Roosting Ecology and Behavior of the Solitary and Foliage-roosting

Hawaiian Hoary Bat (*Lasiurus cinereus semotus*)

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ABSTRACT

The Hawaiian hoary bat (*Lasiurus cinereus semotus*) is a Federally and State of Hawaiʻi listed endangered species and is the only extant, native, terrestrial mammal in the Hawaiian archipelago. With increasing threats, especially from wind energy expansion and potential habitat loss in Hawaiʻi, it is critical to gain a more complete understanding of the life history and ecology of this elusive species in order to better inform conservation and management decisions. This study was motivated by the lack of published data examining the diurnal roost characteristics and roosting behavior of this species.

Hawaiian hoary bats were captured, radio-tagged and tracked to diurnal roosting locations on the east side of Hawaiʻi Island from May 2018 to December 2019. A total of 38 bats were tracked to 52 roost stands and 18 of those bats were located in 24 roost trees. Bats were confirmed at 15 perches within the 24 roost trees. Bats used diurnal roosts in a variety of tree species and in an assortment of habitat stand types including native and non-native habitats. Statistically significant differences were found in both height and diameter at breast height (DBH) between roost trees and randomly sampled trees. Specifically, roost trees were generally larger in both height and DBH than random trees and female bats selected roost trees that were larger in height and with a greater percent canopy cover compared to roost trees selected by male bats. Although data were collected at three maternity roost trees, samples sizes were too small to statistically compare maternity roost tree characteristics versus solitary roost trees or random trees.

Diurnal roost video-monitoring was conducted at two separate sites in Hilo, Hawaiʻi during the 2017 and 2018 reproductive seasons. A total of 114 hours, 50 minutes and 21 seconds (114:50:21) of video imagery was observed and analyzed. Observations of solitary bats accounted for a total of 86:38:17 video-hours while maternity roost observations accounted for a total of 28:12:08 video-hours. While no maternity roosts were observed during 2017, one maternity roost was located and monitored during 2018. An ethogram of behavior at diurnal roosts was created from observations and represents the first detailed description of the behavior of *L. c. semotus* at diurnal roosts.

CHAPTER 1. GENERAL INTRODUCTION

BACKGROUND

The Hawaiian hoary bat (*Lasiurus cinereus semotus*; Chiroptera: Vespertilionidae), known locally as 'ōpe'ape'a is the only extant, native, terrestrial mammal in the Hawaiian archipelago. The name 'ōpe'ape'a references the wing shape of the Hawaiian hoary bat, said to resemble a half-leaf remaining on a taro stalk after the top half is removed for cooking (Pukui and Elbert 1986). The Hawaiian hoary bat has historically been listed as a subspecies of the North American hoary bat (*Lasiurus cinereus cinereus*), however current genetic research recommends elevating it to full species status (Russell *et al*. 2015, Baird *et al*. 2015, 2017). It has been listed as endangered under both the Federal Endangered Species Act and Hawai'i Endangered Species Laws since 1970, and the U.S. Fish and Wildlife Service (USFWS) published a recovery plan for it in 1998 that outlines potential limiting factors, recovery objectives and recovery criteria (USFWS 1998). In 2015, the Hawaiian hoary bat was designated as the Official State Land Mammal of Hawai'i.

Hawaiian hoary bat presence has been documented on all of the main Hawaiian Islands including Hawai'i, Kaua'i, Maui, Moloka'i and O'ahu (Tomich 1986). Genetic studies have produced differing conclusions on the timing of the colonization of the Hawaiian archipelago by North American hoary bat populations of *Lasiurus cinereus cinereus* suggesting their first arrival anywhere from 10,000 to 1.35 million years ago (Russell *et al*. 2015, Baird *et al*. 2015, 2017). Phenotypic divergence from *L. c. cinereus* by the Hawaiian hoary bat resulted in approximately 45% reduction in body mass and 8% reduction in forearm length (Jacobs 1996). Adult Hawaiian hoary bats are small, ranging in size from approximately 12-24 grams. They exhibit reverse body size sexual dimorphism with females slightly larger than males (Jacobs 1996). Their bodies are covered in thick fur including the uropatagium or interfemoral membrane. Their fur is typically a mixture of reddish browns and grays, sometimes tinged to various extents with silvery-white fur producing the frosted or "hoary" effect (see example in Figure 1.1). Hawaiian hoary bats are insectivorous with their diets mainly comprised of moths (Lepidoptera) but also including beetles (Coleoptera), mosquitoes (Diptera), termites (Blattodea) and other nocturnal aerial insects. This has been determined by visual inspection of insect fragments with microscopy in studies by Todd (2012) and Bernard and Mautz (2016), and more recently through metabarcoding guano pellets

demonstrated by Pinzari *et al*. (2019). They are also solitary and foliage-roosting while utilizing a wide range of habitat types from sea level to at least 3,600 m above sea level as documented on Hawai'i Island (Bonaccorso *et al*. 2015, 2016). Acoustic detection studies have demonstrated seasonal patterns of habitat occupancy and acoustic detection on Hawai'i Island with increased activity in the uplands (>1,000 m above sea-level [asl]) during the non-reproductive season (November to April), followed by increased activity in the lowlands (<1,000 m asl) during the reproductive season (Gorresen *et al*. 2013, Bonaccorso *et al*. 2016). These seasonal patterns may reflect Hawaiian hoary bat foraging resources available in more tolerable climatic conditions above the cloud inversion layer common during the winter months of the non-reproductive season, and then warmer, drier conditions favorable for pupping in the lowlands during the reproductive season (Bonaccorso *et al*. 2016). Females typically give birth to twin pups during the reproductive season which consists of a pregnancy period from April to June, lactation from June to August, post-lactation and fledging from August to November, with pups usually fully fledged and independent of their mother by November. While the timings of these seasons likely overlap and may be variable year-to-year as well as among individuals, these general patterns have been demonstrated by capture records (U.S. Geological Survey, unpublished data) as well as previous research by Tomich (1986), Kepler and Scott (1990), Jacobs (1994), and Menard (2001).

Previous studies have investigated Hawaiian hoary bat diet and food habits (Whitaker and Tomich 1983, Jacobs 1999, Pinzari *et al*. 2019), prey abundance and seasonal distribution (Jacobs 1994, Todd 2012, Montoya-Aiona *et al*. 2019, 2020), foraging and home range movements (Bonaccorso *et al*. 2015), and occupancy (Gorresen *et al*. 2008, 2013, 2018, Pinzari *et al*. 2014). However, there are still many areas of research lacking critical information on the species. The recovery plan for the Hawaiian hoary bat established by the USFWS cites a lack of information, particularly on distribution, abundance, habitat needs, limiting factors, ecology and life history that are necessary to assess its status and inform conservation and recovery efforts (USFWS 1998). Moreover, noted threats include collisions with wind turbines (Gorresen *et al*. 2015), habitat loss including roosting habitat, roost disturbance, pesticides and predation (USFWS 1998, Mitchel *et al*. 2005).

With increasing threats, especially from wind energy expansion and potential habitat loss in Hawai'i, it is critical to gain a more complete understanding of the life history and ecology of

this elusive species in order to better inform conservation and management decisions. Currently, there are no published studies directly examining the diurnal roost characteristics or roosting behavior of *L. c. semotus*, compelling the directed research reported in this thesis to examine these issues.

Figure 1.1 Examples of two distinct color morphologies of the Hawaiian hoary bat (*L. c. semotus*). Photo (left) is a dorsal view of an individual with reddish-brown fur and no hoary coloration. Photo (right) is a dorsal view of an individual with hoary coloration on its back and with reddish-brown fur on its uropatagium. Note: these individuals were captured on the same night at the same general netting location.

THESIS OBJECTIVES

This thesis focuses on the roost selection, roosting ecology and roosting behavior of the Hawaiian hoary bat on the east side of Hawaiʻi Island. This information can be used to inform development and selection of mitigation areas and to examine the potential effects of land-clearing or tree-harvesting on bat populations. In addition, this study may provide guidance on key plant species for propagation to benefit bats in restoration or mitigation areas, and the potential effects of roost disturbance and pup-survivorship. The primary objectives were to identify and characterize Hawaiian hoary bat roost locations, habitat and tree attributes, and to identify, describe and characterize behavior of mothers with pups as well as solitary bats particularly during the critical reproductive season.

This thesis has two chapters in which different aspects of the roosting ecology of the Hawaiian hoary bat are examined. Chapter 2 investigates Hawaiian hoary bat roost selection at the habitat stand, tree and perch levels. Hypotheses were twofold: 1) Hawaiian hoary bats will select roosts with physical features that differentiate their roosts from randomly available trees; and 2) reproductive female Hawaiian hoary bats, particularly those with pups, will select roosts that provide net benefits (e.g., protection from predation, thermoregulation) compared to randomly available trees and roosts of non-reproductive female and male bats. Chapter 3 focuses on the diurnal roosting behavior of the Hawaiian hoary bat during the reproductive season. Activity patterns and an ethogram of behavior at diurnal roosts from direct observations is presented. Finally, Chapter 4 is a general discussion with key findings, important management implications, and potential future research.

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CHAPTER 2. ROOST SELECTION AND ROOSTING ECOLOGY OF THE HAWAIIAN HOARY BAT

INTRODUCTION

Forests serve as important roosting and foraging habitat for many bat species, and almost all North American species of bat rely on forests for survival (Taylor 2006). Determining specific roost dynamics is critical, as roost sites are vital to the survival and fitness of foliage roosting bats and their offspring (Vonhoff and Barclay 1996). Bats of the genus *Lasiurus* (Chiroptera: Vespertilionidae) are mainly solitary (non-colonial), and foliage-roosting. Roost studies on North American mainland lasiurine bats such as *Lasiurus seminolus*, revealed that they preferred thinned mature (>50 y old) habitats with low tree density and abundant large over-story trees in mixed pine-hardwood forests (Perry *et al*. 2007a). Furthermore, this study suggested that spatially heterogeneous forests may be preferred due to reduced understory clutter facilitating ease of navigation and increased predator detection as well as allowing more direct sunlight which may have thermal benefits for mothers and pups (Perry *et al*. 2007a). A study that identified characteristics of roost sites at the individual tree level rather than at a stand level was conducted on the North American hoary bat (*Lasiurus cinereus cinereus*) and found that *L. c. cinereus* generally roosted on the easterly sides of trees and most often preferred large, mature (>50 y old) over-story trees of both hardwoods and conifers (Perry and Thill 2007). In contrast to *L. seminolus* in Perry *et al*. (2007a), this study found that *L. c. cinereus* preferred roost sites with a denser understory that may provide protection from terrestrial predators (Perry and Thill 2007). O'Keefe *et al*. (2009) found that *Lasiurus borealis* selected roosts based on proximity to particular landscape features when examining macro-habitat roost factors at stand and landscape scales, since *L. borealis* roosted closer to open areas that may serve as commuting and foraging corridors. Additionally, *L. borealis* preferred large hardwood trees even in landscapes where pines were abundant, and stand age was not a significant factor (O'Keefe *et al*. 2009). In contrast, Perry *et al*. (2007a) and Perry and Thill (2007) found that both *L. seminolus* and *L. c. cinereus* preferred mature (>50 y old) tree stands.

