SIGNAL INTERACTIONS BETWEEN NATIVE AND INTRODUCED FOREST BIRDS OF HAWAIʻI ISLAND AND PREDICTING DISTANCE OF SIGNALS FROM THEIR ENERGY

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Abstract

Passive acoustic monitoring using autonomous recording units (ARUs) offers unique opportunities to investigate both theoretical and applied ecological questions. I used Song Meter SM4s to answer: (1) whether native and introduced birds in Hawai‘i are dividing acoustic space in time and frequency, and (2) whether wildlife managers can improve their density estimates of bird species by achieving unbiased distance measurements from ARUs. First, using recordings I collected from a diversity of vegetation types, I compared the observed overlap between introduced and native bird vocalizations from what was expected under a null model of 500 vocalization randomizations. I found that overlap did not differ from the null distribution and was unaffected by community composition nor vegetation type, suggesting that introduced birds are not having a strong impact on native forest bird communication. Second, using field recordings collected while observing vocalizing birds, I modeled distances between birds and the ARUs, measured from range finders as a function of the random effects of maximum power level (amplitude) of bird vocalizations, the orientation of the bird to the microphone, and wind and rain levels, with the species and call type as fixed effects. Overall, there was no strong relationship between distance and any of the random effects. However, when modeling within individual call types, I found four call types among four species showing relationships between distance and sound power level, suggesting that while this method has potential for wildlife monitoring, it requires further refinement.

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Chapter 1: Signal Interactions Between Introduced and Native Forest Birds on Hawai‘i Island

INTRODUCTION

Vocalizing animals use acoustic signals to attract mates, defend territories, warn conspecifics of danger, and find food. Under the acoustic niche hypothesis, in a pristine environment, each vocalizing species has evolved signals which avoid interference from other species through adjustment of frequency and timing (Krause 1993). For example, in highly biodiverse assemblages of birds (Planqué and Slabbekoorn 2008, Luther 2009), frogs (Deullman and Pyles 1983, Chek et al. 2003), fish (Ruppe et al. 2015), and insects (Sueur 2002, Schmidt et al. 2012), vocalists with overlapping frequencies tend to signal at different times, and those signaling simultaneously tend to occupy different frequency bandwidths, presumably to avoid acoustic overlap.

Introducing novel sounds into these soundscapes, or acoustic environments, however, can disrupt this balance (Hopkins et al. 2022). Anthropogenic noise, for example, can induce changes in native species behaviors and potentially compromise their fitness if these changes reduce the quality of their signals (Slabbekoorn and Ripmeester 2008). Similarly, vocalizing invasive species have been demonstrated to infiltrate native species' acoustic niches, causing them to modify their natural vocalizations through changes in frequency, timing (Bleach et al. 2015), and/or loudness (Both & Grant 2012, Tennessen et al. 2016, Medeiros et al. 2017). Such changes may have adverse effects, including negatively impacting pairing success, compromising foraging opportunities, and/or weakening territorial defense. Alternatively, failing to respond to invasive species signals may result in predation (Hopkins et al. 2022), or acoustic interference, which in the context of mating and territorial calls, can also lead to reduced breeding success and survival (Bradbury & Vehrencamp 2011, cited in Staniewicz et al. 2023).

The most frequently suggested consequence of invasive species vocalizations is their negative impact on native species reproductive success (Both & Grant 2012, Bleach et al. 2015,

Tennessen et al. 2016, Medeiros et al. 2017, Hopkins et al. 2022). For example, experimental playback of American bullfrogs (*Lithobates catesbeianus*) in the Atlantic forest, where they are an invasive species, caused native treefrogs (*Hypsiboas albomarginatus*) to increase their frequencies during and after playback calls, and decrease call duration following playback, which could compromise signaling of male quality vital to mate selection (Both & Grant 2012). However, it may be that these behavioral responses were to introduced noises in general, and not only to introduced species. A later study in the Atlantic forest found that four native frog species changed their calls both temporally and in frequency from bullfrog, native frog, and white noise sounds, regardless of whether they spectrally overlapped or not (Medeiros et al. 2017). Similarly, in Australia, one native frog species altered its calling rate in response to introduced toad playback, but also to native frog and lawn mower noise playback (Bleach et al. 2015). Green treefrogs (*Hyla cinerea*) in North America likewise decreased call length and increased amplitude in response to both invasive Cuban treefrog (*Osteopilus septentionalis*) and white noise within the same frequency range, but not white noise beyond this range (Tennessen et al. 2016). Therefore, it may be the frequency bandwidth (Littlejohn & Martin 1969, Tennessen et al. 2016) and/or timing (Bleach et al. 2015) of introduced sounds, and less so their biotic or abiotic origin, that elicits an inhibitory response. Regardless, introduced sounds which do elicit changes in native male advertisement calls may compromise their attractiveness to females (Both & Grant 2012, Bleach et al. 2015, Tennessen et al. 2016), and their inability to completely avoid overlap may compromise their signal clarity (Brumm et al. 2004, Bleach et al. 2015).

New vocal behaviors may also be energetically suboptimal (Both & Grant 2012, Bleach et al. 2015), or reflect natural behaviors becoming suboptimal. To avoid extra energy expenditure, species may decrease call duration to compensate for increasing their amplitude to be heard above the noise (Tennessen et al. 2016), or increase calling between the calls of the invading species (Bleach et al. 2015). In addition, while species appear to have behavioral plasticity that allows them to adjust to novel noises in their environment, otherwise optimal species-specific strategies, such as decreasing the frequency of their vocalizations to improve transmission, can also result in increased overlap (Medeiros et al. 2017), decreasing their signal-to-noise ratio (Brumm et al. 2004).

When an invasive species becomes an abundant, loud, and dominant contributor to the soundscape, its potential signal overlap with native species, and by extension, its potential impact on them, increases. For example, Farina et al. (2013) and Farina & Pieretti (2014) demonstrated that native Eurasian Blackcaps (*Sylvia atricapilla*) temporally shifted their songs in response to introduced Red-Billed Leiothrix (*Leiothrix lutea*) songs in Northern Italy. One could expect native species in ecosystems having multiple acoustically invasive species to face even more complex challenges, as the constraints of signal competition arise from different directions spectrally and temporally. However, to my knowledge, the simultaneous impacts of multiple introduced species on the sonic environment has so far not been investigated.

Hawai‘i presents a unique opportunity to explore this question, due to the collapse of its avian communities, and its menagerie of introduced bird species. Of its 87 known native forest bird species, only 26 (less than one-third) remain today (Department of Land and Natural Resources, Division of Forestry and Wildlife: Wildlife Program, 2023). By the early 20th Century, the noticeable loss of bird song motivated government organizations and naturalization societies such as the Hui Manu to introduce exotic bird species to Hawai‘i, some specifically chosen for their hardiness and melodious songs (Berger 1974 and Foster 2009, cited therein). While most failed to establish (Foster 2009), Warbling White-eye (*Zosterops japonicus*), Northern Cardinal (*Cardinalis cardinalis*), House Finch (*Haemorhous mexicanus*), Red-Billed Leiothrix, and many others have become the most abundant bird species in Hawaiian lowland forests, (Kendall et al. 2022, Pyle & Pyle 2017, Spiegel et al. 2006, Pratt 1994). Meanwhile, the few remaining Hawaiian forest bird species today face threats from invasive predators, avian malaria, and habitat degradation and fragmentation (Banko & Banko 2009). However, to date there is no published information on whether introduced species are influencing native species communication in Hawai‘i, as they do in other ecosystems (Farina et al. 2013, Medeiros et al. 2017).

A recent study (Hart et al. 2021) found that a high degree of frequency overlap among 10 forest bird species in Hawai‘i (both native and introduced) was apparently compensated for by temporal partitioning of vocalizations, such that there was less simultaneous overlap in frequency and time than expected by chance. However, interactions between native and

introduced species were not within the scope of their study. The three introduced species examined in Hart et al. (2021), the Red-Billed Leiothrix, Northern Cardinal, and Warbling White-Eye, were introduced to Hawai‘i Island between 1928—1932, between 1929—1931, and in 1937, respectively (Pyle & Pyle 2017), representing nearly a century of novel interactions with Hawaiian soundscapes. Sound recordings of Hawaiian avian communities predating these introductions do not, to my knowledge, exist. Therefore, I cannot observe cause-and-effect relationships of novel vocalists on native soundscapes. However, there is a noticeable gradient in representation of introduced bird species across Hawaiian communities, with generally the highest densities of introduced birds in lowland, non-forested habitats such as agricultural fields, and lower densities in high-elevation, contiguous native forest (Foster 2009). I sought to answer whether the representation of introduced bird species is associated with the degree of acoustic niche partitioning in avian communities on the windward slope of Mauna Kea. Few other studies have tested the acoustic niche hypothesis in communities with multiple non-native avian vocalists (Azar & Bell 2017), despite the evidence of introduced birds having an effect on native bird communication in other systems (Farina et al. 2013).

I defined acoustic niche partitioning as less simultaneous overlap in frequency and time than expected randomly, based on a null model generator which randomized the timing of signals. I expected to find less acoustic overlap than expected by chance, i.e. acoustic niche partitioning, even in communities with many introduced birds, because other species have diverged in signal characteristics within the span of mere decades (Grant & Grant 2010). However, I expected to find the most acoustic overlap in the introduced-dominant sites, due to the shorter relative time frame (within the last century, Pyle & Pyle 2017) for new vocalists and native birds to evolve differences in their vocalization structures. I expected the least amount of acoustic overlap in the native-dominant forest bird communities, given their longer timeframe (thousands to millions of years, Lerner et al. 2011) for acoustic partitioning to develop.

METHODS

Song Meter Deployment and Site Characteristics

Sixteen Song Meter (SM4 Wildlife Acoustics Inc.) stations were selected across a variety of vegetation types at Hakalau Forest National Wildlife Refuge (hereafter, Hakalau, 19.832˚N, 155.285˚W, **Figure 1-1A, B**) and a coffee (*Coffee arabica,* Rubiaceae) and cacao (*Theobroma cacao,* Malvaceae) farm in Paukaʻa (19.765˚N, 155.119˚W, **Figure 1-1A, C**) to capture a diversity in community composition with different percentages of introduced bird species. Hakalau stations were in closed ʻŌhiʻa (*Metrosideros polymorpha*, Myrtaceae) wet forest, closed Koa (*Acacia koa*, Fabaceae)-ʻŌhiʻa wet forest, closed Koa-ʻŌhiʻa mesic forest, open Koa-ʻŌhiʻa wet forest, and open Koa-ʻŌhiʻa mesic forest, whereas Paukaʻa stations were in either alien wet grassland or cultivated agriculture (see **Table–1**) based on land classification data from the Hawaiʻi Gap Analysis Project (2001 imagery, open access) and ground truthing. Recordings were collected from June 1 to August 31, 2022. Due to the limited number of Song Meters, some stations were on rotating two-week schedules with others and thus had staggered recording dates, whereas others recorded continuously. Some Song Meters also malfunctioned and recorded fewer days than scheduled. However, all devices recorded for a minimum of 22 days per station. Stations were spaced a minimum of 150 m from each other to avoid detecting the same vocalizations twice, except however, at Paukaʻa; due to limited space, some stations were placed only 75 m apart and were set to record on alternate two-week schedules from their nearest neighbors.

