USING VOCALIZATIONS TO MONITOR HOW CAPTIVE BRED ʻALALĀ 
(CORVUS HAWAIIENSIS) ARE ADAPTING TO THE WILD

A THESIS SUBMITTED TO THE GRADUATE DIVISION OF THE 
UNIVERSITY OF HAWAIʻI AT HILO IN PARTIAL FULFILLMENT 
OF THE REQUIREMENTS FOR THE DEGREE OF 

MASTER OF SCIENCE 
IN 
TROPICAL CONSERVATION BIOLOGY AND ENVIRONMENTAL SCIENCE 

May 2022 

By 
Robert L. Justice III 

Thesis Committee: 
Patrick Hart 
Kristina Paxton 
Alison Greggor 
Jonathan Price 

Keywords: Vocal Repertoire; Animal Behavior; Corvus 
hawaiiensis; Captive release
Acknowledgements

This work was supported by a Disney Foundation, the W.T. Yoshimoto Foundation, and NSF’s Crest Grant.

I would like to thank my committee for supporting me throughout this project, dealing with all my questions, editing a number of drafts, and giving me countless words of advice.

I would like to thank Pat, my advisor, for taking a chance on me and accepting me into his lab, and putting me out in the field where I belong. I definitely would not have been able to get through this program without the help that you provided not only on this project but also with the field work that you provided outside of my project.

Alison Greggor had a vital role in developing the social network data, which was a huge undertaking. This project would not have moved forward without those efforts. Your work and help in re-shaping my paper multiple times has gotten it to its present form.

I would like to specifically thank Kristina Paxton for helping me throughout this process. I do not think I would have been able to get over any let alone all the hurdles that I got through without your help. I can’t really express how helpful of a mentor you were to me throughout graduate school. With few academic mentors in my educational journey, the amount of time and effort that you have given me on this project was instrumental to my success.

I would also like to thank my family for instilling a desire to continue to work hard even when I didn’t feel like it. Without them, I would not have been in a position to succeed the way I have and be the person I am now.
Abstract

The `Alalā is a raucous, intelligent and curious bird that once occupied much of the dry and mesic forests around the island of Hawaii. Currently the remaining population of `Alalā resides only in captivity at the Keauhou Bird Conservation Center on Hawaiʻi island and the Maui Bird Conservation Center, however the long-term goal of these facilities is to reestablish wild populations of `Alalā on both islands. Starting in 2017, 27 captive bred ‘ālala were released at Puʻu Makaʻala Natural Area Reserve on Hawaiʻi island. My research focused on 18 of the 27 captive reared released birds as they transitioned from juveniles to adulthood in the wild. The San Diego Zoo Wildlife Alliance tracking team and I recorded the vocalizations of these individual `Alalā and their associated behaviors using a handheld video camera over 996 field days and a total of 682 video recordings. This allowed me to elucidate the different factors that influenced their vocalizations and pairing success and to uncover the variety of factors that influence their vocal repertoires, such as life stage, social connectedness, paired status, and sex. I found that juvenile repertoire size is a significant predictor of which birds would pair up quickly after maturing to adulthood, and that social connectedness to the group is a good predictor of what behaviors the birds would exhibit as adults. This study is the first to utilize vocalizations associated with specific behaviors to evaluate the potential for pairing success upon reintroduction for a bird that is extinct in the wild.
TABLE OF CONTENTS

ACKNOWLEDGEMENT........................................................................................................... i

ABSTRACT .............................................................................................................................. ii

LIST OF TABLES ................................................................................................................... v

LIST OF FIGURES ................................................................................................................ vi

INTRODUCTION ..................................................................................................................... 1

METHODS ............................................................................................................................. 4
  STUDY OF SPECIES AND AREA ......................................................................................... 4
  POST-RELEASE AND DATA COLLECTION ....................................................................... 5
  SOCIAL NETWORKS .......................................................................................................... 6
  CALL CLASSIFICATION ..................................................................................................... 6
  STATISTICAL ANALYSIS ................................................................................................. 8
    What influences ‘Alalā vocal repertoire size and diversity? .......................................... 8
    Is repertoire size/diversity as a juvenile an indicator of what vocalizations
    will be exhibited as an adult? ......................................................................................... 9
    What are the factors that influence the behaviors that are associated with
    their call types? ............................................................................................................. 9

RESULTS ............................................................................................................................. 10
  How social ranking and connectedness influenced the size and diversity of
  ‘Alalā repertoires during different life stages ................................................................. 10
  What is the relationship between repertoire size and diversity of an individual
  as a juvenile and adult? .................................................................................................... 10
  Predicting the occurrence of calls within different behavioral categories ................. 11

DISCUSSION ........................................................................................................................ 11

TABLES .................................................................................................................................. 15
  TABLE 1. SUMMARY OF VIDEO EFFORT AND DATA RECORDINGS FROM
          10/10/17-7/10/20 IN PU’U MAKA’ALA NATURAL AREA RESERVE .......... 15
  TABLE 2. DESCRIPTION OF SOCIAL BEHAVIOR CATEGORIES USED FOR
          SOCIAL NETWORK ANALYSIS ................................................................................. 16
  TABLE 3. DESCRIPTIONS OF BEHAVIORS ASSOCIATED WITH ‘ALALĀ
          VOCALIZATION ........................................................................................................ 18
  TABLE 4. SUMMARY OF INDIVIDUAL ‘ALALĀ INFORMATION, RELEASE
          COHORT YEAR, DATE MATURED INTO ADULT (ADULT DATE)
          AND FINAL PAIR STATUS BEFORE DEATH ....................................................... 19

FIGURES ............................................................................................................................... 20
  FIGURE 1. MAP A. LOCATION OF PU’U MAKÀ’ALA ..................................................... 20
  FIGURE 2. OVERALL VOCAL REPERTOIRE DIVERSITY BY LIFE STAGE AND
          PAIRED STATUS ....................................................................................................... 21
  FIGURE 3. THE REPERTOIRE SIZE AND REPERTOIRE DIVERSITY OF
          ‘ALALĀ THAT SURVIVED TO ADULTHOOD ...................................................... 22
FIGURE 4. PERCENT OF TOTAL CALLS OF EACH BEHAVIOR TYPE FOR INDIVIDUAL ‘ALALĀ SEPARATED BY THEIR FINAL STATUS……. 23
FIGURE 5. THE DIFFERENT SOCIAL NETWORK MEASURES COMPARED AT THE DIFFERENT FINAL LIFE STAGES OF ALL 18 INDIVIDUAL ‘ALALĀ ………………………………………………………………………………………………………. 24
REFERENCES………………………………………………………………………………………………………25
LIST OF TABLES

Table 1. Summary of video effort and data recordings from 10/10/17-7/10/20 in Pu‘u Maka’ala natural area reserve…………………………………………..

