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HAWAIIAN HOARY BAT (*LASIURUS CINEREUS SEMOTUS*) ACOUSTIC MONITORING AT HAWAI‘I ARMY NATIONAL GUARD (HIARNG) INSTALLATIONS STATEWIDE

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ABSTRACT

Acoustic sampling for occurrence of the endangered Hawaiian hoary bat (*Lasiurus cinereus semotus*) was conducted at 18 "long-term" acoustic monitoring stations on 12 Hawai'i Army National Guard (HIARNG) installations across the islands of Hawai'i, Maui, Moloka'i, O'ahu, and Kaua'i between 2012 and 2018. Bats were confirmed as present at 10 of these installations: Kealakekua Armory, Keaukaha Military Reservation (KMR), Hanapēpe Armory, Kekaha Firing Range (KFR), Pu'unēnē Training Facility, Ukumehame Firing Range (UFR), Kaunakakai Armory, Bellows Regional Training Institute, Kalaeloa, Barber's Point, and the 487th Military Parking Facility, Wahiawā. Seasonal frequency of bat detection was similar to previous acoustic studies for the islands of Hawai'i, Maui, and O'ahu. Hawaiian hoary bats were recorded at HIARNG installations during periods of pregnancy, lactation, and pup fledging. Our acoustic sampling did not record bat vocalizations at Fort Ruger and Waiawa Armory. Foraging activity was observed at nine acoustic monitoring stations on the islands of Hawai'i, Kaua'i, O'ahu, and Maui. No foraging activity was observed on Moloka'i and a single station on O'ahu recorded one feeding buzz in September 2017 at Kalaeloa, Barber's Point. Within-night detections showed bat activity was mostly confined to the first six hours of the night but was also variable among stations. In addition to long-term bat acoustic monitoring at HIARNG installations, Hawaiian hoary bat insect prey sampling with paired acoustic monitoring was conducted at KMR on Hawai'i Island from May through August 2018. Insect abundance and bat activity were sampled within areas where goats and sheep were used to control weeds to determine if grazing by these ungulates attract and support potential prey for the insectivorous Hawaiian hoary bat. The assessment focused on types of flies that are often associated with livestock (muscoid flies, including house flies [Muscidae], blow flies [Calliphoridae], flesh flies [Sarcophagidae], and biting midges [Ceratopogonidae]), and moths that may be impacted by changes in the availability of grass. Insect abundance was found to vary in both space and time across the study area, with numbers of muscoid flies and biting midges increasing in the presence of livestock at some stations. Although these insects appeared to respond to livestock grazing in some instances, we did not find statistically significant responses in bat foraging as measured by echolocation activity between grazed stations and the ungrazed reference station. Thus, we found no evidence that suggested bats are drawn to foraging resources in grazed areas. This result may be influenced by several factors, including the size of Hawaiian hoary bat foraging ranges compared to the scale of study area, the type of ungulate and their dung, and the timing of insect activity. Hawaiian hoary bats use KMR and forage seasonally as evidenced by long-term acoustic studies and their presence in the ungulate grazing areas; however, the relatively small size of the ungulate herd and the area that they graze may not be able to support enough prey to have a significant influence on bat foraging rates.

INTRODUCTION

The Hawaiian hoary bat (*Lasiurus cinereus semotus*, Vespertilionidae) is the only extant, native terrestrial mammal in Hawai'i. Also known as 'Ōpe'ape'a, this endemic species occurs on all of the principal volcanic islands (Tomich 1986). They are foliage roosting, habitat generalists utilizing a wide range of habitat types from sea level to at least 3,600 m above sea level (Bonaccorso *et al.* 2015, 2016) and primarily feed on moths and beetles (Whitaker and Tomich 1983, Jacobs 1999, Todd 2012, Pinzari *et al.* 2019). The species is listed by the U.S. Fish and

Wildlife Service (USFWS) and the State of Hawaiʽi Department of Forestry and Wildlife (DOFAW) as endangered since 1970 and the USFWS published a recovery plan in 1998 (USFWS 1998).

Previous studies using acoustic monitoring have documented bat presence and foraging activity in areas of Hawaiʽi Island (Gorresen *et al.* 2013, Bonaccorso *et al.* 2015, Montoya-Aiona *et al.* 2019b), Kauaʽi (Belwood and Fullard 1984), Maui (Todd *et al.* 2016, Pinzari *et al.* 2019), and Oʽahu (Gorresen *et al.* 2015, Starcevich *et al.* 2019). Whereas recent advances in acoustic monitoring techniques have led to increased knowledge on presence and behavior in some areas of the state, there is little known about populations and ranges of Hawaiian hoary bats particularly on the islands of Kauaʽi, Maui, Molokaʽi, and Oʽahu and at lowland elevations. Acoustic bat surveys at Hawaiʽi Army National Guard (hereafter HIARNG) installations on these islands are valuable in contributing information about statewide distribution and behavior essential for species recovery planning and evaluation.

Beginning in 2012, HIARNG collaborated with the U.S. Geological Survey (USGS), Pacific Island Ecosystems Research Center (PIERC) to evaluate HIARNG installations on the islands of Hawaiʽi, Kauaʽi, Maui, Molokaʽi, and Oʽahu to survey for the potential presence and foraging activity in areas where habitat exists. As forest and woodland habitats used by Hawaiian hoary bats elsewhere are present at HIARNG installations in Hawaiʽi, surveys conducted at these properties will document bat presence and provide insights into seasonal patterns of detection including foraging activity. In turn, this information will be useful in guiding Army National Guard activities to avoid or minimize potential risks and impacts to this endangered species. Here we present information from passive acoustic monitoring for seasonal presence, foraging behavior, and nightly activity patterns on HIARNG installations at 18 "long-term" acoustic monitoring stations on 12 installations statewide for a multi-year effort from August 2012 to September 2018 (Figure 1, Table 1).

In addition to long-term bat acoustic monitoring at HIARNG installations, we paired Hawaiian hoary bat insect prey sampling with acoustic monitoring at Keaukaha Military Reservation (KMR) on Hawaiʽi Island during 2018. At this property, domestic goats (occasionally mixed with domestic sheep) were rotated among grazing plots as part of a weed control program managed by HIARNG. Several studies have documented associations between foraging bats and grazing ungulates. Downs and Sanderson (2010) found that bat activity in several species (*Eptesicus serotinus*, *Pipistrellus*, and *Myotis* spp.) was associated with the presence of cattle rather than their dung, while Ancillotto *et al.* (2017) further supported this association with evidence that small bat species (*Pipistrellus* spp.) forage preferentially over cattle, attracted to livestock pests at night, which included flying mosquitoes and biting midges. However, Gorresen *et al.* (2018) found that Hawaiian hoary bat foraging activity (as identified by feeding buzzes) was not related to beetle or moth biomass in a region comprised of a mix of active and fallow cattle pasture and forest. It should be noted that the result of Gorresen *et al.* (2018) may reflect the relative difficulty of detecting feeding buzzes in field conditions, rather than the actual absence of such a relationship because overall acoustic activity was positively related to beetle biomass in that study. We sampled insect abundance and community within the areas where goats were used for weed control to better understand if grazing ungulates attract and support potential prey for insectivorous Hawaiian hoary bats. Additionally, using acoustic monitoring we assessed bat foraging activity in areas of ungulate grazing.

Our overall project objectives were to: (1) identify potential bat habitat and select locations for deployment of passive acoustic monitoring stations by performing site visits to HIARNG

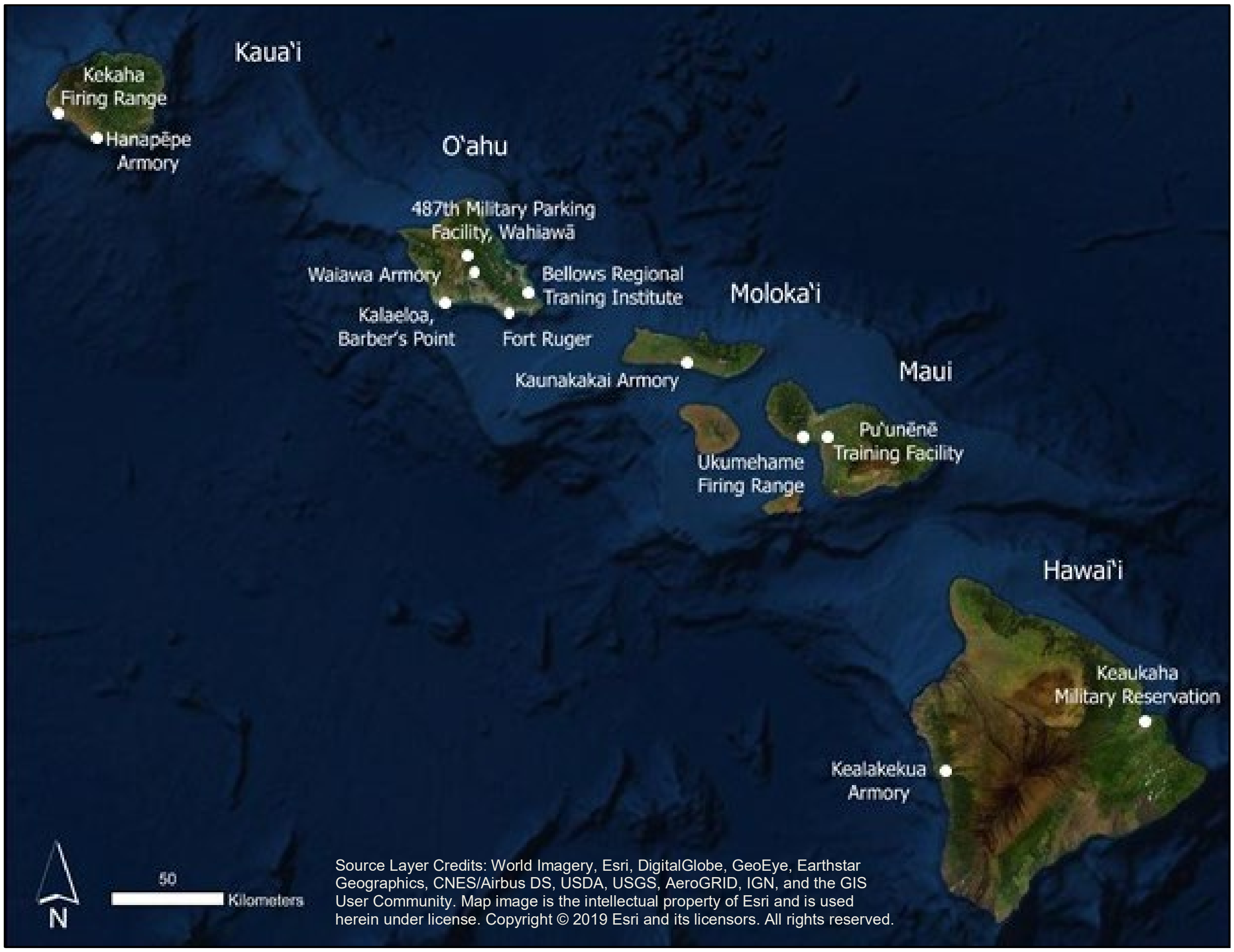

Figure 1. Hawai'i Army National Guard (HIARNG) installations where long-term Hawaiian hoary bat acoustic monitoring was conducted 2012–2018.

installations, (2) determine the presence of bats, frequency of detection, seasonal activity, foraging activity, and nightly activity patterns using long-term passive acoustic monitoring stations, and (3) evaluate the potential association of bat foraging activity and ungulate grazing presence at KMR using passive acoustic monitoring and insect sampling. This report provides a summary of bat acoustic surveys with maps, graphs, and data tables describing seasonal frequency of detection, bat foraging activity, and nightly activity patterns between August 2012 and September 2018 at HIARNG installations statewide. Additional analyses on the association of bat foraging activity and ungulate grazing presence at KMR are also included herein.

Methods

Study Area

Long-term acoustic monitoring was conducted at 18 stations within 12 HIARNG installations on the islands of Hawai'i, Kaua'i, Maui, Moloka'i, and O'ahu from August 2012 to September 2018 (Figure 1). USGS personnel performed site visits at all HIARNG installations and identified areas

Table 1. Long-term Hawaiian hoary bat acoustic monitoring locations on Hawaiʻi Army National Guard (HIARNG) installations including: island, installation name, acoustic monitoring station name, Universal Transverse Mercator (UTM) locations, elevation, and habitat description. Note: developed areas are defined as areas with industrial and/or housing development present.

Island	Installation	Monitoring station	UTM Easting	UTM Northing	Elevation (m above sea level)	Habitat description
Hawaiʻi	Kealakekua Armory	K-Armory	193849	2160451	514	Mid-elevation mesic habitat, sparsely vegetated developed area surrounded by introduced agricultural tree species
	Keaukaha Military Reservation (KMR)	KMR1	285957	2180478	20	Lowland mesic habitat, scattered native and non-native tree and grass species
		KMR2	286763	2179997	18	Lowland wet habitat, densely forested with native and introduced tree and shrub species
		KMR3	286799	2180667	14	Lowland mesic habitat, scattered native tree and non-native grass and shrub species
Kauaʻi	Hanapēpe Armory	HANAPEPE	438549	2422658	72	Lowland dry habitat, sparsely vegetated developed area with few non-native ornamental tree species
	Kekaha Firing Range (KFR)	KFR	422315	2430912	4	Coastal dry habitat, scattered non-native tree and native shrub species
Maui	Puʻunēnē Training Facility	PUUNENE	763661	2303726	35	Lowland dry habitat, sparsely vegetated developed area with few non-native ornamental tree species
	Ukumehame Firing Range (UFR)	UFR	752011	2301645	1	Coastal dry habitat, ephemeral wetland with scattered non-native tree and shrub species
Molokaʻi	Kaunakakai Armory	KAUNAKAI	705891	2333645	12	Lowland dry habitat, sparsely vegetated developed area with few non-native ornamental tree species

