

RESEARCH ARTICLE



Hawaiian hoary bat responses to habitat, season, and non-native insectivore suppression

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Abstract

Habitat loss and non-native species are 2 of the most important factors that influence native species persistence and behaviors globally. The insectivorous Hawaiian hoary bat (*Lasiurus semotus*) is the only extant terrestrial mammal native to the Hawaiian Islands. Non-native invasive insectivore species, which are potential competitors of bats for prey, may influence hoary bat behavior. The goal of this study was to determine how small-scale suppression of invasive insectivores (rodents, ants, and yellowjacket wasps [*Vespula pensylvanica*]) influenced bat activity in grasslands and woodlands. We measured bat activity as a function of the number of distinct minutes in a night containing bat echolocations (bat call minutes) at 20 experimental plots (each 2.25 ha) in a dryland ecosystem on Hawai'i Island, November 2016–January 2018. We included 3 predictor variables: vegetation type (woodland, grassland), season (bat reproductive cycle periods: lactation, mating, pre-pregnancy, and pregnancy), and insectivore treatment type (ant suppressed, yellowjacket wasp suppressed, rodent suppressed, combined ant+wasp+rodent suppressed, and no treatment). Bat activity was associated with all 3 predictors using a negative binomial generalized linear model. Bat call minutes and feeding buzzes were twice as high in woodlands than in the grasslands (2.4 and 2.3 times as high, respectively). Bat activity was slightly lower (0.47 bat call min/night fewer) in plots receiving the combined ant + wasp + rodent treatment compared to all other treatment plots. Feeding buzzes did not differ significantly among treatments.



Mean activity was lowest during lactation (mid-Jun–Aug). Although woodlands appear particularly important for the Hawaiian hoary bat, small-scale bat activity and foraging do not appear to be strongly affected by resource competition with the invasive insectivores in this study.

KEYWORDS

acoustic detection, endangered species, Hawai'i Island, invasive insectivore, *Lasiurus cinereus semotus*, *Lasiurus semotus*, prey competition, woodland

The Hawaiian hoary bat (*Lasiurus semotus*) is the only native terrestrial mammal in the Hawaiian Islands and is listed as federally endangered under the Endangered Species Act. The bat resides on all main islands of Hawai'i, USA. They are solitary, tree-roosting bats that consume aerial insects, primarily moths (Lepidoptera) and beetles (Coleoptera), in open and wooded areas (Belwood and Fullard 1984, Jacobs 1999, Todd 2012, Gorresen et al. 2018, Pinzari et al. 2019). Despite the preponderance of moths and beetles in their diet, individuals forage opportunistically on a wide range of insect orders in native, non-native, human-occupied, and agricultural landscapes (U.S. Fish and Wildlife Service 1998, Todd 2012, Pinzari et al. 2019). Bat activity, feeding behavior, and prey availability can be influenced by habitat, changing weather patterns, and energetic requirements related to the stages of the bat's reproductive cycle in Hawai'i (Menard 2001, Todd 2012, Gorresen et al. 2013). Researchers of multi-year studies on Hawai'i Island reported that hoary bat activity and prevalence fluctuate seasonally with the peak of activity occurring when adults mate and young fledge, decreasing throughout breeding and pregnancy, and increasing again during lactation (Menard 2001, Gorresen et al. 2013). While activity can vary intra- and inter-annually, during 7 years of bat monitoring in our study area, activity has largely corresponded with the reproductive periods (as adapted from Menard 2001) as described above (R. D. Moseley, Colorado State University, unpublished report).

Despite our knowledge of seasonal hoary bat activity patterns on various islands in the Hawaiian archipelago, it is unclear how competition from invasive insectivores may affect food availability and bat activity. Many continental and island ecosystems, including the Hawaiian Islands, have established populations of non-native invasive insectivores, including rodents (e.g., black rats [*Rattus rattus*], house mice [*Mus musculus*]), ants (e.g., Argentine ant [*Linepithema humile*]), and yellowjacket wasps (*Vespula pensylvanica*). These non-native invasive species depredate native and endangered species throughout Hawai'i, and insects are a substantial component of each of these invasive species' diets, including orders that dominate the hoary bat diet (Cole et al. 1992, Gambino 1992, Wilson et al. 2009, Shiels et al. 2013). For example, lepidopterans comprise 70–88% of hoary bat diets on Hawai'i and Kaua'i (Belwood and Fullard 1984, Jacobs 1999), and all of these invasive insectivores consume lepidopterans in larval or adult stages throughout the islands (Cole et al. 1992, Wilson et al. 2009, Shiels et al. 2013). These invasive insectivores consume additional insect orders also documented in hoary bat diets (e.g., Coleoptera and Diptera; Belwood and Fullard 1984, Jacobs 1999), as previously demonstrated with diet studies of yellowjacket wasps (Wilson et al. 2009) and rodents (Shiels et al. 2013), and by sampling invaded and uninvaded ant communities (Cole et al. 1992). Shiels et al. (2013) reported that >90% of black rats and house mice in Hawai'i consumed adult or larval stages of insects, and some orders such as Lepidoptera comprised over half of the rodent's (plant + animal) diet. Roughly a quarter of the total dietary items in yellowjackets sampled on Hawai'i and Maui contained Coleoptera and Lepidoptera (Wilson et al. 2009).

Hawaiian hoary bat foraging behavior may shift within the landscape in response to significant competition where non-native insectivore abundances are high. Todd (2012) reported that Hawaiian hoary bats at high elevation sites without the presence of the invasive insectivorous coqui frog (*Eleutherodactylus coqui*) selected prey based on preference rather than consuming prey proportional to availability compared to lower elevation sites with



dense frog populations. Changes in bat behavior due to competition for prey have also been demonstrated across many bat species and ecosystems (Hickey and Fenton 1990, Arlettaz et al. 1997, Jachowski et al. 2014, Roeleke et al. 2018). Furthermore, such shifts in bat foraging may be on relatively small scales (e.g., a few hectares) to access patches of elevated resources and reduce competition within their foraging- or home-range. For example, Downs and Sanderson (2010) sampled adjacent 3-ha plots in a cattle-grazed pasture and reported that insectivorous bats in the west of England were attracted to the presence of cattle rather than their dung. Bell (1980) used ultraviolet light experiments to demonstrate how insectivorous bats in Arizona, USA, foraged in light-induced prey patches, and Belwood and Fullard (1984) reported that hoary bats foraged opportunistically on swarms of insects underneath electric streetlights in Kaua'i. The nature of microhabitat use and foraging patches is poorly understood and is of particular interest to those managing bat habitat across the Hawaiian Islands.

Habitat conversion or loss due to disturbance can also affect bat presence and activity (Medellin et al. 2000, Gorresen and Willig 2004, Threlfall et al. 2012). Anthropogenic disturbances such as urbanization, military training, and pollution directly alter native ecosystems and can promote additional disturbances such as fire. Many dryland ecosystems of the world, including most in Hawai'i, have experienced fires that facilitate habitat conversion from native woodland to predominantly invasive grassland (D'Antonio and Vitousek 1992, D'Antonio et al. 2011). The introduction of ungulates to Hawai'i has also been a major source of native habitat loss and disturbance. In many cases, such habitat losses are irreversible without human intervention and restoration actions (D'Antonio et al. 2011).