Table 2. Description of social behavior categories used for social network Analysis ……………………………………………………………………

Table 3. Descriptions of behaviors associated with ‘alalā vocalization…………………………………………………………………..

Table 4. Summary of individual ‘alalā information, release cohort year, date matured into adult (adult date) and final pair status before death ………….
LIST OF FIGURES

Figure 1. Map A. Location of pu’u maka’ala…………………………………………………
Figure 2. Overall vocal repertoire diversity by life stage and paired status………..
Figure 3. The repertoire size and repertoire diversity of ‘alalā that survived to adulthood……………………………………………………………………….
Figure 4. Percent of total calls of each behavior type for individual ‘alalā separated by their final status…………………………………………………..
Figure 5. The different social network measures compared at the different final life stages of all 18 individual ‘alalā ………………………………………
Introduction

Despite the importance of animal behavior to a species’ survival and reproductive success, the use of animal behavior research to inform conservation strategies is still underutilized (Greggor et al., 2016; Tobias & Pigot, 2019). The behavioral responses of animals to environmental changes such as habitat fragmentation, resource depletion and predator introduction can occur relatively quickly and be an accurate indication of biodiversity loss (Tadesse, 2018). In particular, changes in acoustic behaviors can serve as an informative measure of the influence of anthropogenic change on wildlife populations. For example, a loss in song diversity associated with population declines has been demonstrated in multiple species including: Dupont’s lark (Chersophilus duponti) in Spain (Laiola & Tella. 2007), regent honeyeaters (Anthochaera phrygia) in Australia (Crates et al., 2021), and a community of Hawaiian honeycreepers in Hawai`i (Paxton et al., 2019). Moreover, reduced song diversity in some populations also corresponded to lower population growth and viability (Laiola et al. 2008; Crates et al. 2021). In bats and cetaceans, anthropogenic noise can interfere with acoustic signaling via echolocation and has been shown to decrease foraging efficiency and mating opportunities, respectively (Schaub et al., 2009; Weilgart et al., 2007). Collectively, these examples highlight the potential use of acoustic signals and associated behaviors as a tool to monitor population health.

Avian vocalizations are one of the most documented forms of animal signaling (Baker, 2001; Catchpole & Slater, 2008) and can be very informative for monitoring by providing baseline data on populations and individuals (Lewis et al., 2021). These vocalizations may be learned or innate and are associated with behaviors that are connected to important life history events such as courtship, territory formation, and individual recognition (Lynch et al., 1996, Lewis et al., 2021). Vocal signals may have faster measurable responses to environmental change than genetic signature because they can be transmitted both vertically (between generations) and horizontally (within generations). An example of this can be seen in birds that live in urban environments that adjust their vocalizations to be heard over anthropogenic ambient noises (Luther & Derryberry, 2011). Learned song features, e.g., minimum frequency, may be altered to a sustained higher frequency level to adapt to urban environments in order to reduce
communication interferences (Shelton et al., 2020). Producing songs with different minimum frequencies over a relatively short time (Shelton et al., 2020) is indicative of the bird’s ability to respond within a generation. Unfortunately, we do commonly see anthropogenic changes, such as habitat fragmentation that can negatively impact the diversity and size of a bird's vocal repertoire.

Birds limited to highly fragmented landscapes, or that live in small populations have been shown to have decreased repertoire sizes potentially as a result of fewer tutors during their song learning period (Hart et al., 2018; Paxton et al., 2019; Valderrama et al., 2012). Similarly, birds in captivity may have fewer opportunities for the exchange of information between conspecifics which may result in the loss of certain call types and differences in the vocal repertoire of captive birds from those of wild birds (Crates et al., 2021; Tanimoto et al., 2017a). These differences may reflect a contrast in both the social and physical settings experienced by the captive reared birds or a possible loss of behavioral traits due to cultural drift (Tanimoto et al., 2017a).

As a species that resides entirely in human care the `Alalā, or Hawaiian crow (Corvus hawaiiensis), was once found in forests through the Island of Hawai`i, but is now extinct in the wild. Like other members of the Corvidae family, `Alalā are highly social and intelligent birds (Banko, 2002) and have complex and diverse vocalizations that play an integral role in social behaviors such as mate attraction, territorial defense, and alarms. Once paired, they spend their time with their partner and form a family group capable of using vocalizations to coordinate cooperative, conflict, and cognition behaviors (Izawa & Watanabe, 2008). As captive reared birds, the `Alalā, may be particularly susceptible to erosion of their vocal repertoire. A comparison of the vocal repertoire of captive reared `Alalā and wild `Alalā recorded in the 1990s found that some calls associated with alarms and territoriality broadcasts were absent in the captive population (Tanimoto et al., 2017a) which could have contributed to reintroduction failure (USFWS, 2009). However, there are likely additional behavioral factors important to the transition from juvenile to adulthood that are associated with increased likelihood of success of captive reared birds upon release to the wild.
Individual differences in behavior were largely ignored as incidental “noise” (Dall et. al., 2004) but is gaining momentum in its significance to species persistence. Only recently, research has started to investigate the importance of the social conditions associated with the adolescent life stage (Ruploh et al., 2012). Transition of these juveniles into adults means they leave what is familiar (family, social group, social rank, group protection) to encounter novel situations (Ruploh et al., 2012). While animal behavior, basically, is influenced by genes, physiology, and development which vary among individuals of a population (Hager, 2010; Marchetti & Price, 1989), the social environment that juveniles experience plays a major role in their fitness, courtship and aggressive behaviors (Fox et al., 2009). Several studies on corvids have demonstrated that social hierarchy influences vocalization and behavior (Izawa & Watanabe, 2008; Kondo & Hiraiwa-Hasegawa, 2015), and that social cohesiveness of individuals within a group not only influences the repertoire size but the composition and evenness of the repertoire as well (Leighton & Tucker, 2021). With this in mind, my study focused on juvenile to adulthood transition behaviors.