Island	Installation	Monitoring station	UTM Easting	UTM Northing	Elevation (m above sea level)	Habitat description
O‘ahu	Bellows Regional Training Institute	BRT1	632515	2361633	6	Lowland mesic habitat, densely forested with non-native tree and shrub species
		BRT2	632530	2361359	6	Lowland mesic habitat, forest edge with non-native tree and shrub species
		BRTFence	633153	2361330	6	Lowland mesic habitat, forest edge near developed area with non-native tree and shrub species
	Fort Ruger	FTRUGER	624940	2351605	40	Lowland mesic habitat, sparsely vegetated developed area with few non-native ornamental tree species
	Kalaeloa, Barber’s Point	KLOA	597242	2357617	15	Lowland dry habitat, sparsely vegetated with non-native shrub species
		KALE1	597415	2357483	28	Lowland dry habitat, sparsely vegetated with non-native shrub species
		KALE2	597792	2358060	33	Lowland dry habitat, sparsely vegetated with non-native tree species
	487th Military Parking Facility, Wahiawā	WAHPL	600982	2375743	259	Lowland mesic habitat, sparsely vegetated developed area surrounded by non-native tree species
	Waiawa Armory	WAIWA	605969	2367864	49	Lowland mesic habitat, forest edge with non-native tree species

with potential bat habitat for the selection of locations for long-term passive acoustic monitoring stations. Acoustic monitoring stations varied in elevation from 1 to 514 m above sea level (asl) (Table 1). On Hawaiʽi Island, one station was placed in a developed area, along a fence line at Kealakekua Armory (K-Armory) surrounded by mid-elevation mesic habitat of agricultural trees and shrubs. Three stations were placed in Keaukaha Military Reservation (KMR) about 700 to 900 m apart. One station (KMR1) was placed in lowland mesic habitat with scattered ʽōhiʽa (*Metrosideros polymorpha*, Myrtaceae) and introduced non-native tree and grass species; another station (KMR2) was placed in lowland wet habitat dominated by ʽōhiʽa and non-native tree and shrub species; and the third station (KMR3) was placed in lowland mesic habitat dominated by non-native grass habitat near a forest edge dominated by non-native trees. The two acoustic stations on Kauaʽi were placed in a developed area in lowland dry habitat with a few non-native ornamental trees along a fence line at Hanapēpe Armory (HANAPEPE) and in a dry coastal area dominated by kīawe (*Prosopis pallida*, Fabaceae) and shrub species ʽilima (*Sida fallax*, Malvaceae) and naupaka (*Scaevola* sp., Goodeniaceae) at Kekaha Firing Range (KFR). Two acoustic stations were placed on Maui; one in a developed area in lowland dry habitat with a few non-native ornamental trees along a fence line at Puʽunēnē Training Facility (PUUNENE) and one in a dry coastal habitat and ephemeral wetland dominated by kīawe at Ukumehame Firing Range (UFR). On Molokaʽi one station was located in a developed area in lowland dry habitat with a few non-native ornamental trees along a fence line at Kaunakakai Armory (KAUNAKAI). Nine stations were placed among five installations on Oʽahu. At Bellows Regional Training Institute, two stations were placed in lowland mesic habitat dominated by kīawe (BRT1 and BRT2) and one was placed along a fence line adjacent to a lowland mesic habitat dominated by non-native tree species and near a road corridor (BRTFence). At Fort Ruger, one station was located in a developed area in lowland mesic habitat with a few non-native ornamental trees (FTRUGER). Three acoustic stations were placed in lowland dry habitat at Kalaeloa, Barber's Point, in sparsely vegetated areas with non-native tree (KLOA, KALE2) and shrub species (KALE1). At the 487th Military Parking Facility in Wahiawā (WAHPL) one station was located in a developed area in lowland mesic habitat surrounded by non-native tree species, and at the Waiawa Armory (WAIWA) one station was placed in lowland mesic habitat along a fence line adjacent to a forest edge dominated by non-native tree species. See Appendix I for aerial maps and habitat photos of acoustic monitoring stations.

Long-term Acoustic Monitoring

Ultrasonic vocalizations (echolocation calls) of Hawaiian hoary bats including foraging calls were recorded from August 2012 to September 2018 (Figure 2). We used SM2Bat+ Song Meter Digital Field Recorders (Wildlife Acoustics, Concord, MA) capable of recording ultrasound between 10 and 100 kHz. Each station consisted of an acoustic recording unit SM2Bat+ in a waterproof housing, 6V external battery, solar panel, and ultrasonic microphone. Each detector had the microphone affixed to the top of metal conduit 2 to 3 m above the ground and connected by cable to the microphone port. We used two types of microphones during this study. SMX-US microphones (Wildlife Acoustics, Concord, MA) were used from 2012 to 2016 but were then discontinued by the manufacturer. We used two SMX-U1 microphones (Wildlife Acoustics, Concord, MA) at all stations after 2016 (Table 2). Both the SMX-US and the SMX-U1 microphone types were omnidirectional and capable of detecting bat calls at distances up to 30 m (Adams *et al.* 2012) under ideal conditions (i.e., no wind or rain, low humidity, etc.), although the range of call detection varied with weather conditions, vegetative clutter, and orientation of the bat relative to the microphone. Upon detection of a vocalizing bat, a sound file was generated with the corresponding date and time and stored to a secure digital (SD) memory card. The SM2Bat+ units remotely recorded from one hour before local sunset until

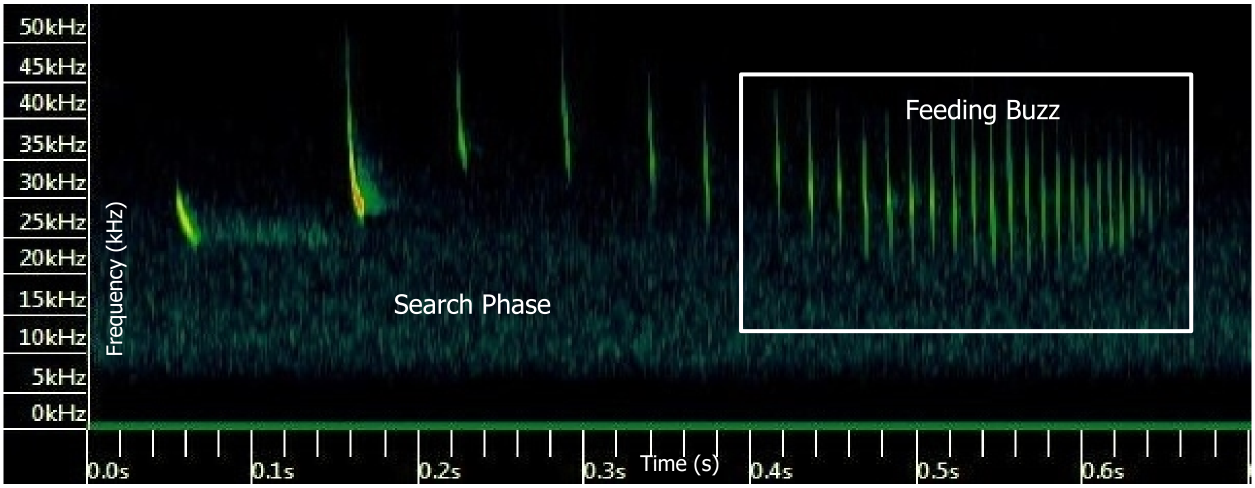

Figure 2. Spectrogram of a Hawaiian hoary bat echolocation call including search phase call pulses (left and center) followed by a feeding buzz (far right) in a single call-event indicative of foraging activity.

one hour after local sunrise and were configured to operate remotely in the field, continuously powered by solar panels and batteries. Bat acoustic monitoring stations were checked every two to three months when SD memory cards were collected and routine maintenance and quality checks on microphone sensitivity were conducted.

Acoustic data were downloaded from SD memory cards and organized in folders of call-events by night using Kaleidoscope software (version 4.1.0, Wildlife Acoustics, Concord, MA). Call-events (also referred to as "bat passes" in some literature) are defined as a sequence of ultrasonic pulses over a span of milliseconds (ms) that can be detected by an ultrasonic microphone as an individual bat flies within the effective range of the microphone (Figure 2). Call-events may contain search phase calls made by a bat moving about an area often for the purpose of searching for prey and may end with a feeding buzz (also referred to as "terminal phase calls"; Griffin 1958; see Figure 2). Feeding buzzes, indicative of foraging activity, are characterized by a rapid series of pulses made by a bat closely approaching a prey item. All echolocation pulses, call-events, and feeding buzzes were counted and verified by audio and visual inspection. Feeding buzzes were counted as the number of individual feeding buzzes identified within a corresponding triggered call-event.

Acoustic recordings of bats were used to produce an index of occurrence, defined as the proportion of nightly samples with at least one bat echolocation detection for each one-month sample period. To capture spatial and temporal variability for the subset of stations with at least one detection, the frequency of detection ("f") per month was calculated for each survey location as the total number of nights with detections divided by the total number of nights sampled, thus effectively weighting the values by sampling effort. A threshold for detection of at least one confirmed call-event with ≥3 echolocation pulses per night was applied to acoustic data to ensure standard Hawaiian hoary bat vocalization parameters. Frequency of detection equal to 1.0 (100%) is equivalent to recording bat calls at a station every night of the month. Zero represents no verifiable bat calls during the sampling period. The detection history at acoustic monitoring stations was used to calculate the proportion of total nights with observed

Table 2. Survey effort at long-term Hawaiian hoary bat acoustic survey effort on Hawaiʽi Army National Guard (HIARNG) installations including: island, installation name, acoustic monitoring station name, total nights sampled, total nights with bat echolocations detected, percentage of nights bats were detected, total number of call-events, total nights with feeding buzzes detected, percentage of nights with feeding buzzes, and the start and end dates for SMX-US and SMX-U1 microphones.

Island	Installation	Monitoring station	Total nights sampled	Nights bats detected	Nights bats detected (%)	Total call-events	Total nights with feeding buzzes	Nights with feeding buzzes (%)	Mic 1 (SMX US) start/end date	Mic 2 (SMX-U1) start/end date
Hawaiʽi	Kealakekua Armory	K-Armory	604	495	82.00	5810	107	17.70	NA	1/20/17 to 9/26/18
	Keaukaha Military Reservation (KMR)	KMR1	1891	300	15.90	1326	70	3.70	9/20/12 to 11/25/16	1/18/17 to 9/3/18
		KMR2	1983	327	16.50	827	61	18.70	9/20/12 to 7/24/16	3/30/17 to 9/28/18
		KMR3	616	348	56.50	1039	35	5.70	NA	12/20/16 to 9/27/18
Kauaʽi	Hanapēpe Armory	HANAPEPE	316	112	35.40	240	5	1.60	NA	1/17/17 to 11/29/17
	Kekaha Firing Range (KFR)	KFR	869	165	19.00	1308	11	1.30	9/14/12 to 11/24/14	1/17/17 to 12/30/17
Maui	Puʽunēnē Training Facility	PUUNENE	316	171	54.10	929	26	8.20	NA	11/16/16 to 9/19/17
	Ukumehame Firing Range (UFR)	UFR	1337	130	9.70	216	9	0.70	8/29/12 to 8/23/15	10/11/16 to 9/19/17

Island	Installation	Monitoring station	Total nights sampled	Nights bats detected	Nights bats detected (%)	Total call-events	Total nights with feeding buzzes	Nights with feeding buzzes (%)	Mic 1 (SMX US) start/end date	Mic 2 (SMX-U1) start/end date
Moloka‘i	Kaunakakai Armory	KAUNAKAI	291	10	3.40	14	0	0.00	NA	12/14/16 to 9/20/17
O‘ahu	Bellows Regional Training Institute	BRT1	119	0	0.00	0	0	0.00	9/13/12 to 6/20/13	NA
		BRT2	1464	2	0.10	2	0	0.00	7/15/13 to 5/2/16	5/3/16 to 11/18/17
		BRTFence	1048	0	0.00	0	0	0.00	7/15/13 to 6/19/15	5/2/16 to 11/18/17
	Fort Ruger	FTRUGER	314	0	0.00	0	0	0.00	NA	1/17/17 to 11/26/17
	Kalaeloa, Barber’s Point	KLOA	376	0	0.00	0	0	0.00	9/13/12 to 12/10/13	NA
		KALE1	307	4	1.30	4	0	0.00	NA	1/17/17 to 11/27/17
		KALE2	287	1	0.30	1	1	0.30	NA	1/19/17 to 11/26/17
	487th Military Parking Facility, Wahiawā	WAHPL	179	10	5.60	10	0	0.00	12/29/15 to 5/8/16	5/9/16 to 11/27/17
	Waiawa Armory	WAIWA	208	0	0.00	0	0	0.00	NA	1/1/17 to 11/27/17

bat activity throughout the survey and the frequency of nightly samples with bat activity averaged over the reproductive and fledging periods (May to October). Hawaiian hoary bat reproductive or "breeding" season (as adapted from Menard 2001) includes periods of pregnancy (typically May to June) and lactation (late June to August). The remainder of the year includes a fledging/post-lactation period (September to October), mating period (October to December), and a pre-pregnancy period (November to April) during which there is little or no reproductive activity or parental care shown by adult females. Overlap and variability in the timing of these seasons may occur year-to-year (Menard 2001, Gorresen *et al.* 2013). Frequency of detection, call-events and feeding buzzes were used to examine seasonal variation, foraging activity, and timing of nightly use at each station. Total counts of echolocation call-events were used to examine nightly activity patterns at stations for samples pooled over the duration of the survey. Timing of nightly Hawaiian hoary bat vocalizations was determined by timestamps of echolocation call-events and pooled over the duration of the survey at each station. Some acoustic monitoring stations had equipment malfunctions that resulted in nights with no recording or lapses in continuous monitoring. Complete acoustic data are available at https://doi.org/10.5066/P9EC7MT1 (Montoya-Aiona *et al.* 2020).

Ungulate Grazing, Insect Abundance, and Bat Association at KMR

The insect prey base potentially available to foraging Hawaiian hoary bats at Keaukaha Military Reservation (KMR) was assessed using a variety of sampling methods including malaise traps, light traps, mosquito traps, and dung traps (Figure 3). Each trap type listed above was initially deployed during a preliminary pilot study aimed to identify the most effective methods for trapping potential prey insects. Malaise traps (model 2875DG; Bioquip Products Inc., Rancho Dominguez, CA) are mesh, tent-like traps that intercept low-flying insects and funnel them into a collecting head containing preservative (50% solution of propylene glycol) located at the top of the trap. Malaise traps are particularly effective at collecting moths (Lepidoptera), flies (Diptera), and small bees and wasps (Hymenoptera). Light traps (model 2851M; Bioquip Products Inc., Rancho Dominguez, CA) attract and intercept night-flying insects and capture them by funneling them into a reservoir at the bottom of the trap. Light traps are most effective at trapping moths, beetles (Coleoptera), and termites (Blattodea), but also often capture some types of flies. We trapped mosquitoes using Centers for Disease Control and Prevention (CDC)-style gravid mosquito traps (Model 1712; John W. Hock Co., Gainesville, FL) using a fermented brew containing 77 g dry timothy hay combined with 0.85 g brewer's yeast and 0.85 g lactalbumin immersed in 5 gallons of water for 5 days that is attractive to female mosquitoes searching for substrate into which to lay their eggs. Finally, dung traps were used to trap beetles that may use sheep and goat dung to feed their larvae. Dung traps consisted of ~1 cup of fresh dung placed on top of wire fencing that sits over a plastic bowl containing water. Adult beetles attracted to the dung are trapped when they fall off the dung and into the water below. Dung was also searched for coprophagic insects within grazing areas.

All traps were placed together in a small area (approximately 25 m^2) protected from livestock via a mobile electric fence (Figure 3) and monitored weekly. Insects collected in each trap were returned to the lab where they were identified using taxonomic keys and reference material housed at the USGS PIERC field station and the University of Hawai'i at Hilo. We expected many different types of insects to be collected using these traps but focused our determinations and analyses on taxa that were expected to be associated directly with livestock or their dung (e.g., biting flies, "filth" flies, and beetles) or rapidly affected by grazing of grass (e.g., moths whose caterpillars feed on grass) and known as a primary food source for the Hawaiian hoary bat (Whitaker and Tomich 1983; Jacobs 1999; Todd 2012; Pinzari *et al.* 2019). The results of the

Figure 3. Several methods were deployed to sample insects that were potential prey for bats including malaise traps (A; tent-like structure in center), dung traps (B), light traps (C), and mosquito traps (D). Insect traps were deployed concurrently within an enclosure protected from livestock by a temporary electric fence.

preliminary pilot study led us to use malaise traps during the main study (see Results section for details).