At each station, a Song Meter was placed 1-1.5 meters above the ground and programmed to record on a five-minute continuous duty cycle (i.e. recording for the initial five minutes followed by five minutes of no recording) from sunrise to 11:00 am, the time of peak vocal activity for Hawaiian forest birds (Hart et al. 2021). To increase the sample size, recordings from Song Meters of a different study at Hakalau were opportunistically used. These were similarly placed and located at the edges of primary or secondary forest, but had schedules of 5:00am to 8:00pm, recording 10 minutes on and 20 minutes off repeatedly (“Aki Cabin”) or 5 minutes on and 15 minutes off repeatedly (“Pedro,” “Pua ʻAkala”). In these cases, only

recordings that fell within the timeframe of the study and between sunrise and 11:00am were used. All recordings were made as .WAV files with a 44.1 kHz sampling rate.

Hakalau is largely Hawai‘i montane rainforest with an average annual temperature of 13.1 ˚C and average annual rainfall of 3550 mm (Giambelluca et al. 2014). There is no dry season, and wet months (>250 mm) can occur throughout the year. Annual cloud frequency is roughly 50% (Giambelluca et al. 2014). The canopy is dominated by Koa and ‘Ōhi‘a lehua, although various tracts were deforested by agriculture and have since been reforested with Koa (Hart et al. 2020). Mid-canopy trees and shrubs include ‘Ōlapa (*Cheirodendron trigynum*, Araliaceae), Kāwa‘u *(Ilex anomala*, Aquifoliaceae) Kōlea (*Myrsine lessertiana*, Primulaceae), Pilo (*Coprosma ochracea*, Rubiaceae), and Pūkiawe (*Leptecophylla tameiameiae*, Ericaceae), as well as the tree fern Hāpu‘u pulu (*Cibotium glaucum*, Cibotiaceae). In open areas ground cover has been taken over by a variety of pasture grasses, including: *Pennisetum clandestinum* (Poaceae) and *Ehrharta stipoides* (Poaceae). Recently some tracts are becoming invaded with gorse (*Ulex europaeus*, Fabaceae) (pers. observation). The relief is gently sloped as one follows the drainages of Mauna Kea Volcano such as Honoli‘i Stream. Parent material is silty clay (Sato et al. 1973) >10,000 years old (Wolf and Morris 1996). Hakalau remains one of the most pristine montane rainforests in the state with the highest endemic forest bird diversity.

The Pauka‘a site (19.765˚N, 155.119˚W) is mostly alien perennial grassland with an average annual temperature of 20.3 ˚C and average annual rainfall of 4950 mm (Giambelluca et al. 2014). Wet months (>250 mm) span the entire year, and annual cloud frequency is roughly 66%. Within the mostly Guinea grass (*Megathyrsus maximus*, Poaceae), dozens of coffee and cacao trees grow in an orchard, with introduced shade trees such a Kukui (*Aleurites moluccanus*, Euphorbiaceae) and Common Guava (*Psidium guajava,* Myrtaceae) and some ‘Ōhi‘a and Koki‘o Ke‘oke‘o (*Hibiscus arnottianus*, Malvaceae) interspersed among them. A grove of Strawberry Guava (*Psidium cattleyanum,* Myrtaceae) and African Tulip (*Spathodea campanulata,* Bignoniaceae) grow beside a stream, and upslope of the property a Rose Gum (*Eucalyptus grandis*, Myrtaceae) forest grows. The relief is gently sloped with steeper gulches descending into Honoli‘i Stream and its tributaries. Parent material is mostly alkalic and transitional basalt at

least 65,000 years old (Wolf and Morris 1996). The songbird community at this site is entirely introduced, except the ʻIo or Hawaiian Hawk (*Buteo solitarius*) which frequent the area.

Acoustic Annotation Methods

Acoustic analysis was adapted from the methods of Hart et al. (2021). One of the sampling days was randomly selected for each site, and of these, the earliest three to six consecutive tracks of five- to ten-minute length having birdsong, but no rain (except occasional drops), were selected. All recordings were visualized and analyzed as spectrograms using the RavenPro Software version 1.4 (K. Lisa Yang Center for Conservation Bioacoustics). Within each 5-minute track, a 0.5-second selection in the quietest part of the recording was made to measure the maximum power level of background noise. Selection boxes were drawn around every vocalization ≥5 decibels (dB) above the background noise and identified to species (**Figure 1-2A**). Begging calls were excluded from analysis with the assumption that their function does not fit into the context of sound partitioning (Tobias et al. 2014). For each selection, the "Add Measurements" feature in RavenPro was used to calculate the following acoustic parameters: begin and end time, low (minimum), high (maximum), and peak (having the greatest energy) frequencies, and average and maximum power levels (SPLs) (**Figure 1-2B**). Four-letter species code, vocalization type (call or song), and the presence of acoustic overlap from another bird (1 for yes, 0 for no) were added manually by annotators. Acoustic overlap was defined as two vocalizations occupying the same frequency and time such that two or more notes intersect. Additional comments were made as necessary, including presence of wind, insects, coqui frogs, helicopters, raindrops, or other noises overlapping with a vocalization, although these were still marked "0" unless the noise came from another bird. To help with standardization, if there was a pause of 0.2 seconds or more between notes, these were selected as different vocalizations rather than one. Likewise, when a vocalization had multiple harmonics, only those ≥5dB above background were selected. Finally, boxes were drawn as tight as possible around notes or phrases while still preserving the parts ≥5dB above background. Annotators (N. Hunt, S. Charlot, and J. Himmelman, see Acknowledgements) were calibrated to follow the same methodology above.

Statistical Analysis

All statistical analyses were performed in R Software (version 4.1.1).

To account for biases in annotation, a standardized selection procedure was created and distributed by NJH, the primary annotator, to the two secondary annotators (SMC, JM). All three annotators made selections from a one-minute recording, each blind to the others' work. Then a chi-squared test for independence was performed on the number of selection overlaps proportional to the total number of selections made by each secondary annotator, relative to those made by the primary annotator, to check for differences in annotator bias.

To compare frequency use between species, the complete frequency range was visualized for each species, measured as the minimum low frequency and the maximum high frequency observed for that species. Then, the mean low frequency and mean high frequency for each species were built into a matrix of species pair combinations for species observed at the same recording station. The proportion of the frequency range of the first species (Species 1) which was overlapped by the second species (Species 2) was calculated and built into this matrix. Each species pair occurred twice, but in different order, such that each species had a calculated proportion of frequency overlap by the other. Next, these species pairs were classified as native-native, native-introduced, and introduced-introduced. Finally, the mean proportion of frequency overlap was calculated for each classification, and compared using One-Way ANOVA and a Tukey's honestly significant difference (HSD) test.

Additionally, the proportion of introduced species vocalizations relative to the total number of vocalizations was calculated for each five-minute track, then averaged across all tracks recorded from the same station. Proportions of introduced species vocalizations were used to compare community composition between stations and field sites.

The null model approach used by Hart et al. (2021) was adapted to examine temporal partitioning of acoustic space. Within the 15- to 30-minute sampling periods at each site, the beginning of each vocalization was randomized, keeping its duration, frequency range, and power level unchanged. This randomization was repeated 500 times to generate a null distribution of heterospecific overlap; the amount expected by chance. Overlap was only examined for heterospecific pairs of vocalizations because within a population, male-male

competition (Todt 1981), pair duetting (Thorpe 1963), and other behavioral circumstances generate overlap that may not be reflective of a species' ability to partition sound.

The number of observed heterospecific pairs of overlapping vocalizations were compared against the null distribution generated by randomizations. These comparisons were also segregated into native-native, native-introduced, and introduced-introduced heterospecific pairs and evaluated for differences in the amount of overlap.

Next, the probability (P) of achieving the observed number of overlapping pairs, or more extreme numbers under the null model, was calculated using the *pnorm* function in R. If P was $\leq$ 0.025, significantly less overlap was observed than expected under the null model, supporting the ANH. If P was $\geq$ 0.975, there was significantly more overlap than expected under the null model, supporting the acoustic clustering hypothesis (Hart et al. 2021, Tobias et al. 2014). The differences in the observed acoustic overlaps and the departure of these observations from the null were compared across Song Meter stations relative to the proportions of introduced species at each station. To check for a hidden effect, a sign test on the differences between the observed and random overlap occurrence was conducted for this second iteration.

RESULTS

The first chi-squared test revealed that one secondary annotator did not differ from the primary ($\chi2$=02.98, n1=76, n2=66, df=1, p=0.084) whereas the other secondary did ($\chi2$=34.14, n1=76, n2=61, df=1, p<0.001). Following recalibration and correction of their previous work, the other secondary annotator performed another one minute of selections, blind to the primary's work, and this time their selected overlaps did not differ in number from the primary observer's ($\chi2$=1.32, n1=26, n2=44, df=1, p=0.25).

Native and introduced species utilized similar frequencies (**Figure 1-3A, B),** however, when divided into species pairs which co-occurred at a recording station, native species had higher proportions of frequency overlap with one another than with introduced species (**Figure 1-4,** difference = 13.5% [9.49%, 17.4%]), and had much great overlap compared with introduced species pairs (difference = 26.2% [21.7%, 30.7%]).

Comparing the null model against the observed number of overlaps revealed no difference between the observations from each station with its null distribution (*Pnorm* values all >0.025, see **Table-2, Figure 1-5**). Native-native, native-introduced, and introduced-introduced heterospecific vocalization pairs all tended to have less overlap than the null distribution, but the differences were not significant, nor were there significant differences in the amount of overlap between native-native, native-introduced, and introduced-introduced species pairs (**Figure 1-6**). However, a sign test revealed that the observed numbers of overlaps were less than the median overlaps from the null distributions more often than expected by chance for 13 out of the recording 16 stations (probability of success= 0.19, successes=3, n=16 trials, p=0.02).

DISCUSSION

The lack of significant difference between the observed vocalization overlaps and the null distribution created through randomization of start time for each recording station fails to provide evidence for forest birds in these communities temporally partitioning their acoustic signals, as predicted by the ANH and demonstrated by Hart et al. (2021). However, there is evidence for a hidden effect, based on the observed number of overlaps for each site being lower, rather than higher or equal to, the median null expectation more frequently than expected randomly. Neither are forest bird species in these communities partitioning frequency, based on the high amount of overlap in their frequency ranges. Native species pairs had the greatest overlap in their frequency ranges compared with native-introduced species pairs and introduced-introduced species pairs. This pattern supports the acoustic clustering hypothesis (Tobias et al. 2014) and may be explained by constraints in native birds' acoustic environment (Cardoso & Price 2010, Morton 1975) or physiology (Memet et al. 2022). However, vocalizations were not more clustered than expected based on random timing.

Alternatively, the lack of acoustic partitioning may be explained by a collapse in acoustic communities following a significant number of avian extinctions. Divergence in morphological traits and frequency use between closely related bird species may be a consequence of, and maintained by, competitive exclusion (Krishnan and Tamma 2016, Grant & Grant 2010). As closely related-species disappeared in Hawai‘i, the barriers reinforcing acoustic divergence due

to competitive exclusion likely deteriorated, resulting in a competitive release in available signal space for those species which survived. Given that many of the Hawaiian bird extinctions preceded the wave of introductions occurring in the early 20th century by decades, there may have been sufficient time for such a relaxation of signal structure in surviving species to occur.

Another, and not mutually exclusive, explanation is population declines resulting in a loss of vocal diversity and higher vocal convergence between species. On Kauai, the ʻAkekeʻe (*Loxops caeruleirostris*), Kauʻi ʻAmakihi (*Chlorodrepanis stejnegeri*), and ʻAnianiau (*Magumma parva*) have all begun to converge in signal structure due to the loss of signal complexity and/or lack of acoustic tutors available, negatively impacting cultural transmission (Paxton et al. 2019). It is unclear whether the convergence I observed between ʻApapane and ʻIʻiwi vocalizations reflects historical patterns or a recent loss of vocal complexity. However, given the high densities of both species at Hakalau, and that ʻIʻiwi have overall remained stable while ʻApapane have increased at the refuge since 1989 (Kendall et al. 2022), this is unlikely. Future research might compare historical vocal complexity and similarity in both species relative to the present day.