Our objective was to determine how small-scale suppression of invasive insectivores (rodents, ants, and yellowjackets) influences hoary bat activity in grassland and woodland plots, and during the stages that correspond to the bat's reproductive cycle as reproductive seasons (i.e., season). We designed our study to take advantage of an existing effort to intensively suppress invasive insectivores to understand their impacts on plant pollination dynamics (Liang et al. 2021). The small-sized plots (2.25 ha) already in place provided an opportunity to test our hypotheses and examine how hoary bats respond to micro-habitat patches after suppression of invasive ants, wasps, and rodents separately and collectively. Such suppression potentially increases insect prey availability for bats by removing those species that mainly consume larval stages of beetles and moths, thereby influencing bat foraging. Furthermore, it is reasonable to assume that reducing invasive insectivores enhances overall health and biodiversity, thereby increasing foraging opportunities. We had 3 specific hypotheses: bats are more active and forage more frequently above plots where potential insectivore competitors are continuously suppressed; bats are active and forage in woodlands and grasslands, but their activity is lower in the grassland because the prey base is simplified and roosting trees are farther away; and bats are more active when adults mate and newly volant juveniles fledge (generally Sep–Dec) because these stages represent the peak of social activity for this species.

STUDY AREA

This study occurred at the United States Army Pōhakuloa Training Area (PTA) on the island of Hawai'i (19°45' 21.59"N, -155°33' 7.79"W), which occupies sub-alpine tropical dryland between the volcanoes of Mauna Kea and Mauna Loa. Though Hawai'i is in the humid tropical Pacific, which generally experiences summer between May and October and winter between October and April, the majority of the installation is situated above the thermal inversion layer, and because of the orographic process, PTA is classified as a cool, tropical dry climate. During the study period (Sep 2016–Jan 2018), average daily temperature at PTA was 14°C and annual precipitation was about 80 mm. Land cover within PTA is a mix of native and non-native vegetation, barren lava, roads, and military facilities. Approximately 80% of PTA has poorly developed soils and the dominant substrate is lava rock. Because of low rainfall, there are no lakes, surface streams, or other major bodies of water on the installation. The United States military began training routinely at PTA in 1943. A patchwork of fenced conservation units now protects



approximately 15,092 ha of native habitat important to bats and other threatened and endangered species from habitat degradation due to military training and invasive species.

We established plots within a 794-ha fenced unit, Kīpuka Kālawamauna East (KKE), at elevation 1,675 m. Kīpuka Kālawamauna East is composed of 2 main vegetation types: a grassland-shrubland mix (i.e., grassland) dominated by approximately 80% invasive fountain grass (*Cenchrus setaceum*) upon rough a'ā lava flows and an open woodland dominated by native 'ōhi'a (*Metrosideros polymorpha*) upon smooth pāhoehoe lava flows. Kīpuka Kālawamauna East was fenced partially in 1998 and the rest was completed in 2010 to exclude non-native ungulates (primarily goats and sheep) and was ungulate-free during the study. Black rats, house mice, Argentine ants, ghost ants (*Tapinoma melanocephalum*), and yellowjacket wasps are all non-native invasive insectivores in woodlands and grasslands throughout the study area.

METHODS

Plot design and invasive insectivore suppression

Within the study area, we established 20 150-m × 150-m (2.25-ha) plots, in 4 geographically defined blocks of 5 plots each, to account for variation in habitat correlated with geographic proximity (Figure 1). Blocks 1 and 2 occurred within grasslands and blocks 3 and 4 occurred within woodlands. The 5 treatment plots included rodent reduction (RR), ant reduction (AR), yellowjacket reduction (YR), rodent + ant + yellowjacket reduction (AIIR), and the untreated control plots. Plots were spaced ≥200 m apart with a wider buffer of ≥400 m around YR and AIIR plots because those included treatments for volant invasives (Figure 1). We applied all 3 treatments to continuously suppress invasive insectivores in their respective plots for 1.5 years. We adjusted suppression efforts as needed to keep target invasive populations significantly lower than those of the untreated control plots. All plot treatments began in July 2016, 4 months before bat monitoring began.

We reduced mouse and rat populations in RR and AIIR plots with Victor kill-traps (Woodstream, Lititz, PA, USA), which were of 2 sizes to account for rat and mouse body size differences. We baited all traps with peanut butter and placed them inside boxes to reduce the chances of trapping non-target vertebrates such as birds (Pender et al. 2013). To account for daily movements of rodents (Shiels et al. 2017), we spaced mouse traps 12.5 m apart and rat traps 25 m apart in a grid across the 2.25-ha plot. There were 169 mouse traps and 49 rat traps in each of the RR and AIIR plots. We checked all snap-traps and re-baited them every 1–2 weeks.

We reduced ant populations throughout AR and AIIR plots approximately every 3–4 months by applying granular formicide bait (Maxforce Complete Granular Insect Bait, Bayer, Research Triangle Park, NC, USA; 1% hydramethylnon, Environmental Protection Agency regulation number 432-1255) at a rate of 3.78 kg/ha using whirlybird spreaders. We ensured even coverage by dividing the plots into 36 smaller squares (25 m by 25 m) and applying 105 g of bait to each square. We treated plots when monitoring results indicated that ant numbers had increased in our treated plots. Each AR and AIIR plot received treatments 6 times throughout our study: in late June 2016, mid-November 2016, early March 2017, late July 2017, late October 2017, and early January 2018. In blocks 1–3, the Argentine ant was the dominant ant species, whereas in block 4, the ghost ant was dominant.

We targeted yellowjackets with fipronil insecticide (activities approved under the Hawai'i Department of Agriculture Experimental Use Permit number EUP-16-01). We mixed fipronil with canned chicken at a rate of 0.1% bait and applied it twice each calendar year. We placed 9 fipronil-laced bait stations within a 50-m × 50-m square in the center of YR and AIIR plots, with the stations spaced 25 m apart. All stations had entry and exit holes to allow yellowjacket workers access (Hanna et al. 2012). We saturated paper wicks with the attractant heptyl butyrate and attached them to bait stations to serve as an additional attractant to yellowjackets, which carried bait back to the nest. Bait stations were set up in the morning and taken down in the afternoon to focus suppression when yellowjackets are active and to reduce effects to nontarget nocturnal insect prey. We monitored stations