Malaise traps were used following the pilot study methodology described above and placed at all sampling stations in the grazed plots as well as the ungrazed reference station. Malaise traps were operated continuously but were emptied of contents at approximately weekly intervals. Insects were identified as described above, sorted into taxa associated with ungulates (biting midges, mosquitos, and muscoid flies) or taxa known to be bat prey (moths), and assessed for abundance by count.

In the northwest corner of the KMR property, goats were contained within grazing plots by electric fencing and rotated among the grazing plots approximately weekly from May–August 2018 (Figure 4). Grazing began the week of 24 May 2018 while insect and acoustic collection at the sampling stations began prior to grazing in the week of 11 May 2018. Five sampling stations with a bat acoustic recording unit and insect trap (4E, 5F-I) were established within the grazing area. For comparison, an additional reference station was established in an ungrazed area with similar non-native grassland habitat approximately 800 m east of the grazing plots (Figure 4). The goat grazing rotation (timing and location) was managed by a contractor independent of insect and bat acoustic sampling.

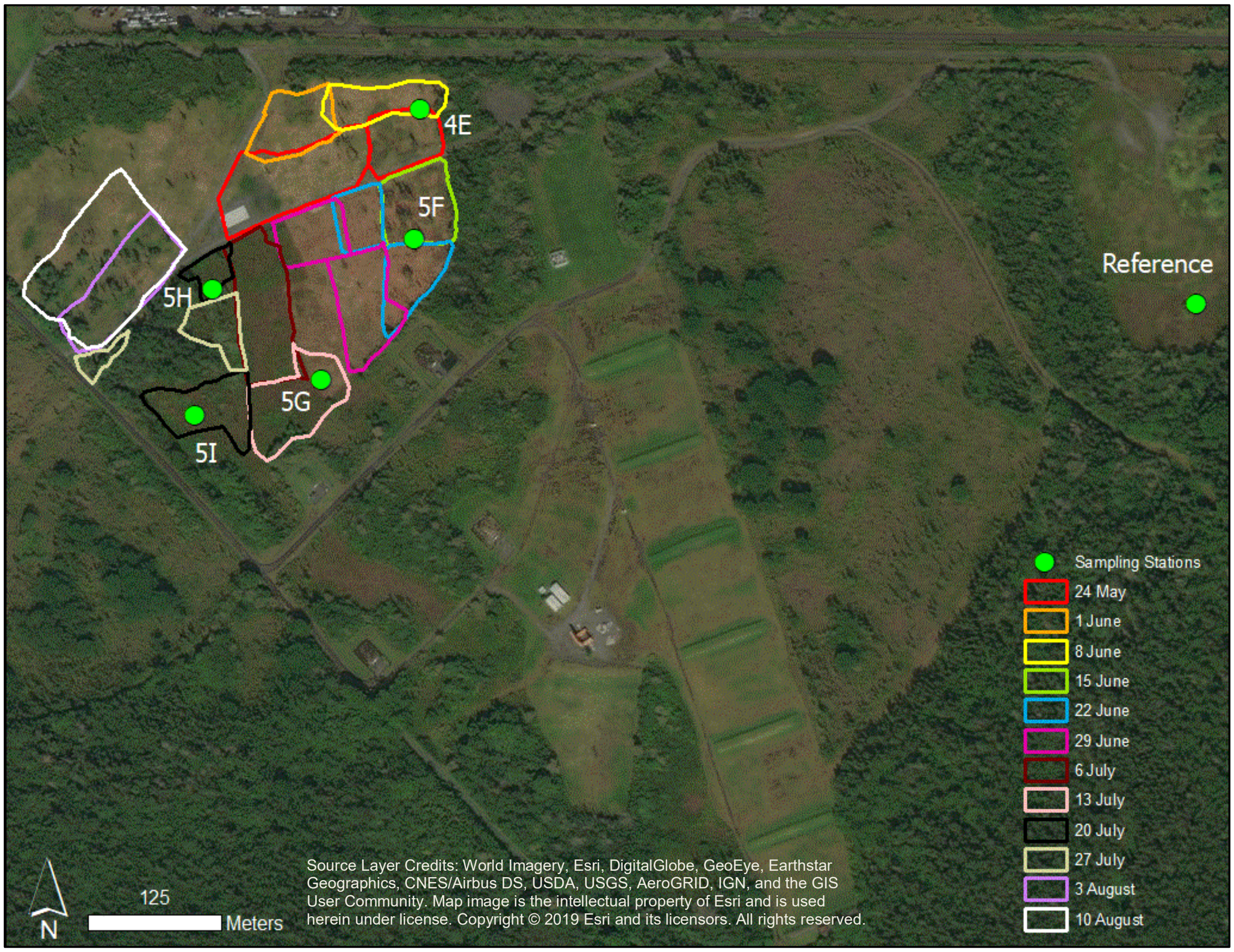

Figure 4. Map of sampling stations, experimental goat grazing plots, and the reference station in an ungrazed area at Keaukaha Military Reservation (KMR) during 2018. Each polygon represents the approximate date and area where goats were present. Note: grazing of goats began the week of 24 May 2018 while insect and acoustic collection at the sampling stations began the week of 11 May 2018.

Acoustic sampling of bat vocalizations and analysis for bat activity, including foraging activity, was conducted using the methodology described for the long-term acoustic monitoring. Ultrasonic microphone model SMX-U1 (Wildlife Acoustics, Concord, MA) was used during this aspect of our study. At each acoustic monitoring station Hawaiian hoary bat echolocation pulses, call-events and feeding buzzes were summed across sampling nights within each sampling week.

To assess the demographics of Hawaiian hoary bats and to identify roosting sites within KMR boundaries, we attempted to capture bats and use thermal imaging to evaluate potential roost trees within KMR. A combination of single-high and triple-high nets of various lengths (6-, 9-, 12-m) was used within the first five hours after sunset at a netting site near the southeast corner of KMR on 18 June and 19 June 2018. We also used an UltraSoundGate Player BL Light acoustic lure (Avisoft Bioacoustics, Glienicke, DE) within 5 m of the netting site with playback of

Hawaiian hoary bat echolocation calls to lure bats to the net site. The protocol for handling bats was approved by the Institutional Animal Care and Use Committee (IACUC #04-039-12) through the University of Hawai'i at Hilo following guidelines of the American Society of Mammalogists.

Thermal imaging (FLUKE Ti450, Fluke Corp., Everett, WA) of potential bat roost trees on KMR property was conducted on the evenings of 13 June and 21 June 2018. Approximately 10 trees were scanned during each of the two surveys. Tree species scanned included 'ōhi'a and mango (*Mangifera indica*; Anacardiaceae), two tree species documented as roost tree species used by Hawaiian hoary bats (Montoya-Aiona *et al.* 2019a).

RESULTS

Long-term Acoustic Monitoring

Bat Presence and Frequency of Detection

Echolocation calls of Hawaiian hoary bats were detected on all islands monitored. Across all acoustic monitoring stations there were a total of 12,525 station-nights from August 2012 to September 2018. Bat echolocation calls were positively identified during 2,075 (16%) of all station-nights at 13 of 18 (72%) acoustic monitoring stations. Bats were not detected (frequency of detection 0%) at five stations on O'ahu: BRT1, BRTFence, FTRUGER, KLOA, and WAIWA. The overall frequency of detection was greatest at K-Armory (82%) followed by KMR3 (57%), both located on Hawai'i Island, and PUUNENE (54%) located on Maui.

Bat acoustic activity was greatest on Hawai'i Island with bat echolocation calls identified during 1,470 station-nights (29%) across all acoustic monitoring stations (K-Armory, KMR1, KMR2, KMR3) including a total of 5,094 station-nights. The overall frequency of detection on Kaua'i was 23% with bat acoustic activity detected during 277 out of 1,185 total station-nights across all acoustic monitoring stations (HANEPEPE, KFR). Similarly, the overall frequency of detection was 18% on Maui across all acoustic monitoring stations (PUUNENE, UFR) with bat acoustic activity detected during 301 station-nights out of 1,653 total station-nights. The overall frequency of detection was generally low (3%) at the single station located on Moloka'i (KAUNAKAI) with bats detected during 10 out of 291 total station-nights. Bat acoustic activity was lowest on O'ahu, for which the frequency of detection was <0.5% and bat echolocation calls were identified on only 17 out of 4,302 total station-nights across all stations monitored on the island (BRT1, BRT2, BRTFence, FTRUGER, KLOA, KALE1, KALE2, WAHPL, WAIWA).

Across all acoustic monitoring stations, peak frequency of detection was generally observed from May through October coinciding with pregnancy (May to June; mean 21%), lactation (July to August; mean 24%), and fledging/post-lactation period (September to October; mean 23%) for Hawaiian hoary bats. Generally the lowest frequency of detection was observed during November through April across all stations (mean 11%). See Table 2 and Table 3 for survey effort and frequency of detection data. Complete acoustic data are available at https://doi.org/10.5066/P9EC7MT1 (Montoya-Aiona *et al.* 2020).

Seasonal Bat Activity

Frequency of bat detection varied seasonally among acoustic monitoring stations. All stations that recorded acoustic activity detected bats during one or more months of the reproductive

Table 3. Sampling effort by month at 18 acoustic monitoring stations at Hawai'i Army National Guard (HIARNG) installations surveyed from August 2012 to September 2018. The proportion of nights with bat echolocations detected relative to the total number of nights the acoustic detector was recording are presented by year and month. The overall percent frequency of detection by month across years is presented in the final row for each station. Note that "–" indicates no data were collected.

Monitoring Station	Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
BRT1	2012	-	-	-	-	-	-	-	-	0/18	0/31	0/5	-
	2013	-	0/17	0/6	0/30	0/12	-	-	-	-	-	-	-
	Overall	-	0%	0%	0%	0%	-	-	-	0%	0%	0%	-
BRT2	2013	-	-	-	-	-	-	0/17	0/31	0/30	0/31	0/30	0/31
	2014	0/31	0/28	0/31	0/30	0/31	0/30	0/31	1/31	0/30	0/31	0/30	0/31
	2015	0/31	0/28	0/31	0/27	0/31	0/30	0/31	1/31	0/15	-	-	0/9
	2016	0/31	0/29	0/31	0/30	0/30	0/30	0/30	0/31	0/30	0/31	0/30	0/31
	2017	0/23	0/28	0/31	0/17	0/31	0/30	0/31	0/31	0/30	0/31	0/18	-
	Overall	0%	0%	0%	0%	0%	0%	0%	1%	0%	0%	0%	0%
BRTFence	2013	-	-	-	-	-	-	0/17	0/20	0/14	0/31	0/30	0/31
	2014	0/31	0/28	0/31	0/20	-	-	0/10	0/31	0/30	0/31	0/28	0/31
	2015	0/31	0/28	0/31	0/22	-	-	-	-	-	-	-	-
	2016	-	-	-	-	0/30	0/30	0/30	0/31	0/30	0/31	0/28	0/30
	2017	0/21	0/28	0/31	0/30	0/31	0/30	0/31	0/31	0/30	0/19	-	-
	Overall	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
FTRUGER	2017	0/15	0/28	0/31	0/30	0/31	0/30	0/31	0/31	0/30	0/31	0/26	-
	Overall	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	-
HANAPEPE	2017	1/14	9/28	7/31	13/30	8/31	16/30	7/31	14/31	21/30	10/31	6/29	-
	Overall	7%	32%	23%	43%	26%	53%	23%	45%	70%	32%	21%	-
KALE1	2017	0/15	0/28	0/31	0/23	0/31	0/30	0/31	1/31	1/30	2/31	0/26	-
	Overall	0%	0%	0%	0%	0%	0%	0%	3%	3%	6%	0%	-
KALE2	2017	0/13	0/28	0/29	0/7	0/31	0/30	0/31	0/31	1/30	0/31	0/26	-
	Overall	0%	0%	0%	0%	0%	0%	0%	0%	3%	0%	0%	-

Monitoring Station	Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
K-Armory	2017	9/12	17/28	28/31	25/30	31/31	30/30	31/31	31/31	18/30	27/29	30/30	9/31
	2018	8/31	18/28	16/31	18/21	31/31	30/30	31/31	31/31	26/26	-	-	-
	Overall	40%	63%	71%	84%	100%	100%	100%	100%	79%	93%	100%	29%
KAUNAKAI	2016	-	-	-	-	-	-	-	-	-	-	-	0/28
	2017	0/31	0/28	1/31	1/30	3/31	0/30	0/31	4/31	1/20	-	-	-
	Overall	0%	0%	3%	3%	10%	0%	0%	13%	5%	-	-	0%
KFR	2012	-	-	-	-	-	-	-	-	15/17	24/31	0/30	0/31
	2013	1/31	0/28	1/31	2/30	0/31	2/30	2/31	21/31	30/30	27/31	7/30	1/31
	2014	0/31	0/28	0/31	1/30	0/31	0/30	0/31	2/31	3/30	1/31	1/23	-
	2015	-	-	-	-	-	-	-	-	-	-	-	-
	2016	-	-	-	-	-	-	-	-	-	-	-	-
	2017	5/15	12/28	6/21	-	1/4	-	-	-	-	-	-	-
	Overall	8%	14%	8%	5%	2%	3%	3%	37%	62%	56%	10%	2%
KLOA	2012	-	-	-	-	-	-	-	-	-	-	0/2	0/31
	2013	0/31	0/28	0/31	0/30	0/31	0/30	0/31	0/31	0/30	0/31	0/30	0/9
	Overall	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
KMR1	2012	-	-	-	-	-	-	-	-	4/11	8/31	6/30	1/31
	2013	0/31	0/28	1/31	1/30	3/31	3/30	7/31	8/31	4/30	0/31	0/30	0/15
	2014	-	-	2/13	0/30	0/31	6/30	16/31	25/31	12/30	4/31	0/30	0/31
	2015	0/31	1/17	-	-	6/10	12/30	12/31	11/31	6/30	1/31	0/30	0/31
	2016	0/31	0/29	0/31	0/30	0/31	0/30	0/30	0/31	0/13	0/31	0/24	-
	2017	0/14	0/28	2/31	0/30	3/31	4/30	21/31	23/31	6/23	8/31	1/30	0/31
	2018	0/31	0/22	4/31	9/25	15/31	13/28	11/26	18/31	2/2	-	-	-
	Overall	0%	1%	7%	7%	16%	21%	37%	46%	24%	11%	4%	1%
KMR2	2012	-	-	-	-	-	-	-	0/12	10/30	13/31	7/30	3/31
	2013	0/31	0/28	0/31	0/30	3/31	6/30	10/31	9/31	2/30	1/31	0/30	0/31
	2014	0/31	0/28	0/31	0/30	0/31	0/30	0/31	3/31	5/30	0/31	0/30	0/31
	2015	0/31	0/28	0/31	3/30	6/31	0/30	1/31	1/31	0/30	0/31	1/30	0/31
	2016	0/31	0/29	0/31	0/30	1/31	0/30	0/24	-	-	-	-	-