In addition to ease of navigation and predator avoidance, energy expenditure and thermoregulation are also important factors in roost selection for bats. Especially for mothers with pups of lasiurine bats which are solitary and tree roosting, therefore they do not have the benefits of social thermoregulation that many colonial species employ in which conspecifics

huddle to reduce heat loss (Menzies *et al*. 2016). Female Hawaiian hoary bats give birth to twin pups at the beginning of the reproductive season which consists of pregnancy (April to June), lactation (June to August), and post-lactation and fledging (August to November), with pups usually fledged and independent of their mother by November (Tomich 1986, Kepler and Scott 1990, Jacobs 1994, Menard 2001, Gorresen *et al*. 2013). Little is known about maternity roost selection during this critical time period. Reproduction and lactation are energetically expensive and may have an effect on roost selection and behavior for reproductive females. In North American hoary bats, roosts selected by lactating *L. c. cinereus* were shown to have protection from wind as well as increased exposure to sunlight, suggesting the importance of reducing energy spent on thermoregulation (Klug *et al*. 2012). Willis and Brigham (2005) also found selection for preferred micro-climate, including wind speeds that were significantly lower at roost sites compared to the opposite side of the same tree for reproductive *L. c. cinereus*. The importance of thermal conditions at roosts was further established by Koehler and Barclay (2000) in their study of post-natal growth of *L. c. cinereus*. Over a 3 year study, post-natal growth rate was positively correlated with roost ambient temperature suggesting that at lower temperatures more energy is devoted to thermoregulation and less energy may be allocated to growth of young (Koehler and Barclay 2000). Reproductive females of *L. c. cinereus* were found to spend more time foraging per night and less time roosting with their young as lactation progressed, but foraging time eventually declined as young became independent (Barclay 1989).

These studies and others highlight the many different factors that determine diurnal roost selection for lasiurine bats including age of tree stands, micro and macro-climate at roost sites, predator avoidance, distance to commuting and foraging corridors, ease of navigation and thermoregulatory considerations especially for maternity roosts. From individual tree level to stand and landscape scales there are many different micro and macro habitat variables to consider. Although these studies help inform general lasiurine roost selection behavior, differences in individual species preferences for roosting habitat make it difficult to extrapolate results that are meaningful for the Hawaiian hoary bat. At present there are no published studies directly examining the roosting ecology and habitat use of *L. c. semotus*. Several studies have acknowledged forests as important resources for the *L. c. semotus*, especially in regard to foraging habitat (Belwood and Fullard 1984, Jacobs 1999, Bonaccorso *et al*. 2015), but none have examined habitats specifically used for roosting. Although early studies suggest the

Hawaiian hoary bat is most often associated with native vegetation (Jacobs 1994), current evidence suggests that they may be more of a generalist in terms of habitat and roosting needs (Gorresen *et al*. 2013, Bonaccorso *et al*. 2015).

Hawaiian hoary bat roost selection was investigated at two spatial scales, the roost tree and habitat stand. Hypotheses were that *L. c. semotus* will select roost sites with physical features that distinguish them from randomly available trees. Moreover, the selection of specific roost sites by reproductive female bats, particularly those with pups, will provide net benefits (e.g., protection from predation, thermoregulation) when compared to randomly available trees and roosts of non-reproductive female as well as male bats.

METHODS

Study Area

The study area covered approximately 1,500 km^2 from the Kaʻahakini to Laupāhoehoe watersheds and included native and non-native mixed forests, timber plantations, agro-ecosystems, lava tubes, and urban/suburban landscapes from sea level to 3,500 m elevation. This region was selected because of previously demonstrated high presence levels for Hawaiian hoary bats (Gorresen *et al*. 2013, Bonaccorso *et al*. 2015, 2016). Multiple locations were used on the east side of Hawaiʻi Island for Hawaiian hoary bat capture from May 2018 through December 2019 (Figure 2.1). Netting locations were selected to include a range of elevations and land-cover types with four lowland (<1,000 m asl) and four upland (>1,000 m asl) fixed netting sites that were rotated among three times a year, as well as an assortment of sites used for opportunistic bat netting.

Figure 2.1 Map of netting sites used for bat capture including fixed sites (orange) and sites used for opportunistic netting (blue) during data collection from May 2018 to December 2019. Note: 500 ft. elevation contours shown in red.

Bat Capture and Tracking

Hawaiian hoary bats were captured under U.S. Fish and Wildlife Service (USFWS) permit TE-003483-33 and State of Hawai'i permit WL19-19 following guidelines from the University of Hawai'i at Hilo, Institutional Animal Care and Use Committee (IACUC). Capture was conducted using denier polyester and/or nylon monofilament mist nets in 6-, 9-, 12-, and 18-m lengths (Figure 2.2). Age, sex, reproductive condition, tissue and guano samples were obtained from each captured bat whenever possible. Age was classified as either adult or juvenile and assessed based on degree of epiphyseal-diaphyseal fusion (Brunet-Rossinni and Wilkinson 2009). Unique, individually color-coded forearm bands were affixed for identification and before release very high frequency (VHF) radio-transmitters (model PIP3, Biotrak Ltd., Wareham,

United Kingdom) were attached with glue (Perma-Type Surgical Cement, Perma-Type Company Inc., Plainville, Connecticut) to the back of the bat (Figure 2.2). Radio-tagged bats were tracked using VHF receivers (model TRX-1000, Wildlife Materials Inc., Murphysboro, Illinois and/or model R410, Advanced Telemetry Systems, Isanti, Minnesota) tuned within the 164.000-164.999 MHz range. Receivers were equipped with non-directional (model SN-150, Cushcraft, Starkville, Mississippi; model 500C, Wildlife Materials Inc., Murphysboro, Illinois) or directional three- or five-element collapsible Yagi antennae (models F164-165-3FB and F164-165-5FB, Wildlife Materials Inc., Murphysboro, Illinois). Tracking was conducted on the ground, from vehicles, and by foot during daytime hours in teams of 2-4 personnel. Vehicles were driven along passable routes with a non-directional antenna affixed to the roof or a directional antenna extended from a window. When possible, field personnel hiked into forest stands with directional antennae and receivers. Upon detection of a radio signal, global positioning system (GPS) coordinates and compass bearings of the signal direction were recorded. Data were recorded at multiple locations and mapped to narrow down the radio-tagged bat's location. When a roost tree was confirmed, a GPS coordinate was recorded at its location.

Figure 2.2 Example of netting site setup used for bat capture (left) and a bat in hand after attaching VHF radio-transmitter and unique, individually color-coded forearm bands (right).

Roost Tree and Habitat Identification

After using the radio signal to determine if a radio-tagged bat was in a tree or group of trees, various tools were used to locate and confirm the bat in a roost tree. A handheld thermal imager (model Ti450, Fluke Corporation, Everett, Washington) was used to scan possible roost tree(s) to determine a possible heat signature of a roosting bat, and binoculars and/or a spotting scope were used to view a bat in a roost tree. When necessary, field personnel observed the area near dusk to identify the tree from which the bat emerged. In some instances, a specific roost tree was not able to be confirmed. In these cases, only broader habitat level ("stand") characteristics were obtained by using Location of a Signal (LOAS) software (version 4.0.3.8, Ecological Software Solutions LLC, Urnäsh, Switzerland) to derive the estimated X,Y coordinates of the bat's roost location from point location and compass bearings collected during radio-tracking.

Each roost tree confirmed was given a unique identification code. The naming convention included the following information: four-character year code, "R" for roost, three-character roost number, followed by "T" for tree (YYYYR00T). For example, the first roost tree identified in 2019 would have the code: 2019R001T. For purposes of habitat classification, each roost tree had an associated roost stand that was defined as a 50-meter radius buffer around the roost tree location point or estimated X,Y coordinates when derived from LOAS. The roost-stand identification code followed the same naming convention as the roost-tree identification code with a four-character year code, "R" for roost, three-character roost number, followed by "S" for stand (YYYYR00S). All roost trees identified and confirmed had an associated roost stand. However, in instances where roost trees were not able to be confirmed, only stand level characteristics were available.

Roost trees were classified to the genus or species level, and roost tree height, diameter at breast height (DBH), percent canopy cover, distance to nearest tree, and elevation were measured. Additionally, if a bat was spotted in the roost tree then percent canopy cover, aspect, and height of the bat's perch were also recorded. For comparison, we identified six trees (≥10 cm DBH to remove understory saplings from analysis) at random bearings and distances within a 50 m radius of each roost tree. The random bearing and distance values were randomly generated, then applied by selecting trees nearest to those values. For each random tree we recorded height and DBH. Tree height, in meters, was measured using a laser range finder (Model Forestry Pro Laser Rangefinder/ Hypsometer, Nikon USA, Mellville, New York). Where possible, the height

of a bat perch, in meters, was also measured by laser range finder. Diameter at breast height (DBH) was measured with DBH tape (Model 283D/10M, Forestry Suppliers, Jackson, Mississippi) by wrapping the diameter tape around the tree at breast height (1.3 m) from base of tree. A tree was measured and classified as a single-bole tree if the trunks forked at a point higher than 1.3 m. If the trunks forked at a point lower than 1.3 m, the tree was classified as multi-trunked and DBH was measured for each trunk and summed. Additionally, if the tree was growing on a slope, DBH was measured on the top part of the slope. Estimated percent canopy cover of roost trees was measured using a spherical densiometer (Convex Model A, Forestry Suppliers, Jackson, Mississippi). Four readings were taken about a roost tree and averaged. Personnel positioned their back toward the reference tree and moved around the tree facing North, East, South and West. Similarly, the estimated percent canopy cover of the bat perch location was measured using a spherical densiometer with personnel taking four readings directly underneath the bat perch facing North, East, South and West. Roost perch aspect (i.e., compass direction) was measured using a compass (Model M-3, Suunto, Vantaa, Finland), where possible.

Elevation, distance from centroid (either roost tree or estimated X,Y coordinates) to forest edge, and mean canopy height in meters were measured with Pictometry software (Version 2-14-8-380, Eagle View Technologies, Bellevue, Washington) (see example in Figure 2.3). Forest edge was defined as the limit of continuous canopy or the boundary in canopy composition (Harper *et al*. 2005). Mean canopy height was determined by measuring 10 random canopy trees within the defined roost stand using the Pictometry software height tool. Habitat classification for tree crown cover, tree height, tree species composition, and understory and ground cover were described using the methodology detailed in Jacobi (1989). Crown cover was categorized as: very scattered trees ("vs", <5% cover, trees widely spaced), scattered trees ("s", 5-25% cover), open canopy ("o", 25-60% cover), and closed canopy ("c", >60% cover). Tree canopy height was assigned as: low stature ("1", 2-5 m), medium stature ("2", 5-10 m), and tall stature ("3", >10 m). When the canopy was distinctly multi-layered, the cover, height, and species composition was noted separately for individual layers. See Jacobi (1989) for species codes and other annotations.

Figure 2.3. Example of stand level measurements recorded and annotated with Pictometry software including centroid (either confirmed roost tree, or estimated X,Y coordinates) distance to forest edge (top, orthogonal view) and ten random trees in the stand measured to calculate mean canopy height of the stand (bottom, oblique view).

Statistical Analyses

Roost tree structural characteristics of height and DBH were compared to randomly selected trees. Height and DBH variables were tested for normality using the Shapiro-Wilk W statistic. Non-normal data were log-transformed and evaluated with the Shapiro Wilk W test statistic. Two-sample t-tests were used to compare transformed data for roost and random trees. Welch's t-tests were used to compare transformed data of roost trees selected by male and female bats including height, DBH, percent canopy cover and distance to nearest tree. Welch's t-tests were also used to compare transformed data of roost perches selected by male and female bats including perch height and percent canopy cover at the perch. Roost perch aspect was analyzed for roost trees where data were available (n = 15), using Rao's spacing test to assess the uniformity of the circular data. Statistical significance for all tests used an alpha = 0.05. All mean values are reported with an associated standard deviation. All analyses were performed in R (version 4.0.0, R Core Team, 2020).