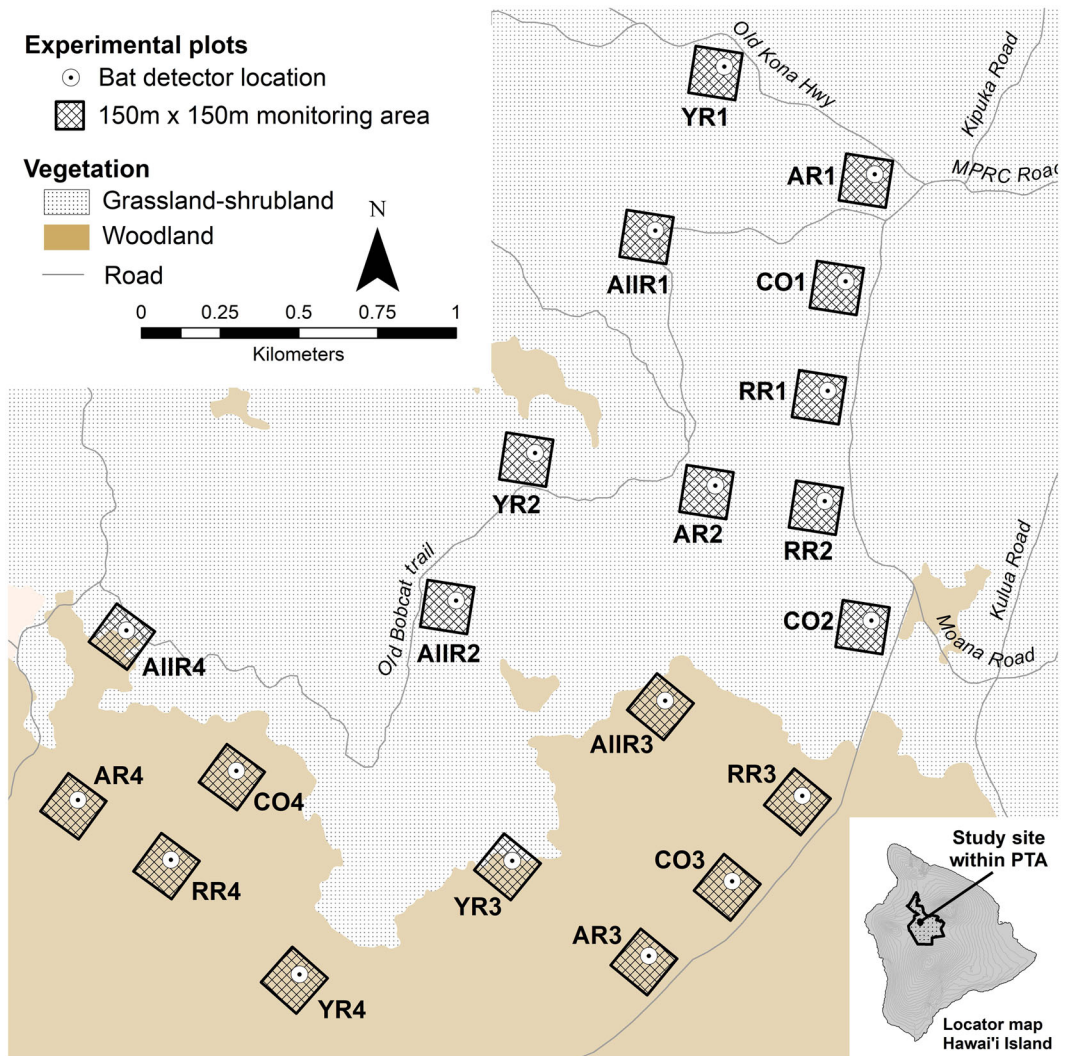


FIGURE 1 Study site containing 20 treatment and control plots and bat detectors at Pōhakuloa Training Area (PTA), Hawai'i, USA, November 2016–January 2018. Plots are labeled with treatment type followed by habitat block number (RR = rodent reduction, AR = ant reduction, YR = yellowjacket reduction, AIIR = rodent + ant + wasp reduction, and CO = untreated control). Plots labeled 1 and 2 are in grasslands and plots labeled 3 and 4 are in woodlands

throughout the day to assess bait consumption. The AIIR and YR plots in block 1 were only treated once for yellowjackets because monitoring indicated that yellowjackets remained nearly absent in that block throughout the study.

We monitored the relative abundance or activity of invasive insectivores before and after each treatment application in all plots, approximately quarterly throughout the study. Each plot contained 17 monitoring stations situated along transects radiating outward from the center of the plot and spaced at 25–35-m increments. During the treatment period, we expected plots receiving treatments would have fewer invasive insectivores than the control plots. We monitored rodent activity with inked tracking cards inside of plastic tracking tunnels (50 cm × 10 cm × 10 cm; Pender et al. 2013) at each of the monitoring stations. We placed peanut butter in the



center of inked cards and left them out for 4 days (3 nights) to collect footprints. Because rat and mouse footprints are easily distinguishable (Shiels et al. 2019), we identified and counted the tunnels with each rodent type upon retrieval. Tracking tunnels represent an index of the relative abundance of the rodent population (Shiels et al. 2019). We monitored ants using 7.6-cm × 6.4-cm index cards baited with a 40% tuna–60% corn syrup mixture using methods similar to those used by Krushelnysky et al. (2011). We set cards on the ground in the shade at each of the monitoring stations for 40 minutes, then we photographed and collected them. We initially identified foraging ants attracted to the cards in the field and later verified and counted them in the office from the photographs. We measured yellowjacket abundance with heptyl butyrate traps elevated 1.5 m above ground at each of the monitoring stations after 4 days (Foote et al. 2011). We counted individual yellowjackets in each trap on the fourth day.

Bat activity and weather data collection

In all 20 plots, we mounted automated acoustic detectors (Anabat Express, Titley Scientific, Brendale, Queensland, Australia) on poles 2 m tall. We secured poles with guy lines fastened to cinderblocks or shrubs. We placed each pole-mounted detector in the southwest corner 50 m from the center of the 150 × 150-m plot, and faced detectors northeast tilted upward at a 45-degree angle. Detectors were equipped with memory cards and powered by rechargeable batteries to record bat calls in all 20 plots between 1900 and 0500. This allowed us to record calls when bats are most active and to extend battery life to 14 nights. Because bat activity fluctuates seasonally, from November 2016–January 2018 we recorded bat activity at all plots for a minimum of 14 nights during each of the following sampling periods: September–December (mating and fledging), January–March (pre-pregnancy), April–mid June (pregnancy), Mid–June–August (lactation).

We recorded nightly precipitation (mm), average nightly wind speed (mph), and nightly temperature (°C) at a solar-powered weather station (Davis instruments and EME Systems, Berkeley, CA, USA) located approximately 5 km southwest of the study site. We obtained nightly measurements from values recorded every 30 minutes between 1900 and 0500. These weather covariates may affect bat foraging and prey availability, as moths and other flying insects may not be as available for bat consumption on particularly wet or windy nights (Belwood and Fullard 1984, Erickson and West 2002, Gorresen et al. 2015). Bonaccorso et al. (2016) reported that bat activity was negatively correlated with wind speed at high elevation caves in the Mauna Loa Forest Reserve on Hawai'i. Voigt et al. (2011) reported that bats may avoid rain because of increased metabolic costs in addition to sensory constraints posed by raindrops. We wanted to account for these possible influences on bat behavior in the analysis.