Monitoring Station	Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
	2017	-	-	1/2	20/30	22/31	24/30	28/31	27/31	29/30	17/31	0/30	0/31
	2018	0/31	2/28	11/31	11/30	25/31	20/30	4/31	1/31	0/28	-	-	-
	Overall	0%	1%	8%	19%	31%	28%	24%	25%	26%	20%	5%	2%
KMR3	2016	-	-	-	-	-	-	-	-	-	-	-	6/11
	2017	0/1	5/28	12/31	23/30	29/31	26/30	26/31	26/31	23/30	12/31	12/30	14/31
	2018	12/31	5/28	12/31	15/30	24/31	20/30	20/31	16/31	10/27	-	-	-
	Overall	38%	18%	39%	63%	85%	77%	74%	68%	58%	39%	40%	48%
PUUNENE	2016	-	-	-	-	-	-	-	-	-	-	4/23	16/31
	2017	17/31	3/28	2/31	12/30	27/31	22/30	23/31	27/31	18/19	-	-	-
	Overall	55%	11%	6%	40%	87%	73%	74%	87%	95%	-	17%	52%
UFR	2012	-	-	-	-	-	-	-	1/3	6/30	6/31	2/30	0/31
	2013	0/31	0/28	0/31	3/30	1/31	0/30	0/31	5/31	3/30	7/31	0/30	0/31
	2014	0/31	1/28	0/31	2/30	1/31	1/30	3/31	1/31	7/30	10/31	4/30	1/8
	2015	-	-	1/16	6/30	2/31	1/30	3/31	5/23	-	-	-	-
	2016	-	-	-	-	-	-	-	-	-	5/21	11/30	7/31
	2017	2/31	0/28	0/31	5/30	2/31	0/30	2/31	9/31	4/19	-	-	-
	Overall	2%	1%	1%	13%	5%	2%	6%	18%	18%	25%	14%	8%
WAHPL	2015	-	-	-	-	-	-	-	-	-	-	-	0/3
	2016	0/28	-	0/7	0/30	0/7	-	-	-	-	-	-	-
	2017	-	-	-	-	-	-	-	4/17	5/30	1/31	0/26	-
	Overall	0%	-	0%	0%	0%	-	-	24%	17%	3%	0%	0%
WAIWA	2017	0/15	0/28	0/31	0/30	0/31	0/30	0/31	0/12	-	-	-	-
	Overall	0%	0%	0%	0%	0%	0%	0%	0%	-	-	-	-

and fledging season (May–October; Figure 5). Year-round acoustic activity was detected at K-Armory and KMR3 on Hawaiʽi Island, KFR on Kauaʽi, and UFR on Maui. Acoustic activity was also detected during every month at HANAPEPE on Kauaʽi except during December when no data were collected. Similarly, acoustic activity was detected at PUUNENE on Maui during every month except October when no data were collected. At KMR1 and KMR2 on Hawaiʽi Island bat acoustic activity was detected during all months except January. Bat occurrence at other stations that detected bat acoustic activity was distributed irregularly or concentrated towards the middle to end of the year and the mean monthly index was relatively low for most stations.

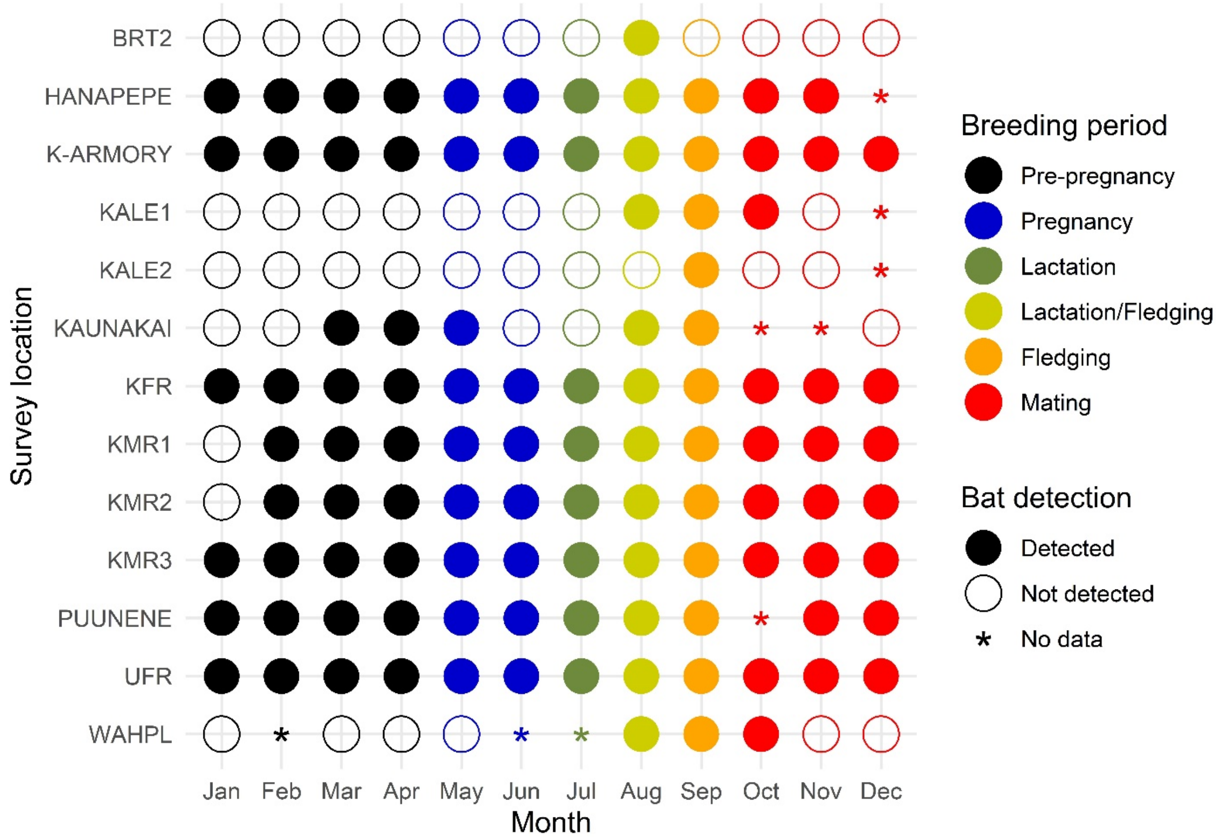

Figure 5. Confirmed bat presence by survey month and location over the station's entire survey period. A solid circle indicates that bats were detected; a hollow circle indicates that no bats were detected; and an asterisk indicates that no data were collected in that month. Circles are colored to distinguish stages of the breeding season including pregnancy (May–June), lactation (late June–August), fledging/post-lactation (September–October), mating (October–December), and a pre-pregnancy period (November–April) during which there is little or no reproductive or parental care shown by adult females.

The mean frequency of bat detections during the reproductive and fledging season had variation at the level of the sampling station even among proximate stations (Figure 6). For example, the frequency of detection at Keaukaha Military Reservation on Hawaiʽi Island for KMR1, KMR2, and KMR3 stations ranged from 11% to 85%. The highest levels (100%) of mean

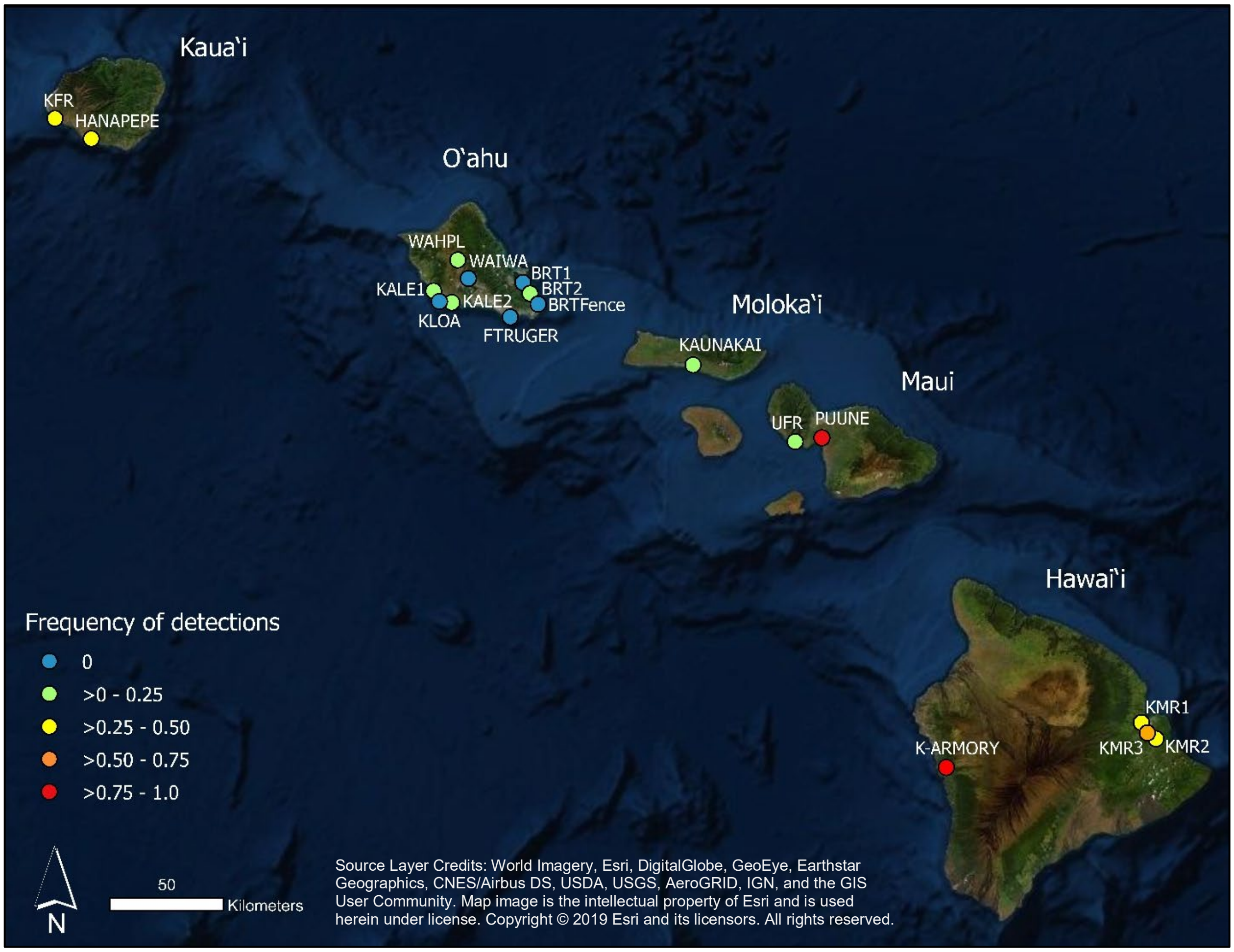

Figure 6. Mean frequency of bat detections across the months of the reproductive and fledging periods (May–October) at Hawai'i Army National Guard (HIARNG) acoustic monitoring stations during 2012–2018.

frequency of detection were at the K-Armory station on Hawai'i Island during May–August and November during Hawaiian hoary bat pregnancy, lactation, and pre-pregnancy periods. On O'ahu, acoustic monitoring demonstrated bat presence only during the lactation and fledging periods (August–October) at WAHPL and KALE1 stations, and bat presence was detected at BRT2 and KALE2 only during August (lactation/fledging) and September (fledging), respectively. At KUANAKAI on Moloka'i, bat presence was detected during March–May (pre-pregnancy, pregnancy) and August–September (lactation, fledging) but not during other months.

Bat Foraging Activity

Foraging activity was observed at nine stations on the islands of Hawai'i, Kaua'i, O'ahu, and Maui (Table 2). No foraging activity was observed at the Moloka'i acoustic monitoring station (KAUNAKAI), and only one acoustic monitoring station on O'ahu recorded a single feeding buzz in September 2017 at the Kalaeloa, Barber's Point (KALE2).

Foraging activity was highest on Hawai'i Island with feeding buzzes detected during 273 of 5,094 station-nights (5%) across all acoustic monitoring stations (K-Armory, KMR1, KMR2, KMR3). Station KMR1 had the greatest number of feeding buzzes during July (23 feeding buzzes) and August (24 feeding buzzes) followed by K-Armory during May (18 feeding buzzes), June (22 feeding buzzes), and August (21 feeding buzzes; Figure 7). Acoustic monitoring stations KMR2 and KMR3 detected fewer feeding buzzes than KMR1 and K-Armory but also showed slight peaks in foraging activity during May and August (Figure 7).

On Kauaʽi, foraging activity was observed at both the HANAPEPE and KFR acoustic monitoring stations. Feeding buzzes were recorded during 16 of 1,185 station-nights (1%) monitored across both acoustic monitoring stations. Station HANAPEPE had feeding buzzes only during February (1 feeding buzz), May (2 feeding buzzes), and September (2 feeding buzzes), while station KFR had comparatively more foraging activity with the greatest number recorded during September (4 feeding buzzes; Figure 8).

On Maui, foraging activity was observed at both the PUUNENE and UFR acoustic monitoring stations during 35 station-nights (2%) that had a total of 1,653 station-nights. Acoustic monitoring station PUUNENE had the greatest number of feeding buzzes during July (6 feeding buzzes) and August (7 feeding buzzes), while station UFR had comparatively less foraging activity with the greatest number recorded during July (2 feeding buzzes) and October (2 feeding buzzes; Figure 9).

Among all stations with foraging activity, peak foraging activity was generally observed during June through September coinciding with pregnancy (May to June), lactation (late June to August), and fledging/post-lactation (September to October) for Hawaiian hoary bats.

Nightly Bat Activity
Nightly acoustic activity, as measured by number of call-events pooled for all sampling nights at each station, varied among acoustic monitoring stations. On Hawaiʽi Island, within-night acoustic activity peaked during the first hour after sunset (1,245 call-events) and decreased throughout the night at the K-Armory station (Figure 10). Within-night bat activity pooled over all sampling nights peaked during the first hour after sunset at stations KMR1 (537 call-events), KMR2 (274 call-events), and KMR3 (409 call-events), with a secondary peak (121, 68, and 175 call-events respectively) 1–2 hours before sunrise (Figure 10).

On Kauaʽi, at the HANAPEPE acoustic monitoring station, within-night activity pooled for all sampling nights occurred irregularly throughout the night with a small peak (67 call-events) in activity six hours after sunset (Figure 11). Alternatively, at the KFR station, within-night activity pooled for all sampling nights steadily increased during the hours past sunset and peaked (361 call-events) four hours after sunset (Figure 11).

On Maui, within-night bat activity at acoustic monitoring station PUUNENE steadily increased during the hours after sunset and peaked (188 call-events) at six hours after sunset before steadily decreasing (Figure 12). At station UFR, within-night activity pooled for all sampling nights occurred irregularly throughout the night with a small peak (51 call-events) two hours after sunset (Figure 12).

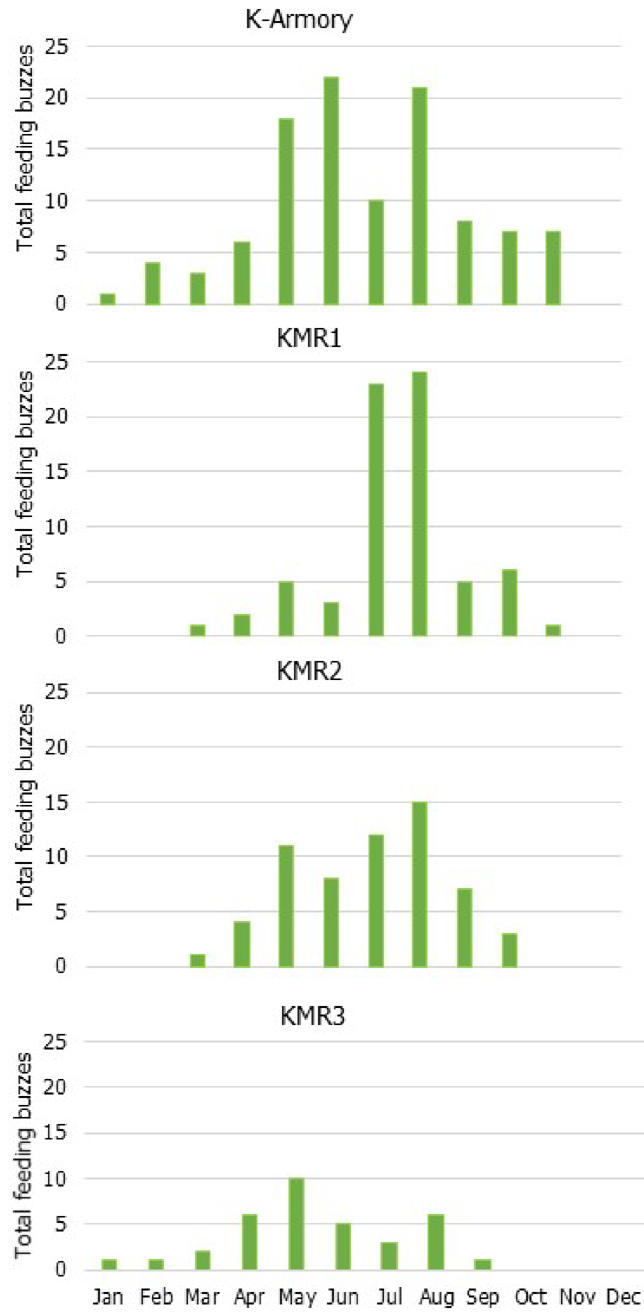

Figure 7. Monthly overall totals of Hawaiian hoary bat feeding buzzes at acoustic monitoring stations on Hawai'i Army National Guard installations on Hawai'i Island. See Table 3 for sampling effort.

On Moloka'i, within-night activity pooled for all sampling nights at the KAUNAKAI acoustic monitoring station occurred irregularly throughout the night starting one hour before sunset and peaked (4 call-events) at four hours after sunset (Figure 13).

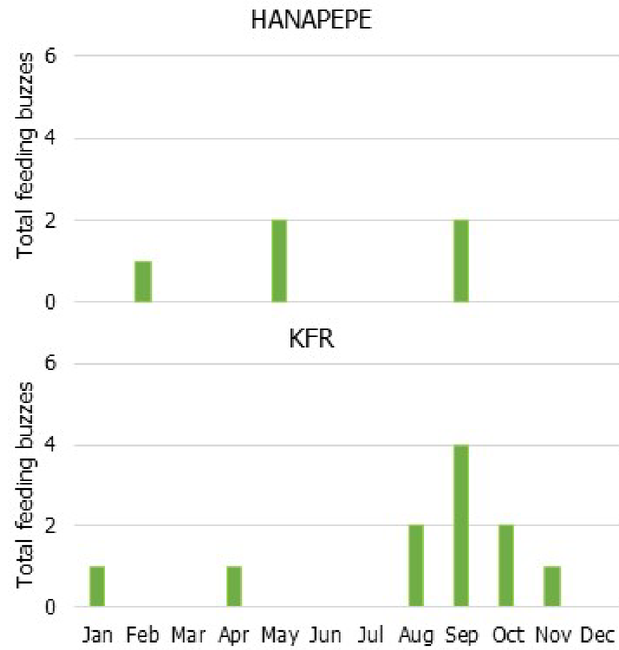

Figure 8. Monthly overall totals of Hawaiian hoary bat feeding buzzes at acoustic monitoring stations on Hawai'i Army National Guard installations on Kaua'i. See Table 3 for sampling effort.

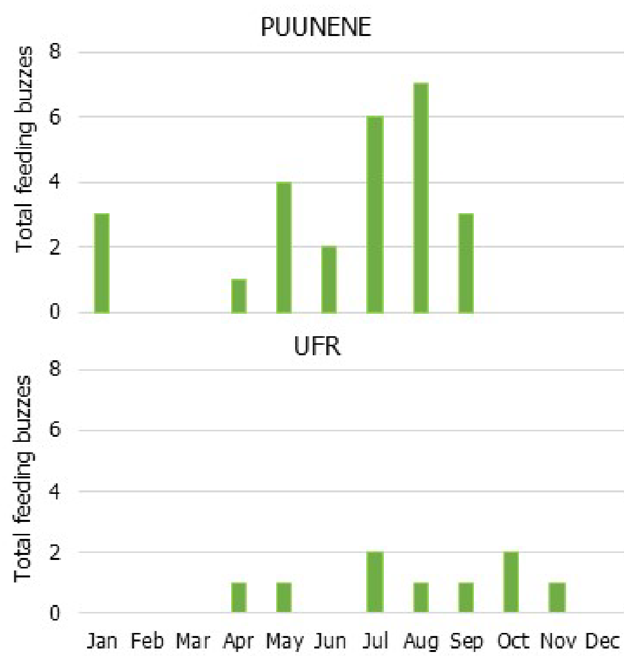

Figure 9. Monthly overall totals of Hawaiian hoary bat feeding buzzes at acoustic monitoring stations on Hawai'i Army National Guard installations on Maui. See Table 3 for sampling effort.

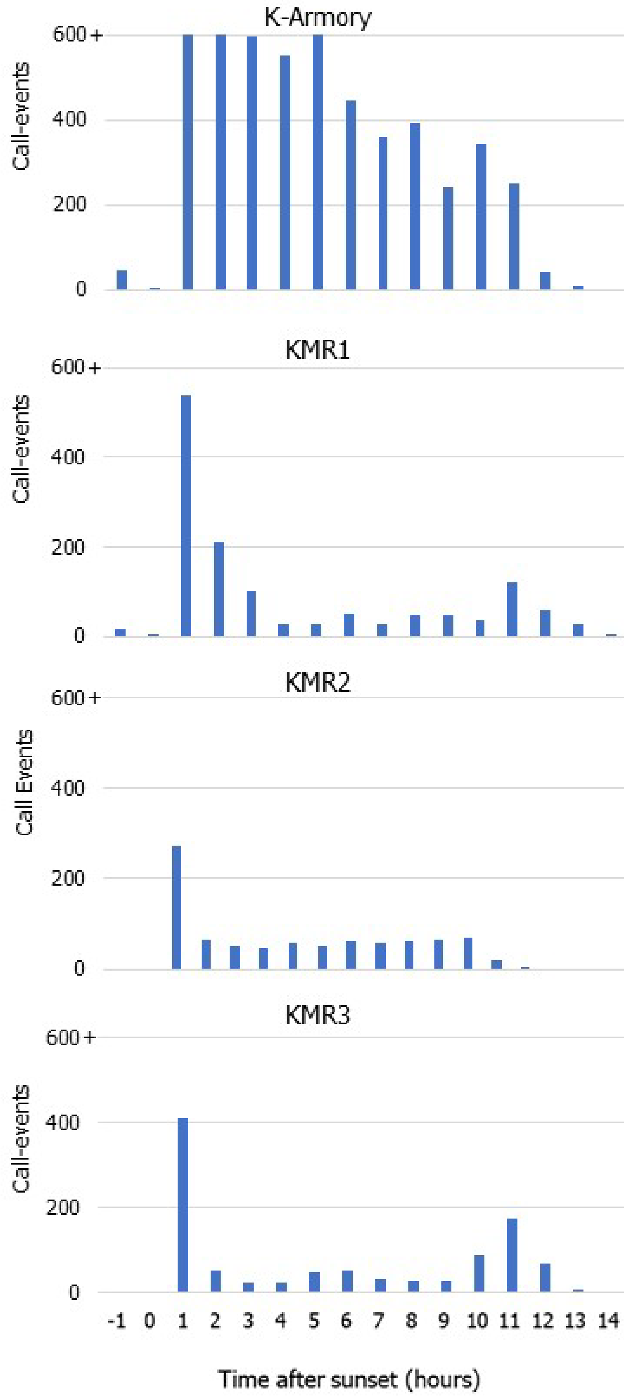

Figure 10. Total number of bat echolocation call-events relative to sunset recorded by station for the entire sampling period on Hawai'i Army National Guard installations on Hawai'i Island. To account for seasonal changes in the length of night, the time of detection was standardized relative to sunset time. See Table 3 for sampling effort.

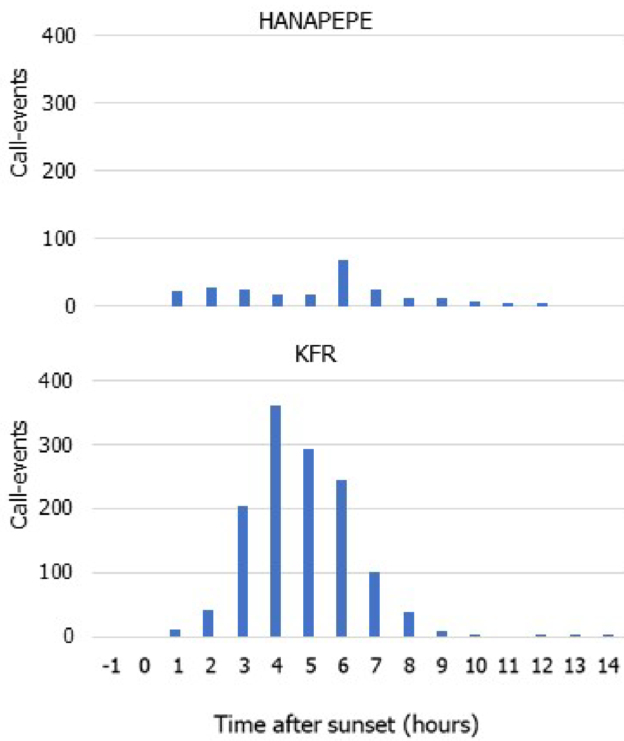

Figure 11. Total number of bat echolocation call-events relative to sunset recorded by station for the entire sampling period on Hawai'i Army National Guard installations on Kaua'i. To account for seasonal changes in the length of night, the time of detection was standardized relative to sunset time. See Table 3 for sampling effort.

On O'ahu, nightly bat acoustic activity was rare and varied among acoustic monitoring stations that detected bats (BRT2, KALE1, KALE2, WAHPL); therefore, within-night activity is shown for all four acoustic monitoring stations on one graph below (Figure 14). Within-night acoustic data pooled for all sampling nights at each station was irregular after sunset with the greatest activity at KALE1 (2 call-events) two hours after sunset and at WAHPL (2 call-events), six to seven hours after sunset (Figure 14).

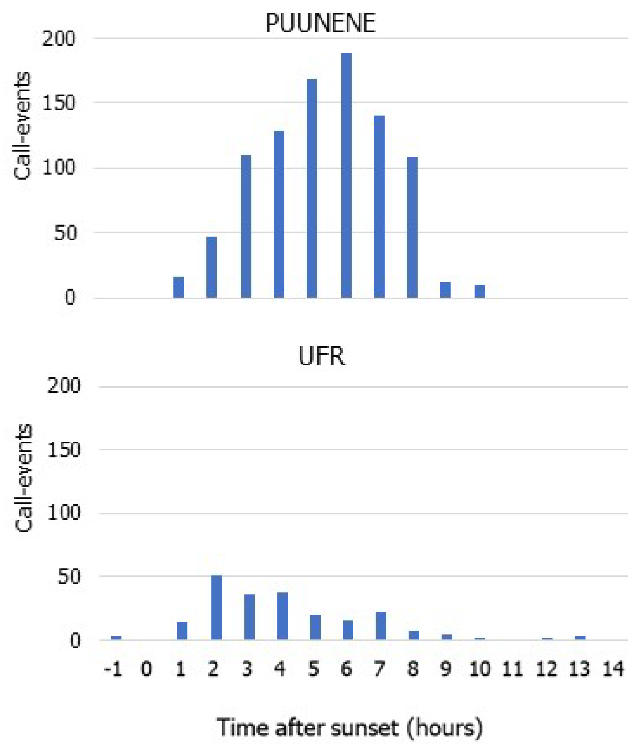

Figure 12. Total number of bat echolocation call-events relative to sunset recorded by station for the entire sampling period on Hawaiʽi Army National Guard installations on Maui. To account for seasonal changes in the length of night, the time of detection was standardized relative to sunset time. See Table 3 for sampling effort.

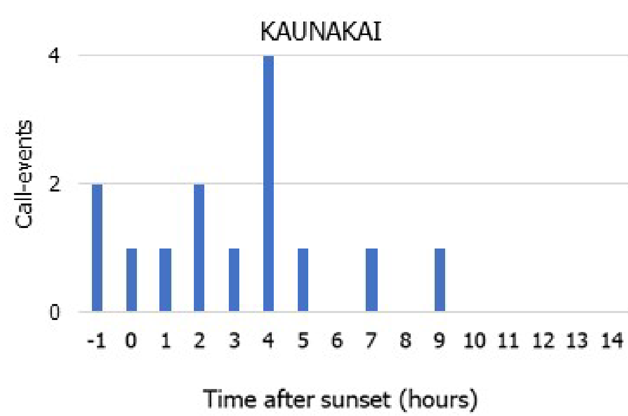

Figure 13. Total number of bat echolocation call-events relative to sunset recorded for the entire sampling period on the Hawaiʽi Army National Guard installation on Molokaʽi. To account for seasonal changes in the length of night, the time of detection was standardized relative to sunset time. See Table 3 for sampling effort.