RESULTS

Roost Characteristics

A total of 61 bats were captured from May 2018 to December 2019. A total of 38 bats (28 male; 10 female; 37 adult; 1 juvenile) were tracked to 52 roost stands and 18 of those bats (11 male; 7 female; 16 adult; 1 juvenile) were identified and confirmed in 24 roost trees (Figure 2.4). Bats were confirmed at 15 perches within the 24 roost trees. Multiple roosts were used by nine bats. Two bats used three stands with two confirmed trees, two bats used two stands with two confirmed trees, three bats used two stands with one confirmed tree, one bat used four stands with three confirmed trees, and one bat used three stands but exact roost trees were not confirmed. One female bat with a pup was not captured or tracked but was located in a different area of the same roost tree as a solitary male bat. There were 23 bats that could not be tracked to any roost level and several additional bats were captured and not radio-tagged during the period of data collection.

Figure 2.4 Map of Hawaiian hoary bat roost locations including both roost stands (yellow) and roost trees (red) used during data collection from May 2018 to December 2019. Note: 500 ft elevation contours shown in red.

Roosts were located in ʻōhiʻa (*Metrosideros polymorpha*) (n = 3), melochia (*Melochia umbellata*) (n = 1), lychee (*Litchi chinensis*) (n = 4), mango (*Mangifera indica*) (n = 1), ironwood (*Casuarina equisetifolia*) (n = 2), gunpowder (*Trema orientalis*) (n = 2), Australian toon (*Toona ciliata*) (n = 2), eucalyptus (*Eucalyptus* spp.) (n = 4), and paperbark (*Melaleuca quinquenervia*) (n = 5) trees. The distance from capture location to roost location ranged from 10 m to 14,559 m (2,492 ± 3,094 m, mean ± SD). Elevation of roost trees ranged from 13 m to 1,576 m asl (350 ± 366 m, mean ± SD). A total of 22 roost trees were located below 1,000 m asl and two roost trees were located above 1,000 m asl. Roost trees ranged in height from 9.0 to 56.2 m (20.9 ± 9.4 m, mean ± SD), DBH ranged from 13.5 to 268.2 cm (75.1 ± 59.5 cm, mean ± SD), percent canopy cover ranged from 2.8 to 97.1% (42.9 ± 34.8%, mean ± SD), and distance to nearest tree ranged from 0.5 to 21.9 m (5.1 ± 5.3, mean ± SD) (Table 2.1). Randomly selected

trees ranged in height from 5.9 to 39.5 m (16.3 ± 7.5 m, mean ± SD), and DBH ranged from 19.7 to 66.1 cm (40.8 ± 14.5 cm, mean ± SD) (Table 2.1). There were statistically significant differences between roost tree values and the mean values derived for sets of associated random trees for both tree height ($t = -2.26$, $df = 46$, p-value = 0.03), and tree DBH ($t = -2.29$, $df = 46$, p-value = 0.03). Moreover, roost trees were generally larger on average in both height and DBH compared to randomly sampled trees. There were statistically significant differences between roost tree values for male (n = 16) versus female (n = 9) bats for tree height ($t = -2.78$, $df = 22$, p-value = 0.01), and percent canopy cover ($t = 2.80$, $df = 22$, p-value = 0.01), but not tree DBH ($t = 1.61$, $df = 22$, p-value = 0.12) or distance from roost tree to nearest tree ($t = -0.24$, $df = 14$, p-value = 0.81). Moreover, roost trees used by females were larger in height (26.9 ± 12.0 m, mean ± SD) compared to those used by males (17.8 ± 6.1, mean ± SD), and roost trees used by females had greater percent canopy cover (59.5 ± 28.1%, mean ± SD) compared to those used by males (36.7 ± 37.0%, mean ± SD). Small sample sizes did not allow for maternity (n = 3) versus non-maternity (n = 22) roost tree comparisons. See Appendix for complete roost tree metrics.

Table 2.1 Roost tree height and DBH for each roost tree (n = 24) and mean height, mean DBH, and standard deviation (SD) for 6 random trees (n = 144) within 50 m of each roost tree.

Roost ID	Stand ID	Roost Tree		Random Trees			
		Height (m)	DBH (cm)	Mean Height (m)	SD	Mean DBH (cm)	SD
2018R002T	2018R002S	13.4	17.4	11.8	5.3	21.0	7.1
2018R003T	2018R003S	33.4	52.3	28.5	6.8	59.3	21.4
2018R007T	2018R007S	24.0	60.0	16.7	5.1	24.4	8.6
2018R010T	2018R010S	22.5	43.5	22.3	10.3	43.8	46.8
2019R001T	2019R001S	9.0	13.5	9.2	1.3	19.7	8.2
2019R003T	2019R003S	20.5	199.0	11.4	4.7	25.9	27.5
2019R006T	2019R006S	19.6	58.3	17.7	4.2	32.6	13.6
2019R007T	2019R007S	23.5	58.8	17.2	7.1	25.6	16.4
2019R008T	2019R008S	12.8	18.4	11.1	30.1	20.5	10.2
2019R009T	2019R009S	18.0	21.2	17.7	4.8	43.5	45.0
2019R010T	2019R010S	13.8	136.4	5.9	2.3	41.0	27.7
2019R011T	2019R011S	14.3	107.1	8.5	4.1	59.9	42.3
2019R012T	2019R012S	14.6	92.4	12.6	5.0	66.1	29.0
2019R013T	2019R013S	17.0	268.2	15.4	3.8	52.0	34.4
2019R018T	2019R018S	23.5	53.7	20.4	3.5	60.9	25.2
2019R019T	2019R019S	56.2	82.7	39.5	18.9	40.2	22.2
2019R020T	2019R020S	12.9	33.5	12.3	8.2	37.5	30.1
2019R023T	2019R023S	26.4	86.0	25.5	7.2	45.0	40.0
2019R025T	2019R025S	15.2	81.2	13.2	7.2	60.1	40.4
2019R027T	2019R027S	18.8	57.4	8.7	5.2	39.1	27.7
2019R029T	2019R029S	20.2	56.1	13.1	7.5	58.6	43.3
2019R030T	2019R030S	23.6	116.0	18.1	15.1	37.1	23.8
2019R031T	2019R031S	21.4	73.1	11.7	5.4	30.1	11.0
2019R038T	2019R038S	26.0	17.5	22.9	5.3	36.3	27.5

Three maternity roosts were identified during 2019 in lychee (2019R013T), eucalyptus sp. (2019R023T), and paperbark (2019R031T) trees. Maternity roosts were located at elevations of 41 m (2019R013T), 439 m (2019R023T), and 73 m (2019R031T) asl. Two female bats were captured, and tracked to roosts 2019R023T and 2019R031T where they were then spotted with two pups and one pup, respectively. A male bat was captured and tracked to 2019R013T where a subsequent search of the entire tree with a thermal imager revealed a mother with one pup (not previously captured), in a different area of the same tree. The distance from capture location to roost location for bats at maternity roosts was 819 m (2019R023T) and 5140 m (2019R031T). Distance from capture location to roost location for the female bat at 2019R013T was not

calculated because the bat was not captured away from the maternity roost site at which it was identified.

For the 15 roost perches that were confirmed in roost trees, roost perch height ranged from 4.8 to 23.8 m (13.8 ± 6.7 m, mean ± SD), perch canopy cover ranged from 4.1 to 98.7% (50.4 ± 33.9%, mean ± SD), and perch aspect ranged from 110 to 334° (226 ± 81°, mean ± SD) with the following distribution, ESE (n = 1), SE (n = 3), SSE (n = 1), S (n = 1) SSW (n = 1), WSW (n = 2), W (n = 2), NW (n = 3), and NNW (n = 1) (Figure 2.5). Anecdotal evidence indicated a preference for roost perches on the outer peripheries of roost trees away from the tree bole. There were no statistically significant differences between perch height (t = 1.01, df = 12, p-value = 0.33), and percent canopy cover (t = 1.64, df = 9, p-value = 0.14) between males and females. The test of roost perch aspect did not reject the null hypothesis of a uniform distribution (Rao's spacing test statistic = 159, level = 0.05, critical value = 165.75). Sample sizes did not allow for maternity (n = 3) versus non-maternity (n = 12) roost perch comparisons. See Appendix for complete roost perch metrics.

Figure 2.5 Compass direction (aspect) of roost perch (n = 15) in relation to the bole of the roost tree.

For the 52 identified roost forest stands, mean canopy height ranged from 11.3 to 44.4 m (23.7 ± 8.1 m, mean ± SD), and distance to forest edge ranged from 0.5 to 188.1 (29.3 ± 42.3 m, mean ± SD). Stand canopy cover classifications included closed >60% cover (n = 25), open

(>25% - 60% cover) (n = 10), scattered (>5 - 25% cover) (n = 5), and very scattered (<5% cover) (n = 12). See Appendix for complete roost stand metrics.

DISCUSSION

Hawaiian hoary bats used diurnal roosts in a variety of tree species and in an assortment of habitat stand types including native and non-native habitats. Similar to *L. c. cinereus* (Perry and Thill 2007a); this plasticity in roost selection may account for their seemingly broad distribution across the landscape. The hypothesis that bats would select roost sites with physical features that differentiate roosts from randomly available trees was supported. Hawaiian hoary bat roost trees were larger in both height and DBH than randomly sampled trees. Similarly, in the Perry *et al.* (2007b) study of *Lasiurus borealis*, while height and DBH of roost trees did not differ between sexes, roost trees used by both sexes were greater in height and DBH than random trees. However, Hawaiian hoary bat sex comparisons showed that females roosted in trees that were larger in height and had a greater percent canopy cover compared to those used by males. Distance to nearest tree and DBH of roosts used by females compared to males was not statistically significant. In contrast, females of *L. borealis* roosted in trees that were further away from other trees compared to male roost trees suggesting that females selected trees that reduced shading and increased solar radiation for thermoregulation processes (Perry *et al.* 2007b). Both Elmore *et al.* (2004), and Perry *et al.* (2007b) suggest that overall, female bats may be more discerning than males in their roost selection which is also supported by these data for the Hawaiian hoary bat. Statistical comparisons between maternity roost characteristics versus solitary roosts or random trees could not be conducted because sample sizes for maternity roosts were not large enough for sufficient power (n = 3).

Bats were more readily tracked to roosts in lowland habitats, which mostly consisted of non-native timber plantation and orchard or urban/suburban habitats compared to native or mixed native habitats that are more prevalent higher in elevation. Extensive roads and trail networks aided in lowland tracking compared to upland habitats. Therefore, potential roosts in upland habitats and in native tree species may be underrepresented in these data.

Despite obvious physical differences in tree geometry and canopy characteristics among roost tree species, most bats showed a preference for roost perches on the outer peripheries of trees, away from the bole. This is common behavior also seen in North American hoary bats

where roosts had sufficient flyways to emerge from the surrounding canopy (Klug *et al.* 2012). Although roost perch aspect was not statistically different from uniform distribution, there seemed to be a trend in preference for the westerly and southerly orientation of perches in roost trees which is the opposite side of prevailing windward weather in the Hawaiian archepelago. Klug *et al*. also found a preference for roosting on the lee-side of trees for *L. c. cinereus* in Canada for both resident and non-resident migrating bats in their study area and assumed an estimated 1.60 kJ/day energy savings by roosting on the lee-side, consistent with a similar study by Willis and Brigham (2005). Moreover, sunlight exposure may also be a factor in roost perch aspect where exposure to sunlight in the evenings may help facilitate rewarming before emerging from the roost for nightly foraging. Willis and Brigham (2005) found that *L. c. cinereus* in Canada roosted on the south side of tree canopies and Klug *et al*. (2012) found that lactating females of *L. c. cinereus* also chose roosts with less variable sunlight exposure and had south-facing canopy openings which aid in warming roosts during the day. While sex comparisons between Hawaiian hoary bat females and males for roost perch percent canopy cover and height were not statistically significant, females did select trees with greater overall tree percent canopy cover. This indicates the females prefer denser trees than males possibly for increased protection from predation and/or thermoregulation purposes. Perhaps with a larger sample size, evidence of selection for roost perch aspect, percent canopy cover and height may become more apparent for *L. c. semotus*.

Although some suggest that *L. c semotus* may be widespread across habitat types in the Hawaiian archipelago (Jacobs 1994, Gorresen *et al*. 2013), population abundance and distribution patterns are not well established. Furthermore, genetically distinct populations with limited gene flow among the Hawaiian Islands (Pinzari 2019), may be vulnerable to extirpation if critical habitat factors change. As such, conservation strategies should address both seasonal roosting and foraging requirements (Pierson 1988). The information gathered here may help managers make informed decisions assisting the recovery of *L. c. semotus* and for improved selection and design of bat mitigation areas that may offer a balance of seasonal roosting habitat, and guidance on key plant species for propagation to benefit bats in restoration-mitigation areas.

Although this study marks the first directed research for quantifying diurnal roost habitat for Hawaiian hoary bats, further research should include continued effort in tracking females to maternity roosts and evaluating selection compared to males and non-reproductive females.

Moreover, obtaining additional roost data in upland habitats may give a better picture of seasonal roosting variations. The information gathered in this study may assist in improved selection and design of bat mitigation areas that may offer a balance of roosting habitat important for Hawaiian hoary bat recovery efforts.

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Hawaiian hoary bat roost tree, perch and stand metrics collected from May 2018 to December 2019. Habitat type classification was described using methods and characterizations of Jacobi (1989). Note: for roost 2019R013T both a male solitary bat and female bat with a pup (maternity roost) were located at different perches within the same tree during 2019, no Bat ID available for the female with pup because she was not captured during this study.

Roost Tree Metrics (n = 24)

Roost ID	Stand ID	Bat ID	Sex	Age	Roost type	Roost tree species	Tree height (m)	DBH (cm)	Canopy cover (%)	Distance to nearest tree (m)	Elevation (m)	Habitat classification
2018R002T	2018R002S	2018HHB003	M	A	Solitary	*Toona ciliata*	13.4	17.4	9.8	4.3	337.3	c3xt,2Psc (M:mf,xs)
2018R003T	2018R003S	2018HHB003	M	A	Solitary	*Eucalyptus* sp.	33.4	52.3	5.6	7.5	245.7	c3xt,2Psc (M:xs)
2018R007T	2018R007S	2018HHB008	F	A	Solitary	*Mangifera indica*	24.0	60.0	30.1	7.2	56.4	c3xt,2xt (M:xx,xh)
2018R010T	2018R010S	2018HHB011	M	A	Solitary	*Eucalyptus* sp.	22.5	43.5	7.2	1.2	454.3	c3xt,Me,2Psc (M:mf,xs)msc
2019R001T	2019R001S	2019HHB001	M	A	Solitary	*Metrosideros polymorpha*	9.0	13.5	13.7	2.5	1225.4	s2Me (M:mf,ns)sng
2019R003T	2019R003S	2019HHB005	F	A	Solitary	*Metrosideros polymorpha*	20.5	199.0	42.8	21.9	1575.9	o3Me,2Me (W:tf,ns)
2019R006T	2019R006S	2018HHB002	F	A	Solitary	*Toona ciliata*	19.6	58.3	41.0	2.7	325.8	o3xt,2Psc (M:xs,tf)msc
2019R007T	2019R007S	2018HHB002	F	A	Solitary	*Trema orientalis*	23.5	58.8	47.2	0.5	318.8	o3xt,2Psc (M:xs)
2019R008T	2019R008S	2019HHB017	M	A	Solitary	*Melochia umbellata*	12.8	18.4	10.0	2.3	171.6	vs2xt (M:xs)
2019R009T	2019R009S	2019HHB017	M	A	Solitary	*Trema orientalis*	18.0	21.2	2.8	0.6	171.7	s3xt,2xt (M:xs)
2019R010T	2019R010S	2019HHB018	M	A	Solitary	*Litchi chinensis*	13.8	136.4	71.1	14.1	12.7	vs3xt (M:xg,xx)
2019R011T	2019R011S	2019HHB018	M	A	Solitary	*Litchi chinensis*	14.3	107.1	91.2	10.7	13.6	vs3xt (M:xg,xx)

Roost ID	Stand ID	Bat ID	Sex	Age	Roost type	Roost tree species	Tree height (m)	DBH (cm)	Canopy cover (%)	Distance to nearest tree (m)	Elevation (m)	Habitat classification
2019R012T	2019R012S	2019HHB019	M	A	Solitary	*Litchi chinensis*	14.6	92.4	90.6	14.3	16.5	vs3xt (M:xg,xx)
2019R013T	2019R013S	2019HHB020, NA	M, F	A, A	Solitary, Maternity	*Litchi chinensis*	17.0	268.2	90.6	0.5	41.0	vs3xt (M:xg,xx)
2019R018T	2019R018S	2019HHB034	F	A	Solitary	*Metrosideros polymorpha*	23.5	53.7	91.2	5.4	690.1	s3Me,2xt (M:tf,xs,xg)
2019R019T	2019R019S	2019HHB035	F	J	Solitary	*Eucalyptus* sp.	56.2	82.7	76.3	3.1	354.6	s3xt,2xt (M:xg,xx)
2019R020T	2019R020S	2019HHB037	M	A	Solitary	*Casuarina equisetifolia*	12.9	33.5	97.1	1.8	361.0	vs3xt,2Psc (M:xg,xx)
2019R023T	2019R023S	2019HHB040	F	A	Maternity	*Eucalyptus* sp.	26.4	86.0	93.24	5.5	438.6	c3xt,2Psc (M:xs,tf)msc
2019R025T	2019R025S	2019HHB047	M	A	Solitary	*Melaleuca quinquenervia*	15.2	81.2	15.0	3.6	274.0	vs3xt,2xt (M:xg,xx)
2019R027T	2019R027S	2019HHB047	M	A	Solitary	*Melaleuca quinquenervia*	18.8	57.4	20.7	3.4	274.3	vs3xt,2xt (M:xg,xx)
2019R029T	2019R029S	2019HHB046	M	A	Solitary	*Melaleuca quinquenervia*	20.2	56.1	22.5	4.5	295.0	vs3xt,2xt (M:xg,xx)
2019R030T	2019R030S	2019HHB047	M	A	Solitary	*Melaleuca quinquenervia*	23.6	116.0	34.5	4.0	301.9	vs3xt,2xt (M:xg,xx)
2019R031T	2019R031S	2019HHB048	F	A	Maternity	*Melaleuca quinquenervia*	21.4	73.1	23.6	0.5	82.9	o3xt,2xt (M:xg,xx)
2019R038T	2019R038S	2019HHB074	M	A	Solitary	*Casuarina equisetifolia*	26.0	17.5	4.1	0.5	372.3	o3xt (M:xx,xg,mf)

Roost Perch Metrics (n = 15)

Roost ID	Stand ID	Bat ID	Sex	Age	Roost type	Roost tree species	Roost perch canopy cover (%)	Roost perch height (m)	Roost perch aspect (°)
2019R001T	2019R001S	2019HHB001	M	A	Solitary	*Metrosideros polymorpha*	15.5	7.5	140
2019R006T	2019R006S	2018HHB002	F	A	Solitary	*Toona ciliata*	9.8	16.8	150
2019R008T	2019R008S	2019HHB017	M	A	Solitary	*Melochia umbellata*	4.1	9.9	110
2019R010T	2019R010S	2019HHB018	M	A	Solitary	*Litchi chinensis*	75.6	6.7	311
2019R011T	2019R011S	2019HHB018	M	A	Solitary	*Litchi chinensis*	65.2	7.3	183
2019R013T	2019R013S	2019HHB020	M	A	Solitary	*Litchi chinensis*	66.2	5.2	255
2019R013T	2019R013S	NA	F	A	Maternity	*Litchi chinensis*	90.6	4.8	310
2019R018T	2019R018S	2019HHB034	F	A	Solitary	*Metrosideros polymorpha*	98.7	20.3	270
2019R019T	2019R019S	2019HHB035	F	J	Solitary	*Eucalyptus* sp.	62.6	23.8	281
2019R020T	2019R020S	2019HHB037	M	A	Solitary	*Casuarina equisetifolia*	84.9	11.1	325
2019R023T	2019R023S	2019HHB040	F	A	Maternity	*Eucalyptus* sp.	87.0	23.4	198
2019R027T	2019R027S	2019HHB047	M	A	Solitary	*Melaleuca quinquenervia*	40.2	13.2	130
2019R030T	2019R030S	2019HHB047	M	A	Solitary	*Melaleuca quinquenervia*	20.2	17.3	128
2019R031T	2019R031S	2019HHB048	F	A	Maternity	*Melaleuca quinquenervia*	26.4	18.8	334
2019R038T	2019R038S	2019HHB074	M	A	Solitary	*Casuarina equisetifolia*	9.0	20.2	268

Roost Stand Metrics (n = 52) Note: only Stand ID is available for stands where no specific roost tree was identified.

Stand ID	Roost ID	Bat ID	Sex	Age	Roost type	Habitat classification	Elevation (m)	Distance to forest edge (m)	Mean canopy height (m)
2018R001S	NA	2018HHB002	F	A	Solitary	c3xt,2Psc (M:xs)	331.7	10.4	37.1
2018R002S	2018R002T	2018HHB003	M	A	Solitary	c3xt,2Psc (M:mf,xs)	337.3	11.7	25.0
2018R003S	2018R003T	2018HHB003	M	A	Solitary	c3xt,2Psc (M:xs)	245.7	176.2	33.5
2018R004S	NA	2018HHB004	M	A	Solitary	c3xt,2Psc (M:xs,mf)	281.0	69.7	18.7
2018R005S	NA	2018HHB005	M	A	Solitary	o3xt,2Psc (M:mf,xs)	339.6	2.3	34.5
2018R006S	NA	2018HHB007	M	A	Solitary	c3xt (M:xs,xg)	147.6	39.7	21.7
2018R007S	2018R007T	2018HHB008	F	A	Solitary	c3xt,2xt (M:xx,xh)	56.4	6.0	22.7
2018R008S	NA	2018HHB009	M	A	Solitary	c3xt (M:xs)	219.2	42.8	38.2
2018R009S	NA	2018HHB010	M	A	Solitary	c3xt (M:tf,xs)	333.6	28.8	35.3
2018R010S	2018R010T	2018HHB011	M	A	Solitary	c3xt,Me,2Psc (M:mf,xs)msc	454.3	8.5	27.8
2018R011S	NA	2018HHB011	M	A	Solitary	o3xt,Me (M:mf)	416.6	9.6	17.1
2018R012S	NA	2018HHB003	M	A	Solitary	c3xt (M:xs)	252.3	125.2	39.4
2019R001S	2019R001T	2019HHB001	M	A	Solitary	s2Me (M:mf,ns)sng	1225.4	1.8	11.4
2019R002S	NA	2019HHB004	M	A	Solitary	c3xt (M:xs)	342.7	13.8	22.7
2019R003S	2019R003T	2019HHB005	F	A	Solitary	o3Me,2Me (W:tf,ns)	1575.9	188.1	17.7
2019R004S	NA	2019HHB008	M	A	Solitary	c3xt (M:xs)	446.5	3.6	18.2
2019R005S	NA	2019HHB009	M	A	Solitary	c3xt (M:xs)	411.4	2.9	34.0
2019R006S	2019R006T	2018HHB002	F	A	Solitary	o3xt,2Psc (M:xs,tf)msc	325.8	9.8	26.5
2019R007S	2019R007T	2018HHB002	F	A	Solitary	o3xt,2Psc (M:xs)	318.8	19.5	24.6
2019R008S	2019R008T	2019HHB017	M	A	Solitary	vs2xt (M:xs)	171.6	17.5	12.4
2019R009S	2019R009T	2019HHB017	M	A	Solitary	s3xt,2xt (M:xs)	171.7	11.6	14.9
2019R010S	2019R010T	2019HHB018	M	A	Solitary	vs3xt (M:xg,xx)	12.7	8.5	18.7
2019R011S	2019R011T	2019HHB018	M	A	Solitary	vs3xt (M:xg,xx)	13.6	6.1	20.4
2019R012S	2019R012T	2019HHB019	M	A	Solitary	vs3xt (M:xg,xx)	16.5	1.2	19.2
2019R013S	2019R013T	2019HHB020, NA	M, F	A, A	Solitary, Maternity	vs3xt (M:xg,xx)	41.0	3.2	16.7
2019R014S	NA	2019HHB024	M	A	Solitary	s3xt2Me(M:mf,ns)sng	1047.1	2.4	18.7

Stand ID	Roost ID	Bat ID	Sex	Age	Roost type	Habitat classification	Elevation (m)	Distance to forest edge (m)	Mean canopy height (m)
2019R015S	NA	2019HHB025	M	A	Solitary	c3xt (M:xs,tf)	555.2	19.5	14.7
2019R016S	NA	2019HHB027	F	A	Solitary	o3xt,Me (M:xg,xx)	474.8	17.5	15.6
2019R017S	NA	2019HHB033	F	A	Solitary	vs3Me (M:xg,xx)sng	756.3	2.7	17.4
2019R018S	2019R018T	2019HHB034	F	A	Solitary	s3Me,2xt (M:tf,xs,xg)	690.1	27.1	20.8
2019R019S	2019R019T	2019HHB035	F	J	Solitary	s3xt,2xt (M:xg,xx)	354.6	3.3	44.4
2019R020S	2019R020T	2019HHB037	M	A	Solitary	vs3xt,2Psc (M:xg,xx)	361.0	0.8	24.1
2019R021S	NA	2019HHB038	M	A	Solitary	c3xt (M:xs,tf)msc	427.0	91.6	33.8
2019R022S	NA	2019HHB039	M	A	Solitary	c3xt (M:tf,xs)msc	451.1	87.3	28.2
2019R023S	2019R023T	2019HHB040	F	A	Solitary	c3xt,2Psc (M:xs,tf)msc	438.6	21.1	29.0
2019R024S	NA	2019HHB043	M	A	Solitary	c3xt (M:xs)	498.0	3.6	29.5
2019R025S	2019R025T	2019HHB047	M	A	Solitary	vs3xt,2xt (M:xg,xx)	274.0	3.0	16.8
2019R026S	NA	2019HHB047	M	A	Solitary	vs3xt,2xt (M:xg,xx)	272.1	6.5	14.7
2019R027S	2019R027T	2019HHB047	M	A	Solitary	vs3xt,2xt (M:xg,xx)	274.3	1.1	14.2
2019R028S	NA	2019HHB046	M	A	Solitary	c3xt,2xt (M:tf,xs)	348.3	12.6	24.8
2019R029S	2019R029T	2019HHB046	M	A	Solitary	vs3xt,2xt (M:xg,xx)	295.0	4.2	13.2
2019R030S	2019R030T	2019HHB047	M	A	Solitary	vs3xt,2xt (M:xg,xx)	301.9	5.4	17.4
2019R031S	2019R031T	2019HHB048	F	A	Solitary	o3xt,2xt (M:xg,xx)	82.9	4.0	20.0
2019R032S	NA	2019HHB049	F	A	Solitary	o3xt (M:xx)	162.2	0.6	23.6
2019R033S	NA	2019HHB001	M	A	Solitary	o3Me (M:xg)sng	1653.5	3.1	17.7
2019R034S	NA	2019HHB072	M	A	Solitary	c3xt (M:mf)	551.3	57.3	20.1
2019R035S	NA	2019HHB071	M	A	Solitary	c3xt (M:mf,tf)	725.6	78.5	37.6
2019R036S	NA	2019HHB071	M	A	Solitary	c3xt,2Psc (M:xs, tf)	683.0	90.3	32.8
2019R037S	NA	2019HHB071	M	A	Solitary	c3xt (M:mf,tf)	651.6	58.3	28.5
2019R038S	2019R038T	2019HHB074	M	A	Solitary	o3xt (M:xx,xg,mf)	372.3	12.7	28.7
2019R039S	NA	2019HHB073	M	A	Solitary	c3xt (M:xs)	357.1	33.5	20.8
2019R040S	NA	2019HHB075	M	A	Solitary	c3xt (M:xs)	403.3	43.4	17.1

CHAPTER 3. DIURNAL ROOSTING BEHAVIOR OF THE HAWAIIAN HOARY BAT DURING THE REPRODUCTIVE SEASON

INTRODUCTION

Bats may spend more than half their lives at their diurnal roosts which serve as important areas used for shelter, rest, digestion, and care for young (Fleming *et al*. 1998). While bats may roost in both "natural" (caves, rock crevices, trees including cavity, bark and foliage, etc.) and anthropogenic (mines, buildings, bridges, etc.) structures, research is often focused on roosts that are more readily investigated like those of cave, bridge and building dwelling species (Pierson 1988). Some studies suggest that roosts may be limiting in some species (Humphrey 1975, McCracken 1988, Kunz and Lumsden 2003, Moretto and Francis 2017), and despite their importance in the life history of bats, especially maternity roosts, relatively little is known about bat behavior at diurnal roosts (Kunz 1982). Daily activity budgets have been investigated in maternity colonies of *Myotis lucifugus* (Burnett and August 1981), *Pipistrellus subflavus* (Winchell and Kunz 1996), *Leptonycteris curasoae* (Fleming *et al*. 1998), and a single harem male colony of *Artibeus lituratus* (Muñoz-Romo 2006). Detailed ethograms for *Artibeus lituratus* (Muñoz-Romo 2006) as well as a few megachiropteran species such as *Pteropus poliocephalus* (Nelson 1965), *Pteropus alecto* (Markus and Blackshaw 2002) and *Pteropus vampyrus* (Hengjan *et al*. 2017) have also been produced. However, these studies focused on colonial bat species and a common theme among these studies includes social behavior between conspecifics at roosts. While research on the behavior and activity budgets of bats have thus far focused mainly on colonial species, solitary and elusive species like the Hawaiian hoary bat (*Lasiurus cinereus semotus*) have rarely been investigated.

Information on Hawaiian hoary bat behavior has been limited to acoustic surveys (Belwood and Fullard 1984), anecdotal accounts (Baldwin 1950, Fujioka and Gon 1988, Kepler and Scott 1990) or focused on nocturnal behavior at wind-turbine facilities (Gorresen *et al*. 2015, 2017). There is minimal information on behavior at diurnal roosts, especially for mother-pup interactions during the reproductive season, which consists of pregnancy (April to June), lactation (June to August), and post-lactation and fledging (August to November) (Tomich 1986, Kepler and Scott 1990, Jacobs 1994, Menard 2001, Gorresen *et al*. 2013). Female Hawaiian hoary bats give birth to twin pups at the beginning of reproductive season with pups usually fledged and independent of their mother by November (Tomich 1986), and little is known about

mother-pup interactions and roost environment during this critical time period. For bats, reproduction and lactation are energetically expensive and may have an effect on roost selection and behavior for reproductive females compared to males or non-reproductive females (e.g., Hamilton and Barclay 1994). Also, because the Hawaiian hoary bat is a solitary and foliage roosting species it does not have the advantages of social interactions and intraspecific cooperation that colonial species have that may provide a number of fitness benefits including reduced thermoregulatory costs (Menzies *et al*. 2016). While energetic demands are an important factor in diurnal roost selection (e.g., Winchell and Kunz 1996, Menzies *et al*. 2016), investigating behavior at diurnal roosts may give a better understanding of their function and serve in the development of conservation standards through a better understanding of potential effects of predators and disturbance at roosts.

The objective of this study was to observe *L. c. semotus* at diurnal roosts and create an ethogram of observed behavior in order to gain a better understanding of the behavioral ecology of this elusive species. Vulnerability to predation or disturbance, interactions between mothers and pups and pup-survivorship are important aspects of Hawaiian hoary bat ecology, that require direct observation at roosts. This information may aid land managers and policy makers in deciding what factors should be considered when designing protection, conservation and mitigation measures for this species.

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METHODS

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Study Sites

Diurnal roost video-monitoring was conducted at two separate sites (AMA, DOF) in Hilo, Hawaiʻi during the reproductive seasons of 2017 and 2018 (Figure 3.1). In previous studies (Bonaccorso *et al*. 2015) bats were captured, banded, radio-tagged and tracked to both of these roost sites. In subsequent years, these roost sites were periodically monitored for bat presence. While none of the previously banded bats were observed during this study, other individuals were present and opportunistically monitored.

Roost site AMA was located at a private residence near the Wailuku river and bordered by an agricultural area at an elevation of approximately 56 m asl. Site AMA had one lychee tree (*Litchi chinensis*) (AMA_L1) with six distinct roost perch locations identified as occupied by bat(s) during at least one sample period (Figure 3.2). The second site, DOF was located at an

arboretum near downtown Hilo at an elevation of approximately 14 m asl and consisted of three separate lychee trees (DOF_L1, DOF_L2, and DOF_L3) and one paradise nut tree (*Lecythis zabucajo*) (DOF_PN1) which collectively had a total of ten distinct roost perch locations identified as occupied by bat(s) during at least one sample period (Figure 3.3).

Figure 3.1 Map of study sites (AMA, DOF) monitored during the 2017 and 2018 reproductive seasons.

Figure 3.2 Approximate roost perch locations within the AMA_L1 roost tree monitored during the 2017 and 2018 reproductive seasons.

Figure 3.3 Approximate roost perch locations within the DOF_L1, DOF_L2, DOF_L3, and DOF_PN1 roost trees monitored during the 2017 and 2018 reproductive seasons.

Video Monitoring

Video monitoring at diurnal roosts was conducted approximately once per week from 24 May 2017 to 14 September 2017 for a total of ~55 video-hours combined for both AMA and DOF roost locations, and from 29 May 2018 to 28 August 2018 for a total of ~59 video-hours combined for both AMA and DOF roost locations (Table 3.1).

Roost trees were scanned with binoculars and/or a thermal imager (model Ti400, Fluke Corporation, Everett, Washington) to determine bat presence/absence. When a roosting bat was confirmed in a tree, a digital single-lens reflex (DSLR) video camera (various models) was setup on a tripod under or near a roost perch (Figure 3.4). Video of bat activity was recorded onto secure digital (SD) memory cards in approximately 15 minute intervals to allow for refocusing or adjustment if applicable. Video-monitoring was conducted in the first 6-8 hours after sunrise due to personnel and weather constraints. If more than one bat was observed in a study site, attempts were made to video monitor separately at both locations when possible.

Complete demographic information (age, sex, etc.) or identity of individual bats that were video monitored was not possible to ascertain because bats were not captured or banded in this study. Therefore, bats monitored were classified as "solitary" for a single bat of unknown sex or "maternity" when a mother-pup(s) group was identified.

Table 3.1 Video monitoring effort during the 2017 and 2018 reproductive seasons.