Acoustic sampling and call review

We used omni-directional microphones and recorded bat calls at a frequency division ratio of 8 and digital sensitivity of 115. These microphones record in a multi-directional fashion, but they are strongest in the direction they are pointed. Bats belonging to the *Lasiurus* genus have a call frequency ranging between 15 and 30 kHz but may also call at higher frequencies when foraging (Gorresen et al. 2017, Corcoran and Weller 2018). Bat calls are best detected on cool dry nights owing to the mechanisms of sound travel. While microphone detection distance is based on many variables including pulse frequency, intensity of the signal, temperature, and humidity, we expected microphones to detect calls from high flying bats in open areas at distances no greater than 100–150 m and spaced detectors accordingly.

We analyzed all calls using zero-crossings analysis and visually scanned each spectrogram in AnalookW (version 4.2n, Titley Electronics). We counted a file if it contained ≥2 echolocation pulses, to ensure standard vocalization parameters for true bat detection, and categorized files containing evidence of feeding behavior separately from general search or approach-phase calls. Although acoustic monitoring alone does not provide the number of



individuals detected in a night, distinguishing between call type can help identify how bats interact with the environment on a nightly basis and may indicate preference for a sampled area. To avoid falsely inflating bat detection events, we used an activity index based on the number of unique 1-minute intervals during the 10-hour night in which we recorded echolocations (Hayes 1997, Miller 2001). We refer to these intervals as bat call minutes and use this metric as count data to describe bat activity in each plot. Furthermore, we calculated the number of calls specific to feeding activity each night and refer to them as feeding buzzes. These terminal-phase calls are characterized by a rapid increase in the number of echolocation pulses, which indicate that a bat is targeting small flying prey (Griffin et al. 1960). Quantifying feeding buzzes offers insight into the foraging suitability of the study site. Because these feeding buzzes are typically recorded less frequently, and less reliably for this species, we used direct counts and did not index them for this study.

Analyses

We used a generalized linear model (GLM) to model expected mean nightly bat activity in count models under a negative binomial distribution with a log link function. We conducted all analyses using the statistical program R (R Core Team 2020). We used the `glm.nb` function in the MASS package (Venables and Ripley 2002) to model the number of bat call minutes and the number of feeding buzzes as response variables in models. Predictors were block (sampling blocks 1–4), invasive insectivore treatment, and season. We performed a deviance goodness-of-fit test using the `pchisq` function in program R, where the test statistic is chi-square distributed and where degrees of freedom are equal to the number of parameters subtracted from the number of data points. When using this function, a P -value < 0.05 suggests poor model fit. We calculated incident rate ratios for parameter estimates to estimate effect size.

We used the `emmeans` package (Lenth 2021) and `multcomp` package (Hothorn et al. 2008) to generate estimated marginal means and perform pairwise comparisons and *post hoc* Tukey tests for the levels of each predictor. After finding a strong block effect, indicating differences between woodlands and grasslands, we then separated the data and performed *t*-tests to compare the mean number of bat call minutes and the mean number of feeding buzzes in grasslands ($n = 10$, blocks 1 and 2) and woodlands ($n = 10$, blocks 3 and 4).

Because there was extensive spatial variability for most invasive insectivore abundances among plots before and after applying treatments, we correlated average insectivore abundance measurements with the average number of bat calls detected in a night rather than the number of bat call minutes. We did not use the number of bat call minutes as an index of activity in this case so we could better compare bat detections with the abundance of invasive insectivores and keep them on the same scale. We organized invasive insectivore monitoring by plot ($n = 20$), invasive species (mouse, rat, total rodent, ant, yellowjacket), and monitoring date (at least quarterly). When testing for correlations between bat calls and rodent abundance, we selected bat calls and rodent abundance data from 3-month periods around each monitoring event, whereas for correlations between bat calls and invasive insect abundance, we used monthly averages of bat calls, ant, and yellowjacket counts. We chose different time periods to better reflect maturity for invasive insectivores (i.e., 2–3 months for rodents and < 1 month for ants and yellowjackets). We sampled rats and mice only in RR, AIIR, and control plots, so we assumed (on a block-specific basis) the same rodent abundances in the AR and YR plots as in the control plot. Because we anticipated a difference in bat and rodent activity between vegetation types, we conducted additional correlations by separating grassland plots from woodland plots.

Although we account for differences in bat activity throughout the reproductive periods in our described models, we also separately modeled nightly weather variables as predictors on a finer scale for bat activity. We performed a multiple linear regression analysis to evaluate associations between our response variable for bat activity (bat call minutes) and the predictor variables ambient temperature, wind speed, and rainfall. We chose these predictor variables because of their likelihood to influence the availability of aerial insect prey and potential to



impede bat flight during particularly windy or rainy nights. We did not include weather variables as predictors in the general bat activity models to avoid overparameterizing those models.

RESULTS

We successfully reduced the invasive insectivores through our treatment methodology. Aside from the YR plots, we were able to reduce each invasive insectivore in respective treatment plots (i.e., AR, RR, and AllR) by approximately 2-fold relative to untreated control plots (Table 1). Suppression was most pronounced in the rodent and ant reduction plots. We reduced tracking tunnel percentages (which is an indication of population abundance) by approximately 10-fold for rats and nearly 2-fold for mice relative to untreated control plots (Table 1).

We surveyed bats during 4,183 detector nights and recorded 8,341 acoustic detections, which account for 7,720 distinct bat call minutes. The negative binomial GLM revealed significant relationships with bat call minutes (Table 2) and the 3 predictor variables (block, treatment, season). The best model was minutes~block + treatment + season and the deviance goodness-of-fit test indicated adequate fit to the data ($P = 1.0$). The interaction model (minutes~block $\times$ treatment $\times$ season) was also significant but with 80 parameters it was overparameterized and difficult to interpret the effects properly. Instead, we used the additive model and performed pairwise contrasts for each predictor independently. Pairwise contrasts and Tukey tests indicated that block 4 had the highest estimated marginal mean number of bat calls followed by block 3, and blocks 1 and 2 had lower means that did not differ ($P = 0.211$; Figure 2). Plots receiving all treatments (i.e., AllR) had the lowest estimated marginal mean, whereas the remaining treatments had significantly higher means that did not differ from each other (Figure 3). Finally, estimated marginal means of bat call minutes were lowest during lactation, followed by pregnancy. The highest means occurred during mating and pre-pregnancy, which did not differ (Figure 4).