Hawaiʻi is a highly disrupted system and therefore challenges the assumptions of the acoustic niche hypothesis, which assumes an intact, biodiverse community. In comparison with a Costa Rican avian community, a Hawaiian community had less partitioning in frequency and in time (Hart et al. 2021). Given Costa Rica's high biodiversity, it likely better fits the conditions of the ANH and therefore has better sound partitioning.

Even within highly biodiverse systems, however, the evidence for acoustic partitioning can be obscured. Uneven distribution of the body sizes in forest birds in Hawaiʻi and the associated constraints of morphology on frequency use may bias the distribution of frequencies. Memet et al. (2022) found that when using a null model that corrected for such bias, 3 out of 5 neotropical bird communities exhibited evidence of frequency partitioning.

My results may have differed from Hart et al. (2021) because while they recorded during the peak breeding season (March–April) for Hawaiian forest birds, I recorded primarily during the summer months following breeding. It is possible that summer months are less important for

native acoustic partitioning than spring months, when it is most needed for advertisement and territorial calls. Likewise, Farina et al. (2013) found that vocal activity of introduced Red-Billed Leiothrix in Italy varies throughout the year differently than native birds. This suggests that introduced species in Hawai‘i may similarly prioritize signal partitioning, if at all, during different months from native birds. Future research might compare the amount of acoustic partitioning between seasons.

Similar to this study, consensus of resource competition among and between native and introduced forest birds in Hawai‘i (Moulton and Pimm 1983, Moulton 1985, Mountainspring and Scott 1985, Foster 2005, Freed and Cann 2009) has largely been inconclusive. Moulton and Pimm (1983) observed that the probability of introduced bird species extinction increased with the number of species introductions, which they attributed to potential competition. A following study of extinction risk increasing between introduced bird species having similar bill size supported this more specifically as dietary niche competition (Moulton 1985). These two studies suggest that lowland Hawaiian bird communities hosting a diversity of introduced species are saturated, which may explain the lower frequency overlap I observed between introduced-introduced species pairs. Reciprocally, then, high-elevation communities may be unsaturated and thus have less competition for resources, including sound space. The observation of three introduced species, Red-Billed Leiothrix, Warbling White-eye, and Japanese Bushwarbler (*Cettia diphone*), exhibiting positive population growth rates in native forest of Maui, but not at the expense of density of Alauahio (*Paroreomyza montana*), which shared dietary preferences with these species (Foster 2005), supports the notion unsaturated montane forest bird communities. Mountainspring and Scott (1985), however, after controlling for habitat structure, found more positive associations between bird species than negative (76 versus 10), and found that native-introduced pairs had higher proportions of negative correlations than native-native or introduced-introduced species pairs. While my study found no evidence for acoustic competition between introduced and native forest birds, future research could examine other resource partitioning, informed by more detailed understanding of life histories, and with more thorough analysis than correlation. For example, sites of different community compositions could help to reveal whether competition for food and nesting resources exhibit the same neutral effect I have

observed for acoustic space, or whether introduced birds present yet another pressure on native bird populations.

Future studies could use playback experiments with more common native species and with introduced species to determine their responses to native, introduced, and white-noise (as a control) playback. This would allow for an experimental approach to see how species may partition sound in real time, and, to my knowledge, this would be the first instance of doing so in a hybrid community of forest birds. Previous playback studies in frogs have demonstrated that, exposed to recordings of introduced species, native species will alter their frequencies, timing, and/or amplitude (Both & Grant 2012, Bleach et al. 2015, Tennesen et al. 2016, Medeiros et al. 2017), in some cases, even if the native species calls in a different frequency range as the stimulus. However, native species also responded to other native species stimulus (Bleach et al. 2015, Medeiros et al. 2017) and white noise control (Tennessen et al. 2016, Medeiros et al. 2017). In a playback experiment between and introduced and native bird species, the native bird did not alter its frequency, but did adjust its timing to sing in between the calls of the introduced bird (Farina & Pieretti 2014). While playback studies are helpful in examining short-term behavioral responses of native birds to acoustic invaders, they are generally conducted within short time scales, and fail to capture lag responses in native species, long-term consequences, and evolutionary changes in a changing soundscape. Long-term monitoring of native species' responses to introduced species across seasons and years may better demonstrate whether they compete for acoustic resources.

TABLES

Table 1-1. Description of each Song Meter station location, date selected for analysis, bird community composition (by percent of introduced birds) and recording effort. Vegetation types with * denote those that were reclassified from 2001 imagery based on 2022 ground-truthing.

Song Meter ID	Latitude	Longitude	Elevation (ft)	Vegetation Type	Date	Number of Species	Proportion of Introduced Vocalizations	Recording Effort (days)
1AFENCE	19.784281	155.295655	5324	Closed Koa-ʻŌhiʻa wet forest	20 Jun 2022	9	0.094	88
1AHI	19.784011	155.306933	5545	Closed Koa-ʻŌhiʻa wet forest	17 Jul 2022	14	0.29	40
8ALOW	19.829676	155.256316	4347	Closed ʻŌhiʻa wet forest	11 Jul 2022	9	0.092	64
8AMID	19.827862	155.263814	4544	Closed ʻŌhiʻa wet forest	8 Aug 2022	11	0.044	45
8AFENCE	19.828882	155.284288	4987	Closed ʻŌhiʻa wet forest	3 Jul 2022	8	0.044	92
8AHI	19.827957	155.299087	5249	Closed Koa-ʻŌhiʻa wet forest	30 Jul 2022	9	0.14	64
AKICAB	19.820895	155.331577	6539	*Open Koa mesic forest	10 Jun 2022	13	0.62	42
HART1	19.764629	155.119141	856	Alien wet grassland	9 Aug 2022	12	1	39
HART2	19.764852	155.117718	781	Cultivated agriculture	12 Jun 2022	11	1	39

Table 1-1. (Continued) Description of each Song Meter station location, date selected for analysis, bird community composition (by percent of introduced birds) and recording effort. Vegetation types with * denote those that were reclassified from 2001 imagery based on 2022 ground-truthing.

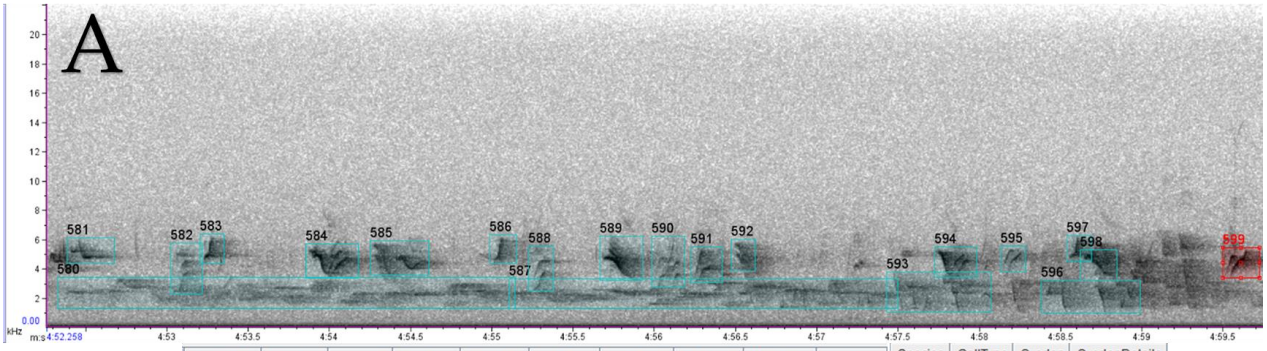
Song Meter ID	Latitude	Longitude	Elevation (ft)	Vegetation Type	Date	Number of Species	Proportion of Introduced Vocalizations	Recording Effort (days)
HART3	19.763518	155.117559	732	Cultivated agriculture	10-Jun-22	8	1	22
PEDRO	19.819475	155.315384	5965	Closed Koa-ʻŌhiʻa mesic forest	27 Jul 2022	14	0.55	85
PEDRO1	19.830781	155.300258	5390	Open Koa-ʻŌhiʻa wet forest	21 Aug 2022	12	0.4	24
PEDRO2	19.83219	155.303123	5446	Open Koa-ʻŌhiʻa wet forest	8 Jul 2022	15	0.41	62
PEDRO3	19.829044	155.316021	5889	*Open Koa mesic forest	3 Jul 2022	14	0.4	51
PUA AKALA	19.786567	155.323975	6237	Closed Koa-ʻŌhiʻa mesic forest	17 Jul 2022	14	0.15	76
PUA AKALA1	19.788281	155.325994	6283	Open Koa-ʻŌhiʻa mesic forest	26 Aug 2022	12	0.44	39

Table 1-2. Summary observations for each Song Meter station, including the number of possible vocalization pairs, the observed number of overlapping vocalizations, the mean of the null distribution of overlaps based on 500 randomizations of all vocalizations across consecutive tracks within each site, the standard deviations of these means, and the probability of obtaining the observed number of overlaps based on the null distribution of each randomization (Pnorm). A Pnorm value < 0.05 indicates an observation significantly different from expected by the null.

Recording Station	Pairs of Vocalizations	Overlapping Pairs	Mean null overlaps	SD Null overlaps	Pnorm values
1	23093	26	61.74	55.32	0.26
2	19222	25	55.01	57.38	0.30
3	16180	41	51.04	50.68	0.42
4	29854	89	137.30	94.85	0.31
5	122167	161	277.74	210.38	0.29
6	25406	28	56.44	62.58	0.32
7	52678	50	139.03	110.33	0.21
8	15070	13	32.88	36.17	0.29
9	25611	36	83.72	71.05	0.25
10	44532	44	104.97	82.46	0.23
11	16604	17	48.06	57.75	0.30
12	80998	99	189.48	153.19	0.28
13	47649	98	109.52	101.03	0.45
14	138242	119	243.53	192.28	0.26
15	12664	23	32.78	44.41	0.41
16	43186	33	78.16	87.28	0.30

FIGURES

Figure 1-1. Overview of Hawai‘i Island **(A)** and photo insets of field sites at Hakalau Forest National Wildlife Refuge **(B)** and Pauka‘a agricultural site **(C)**. Hakalau vegetation is mostly either Primary Wet ‘Ōhi‘a/Koa Forest or Secondary Wet/Mesic Koa Forest, whereas the Pauka‘a site is dominated by Alien Grassland and Agriculture. Vegetation classes designated by the Hawai‘i GAP Analysis Project.