Date	Site	Tree species	Roost tree ID	Perch ID	Roost type	Total duration of video monitoring (s)
5/24/2017	DOF	*L. chinensis*	DOF_L1	L1P1	Solitary	15316
5/31/2017	DOF	*L. chinensis*	DOF_L1	L1P1	Solitary	7744
5/31/2017	DOF	*L. chinensis*	DOF_L2	L2P2	Solitary	6518
6/2/2017	DOF	*L. chinensis*	DOF_L1	L1P1	Solitary	10455
6/2/2017	DOF	*L. chinensis*	DOF_L2	L2P3	Solitary	10077
6/7/2017	DOF	*L. chinensis*	DOF_L1	L1P1	Solitary	10446
6/16/2017	DOF	*L. chinensis*	DOF_L1	L1P3	Solitary	20913
6/19/2017	DOF	*L. chinensis*	DOF_L2	L2P1	Solitary	7987
6/19/2017	DOF	*L. chinensis*	DOF_L2	L2P2	Solitary	7790
6/23/2017	DOF	*L. chinensis*	DOF_L2	L2P2	Solitary	5504
7/5/2017	DOF	*L. chinensis*	DOF_L1	L1P3	Solitary	25140
7/7/2017	DOF	*L. chinensis*	DOF_L1	L1P3	Solitary	8145
7/19/2017	DOF	*L. chinensis*	DOF_L1	L1P3	Solitary	16179
8/2/2017	DOF	*L. chinensis*	DOF_L1	L1P1	Solitary	12262
8/16/2017	AMA	*L. chinensis*	AMA_L1	L1P5	Solitary	7851
8/24/2017	AMA	*L. chinensis*	AMA_L1	L1P5	Solitary	3761
8/31/2017	AMA	*L. chinensis*	AMA_L1	L1P5	Solitary	3620
9/14/2017	DOF	*L. chinensis*	DOF_L1	L1P4	Solitary	11663
9/14/2017	DOF	*L. chinensis*	DOF_L1	L1P5	Solitary	7424
5/29/2018	AMA	*L. chinensis*	AMA_L1	L1P7	Solitary	7739
6/1/2018	AMA	*L. chinensis*	AMA_L1	L1P7	Solitary	4801
6/13/2018	DOF	*L. chinensis*	DOF_L2	L2P5	Solitary	4160
6/14/2018	DOF	*L. chinensis*	DOF_L3	L3P1	Solitary	5622
6/14/2018	DOF	*L. zabucajo*	DOF_PN1	PN1	Solitary	2715
6/19/2018	DOF	*L. chinensis*	DOF_L2	L2P5	Solitary	14641
6/19/2018	DOF	*L. chinensis*	DOF_L3	L3P1	Solitary	15171
6/20/2018	DOF	*L. chinensis*	DOF_L3	L3P1	Solitary	5278
6/27/2018	AMA	*L. chinensis*	AMA_L1	L1P7	Maternity	13685
7/2/2018	AMA	*L. chinensis*	AMA_L1	L1P8	Solitary	27506
7/9/2018	AMA	*L. chinensis*	AMA_L1	L1P8	Solitary	25469
7/13/2018	AMA	*L. chinensis*	AMA_L1	L1P7	Maternity	7153
7/20/2018	AMA	*L. chinensis*	AMA_L1	L1P9	Maternity	12198
7/27/2018	AMA	*L. chinensis*	AMA_L1	L1P10	Maternity	26167
8/16/2018	AMA	*L. chinensis*	AMA_L1	L1P11	Maternity	7210
8/17/2018	AMA	*L. chinensis*	AMA_L1	L1P11	Maternity	26164
8/21/2018	AMA	*L. chinensis*	AMA_L1	L1P11	Maternity	3168
8/28/2018	AMA	*L. chinensis*	AMA_L1	L1P11	Maternity	5779

Figure 3.4 Video monitoring equipment setup at a roost tree (AMA_L1).

Video Analysis

All video was reviewed in its entirety at normal playback speed. Behaviors were described according to observed activities, grouped into categories, and described referring to Fleming *et al.* (1998), Marcus and Blackshaw (2002), Muñoz-Romo (2006), and Hengjan *et al.* (2017). Behaviors were documented in two ways; the number of times (discrete events) a behavior was observed as well as the duration of total time spent engaged in the behavior. Behavioral categories applicable to *L. c. semotus* included, excretion, grooming, social behavior, and non-categorized (behaviors that could not otherwise be classified). At maternity roosts only the behavior of the mother was quantified.

Pearson's Chi-square goodness of fit tests were used to examine whether the proportion of different types of events and times per event statistically deviated from parity for both solitary and maternity roost observations. Statistical significance for all tests used an alpha = 0.05. All analyses were performed in R (version 4.0.0, R Core Team, 2020).

RESULTS

Ethogram

During the 2017 and 2018 reproductive roost monitoring seasons, 11 discrete behaviors were identified (Table 3.2). Example context is available for further clarity. See Appendix for example images of observed behaviors.

Table 3.2 Ethogram of Hawaiian hoary bat diurnal roosting behavior during the 2017 and 2018 reproductive seasons.

Behavioral category	Behavior	Description	Context
Excretion	Defecate	Hanging bipedally or monopedally, wings extended from shoulders with bent wrists while body is pushed back away from wings, fecal pellet(s) passing between wing opening	Expel fecal waste
	Urinate	Hanging bipedally or monopedally, wings folded but extended from shoulders with bent wrists, while body is pushed back away from wings, with urine stream or drops passing between wing opening	Expel urine waste, does not seem to be used for scent marking
Grooming	Lick	Vigorous licking motion with tongue of front of body including chest, stomach, wings, genitalia, uropatagium, feet, etc.	Self-maintenance, cleaning function of wing or body
	Scratch	Vigorous clawing or scratching motion with foot claws across head and body	Self-maintenance, grooming function of body
Social behavior	Maternal care	Mother and pup(s) interactions including nursing, grooming (licking and scratching), body adjustments	Includes all social interactions between mother and pup(s)
Non-categorized (Other)	Hang relax	Hanging bipedally or monopedally with eyes open	Standard non-sleeping, roosting position
	Hang alert	Hanging bipedally or monopedally with ear movement and eyes open looking around	Attentive roosting position
	Movement	Full body movements and/or adjustments including rotation at roost perch	Adjusting or improving body position on roost perch
	Sleep	Eyes closed, wings folded across body with uropatagium sometimes folded over wings, head and chin tucked toward body; sometimes thumbs or wrists covering eyes	Non-active, rest position
	Stretch	Extension of one or both wings from shoulders and wrists; wing(s) extended or tensed and body sometimes tensed for several seconds before relaxation	Deliberate activity, usually interrupts sleep or preceding sleep
	Yawn	Slow, wide opening or gaping of mouth with inhalation of air followed by shorter exhalation	Involuntary action, usually interrupts sleep or preceding sleep

Diurnal Roost Activity

A total of 114 hours, 50 minutes and 21 seconds (114:50:21) of video was observed and analyzed for the 2017 and 2018 reproductive seasons. Observations at solitary bat roosts accounted for a total of 86:38:17 video-hours while maternity roost observations accounted for a total of 28:12:08 video-hours.

During the 2017 reproductive monitoring season all bats monitored were classified as a solitary bat(s) of unknown sex, no maternity roosts were observed. Since bats were not banded it unknown how many individual bats were observed among roost perches and monitoring periods. However, of the 12 monitoring periods at the DOF roost trees, there were four monitoring periods (31 May, 2 June, 19 June, and 14 September) when two bats were monitored simultaneously at different roost perches. Bats used seven different roost perches within two roost trees (DOF_L1 and DOF_L2) during the 2017 reproductive season. However, at the AMA roost tree (AMA_L1) only one perch was occupied for three consecutive monitoring periods on 16, 24 and 31 August 2017.

During the 2018 reproductive season one maternity roost was observed at the AMA study site. On 27 June 2018 a mother with two infant pups was first observed at a roost perch (L1P7). It is important to note that a solitary bat (no pups present) was first monitored at that location on 29 May 2018 and again on 1 June 2018. This was likely the pregnant mother prior to parturition but is unconfirmed. The mother and pups moved among two roost perches (L1P7, and L1P9) during monitoring periods from 27 June to 20 July 2018 though no roost switching behavior was ever observed on video. On 27 July 2018 the mother and only one pup was located at a new perch (L1P10). It is unknown if the family trio was predated upon, one of the juvenile pups fledged, or other factors that resulted in this change in family structure. The mother-pup pair was observed at yet another roost perch (L1P11) during monitoring periods from 16 August to 28 August 2018 which was the end of observations for 2018. At the DOF study sites bat(s) were observed at three different perches within three roost trees (DOF_L2, DOF_L3, DOF_PN1). There were two monitoring periods (14 June, and 19 June) when two bats were monitored simultaneously at different roost perches.

Overall, there were varying degrees of occupancy at roost perches. The roost perch occupied the most often was L1P1 at roost tree DOF_L1 which was used during five video-monitoring periods (24 May, 31 May, 2 June, 7 June, and 2 August 2017). Seven roost perches

were occupied only once during video-monitoring (DOF_L1 (L1P4, L1P5), DOF_L2 (L2P1, L2P3), DOF_PN1 (PN1), AMA_L1 (L1P9, L1P10).

During video-monitoring, solitary bats at their diurnal roosts spent 93% of their time sleeping (Figure 3.5), whereas the mother bat at maternity roosts spent 86% of her time sleeping (Figure 3.6). Additionally, for solitary bats 6% of their time was spent engaged in grooming behaviors (licking, scratching), and all other behaviors accounted for less than 2% combined. During maternity roost video-monitoring, maternal care accounted for 9% of the mother's time. Maternal care included grooming (licking, scratching), body adjustments, nursing and any other behavior that involved both mother and pup(s). Self-grooming behavior (licking, scratching) accounted for 3% of the mother's time, whereas all other behaviors accounted for less than 2% combined. Removing maternal care and focusing just on individual behavior of the mother at the maternity roost revealed similar patterns of activity as solitary roosting bats where 94% of her time was spent sleeping, 2% was spent engaged in self-grooming behaviors (licking, scratching), and all other behaviors accounted for 2% combined (Figure 3.7).