Of the 8,341 distinct calls recorded, about 6% ($n = 512$) were feeding buzzes. When we analyzed feeding buzzes, the best approximating model was feeding buzz~block + treatment + season and the deviance goodness-of-fit test indicated adequate fit to the data ($P = 1.0$). Block and season were significant predictors of feeding activity, whereas treatment was not (Table 3). Pairwise contrasts and Tukey tests indicated that the mean number of feeding buzzes was significantly higher in the woodland (blocks 3 and 4) than the grassland (blocks 1 and 2) plots (Figure 5A). Pairwise contrasts and Tukey tests also indicated that feeding activity was highest during mating and

TABLE 1 Summary of invasive insectivore abundances (mean $\pm$ SE) during Hawaiian hoary bat activity sampling September 2016–January 2018 in the 5 treatments ($n = 4$ plots per treatment). We estimated rodent abundance using tracking tunnels (% of 17 tunnels per plot with tracks), and estimated ants and yellowjackets using counts (on baited cards for ants, and live traps for yellowjackets; 17 per plot). We assumed rodent tracking was equivalent in ant, yellowjacket, and untreated control plots. We collected data on Hawai‘i Island, USA, at Pōhakuloa Training Area

Treatment	% rat tracking		% mouse tracking		% rodent tracking		Ant abundance		Yellowjacket abundance	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Rodent	3.55	1.08	40.35	6.51	43.31	6.43	36.31	12.13	3.42	1.77
Ant	35.01	7.59	75.00	7.97	93.45	6.26	14.44	7.42	4.73	2.88
Yellowjacket	35.01	7.59	75.00	7.97	93.45	6.26	40.43	9.99	3.51	2.01
All treatments	2.26	1.63	41.99	6.25	44.02	5.90	8.84	4.54	3.70	2.41
Control	35.01	7.59	75.00	7.97	93.45	6.26	29.90	13.73	6.42	3.01



TABLE 2 The model parameters (estimate), standard error (SE), Z value, and lower (LCI) and upper (UCI) 95% confidence intervals from the top-ranked model for the negative binomial regression analyses on Hawaiian hoary bat call minutes by sampling block, invasive insectivore treatment, and reproductive season. Block 1, the combined ant + wasp + rodent treatment (AIIR), and lactation served as the statistical baselines for each of the 3 categorical variables and are represented by the model intercept. Pr(>|Z|) represents the likelihood of obtaining a result as extreme, or more extreme than observed, under the null hypothesis. We calculated incident rate ratios (IRR) to determine effect size. We collected data on Hawai'i Island, USA, at Pōhakuloa Training Area, November 2017–January 2018

	Estimate	SE	Z	Pr(> Z)	LCI	UCI	IRR
(Intercept)	−0.925	0.113	−8.210	≤0.001	−1.146	−0.701	
Block 2	−0.144	0.085	−1.699	0.063	−0.315	0.029	0.866
Block 3	0.592	0.077	7.687	≤0.001	0.441	0.744	1.808
Block 4	1.131	0.082	13.823	≤0.001	0.960	1.304	3.100
Ant treatment	0.453	0.092	4.919	≤0.001	0.271	0.636	1.574
Control	0.360	0.094	3.826	≤0.001	0.173	0.548	1.433
Rodent treatment	0.279	0.094	2.982	0.003	0.095	0.463	1.322
Yellowjacket treatment	0.284	0.092	3.100	0.002	0.103	0.465	1.328
Mating	0.956	0.093	10.246	≤0.001	0.762	1.149	2.601
Pre-Pregnancy	0.953	0.098	9.744	≤0.001	0.758	1.147	2.593
Pregnancy	0.672	0.103	6.541	≤0.001	0.470	0.874	1.959

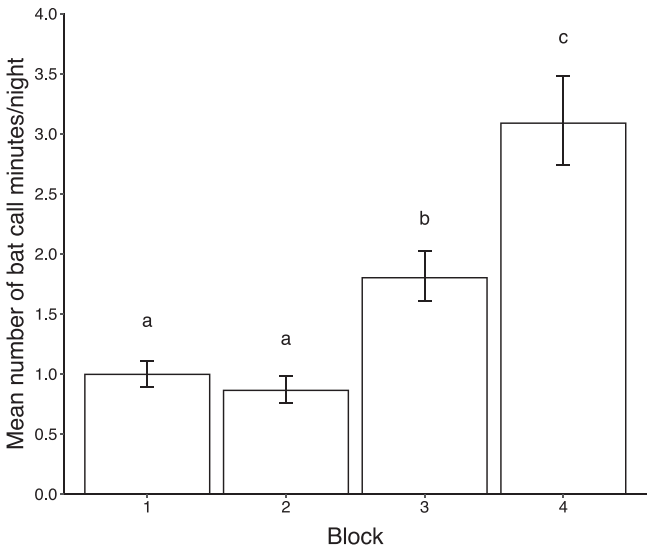


FIGURE 2 Mean number of minutes in a night containing Hawaiian hoary bat echolocations in all 4 blocks at Pōhakuloa Training Area, Hawai'i, USA, November 2016–January 2018. Blocks 1 and 2 are in grasslands and blocks 3 and 4 are in woodlands. Estimated marginal means and 95% confidence intervals are based on a negative binomial generalized linear regression model and are back-transformed from the log scale to the response scale. We computed pairwise comparisons between the levels of block and *post hoc* Tukey adjusted *P*-values on the log scale with a family-wise error rate of 0.95. Letters in common are not significantly different

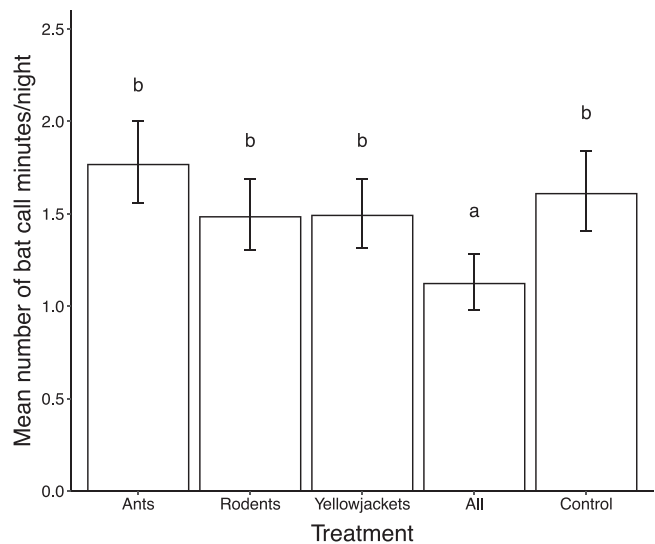


FIGURE 3 Mean number of minutes in a night containing Hawaiian hoary bat echolocations in all 5 treatment types at Pōhakuloa Training Area, Hawai‘i, USA, November 2016–January 2018. Estimated marginal means and 95% confidence intervals are based on a negative binomial generalized linear regression model and are back-transformed from the log scale to the response scale. We computed pairwise comparisons between the levels of treatment and *post hoc* Tukey adjusted *P*-values on the log scale with a family-wise error rate of 0.95. Letters in common are not significantly different. The all treatment represents ant + rodent + yellowjacket reduction