I conducted a longitudinal study over the course of three years that followed the transition to adulthood in captive-reared `Alalā after being released as juveniles into the wild. My goal was to understand if the released juveniles were developing appropriate vocalizations important to mate acquisition in the wild, as well as uncovering the influence of vocalizations on their social structure. As juveniles, `Alalā are socially connected with one another, but when they reach maturity, they are very selective in their mate choice, and after selecting a mate they separate into defended territories (Banko et al., 2002). By combining vocal observation and social network data, we were able to examine 1) What influences `Alalā vocal repertoire size and diversity, and 2) What is the relationship between juvenile and adult vocal repertoire size and diversity. Because previous studies on corvids have shown mated-pairs and socially dominant individuals make the most diverse array of call types and have the highest mating success (Kondo & Hiraiwa-Hasegawa, 2015), I expected that pair bonded individuals would have a higher repertoire size and diversity. Moreover, birds that are more socially connected as juveniles would have a larger vocal repertoire size and diversity when compared to less connected birds. Lastly, I used social network data to look into 3) the factors that shape the different types of calls displayed by the `Alalā. If we are able to extract information from
individual birds' repertoires that may be related to more aggressive behaviors, and thus potentially fitness, this could serve as a very useful tool in the monitoring of captive released animals as well as understanding how animal social structures are formed.

**Methods:**

*Study species and area:*

`Alalā reared at the San Diego Zoo Wildlife Alliance’s (SDZWA) Maui and Keauhou Bird Conservation Breeding Centers were released into the wild at Pu`u Maka`ala Natural Area Reserve (NAR) (Figure 1) in October 2017 (4 females, 7 males) and October 2018 (5 females, 5 males; Table 1). Birds in both release cohorts were 15-18 months old at release. `Alalā have been observed to live up to 18 years in the wild (1 female) and 25 years in captivity (1 male) (Banko et al., 2002). The age at first breeding is approximately 2-3 years for females and males. `Alalā are monogamous and often have long-term pair bonds, although extra-pair copulations have been observed, and in the event of death of a partner, a widow will attempt to pair bond again (USFWS, 2009). In this study, I classified the birds as either juveniles or adults depending on the sexual maturity of their cohort determined by observation of their pairing behavior. Apart from birds that showed pairing behavior prior to their third breeding season, all the birds were classified as adults starting March 3rd in their third year of life. I then further categorized adult birds by pair status: paired, unpaired, or widowed. Widowed birds were classified based on known or presumed death of their partner. Presumed death was based on the disappearance of the birds for more than a week.

The study area, Pu`u Maka`ala NAR, consists of 18,730 acres of old-growth `ōhi`a (*Metrosideros polymorpha*) and *koa* (*Acacia koa*) dominated forest interspersed with small patches of kīpuka forest and open pasture. Years of ungulate exclusion through fencing has resulted in a thriving under and midstory, dominated by native vegetation including many fruiting plants important to the `Alalā diet such as `ōlapa (*Cheirodendron trigynum*), hō`awa (*Pittosporum amplectens*) and `ōhelo `ai (*Vaccinium reticulatum*; Sakai et al., 1986). While fruit is a main component of `Alalā diet, they are considered generalist foragers, and also commonly
consume invertebrates, nectar, flowers, and the eggs and nestlings of other forest birds (Sakai et al., 1986).

**Post-release monitoring and data collection:**

Prior to release, each bird was uniquely color banded and fitted with a Very High Frequency (VHF) transmitter to allow released birds to be located daily and facilitate the collection of vocalizations and behavioral data for each bird. Along with the SDZWA tracking team, I, opportunistically, collected behavioral data for social network analyses and recorded vocalizations of individual `Alalā from October 2017 to July 2020 (Table 1). Food hoppers with supplemental food were spaced throughout the release areas and filled each day around 07:00, which attracted birds to the feeders and offered a unique opportunity for reliable re-sightings, observations and recordings. In cases where birds were not found after approximately one hour post morning feeding, I used radio telemetry to locate them in the NAR. Observations later in the day typically aimed to find birds away from the hopper locations in order to observe a wider variety of behaviors. As of early February 2019, a weekly focal follow of 15-30 minutes per bird was conducted to facilitate longer observations, farther from the feeding stations.

At each encounter with an `Alalā, the field team and I collected behavioral data and noted all social interactions associated with feeding, aggression, and breeding (Table 2), along with the time, GPS location, and general habitat characteristics associated with each observation. I adapted the nine social behavior categories used in this study based on ethograms of related corvid species (Greggor et al., 2016b; Jolles et al., 2013; Logan et al., 2012) and behaviors commonly seen at the SDZWA conservation breeding centers. For behaviors that involved directed interactions (e.g. aggression of one bird towards another bird), I indicated the bird that initiated the behavior and the bird that received the behavior for use in directed networks.

In a subset of observations, I recorded the vocalizations of individual `Alalā and their associated behaviors using a handheld video camera (JVC Everio). In order to capture a wide variety of behaviors associated with vocalizations I recorded birds between 06:45 and 16:00. During each recording, I focused on recording the vocalizations of an individual `Alalā, however, vocalizations of other `Alalā in close proximity to the focal bird and in the field of view of the recorder were documented as well. For each recording, I identified the vocalizing
`Alalā based on their unique color band combination and also documented the specific vocalization, the behavior associated with each vocalization, the I.D.(s) of any birds involved in an interaction, the overall context of the video, as well as the date, time, and GPS location of the observation.

Social Networks:

I divided the social behaviors documented during observations into three social behavior categories: 1) affiliative interactions (AFF; co-feeding and co-sitting), 2) aggressive interactions (chasing and displacing), and 3) pair bonding interactions (PB; allofeeding, allopreening, breeding solicitations, copulation) (Table 2). Observations within each of the three categories were divided into time periods based on when the number of birds in the NAR remained stable (e.g. a new time period was started if a bird died or if new birds were released). I used the R package ‘asnipe’ (Farine et al., 2013) to calculate social networks separately for each social behavior category and each time period. Affiliative and PB networks were derived from undirected behaviors, while the aggressive network was based on directed behaviors. A network permutation was run to determine whether the network had sufficient observations to differ from chance.