Begin Time (s)	End Time (s)	Low Freq (Hz)	High Freq (Hz)	Begin File	Delta Freq (Hz)	Delta Time (s)	Peak Freq (Hz)	Max Power (dB)	Avg Power (dB)	Species	CallType	Overlap	OverlapDetails
294.987	295.155	4343.7	6294.7	PUAKHA...	1951.0	0.168	5038.8	74.2	58.6	HCRE	C	0	
295.107	297.498	1250.4	3313.0	PUAKHA...	2062.6	2.391	2756.2	72.3	52.7	RBLE	S	1	
295.227	295.381	2439.8	5520.1	PUAKHA...	3080.3	0.154	3617.6	71.0	52.5	HCRE	C	0	
295.664	295.928	3171.8	6191.1	PUAKHA...	3019.3	0.264	4651.2	92.7	70.1	HAAK	C	0	
295.986	296.188	2744.8	6221.1	PUAKHA...	3476.3	0.202	4392.8	70.9	52.2	HCRE	C	1	
296.226	296.418	3019.3	5459.1	PUAKHA...	2439.8	0.192	4005.2	79.3	60.0	HCRE	C	0	
296.473	296.621	3812.2	5977.6	PUAKHA...	2165.4	0.149	4608.1	73.6	59.6	HCRE	C	0	
297.431	298.071	1006.4	3751.2	PUAKHA...	2744.8	0.640	2368.7	73.5	53.7	OMAO	S	0	
297.724	297.985	3415.8	5484.9	PUAKHA...	2069.1	0.261	4694.2	87.7	67.3	HAAK	C	0	
298.131	298.283	3781.7	5550.6	PUAKHA...	1768.9	0.152	4737.3	75.1	57.8	HCRE	C	0	
298.381	298.989	960.3	3202.3	PUAKHA...	2242.0	0.609	2368.7	77.3	57.4	OMAO	S	0	
298.538	298.691	4491.0	6257.9	PUAKHA...	1766.9	0.154	4780.4	91.3	70.7	HCRE	C	0	
298.620	298.846	3202.3	5245.6	PUAKHA...	2043.3	0.226	4780.4	91.3	70.2	APAP	C	0	
299.499	299.724	3354.8	5398.1	PUAKHA...	2043.3	0.226	4565.0	90.0	70.3	HCRE	C	0	

Figure 1-2. Example of selections **(A)** made in RavenPro with relevant measurements **(B)** added to the selection table.

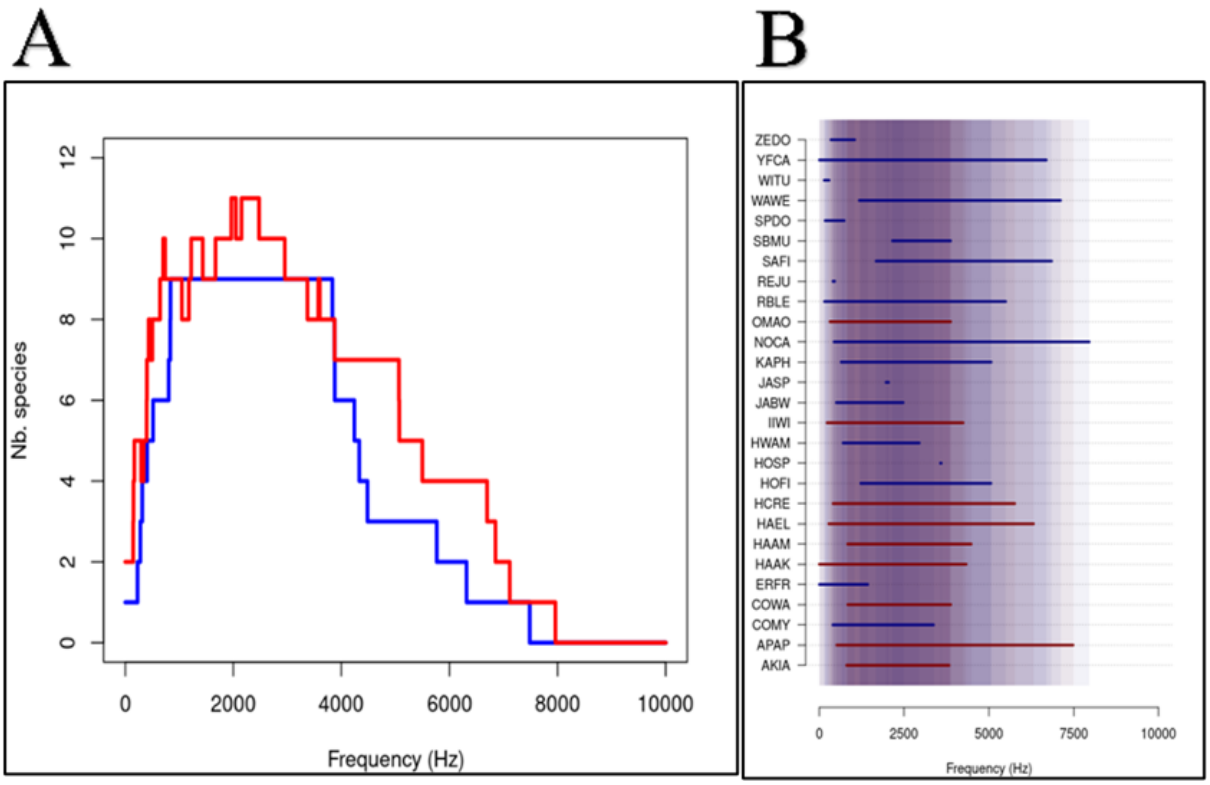


Figure 1-3. Frequency use **(A)** of native species (blue) and introduced species (red). A list of detected species **(B)** with their vocalization frequency ranges, with shaded background representing potential overlapping in a given frequency; the darker the background, the higher the number of species using this frequency.

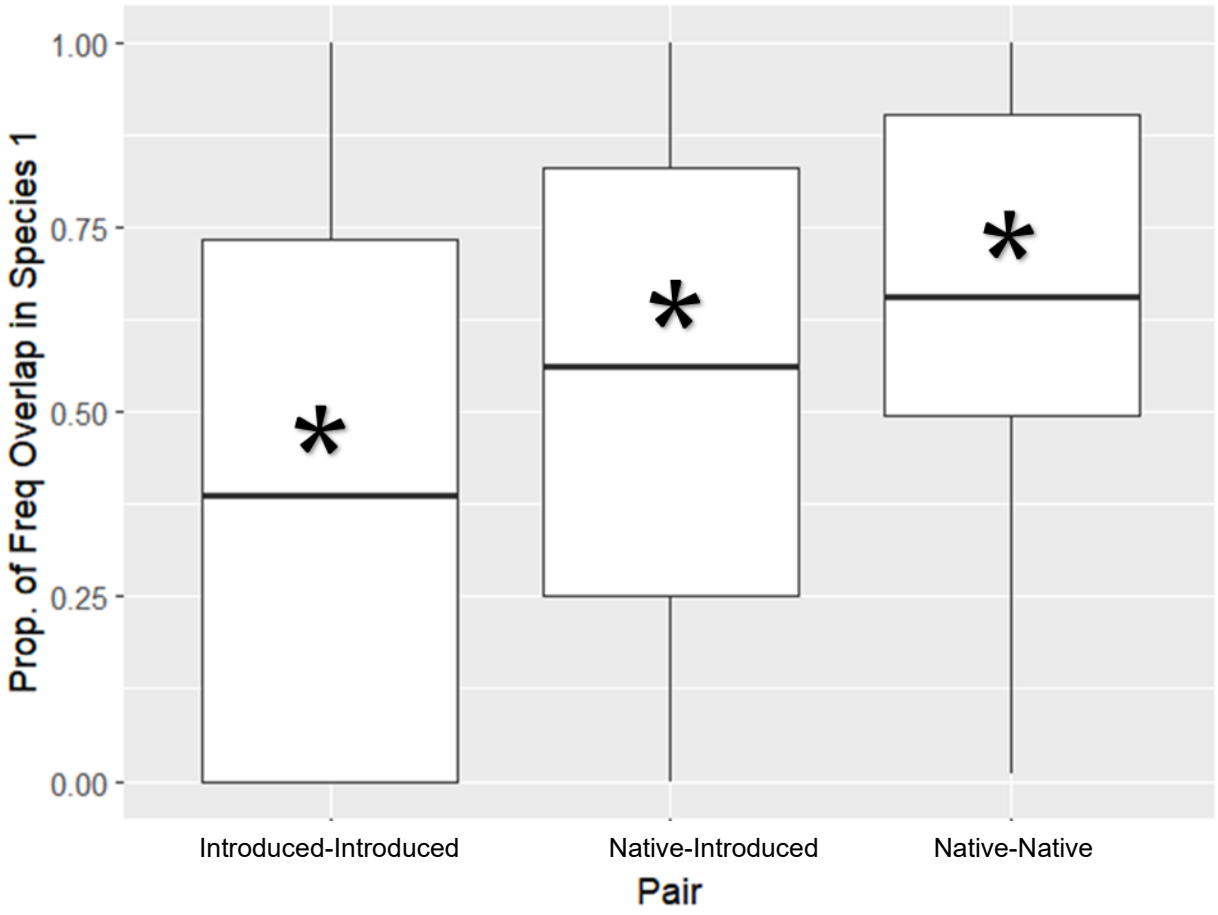


Figure 1-4. Comparison of the proportion of frequency range (taken as mean lowest and mean highest frequency of species) of a first species in a species pair overlapped by a second species, controlling for occurrence at the same recording station, and grouping by species origin. All groupings differed in the proportion of overlap.

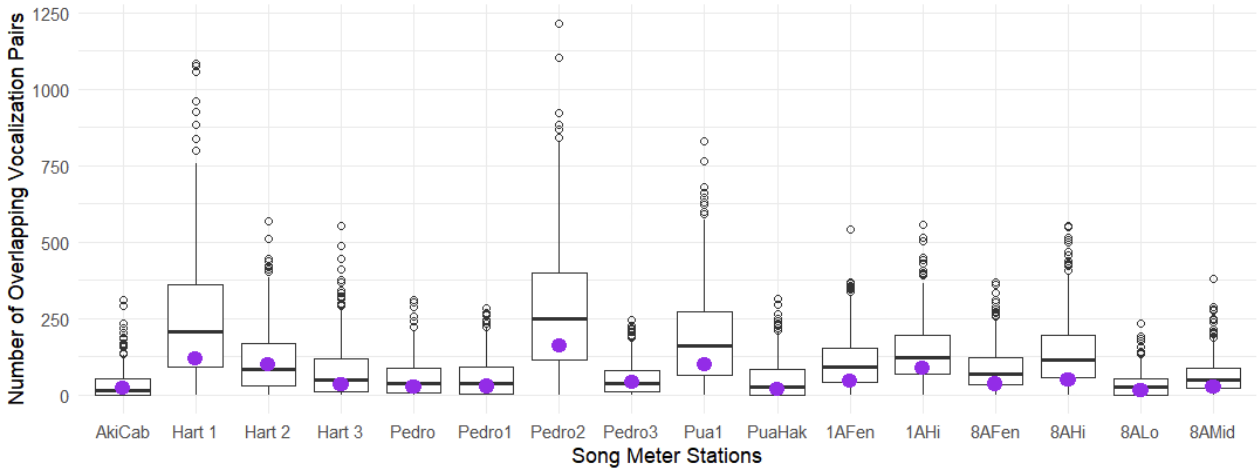


Figure 1-5. Boxplots representing the distributions of heterospecific vocalization overlap based on 500 randomizations of all vocalizations, occurring across consecutive tracks (15-30 minutes) within each station. Purple dots are the observed number of overlaps, whereas boxplots represent the range, median, lower and upper quartiles of the null distribution. Open circles show outliers.