Figure 3.5 Overall percentage of time (seconds) engaged in a behavior at solitary bat roosts during the 2017 and 2018 reproductive seasons. Note: total time = 311,897 s.
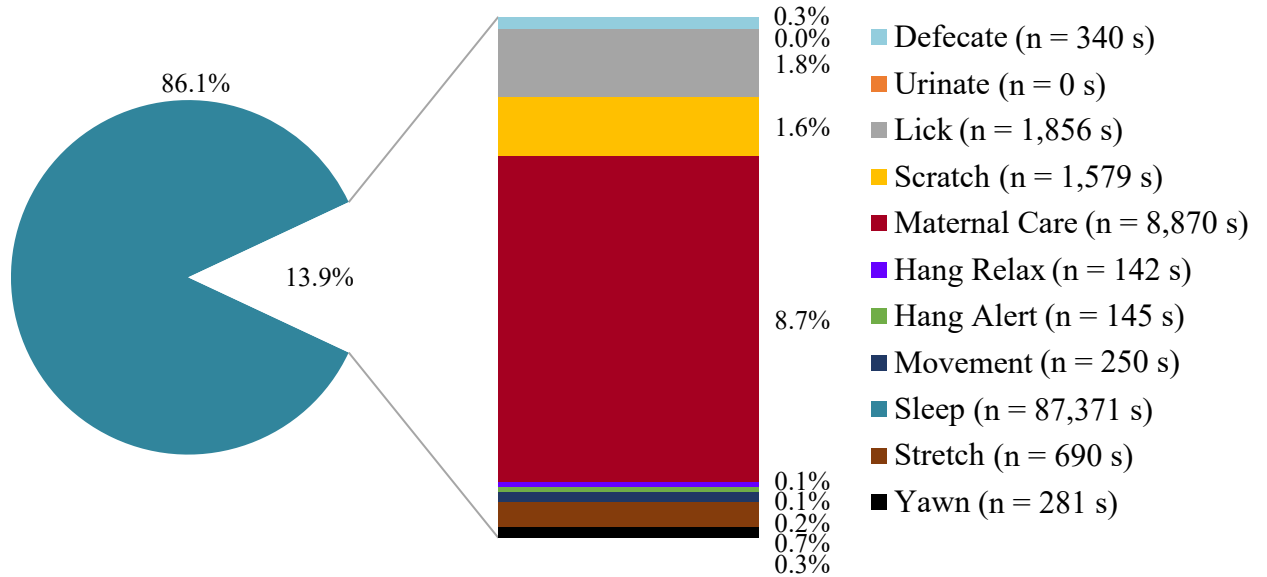
Figure 3.6 Overall percentage of time (seconds) engaged in a behavior at maternity roosts during the 2018 reproductive season. Note: total time = 101,524 s.
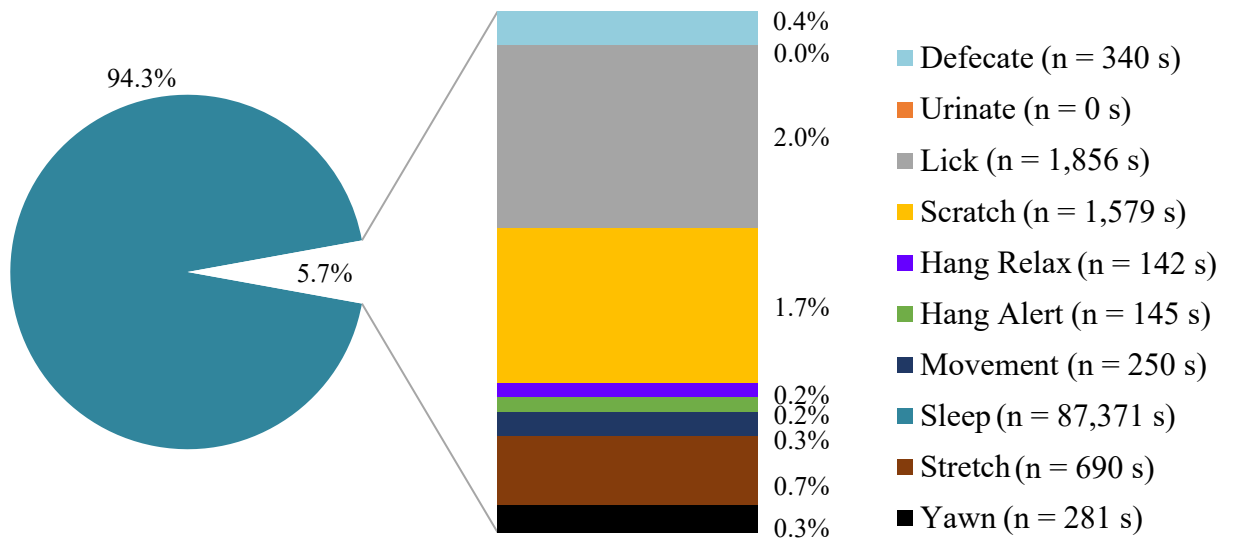

Figure 3.7 Overall percentage of time (seconds) engaged in non-maternal behavior at maternity roosts during the 2018 reproductive season. Note: total time = 92, 654 s.

Pearson's Chi-square goodness of fit tests were used to examine whether the proportion of total time per event statistically deviated from parity for solitary and maternity roost observations. The observed data were statistically different than expected values for both solitary ($\chi^2 = 138,459$, df = 9, p = 2.2e-16) and maternity ($\chi^2 = 734,829$, df = 10, p = 2.2e-16) roost observations.

During video-monitoring a total of 674 discrete behavior events were observed at solitary bat roosts. The most common behavior for solitary bats was grooming (licking, scratching) (43%, 294 events) (Figure 3.8). Stretching, yawning, and movement accounted for 100 (15%), 114 (17%), and 99 (15%) events respectively while defecating and urinating accounted for only 35 events combined (5%). Hang alert and hang relaxed were rarely observed (5%, 32 events) for solitary bats. During video-monitoring at maternity roosts a total of 411 discrete behavior events were observed. Maternal care was the most common behavior observed (54%, 220 events) followed by yawning (15%, 63 events), stretching (11%, 43 events), scratching (8%, 31 events), and licking (6%, 23 events) (Figure 3.9). While defecation was rarely observed (3%, 11 events), urination was never observed at maternity roosts. Similarly, the behaviors of hang relax, hang alert and movement were rare events (5%, 20 events combined). Removing maternal care and focusing just on individual behavior of the mother at the maternity roost revealed that yawning (33%, 63 events), and stretching (23%, 43 events) were the most commonly observed behaviors followed by self-grooming behaviors of scratching (16%, 31 events), and licking (12%, 23 events) (Figure 3.10). Rarer events included, movement (7%, 13 events), defecate (6%, 11 events), hang alert (3%, 6 events) and hang relax (0.5%, 1 event).

Pearson's Chi-square goodness of fit tests were used to examine whether the proportion of different types of events statistically deviated from parity for solitary and maternity roost observations. The observed data were statistically different than expected values for both solitary ($\chi^2 = 398.09$, df = 8, p = 2.2e-16) and maternity ($\chi^2 = 952.38$, df = 9, p = 2.2e-16) roost observations.
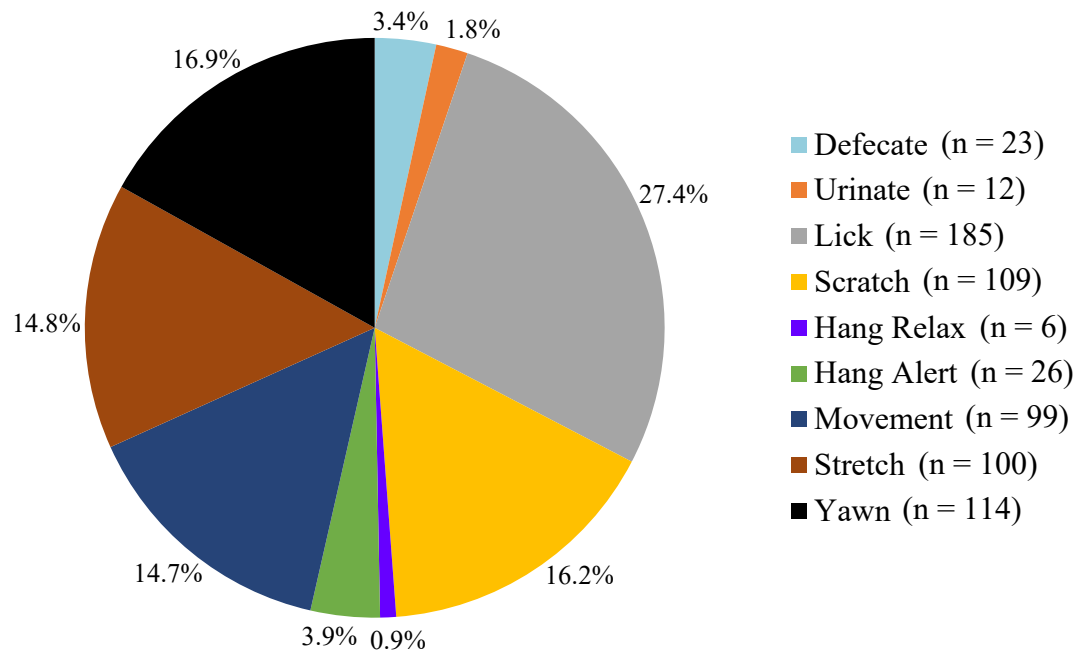
Figure 3.8 Total behavior events observed at solitary bat roosts during the 2017 and 2018 reproductive seasons. Note: total events = 674.
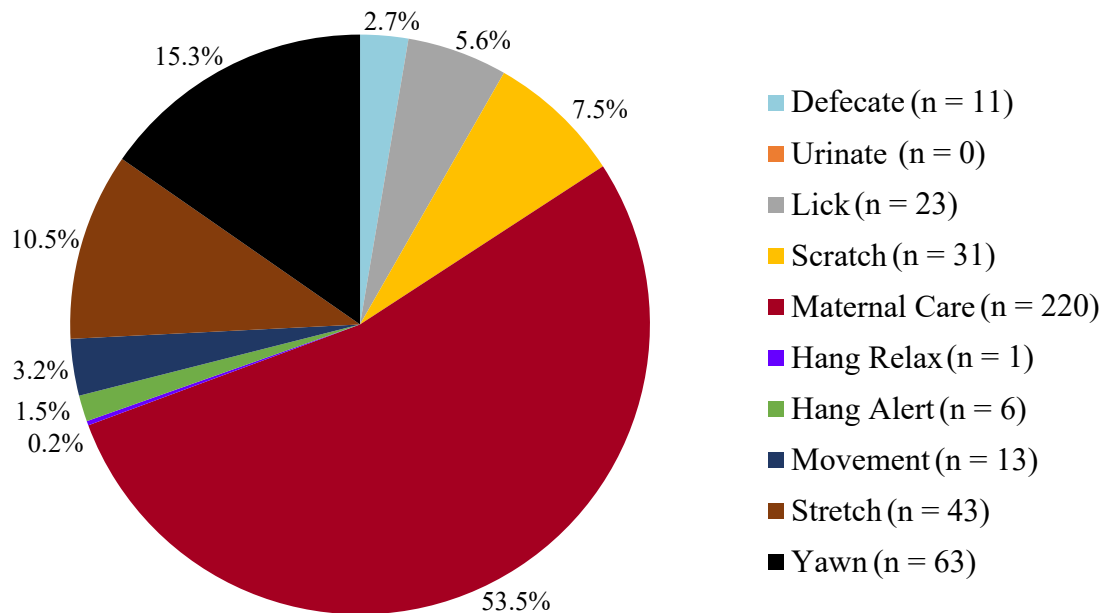

Figure 3.9 Total behavior events observed at maternity roosts during the 2018 reproductive season. Note: total events = 411.
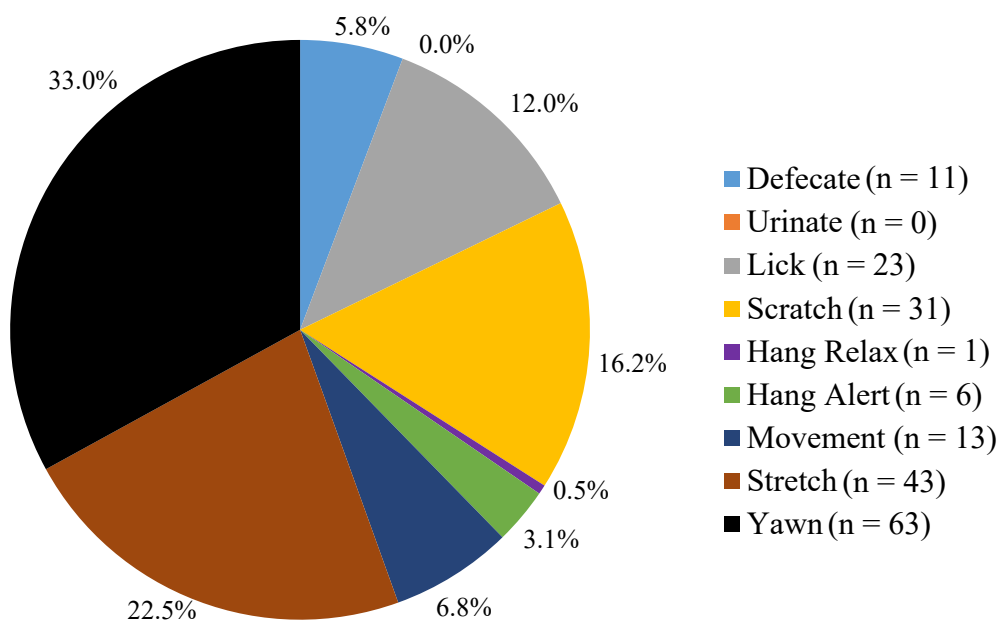
Figure 3.10 Total non-maternal behavior events observed at maternity roosts during the 2018 reproductive season. Note: total events = 191.