I calculated betweenness from undirected AFF and PB social networks to quantify how well connected the individual was to the other `Alalā that were on the landscape during each time period. I also calculated out-degree from the directed aggressive social network to quantify the amount of aggressive interactions that each individual exhibited to better understand how this shaped the likelihood of pairing up as an adult. Network metrics were calculated for each time period, and a weighted mean value of the network metric was created for all time periods that occurred within each life history stage (juvenile, breeding), weighted by the number of observations taken during that period.

Call Classification:

Digital video recordings were converted to 16-bit WAV format at a 44.1 kHz sampling rate. I then made selections of all vocalizations on each recording in Raven Pro (version 1.5; Bioacoustics Research Program, Cornell Lab of Ornithology, Ithaca, NY, U.S.A.) using a Hann
window type with a discrete Fourier transform (DFT) size of 1024 samples, 50% time overlap, and a 3 dB filter bandwidth at 84.6 Hz. Calls vocalized > 0.5 seconds apart were selected individually while groups of calls vocalized < 0.5 seconds apart were selected as a call phrase. Only a single representative of each unique call type within a call phrase was included in the proceeding steps to avoid bias that may arise when comparing calls that are repeated within a call phrase. Vocalizations in which the vocalizing `Alalā could not be identified, along with vocalizations that overlapped with noise (e.g., other `Alalā, helicopters, wind) that obscured key distinguishing characteristics of the vocalizations were excluded. In addition, only individuals with at least 5 videos and > 200 vocalizations were included in subsequent analyses. I categorized each vocalization into one of the following behavioral categories based on the associated behaviors exhibited in the video: aggressive (AG), alarm (AL), territorial (TB), courtship (CO), social-contact (SC), submissive (SU), and close quarter contact (SM). Calls for which no associated behavior could be determined were categorized as miscellaneous (MI)(Table 3).

To classify `Alalā vocalizations into call types, I used the web-based software KOE, which uses interactive ordination plots to classify large numbers of vocalizations in an objective manner (Fuzukawa, 2020). In KOE, ordinations were constructed using the t-distributed Stochastic Neighbor Embedding (t-SNE) technique based on specific acoustic features from each vocalization. To prevent biasing selections based on the distance of a vocalization from a recorder or individual variation I did not include acoustic features of a vocalization that involved duration, power, amplitude, or harmonics. I first classified vocalizations into broad call type categories in KOE based on visual and aural review of vocalizations clustered on the interactive ordination plots. I then reviewed call types in Raven Pro to refine call type classifications as the spectrogram resolution in Raven was better suited for fine-scale classification. I used acoustic, temporal, and contextual criteria to differentiate call types from each other. I categorized vocalizations within an individual call type as variants if they exhibited slight differences presumed to be due to individual variation, morphology, or locomotion (Benti et al., 2019; Boeckle et al., 2018; Laiolo & Rolando, 2003; Tanimoto et al., 2017a). For consistency, vocal libraries were classified by one individual exclusively, then verified with past `Alalā libraries (Tanimoto et al., 2017b) to ensure consistency.
Statistical Analysis:

All statistical analyses were conducted in R (version 4.0.3; R Development Core Team, 2020). I first created vocalization accumulation curves of each individual to determine if the full repertoire size was captured using the R package ‘vegan’ (Oksanen et al., 2020). To account for differences in sampling effort between individuals, I standardized repertoire size by dividing the total number of unique call types identified by the total number of recorded calls. Thus, the standardized repertoire size represents the proportion of unique call types vocalized out of all vocalizations recorded for each bird. I calculated repertoire diversity for each individual using the Simpson’s diversity index (Oksanen et al., 2020) which includes not only the number of unique call types (e.g. richness), but also the relative abundance of each call type (e.g. evenness) (Simpson et al., 1949). The Simpson diversity index ranges between 0 and 1, with higher values indicating a greater repertoire diversity (Simpson et al., 1949).

What influences ‘Alalā vocal repertoire size and diversity?

I used linear models to determine which factors most strongly influenced ‘Alalā vocal repertoire size and repertoire diversity over the entire study period. In each model, I included the following explanatory variables: betweenness metric from both the AFF and PB social networks as a measure of social connectedness, the bird’s final pairing status (paired, unpaired, juvenile), and the sex of the bird. A bird’s final pairing status was based on whether a bird paired with another ‘Alalā at any point during the period of the study. Birds that died before they reached sexual maturity were classified as a juvenile. I log transformed repertoire diversity to improve normality, and used residual plots to assess model fit. I assumed statistical significance at alpha ≤ 0.05 and for significance tests I conducted post-hoc analyses with Tukey’s HSD (family-wise error rate = 0.05) to determine differences among groups. To identify the factors that influence the repertoire beta diversity I used a Permutational Multivariate Analysis of Variance (PERMANOVA; Anderson et al., 2001). Beta diversity was measured using a Bray-Curtis measure of dissimilarity (Bray & Curtis, 1957). The Bray-Curtis coefficient measures the difference in abundance and richness of call types between each pair of individuals, with a value of 1 indicating no shared call types and a value of 0 indicating the abundance and identity of all call types are the same between individuals. I standardized call types and individuals by their maxima so that rare and abundant call types were considered and to account for unequal sample
size among individuals. For the PERMANOVA model, the same explanatory variables as described above were included.

Is repertoire size/diversity as a juvenile an indicator of what vocalizations will be exhibited as an adult?

To examine the relationship between a bird’s juvenile and adult vocal repertoire size and diversity and how a bird’s final pairing status (paired, unpaired) as an adult may influence this relationship, I used a linear mixed model with a logit link function, using the R package ‘lmer’ (Bates et al., 2015). Each bird’s vocal repertoire size and diversity was calculated separately for juvenile and adult life stages based on vocalizations recorded during each life stage. Only birds that survived to adulthood were included in this analysis. In each model, I included the bird’s life stage (juvenile, adult), final pairing status, (paired, unpaired), and the interaction of the two variables as fixed factors. In addition, individual ID was included as a random factor to account for repeated measures of vocal repertoire size and diversity from the same individual. I log transformed juvenile and adult vocal repertoire size to improve normality and used residual plots to assess model fit and then conducted post-hoc analysis for significant interactions using the R package ‘emmeans’ (Russell Lenth, 2020).

What are the factors that influence the behaviors that are associated with their call types?