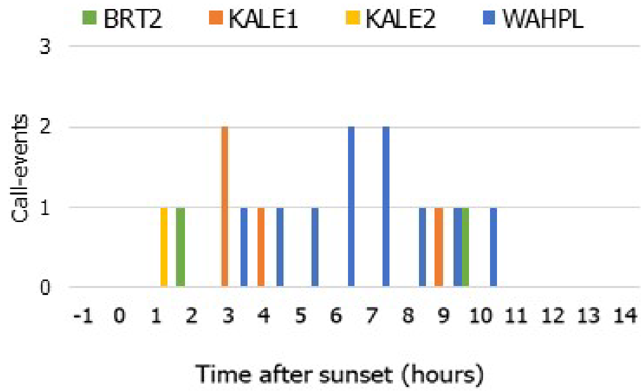

Figure 14. Total number of bat echolocation call-events by time after sunset recorded for the entire sampling period at each station where bats were detected on Hawai'i Army National Guard installations on O'ahu. To account for seasonal changes in the length of night, the time of detection was standardized relative to sunset time. See Table 3 for sampling effort.

Ungulate Grazing, Insect Abundance, and Bat Association at KMR

Ungulate Grazing and Insect Abundance Patterns

Our pilot study found malaise traps to be the most effective method for collecting insects potentially associated with goats and sheep or known to be important bat prey. In particular, malaise traps were effective at collecting moths and several species of flies that are often associated with livestock such as biting midges (Ceratopogonidae) and muscoid flies, including house flies (Muscidae), blow flies (Calliphoridae), and flesh flies (Sarcophagidae). In contrast, light traps and dung traps collected few insects. The effectiveness of light traps was likely diminished by ambient light from nearby buildings that competed with the light traps for the attention of moths and other insects (e.g., night-flying beetles). As a result, we used malaise traps to assess moth abundance. Several individual beetles were collected in dung traps (dung beetles [Scarabaeidae] and burrowing bugs [Cydnidae]), but numbers were too low to allow analysis, so the method was not used in the larger-scale study. These results suggesting that few beetles were attracted to dung in our study area were corroborated by the absence of beetle larvae in dung that was searched for coprophagic insects. Mosquitoes were captured in the mosquito traps (an average of 1.2 individuals/day), but the capture rate was variable (54% of all mosquitoes were collected during 3 out of 44 non-consecutive sample periods), and it was clear that there was no relationship between mosquito abundance and the presence of goats. As a result, we discontinued the use of mosquito traps. Ultimately, we assessed abundances of biting midges, mosquitoes, moths, and muscoid flies based on the use of malaise traps.

Overall, we collected 12,413 insects including 7,020 moths, 3,549 muscoid flies, 1,838 biting midges, and 6 mosquitoes. Because mosquitoes were rarely collected, they were excluded from further analysis. Insect abundance patterns were different across the collection dates for each insect type. The means per sample period for grazed stations are presented because of their proximity and experimental condition while the total is presented for the reference station because it was a single non-experimental station (Figure 15). Mean moth abundance at the grazed stations showed one large peak around 1 June 2018, but then moth abundance tapered

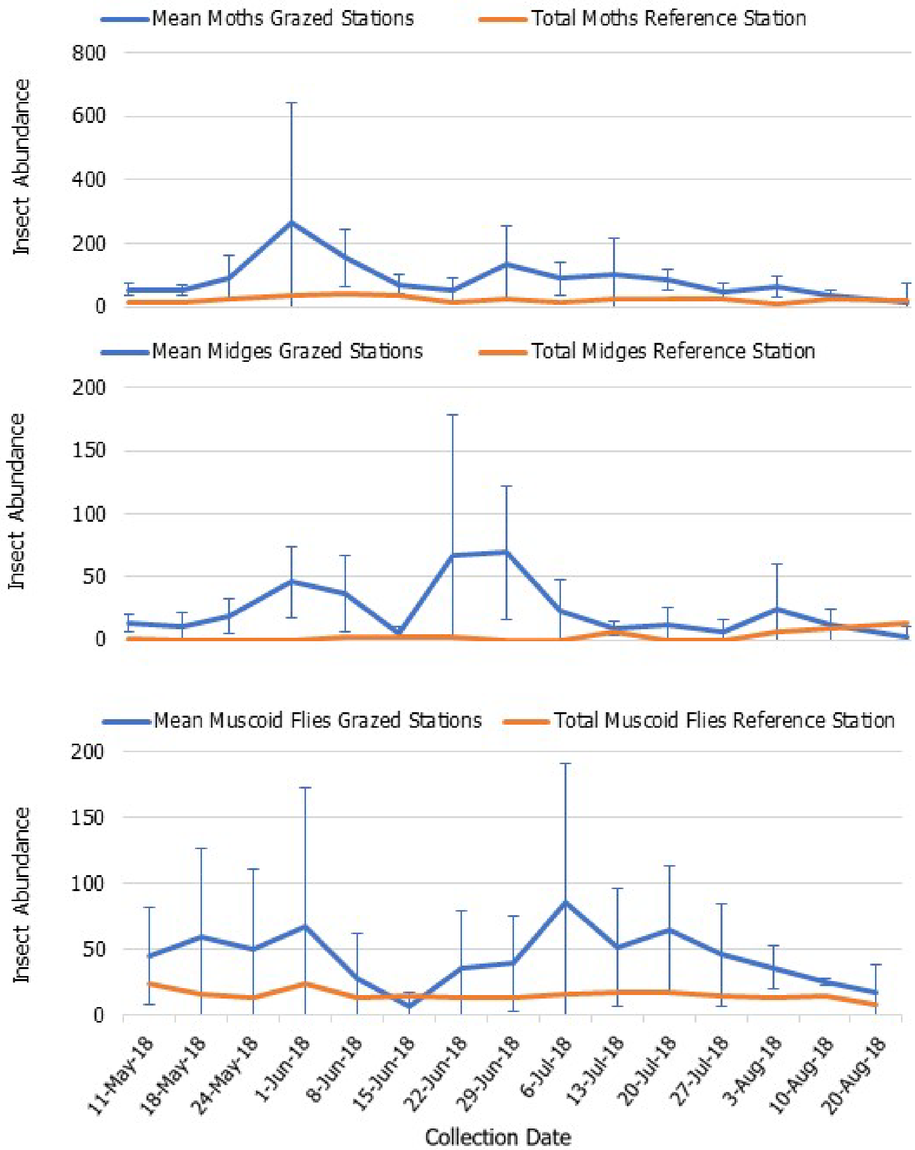

Figure 15. Insect groups identified and abundance counts from weekly malaise trap collections within grazed and reference sampling stations at Keaukaha Military Reservation (KMR). Collection date is the date that malaise trap contents were collected and contain insects from the preceding week. "Mean Grazed Stations" is pooled data from the five stations in the experimental grazing plots presented as mean with standard deviation. "Total Reference Station" is the total count from insect collection at the ungrazed reference station only.

off in the following weeks. Mean moth abundance at the grazed stations was only slightly higher than the total moths collected at the reference station. Mean biting midge abundance was higher at the grazed stations than total midges collected at the reference station, showing two peaks around early June and 22–29 June 2018. Mean muscoid fly abundance was greater than total muscoid flies collected at the reference station for the duration of the study except for one period during 15 June 2018.

Abundance patterns were also different across individual sampling stations for each insect type (Figure 16). At station 4E, muscoid fly abundance peaked during pre-grazing and grazing stages, while all three insect types showed lesser peaks in the post-grazing stage. At station 5F, insect abundances peaked during the grazing stage; moth abundance remained higher; and biting midges had a second peak during the post-grazing stage. At station 5G, moths and biting midge abundance showed no large peaks, and only muscoid fly abundance peaked in grazing, and slightly later during the post-grazing stage. At station 5H, moths and biting midges showed peaks in abundance during the pre-grazing stage, while muscoid fly abundance was low across the pre-grazing period and showed a small increase during grazing. At station 5I, moth abundance showed peaks during the pre-grazing stage, while biting midge and muscoid fly abundance remained mostly low over all stages. At the ungrazed reference station, biting midge abundance was very low; there were no apparent peaks in muscoid fly abundance; and moth abundance was mostly greater than the other two insect types and showed a few large peaks over time.

We analyzed insect counts of moths, muscoid flies, and midges separately as a function of distance and time (lag) from the active grazing area. At time "0 weeks" goats were actively grazing and time "5 weeks" goats had been absent from the grazing area for five weeks. There was no apparent relationship between distance and time from active pasture and insect abundance (Figure 17).

Bat Activity and Ungulate Grazing Presence

Echolocation calls of Hawaiian hoary bats were detected at all stations in the ungulate grazing plots as well as the reference station outside of the experimental grazing plots (except at station 5G, which had an equipment failure). There were no differences in echolocation pulses in reference versus grazed plots (Figure 18), and there were no differences in echolocation pulses as a function of distance and time (lag) from active grazing area (Figure 19). Where at time "0 weeks" ungulates were actively grazing and time "5 weeks" ungulates were absent from the grazing area for five weeks. We also analyzed total echolocation pulses and feeding buzzes as a function of insect count for midges, moths, and muscoid flies at grazed and reference stations (Figures 20 and 21). There were no differences between echolocation pulses or feeding buzzes and insects in grazed and reference stations. Finally, we looked at total feeding buzzes and pulses in reference and grazed stations and found that the grazed stations had more echolocation pulses and feeding buzzes than the reference station (ANCOVA, $t_{604} = 2.56$, $P = 0.01$; Figure 22).

We found no evidence of roosting bats during two thermal searches (13 and 21 June 2018) of potential roost trees within KMR boundaries. However, one bat was observed on thermal imagers flying overhead shortly after sunset on 21 June 2018. The bat remained in the area for approximately 15 minutes before field personnel lost line-of-sight. During two netting nights (18 and 19 July 2018) no bats were captured or observed; therefore, we were unable to conduct dietary analysis of guano or Hawaiian hoary bat demographics in KMR.

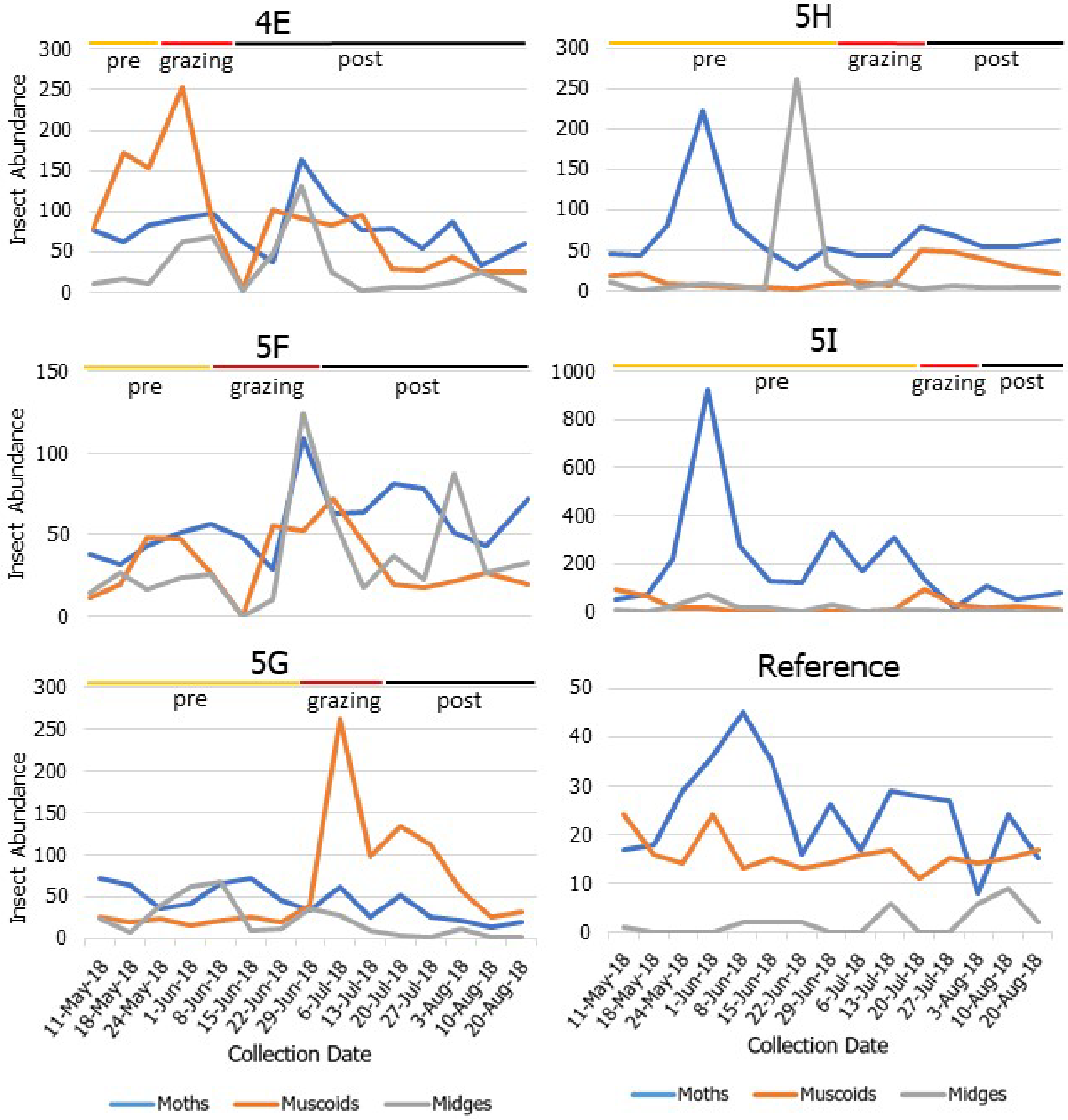

Figure 16. Insect abundance of moths, muscoid flies, and biting midges over time for the five sampling stations and the reference station. Stage of grazing at each sampling station is described by time prior to grazing, “pre” (yellow line); during the time goats were present around the station, “grazing” (red line); and time after goats had been moved away from the station, “post” (black line).

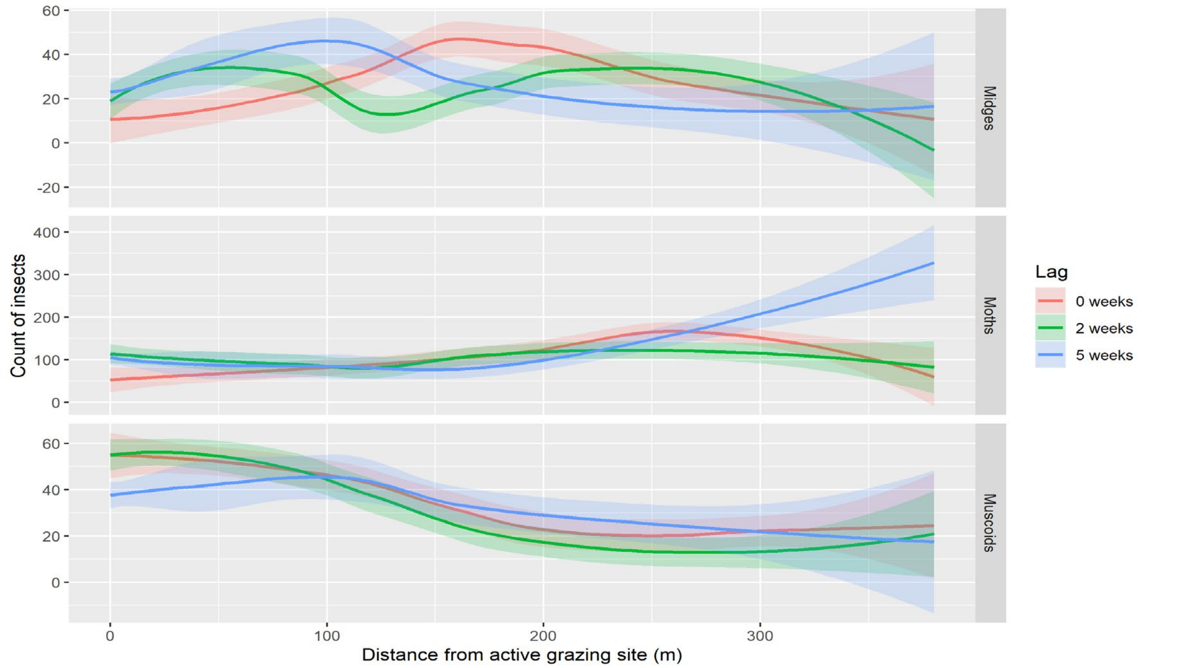

Figure 17. Counts of midges, moths, and muscoid flies combined as a function of distance (m) and time (lag) from active grazing area. Where at lag "0 weeks" goats were actively grazing and lag "5 weeks" goats had not been grazing in the area for five weeks. Overall trends are shown with a loess smooth curve, and 95% confidence intervals are shown with color shades.