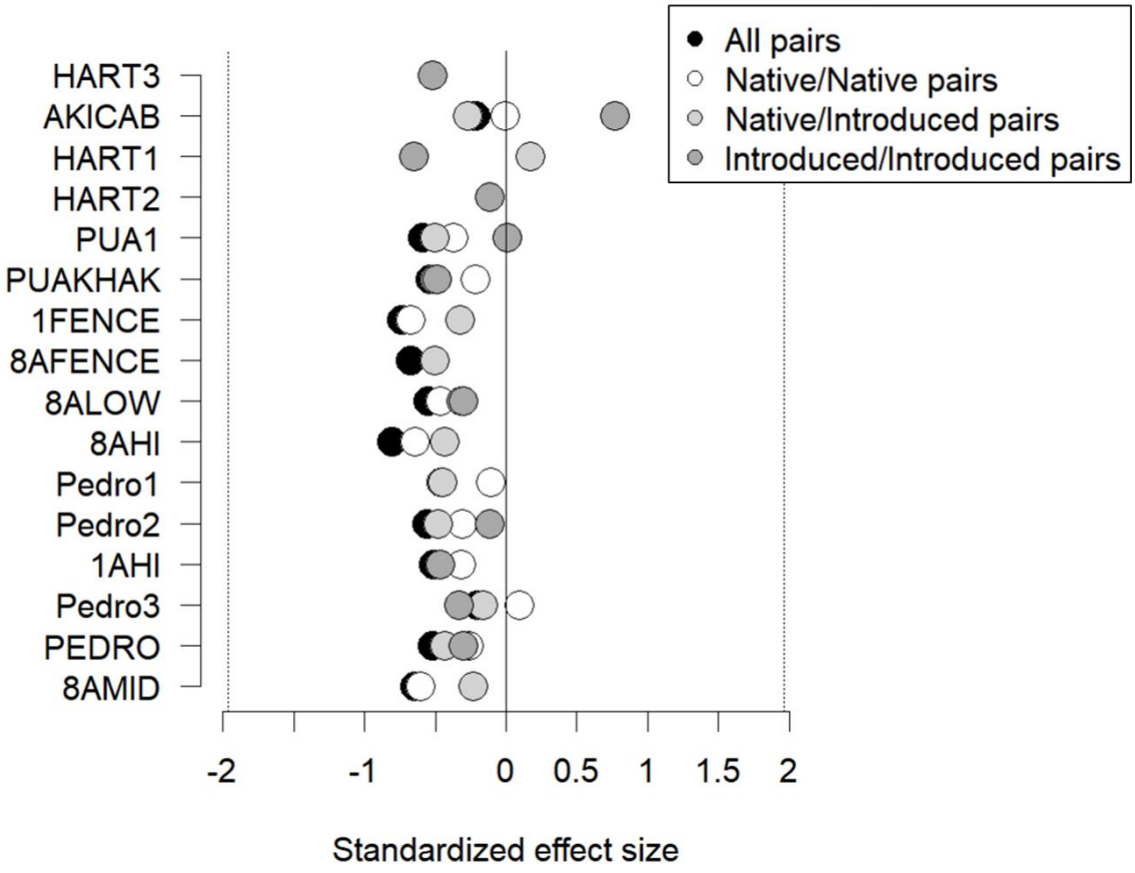


Figure 1-6. Standard effects sizes (SES) for 500 randomizations for all native-native, native-alien, and alien-alien vocalization pairs, with consecutive 5-minute tracks at sites combined. SES shows no significant difference between the randomized null distribution and observations of overlap (SES of magnitude greater than ±1.96 represents significant departure from null.)

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Chapter 2: Distance Estimation Based on Maximum Power Level of Recorded Bird Vocalizations in Hawai‘i

INTRODUCTION

Passive acoustic monitoring (PAM) using autonomous acoustic recorders (ARUs) offers new possibilities for surveying wildlife which are less invasive, less reliant on field expertise, less expensive when accounting for human labor, safer, and capable of data collection in remote areas at larger spatiotemporal scales than traditional methods (Au & Lammers, 2016; Marques et al. 2012; Farina & Pieretti 2017). However, one of the challenges for managers is estimating population density from recordings, which can be highly complex datasets, and lack the visual sensory component necessary for verifying animal locations and distinguishing between individuals.

Two strategies to avoid resampling the same individual in an acoustic dataset include incorporating cue rates and using the average proportion of time spent vocalizing by one species. A cue rate represents the average number of vocalizations made within a given time period based on behavioral observations of that species (Morreti et al. 2010). Average proportion of time spent by individuals of a species vocalizing (Ward et al. 2012) is often used in the context of monitoring along a census transect (Kügler et al. 2021; Marques et al. 2012). Density is then calculated using these averages and the number of calls per sample area. These assume 100% detection within a defined area, and that detections outside of this area can be excluded. However, if there are uncertainties in detection, the density estimate will need to include a detection probability function, which requires the distance from the recorder to the sound source.

One method of distance estimation employs the timing of sound to single sensors or an array of sensors (Efford et al. 2009, Marques et al. 2012). For example, one study used the differences in arrival times of normal modes of North Pacific right whale (*Eubalaena japonica)* vocalizations to estimate distance (Marques et al. 2011). Efford et al. (2009) successfully modeled population density from location data over a single sampling interval, using the spatial pattern of either binary (detected/not detected) or signal strength-based (signals exceeding a certain sound energy threshold in dB) detections across an array of acoustic detectors.

Another technique is to use the inverse relationship between sound pressure (p), or the pressure in a sound wave relative to the air pressure, and the distance (r) to its source, or $p \propto 1r$. This relationship has been employed for underwater navigation using sonar (e.g. Lee et al. 2019) and in a few wildlife monitoring studies, in which the sound pressure level (SPL), or perceived loudness of a sound by an acoustic recorder, is used to predict the distance to the animal which produced it (Darras et al. 2018, Sebastian-Gonzalez et al. 2018, Yip et al. 2019, Graf and Hatlauf 2021). SPL is typically measured in decibels (dB), which use a logarithmic scale to measure the sound pressure of a sound wave relative to a reference pressure. Specifically,

$$Lp = 20\log 10 \frac{p}{pref}$$

where L_p is the SPL in dB, p is the sound pressure (in Pascals), and p_{ref} is the reference sound pressure (The Engineering Toolbox 2004). Application of the signal-strength based detection method (Efford et al. 2009), such as determining that Bell Minor (*Manoria melnophrys*) calls louder than 70dB are within a 50-m radius of the recording device (Lambert and McDonald 2014), also applies the inverse relationship between sound pressure and distances on a fundamental level. Specific distances, however, are also possible to predict from SPL.

Darras et al. (2018) found that observers could estimate distances for five bird species from sound recordings, with high correlation (0.76-0.96) with the measured distances, if provided with a calibration sequence of tones of various frequencies, recorded at various distances, or given knowledge of the closest and farthest bird detections. In a second experiment, they found that point counts outperformed ARUs in detection if the survey radius was unlimited, but that under fixed-radius and distance sampling modeling, ARUs captured significantly more species richness and density, respectively, than point counts, based on measured horizontal distances to visually detected birds. However, the authors could have introduced an even more objective method for estimating bird distances: rather than using human cognition to assess the power level and frequency, using an acoustic software to compute these parameters, then predicting distances from a regression of measured distances and associated power levels from recorded birds.

This is precisely the method Sebastian-Gonzalez et al. (2018) used to improve density estimation from single ARUs. Density of Hawai‘i ‘Amakihi (*Cholordrepanis virens*) was

calculated from cue rates, environmental conditions, and estimates of each detected bird's distance to the recorder based on the power level of the vocalization. The latter relationship was modeled using recordings of vocalizing birds whose distances were measured from the microphone using a rangefinder. Distance between a cue and its source could be reliably predicted by its power level with no significant effects from rain or wind, and did not require a calibration sound transmission sequence as in Darras et al. (2018). These methods and an automated detection algorithm produced population density estimates similar to those from human surveyors, however, the possible difference in estimation error between the two methods was not assessed.

Yip et al. (2019) used reference recordings with measured distances of Ovenbird (*Seirus aurocapilla*) and Common Nighthawk (*Chordeiles minor*) cues to predict distances of vocalizations from other recordings based on their relative sound level (RSL), which measures the energy of a sound wave received by a microphone relative to the microphone's maximum output. Ovenbird cues were located using an acoustic array grid and their time of arrival to each recorder, whereas nighthawk distances were measured using a transect of ARUs, a playback speaker to attract birds, and a human observer recording horizontal distance, height, bearing, and time of each response vocalization relative to the start of the transect. Using regressions of the recorded distances and RSLs, the authors were able to predict both distance and population density from RSL, without significant differences in density estimates from those modeled from known distances, despite some error in predicted distance. Density estimates also had less error than densities modeled from human-estimated distances extracted from previous literature.

Subsequently, Graf and Hatlauf (2021) used camera traps and a microphone array to measure golden jackal (*Canis aureus*) distances to microphones and their associated SPLs, respectively. They then built a model to predict jackal group distances from SPLs and applied it to transect recordings of jackal responses to playback. Distances could be reliably estimated up to 400m based on SPL, and there was a significant difference between distance estimation from front- versus back-facing jackal responses relative to the microphone, with back-facing responses not performing well at distance estimation, emphasizing the importance of orientation.

An advantage of estimating density from acoustic or other proximity detectors is that it can improve the precision of population monitoring by removing human bias from distance

estimations (Efford et al. 2009, Yip et al. 2019, Graf and Hatlauf 2021). In some circumstances, such as underwater or in thick forest, acoustic detectors can also detect animals further than human surveyors (Marques et al. 2013), which may explain why, according to one review, ARU-based studies have often detected just as many, and sometimes more, bird species than human observers (Darras et al. 2019). With proper application, the authors suggest, ARUs may even surpass human surveyors by providing more coverage, spatial and temporal resolution, standardization, and verifiable datasets, while still yielding comparable information about abundance, density, occupancy, and species richness.

While the number of studies estimating animal distances from recordings is small (Darras et al. 2018; Sebastian-Gonzalez 2018; Yip et al. 2019; Graf and Hatlauf 2021), consistent patterns between them include the inverse relationships between distance and SPL of vocalizations (inverse square law), true distance and the accuracy of distances predicted from SPLs, and, in playback experiments, distance and the number of individuals responding (Graf and Hatlauf 2021). The latter observation suggests a distance threshold in the ability of individuals to detect others of their own species, and similarly there are constraints to acoustic monitoring. In the case of golden jackals, distance can be reliably estimated from relative sound level (RSL) up to 400m (Graf and Hatlauf 2021).

For terrestrial, non-flying animals, camera traps can be combined with acoustic arrays to estimate distances of vocalizing individuals and relate these to the recorded SPL (Graf and Hatlauf 2021). However, for birds, bats, and arboreal creatures which cannot easily be detected by camera traps, it is necessary to measure distances using more active observation methods such as range finders (Sebastian-Gonzalez et al. 2018, Yip et al. 2019). In addition, while some have accounted for orientation of the vocalists to the microphone (Graf and Hatlauf 2021), they may not have accounted for environmental variables such as wind, which can distort sound waves (Barlow 1929) and rain, which can increase attenuation of sound, decrease signal to noise ratio, and decrease the calling rate of birds (Lengagne and Slater 2002). Further research should be done regarding how wind and rain change the relationship between distance and amplitude.

This study seeks to find a relationship between the amplitude of bird vocalizations and their distances to the microphone, while accounting for the orientation of the bird, wind, and rain, to assist with future wildlife population monitoring using ARUs. We hypothesized that we

would observe an inverse relationship between the maximum power level (dB) of the cue and its distance to the recording device, as measured by a range finder. We also expected that birds directly oriented to the microphone (close to 0˚) would improve their sound transmission and therefore have steeper slopes relating distance (y) and power level (x). In addition, we predicted that this relationship would appear different between different call types, due to their different functional uses such as advertisement versus contact calls. Finally, we expected higher levels of rain and wind to weaken this relationship through distortion and attenuation of sound waves, respectively.