To understand what factors may predict the occurrence of different vocalization categories associated with `Alalā behaviors, I used a Cumulative Link Mixed Model (CLMM) with a logit link function, using the R package ‘ordinal’ (Christensen, 2019). The original 8 behavioral vocalization categories were combined into 5 ordinal categories (SU, SC, AL, AG, and TB) that ranked behavior from least to most ‘dominant’. Close quarter contact calls were reclassified into the SU category because they were typically between pairs used in a submissive manner with their partner. Miscellaneous calls were removed due to the difficulty of classifying vocalizations of unknown behavior on an ordinal scale. In addition, I removed courtship calls because there were only 12 calls classified into this behavioral category. As fixed factors in the model, I included out-degree measured from the aggression social network as a measure of outward aggression, betweenness measured from the AFF and PB social networks as a measure of social connectedness, status (juvenile, unpaired, paired, widowed), and sex of the bird. All social
network measures were based on social networks constructed at the time a vocalization was recorded. Likewise, the status of birds was determined based on their pairing behavior at the time a vocalization was recorded.

Results

I recorded 10,425 vocalizations from 18 captive reared `Alalā released in the wild for an average of 579.2 ± 198.8 days post-release (Table 4). I captured a total of 43 unique call types with an average of 37.8 ± 14.7 videos per bird and 19.8 ± 8.9 unique call types per bird (Table 4). Accumulation curves for all individuals did not reach an asymptote indicating that `Alalā were either still learning new vocalizations or I had not yet captured their full repertoire.

How social ranking and connectedness influenced the size and diversity of `Alalā repertoires during different life stages

`Alalā vocal repertoire size and alpha diversity were generally not influenced by the social connectedness of a bird based on behaviors of pair bonding (size: t = 0.98, p = 0.35, diversity: PB: F1,12= 2.81, p = 0.12), affiliating with other birds (size: t = -0.23, p = 0.82, diversity: F1,12= 0.34, p = 0.57) or the sex of the bird (size: t = 1.55, p = 0.15, diversity: F1,12= 0.04, p = 0.85). However, juveniles that died in the wild prior to reaching adulthood had significantly lower vocal repertoire alpha diversity compared to unpaired or paired adults (F2,12= 5.52, p = 0.02) (Figure 2). In contrast to alpha diversity, beta repertoire diversity, measured using Bray-Curtis dissimilarity indices, was not only influenced by a bird’s final pair status (PERMANOVA: F2,12 = 2.201, R2 = 0.20, p = 0.02), but also the juvenile connectedness of the bird based on behaviors of affiliating with other birds (AFF betweenness: F1,12 = 2.23, R2 = 0.10, p = 0.04) and the sex of the bird (F = 2.28, R2 = 0.10, p = 0.05). However, social connectedness related to behaviors associated with pair bonding was not significantly related to vocal repertoire beta diversity (F1,12 = 1.71, R2 = 0.08, p = 0.11).

What is the relationship between repertoire size and diversity of an individual as a juvenile and adult?

I found a significant interaction between life stage and pair status for both the size and diversity of a bird’s repertoire (size: F1,11 = 8.76, p = 0.01, diversity: F1,11 = 10.23, p = 0.01;
Repertoire size and diversity for `Alalā that remained unpaired did not differ between their juvenile and adult phases (size: \( t = 0.42, p = 0.68 \); diversity: \( t = -2.113, p = 0.06 \)). In contrast, `Alalā that formed a pair with another `Alalā had a larger vocal repertoire size as a juvenile than as an adult (size: \( t = -5.39, p = .0001 \)). However, the diversity of calls within the adult phase of a paired `Alalā was greater than during their juvenile phase (\( t = -2.80, p = 0.02 \)) (Figure 3).

**Predicting the occurrence of calls within different behavioral categories**

All behavioral categories (e.g., AG, SU, TB) were exhibited during each life stages (Figure 4), however the frequency of calls within each behavioral category differed in association with a bird’s life stage (\( F_{3,11} = 354.14, p < 0.001 \)), the social connectedness of a bird (PB: \( F_{1,11} = 15.71, p < 0.001 \); AFF: \( F_{1,11} = 8.12, p = .004 \)), and the amount of outward aggressive interactions with other `Alalā (\( F_{1,11} = 26.26, p < 0.001 \)). However, there was no difference in the likelihood of vocalizing calls associated with different behavioral categories between males and females (\( F_{1,11} = 0.57, p = 0.45 \)). The vocalizations of both juvenile and unpaired birds were dominated primarily by submissive calls, while paired and widowed birds primarily used territorial broadcast and aggressive calls (Figure 4). Similarly, the affiliate measures associated with the social network indicated `Alalā that affiliated with few individuals (e.g., paired birds) had a larger likelihood of vocalizing call types associated with dominant behaviors such as territorial broadcasts and aggression (Figure 5).

**Discussion**

This longitudinal study yielded a large collection of acoustic and behavioral data for individuals over a 3-year period, allowing us to link behaviors, life stages and social connectivity to specific vocalizations for the critically endangered `Alalā (*Corvus hawaiiensis*). Combining these data with social network metrics helped us better understand the relationship between social dynamics and avian vocalizations in the wild. I found that `Alalā that formed pair bonds had larger repertoire sizes as juveniles than as adults, and that their adult repertoires were more diverse. Further, juveniles that exhibited smaller vocal repertoires were less likely to form pair bonds in their first year as a mature adult. These results indicate that juvenile repertoire size and
position within the social hierarchy may be good indicators of the likelihood of pairing success of captive reared individuals released into the wild.

In accordance with my findings, multiple studies suggest that larger repertoire sizes are related to increased pairing and mating success in birds (Creanza et al., 2016; Garamszegi et al., 2012; Potvin et. al., 2015; Searcy, 1984; 1992). These studies hypothesize that larger repertoire sizes may indicate a more attractive mate (Garamszegi et al., 2012), suggesting better male fitness and territory defense (Potvin et al., 2015). Juvenile and adult repertoire size did not vary for birds that remained unpaired in this study, suggesting that changes in life stage may not be the only factor leading to changes in vocal repertoires. Some birds may learn and retain more calls, while others may refine their repertoires rather than increase them (Rundstrom & Creanza, 2021). It is possible that the `Alalā, like other bird species, use repertoire size as an indicator of fitness in mate selection.

Beyond repertoire size, our data demonstrates further changes in `Alalā vocal behavior once two birds form a pair. Changes in repertoire size and diversity after birds pair has been shown to occur in other avian species (e.g. call repertoire composition changes in zebra finches (Taeniopygia guttata) (Gill et al., 2015) and reductions in song-type variety in rufous-and-white wrens (Thryothorus rufalbus) (Hennin et al., 2009). When we examined the birds that transitioned into paired adults, we found that their repertoire size became smaller, but the diversity of their repertoire actually increased, indicating that these birds were using a smaller total number of unique vocalizations but a more even variety of the calls more often. Closer inspection into these vocalizations revealed more similarities in call types used by paired individuals. This convergence may reflect similar change in behavior, representing a lack of need to perform such a wide range of vocalizations, such as the submissive calls or common contact (SC01), and only expend energy on calls that are relevant to pair bonded individuals such as territorial broadcasts, aggression calls, and courtship calls (Sewall, 2012).

`Alalā social connectedness and how they were affiliated with other `Alalā influenced the diversity of their vocalizations. Past studies have shown that matched calls among members of a social group provides various benefits like facilitating cooperative defense of resources, such as food, from competing groups (King & McGregor, 2015; Sewall, 2012). We saw that birds with
a lower affiliated betweenness score as a juvenile were more likely to have a more diverse vocal repertoire as an adult. While we did not see repertoire size differences between paired and unpaired adults, changes in repertoire diversity were much more apparent in paired individuals as they matured into adults. Unpaired individuals kept a similar repertoire size and diversity as they matured and exhibited more submissive and less aggressive behaviors compared to their paired counterparts. Given that vocal matching is a learned behavior and not innate (King & McGregor, 2015; Sewall, 2012), changes in the diversity or evenness of vocalizations indicates that the birds were learning in their new environment. Given that we have seen changes in birds’ vocal repertoires based on wild vs. captive rearing (Tanimoto et al., 2017) in the past, it could be an option for the releases of newly captive reared birds to be within the same vicinity of other birds to allow the learning of these “wild” behaviors. An important thing to note is that newly released birds would have to be exposed to the calls, but not infringing on the food resources and established territories of already established pairs.

Identifying key elements in a juvenile’s repertoire that correlate with important survival behaviors is a huge step in understanding the transition periods in their lives. The ability to identify and measure indicator vocalizations and their associated behaviors would allow us to predict the likelihood a given bird will pair bond quickly, a powerful new tool to identify birds that could potentially be more successful in the wild. The longitudinal nature of this study and the method of using animal communication and associated behaviors to monitor populations are both relatively unique in behavioral ecology. Usage of bioacoustics technology to extract individuality information has been used in many avian species, such as singing honeyeaters (Gavicalis virescens) (Fox et al., 2008), great spotted kiwis (Apteryx haastii) (Dent & Molles, 2016), tawny owl (Strix aluco) (Choi et al., 2019) green backed flycatchers (Ficedula elisae) (Chen et a., 2020), but none of these studies looked at associated behaviors (but see Dent & Molles, 2016). In our study, collecting behavioral data across the juvenile stage and into adulthood has provided better insights than just studying each life stage individually. Knowledge of the way vocal behaviors transition over a life-stage continuum can contribute to conservation outcomes if those behaviors provide insight into a population’s response to different actions (Teixera et al., 2019). For example, vocal behaviors may signal habitat quality or changes (Goretskaia et al., 2018). High quality habitats support not just the species but also support behaviors that promote species persistence. Therefore, a measure of the effectiveness of habitat
restorations may be detection of juveniles with a larger vocal repertoires following the conservation action.

Although many of the `Alalā in this study died, and the rest were brought back into captivity, the data that was collected during their time in the wild has important implications to the future success of reintroductions of this species. By extracting information from the vocalizations of juveniles that eventually formed pair bonds as adults, we identified acoustic signs that set them apart from juveniles that did not pair. This individualized information during their juvenile life-stage could be foundational to future investigations of the `Alalā and more broadly, be useful in developing a template for more successful future releases of countless other bird species from captivity into the wild.
# Tables

Table 1. Summary of video effort and data recordings from 10/10/17-7/10/20 in Pu‘u Maka‘ala Natural Area Reserve

<table>
<thead>
<tr>
<th>Individual ID</th>
<th>Total Videos</th>
<th>Call Total</th>
<th>Start Date</th>
<th>End Date</th>
<th>Date Span</th>
<th>Unique Call Types</th>
<th>Unique Behavior Types</th>
<th>Observation Time</th>
<th>Standard Repertoire</th>
</tr>
</thead>
<tbody>
<tr>
<td>BWWM</td>
<td>5</td>
<td>101</td>
<td>10/10/17</td>
<td>5/30/19</td>
<td>598</td>
<td>11</td>
<td>7</td>
<td>3.89</td>
<td>0.1089</td>
</tr>
<tr>
<td>YOWM</td>
<td>18</td>
<td>210</td>
<td>10/17/17</td>
<td>12/3/19</td>
<td>778</td>
<td>14</td>
<td>7</td>
<td>22.73</td>
<td>0.0667</td>
</tr>
<tr>
<td>RWRM</td>
<td>19</td>
<td>308</td>
<td>1/3/20</td>
<td>7/10/20</td>
<td>190</td>
<td>10</td>
<td>6</td>
<td>117.84</td>
<td>0.0325</td>
</tr>
<tr>
<td>RMGO</td>
<td>23</td>
<td>235</td>
<td>1/13/19</td>
<td>1/3/20</td>
<td>356</td>
<td>11</td>
<td>6</td>
<td>55.89</td>
<td>0.0468</td>
</tr>
<tr>
<td>OOWM</td>
<td>25</td>
<td>319</td>
<td>2/25/18</td>
<td>12/6/19</td>
<td>650</td>
<td>24</td>
<td>8</td>
<td>29.97</td>
<td>0.0752</td>
</tr>
<tr>
<td>RMYO</td>
<td>26</td>
<td>280</td>
<td>12/11/18</td>
<td>1/18/20</td>
<td>404</td>
<td>16</td>
<td>7</td>
<td>78.56</td>
<td>0.0571</td>
</tr>
<tr>
<td>OWWM</td>
<td>28</td>
<td>333</td>
<td>6/3/18</td>
<td>12/2/19</td>
<td>548</td>
<td>10</td>
<td>6</td>
<td>69.26</td>
<td>0.03</td>
</tr>
<tr>
<td>RMWO</td>
<td>29</td>
<td>423</td>
<td>1/2/19</td>
<td>1/3/20</td>
<td>367</td>
<td>9</td>
<td>4</td>
<td>79.77</td>
<td>0.0213</td>
</tr>
<tr>
<td>GWWM</td>
<td>31</td>
<td>381</td>
<td>10/30/17</td>
<td>6/15/20</td>
<td>960</td>
<td>19</td>
<td>7</td>
<td>89.86</td>
<td>0.0499</td>
</tr>
<tr>
<td>GOWM</td>
<td>35</td>
<td>381</td>
<td>6/20/18</td>
<td>7/10/20</td>
<td>752</td>
<td>26</td>
<td>9</td>
<td>147.56</td>
<td>0.0432</td>
</tr>
<tr>
<td>YWWM</td>
<td>38</td>
<td>381</td>
<td>2/22/18</td>
<td>2/7/20</td>
<td>716</td>
<td>31</td>
<td>8</td>
<td>87.48</td>
<td>0.0481</td>
</tr>
<tr>
<td>BOWM</td>
<td>40</td>
<td>381</td>
<td>1/1/18</td>
<td>6/12/20</td>
<td>894</td>
<td>33</td>
<td>9</td>
<td>84.24</td>
<td>0.0486</td>
</tr>
<tr>
<td>ROWM</td>
<td>41</td>
<td>381</td>
<td>2/20/18</td>
<td>4/24/20</td>
<td>795</td>
<td>29</td>
<td>8</td>
<td>93.11</td>
<td>0.0333</td>
</tr>
<tr>
<td>VORM</td>
<td>43</td>
<td>381</td>
<td>11/6/18</td>
<td>10/14/19</td>
<td>343</td>
<td>11</td>
<td>5</td>
<td>108.61</td>
<td>0.0135</td>
</tr>
<tr>
<td>RMPW</td>
<td>44</td>
<td>381</td>
<td>2/27/19</td>
<td>7/10/20</td>
<td>500</td>
<td>21</td>
<td>8</td>
<td>187.72</td>
<td>0.0309</td>
</tr>
<tr>
<td>SWRM</td>
<td>56</td>
<td>381</td>
<td>10/9/18</td>
<td>12/2/19</td>
<td>420</td>
<td>15</td>
<td>6</td>
<td>127.38</td>
<td>0.0194</td>
</tr>
<tr>
<td>RMWW</td>
<td>57</td>
<td>381</td>
<td>12/11/18</td>
<td>7/10/20</td>
<td>578</td>
<td>13</td>
<td>6</td>
<td>231.77</td>
<td>0.0114</td>
</tr>
<tr>
<td>RMGW</td>
<td>60</td>
<td>381</td>
<td>11/4/18</td>
<td>7/10/20</td>
<td>615</td>
<td>31</td>
<td>8</td>
<td>192.57</td>
<td>0.0462</td>
</tr>
<tr>
<td>RMPO</td>
<td>68</td>
<td>381</td>
<td>12/9/18</td>
<td>6/19/20</td>
<td>559</td>
<td>34</td>
<td>9</td>
<td>194.37</td>
<td>0.0354</td>
</tr>
<tr>
<td>Averages</td>
<td>37.83</td>
<td>573.56</td>
<td>8/20/18</td>
<td>3/20/20</td>
<td>579.17</td>
<td>19.83</td>
<td>7.06</td>
<td>111.04</td>
<td>0.0394</td>
</tr>
</tbody>
</table>
Table 2. Description of social behavior categories used for social network analysis. For directed behaviors we identified the initiator and the receiver bird during data collection. Behaviors and their biological significance were adapted from past corvid literature.

<table>
<thead>
<tr>
<th>Social behavior</th>
<th>Description</th>
<th>Social behavior type</th>
</tr>
</thead>
<tbody>
<tr>
<td>Co-Feeding</td>
<td>Two or more birds feeding together. A directed behavior that exhibits social tolerance of each individual</td>
<td>Affiliative Interaction</td>
</tr>
<tr>
<td>Co-Sitting</td>
<td>Two or more birds sitting within shoulder distance of one another. A non-directed behavior.</td>
<td>Affiliative Interaction</td>
</tr>
<tr>
<td>Submissive Begging</td>
<td>Begging used higher pitched vocalization, many times with beak open. Wing posturing was usually included with their vocalizations. A directed behavior with a clear initiator and receiver.</td>
<td>Affiliative Interaction</td>
</tr>
<tr>
<td>Chase</td>
<td>Closely following one or more birds while the other bird(s) were evasive in flight. An aggressive directed behavior.</td>
<td>Outward Aggression Interaction</td>
</tr>
<tr>
<td>Displace</td>
<td>When one bird actively moves another bird from a position on a branch and/or lands directly in the spot that another bird was located. An aggressive directed behavior.</td>
<td>Outward Aggression Interaction</td>
</tr>
<tr>
<td>General aggression</td>
<td>Covers all other types of aggression, including posturing threats, contact aggression with beak, wings or feet. A directed behavior.</td>
<td>Outward Aggression Interaction</td>
</tr>
<tr>
<td>-------------------</td>
<td>----------------------------------------------------------------------------------------------------------------</td>
<td>--------------------------------</td>
</tr>
<tr>
<td>Allofeed</td>
<td>When the initiating bird places food inside the beak of another bird. A pair bonding directed behavior.</td>
<td>Pair bonding interaction</td>
</tr>
<tr>
<td>Allopreen</td>
<td>When the initiating bird uses its beak to touch or groom the feathers or beak of another. A pair bonding directed behavior.</td>
<td>Pair bonding interaction</td>
</tr>
<tr>
<td>Breeding solicitation</td>
<td>Typically seen with the male cooing toward the female, females would respond with tail wagging. A pair bonding directed behavior.</td>
<td>Pair bonding interaction</td>
</tr>
<tr>
<td>Breeding copulation</td>
<td>After a sequence of a breeding solicitation, the male will climb onto the back of the female. Copulations are noted regardless of whether they are successful. (Never seen over the course of this study). An undirected behavior.</td>
<td>Pair bonding interaction</td>
</tr>
</tbody>
</table>
Table 3. Descriptions of behaviors associated with `Alalā vocalizations.

<table>
<thead>
<tr>
<th>Behavior</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>AG – Aggression</td>
<td>Vocalizations used to exert dominance toward a conspecific or human within the immediate vicinity.</td>
</tr>
<tr>
<td>AL – Alarm</td>
<td>Vocalizations used to warn conspecifics of potential danger, such as a predator or human.</td>
</tr>
<tr>
<td>CO – Courtship</td>
<td>Calls used to communicate breeding intentions.</td>
</tr>
<tr>
<td>SC – Social Contact</td>
<td>Vocalizations used to locate conspecifics outside of the immediate vicinity.</td>
</tr>
<tr>
<td>SM – Close Contact</td>
<td>Vocalizations used to communicate with affiliates within the immediate vicinity.</td>
</tr>
<tr>
<td>SU – Submission</td>
<td>Vocalizations used to indicate social status or request food.</td>
</tr>
<tr>
<td>TB – Territorial Broadcast</td>
<td>Vocalizations projected over a large area to indicate the boundaries of a territory.</td>
</tr>
<tr>
<td>MI – Miscellaneous</td>
<td>Vocalizations with either an unclear associated behavior or multiple behavioral contexts.</td>
</tr>
</tbody>
</table>
Table 4. Summary of individual `Alalā identity, release cohort year, date matured into adult (adult date), and final pair status before death. Betweenness and aggression metrics are averaged across networks.

<table>
<thead>
<tr>
<th>Color band Combo</th>
<th>Hawaiian Name</th>
<th>Cohort</th>
<th>Sex</th>
<th>Affiliative Betweenness</th>
<th>Pair bond Betweenness</th>
<th>Outward Aggression</th>
<th>Adult Date</th>
<th>Final Status</th>
</tr>
</thead>
<tbody>
<tr>
<td>BOWM</td>
<td>Mana`olana</td>
<td>2017</td>
<td>M</td>
<td>3.31</td>
<td>11.17</td>
<td>4.35</td>
<td>3/13/19</td>
<td>Widow</td>
</tr>
<tr>
<td>GOWM</td>
<td>Palekana</td>
<td>2017</td>
<td>M</td>
<td>7.33</td>
<td>28.00</td>
<td>4.69</td>
<td>3/1/19</td>
<td>Paired</td>
</tr>
<tr>
<td>GWWM</td>
<td>Lili`uwelo</td>
<td>2017</td>
<td>F</td>
<td>2.43</td>
<td>2.65</td>
<td>7.25</td>
<td>12/12/18</td>
<td>Widow</td>
</tr>
<tr>
<td>OOWM</td>
<td>Ho`oikaika</td>
<td>2017</td>
<td>M</td>
<td>7.49</td>
<td>5.38</td>
<td>11.80</td>
<td>12/12/18</td>
<td>Paired</td>
</tr>
<tr>
<td>OWWM</td>
<td>Manaiakalani</td>
<td>2017</td>
<td>F</td>
<td>6.36</td>
<td>0.00</td>
<td>0.56</td>
<td>3/13/19</td>
<td>Paired</td>
</tr>
<tr>
<td>RMGW</td>
<td>Ho`omalu</td>
<td>2018</td>
<td>F</td>
<td>10.27</td>
<td>26.58</td>
<td>5.35</td>
<td>12/16/19</td>
<td>Paired</td>
</tr>
<tr>
<td>RMOO</td>
<td>Aumoamoa</td>
<td>2018</td>
<td>M</td>
<td>14.63</td>
<td>13.08</td>
<td>2.60</td>
<td>2/1/20</td>
<td>Juvenile</td>
</tr>
<tr>
<td>RMPO</td>
<td>Ulu</td>
<td>2018</td>
<td>M</td>
<td>5.07</td>
<td>0.32</td>
<td>4.79</td>
<td>12/16/19</td>
<td>Paired</td>
</tr>
<tr>
<td>RMPW</td>
<td>Maika`iloa</td>
<td>2018</td>
<td>F</td>
<td>19.70</td>
<td>10.71</td>
<td>2.63</td>
<td>3/1/20</td>
<td>Unpaired</td>
</tr>
<tr>
<td>RMWO</td>
<td>Kūkia`imauna</td>
<td>2018</td>
<td>M</td>
<td>31.63</td>
<td>3.01</td>
<td>2.75</td>
<td>1/13/20</td>
<td>Juvenile</td>
</tr>
<tr>
<td>RMWW</td>
<td>Kū<code>oko</code>a</td>
<td>2018</td>
<td>F</td>
<td>12.45</td>
<td>0.19</td>
<td>2.82</td>
<td>4/27/20</td>
<td>Paired</td>
</tr>
<tr>
<td>RMYO</td>
<td>Kaleo</td>
<td>2018</td>
<td>M</td>
<td>8.67</td>
<td>33.64</td>
<td>3.60</td>
<td>1/16/20</td>
<td>Juvenile</td>
</tr>
<tr>
<td>ROWM</td>
<td>Kia<code>ikūmokuhā lī</code>i</td>
<td>2017</td>
<td>M</td>
<td>9.73</td>
<td>11.81</td>
<td>3.79</td>
<td>3/1/19</td>
<td>Widow</td>
</tr>
<tr>
<td>RWRM</td>
<td>Kulani</td>
<td>2018</td>
<td>F</td>
<td>6.39</td>
<td>9.79</td>
<td>3.18</td>
<td>3/1/20</td>
<td>Unpaired</td>
</tr>
<tr>
<td>SWRM</td>
<td>`Eleu</td>
<td>2018</td>
<td>F</td>
<td>12.70</td>
<td>9.07</td>
<td>5.96</td>
<td>1/13/20</td>
<td>Juvenile</td>
</tr>
<tr>
<td>VORM</td>
<td>Makalapua</td>
<td>2018</td>
<td>M</td>
<td>1.88</td>
<td>18.71</td>
<td>4.43</td>
<td>11/3/19</td>
<td>Juvenile</td>
</tr>
<tr>
<td>YOWM</td>
<td>Mele</td>
<td>2017</td>
<td>M</td>
<td>16.43</td>
<td>10.81</td>
<td>1.18</td>
<td>3/1/19</td>
<td>Unpaired</td>
</tr>
<tr>
<td>YWWM</td>
<td>Ola</td>
<td>2017</td>
<td>F</td>
<td>5.43</td>
<td>9.92</td>
<td>2.21</td>
<td>3/1/19</td>
<td>Paired</td>
</tr>
</tbody>
</table>
Figures

Figure 1: A) Location of Puʻu Makaʻala Natural Area Reserve on Hawaiʻi Island. B) Detailed map of Puʻu Makaʻala Natural Area Reserve were ʻAlalā were released (red X). The ