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WINTER DISTRIBUTION AND USE OF HIGH ELEVATION CAVES AS FORAGING SITES BY THE ENDANGERED HAWAIIAN HOARY BAT, *LASIURUS CINEREUS SEMOTIS*

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ABSTRACT

We examine altitudinal movements involving unusual use of caves by Hawaiian hoary bats, *Lasiurus cinereus semotus*, during winter and spring in the Mauna Loa Forest Reserve (MLFR), Hawai'i Island. Acoustic detection of hoary bat vocalizations, were recorded with regularity outside 13 lava tube cave entrances situated between 2,200 to 3,600 m asl from November 2012 to April 2013. Vocalizations were most numerous in November and December with the number of call events and echolocation pulses decreasing through the following months. Bat activity was positively correlated with air temperature and negatively correlated with wind speed. Visual searches found no evidence of hibernacula nor do Hawaiian hoary bats appear to shelter by day in these caves. Nevertheless, bats fly deep into caves as evidenced by numerous carcasses found in cave interiors. The occurrence of feeding buzzes around cave entrances and visual observations of bats flying in acrobatic fashion in cave interiors point to the use of these spaces as foraging sites. *Peridroma* moth species (Noctuidae), the only abundant nocturnal, flying insect sheltering in large numbers in rock rubble and on cave walls in the MLFR, apparently serve as the principal prey attracting hoary bats during winter to lava tube caves in the upper MLFR. Caves above 3,000 m on Mauna Loa harbor temperatures suitable for *Pseudogymnoascus destructans* fungi, the causative agent of White-nose Syndrome that is highly lethal to some species of North American cave-dwelling bats. We discuss the potential for White-nose Syndrome to establish and affect Hawaiian hoary bats.

INTRODUCTION

Altitudinal migration of an animal population infers an annual return movement of all or part of the population between breeding and non-breeding areas that differ in elevation (Dixon and Gilbert 1964; Rabenold and Rabenold 1985). Altitudinal migration occurs in at least 61 species of bats (McGuire and Boyle 2013). The underlying reasons for most of these migrations usually are driven by seasonal roosting requirements including those involving hibernation or by seasonal segregation of males and females as occurs in North American hoary bats, *Lasiurus cinereus cinereus* (Cryan *et al.* 2014).

First documentation of a potential altitudinal migration by Hawaiian hoary bats, *Lasiurus cinereus semotus*, was made by Menard (2001) based on historical museum specimen collection records and substantiated by acoustical monitoring in Todd (2012) and Gorresen *et al.* (2013). The extensive 5-year acoustic data set of Gorresen *et al.* (2013) describes this bat species as breeding in lowlands at or below 1,000 m with much of the population active in montane regions during winter through early spring on Hawai'i Island. However, the latter data set did not sample above 2,000 m asl, whereas, Hawaiian hoary bats historically are known to have a distributional range from sea level to near 4,000 m elevation (Hawai'i Natural Heritage Program 2001). Thus a notable part of the species' behavior and ecology, that taking place above 2,000 m, has not been investigated and the ecological reasons for its annual altitudinal movement patterns remain poorly understood.

The association of Hawaiian hoary bat carcasses present deep inside lava tube caves on the north east flank of Mauna Loa and occasional observations of live bats roosting in rock crevices elsewhere has been reported by Tomich (1974 and 1986). Tomich attributed all bat carcasses found in caves of Hawai'i as "appear to have entered the caves accidentally". Tomich (1986) also reported fat deposits of 20–25% of total body mass during early winter for Hawaiian hoary

bats as possible preparation for “lesser activity during cooler months”; however he cautioned that “winter torpor or colonial occupancy of deep cave shelters is yet to be demonstrated” (Tomich 1974).

Understanding the use of high elevation habitats by the Hawaiian hoary bat is an important management issue for this endangered subspecies because 1) these habitats are used to an unknown extent during the poorly documented winter portion of the bat’s annual cycle and 2) high elevation habitats on Hawai’i Island include numerous caves with microclimates that potentially could harbor *Pseudogymnoascus destructans*, the fungus that is the causative agent of White-nose Syndrome (WNS). WNS has caused fatalities leading to population declines for several species of bats in eastern continental North America (Lorch *et al.* 2011, Blehert *et al.* 2009). The fungus infects the skin of bats while they hibernate leading to physiological and energetic disruption of hibernation such that fatality rates can be enormous in infected populations (Lorch *et al.* 2011, Warnecke *et al.* 2012, Minnis and Lindner 2013). It recently has been found that *Lasiurus borealis* and *Lasionycteris noctivagans*, two tree-roosting, migratory bats, can be carriers of *P. destructans* (USFWS 2014, Bernard *et al.* 2015); thus locating the wintering grounds of hoary bats as well as learning about the possible use of winter torpor are important steps in learning if there is potential vulnerability to WNS by hoary bats (Cryan *et al.* 2014).

Our current study examines the winter ecology and movement patterns of Hawaiian hoary bats at elevations between 2,200 and 3,600 m in the Mauna Loa Forest Reserve (MLFR). We surveyed the airspace surrounding 13 cave entrances as well as the cave interiors with the following objectives: 1) document monthly patterns of bat presence in the vicinity of cave entrances by quantifying acoustic activity with ultrasonic recording detectors; 2) survey cave interiors to visually look for evidence of hibernacula; and 3) assess if there is a potential risk of White-nose Syndrome effecting Hawaiian hoary bats in caves of the MLFR. Finally, we examine the hypothesis that Hawaiian hoary bat flight activity and foraging in the MLFR is influenced by local weather conditions.

METHODS

Study Area

Our study was conducted in the MLFR, Hawai’i Island (Figure 1). The MLFR spans elevations from approximately 2,000 m to the summit of Mauna Loa Volcano at 4,169 m asl. We placed acoustic recording stations in the immediate vicinity of 13 lava tube cave entrances at elevations between 2,261 and 3,562 m (Table 1). Many additional lava tubes occur in the reserve; however, we selected lava tubes for acoustic sampling to provide a large gradient of elevation and with a known presence of bat remains. The lava tubes in our study formed from eruptions of Mauna Loa Volcano, some as recently as 172 years before present (ybp) with the oldest dated as 3,000 ybp (Wolfe and Morris 1996). The lava fields of MLFR consist almost exclusively of tholeiitic basalt forming two principle types of lava flows: a’a and pāho’ehō’e (Wolfe and Morris 1996). Younger lava fields around our study caves are barren lava with almost no vegetation present (Figure 2). Older lava fields support scattered low shrubs (Figure 3) that include pūkiawe (*Styphelia tameiameia*), ‘a’ali’i (*Dodonaea viscosa*), ‘ōhelo ‘ai (*Vaccinium reticulatum*) and the dwarf trees of ‘ōhi’a lehua (*Metrosideros polymorpha*). Some habitat islands of dwarf forest consisting primarily of ‘ōhi’a lehua also occur in the reserve, but are not a common landscape feature above 2,000 m. Precise lava tube cave coordinates are

withheld by agreement with the Hawai'i Division of Forestry and Wildlife due to the sensitive ecological and cultural attributes of these caves. We list the 13 caves (Table 1) by numerical codes (1–13) with increasing elevation.

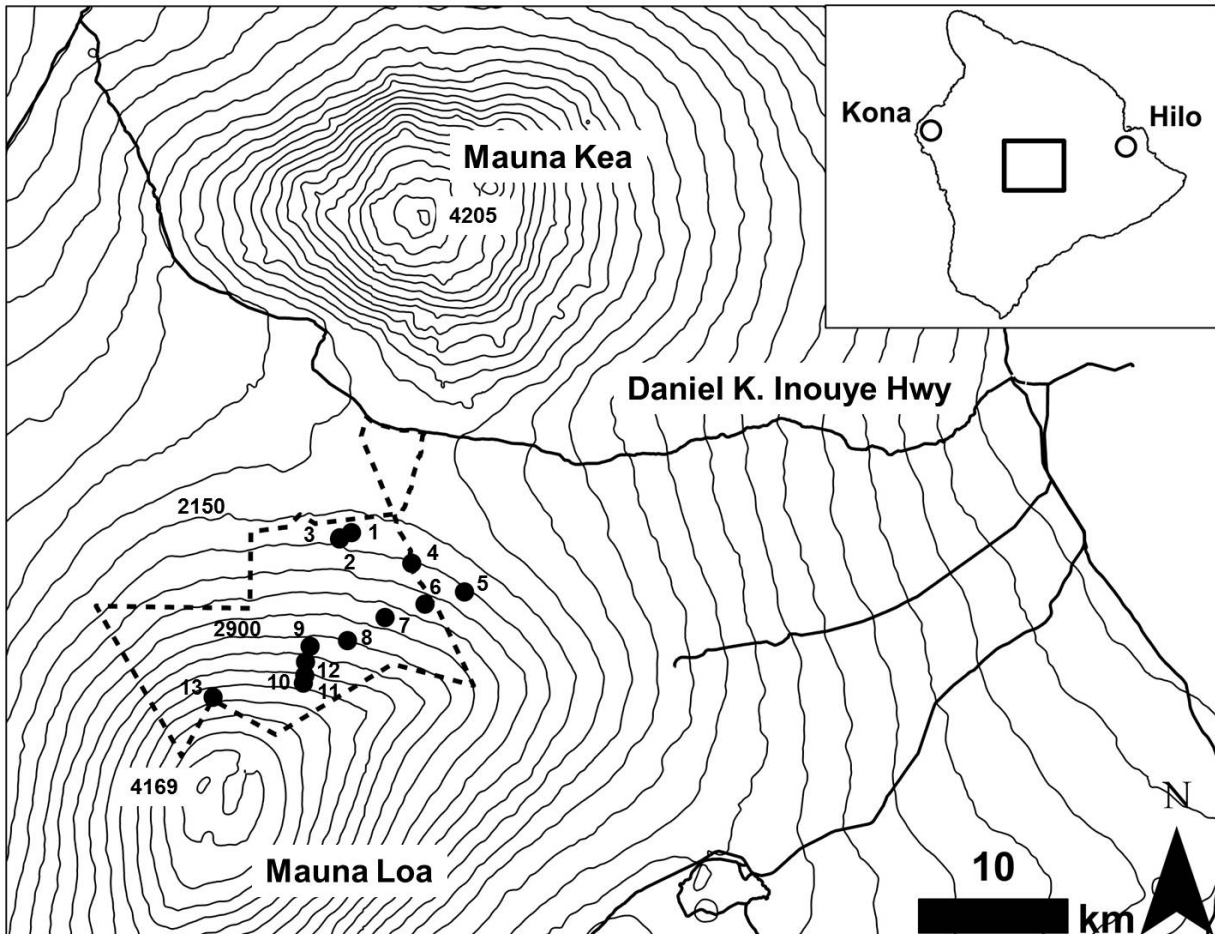


Figure 1. Hawai'i Island with the study area (rectangle of inset map) in the Mauna Loa Forest Reserve. Reserve boundaries are indicated by dashed lines, principle roads by heavy black lines, and contours of elevation in m asl by concentric thin black lines. The 13 lava tube cave entrances are numbered dots (caves 2 and 3 are superimposed).

Table 1. Cave number, elevation, substrate age, and nights sampled for bat activity at 13 lava tube caves in the Mauna Loa Forest Reserve.

Cave Number	Elevation (m)	Substrate Age*	Nights Sampled
1	2,261	1	111
2	2,277	4	27
3	2,286	4	154
4	2,341	3	104
5	2,341	4	129
6	2,533	4	131
7	2,725	3	129
8	2,979	3	157
9	3,045	2	76
10	3,191	2	96
11	3,338	2	114
12	3,393	2	111
13	3,562	3	56

*Substrate age classes (Wolfe and Morris 1996) in years before present: 1 = 172, 2 = 200–750, 3 = 750–1,500, 4 = 1,500–3,000.

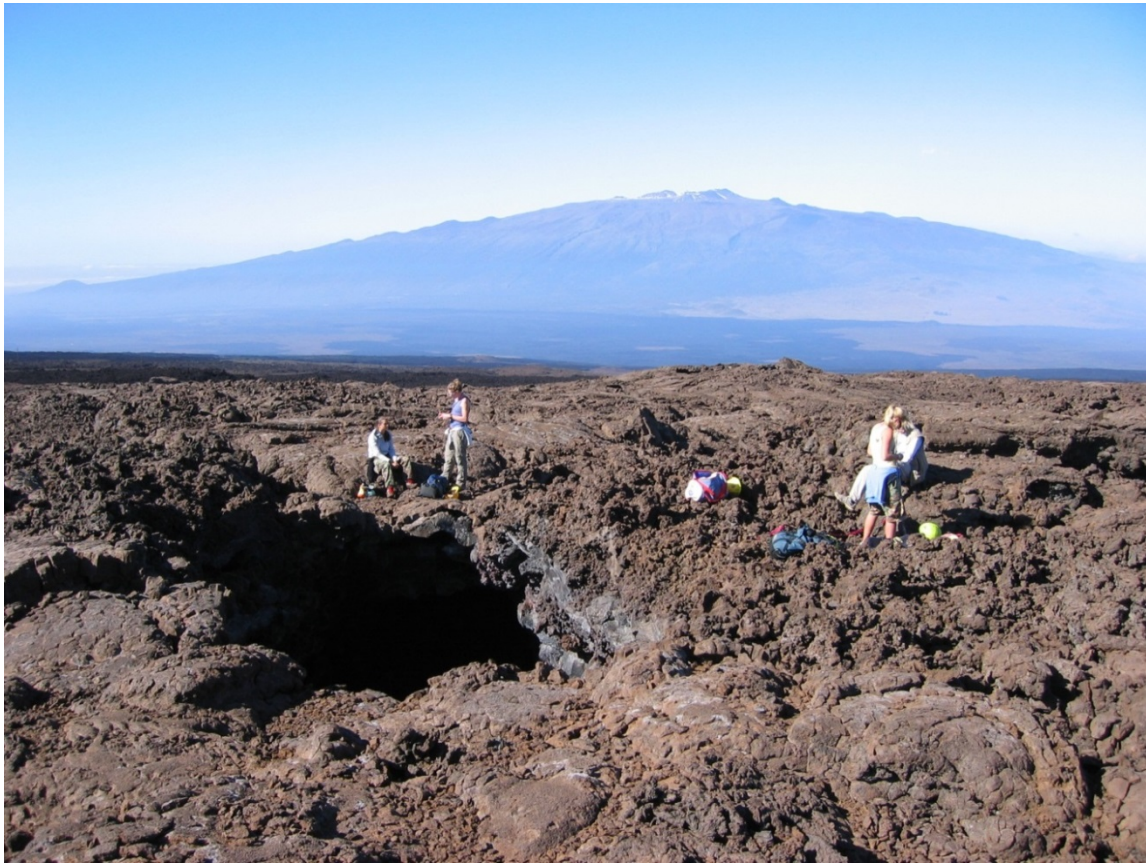


Figure 2. Entrance to cave 8 showing barren a'a lava. Mauna Kea is the volcanic peak in the background.



Figure 3. Pāho'ehō'e lava flow (1,500 to 3,000 ybp) at the entrance to cave 3 and co-author, K. Montoya-Aiona.

Annual rainfall in the MLFR averages approximately 200 mm (Giambelluca *et al.* 2013). Although heavy fogs add some moisture in addition to rainfall, the reserve is situated above the usual cloud inversion layer (ca 1,700 m; Giambelluca and Schroeder 1998) and many nights are clear.

Acoustic Detection Protocols

Ultrasonic vocalizations of Hawaiian hoary bats, including search phase and terminal phase calls (Griffin 1970) hereafter referred to as "feeding buzzes", were recorded from November 2012 through April 2013. SM2Bat+ (SM2Bat) Song Meter Digital Field Recorders (Wildlife Acoustics, Concord, MA) capable of recording ultrasound between 20 and 100 kHz were deployed at each of 13 cave entrances in our study area. Cave 2 was dropped from further recordings in December 2012. Our recording stations ranged between 2,261 and 3,562 m asl. Each SM2Bat was programmed to record from one hour before local sunset until one hour after local sunrise. Recordings were made a total of 1,395 site specific recording-nights. SM2Bat units consisted of

a waterproof housing, an external temperature sensor, 4 D-cell batteries, and each was attached by a wood mount onto a 3-meter galvanized steel pole (Figure 4). High frequency SMX-US microphones (Wildlife Acoustics) were placed approximately 2 to 3 m above the lava substrate and connected by cable to the SM2Bat microphone port.



Figure 4. An acoustic recording station with SM2Bat recording unit (green box) attached to a galvanized steel pole. An extension cable connected to a high frequency microphone is wrapped around the pole to secure it from high winds.

High frequency microphones are capable of recording bats at distances up to 100 m under ideal conditions; however, the range of call detection varies with weather conditions and orientation of the bat's head relative to the microphone. Upon detection of a vocalizing bat a sound file is generated with the appropriate date and time.

We set SM2Bats to record in zero-crossings mode. Sequences of ultrasonic pulses from a bat, defined as a "call event", were filtered to remove background noise, and counted for each sampling night using Kaleidoscope (Wildlife Acoustics, version 1.1.0). Individual echolocation "pulses", including those from search and feeding buzz calls, also were counted within each call event using AnalookW (version 3.8; Corbin 2012). We visually inspected call events to count feeding buzzes indicative of attacks on prey (Britton and Jones, 1999 and Griffen et al. 1960). Feeding buzzes are recognized by a rapid increase in pulse repetition rate and decrease in inter-pulse interval.

Statistical Analysis

All statistical analyses were conducted using the program R (version 3.1.2, R Development Core Team, 2014) except where other programs are noted. Detection probability values, henceforth referred to as “detectability” from occupancy analysis (MacKenzie *et al.* 2006) represent the probability of detecting a bat at a microphone on a given sampling night. Detectability was calculated during each sampling month using Presence (version 6.4: J. Hines 2006). Detectability of 1.0 was equivalent to recording bat calls at all detectors every sampling night. A threshold of at least one confirmed call event with ≥ 3 echolocation pulses/night was applied to all data. Zero detectability represented no verifiable bat calls during an entire sampling period. Monthly differences in activity parameters and detectability were analyzed for significance using ANOVA.

A spatial distribution analysis of monthly mean bat activity across 12 lava tube entrances was calculated and mapped using the weighted standard deviational ellipse tool in ArcGIS (version 10.2.1, ESRI, 2013). We used a one standard deviation ellipse polygon for each month weighted by the number of echolocation pulses recorded. Each monthly ellipse illustrates central tendency of distribution of bat activity across the 12 caves. Smaller ellipses represent more concentrated areas of bat activity.

We compiled hourly measurements of wind speed, barometric pressure, and precipitation from the Global Monitoring Division at the Mauna Loa Observatory located adjacent to cave 6 in Figure 1 (NOAA Earth Systems Research Laboratory 2014) to test if these variables influence bat activity. Mean hourly temperature was recorded from external sensors on SM2Bat units at five minute intervals.

We used both multiple regression and quantile regression to examine potential patterns between bat echolocation activity and temperature, wind speed, and barometric pressure. Because measureable precipitation occurred only on two nights during our study, we removed it from the analysis. We restricted these analyses to data from caves 11 and 12 because bat activity was greatest at these caves and expected to be strongly weather dependent due to the extreme conditions at the high elevations represented. Additionally, we examined the relationship between bat echolocation activity and wind speed with a t-test to compare the means of hourly bat activity above and below wind speeds of 6 m/sec.

Linear quantile regression of bat activity with temperature, wind speed, and barometric pressure were examined using quantiles 0.10, 0.25, 0.50 (median), 0.75, and 0.90 (Cade and Noon 2003). For example, the 0.10 quantile examines the relationship between 90% of bat echolocation activity and a weather variable such as temperature while the 0.90 quantile examines the relationship between the upper 10% of the bat echolocation activity and a weather variable. Statistics for quantile regression including slope coefficients, standard errors, 95% CIs, t-statistics, and p-values were calculated using the rank inversion method and default settings in the package “quantreg” (Koenker 2001, Koenker and Hallock 2007).

Visual Searches for Hibernacula

Each of the 13 caves in our study was examined one to three times between November 2012 and February 2013 by visual searches of all substrates from floor to ceiling. Searches were conducted by at least two persons slowly walking the length of the cave. We looked for signs of

bats including live animals flying or roosting, mummified or skeletonized carcasses, guano, or substrate staining caused by roosting bats. All signs of bats were noted in detail and mapped.

RESULTS

Seasonal Acoustic Patterns

Hawaiian hoary bats were detected vocalizing in the airspace around all of our 13 monitored cave entrances. During 1,395 detector nights, vocalizations were recorded at a mean of $46.6\% \pm 16.2\%$ of the nights sampled (Table 2). The numbers of recorded vocalizations (Figure 5) at caves 11 and 12 far exceed those of all other caves. In December 2012, cave 2 was dropped from further sampling. Pooled monthly mean detectability from the remaining 12 caves over the entire survey (Figure 6.) was significantly higher during November and December ($F_{5,59} = 7.8$, $p < 0.001$); however, there was no significant difference in pulse number recorded between months ($F_{5,55} = 1.71$, $p = 0.15$).

Table 2. Call event and echolocation pulse summary at caves in the Mauna Loa Forest Reserve from November 2012 to April 2013.

Cave Number	Nights with Bat Calls	Call Events	Pulses	Call Events /Night \pm SD	Pulses/Night \pm SD	% Nights with Calls/Month \pm SD
1.	71	161	684	1.74 ± 1.01	9.80 ± 10.53	51 ± 0.14
2.	17	28	104	1.64 ± 0.99	6.88 ± 5.51	58 ± 0.00
3.	56	86	415	1.53 ± 0.85	7.94 ± 10.19	37 ± 0.17
4.	48	125	444	2.60 ± 1.65	9.41 ± 7.57	42 ± 0.40
5.	75	264	1,656	3.52 ± 2.96	22.0 ± 28.50	59 ± 0.42
6.	65	163	857	2.29 ± 1.59	12.07 ± 13.00	54 ± 0.22
7.	73	238	1,216	3.26 ± 2.63	16.65 ± 21.72	59 ± 0.36
8.	45	77	568	1.65 ± 0.92	12.60 ± 15.39	29 ± 0.19
9.	44	86	616	2.00 ± 1.24	13.62 ± 14.67	38 ± 0.13
10.	54	310	2,822	4.68 ± 4.61	50.11 ± 65.40	60 ± 0.33
11.	55	1032	10,370	18.10 ± 40.54	181.00 ± 459.63	52 ± 0.25
12.	67	1334	15,215	19.91 ± 26.35	227.08 ± 408.82	62 ± 0.26
13.	2	10	116	5.00 ± 0.00	58.00 ± 56.57	5 ± 0.08
Total	672	3,914	35,083	5.22 ± 6.23	48.24 ± 78.58	47 ± 16

In November, echolocation activity as shown by mean ellipses (Figure 7) was concentrated below 3,000 m around caves 1, 3, 4, 7, and 8. In December and January, activity ellipses were located above 2,900 m around caves 8, 9, 10, 11, and 12. In February and March, bat activity was distributed over a large range of elevations and caves from 2,300 to 3400 m. The highest cave sampled, cave 13 (3,562 m), as well as cave 5 (2,341 m) generally had little bat activity throughout our study.

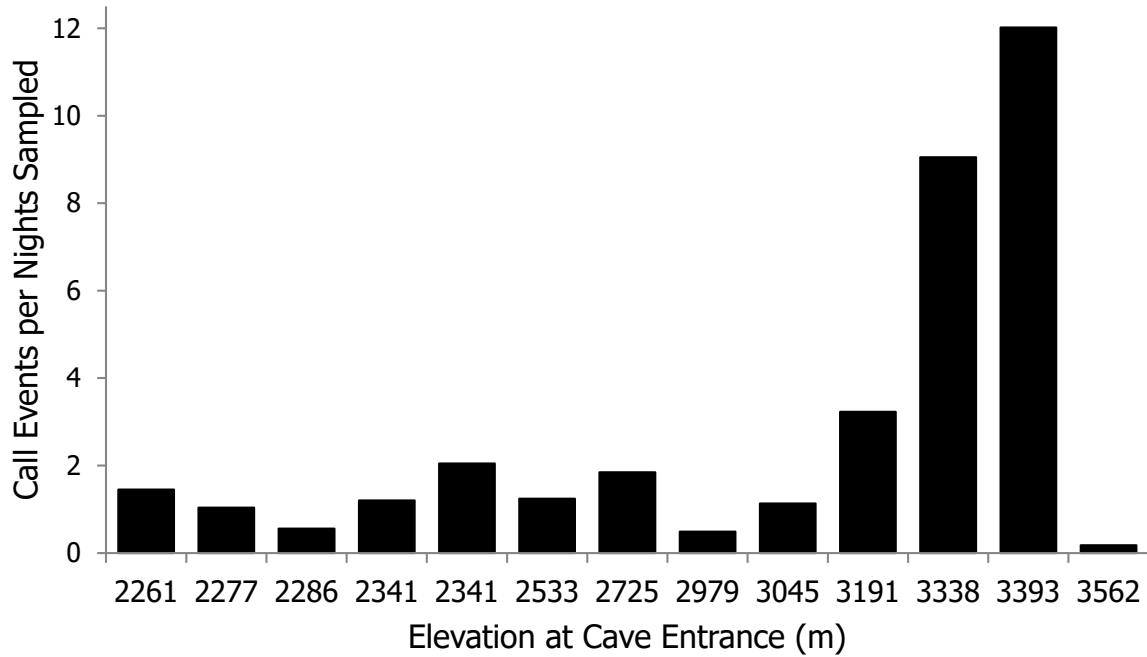


Figure 5. Cumulative call events recorded at 12 cave entrances from November 2012 to April 2013. Call events are standardized to number of sample nights for each cave. Caves are listed by increasing elevation.

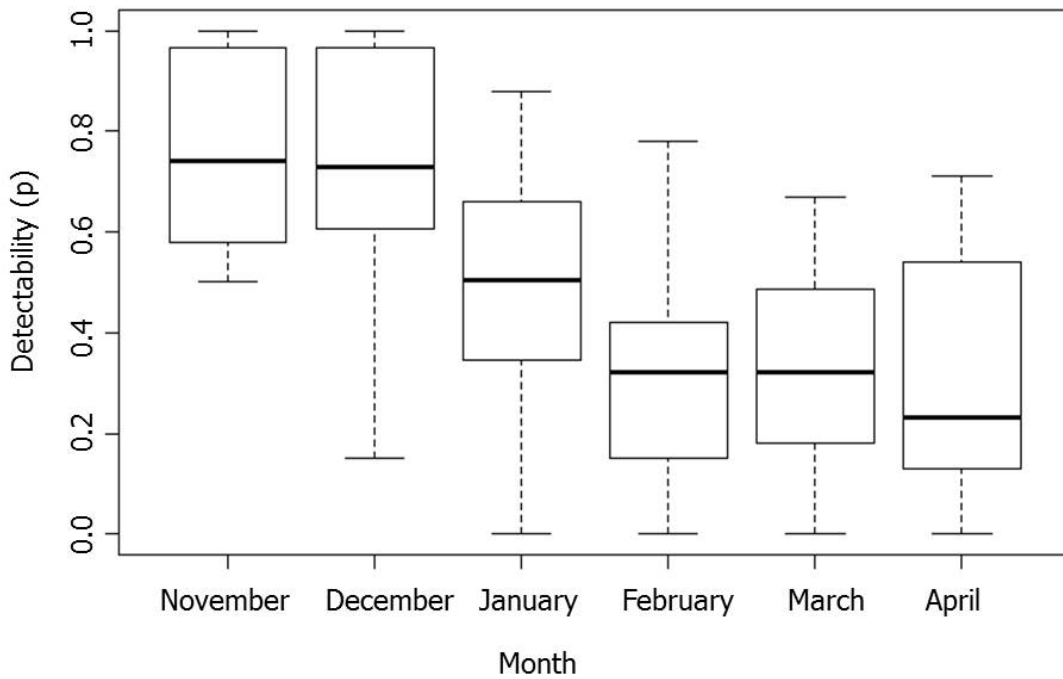


Figure 6. Pooled monthly detectability of bat echolocation calls from all caves. Boxes are interquartile ranges, bold black lines are medians, and dashed lines are minima and maxima.

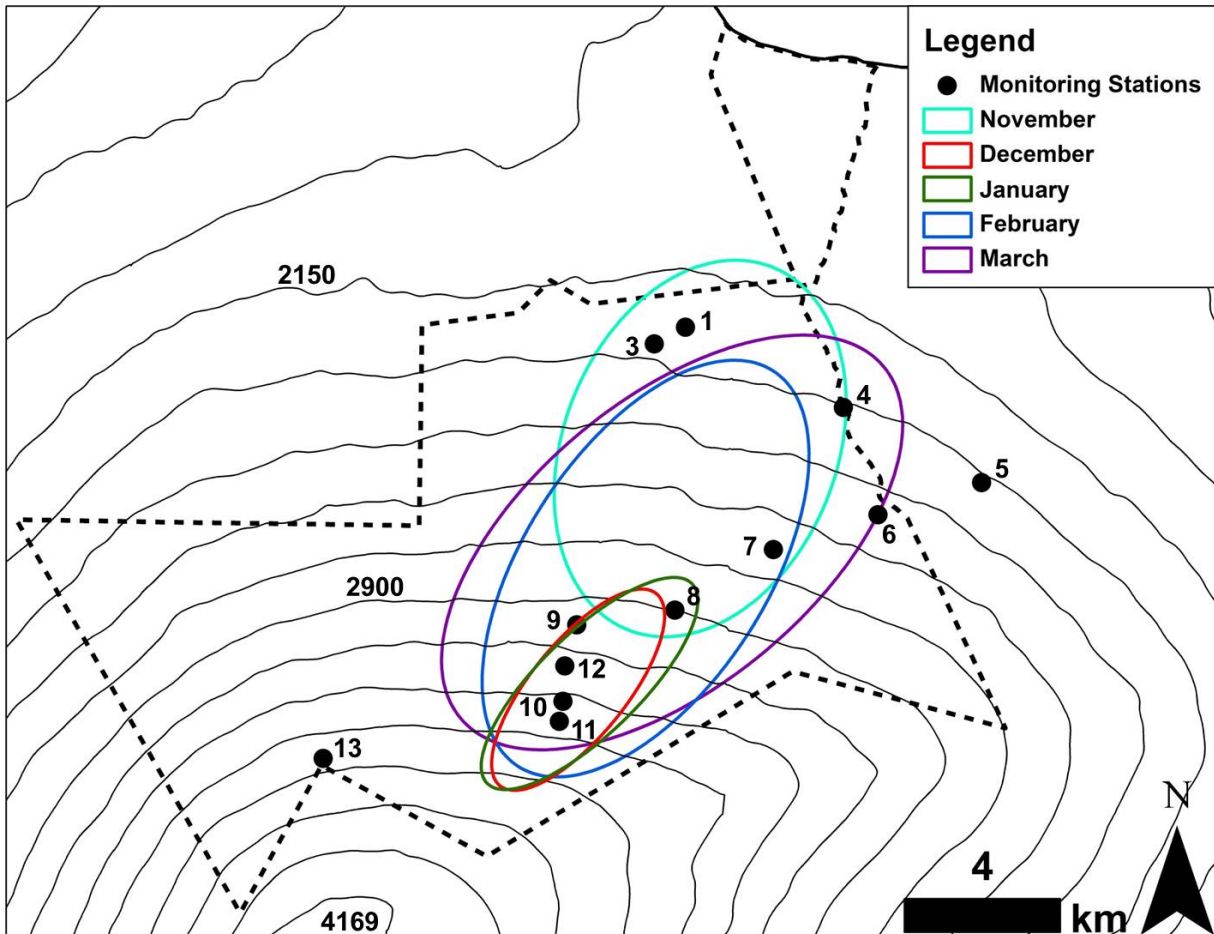


Figure 7. Ellipses of mean echolocation pulse number at cave entrances in the Mauna Loa Forest Reserve, November 2012 to March 2013. Cave numbers and elevations are listed in Table 1.

Hourly Within Night Bat Activity

Echolocation calls often were recorded through prolonged portions of the night at caves situated below 3,000 m asl. For example, during December 2012, bat calls were recorded at cave 5 (2,340 m asl) from about 1700 (sunset) until 0400 hr when air temperatures fell to about 8 °C, the minimum air temperature recorded at this cave entrance during that month (upper graph, Figure 8). The maximum number of echolocation pulses/hr recorded was 145. Throughout January average nightly temperatures approached 5 °C by 2300 hr at cave 5 and bat calling sharply decreased coinciding with this temperature (lower graph, Figure 8).

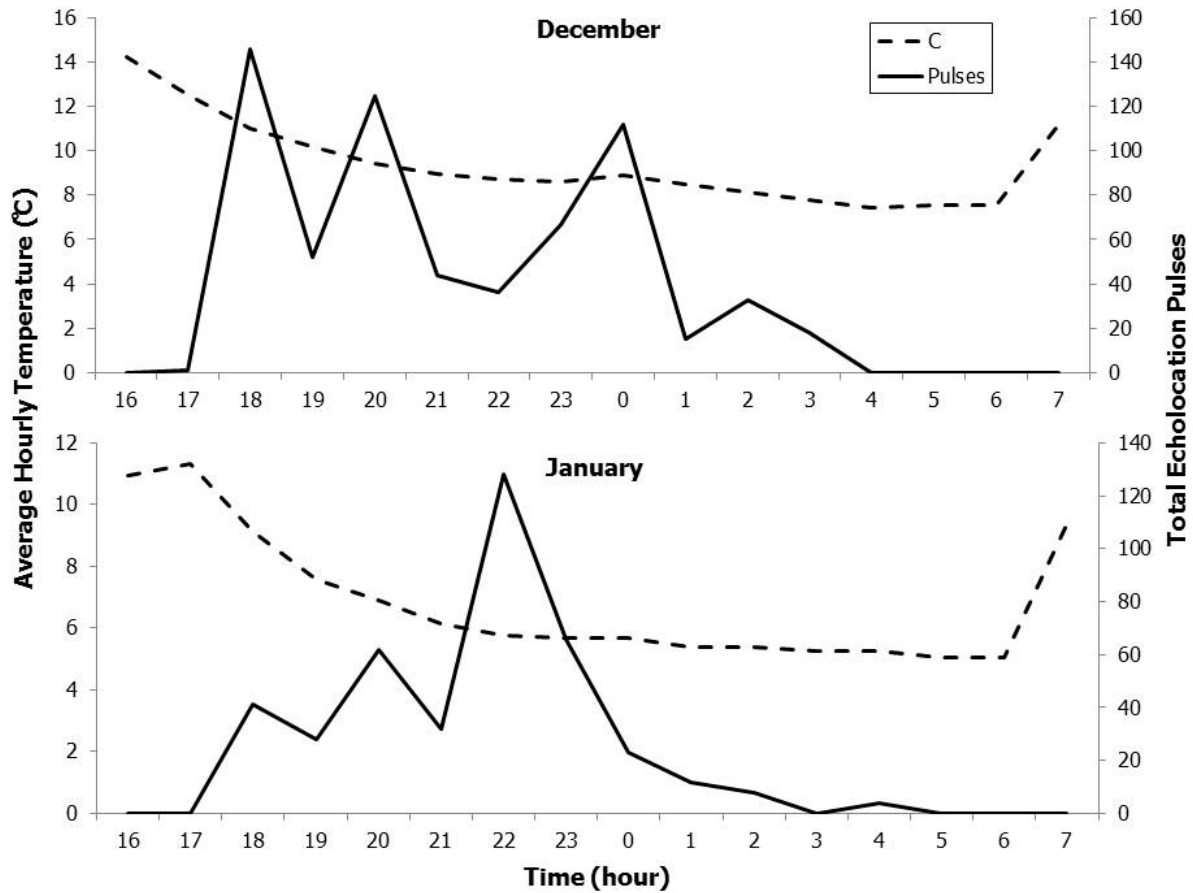


Figure 8. Hourly mean air temperature (°C) and bat echolocation pulse number during December 2012 and January 2013 at cave 5; 2,340 meters asl.

Bat calling peaked in the first two hours of darkness at all cave entrances above 3,000 m asl during December through February with little subsequent calling in subsequent hours as air temperatures fell below 8 °C (see example for cave 12 in Figure 9). Even with a narrow temporal window of activity early in the night, the total number of call pulses recorded at caves 11 and 12 were an order of magnitude greater than at any other caves during winter months (Table 2).

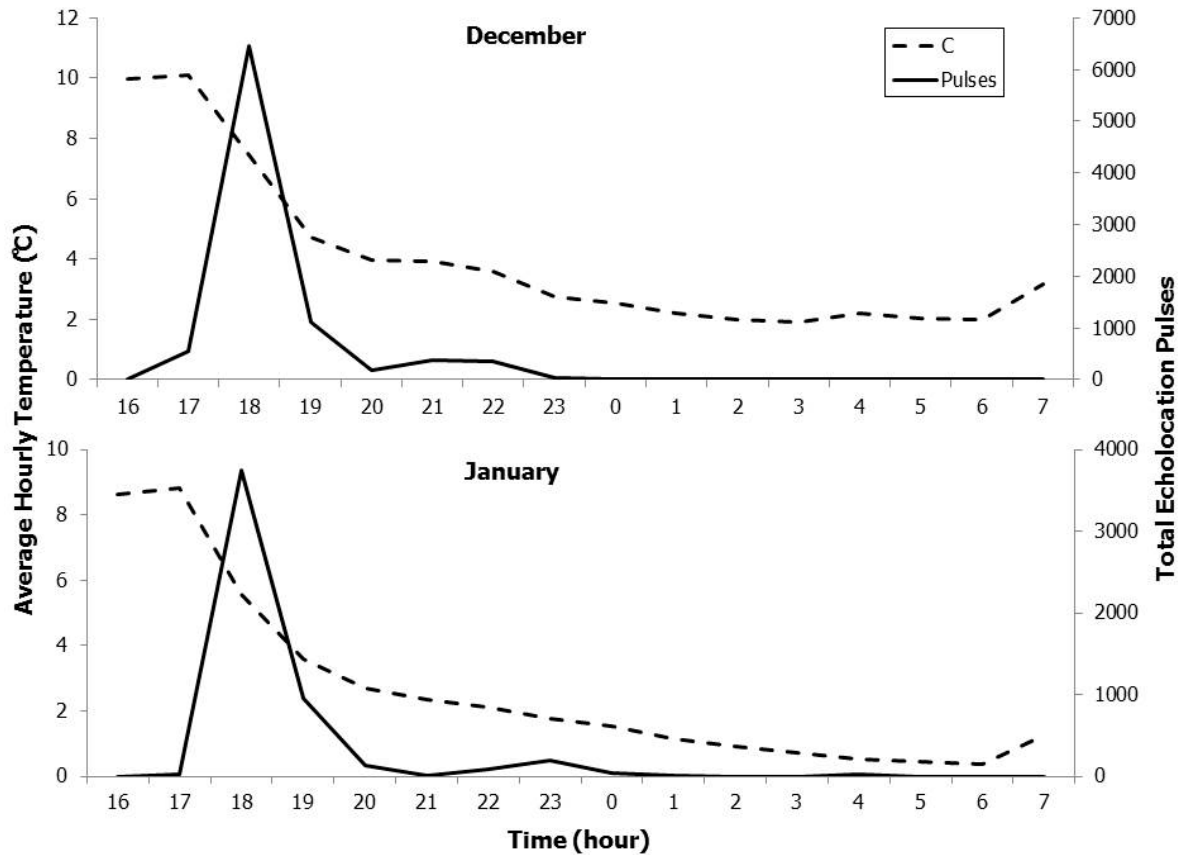


Figure 9. Hourly mean air temperature and bat echolocation pulse number during December 2012 and January 2013 for cave 12; 3,400 meters asl.

Influence of Weather on Bat Activity

Our analysis of the influence of weather variables on bat echolocation activity is focused around two high elevation caves, 11 and 12, where calling activity was most frequent. We sampled 1,470 hourly periods, 203 of which had bats present and thus were used in multiple regression and quantile regression analyses. Bats were not detected during 1,267 of the hourly observations.

Multiple regression of mean hourly echolocation activity greater than zero against temperature, wind speed, and barometric pressure measured at caves 11 and 12 (Figure 10) indicated that these variables had a significant influence on bat activity ($F_{3,175} = 5.8$, $p = 0.0008$, $R^2 = 0.0905$, $R^2_{\text{Adjusted}} = 0.0749$). Although the linear model was significant these weather variables explained only 9% of the variation observed in activity. Temperature, the most significant predictor, was positively correlated with echolocation activity ($\beta = 0.29$, $t = 3.7$, $p = 0.0002$, $R^2 = 0.07$; Figure 10a). Wind speed was almost significant and negatively correlated with echolocation activity ($\beta = -0.15$, $t = -1.9$, $p = 0.0530$, $R^2 = 0.01$; Figure 10b). Barometric pressure was not a significant predictor of echolocation activity ($\beta = -0.0004$, $t = -0.005$, $p = 0.9960$, $R^2 = -1.55e05$; Figure 10c). No significant interactions were found between any of these variables when tested in the linear model.

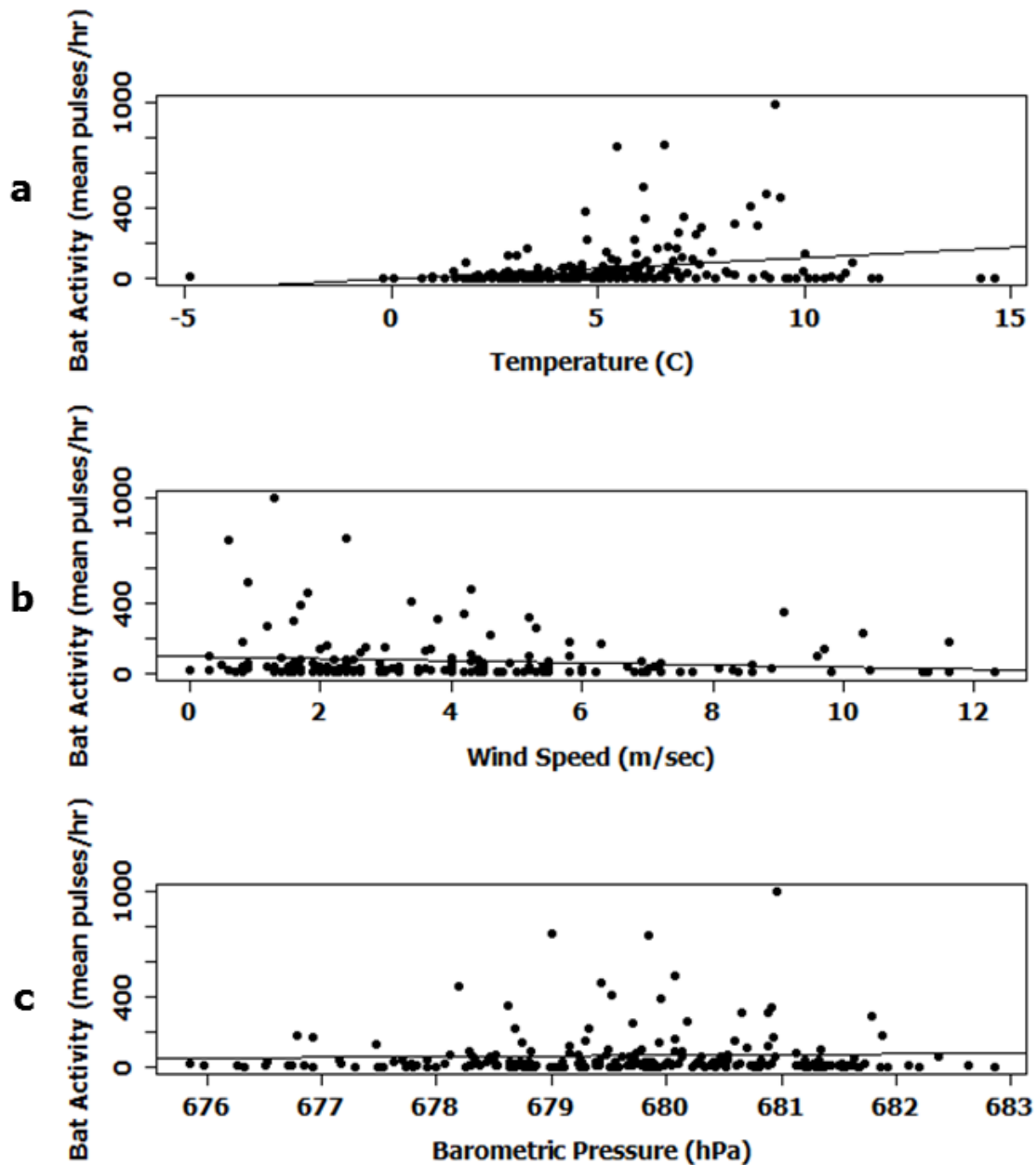


Figure 10. Relationship between mean hourly echolocation activity at caves 11 and 12 and a) temperature, b) wind speed, c) barometric pressure. Solid black circles represent hourly calling events. Regression lines represent the best fit line.

Quantile regression showed a significant positive relationship between hourly activity and temperature at the 75th and 90th quantiles (Figure 11a and Table 3). This relation with echolocation activity varies across the temperature scale and was strongest at the 90th quantile. Comparisons between the temperature slope coefficients at all quantiles 0.10, 0.25, 0.50, 0.75, 0.90 ($F_{4,1011} = 3.26$, $p < 0.05$) were significant.

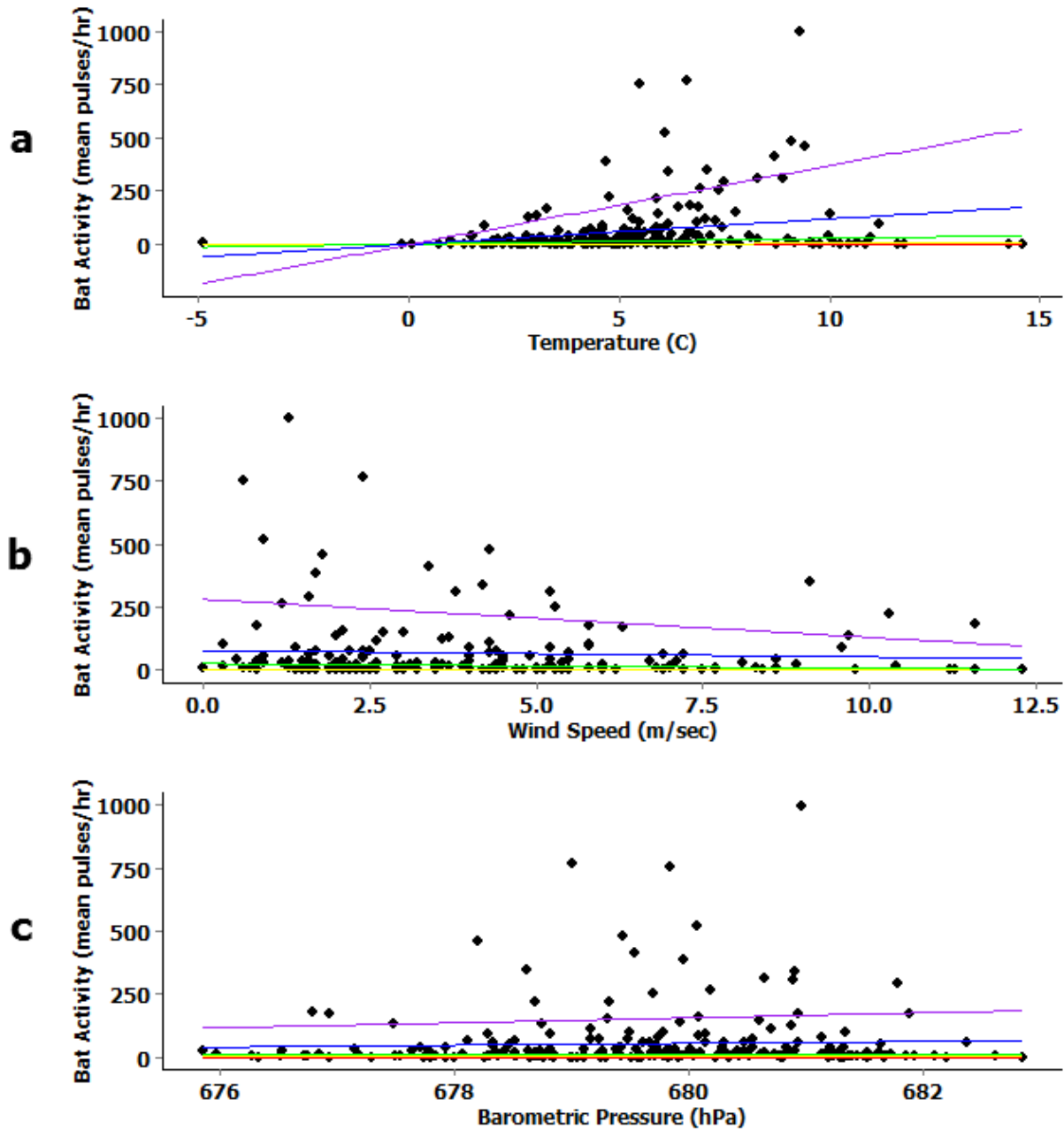


Figure 11. Relationship between mean hourly echolocation activity at caves 11 and 12 and a) temperature, b) wind speed, c) barometric pressure. Black diamonds represent hourly calling periods. Regression lines represent quantiles of 0.10 (red), 0.25 (yellow), 0.50 median (green), 0.75 (blue), and 0.90 (purple).

Table 3. Quantile regression of temperature, wind speed, and barometric pressure with echolocation activity.

Temperature						
Quantile	Estimate	SE	Lower 95% CI	Upper 95% CI	t-value	p-value
0.10	0.44	0.11	-0.09	0.09	0.38	0.70
0.25	0.27	0.32	-0.17	0.69	0.86	0.38
0.50	2.72	1.67	0.39	4.32	1.62	0.10
0.75	11.91	6.17	5.75	17.77	1.93	0.05
0.90	37.11	10.44	21.01	42.22	3.55	0.0004
Wind Speed						
Quantile	Estimate	SE	Lower 95% CI	Upper 95% CI	t-value	p-value
0.10	-0.20	0.06	-0.43	-0.04	-2.99	0.003
0.25	-0.32	0.24	-0.81	-0.07	-1.30	0.19
0.50	-1.80	5.56	-2.88	0.79	-1.70	0.09
0.75	-2.60	5.56	-7.91	9.42	-0.46	0.64
0.90	-15.11	13.38	-26.32	7.10	-1.09	0.27
Barometric Pressure						
Quantile	Estimate	SE	Lower 95% CI	Upper 95% CI	t-value	p-value
0.10	0.10	0.18	-0.23	0.23	0.57	0.56
0.25	-0.11	0.55	-0.47	0.69	-0.19	0.84
0.50	0.00	1.88	-3.22	2.20	0.00	1.00
0.75	3.75	7.86	-12.58	11.98	0.47	0.63
0.90	9.88	31.33	-4.47e01	4.6e01	0.31	0.75

Quantile regression showed a negative significant relationship between hourly echolocation activity and wind speed at the 10th quantile (Table 3 and Figure 11b). Overall, there was a negative trend, suggesting reduced bat activity at higher wind speeds (Figure 11b). Wind speed slope coefficients at all quantiles, including 0.10 vs 0.25 did not significantly differ. An unpaired t-test found no significant differences between the means of bat activity below or above wind speeds of 6 m/sec. Finally, there were no significant relationships between echolocation activity and barometric pressure using the quantile analysis (Table 3 and Figure 11c).

Foraging Activity

The percentage of nights having feeding buzzes pooled for all caves peaked during December and January and again during April (Figure 12). Feeding buzzes usually were observed only at air temperatures $> 6^{\circ}\text{C}$. Feeding buzzes were observed at all 12 caves that were monitored the entire study (Table 4); however, only cave 12 had > 50 feeding buzzes/month recorded. In December, multiple echolocating bats were observed in single call files at Cave 11 ($n = 10$) and at Cave 12 ($n = 27$).

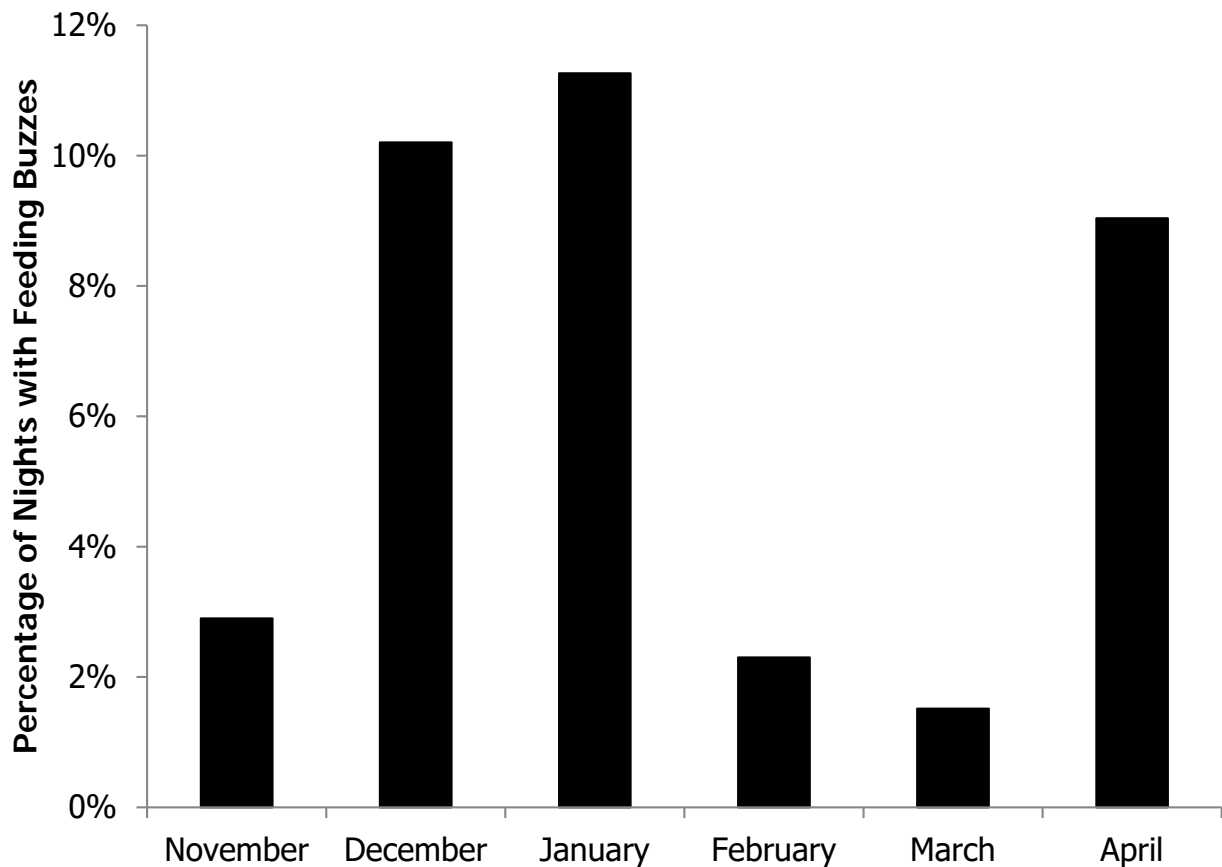


Figure 12. Percentage of nights having feeding buzzes pooled from 12 Mauna Loa Forest Reserve caves.

Table 4. Number of feeding buzzes recorded at cave entrances from November 2012 to April 2013 in the Mauna Loa Forest Reserve.

Cave Number	November	December	January	February	March	April
1	-	0	0	2	0	4
3	2	0	2	0	0	1
4	0	0	1	0	0	0
5	2	1	1	1	0	0
6	0	1	2	2	0	1
7	0	0	1	0	0	0
8	1	0	2	0	0	0
9	-	-	4	0	1	1
10	1	4	11	0	0	3
11	-	9	0	0	11	6
12	-	66	58	1	1	5
13	-	0	0	-	0	-

Visual Surveys of Cave Interiors

We visually searched for signs of bat use within caves during winter months, looking for living animals, carcasses, guano deposits, or wall staining. No signs of hibernacula or day roosts present or past were found in any Mauna Loa Caves. We did find skeletal remains (Figure 13), partially decomposed mummies with fur (Figure 14), and one fresh carcass (cave 11) perhaps only several days old (Figure 14). Twenty carcasses were found in cave 2, ~100 in cave 3, ~200 in cave 8, and seven in cave 12.

We also found living and dead cutworm moths of the genus *Peridroma* (Noctuidae) in all caves. The genus *Peridroma* is broadly distributed in Eurasia, Northern Africa, the Middle East, and North America in addition to Hawai'i and other Pacific islands. Several endemic species have been described for Hawai'i and additional species are likely to be described in the future. *Peridroma* occurring in the MLFR (Figure 15) have a body length of about 20 mm representing a prey size suitable for Hawaiian hoary bats (Jacobs 1999). Populations in MLFR now mostly live in rock rubble on the floors of the lava tubes although immense populations of these moths covered walls and ceilings of many lava tubes on the Island of Hawai'i in historic times (F. Howarth, personal communication). *Peridroma* populations declined severely early in the 20th Century as a result of biological controls released to protect sugar cane from the larvae of this grass feeding genus.



Figure 13. Skeleton of a Hawaiian hoary bat on a cave floor. Photo by F. Bonaccorso.



Figure 14. Partially decomposed and mummified Hawaiian hoary bat on rubble of a cave floor (Left Photo: F. Bonaccorso) and a few day old Hawaiian Hoary Bat carcass with a fungal infestation on a cave floor (Right Photo: C. Todd).



Figure 15. A *Peridroma* sp. moth on an ice flow covering the floor of cave 13 (Photo: S. Smith).

DISCUSSION

Echolocation Activity

Hawaiian hoary bats echolocation calls were recorded at high elevation cave entrances and surrounding environs in the MLFR during each month from November 2012 through April 2013. The detectability indices and the total number of call events were relatively high in November and December, intermediate in January, and low but consistently representing bat presence in February through April. Caves 11 and 12, both located above 3,000 m asl, together accounted for 60.4% of all call events and 72.9% of all echolocation pulses recorded. Caves 11 and 12 also currently shelter the two largest known populations of cutter moths (*Peridroma*) among our study caves (S. Smith, personal communication). All other nocturnal flying insects found inside and out of caves in our study were uncommon in a one-night qualitative comparison of night-time insect activity around an ultraviolet light source.

Foraging behavior was demonstrated by recordings of “feeding buzzes” at all cave entrances that we monitored. The low numbers of feeding buzzes detected relative to search calls in our study is typical of many acoustic surveys. Recognizable feeding buzzes often are detected only under excellent recording conditions when bats are near a microphone with the head oriented toward the microphone.

Cave 12 was associated with most of the feeding buzz activity in our study and shelters the largest population of *Peridroma* moths, the only important prey group in the area. The absence of any observation of roosting activity resulting from our visual cave inspections supports the conclusion that feeding on *Peridroma* moths may be the key reason that Hawaiian hoary bats are active in and around the high elevation caves in the MLFR.

During December and January, Hawaiian hoary bats foraged until approximately 0100 hr around cave entrances located at lower elevations in our study area; whereas at elevations above 3,000 m asl bat foraging was restricted to the first two hours of the night. Foraging activity was positively correlated with air temperature and negatively with wind speed. Temperatures below 6 °C had almost no associated bat activity. For example, during December and January at cave 12 (3,393 m asl), air temperatures fell below 6 °C around 1900 hr and virtually all bat echolocation recordings were observed before 1900 hr (most heavily concentrated between 1800 and 1900 hr).

Our study area generally has low occurrence of fog and rain due to the effects of the cloud inversion layer which hovers at approximately 1,700 m asl in this region (Giambelluca et al. 1998 and 2013). The rarity of measureable precipitation ($n = 2$ nights) in the MLFR during our five month study eliminated rainfall as a variable in our analysis. We surmise that individual Hawaiian hoary bats may be particularly likely to travel to the MLFR to forage on *Peridroma* moths during times when unfavorable localized climatic conditions, particularly common in winter months, render foraging at lower elevations ineffective (Bonaccorso *et al.* 2015).

We conclude that high elevation caves on Mauna Loa, as a result of providing sheltering sites for populations of *Peridroma* moths, offer Hawaiian hoary bats a food source that is particularly important during winter months. Bat foraging activity evidenced by the amount of search and feeding buzz calls in the MLFP is correlated with relatively low wind speeds, air temperatures above 6 °C, and although we could not assemble enough local data to provide statistical rigor, probably with conditions free of heavy fog and rain. Low temperatures, high wind speeds, fog, and rain all are reported to interfere with hoary bat foraging efficiency and/or insect activity elsewhere (Belwood and Fullard 1984, Arnett et al. 2008, Gorresen *et al.* 2015) and in general increase metabolic costs (Voigt *et al.* 2011), thus causing bats either to retreat into night roosting sites or to opportunistically move to areas of clear, calm weather.

Winds above six m/sec generally reduce vespertilionid flight activity (Arnett et al. 2008, Schuster et al. 2015). Hawaiian hoary bat echolocation activity in the MLFR also was negatively correlated with wind speed and little activity occurred during periods of wind speed > 6 m/sec.

One possible way for bats in Hawai'i to avoid inclement weather conditions while hunting for aerial nocturnal insects is to fly to elevations above the cloud inversion layer, a condition frequently occurring above 1,700 m asl in the MLFR (Giambelluca and Schroeder 1998). Our data show that Hawaiian hoary bats make particularly heavy use of the high elevation caves in the MLFP during December and January, thus the MLFP and other areas of similar elevation with lava tube caves may be particularly important as winter foraging areas.

Potential Use of Caves as Roosting Hibernacula by Hawaiian Hoary Bats

No hibernacula, nor any sign of cave use by Hawaiian hoary bats for the purpose of roosting, were found in any of the caves visually searched by our staff. The more than 300 bat skeletons and mummies in the five caves having bat carcasses are likely to have resulted over time from bats that became disoriented and unable to leave a cave after entering to forage on cave-sheltering moths. The majority of all carcasses were found within large chambers with restricted exit spaces (crawl spaces for humans) leading to the cave entrance, thus creating a "fish trap funnel" condition.

Previous authors have hypothesized that Hawaiian hoary bats most likely undergo altitudinal

migration in order to seek microclimates to facilitate winter torpor (Menard 1999, Gorresen *et al.* 2013). Although we have not excluded winter torpor as possibly being part of the life cycle of Hawaiian hoary bats, our observations suggest that the use of high elevation lava tubes for this purpose is not likely. We conclude that Hawaiian hoary bats approach and enter caves in the MLFR for the pursuit of nocturnal flying moths as prey items during foraging flights.

Given that there are no suitable trees to serve as roosts in the upper portion of the MLFR and very few in the lower portion of this reserve it is likely that bats commute to the reserve only for foraging and return to forested areas at lower elevations surrounding the MLFR for daily roosting. Thus the movements by Hawaiian hoary bats into and out of the MLFR are not a “seasonal migration” but a seasonal use of a unique foraging area that offers an attractive food resource in tolerable climatic conditions above the usual cloud inversion layer found in this region. We suggest that individual bats will make optimal foraging decisions on a nightly basis about whether to commute to the MLFR or not based on local weather conditions in the portions of their respective winter foraging ranges at lower elevations and closer to roosting sites.

Assessing the Potential Risk of White-nose Syndrome in Hawaii

Because extensive winter searches of caves with and without bat carcasses present in the MLFR have not been found to have bat hibernacula or any form of day-roosting behavior by bats, the risk of White-nose Syndrome (WNS) to Hawaiian Hoary Bats is perhaps low. Bats of several species in North America are highly susceptible to WNS as they hibernate in caves with air temperatures below 14°C. There may yet be a risk for Hawaiian hoary bats from temporary “night roosting” within foraging caves if the *Pseudogymnoascus destructans* fungus is present in the MLFR. The microclimates, in terms of temperatures and humidity in caves on Mauna Loa, are suitable for *P. destructans* and other fungi for growth/survival. One fresh bat carcass found on a cave floor during our surveys had the facial region covered by a fungus (Figure 15); however, from this photo it has been determined that the fungus was not *P. destructans* (D. Blehart, personal communication).

The recent findings of *P. destructans* spores in the fur of eastern red bats and silver-haired bats, two species of foliage roosting bats that rarely enter caves, suggest that hoary bats may also carry spores if exposed to the fungus (USFSW 2013, Bernard *et al.* 2015). If Hawaiian hoary bats make short “night roosts” on cave substrates in the midst of foraging activity inside caves, there is a possibility bats may come in contact with the fungus should it be present in Hawai‘i. As yet, no studies have attempted to identify the presence/absence of *P. destructans* in Hawai‘i. Given the frequent winter/spring use of caves by Hawaiian Hoary Bats as demonstrated by large numbers of bat carcasses within caves, our visual observations of bats flying at night in caves, the high volume of vocal activity at cave entrances, as well as the movement of visiting humans between North American and Hawai‘i, prudence may warrant that surveys for the presence of *P. destructans* (Lindner *et al.* 2011, Turner *et al.* 2014) be conducted to further explore possible exposure of hoary bats to this fungus.

Although no evidence of roosting behavior associated with caves was found in our study, Hawaiian hoary bats frequently enter caves and sometimes die in caves. These bats are likely to encounter cave substrates either in collisions during prey capture or for the purpose of short duration “night roosting”. There is certain to be some contact between bats and cave substrates. The air temperatures found inside caves above 2,500 m asl are suitable for growth

of *P. destructans*, thus there is at least some possibility of risk for Hawaiian hoary bats to come in contact with this fungus if present. At this time it is not known if the fungus is present in Hawaiian cave ecosystems; however given that visitation of recreational cavers from North America is a common occurrence, introduction from contaminated clothing and equipment does bear a risk that the fungus if not already present in Hawai'i will become established. Whether the behavior and immunology of Hawaiian hoary bats would render disease risk from WNS moot or not is simply not known.

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