DISCUSSION

Roosting behaviors observed for the Hawaiian hoary bat were similar to those observed in solitary individuals of other bat species. However, many studies focus on colonial bat species therefore numerous social behaviors noted in these species were not observed for *L. c. semotus*. For example, thermoregulatory behavior commonly observed in temperate bat species (e.g. Markus and Blackshaw 2002) such as "wing-fan" where bats fan their wings to cool their body temperature, was not observed in any video-monitoring indicating *L. c. semotus* may not engage in this behavior often or at all. This may suggest that Hawaiian hoary bats select for roosts with favorable thermoregulatory conditions and less energy is spent regulating body temperature. However, while the roosts observed in this study were located at low elevation (<100 m asl) bats roosting in higher elevations (>1,000 m asl) may exhibit additional behaviors in response to lower ambient temperatures including engaging in short bouts of torpor (pers. observation). Additional observations, particularly during the crepuscular time period prior to bats emerging from a roost, as well as observations at roosts in upland habitat and during additional seasons are

necessary to gather a full range of conditions and behaviors and a more detailed picture of a daily and seasonal activity budgets for *L. c. semotus*.

Quantifying roost occupancy was difficult to ascertain without having identified individual bats but it was apparent that there were certain degrees of roost perch switching occurring for both the maternity and solitary bats at both sites. Anecdotal accounts of bat presence during the reproductive season as far back as 2005 at site DOF (Bonaccorso *et al*. 2015) and even longer (~40 years) at the site AMA (landowner, pers. observation) indicates long-term use of these sites by at least a small subset of the bat population on Hawai'i Island. Capture and genetic analysis may reveal if there is natal philopatry at these sites.

Lower levels of activity were observed for solitary bats at roosts compared to levels of activity at maternity roosts. However, further observations particularly for maternity roosts will be necessary to statistically analyze these differences. Pearson's Chi-square goodness of fit tests showed that the proportion of different types of events and time per event statistically deviated from parity for both solitary and maternity roost observations. That is, proportion of different types of events and time per event were not equally distributed throughout the roost observation periods. This was not an unexpected result as some behaviors are expected to account for more time (i.e., sleep) at Hawaiian hoary bat diurnal roosts.

Maternal care was mostly comprised of grooming behavior (licking) and short body adjustments that may facilitate nursing. Predation or disturbance events at the maternity roosts were not observed on video during the observation periods. Nevertheless, the maternity roosts that were observed in this study began with observations of a mother and two pups. However, sometime between the 20 July and 27 July 2018 observation periods only one pup was present with its mother until the end of monitoring for the season. While the mother and pups jointly switched roost perches (L1P7 to L1P9) approximately 2-3 m between those perches, they remained in the same general area of the roost tree. However, when they switched roost perches again (L1P9 to L1P10) the distance between those perches was approximately 17-18 m and across to the opposite side of the roost tree. It was also around the time of this perch switch that one of the pups was unaccounted for at the new perch location (L1P10). While it is difficult to speculate what event may have occurred that resulted in this circumstance, it is an otherwise interesting anecdote and though predation or threat of predation was not observed during this study, it cannot not be ruled out. Gathering additional information and observations at maternity

roosts may provide information on pup survivorship until fledging which is a critical metric for population viability analyses and has important management applications.

While the methods of video recoding in this study did not allow for recording of vocalizations at the roost level, other studies using ultrasonic bat echolocation detectors at maternity roosts (Montoya-Aiona *et al*. 2020) did not record distinct daytime vocalizations between mothers and pup(s). Furthermore, more than 95% of recorded echolocations were between the nighttime hours of 18:00 to 05:59 with less than 5% bat echolocations recorded from 06:00 to 17:59, of which were mostly confined to dawn and dusk hours where the mother was likely emerging from or returning to the roost area (Montoya-Aiona *et al*. 2020). Further studies with paired echolocation detectors and video recording at maternity roost sites could be used to determine if there are daytime vocalizations and associated observed behavior at roosts.

The ethogram presented here represents the first detailed description of the behavior of *L. c. semotus* recorded at diurnal roosts. It serves as a baseline of diurnal behavior for the species with important conservation implications. Examining the behaviors observed at solitary and maternity roosts as well as their context may help give insight into limiting factors for the Hawaiian hoary bat such as roost disturbance, predation and pup survivorship.

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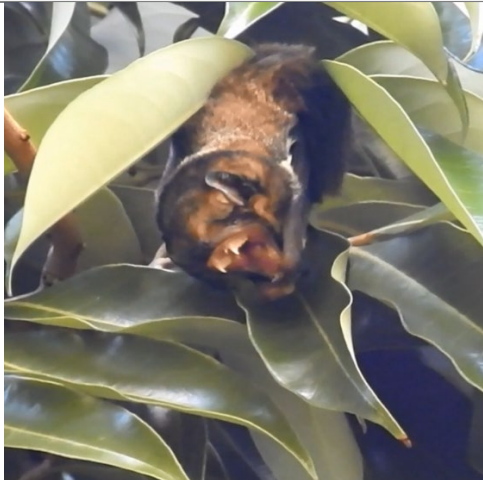Example still images of Hawaiian hoary bat diurnal roosting behavior.

Behavioral category	Behavior	Example image	Example context
Excretion	Defecate, Urinate		Posture common for excretion, urine or fecal pellets pass through wing opening
Grooming	Lick		Head bent forward toward body, licking wing membrane
	Scratch		Scratching top of head with foot

Behavioral category	Behavior	Example image	Example context
Social behavior	Maternal care		Mother with two pups nursing under her wings
Non-categorized (Other)	Hang relax		Relaxed posture, eyes open
	Hang alert		Alert posture, eyes open, ears held back and attentive

Behavioral category	Behavior	Example image	Example context
	Movement		Turning body, holding branch with thumb while adjusting foot hold on perch
	Sleep		Sleeping posture, uropatagium folded over body and wings, head tucked with wrists covering eyes
	Stretch		Body arched, stretching to one side, prior to extending wing(s)

Behavioral category	Behavior	Example image	Example context
	Yawn		Yawn with mouth gaping, eyes open

CHAPTER 4. GENERAL DISCUSSION

SUMMARY OF KEY FINDINGS

This thesis research focused on two relatively unknown areas of Hawaiian hoary bat ecology; roost selection and roosting behavior. Chapter 2 investigated roost selection at the habitat stand, roost tree and roost perch level. Hawaiian hoary bats roosted in a variety of tree species and habitat stand types including native and non-native habitats at a range of elevations. A majority of roosts were located at lowland (<1,000 m asl) elevations and all maternity roosts (n = 3) were located below 500 m asl. Roost trees selected by Hawaiian hoary bats were larger in both height and DBH than randomly sampled trees and females selected roost trees that were larger in height and with a greater percent canopy cover compared to roosts selected by males. There were not statistically significant differences in roost tree DBH or distance to nearest tree between males and females. Statistical comparisons between maternity roost characteristics versus solitary roosts or random trees could not be conducted because sample sizes for maternity roosts were not large enough for sufficient power. There were not statistically significant differences between roost perch canopy cover and height between males and females. Although roost perch aspect was not statistically different from uniform distribution, there was a trend toward the northwest to southeast sides of roost trees.

Chapter 3 explored the diurnal roosting behavior of the Hawaiian hoary bat. A total of 11 discrete behaviors in four behavioral categories were identified and described. Lower levels of activity were observed for solitary bats at roosts compared to levels of bat activity at maternity roosts. At maternity roosts, maternal care was mostly comprised of grooming behavior and short body adjustments. Observations at the maternity roosts showed a change in family structure from a mother with two pups to a mother with only one pup in the middle of the reproductive season of 2018. There was also a degree of roost perch switching during the reproductive season, the reasons for which remain unknown. Although predation or disturbance at the roost locations were not observed on video recordings, they could not be ruled out.

MANAGEMENT IMPLICATIONS

The results of this thesis are consistent with research on other lasiurine bats showing that bats generally select larger trees (both height and DBH) compared to those available in the

landscape (Perry and Thill 2007, Perry *et al.* 2007). Large trees did not appear to be a limited resource in habitat stands in the study area. However, large scale clearing and trimming projects may result in perturbations that reduce the density of suitable roost trees. This may have negative fitness consequences regardless of whether some suitable roost trees remain for bats to use. Although one-way movements by Hawaiian hoary bats within a night have been measured over distances of up to 11.3 km (Bonaccorso *et al.* 2015), these types of movements are undoubtedly energetically expensive. Reducing suitable roosting habitat may result in bats spending greater energy moving to foraging resources or between roosts. Furthermore, maintaining a diversity of roosting options at a variety of habitats and elevations may be necessary. Though current mitigation guidance emphasizes a management preference for restoring native habitats in order to provide net environmental benefits (Amlin and Siddiqi 2015), Hawaiian hoary bats were found in a variety of habitat types and elevations, therefore diversity in mitigation areas may be important to encompass the full range of roost types across the landscape.

Roost disturbance and predation were not observed during video recording but could not be ruled out. The vulnerability of Hawaiian hoary bats to roost disturbance or predation is still unknown and may have different implications at roosts of solitary bats versus maternity roosts. Solitary bats may be more likely and able to flee a roost tree if disturbed. While transport of non-volant pups has been observed for both frugivorous and nectarivorous species (e.g., Hernández-Mijangos *et al.* 2009), the carrying of juveniles by small aerial insectivorous species is uncommon (Kunz and Hood 2000). While a change in mother-pup(s) dynamic occurred midway through the 2018 reproductive season, pup survivorship until fledging was unable to be fully established. Although three maternity roosts were identified in 2019 and reported in Chapter 2, they were not able to be video-monitored for roosting behavior due to accessibility and personnel reasons. Notably, two maternity roosts each consisted of a mother and one pup while the third was a mother with two pups. Though the reasons for these differing mother-pup(s) assemblages are currently unknown, Hawaiian hoary bat fecundity and pup-survivorship to fledging may be considered critical factors in conservation and management decisions.

FUTURE RESEARCH

This thesis has provided new data on the ecology of the Hawaiian hoary bat considered critical by Federal and State of Hawaiʻi entities (USFWS 1998, Amlin and Siddiqi 2015).

However, additional study of this elusive species is needed to collect sufficient data to make statistical evaluations of maternity roost selection. Increased effort on tracking bats in upland habitats (>1,000 m asl) should also be considered. Most of the roost trees identified in this study were located in lowland (<1,000 m asl) habitats which was at least partially due to the relative ease of radio-tracking along established roads and trails present in the lowlands. Although considerably more labor-intensive, increasing roost sample sizes in upland habitats may make seasonal roosting habitat as well as elevational analyses possible.

Emphasis on tracking female bats to maternity roosts is particularly important to understand maternity roost habitat characteristics and potentially gathering additional behavioral observations at these roosts. Information on predation and disturbance at roosts as well as pup-survivorship until fledging requires intensive monitoring efforts at maternity roosts. Gathering additional information and observations at maternity roosts may provide information on pup survivorship until fledging, roost disturbance and potential predation which have important management applications. Future studies may provide additional data on these as well as address remaining data gaps in the understanding of the habitat use and behavioral ecology of the Hawaiian hoary bat.

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