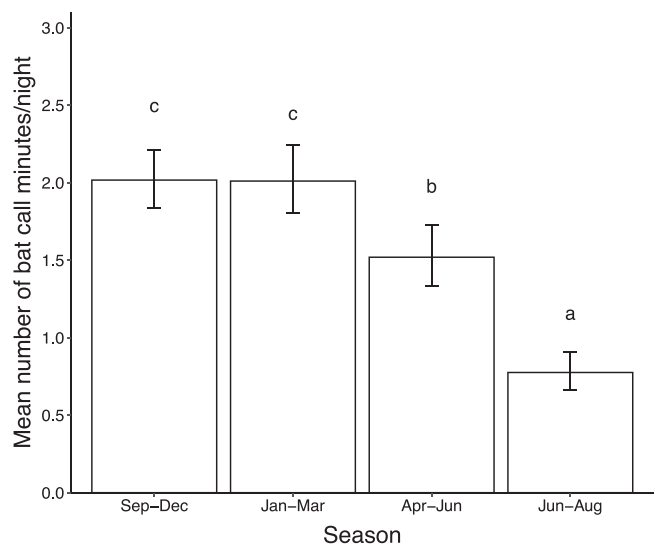


FIGURE 4 Mean number of minutes in a night containing Hawaiian hoary bat echolocations during all 4 reproductive seasons (Sep–Dec = mating and fledging, Jan–Mar = pre-pregnancy, Apr–Jun = pregnancy, and Jun–Aug = lactation) at Pōhakuloa Training Area, Hawai‘i, USA, November 2016–January 2018. Estimated marginal means are based on a negative binomial generalized linear regression model and are back-transformed from the log scale to the response scale. We computed pairwise comparisons between the levels of season and *post hoc* Tukey adjusted *P*-values on the log scale with a family-wise error rate of 0.95. Letters in common are not significantly different



TABLE 3 The model parameters (estimate), standard error (SE), Z value, and lower (LCI) and upper (UCI) 95% confidence intervals from the top-ranked model for the negative binomial regression analyses on Hawaiian hoary bat feeding buzzes by sampling block, invasive insectivore treatment, and reproductive season. $\Pr(>|Z|)$ represents the likelihood of obtaining a result as extreme, or more extreme than observed, under the null hypothesis. We calculated incident rate ratios (IRR) to determine effect size. Block 1, the combined ant + wasp + rodent treatment (AllIR), and lactation served as the statistical baselines for each of the 3 categorical variables and are represented by the model intercept. We collected data on Hawai'i Island, USA, at Pōhakuola Training Area, November 2017–January 2018

	Estimate	SE	Z	$\Pr(> Z)$	LCI	UCI	IRR
(Intercept)	-3.217	0.266	-12.100	≤ 0.001	-3.752	-2.696	
Block 2	-0.758	0.230	-3.289	0.003	-1.233	-0.300	0.469
Block 3	0.717	0.166	4.312	≤ 0.001	0.398	1.038	2.048
Block 4	0.765	0.184	4.160	≤ 0.001	0.376	1.160	2.149
Ant treatment	0.508	0.211	2.406	0.082	0.091	0.930	1.663
Control	0.268	0.221	1.217	0.510	-0.167	0.705	1.308
Rodent treatment	0.320	0.218	1.471	0.301	-0.107	0.750	1.377
Yellowjacket treatment	0.362	0.211	1.715	0.453	-0.057	0.785	1.437
Mating	1.036	0.210	4.941	≤ 0.001	0.606	1.476	2.818
Pre-pregnancy	0.064	0.232	0.274	0.456	-0.395	0.527	1.066
Pregnancy	-0.476	0.268	-1.776	0.246	-1.004	0.045	0.621

means were lower during all other reproductive periods and not significantly different from each other (Figure 5B). The mean number of feeding buzzes did not differ across all treatments (Table 3).

We used an independent samples *t*-test to compare the number of bat call minutes and feeding buzzes in woodland and grassland plots. The mean number of nightly bat call minutes was higher (2.3 times) in the wooded plots ($\bar{x} = 2.71$, $SD = 5.36$) than in the grassland plots ($\bar{x} = 1.13$, $SD = 2.66$); $t_{2,728.3} = 11.96$, $P < 0.001$). The mean number of feeding buzzes was also higher (2.5 times) in the wooded plots ($\bar{x} = 0.18$, $SD = 0.63$) than in the grassland plots ($\bar{x} = 0.08$, $SD = 0.56$; $t_{3,883.3} = 5.35$, $P < 0.001$). Of the 7,720 bat call minutes recorded across all plots, 68% ($n = 5,232$) were in the woodland plots and 32% ($n = 2,488$) were in the grassland plots. Of the 512 feeding buzzes recorded, 66% ($n = 340$) were in woodland plots and 34% ($n = 172$) were in grassland plots.

Results of the Pearson correlation indicated that there was no association between the monthly mean number of bat calls and ant ($P = 0.157$) or wasp ($P = 0.531$) abundance. The percentage of tracking tunnels with detections showed rodent abundance was not significantly correlated with the average of bat calls ($t_{109} = -0.74$; $P = 0.463$; $R = -0.07$). Rats were positively correlated with mean nightly bat calls ($t_{109} = 2.262$; $P = 0.026$; $R = 0.21$), and mice were negatively correlated with mean nightly bat calls ($t_{109} = -3.588$; $P < 0.001$; $R = -0.33$). We further separated data by vegetation type and bat activity within grassland plots was positively correlated with the abundance of rats ($t_{51} = 5.17$, $P < 0.001$, $R = 0.59$) and negatively correlated with the abundance of mice ($t_{51} = -3.46$, $P = 0.001$, $R = -0.44$). There were no significant correlations between activity and invasive insectivore abundances within woodland plots.

A multiple linear regression model showed that the mean number of bat call minutes was correlated with temperature, wind speed, and rainfall, but these predictors only accounted for $< 0.5\%$ of the variability ($F_{3, 4,179} = 6.81$, $P < 0.001$, $R^2 = 0.001$). Rain, the most significant weather predictor, was negatively correlated with bat activity ($\beta = -0.209$, $t = -3.833$, $P < 0.001$, $R^2 = 0.003$) and ranged from 0–17.60 mm. Wind was also negatively correlated with bat activity ($\beta = -0.097$, $t = -2.082$, $P = 0.037$, $R^2 = 0.001$) and ranged 0–12.49 km/hr, but little

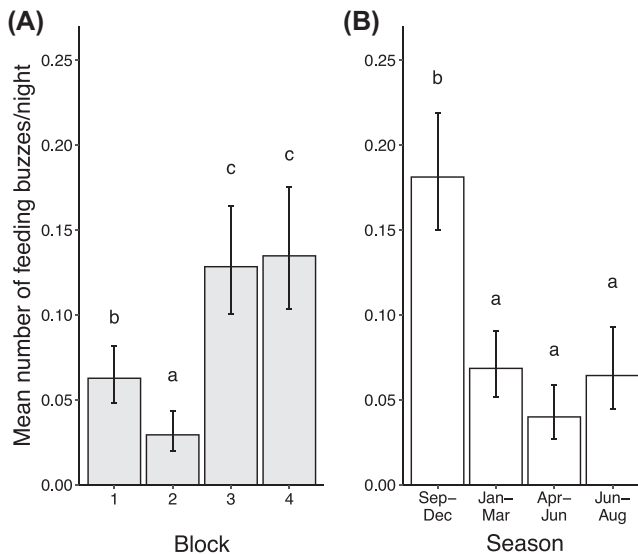


FIGURE 5 Mean number of recorded Hawaiian hoary bat feeding buzzes per night in all 4 habitat blocks (A) and during all 4 reproductive seasons (B; Sep–Dec = mating and fledging, Jan–Mar = pre-pregnancy, Apr–Jun = pregnancy, and Jun–Aug = lactation) at Pōhakuloa Training Area, Hawai‘i, USA, November 2016–January 2018. Estimated marginal means and 95% confidence intervals are based on a negative binomial generalized linear regression model and are back-transformed from the log scale to the response scale. We computed pairwise comparisons between the levels of both factors and *post hoc* Tukey adjusted *P*-values on the log scale with a family-wise error rate of 0.95. Letters in common are not significantly different. Blocks 1 and 2 are in grasslands and blocks 3 and 4 are in woodlands

variation was explained by these predictors combined. Bat activity was not significantly correlated with temperature ($\beta = -0.047$, $t = -1.768$, $P = 0.077$, $R^2 = 0.001$), which ranged from 5.38–19.35°C.

DISCUSSION

Although the abundance of invasive insectivores varied considerably among our plots because of our suppression efforts and preexisting heterogeneity, bats were consistently present in all treatment and control plots and foraged in grasslands and woodlands throughout the year. Although our 2.25-ha plots were large enough to demonstrate the negative effects of the invasive insectivores on insect pollination and visitation to flowering plants (Liang et al. 2021), acoustic bat activity did not differ between control and treatment plots. Vegetation type appeared to be more important than the abundance of invasive competitors in explaining variation in bat activity, with woodland plots having 2.4 times the amount of activity as grassland plots. Contrary to our expectations, there was no strong seasonal peak in bat activity when adults mate and young fledge within our plots, and the lowest bat activity in our study occurred during the summer months when females typically lactate.

The importance of woodlands for bats has been repeatedly highlighted in studies in agricultural, urban, and tropical rainforest settings (Lumsden and Bennett 2005, Fischer et al. 2010, Heim et al. 2015, Treitler et al. 2016). These studies of insectivorous bats have demonstrated that proximity to woodlands, even small patches of trees, results in greater bat activity (Heim et al. 2015, Treitler et al. 2016). As hypothesized, this pattern was also evident in our study as woodlands had more bat call minutes and feeding buzzes than nearby grasslands. Previous habitat preference and insect availability studies have not explicitly compared prey suitability and availability between



woodlands and grasslands on Hawai'i Island (Todd 2012) or Maui (Todd et al. 2016, Pinzari et al. 2019) but instead emphasize the plasticity of prey selection and strategy based on the individual and available prey taxa. Lactating females and juveniles often select prey that are less able to avoid capture, which enhances their foraging efficiency (Anthony and Kunz 1977, Belwood and Fullard 1984, Valdez and Cryan 2009). In such cases, the size of the prey available in the habitat would be more relevant than the vegetation type with regard to foraging efficiency.

The woodland areas may be a reservoir for insect prey relative to the grasslands (Grindal and Brigham 1998). This may indicate bat preference for potential prey type or size in this particular woodland or an otherwise attractive habitat for foraging, though we could not test this hypothesis. It is also possible that the grassland in this study contained less beneficial prey than a grassland that does not exclude ungulates as suggested by Todd et al. (2016). Dung beetles and flies are associated with cattle dung, and Todd (2012) reported both prey types in fecal pellets of bats captured near cattle ranches on Hawai'i Island. Montoya-Aiona et al. (2020) reported that although insects responded to grazed areas in some instances, there was no evidence that hoary bat foraging activity was higher in grazed than ungrazed areas. The elevated bat activity in the woodland plots may also be due to the prevalence of 'ōhi'a, one of the few tree species that provide sufficient roosting habitat for Hawaiian hoary bats in the study area. Proximity to such roost trees would likely increase echolocation as individuals navigate to and from their roost. Similarly, to facilitate navigation and avoid colliding with obstacles, bats may echolocate more often in the taller and slightly denser vegetation of the woodland than in open grasslands (Jacobs 1999). But the requirement for more echolocation could not solely explain the greater bat activity because feeding buzzes were also significantly greater in the woodland than in the grassland, which indicates higher foraging activity there. Notably, the 'ōhi'a in the open woodland in this study have lower tree density and minimal ground cover relative to most mesic and wet forests in Hawai'i; therefore, we cannot assume that bat activity levels would be similarly high to those in denser forest patches even if 'ōhi'a trees are dominant.

Based on activity and abundance measures, bats and rats, but not mice, appear to be most active and abundant in the woodland plots. Bat and rat abundances were positively correlated within the grassland plots, despite mice being numerically dominant over rats and negatively correlated with bats. This suggests that bats and rats may have been attracted to microhabitats within the grasslands where fewer mice were present. The presence of trees and shrubs are important habitat features for black rats, just as grass cover is for house mice (Shiels et al. 2017). These general habitat features likely contributed to the variation in bat and rodent activity that we observed in the 2 vegetation types. Thus, important microhabitats could have been, for example, areas with more woody plants or other features that both rats and bats prefer. In that case, shared habitat preferences, rather than direct interspecific interactions, would be responsible for the positive association observed between rat abundance and bat activity. We did not collect vegetation data at a fine enough scale to evaluate microhabitat relationships for either species. Habitat preference may also explain the negative correlation between mouse abundance and bat activity. Bats did not forage more in rodent-suppressed plots, which indicates that habitat preference rather than prey competition may be a more likely explanation for the negative correlation between bats and mice in the grassland.

In contrast to our hypothesis, there were not strong patterns related to bat activity or foraging in plots where we suppressed invasive insectivores. We expected higher bat foraging in the treatment plots based on potential dietary overlap and the possibility of resource competition between the insectivores we studied. We saw an effect opposite to our expectations within the ant + wasp + rodent-suppressed (AIIR) plots, as activity was lower relative to all other treatments. Because we deployed fipronil to target yellowjackets for limited periods during the day it is unlikely that we affected non-target nocturnal aerial insect prey, and although Maxforce was potentially available to some insect larvae any effects to adult insect prey availability in suppressed plots is likely to be minor. A possible explanation for this difference is that the AIIR treatment plots were the most frequently visited by the field staff of all 20 plots, and the direct or indirect effects of increased physical disturbance from trampling in these treatment plots may have deterred bats to some extent. The magnitude of this difference in bat activity between AIIR plots and the average of the other treatment plots was quite low, equating to approximately 0.47 bat call minutes/night (i.e., 1.12 vs. 1.58 bat call min/night, respectively). Therefore, although this result was statistically significant, it is unlikely to be biologically significant.



The lack of an expected effect on bat activity within the invasive insectivore treatment plots may result from the difference in prey species or life stages (i.e., flying adults vs. non-flying larvae or adults) targeted by each insectivore. This may explain the apparent lack of prey competition between bats and the invasive insectivores. For example, rats, mice, yellowjackets, and ants generally consume larval stages of insects like moths (Lepidoptera) and beetles (Coleoptera) on the ground or vegetation (Cole et al. 1992, Gambino 1992, Wilson et al. 2009, Shiels et al. 2013), whereas hoary bats consume the adult forms of these aerial insects in flight (Todd 2012, Gorresen et al. 2018, Pinzari et al. 2019). Additionally, because no other bat species are present in Hawai'i, hoary bats experience little competition for nocturnal aerial insects, and they are opportunistic insectivores with flexible diets. Although we successfully suppressed invasive insectivores, we did not sample the insect community available during the study period and did not study the diets of the insectivores. The area may not have been particularly productive in prey for bats before the study, such that removing the invasive insectivores failed to cause a substantial change in the prey base available for bats. Knowledge of the baseline insect community, particularly nocturnal species, would help to evaluate the apparent absence of dietary competition that we uncovered.

The scale of the treatment plots and monitoring areas may have also influenced our conclusion that insectivore suppression treatments were largely ineffective at altering hoary bat activity. The effect of microhabitat changes on Hawaiian hoary bats is poorly understood, which led us to investigate these small-scale changes to determine whether any effect was apparent. Differences in bat activity among invasive insectivore treatments may not have been as strong as if we had increased spatial sampling to better match the nightly foraging area of hoary bats. Bat foraging areas can be quite large, and Hawaiian hoary bats have been documented using nightly foraging ranges on Hawai'i Island of 230.7 ± 72.3 ha, and 11% (25.5 ± 6.9 ha) of that as a core use area (Bonaccorso et al. 2015). Suppressing invasive insectivores on the scale of hoary bat foraging range or core use areas was not possible with our available resources for this study. Thus, the scale at which hoary bats forage and detect prey likely affected our results. While we were able to detect differences in bat activity between the 2 vegetation types, each of which spanned a much larger contiguous area, the 2.25-ha patches in which the insectivore treatments were applied may not have been large enough to influence bat foraging behavior.

Bat activity in our study differed significantly across reproductive periods, although the magnitude of change was small across periods, and the peak season was unlike previous multi-year studies on Hawai'i Island (Menard 2001, Gorresen et al. 2013, Montoya-Aiona et al. 2020) and at PTA specifically (R. D. Moseley, unpublished data). These researchers reported that hoary bats were most active during the late summer and early fall and least active during winter. Although we expected activity to be highest around September–December (mating and fledging) relative to other months, we did not expect activity levels to be similarly elevated in January–March (pre-pregnancy) during our study. Similarly, the lower level of activity during lactation (Jun–Aug) was an unexpected result given that it represents one of the most energetically costly reproductive periods for females. The lower activity during lactation may suggest that there were more non-lactating bats (i.e., males or juveniles of either sex) than lactating females foraging in our study area. The mean number of feeding buzzes was highest during mating but did not vary throughout the remaining reproductive periods, which further suggests lactating females may have been rare in our study site. Lactating females may forage closer to roosting sites to reduce the energetic costs of foraging and nursing at night. Henry et al. (2002) reported that home range decreased 50% for lactating female little brown bats (*Myotis lucifugus*) between pregnancy and lactation and that lactating bats returned 1–2 times/night to nurse pups.

The weather variables were not good predictors for explaining bat activity and foraging, and these variables did not provide clarity on seasonal patterns. Bat behavior in response to seasonal changes in energetic costs may have been more represented in the prior occupancy and activity study at PTA (R. D. Moseley, unpublished report) because it was a longer study and sampled more vegetation types than we did in our study. That 3-year study began in 2014 and revealed that bat activity levels followed consistent seasonal reproductive patterns as described by Menard (2001) when sampled at multiple sites across PTA. Inter-annual variability in bat activity in the same study



area is common with acoustic surveys of hoary bats (Rodhouse et al. 2012, Gorresen et al. 2013, Pinzari et al. 2019) and the comparatively short study period (14 months) may reflect an overall departure in the expected bat activity patterns from subsequent years in the study area, specifically.

The overall lower number of feeding buzzes relative to search-phase calls is a common result in many acoustic surveys of bats (Rodhouse et al. 2012, Bonaccorso et al. 2016, Pinzari et al. 2019, R. D. Moseley, unpublished report). Prey type can also influence bat foraging strategy (Fenton and Fullard 1979, Fullard 2001, Corcoran and Weller 2018). Researchers of hoary bats report that they may produce softer and more directional calls or not call at all while foraging to optimize the capture of moths (Gorresen et al. 2017, Corcoran and Weller 2018). Because Hawaiian hoary bats do not forage in high densities and individuals rarely overlap foraging and core use areas (Bonaccorso et al. 2015), detecting habitat preference based on the behavior of relatively few bats is challenging. The tendency of acoustic studies to under-sample insectivorous bats may produce misleading conclusions about how the species uses a given habitat if there is too much emphasis on the number of feeding buzzes recorded. For this reason, we do not rely solely on the feeding buzzes as indicators of activity and habitat preference. Our sampling methodology across all 20 plots is sufficiently robust to evaluate differences in general bat activity even if microphones failed to detect all occurrences of foraging.

MANAGEMENT IMPLICATIONS

The Hawaiian hoary bat frequents both vegetation types studied in this high-elevation dryland ecosystem, and it is found year-round, even when populations of sympatric insectivores fluctuate. Bats frequented and fed in woodlands twice as much as in grasslands and management actions that retain woodlands should be prioritized to maintain potential roost sites and quality foraging habitat. Because of the cryptic nature of this species, detection can be challenging. Landowners and managers in Hawai'i are often interested in whether bats are present on their lands or nearby, and our findings suggest that the greatest likelihood of acoustic bat detection will occur in woodlands in September–March, when bat calls were most numerous. Hawaiian hoary bat activity may decrease slightly when the invasive insectivores (ants, yellowjackets, and rodents) are simultaneously suppressed in small-scale patches. Because the magnitude of simultaneously suppressing these invasive insectivores on bat activity was so small, and the local and global impacts of these invasive insectivores are so harmful for native species, managers should continue to individually suppress or eradicate invasive rodents, ants, and yellowjackets where they are problematic. Managers can further expect that such conservation actions on small scales (i.e., 4 ha plots) are unlikely to substantially affect hoary bat activity.

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CONFLICT OF INTERESTS

The authors have no conflicts of interest to report.



ETHICS STATEMENT

All activities involving vertebrates were approved under the United States Department of Agriculture (USDA) National Wildlife Research Center's (NWRC) Institutional Animal Care and Use Committee study protocol QA-2452.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in figshare at <https://doi.org/10.6084/m9.figshare.15088248> and <https://doi.org/10.6084/m9.figshare.16828567>.

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