the six bimonthly surveys: January, May, September, and October; however, no bat calls were detected in March or July. Detectability of bat calls was above 0.50 in January, May, and September. Foraging buzzes, indicating feeding activity, were recorded in all months that bats were present.

INTRODUCTION

Although the Hawaiian hoary bat (*Lasiurus cinereus semotus*) was first collected in 1861 (Gray 1862) and occurs on all major volcanic islands in Hawai'i (Tomich 1986), the ecology (Jacobs 1994) and even the systematics (Morales and Bickham 1995) of this bat still are poorly understood. The U.S. Fish and Wildlife Service (USFWS) listed this endemic subspecies as "endangered" in 1970 and published a recovery plan for the species in 1998 (USFWS 1998). Aside from brief publications dealing with Hawaiian hoary bat distribution, echolocation, or diet, studies of bats of at least one-year in duration have been published only recently (Fraser *et al.* 2007, Fraser and HaySmith 2009, Todd 2012, Gorresen *et al.* 2013, Bonaccorso *et al.* in press). Two acoustic surveys previously demonstrated that Hawaiian hoary bats occur in Kaloko-Honokōhau National Historical Park (NHP; hereafter, the Park). Fraser *et al.* (2007) detected Hawaiian hoary bats in the Park only in March and April during surveys conducted with handheld bat detectors from March through July 2005. In a brief survey, 2–7 October 2009, one Anabat II system was deployed in the Park (A. Johnson-Campbell personal communication) and recorded from 1 to 16 call events (see Appendix for definitions of terms) for each of the five nights. All call events in the latter study were short sequences of pulses without feeding buzzes, suggesting that Hawaiian hoary bats at those instances quickly transited the area around the microphone without foraging.

Reproductive activity in female Hawaiian hoary bats including pregnancy, lactation, and parental care of maternally dependent pups (usually twins) occurs from May through October (Tomich 1986). By November, young of the year are completely independent of the mother, both in foraging and roosting. During September through October, Hawaiian hoary bats appear to congregate at higher than normal densities at traditional "swarming sites" (D. Foote personal observation; F. Bonaccorso personal observation) during which time copulations have been observed both on Maui (J. King personal communication) and on Hawai'i (C. Todd personal communication). Females likely store sperm over the winter, and the reproductive cycle results in pregnancies in the following May–June with parturition mostly in July (Tomich 1986).

We hypothesize that echolocation call events recorded for Hawaiian hoary bats should be more numerous during the May to October reproductive season. The reasons for increased vocal

activity during the reproductive season being: 1) adult females have increased energetic demands during pregnancy and lactation; 2) populations of Hawaiian hoary bats should be largest each year after young bats fledge; and 3) subadult bats are less efficient predators than adults and active over longer periods each night.

This report summarizes seasonal occupancy of the Hawaiian hoary bat at Kaloko-Honokōhau NHP over a one-year period and includes analyses of bat-vocalization data collected from six bimonthly sampling periods of approximately one week each. These data provide detailed information on the seasonal presence of bats in the Park, and make it possible to draw inferences about foraging activity, occupancy by season, frequency and timing of simultaneous multiple bat detections, and habitat use.

METHODS

Study Area

Our study was conducted at Kaloko-Honokōhau NHP on the island of Hawai'i. The Park comprises 469 ha with almost half of this area in marine waters. Within the Park there are coral reefs, beaches, rocky shores, anchialine pools, two historical man-made brackish fishponds and associated wetlands, dry forest, cultural and archeological sites, and lava fields described in detail by U.S. National Park Service (1994) and Cogan *et al.* (2011).

We recorded bat vocalizations at four locations: Kaloko Fishpond, Māmalahoa Trail, 'Aimakapā Fishpond, and South Boundary (Figures 1 and 2, Table 1). All stations consisted of one ultrasonic recording unit and were 1 to 10 m above sea level. Kaloko and 'Aimakapā stations were along wooded shorelines of the respective fishponds. Māmalahoa Trail and South Boundary were in xeric lava fields respectively dominated by invasive haole koa trees (*Leucaena leucocephala*, Mimosoideae) and fountain grass (*Cenchrus setaceus*, Poaceae).

Bat Detection and Recording Equipment

Echolocation pulses of Hawaiian hoary bats were recorded using Anabat SD1 Bat Detectors (hereafter, SD1; Titley Electronics, Ballina, Australia) as the primary recording device. Each bat detector was programmed to record from 1700 to 0730 hrs the next morning. We deployed SD1 units on 42 nights between 17 October 2011 and 26 September 2012 over a total monitoring time of 504 hrs. During each bimonthly survey, one SD1 unit recorded during seven consecutive nights at each of the four recording stations. Based on the tested effective range of the SD1 microphones, we monitored a total area of 11,309 m².

In October 2011 and in May and September 2012, supplemental recordings were made with SM2Bat Song Meter Digital Field Recorder Platforms (hereafter, SM2; Wildlife Acoustics, Concord, MA). These new SM2 units were available only on a limited basis for this project. SM2 detectors were deployed on 19 nights for 228 hours of recording. Based on the tested effective range of the SM2 microphones, we monitored a total area of 62,831 m².

Both SD1 and SM2 recording units logged bat calls on compact flash-memory cards and included timing devices and ports to connect cables to microphones. Each SD1 was powered by an external 12-volt battery, and both were enclosed in a water-resistant plastic box. An ultrasonic Hi-Mic microphone was mounted inside PVC pipe oriented with the microphone toward the ground to prevent rain damage. A 15 x 15 cm plexiglass plate was attached 12 cm below the microphone at a 45-degree angle to reflect and enhance calls from bats flying above

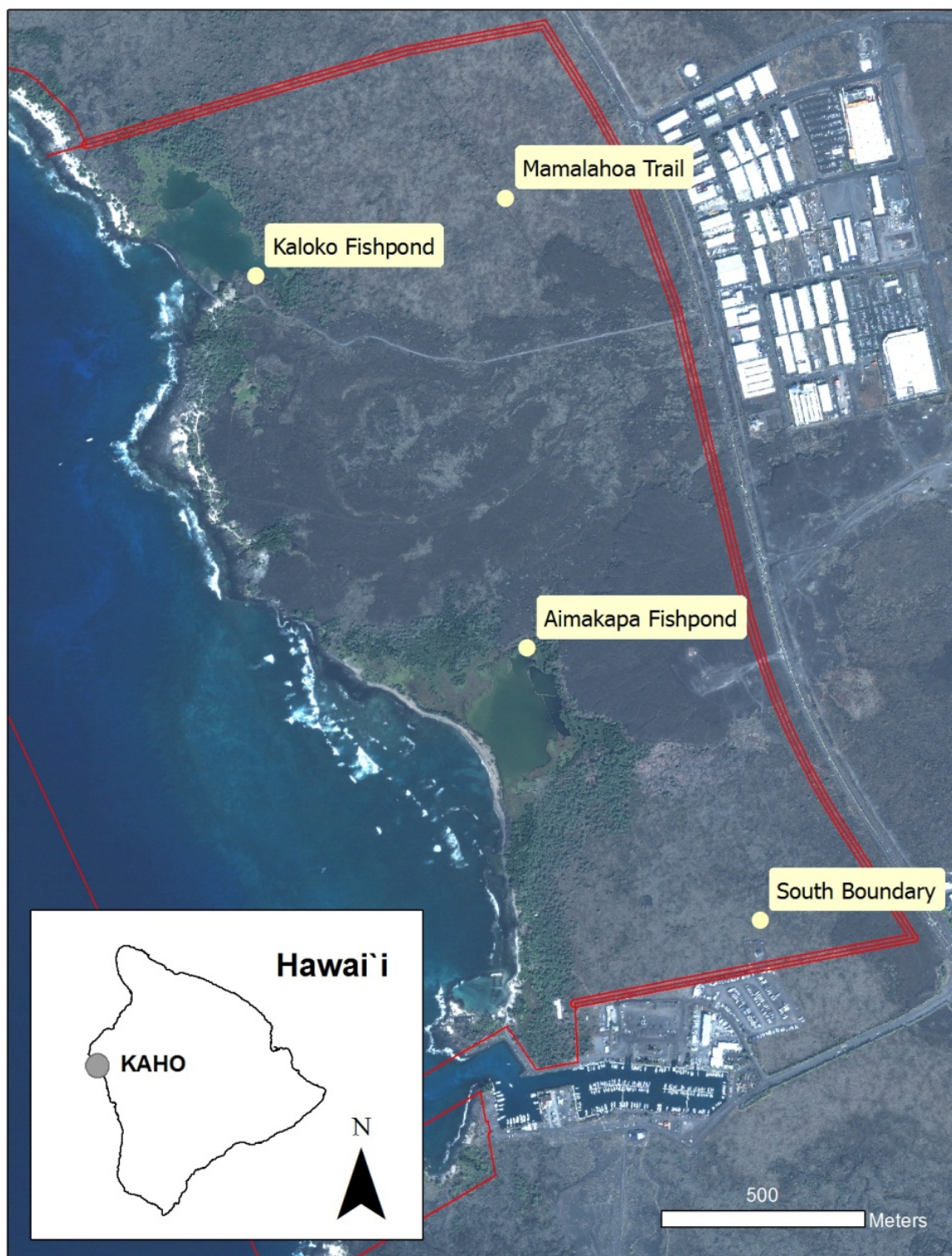


Figure 1. Map of bat-monitoring stations and park boundaries (red lines) at Kaloko-Honokōhau National Historical Park (KAHO), Hawai'i.

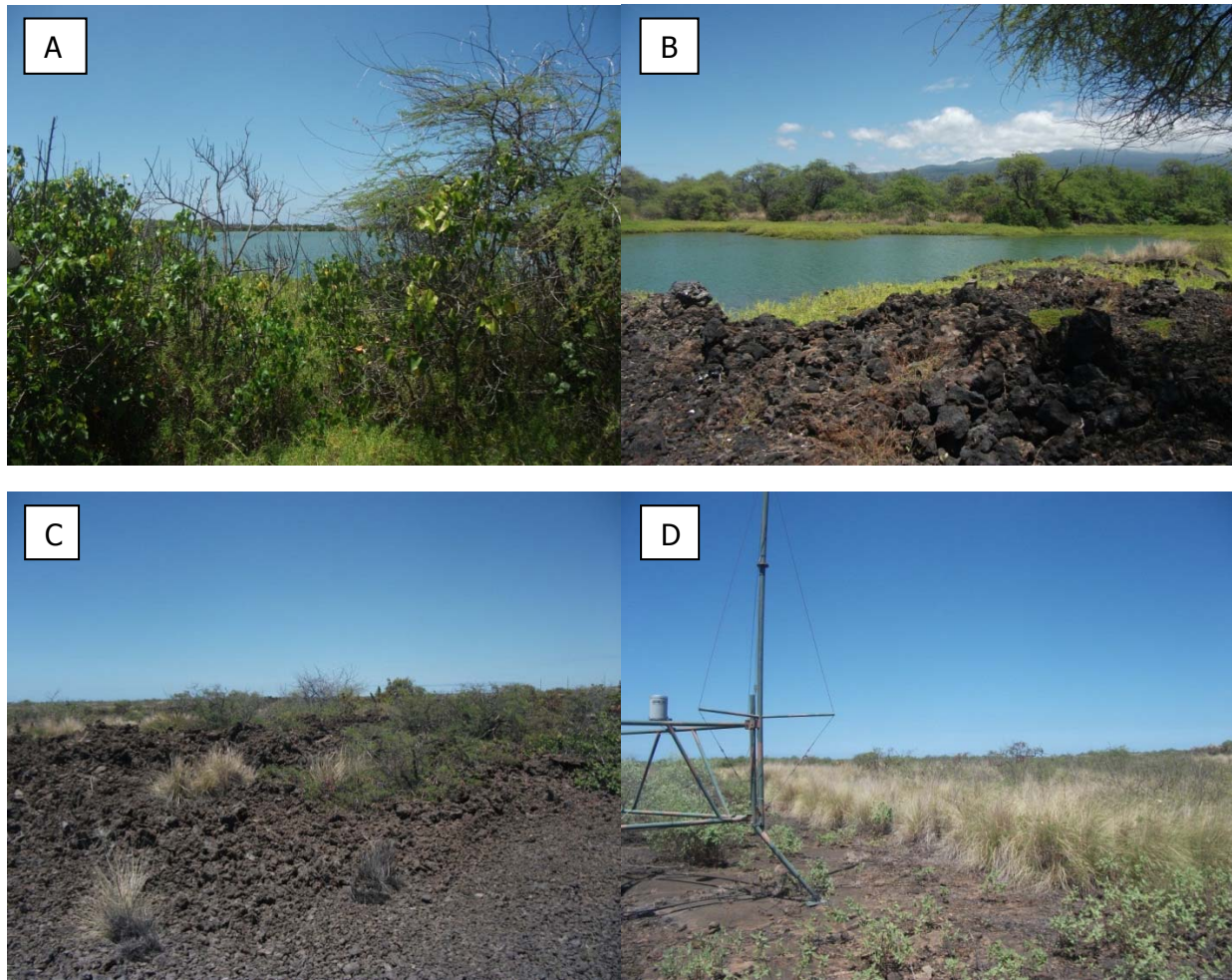


Figure 2. Habitat and vegetation around the four acoustic recording stations: A. 'Aimakapā Fishpond; B. Kaloko Fishpond; C. Māmalahoa Trail; D. South Boundary.

Table 1. Recording stations at Kaloko-Honokōhau National Historical Park, Hawai'i, with GPS Easting and Northing (UTM units) and habitat characterization.

Location	Easting	Northing	Habitat
Kaloko Fishpond	2179588	811209	wetland shoreline
N. Māmalahoa Trail	2179779	811824	lava and haole koa
'Aimakapā Fishpond	2178674	811877	wetland shoreline
South Boundary	2178005	812450	lava and fountain grass

the microphone (Figure 3). The PVC pipe and microphone then were affixed to the top of a 7-m steel pole anchored into the soil substrate and/or tethered to a tree. Anabat Hi-Mic microphones in this configuration have an omnidirectional maximum effective range of 30 m. All microphones were inspected for operational efficiency before each bimonthly deployment.

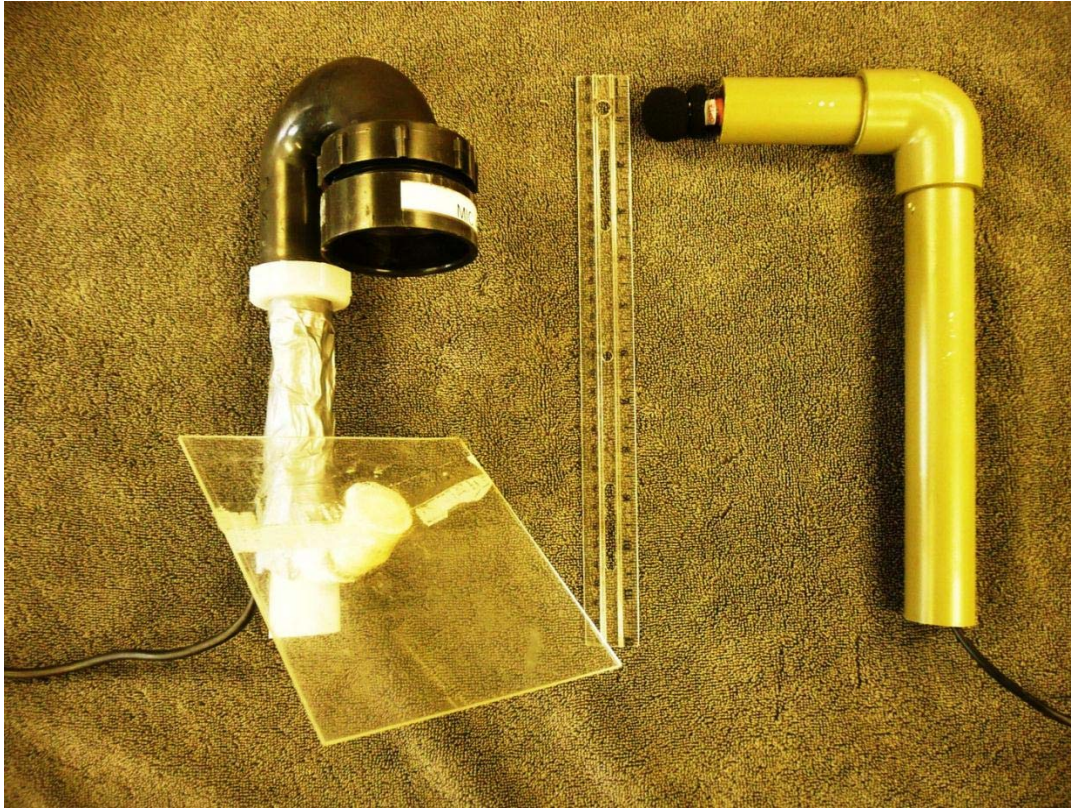


Figure 3. Anabat Hi-Mic microphone unit (left) and SM-USX microphone unit (right).

SM2 units were powered with four internal D-cell batteries or two external 12-volt, 7.2 amp-hr batteries wired in series. A cable from the SM2 connected to a high-frequency SM-USX microphone mounted partially within a PVC sleeve oriented parallel to the ground (Figure 3) and atop a pole of 7 m height. Both the SM2 and the SM-USX are waterproof units. The SM-USX microphone records high-quality omnidirectional calls at distances of up to 100 m under ideal conditions; however, the quality of call recordings vary with the orientation of a bat's head relative to the microphone, the distance to the microphone, and humidity. The relative performance qualities of Anabat and Wildlife Acoustics systems have been evaluated by Adams *et al.* (2012), and each offers different advantages in recording hoary bats.

Data Analysis

SD1 recordings were downloaded from compact flash cards using the program CFCread (version 4.2.1, Titley Scientific). Recordings were organized in folders of call-events by night. Analook software (version 3.3.6, Titley Scientific) enabled collected call events to be downloaded, displayed, and managed for computers. "Zero-crossings analysis" created frequency/time graphs of detected signals from which echolocation pulses were identified and counted.

SM2 recordings were downloaded from compact flash cards and converted to call event ".wav files" using Wac2Wav software (version 2.9.1, Wildlife Acoustics). We used SongScope (version 3.3, Wildlife Acoustics) to filter most background noise (e.g., wind, rain, insect calls) from the files and to count individual echolocation pulses produced by bats. CallViewer (version 18,

M. Skowronski 2008, developer) was used to create frequency/time graphs (Figures 4–6), which depict series of echolocation pulses within a recorded call event.

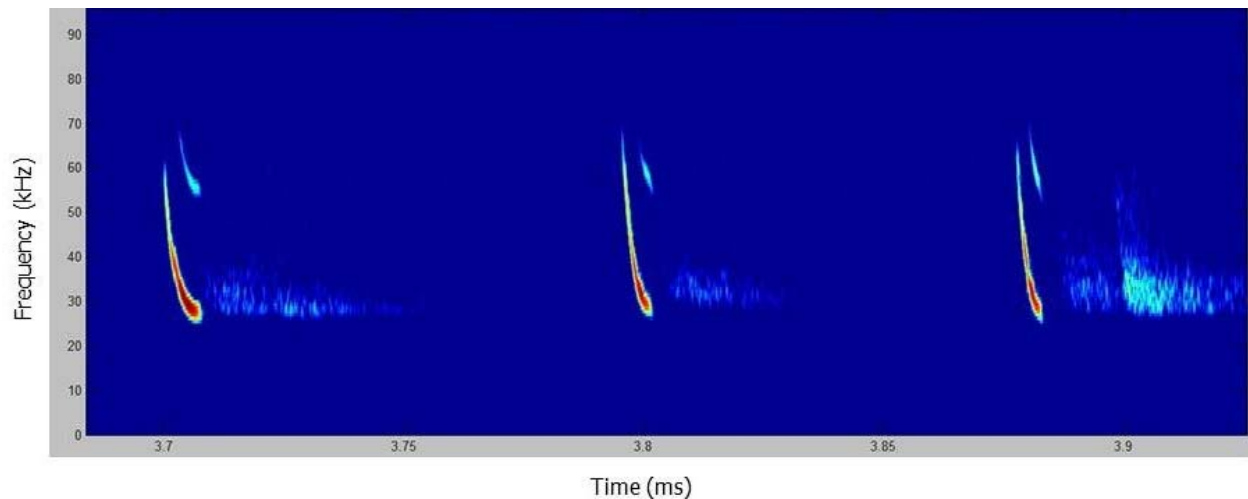


Figure 4. Typical search-phase pulses in a call event. The sonogram shown here depicts three pulses from a Hawaiian hoary bat at Kaloko-Honokōhau National Historical Park, Hawai'i.

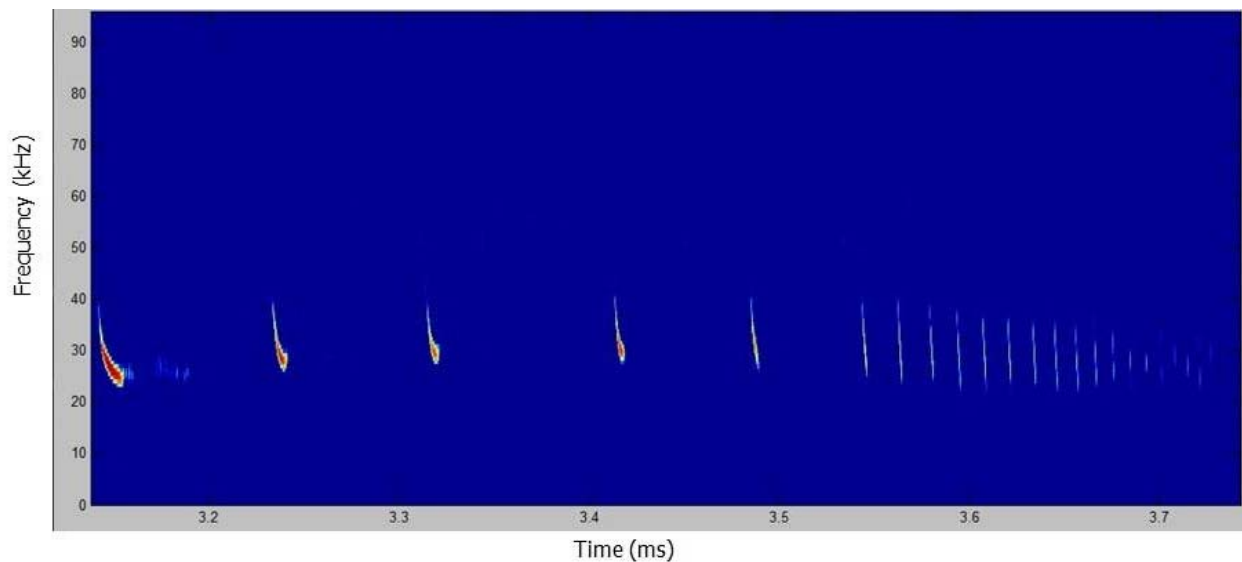


Figure 5. Search-phase pulses (left and center) followed by a feeding buzz (far right) in a single call event.

“Bat detectability” as an index for occupancy analysis was calculated with the program PRESENCE (version 4.2, Hines 2006). Maximum detectability of 1.0 was equivalent to every recording station detecting a minimum threshold of three confirmed bat echolocation pulses within at least one call event every night during a seven-night sampling period. Zero

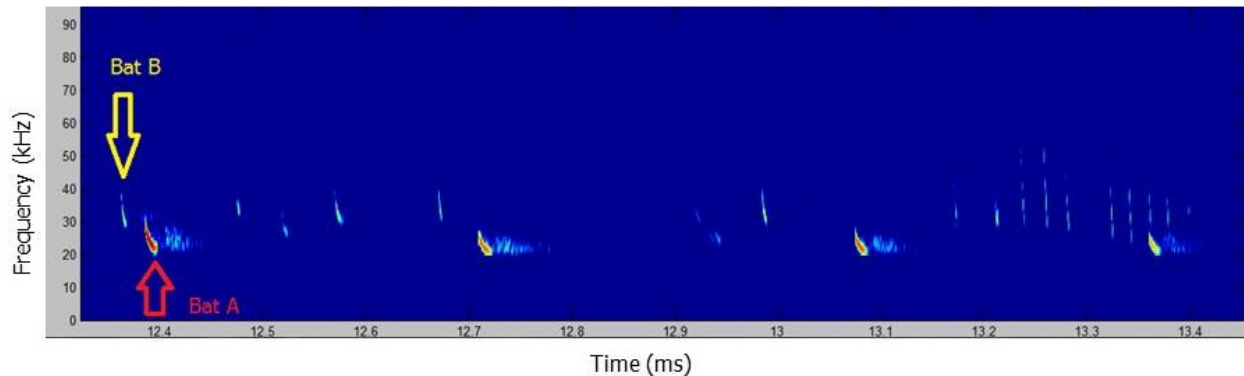


Figure 6. Search-phase pulses produced by two bats near a single microphone. Bat A (lower portion of sonogram) is closer to the microphone. Bat B is emitting search-phase pulses (left and center), then emits a feeding buzz (far right).

detectability represented no call event identification exceeding the threshold value at any station during a sampling period.

All call events were verified by audio and visual inspection. We conservatively discarded any recorded events of sound that did not conform to standard hoary bat vocalization parameters. The cumulative number of echolocation pulses for all call events was summed by recording station and night during a survey period. Finally, we tabulated the number of nights with feeding buzzes and also tabulated the number of nights containing call events with group activity (i.e., more than one echolocating bat was recorded by a single microphone with individual pulses overlapping in time for two or more call events). Thus, our acoustic surveys provide site-specific quantitative information on the presence or absence of bats, foraging activity, and the presence of multiple bats around a given microphone.

All statistical tests were conducted using Microsoft Excel 2010. Means are shown with standard errors, and *P* values were set at a 0.05 threshold.

Characteristics of Hawaiian Hoary Bat Calls

The calls, or echolocation pulses, of Hawaiian hoary bats are frequency modulated, whereby a single sound pulse sweeps through a range of frequencies over time. A typical pulse in a Hawaiian hoary bat call begins at a frequency of 60–70 kHz and sweeps downward to about 25 kHz within a few milliseconds (ms). Each pulse appears as a J-shaped band of energy in a sonogram (Figure 4). When a bat searches for potential insect prey there is an inter-pulse interval of about 8–10 ms, hence the term “search call.” An individual call event representing a bat flying past a recording microphone and producing a series of pulses can involve a few pulses at a rate of about one pulse per 7–8 ms in the initial search phase or hundreds of pulses throughout a feeding buzz broadcast at up to 10 pulses/ms (Figure 5). The feeding buzz serves to obtain frequent echoes that carry information on the trajectory of the insect that the bat can use to attempt an intercept in flight. If two or three bats are in close proximity and echolocating at the same time, these calls often can be distinguished within one sonogram as the timing of the pulses are out of time with each other (Figure 6). Hawaiian hoary bat calls are unique among all the sounds (wind, rain, insects, machines) produced by nature or by man in the

Hawaiian environment. Thus, great confidence can be placed in identifying and quantifying Hawaiian hoary bat calls.

RESULTS

Acoustic Detections of Bats

Call events produced by Hawaiian hoary bats were recorded during October, January, May, and September with Anabat SD1 units (Table 2), but no call events were recorded during March or July. The greatest number of call events and the highest detectability values using the SD1 system (Figure 7) were observed in September. During the 42 nights that recording was conducted, call events were recorded on 16 nights (38% of the nights sampled). There were 56 total call events recorded representing a mean of 0.53 ± 0.35 call events per microphone per night over the duration of the study. The mean number of pulses per event was 4.54 ± 0.52 . All call events recorded by SD1 units consisted of search calls without feeding buzzes.

Table 2. SD1 records of call events and pulses at Kaloko-Honokōhau National Historical Park.

Month/year	Nights sampled	Recording stations	Nights with bat activity	Call events	Total pulses
October 2011	7	3	2	2	6
January 2012	7	4	6	21	84
March 2012	7	4	0	0	0
May 2012	7	2	2	2	11
July 2012	7	3	0	0	0
September 2012	7	2	6	31	176
Totals	42		16	56	277

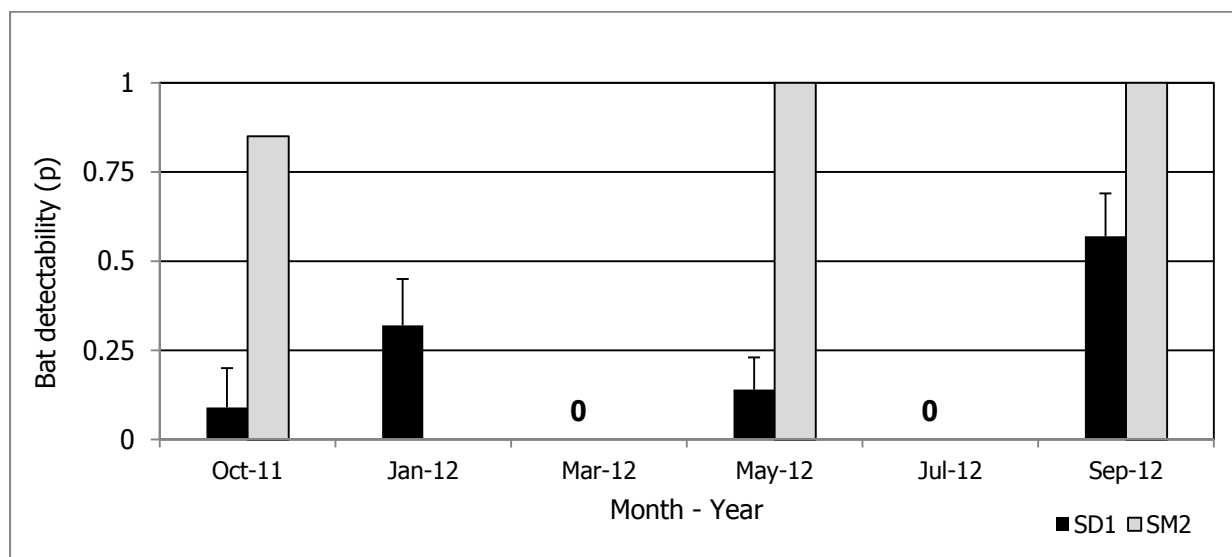


Figure 7. Mean bat detectability for recording stations using pooled SD1 recorders (black bars) and single SM2 recorders (gray bars). Zero values in March and July indicate that sampling was conducted, but no confirmed bat calls exceeding the threshold value were recorded. Vertical lines represent the upper half of one standard error.

Supplementary recordings from SM2 detectors in October 2011 at the Kaloko Fishpond, May 2012 at the 'Aimakapā and Kaloko Fishponds, and September 2012 at the Kaloko Fishpond captured 469 call events (Table 3). Call events were detected on 18 of 19 total nights (94.7%) during survey periods using the SM2.

Table 3. SM2 records of call events and total pulses at Kaloko-Honokōhau National Historical Park, Hawai'i.

Month/year	Nights sampled	Recording stations	Nights with bat activity	Call events	Total pulses
October 2011	7	1	6	82	1,261
May 2012	7	2	7	324	13,912
September 2012	5	1	5	63	1,865
Totals	19		18	469	17,038

An SM2 and an SD1 paired side by side for five nights at the Kaloko Fishpond in September recorded 63 call events with 1,865 pulses and 16 call events with 106 pulses, respectively, during the only period of successful simultaneous recording. Two additional attempts to pair these two types of ultrasonic recorders were not successful due to equipment failure in SD1 units.

Timing of Nightly Bat Activity

No acoustic activity was observed in the Park before 1800 hrs or after 0300 hrs during our study (Figure 8). A major peak in activity from the pooled results of all ultrasonic detectors occurred between 1800 and 2000 hrs with activity trailing off through successive hours. A small secondary peak in bat activity was observed between 0100 and 0300 hrs during May.

Bat Call Activity Relative to Reproductive Seasons

To assess seasonal bat activity, we used only SD1 data since these were the only recording units collecting data in both reproductive and non-reproductive seasons. Both call events and echolocation pulses were standardized to reflect survey effort. There was no significant difference between the mean number of call events recorded per microphone per survey, during the reproductive season, 11.0 ± 17.3 (May through October), and the non-reproductive season, 7.7 ± 11.6 (two-sample t-test; $t = 0.28$, $P = 0.79$, $n = 3$, $df = 4$). Nor was there a significant difference in total echolocation pulses recorded per microphone per survey during the reproductive season, 62.33 ± 98.59 , and the non-reproductive season, 30 ± 46.9 (two-sample t-test; $t = 0.51$, $P = 0.63$, $n = 3$, $df = 4$). There was no significant difference in detectability between the reproductive (0.2 ± 0.3) and non-reproductive (0.1 ± 0.1) seasons (two-sample t-test; $t = 0.51$, $P = 0.64$, $n = 3$, $df = 4$; Figure 9).

Foraging and Group Activity

From the SM2 recordings, we found feeding buzzes indicative of foraging activity during October ($n = 3$), May ($n = 56$), and September ($n = 2$). All foraging events occurred at Kaloko or 'Aimakapā Fishponds, suggesting that wetland habitats provide suitable insect prey.

We observed simultaneous call events with two echolocating bats present around a microphone only during May at which time there were 60 instances of paired vocalizations recorded mostly

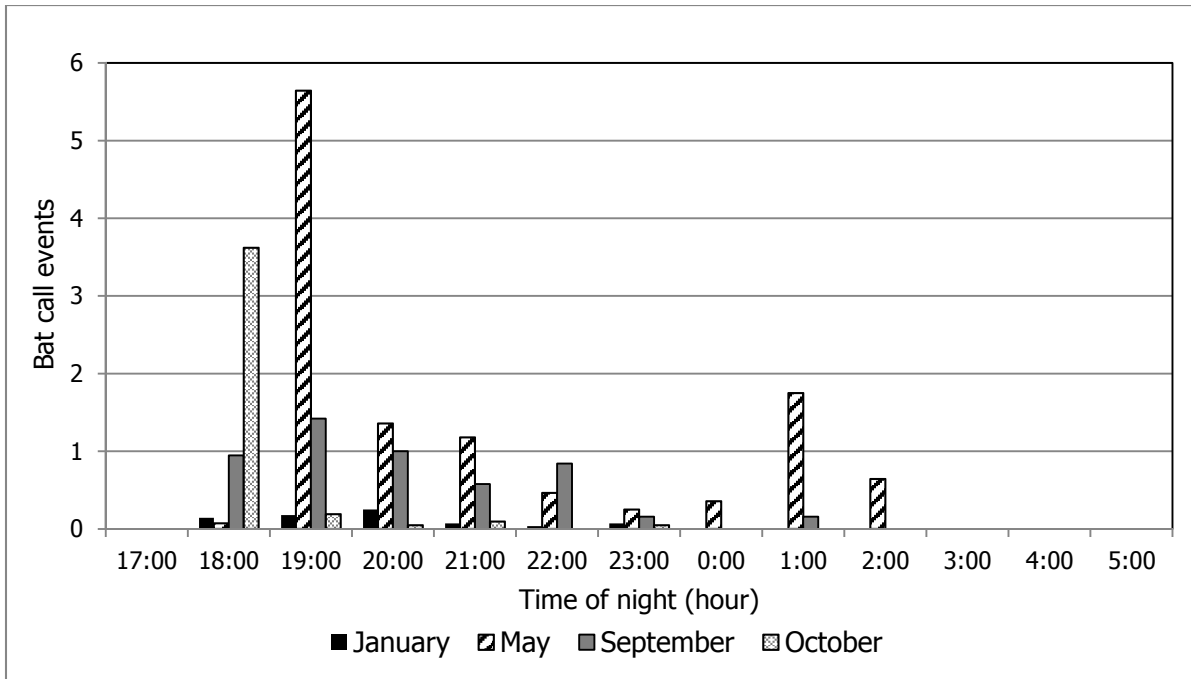


Figure 8. Timing of nightly bat call events at Kaloko-Honokōhau National Historical Park, Hawai'i.

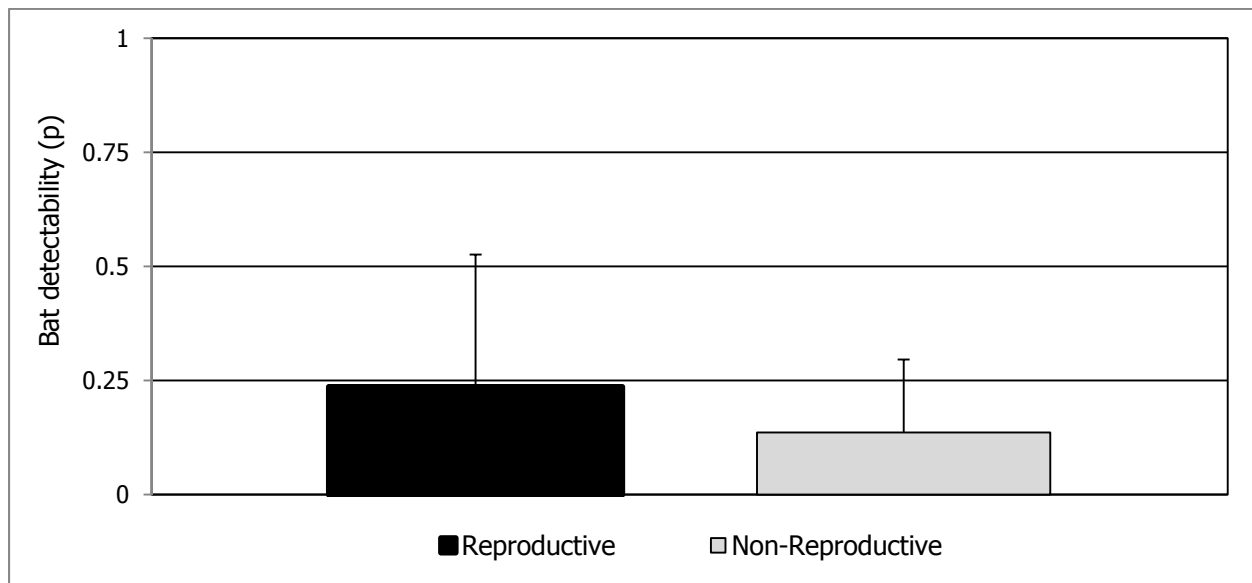


Figure 9. Mean detectability of bats at Kaloko-Honokōhau National Historical Park, Hawai'i, during reproductive and non-reproductive periods.

by SM2 units. All recordings with multiple bats were observed at the fishponds during times when only adult bats were present in the population.

Habitat Use

Kaloko Fishpond (38 call events) and 'Aimakapā Fishpond (14 call events) overwhelmingly were the areas of greatest bat activity within the Park. Only four call events were recorded over the xeric lava beds at the South Boundary ($n = 2$) and at the Northern Māmalahoa Trail ($n = 2$). Using only data collected with SD1 systems, a two sample t-test indicated significantly more bat call events at the pond shoreline habitat (6.50 ± 9.47) than at the xeric lava/shrub habitats (0.40 ± 0.52 ; $t = 2.04$, $n = 10$, $df = 16$, $P = 0.05$).

DISCUSSION

Vocalizations from Hawaiian hoary bats were recorded in Kaloko-Honokōhau NHP during four of the six bimonthly survey periods in this study (Figure 7). During January, May, and September, bats were detected using SD1 recording systems at mean values ≥ 0.5 detectability (Figure 7); thus indicating persistent activity during those months. During October, bats were less active and the mean detectability value was well below 0.5. Our sampling efforts during March and July recorded no bat calls, and thus the detectability index was zero in those months. Fraser *et al.* (2007) surveyed Hawaiian hoary bats in the Park between March and July 2005 using hand-held ultrasonic bat detectors, and, with the exception of one call event detected in March, they detected frequent bat presence only in April. Our study is in agreement with Fraser *et al.* (2007) indicating little to no bat activity in the Park during the months of March and July; however, the caveat must be stated that the more sensitive and far-ranging SM2 units were not available during those months.

The supplemental recordings using SM2 units recorded significantly more total bat calls and a larger number of sound pulses per bat than the SD1 units in the three sampling periods for which simultaneous recording was conducted (Table 3). The significantly larger number of pulses per detection event with the SM2 units placed beside SD1 units for comparison of simultaneous recordings may be attributed to the greater range and quality of the SM-USX microphones in recording Hawaiian hoary bat calls among the environmental characteristics including other natural sounds in the environment at the Park. Our comparative results from the SM2 and SD1 bat detection systems are consistent with conclusions made by Adams *et al.* (2012) for North American hoary bat calls in other geographic locations. Additional acoustic monitoring with SM2 units over an annual cycle at the Park would be desirable in order to have a more complete view of seasonal occupancy and habitat use by Hawaiian hoary bats.

The occurrence of peak activity in the first two hours after sunset in the Park (Figure 8) is similar to the nightly activity patterns often shown by Hawaiian hoary bats elsewhere (Fraser *et al.* 2007, Todd 2012). The nightly average peak activity between 1800 and 2000 hrs were most strongly influenced by bat activity recorded in September and October. These months correspond to the annual fledging of Hawaiian hoary bats. During September–October the number of total bats in the foraging (flying) population is expected to be at an annual peak and the amount of total calling per night also should be greatest because fledgling bats often forage close by their mothers at this time of year (F. Bonaccorso personal observation). This high call rate is augmented because young bats are inefficient hunters of insect prey and presumably remain active for longer periods than adult bats (Jacobs 1994). It is notable that we did not observe multiple bat calls in the Park on our sonograms during this period as might be expected.

Although we observed no statistically significant differences in the number of call events of echolocating bats, or the number of total echolocation pulses, or in the index of detectability between the reproductive season and non-reproductive seasons, there were trends toward more vocalizations in all the above detected in the reproductive season. Our hypothesis that increased echolocation activity should occur within the reproductive season was thus supported only by weak trends and not statistically significant differences. We suspect that Kaloko-Honokōhau NHP, although offering aerial insect prey for foraging bats, particularly over and around the fishpond areas, may not offer consistent insect productivity as rich as some other regional habitats such as mature dry forest. However, periodic outbreaks of insect prey may be associated with common plants in the Park and may increase the value of foraging habitat for bats episodically. For example two night flying insects, the kiawe borer (*Placosternus crnicornis*) and the coconut leafroller (*Omiodes blackburni*) are periodically common in the Park (D. Foote personal communication). Outbreaks of other geometrid moths also have been recorded on kiawe (*Prosopis pallida*), a common plant in and around the Park (D. Foote personal communication). Such pulses of prey availability may attract bats for foraging during insect outbreaks. This hypothesis deserves further research. It also would be valuable to know the sex and age group of individual bats foraging over the fishponds at the Park. Do both sexes forage in the Park? Are subadults foraging with or without mothers there?

Bats primarily are active along wooded shorelines adjacent to fishponds and perhaps over the ponds themselves; whereas little activity is apparent from our recordings over the inland xeric habitats of barren lava and scattered shrubs. Given the sparse vegetation that covers most of the Park, insect abundance may not be sufficient to support bats in areas other than at the fishponds. Furthermore, within the Park there are virtually no suitable large, densely foliated trees preferred elsewhere (Bonaccorso *et al.* in press) by Hawaiian hoary bats as roosts. Hawaiian hoary bats may use the Park as a secondary foraging area when food resources are not particularly abundant elsewhere. The bats that do utilize the Park as a foraging area primarily are actively calling one to two hours after sunset perhaps after foraging for some time closer to roosting areas outside the Park. Research in the future may best be directed at documenting sex and age groups of bats in the Park, sampling the potential prey base of nocturnal aerial insects, radio-tracking of individuals following mist-net capture of bats in the Park, and conducting acoustic sampling continuously over an annual cycle to determine if previous patterns are typical or annually variable.

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LITERATURE CITED

- Adams, A. M. K. Jantzen, R. M. Hamilton, and M. B. Fenton. 2012. Do you hear what I hear? Implications of detector selection for acoustic monitoring of bats. *Methods in Ecology and Evolution* 3:992–998.
- Bonaccorso, F. J., C. M. Todd, A. C. Miles, and M. P. Gorresen. In press. Scales of movement in the endangered Hawaiian hoary bat, *Lasiurus cinereus semotus* (Chiroptera: Vespertilionidae). *Journal of Mammalogy*.
- Cogan, D., K. Schulz, D. Benitez, G. Kudray, and A. Ainsworth. 2011. Vegetation inventory project: Kaloko-Honokōhau National Historical Park. Natural Resource Report NPS/KAHO/NRR—2011/462. National Park Service, Fort Collins, CO. 124 pp.
- Fraser, H., and L. HaySmith. 2009. Hawaiian hoary bat monitoring protocol—Pacific Island Network. Natural Resource Report NPS/PWR/PACN/NRR—2009/DRAFT. National Park Service, Fort Collins, CO. 168 pp.
- Fraser, H. R., V. Parker-Geisman, and G. R. Parish, IV. 2007. Bat inventory in national parks on Hawai'i, Maui, and Moloka'i. Technical Report 140. Pacific Cooperative Studies Unit, University of Hawai'i at Mānoa, Honolulu, HI. 25 pp.
- Gorresen, M. P., F. J. Bonaccorso, C. A. Pinzari, C. M. Todd, K. Montoya-Aiona, and K. Brinck. 2013. A five-year study of Hawaiian hoary bat (*Lasiurus cinereus semotus*) occupancy on the island of Hawai'i. Technical Report TR-41. Hawai'i Cooperative Studies Unit, University of Hawai'i, Hilo, HI. 48 pp.
- Gray, J. E. 1862. Notice of a species of *Lasiurus* sent from the Sandwich Islands by Mr. W. H. Pease. *Proceedings of the Zoological Society of London* 30:143.
- Hines, J. E. 2006. Presence 4—Software to estimate patch occupancy and related parameters. U.S. Geological Survey Patuxent Wildlife Research Center, Laurel, MD. Available at: <http://www.mbr-pwrc.usgs.gov/software/presence.html> Accessed on 25 March 2014.
- Jacobs, D. 1994. Distribution and abundance of the endangered Hawaiian hoary bat, *Lasiurus cinereus semotus*. *Pacific Science* 48:193–200.
- Morales, J. C., and J. W. Bickham. 1995. Molecular systematics of the genus *Lasiurus* (Chiroptera: Vespertilionidae) based on restriction-site maps of the mitochondrial ribosomal genes. *Journal of Mammalogy* 76:730–749.
- Todd, C. M. 2012. Effects of prey abundance on seasonal movements of the Hawaiian hoary bat (*Lasiurus cinereus semotus*). MS thesis. University of Hawai'i, Hilo, HI.
- Tomich, P. Q. 1986. *Mammals in Hawai'i*. Second edition. Bishop Museum Press, Honolulu, HI. 375 pp.
- USFWS [U.S. Fish and Wildlife Service]. 1998. Recovery plan for the Hawaiian hoary bat (*Lasiurus cinereus semotus*). Region 1, U.S. Fish and Wildlife Service, Portland, OR. 50 pp.

U.S. National Park Service. 1994. General management plan/environmental impact statement
Kaloko-Honokohau National Historical Park, Hawaii. 347 pp. Available at:
<http://www.nps.gov/kaho/parkmgmt/planning.htm> Accessed on 25 March 2014.

APPENDIX: TERMINOLOGY

The following terms are defined as used in this study.

Echolocation: high frequency calls made by bats while searching for prey and tracking prey flight paths (but can also be used for orientation in flight)

Pulse: an individual sound wave emitted by a calling bat

Call event: a sequence of ultrasonic pulses over a time span of milliseconds (ms) detected by a microphone as an individual bat flies past the effective range of the microphone

Feeding buzz: a rapid series of pulses made by a bat closely approaching a prey item and thus indicating feeding activity by the bat

Search call: a series of pulses made at a rate of about one call per 8–10 ms by a bat searching for prey