METHODS

Measuring Distances while Recording Songs

Recordings and observations of vocalizing birds of any species were made from June 10 to July 12, 2022 in the Pua Akala and Pedro tracts of Hakalau Forest National Wildlife Refuge (see Chapter 1 Methods, 19.832˚N, 155.285˚W). Pairs of observers, trained in bird identification, arrived at one of several locations in the refuge at or shortly following dawn, and followed birds until vocal activity dissipated (usually at or before 11:00 am). Observations were also collected within 2 hours of dusk when vocal activity increased again. Observers noted the site name and estimated the wind and rain conditions on a Beaufort scale, then converted these to the conventions used by Sebastian-Gonzelez et al. (2018). Having no microclimate sensor, observers estimated rain levels as the following: no rain or misty was estimated as 0 (<0.5mm/12 min); light drizzle to light rain was estimated as 1 (0.5mm–1mm/12min); heavy rain was estimated as 2 (>1mm/12min). For wind, smoke rising vertically or drifting was estimated as 0 (<=15km/h); wind rustling leaves to blowing small twigs in constant motion was estimated as 1 (15-30 km/h); and any wind raising dust or larger materials was estimated as 2 (>30km/h).

In each pair of surveyors, Observer A chose a vocalizing bird that could be clearly identified and visually located, then measured its angular distance while it vocalized using a rangefinder (Nikon Forestry 550 or Vortex Optics Ranger 1800). Meanwhile, Observer B held a Song Meter (SM4, Wildlife Acoustics Inc.) and wrote down observations. Observer A audibly indicated the time of each vocalization, the species of bird, the measured distance to the bird, and

its orientation to the observer, with 0 degrees pointing directly at the observer, 180 degrees facing directly away, and all other measurements being between these values, estimated to the nearest 10 degrees. Observer B stayed as close to Observer A as possible so that the distance between the sound recorder and the rangefinder was minimal (less than 60cm). Efforts were made to take a variety of distances, sometimes from the same vocalizing individual, which required moving away from or closer to a bird. However, whenever possible, observers tried to move throughout the survey area and between sites to collect data from a variety of individuals.

Acoustic Analysis

Sonograms of field recordings were visualized and aurally inspected using RavenPro Version 1.5 (K. Lisa Yang Center for Conservation Bioacoustics). Observers skipped to the timestamp of each vocalization having an associated distance measurement, as recorded in the field. The measurements recorded from the field were verified by listening to the voice of the observer on the recording. A selection box was drawn about each vocalization, and set to automatically measure a set of parameters, including begin time, end time, low frequency, high frequency, dominant frequency, maximum sound pressure level, and average sound pressure level. Species, call type, orientation, measured distance of the bird to the recorder, wind rating, and rain rating were manually entered for each selection by the annotators.

Statistical Analysis

First, a global linear mixed model (lmer) was built using the **lme4** package in R (version 4.1.1) to predict the distance of a bird to a recorder, based on the complete dataset of vocalizations. Fixed effects included maximum power level, peak frequency, orientation, and levels of wind and rain. Call type and species were included as nested random effects. The model was compared against a null model with only the nested random effects of species and call type.

Next, model selections were made separately for individual call types within each species, including multiple linear regression and multiplicative models. Those with insufficient sample size (<10 per call type) were combined with other call types for distance estimation or dropped if they did not fall within the same range of maximum power levels or average power levels as the other call types. Models were selected based on Akaike's Information Criterion, corrected for small sample sizes (AIC_c) to predict distance as a response to maximum or average

sound pressure level, with peak frequency (frequency of the vocalization having the greatest power level), orientation, wind, and rain as covariates. Variables were log-transformed when they were right-skewed in distribution to meet normality assumptions. We selected the best significant model (if any) for each call type using the function **dredge** in R. We also used the **emmean**s function in R to obtain the estimated marginal means for distances at different levels of wind and rain. Estimated marginal means, also known as least-squares means, are estimates of the fixed effects which take into account variation from the random effects. They are calculated from the linear model equation coefficients multiplied by the means of each variable across each level of every categorical variable. This can be especially useful when there are unbalanced sample sizes across different variables.

RESULTS

We identified 23 vocalization types of 15 species from 736 recorded vocalizations with measured distances and orientations.

The global lmer including the fixed effects of max power level, wind, and rain, as well as the nested effects of species and call type, had a better fit ($R^2_{marginal}$= 0.073, $R^2_{conditional}$ = 0.48, AIC = 5739.9, **Table 2-1**) than the null model with only the nested effects of species and call type ($R^2_{conditional}$ = 0.308, AIC = 5796.3). It also revealed that wind (estimate: -2.27, p=0.019 , **Figure 2-1**) and rain (estimate: 4.48, p=0.0013 **Figure 2-2**) had slightly significant effects on the distance estimation based on emmeans. Wind of 0 had a stronger effect (emmeans 25.3 [CL: 19.6, 31],) than wind of 1(emmeans 23 [CL: 17.3, 28.8]), while rain of 1 had a stronger effect (emmeans 26.4 [CL: 20.4, 32.4]) than rain of 0 (emmeans 21.9 [CL: 16.3 27.5]). Some of the variation was also explained by max power level (Estimate: -0.38 [CL: -0.48, -0.27], sd^2= 2.02, p<0.001). Variance was largely unexplained (residual sd^2= 128.21), but with some from species (sd^2 = 90.77) and then from call nested within species (sd^2= 9.41).

Three of the models built for each species and vocalization type had significant relationships between distance and maximum power level (max power): ‘Apapane song (**Table 2-2**; **Figure 2-3**, $F_{2,10}$=18.23, AIC_c = 98.05), I‘iwi call type II (**Table 2-3**, **Figure 2-4**, $F_{1,35}$=23.06, AIC_c = 5.10), and Yellow-fronted Canary song (**Table 2-5**, **Figure 2-5**, $F_{1,28}$ =

15.02, AIC_c = 237.07). Warbling White-eye twitter call distances did not show strong fit with max power (AIC_c =78.39), but they did show a significant relationship with average power level and wind (**Figure 2-6**, $F_{6,46}$=7.53, AIC_c = 67.33) when they were log-transformed.

DISCUSSION

Most of the vocalizations did not show a relationship between power level and distance, which is similar to the findings, mostly unpublished, from other acoustic ecologists. Dawson and Efford (2009) called localization of sound from fewer than three recorders "impossible." Spiesberger (2001) suggested that amplitude is less reliable than time of arrival for locating sounds due to constructive and destructive interference of signals, and suggested using an acoustic array with at least N +1 recorders for the number of dimensions (N) desired in locating the sound, and sometimes more to account for error.

Without obstructions, and in a homogenous medium, sound energy spreads spherically from its source such that for every doubling of distance, amplitude decreases by 6dB (Wiley and Richards 1982). These conditions would make distance estimation from power level a mere calculation, except they are almost never met. For one, the medium is almost never homogenous or constant, and attenuation in the atmosphere can even change with temperature and humidity fluctuations. The strong effects of wind and rain in our linear mixed model support this, and future studies should include more precise and detailed weather data for this reason. Sound attenuation also occurs from absorption and scattering through the environment, and this increases with frequency (Wiley and Richards 1982). Lower frequency sounds would theoretically be easier to locate in dense vegetation than higher sounds, although this was not reflected in our observations: ʻOmaoʻo songs and calls did not show significant relationships with distance. Sebastian-Gonzalez et al. (2018) also experienced some difficulties with predicting distance from some SPL measurements, even though their ʻAmakihi model fit the data well, and they attribute this to variability in sound transmission patterns. As much as possible, we tried to conduct observations in similar habitat types. However, differences in density between Koa stands and ʻōhiʻa, for example, could cause differences in transmission properties and thus make distance difficult to estimate from SPL (Morton 1975, Forrest 1994).

Another breach of the assumption of spherical spread is that birds can direct their signals in relation to signal function; for example, omnidirectional alarm calling versus directional mating calls (Patricelli et al. 2007). ‘Oma‘o are notorious for throwing their voices, and having a lot of individual variation in their vocalizations (R. Camp, pers. commentary). The lack of relationships in many species may be partly because of individual variation in sound intensity (Yip et al. 2019) and the ability of birds to modulate the amplitude of their calls (Pytte et al. 2003) and songs (Brumm 2004) in the context of increased environmental noise. We suggest that amplitude modulation is yet one more variable to be considered in distance estimation from power level, but that species do have limits within which these amplitudes fall, which may help in formulating correction factors.

However, the four models which did show significant relationships demonstrate that for some species and call types, distance estimation is possible from single recorders, and that this will only improve with refinement of methods. In these cases, distance estimates from power level will be less biased than human estimates, and result in more accurate density estimates (Yip et al. 2019). Population monitoring from single acoustic recorders may still be possible (Efford et al. 2009, Sebastian-Gonzalez et al. 2018), however larger acoustic arrays will greatly improve accuracy (Spiesberger 2001). Detection functions and cue rates should be investigated both for threatened and endangered native species, and introduced species, to monitor incipient movement or population growth into new areas.

Future studies would do well to collect more observations from different individuals, to collect more observations such that there is sufficient sample size to compare relationships between distance and power level in different habitat types, and include human distance estimations to compare with those measured from rangefinders (Sebastian-Gonzalez et al. 2018, Yip et al. 2019).

TABLES

Table 2-1. Predictors of distance included in the top 10 linear models for the complete dataset of vocalizations, their associated degrees of freedom (df), -log(likelihood), AIC (Akaike's Information Criterion) values, and weights. The model including the fixed effects of maximum power level, wind, and rain, plus the nested random effects of species and call type, has the lowest AIC value and the highest weight, and is therefore the best fit.

	df	logLik	AIC	delta	weight
max power+wind+rain+(1|species/calltype)	7	-2861.04	5736.07	0.00	0.90
max power+rain+(1|species/calltype)	6	-2864.65	5741.30	5.22	0.07
max power+ori+wind+rain+(1|species/calltype)	8	-2863.85	5743.71	7.63	0.02
max power+wind+rain+(1|species)	6	-2866.41	5744.81	8.74	0.01
max power+wind+(1|species/calltype)	6	-2867.41	5746.82	10.75	0.00
max power+ori+rain+(1|species/calltype)	7	-2867.20	5748.39	12.32	0.00
max power+rain+(1|species)	5	-2870.02	5750.05	13.98	0.00
max power+freq+wind+rain+(1|species/calltype)	8	-2867.96	5751.93	15.85	0.00
max power+ori+wind+rain+(1|species)	7	-2869.32	5752.64	16.56	0.00
max power+wind+(1|species)	5	-2871.89	5753.78	17.70	0.00

Table 2-2. Predictors of distance included in the top 10 linear models for ‘Apapane songs, their associated degrees of freedom (df), -log(likelihood), and AIC_c (Akaike’s Information Criterion, corrected for small sample sizes) values. The model including both peak frequency and maximum power has the lowest AIC value and degrees of freedom and the highest weight. It is therefore the best fit and most parsimonious. Models within 2 AIC_c units of this are also good fits, but have less weight are equally or less parsimonious.

	df	logLik	AICc	delta	weight
frequency + max power	4	-42.52	98.05	0.00	0.26947427
max power + wind	4	-42.75	98.50	0.45	0.21498139
frequency + max power + rain	5	-40.07	98.71	0.67	0.19319637
frequency + max power + wind	5	-40.20	98.97	0.92	0.16983161
max power	3	-46.84	102.34	4.29	0.03152587
max power + rain + wind	5	-42.11	102.78	4.74	0.02525057
max power + rain	4	-44.99	102.97	4.92	0.02297231
max power + orientation + rain	5	-42.51	103.59	5.55	0.01684343
frequency + max power + orientation	5	-42.51	103.59	5.55	0.01683519
frequency + max power + rain + wind	6	-38.83	103.67	5.62	0.01622060

Table 2-3. Predictors of distance included in the top 10 linear models for ‘I‘iwi call type II, their associated degrees of freedom (df), -log(likelihood), and AIC_c (Akaike’s Information Criterion, corrected for small sample sizes) values. The model including both maximum power and wind has the lowest AIC_c value and the highest weight. However, the model with only maximum power is within 2 AIC_c units and has one less degree of freedom, making it more parsimonious.

	df	logLik	AICc	delta	weight
max power + wind	4	2.43	4.38	0.00	0.23952102
max power	3	0.81	5.10	0.72	0.16748836
max power + rain	4	1.84	5.58	1.19	0.13204050
max power + rain + wind	5	2.74	6.46	2.08	0.08468576
log(frequency) + max power + wind	5	2.45	7.04	2.65	0.06351433
max power + orientation + wind	5	2.43	7.07	2.68	0.06256918
log(frequency) + max power	4	0.84	7.57	3.18	0.04879404
max power + orientation	4	0.82	7.60	3.22	0.04793507
log(frequency) + max power + rain	5	1.89	8.15	3.77	0.03637371
max power + orientation + rain	5	1.84	8.26	3.88	0.03448042

Table 2-4. Predictors of distance included in the top 10 linear models for Yellow-fronted Canary songs, their associated degrees of freedom (df), -log(likelihood), and AIC_c (Akaike's Information Criterion, corrected for small sample sizes) values. The model including only maximum power has the lowest AIC_c value, the highest weight, and the fewest degrees of freedom, making it the most parsimonious model.

	df	logLik	AICc	delta	weight
max power	3	-115.07	237.07	0.00	0.23280298
frequency + max power	4	-114.04	237.69	0.62	0.17077569
frequency + max power + rain	5	-112.89	238.28	1.21	0.12695925
max power + rain	4	-114.71	239.01	1.94	0.08814489
max power + wind	4	-114.94	239.48	2.41	0.06973885
max power + orientation	4	-115.07	239.74	2.67	0.06117421
frequency + max power + wind	5	-113.92	240.33	3.26	0.04552838
frequency + max power + orientation	5	-114.02	240.54	3.48	0.04096143
frequency + max power + orientation + rain	6	-112.87	241.40	4.33	0.02674145
frequency + max power + rain + wind	6	-112.89	241.43	4.36	0.02632737

Table 2-5. Predictors of distance included in the top 10 linear models for Warbling White-eye twitter calls, their associated degrees of freedom (df), -log(likelihood), and AIC_c (Akaike's Information Criterion, corrected for small sample sizes) values. The model including frequency, orientation, average power, and wind has the lowest AIC_c value and the highest weight. However, the model with only average power and wind is within 2 AIC_c units and has two less degrees of freedom, making it more parsimonious.

	df	logLik	AICc	delta	weight
frequency + orientation + average power + wind	6	-26.44	66.88	0.00	0.19938692
orientation + average power + wind	5	-27.96	67.32	0.45	0.15951186
average power + wind	4	-29.21	67.33	0.45	0.15917552
frequency + average power + wind	5	-28.11	67.62	0.74	0.13784388
frequency + orientation + rain + average power + wind	7	-26.27	69.28	2.40	0.06002280
rain + average power + wind	5	-29.09	69.58	2.71	0.05155211
orientation + rain + average power + wind	6	-27.83	69.66	2.78	0.04970502
frequency + rain + average power + wind	6	-27.98	69.95	3.07	0.04288397
frequency + average power	4	-30.78	70.46	3.58	0.03321590
frequency + orientation + average power	5	-29.80	70.99	4.12	0.02546281

FIGURES

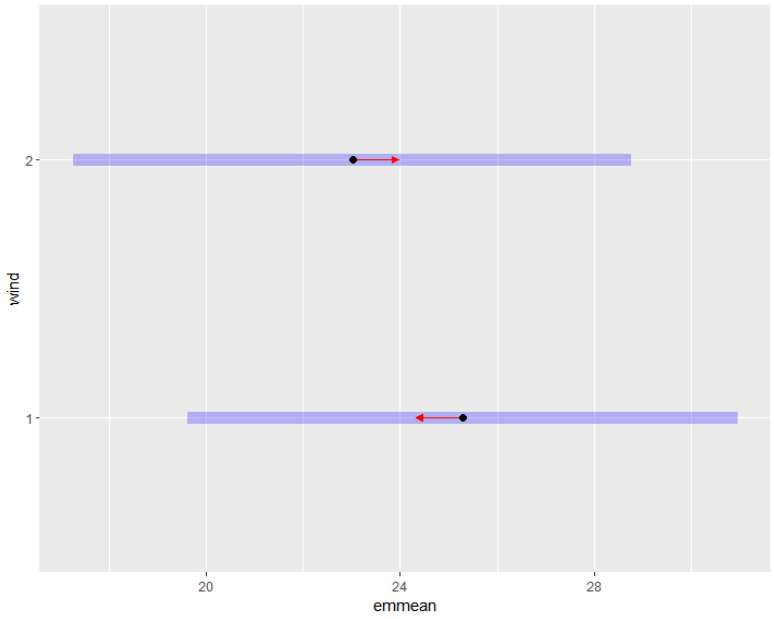

Figure 2-1. Comparison of emmeans between levels of wind for the entire dataset of vocalizations and distances. Wind of 0=25.3, Wind of 1=23. Red arrows show direction of pull on the slope of the distance over the maximum power level.

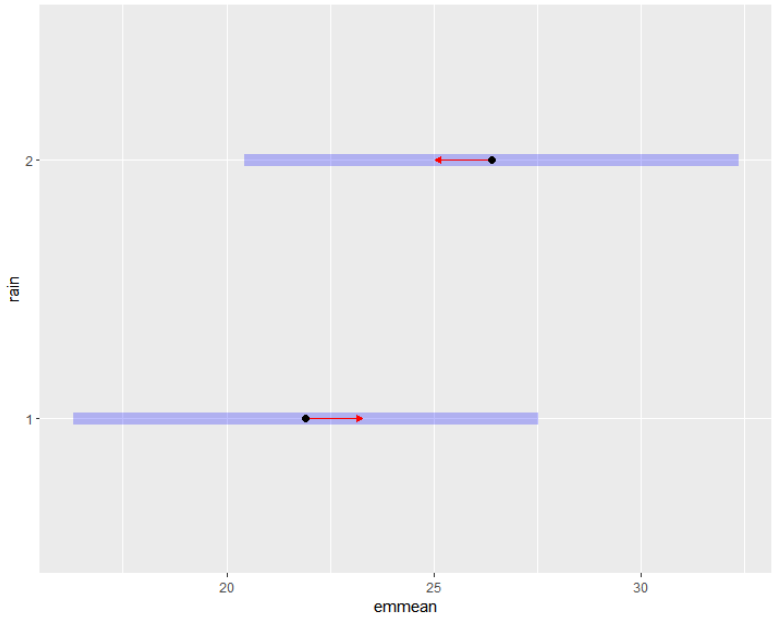

Figure 2-2. Comparison of emmeans between levels of rain for the entire dataset of vocalizations and distances. Rain of 1=26.4, Rain of 0=21.9. Red arrows show direction of pull on the slope of the distance over the maximum power level.

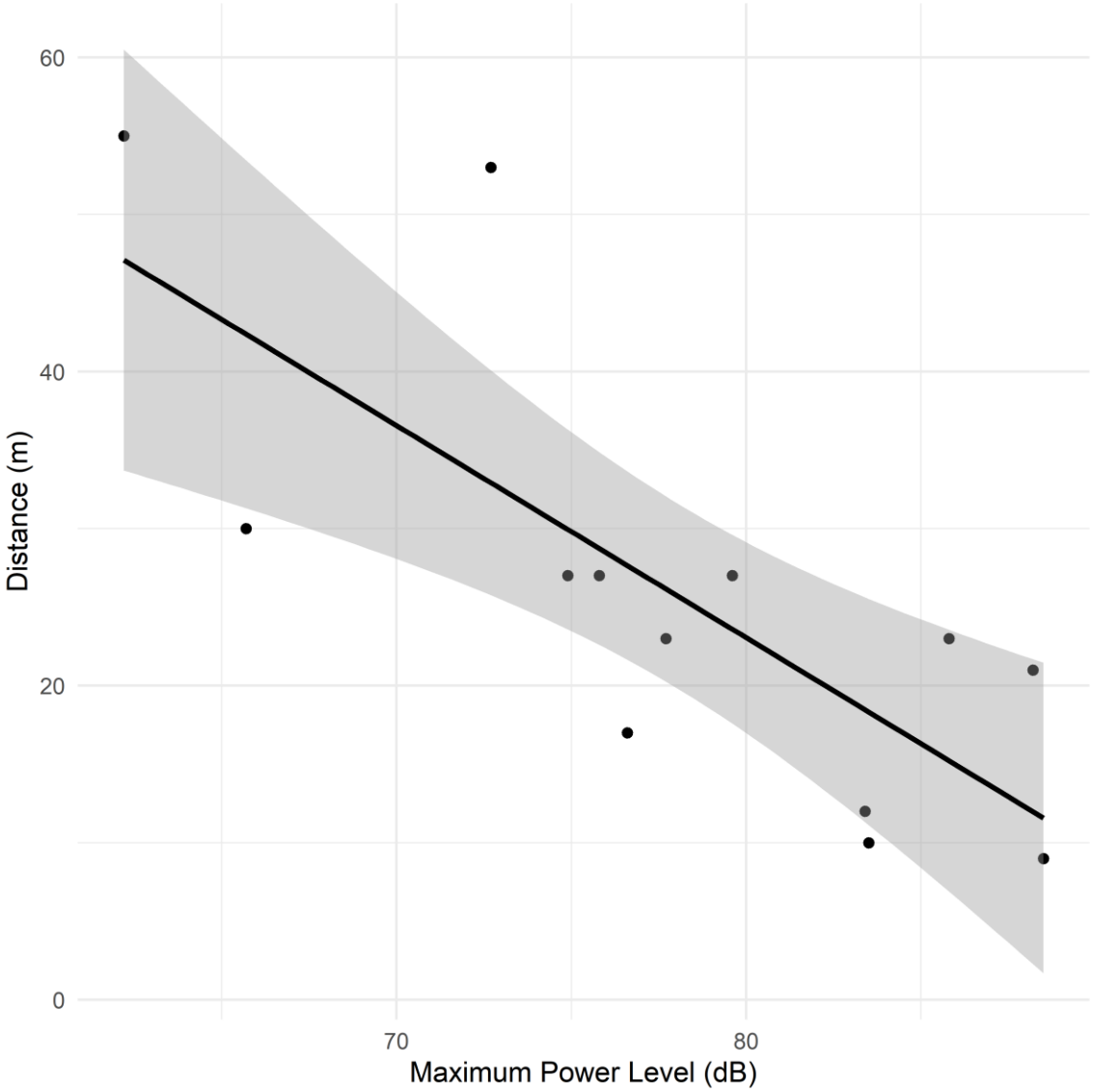

Figure 2-3. Regression line fitted to observations (black circles) of ‘Apapane song distances and maximum power levels. Shaded region represents 95% confidence interval about the slope estimate. Slope = -1.41; SE = 0.30; t value=-4.68; p = 0.0002, adjusted R^2= 0.698. Frequency also had significant effect on distance estimation (see **Table 2-1**), however there was an insufficient sample size to determine slope adjustments based on frequency.

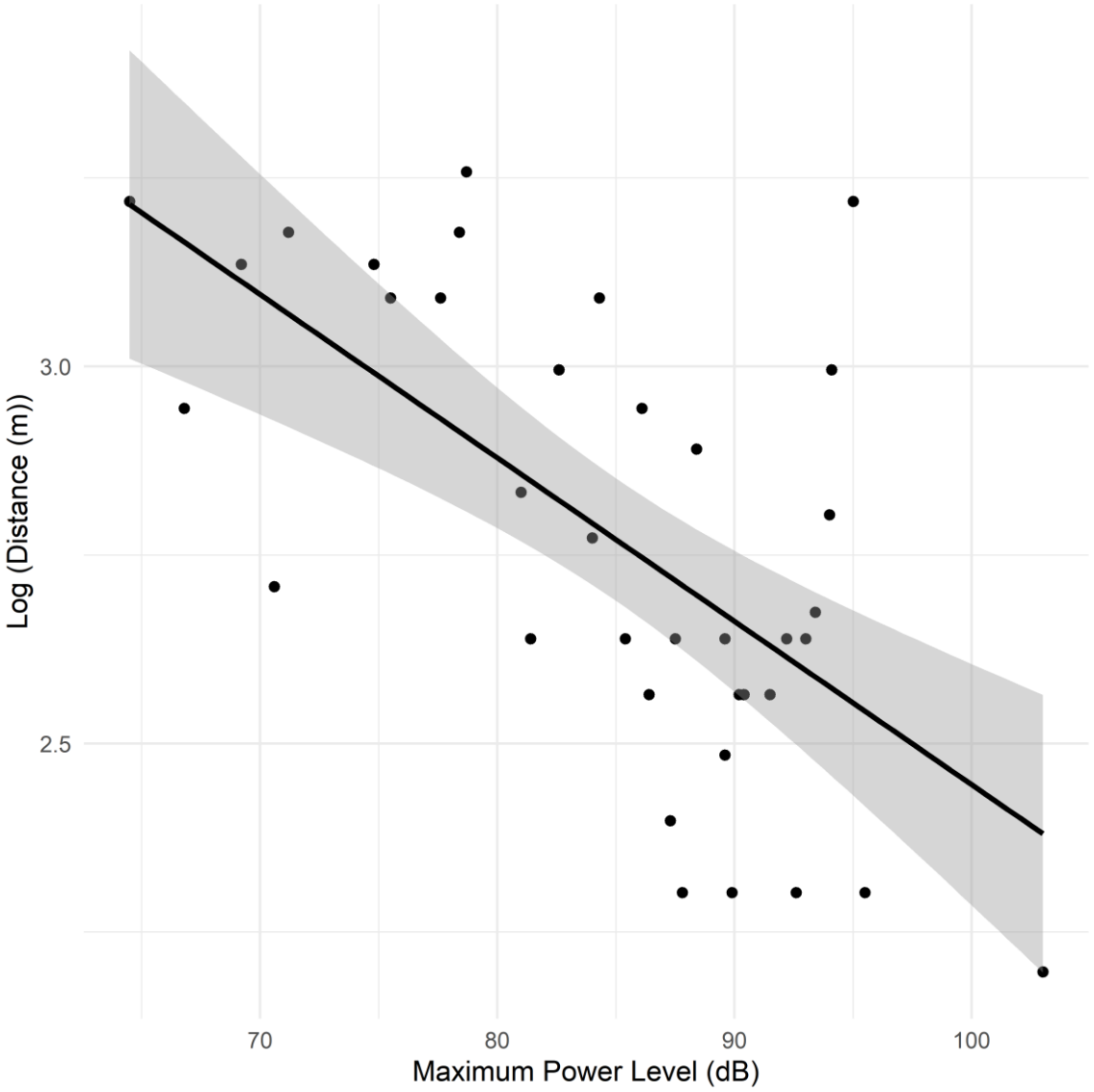

Figure 2-4. Regression line fitted to observations (black circles) of ‘I‘iwi call II distances (log transformed) and maximum power levels. Shaded region represents 95% confidence interval about the slope estimate. Slope = -0.022; SE = 0.0045; t value=-4.80; p <0.001, adjusted R^2= 0.38.

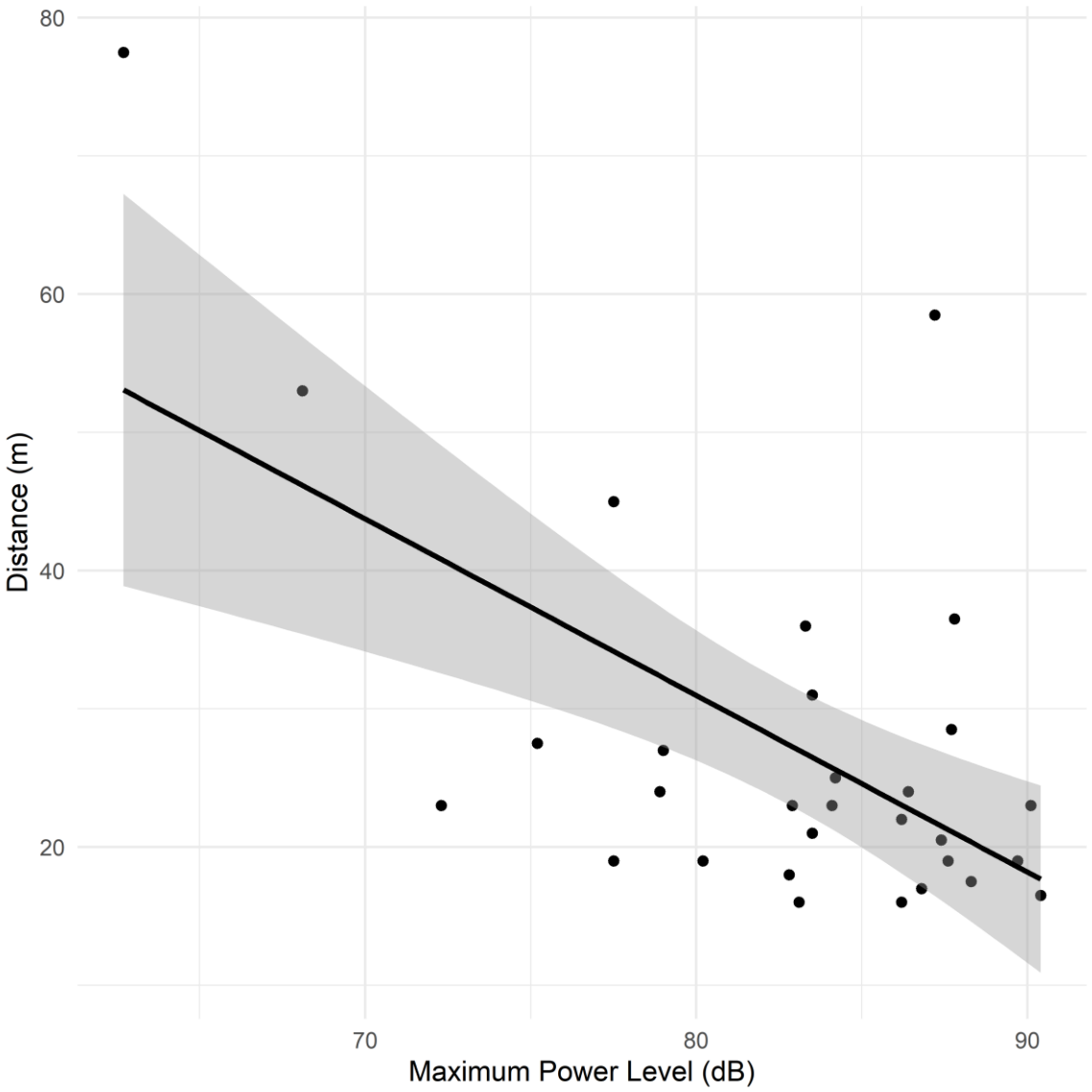

Figure 2-5. Regression line fitted to observations (black circles) of Yellow-fronted Canary song distances and maximum power levels. Shaded region represents 95% confidence interval about the slope estimate. Slope = -1.28; SE = 0.33; t value= -3.88; p=0.001, and adjusted R^2 = 0.33.

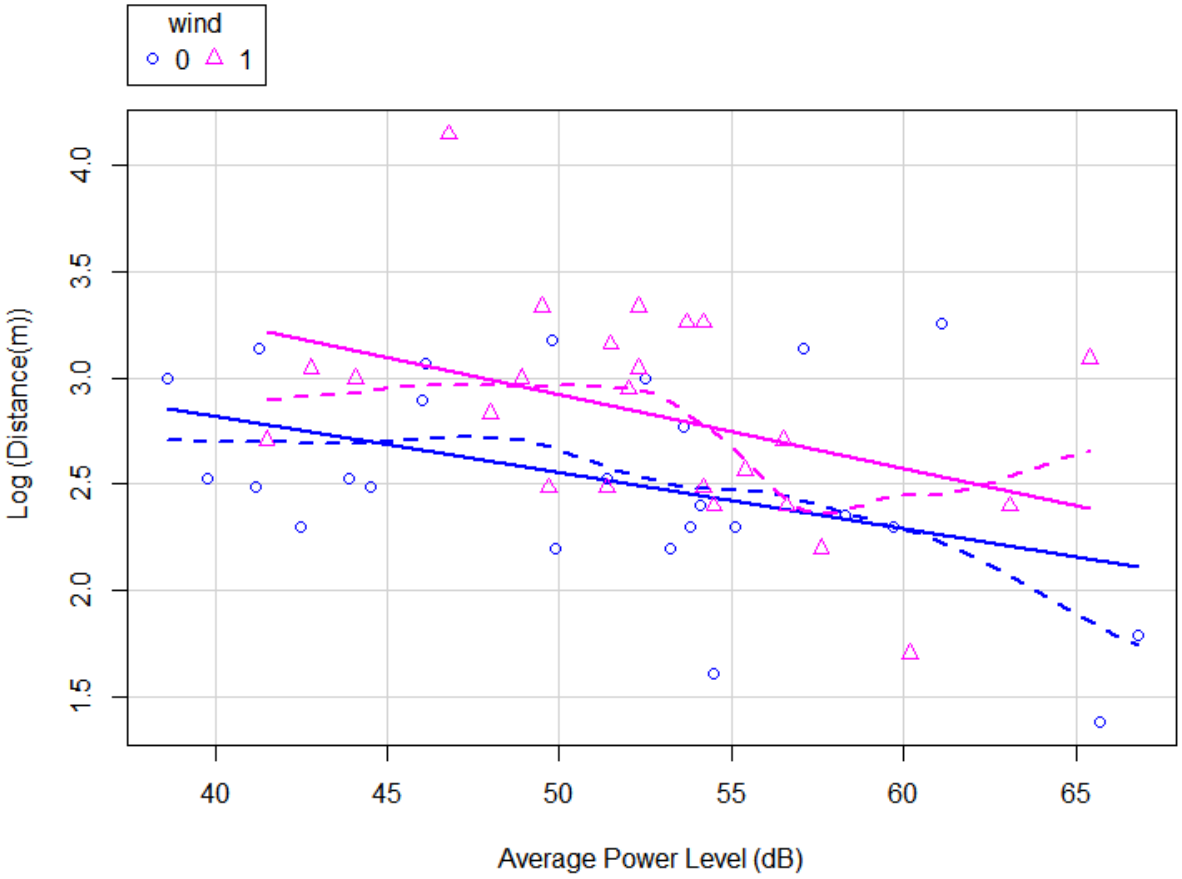

Figure 2-6. Linear regression lines (solid) showing the relationship between average power level and the log of distance when wind rating is 0 (blue, bottom) or 1 (pink, top). Open circles and triangles are observations under wind conditions of 0 and 1, respectively. Dotted lines are LOESS smoothers. Under a wind condition of 0, slope = -0.029; SE = 0.0095; t value= -3.07; p=0.0036, and adjusted R^2= 0.21. A wind condition of 1 steepens this slope and shifts it up by 0.34 log units.

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