Figure 18. Total bat echolocation pulses in grazed stations versus reference station. Overall trend is shown with a loess smooth curve, and 95% confidence intervals are shown with color shades.

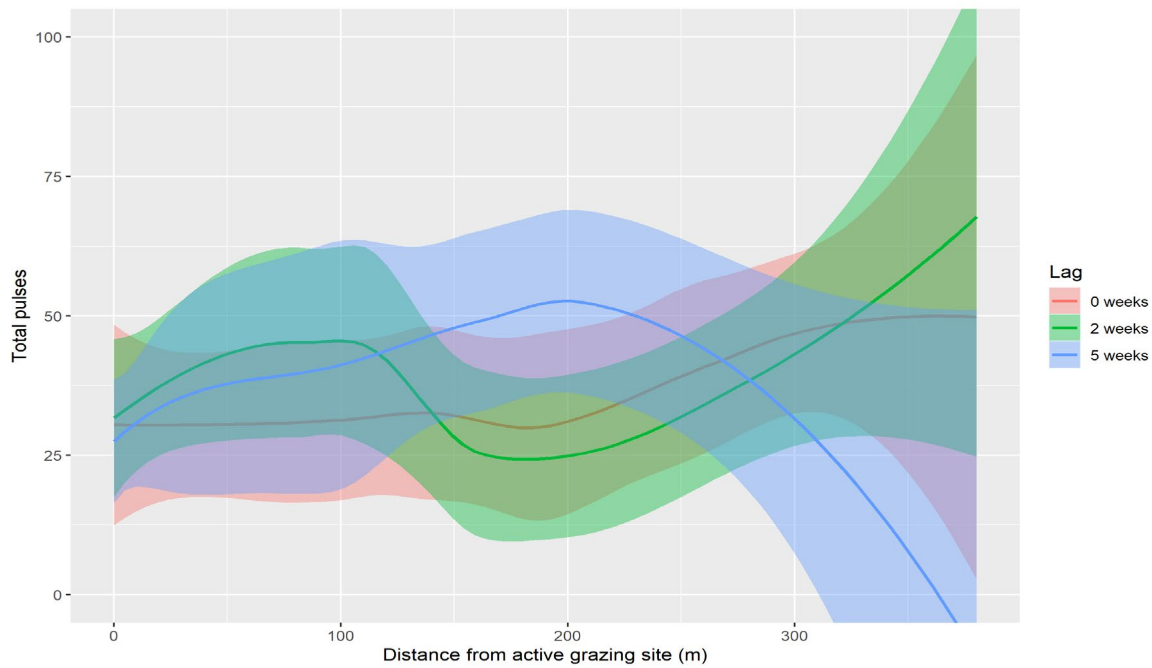

Figure 19. Total bat echolocation pulses as a function of distance and time (lag) from active grazed sampling station. Where at lag "0 weeks" ungulates were actively grazing and lag "5 weeks" ungulates had not been grazing in the area for five weeks. Overall trends are shown with a loess smooth curve and 95% confidence intervals are shown with color shades.

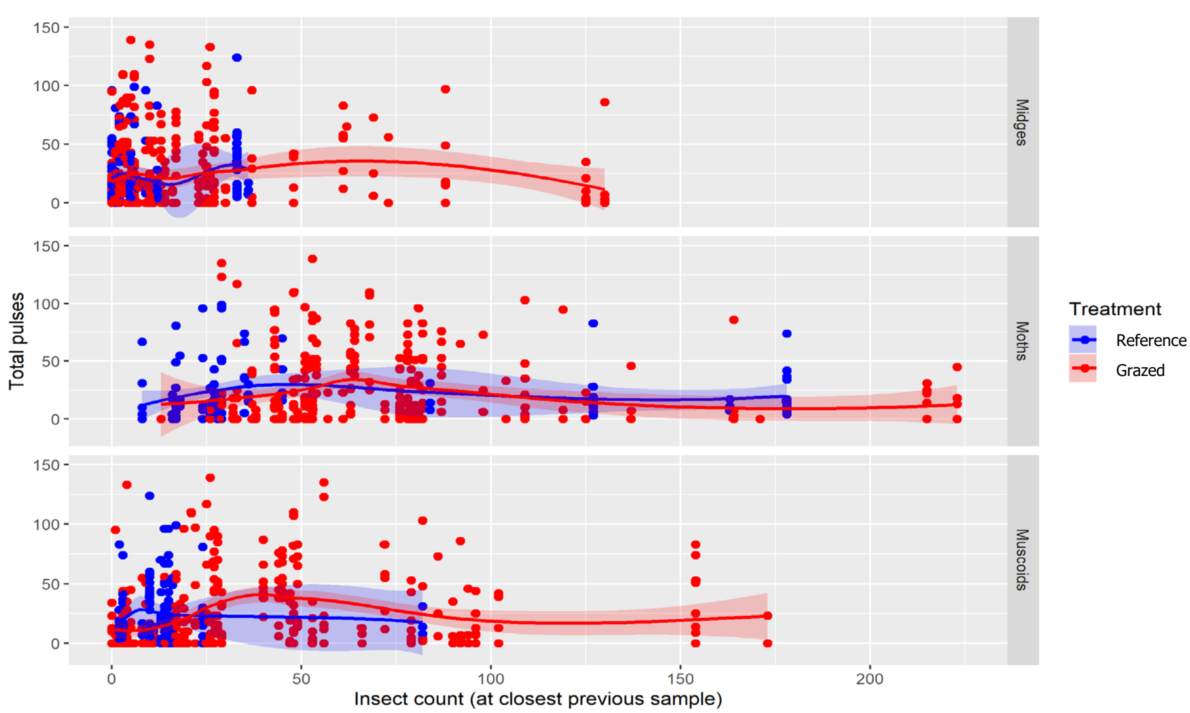

Figure 20. Total bat echolocation pulses and insect counts for midges, moths, and muscoid flies at grazed stations and the ungrazed reference station, counted to the closest previous collection sample date. Overall trends are shown with a loess smooth curve, and 95% confidence intervals are shown with color shades.

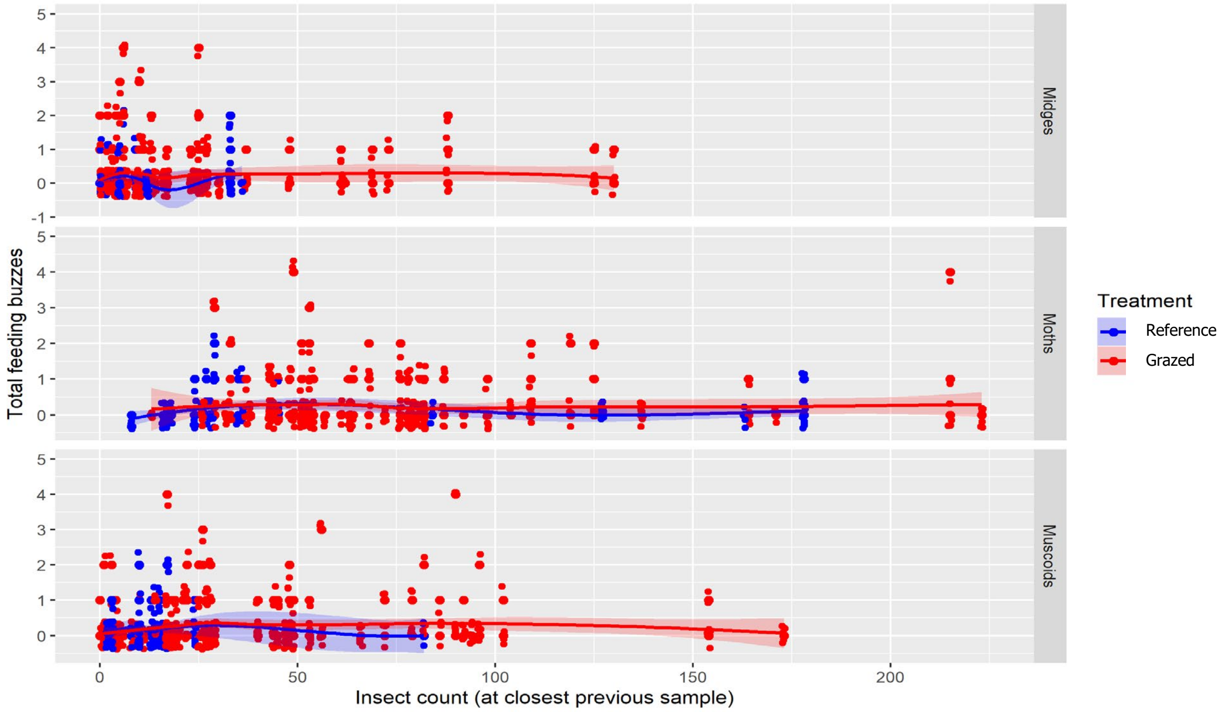

Figure 21. Total feeding buzzes and insect counts for midges, moths and muscoid flies at grazed and ungrazed reference stations counted at the closest previous collection sample date. Overall trends are shown with a loess smooth curve, and 95% confidence intervals are shown with color shades.

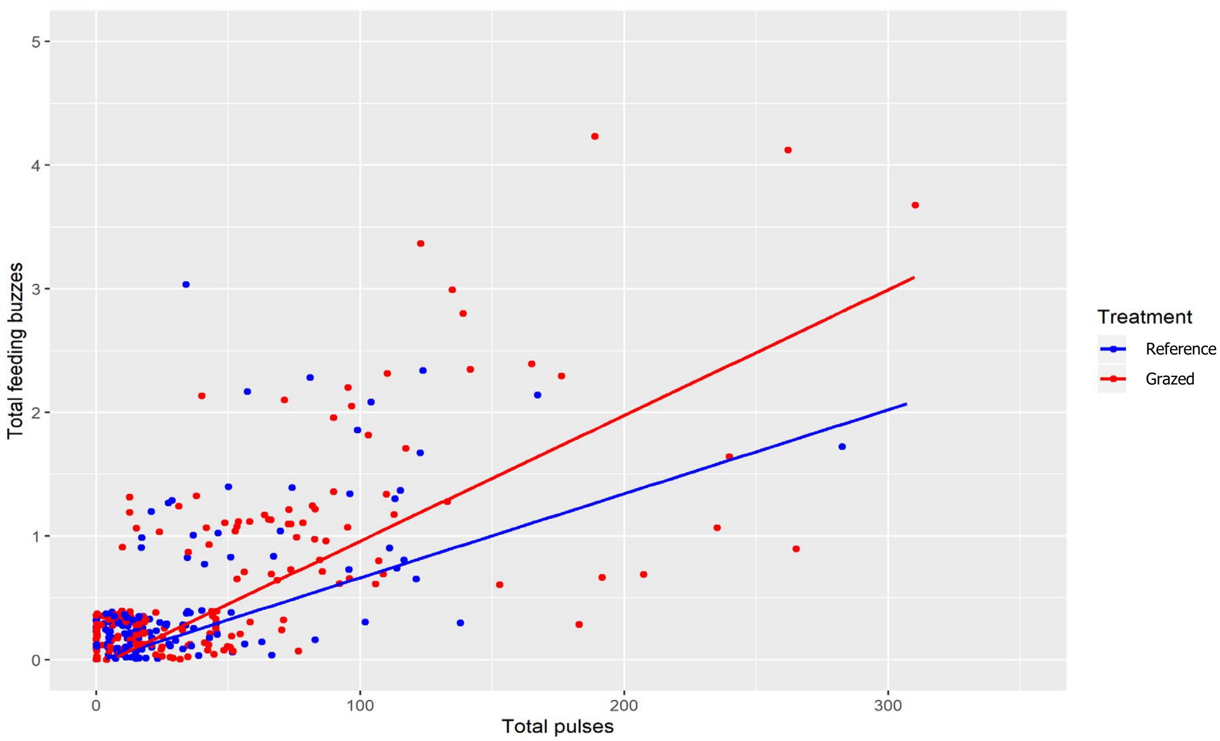

Figure 22. Total bat echolocation pulses and feeding buzzes at grazed and ungrazed reference stations with trend lines.

Discussion

Acoustic monitoring confirmed that Hawaiian hoary bats were present at 13 of 18 acoustic monitoring stations on 10 of 12 HIARNG installations on the islands of Hawai'i, Kaua'i, Maui, Moloka'i, and O'ahu. Bat occurrence and foraging activity was distributed irregularly but mostly concentrated in May through October during the pregnancy, lactation, post-lactation, and fledging periods. During the pregnancy and lactation periods, adult females can be expected to have their highest energy demands needed to forage in order to support reproductive activities, and, during the post-lactation and fledging period, the total bat population should be at its annual maximum, thus contributing to increased bat activity and foraging (Gorresen *et al.* 2013).

Hawaiian hoary bats are regarded as habitat generalists occurring from sea level to 3,600 m asl (Gorresen *et al.* 2013, Bonaccorso *et al.* 2016). While increased frequency of detection and foraging activity is often associated with forest and corridor habitat (areas of narrow, open conduit for unimpeded flight such as roads, windrows of trees, etc.; Gorresen *et al.* 2013, Montoya-Aiona *et al.* 2019b), bat presence has been detected in areas with little vegetation including urban environments (Bonaccorso *et al.* 2019) similar to HIARNG installations in our current study where developed areas were present. Therefore, even when detection rates were low, bats do occur and make use of habitats similar to those within the installations monitored.

The seasonal patterns of occurrence that we detected are similar to patterns previously observed in acoustic monitoring studies on the islands of Hawai'i (Gorresen *et al.* 2013, Montoya-Aiona *et al.* 2019b), Maui (Pinzari *et al.* 2019), and O'ahu (Bonaccorso *et al.* 2019, Starcevich *et al.* 2019) with peak acoustic activity also detected between May and October. Additional studies on Hawai'i Island (Menard 2001, Gorresen *et al.* 2013, Bonaccorso *et al.* 2016) suggest bats make seasonal movements from coastal lowlands at or below 1,000 m asl during the pregnancy through fledging periods (May–October) to interior highlands up to 3,600 m asl during the pre-pregnancy period (January–March). Our acoustic monitoring stations were well below 1,000 m asl with the highest at 514 m asl; however, our observed patterns of seasonal occurrence support the reproductive seasonality observed in the lowlands.

Foraging activity was detected infrequently and at only nine acoustic monitoring stations on the islands of Hawai'i, Kaua'i, O'ahu, and Maui. Peaks in foraging activity were detected at most stations in August and September coinciding with hoary bat fledging in Hawai'i. The difficulty in detecting feeding buzzes has been noted in other acoustic monitoring studies (Bonaccorso *et al*. 2016, Gorresen *et al*. 2018, Pinzari *et al*. 2019), and the limitations of acoustic detection equipment and microphone effective detection range may reduce the number of feeding buzzes recorded. Therefore, foraging activity is believed to be underrepresented across acoustic monitoring stations.

Generally, within-night acoustic activity was confined to the first six hours after sunset. On Hawai'i Island, Montoya-Aiona *et al.* (2019b) found that in reproductive months (May–October) nightly activity began shortly after local sunset and quickly decreased, while in the non-reproductive season (November–April) nightly echolocation activity begins at sunset and persists through the night until nearly sunrise. However, on O'ahu there were no clear patterns of nightly activity across acoustic monitoring stations (Pinzari *et al*. 2019). The irregularity in nightly activity may be influenced by many variables including irruption events of insect prey, weather events, and localized habitat changes (Gorresen *et al*. 2013, Banko *et al*. 2014).

Although grazing by goats appears to increase the abundance of potential bat prey insects such as muscoid flies and biting midges, we did not find apparent differences in bat echolocation activity and insect counts between grazed and ungrazed reference stations to suggest hoary bats are drawn to foraging above the grazing goats. Nor did we find relationships between bat echolocation activity and the distance to the herd or time since an area was grazed. It is not clear why bats did not respond to measured increases in the availability of insects, but it may be due to factors such as the relatively large foraging range of bats in the area compared to the size of the areas being grazed, the type of animal grazed and their dung, and the daily activity patterns of the insects. For example, the area grazed by goats and sheep (~15 ha) was much smaller than the area typically used for foraging by Hawaiian hoary bats (230.7 ± 72.3 ha) and core use areas (CUA; 25.5 ± 6.9 ha; Bonaccorso *et al.* 2015). As a result, a pulse in insect prey associated with livestock in our study may have been insignificant compared to prey found elsewhere in the area (e.g., moths attracted to lights at nearby buildings). In contrast, others have found positive associations between livestock and bat foraging activity, but in those studies the areas grazed were much larger (e.g., 1,300 ha, Ancillotto *et al.* 2017) and included cattle rather than goats and sheep (a single herd of 21 cattle, Downs and Sanderson 2010; nine herds up to 60 head/herd, Ancillotto *et al.* 2017). It is possible that the larger biomass of cattle and their dung, or the quality of cattle dung (e.g., higher moisture or nutrient levels), used in those studies led to considerably more insects, and therefore a significant response by bats. It is not known how active muscoid flies and biting midges are at night, but movement of livestock during the night likely disturbs the flies resting on or adjacent to the animals, leading to flight behaviors that bats may detect. Alternatively, they may be entirely inactive at night and not available to bats as prey.

We were not able to collect information on the numbers of goats and sheep within each grazing plot and this also varied with the grazing regime and size of paddock. Goat dung also contains less moisture than cattle dung, which would reduce the use of goat dung by scarab beetles that require wet conditions. This may explain why we did not collect many scarab beetles during our pilot insect sampling. Potential bat prey such as moths associated with grass may have been slightly depressed by grazing, as they require long grass habitats to complete their life cycles. At five weeks lag time, there was an increase in moth abundance as distance from active goat grazing increased. The life cycles of goat associated bat prey, such as muscoid flies, are 15–25 days. Muscoid fly count also decreased as distance from active goat grazing increased, for lag times at 0 and 2 weeks. Biting midges have life cycles between two and six weeks, this may explain why our data showed the largest peak in abundance around six weeks after grazing began. In summary, Hawaiian hoary bats use Keaukaha Military Reservation (KMR) and forage seasonally as evidenced by long-term acoustic studies and their presence in the ungulate grazing areas; however, the relatively small grazing ungulate herd size and grazing area may not be able to support enough prey to have a significant influence on bat foraging rates.

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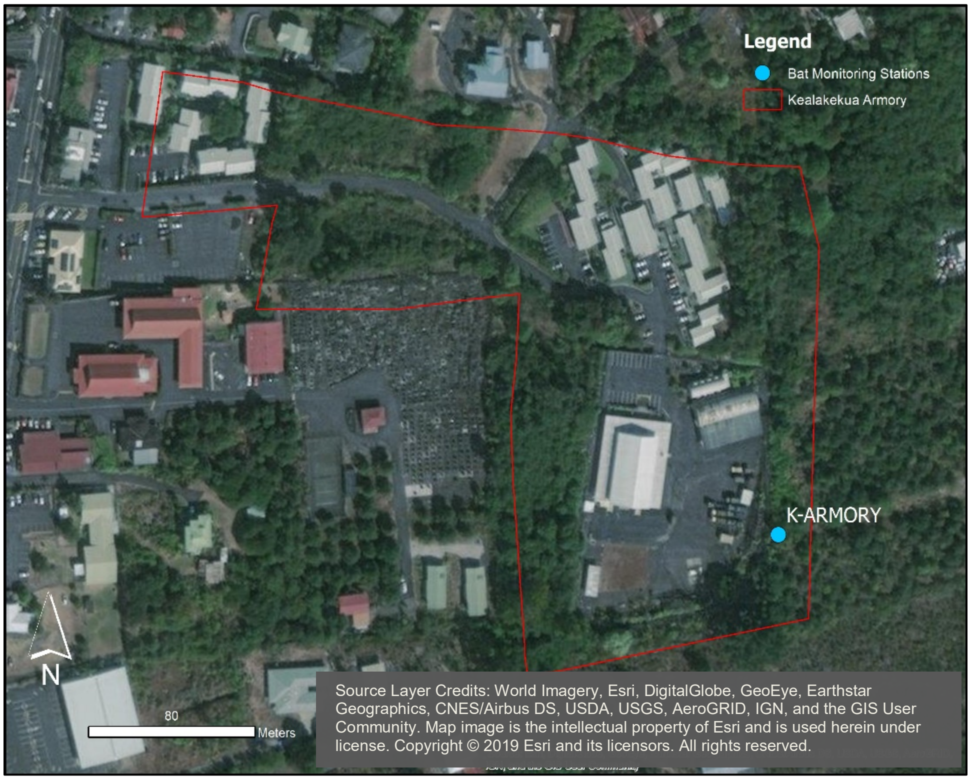
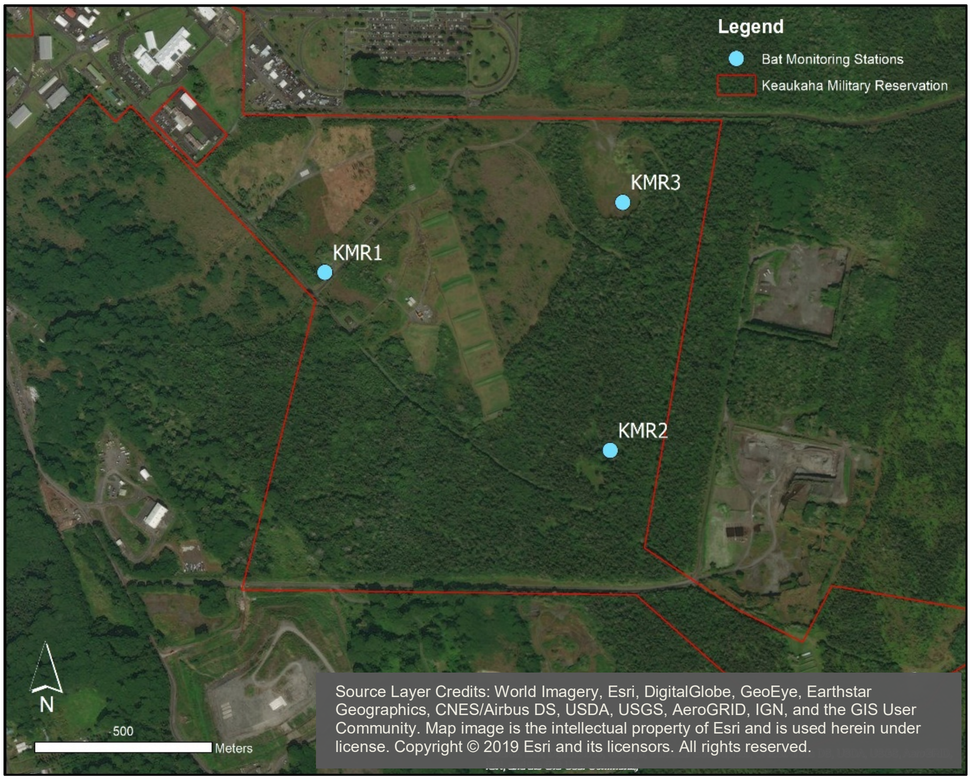
APPENDIX I. LONG-TERM BAT ACOUSTIC MONITORING STATIONS

Aerial maps and habitat photos of HIARNG installations with Hawaiian hoary bat long-term acoustic monitoring stations.



Appendix I, Figure 1. Hawai'i Island-Kealakekua Armory aerial map of bat acoustic monitoring station.

Appendix I, Figure 2. Hawai'i Island-Kealakekua Armory bat acoustic monitoring station (K-Armory) and surrounding habitat.



Appendix I, Figure 3. Hawai'i Island-Keaukaha Military Reservation aerial map of bat acoustic monitoring stations.

Appendix I, Figure 4. Hawai'i Island-Keaukaha Military Reservation bat acoustic monitoring stations and surrounding habitat from left to right: KMR1, KMR2, KMR3.

Appendix I, Figure 5. Kaua'i-Hanapēpe Armory aerial map of bat acoustic monitoring station.

Appendix I, Figure 6. Kaua'i-Hanapēpe Armory bat acoustic monitoring station (HANAPEPE) and surrounding habitat.

Appendix I, Figure 7. Kaua'i-Kekaha Firing Range bat aerial map of bat acoustic monitoring station.

Appendix I, Figure 8. Kaua'i-Kekaha Firing Range bat acoustic monitoring station (KFR) and surrounding habitat.

Appendix I, Figure 9. Maui-Puʻunēnē Training Facility aerial map of bat acoustic monitoring station.

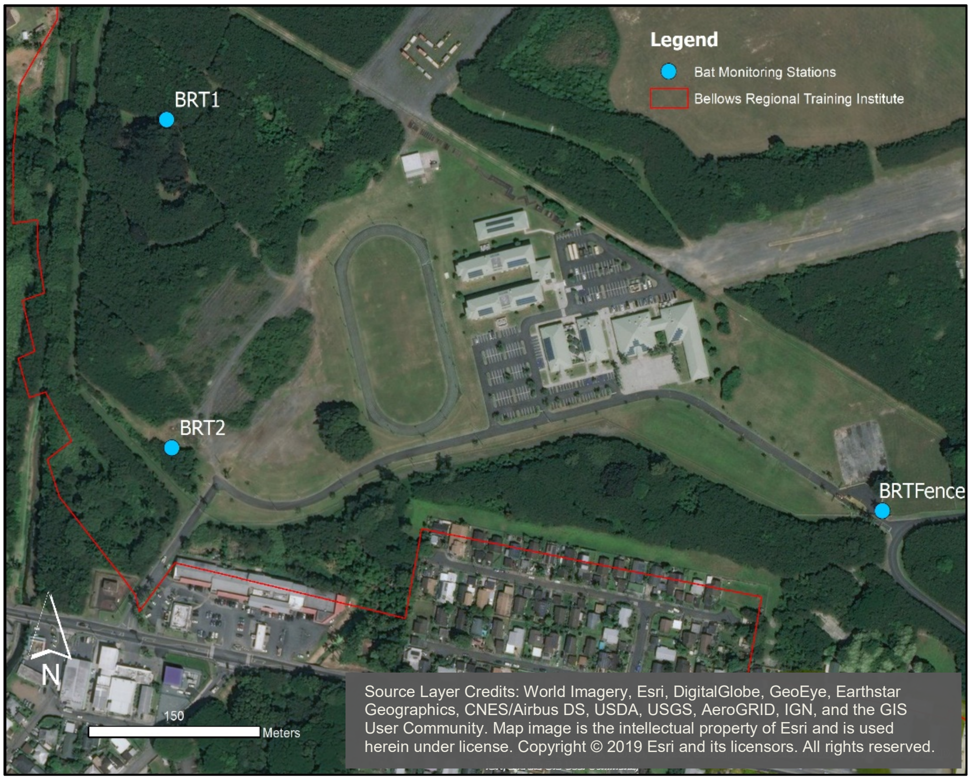
Appendix I, Figure 10. Maui-Puʻunēnē Training Facility bat acoustic monitoring station (PUUNENE) and surrounding habitat.

Appendix I, Figure 11. Maui-Ukumehame Firing Range aerial map of bat acoustic monitoring station.


Appendix I, Figure 12. Maui-Ukumehame Firing Range bat acoustic monitoring station (UFR) and surrounding habitat.

Appendix I, Figure 13. Moloka'i-Kaunakakai Armory aerial map of bat acoustic monitoring station.

Appendix I, Figure 14. Moloka'i-Kaunakakai Armory bat acoustic monitoring station (KAUNAKAI) and surrounding habitat.



Appendix I, Figure 15. Oʻahu-Bellows Regional Training Institute aerial map of bat acoustic monitoring stations.

Appendix I, Figure 16. Oʻahu-Bellows Regional Training Institute surrounding habitat of bat acoustic monitoring stations.

Appendix I, Figure 17. O'ahu-Fort Ruger bat acoustic aerial map of bat acoustic monitoring station.

Appendix I, Figure 18. O'ahu-Fort Ruger bat acoustic monitoring station (FTRUGER) and surrounding habitat.

Appendix I, Figure 19. O'ahu-Kalaeloa, Barber's Point aerial map of bat acoustic monitoring stations.


Appendix I, Figure 20. O'ahu-Kalaeloa, Barber's Point bat acoustic monitoring stations and surrounding habitat from left to right: KLOA, KALE1, KALE2.

Appendix I, Figure 21. Oʻahu-487th Military Parking Facility aerial map of bat acoustic monitoring station.

Appendix I, Figure 22. Oʻahu-487th Military Parking Facility bat acoustic monitoring station (WAHPL) and surrounding habitat.

Appendix I, Figure 23. O'ahu-Waiawa Armory aerial map of bat acoustic monitoring station.


Appendix I, Figure 24. O'ahu-Waiawa Armory bat acoustic monitoring station (WAIWA) and surrounding habitat.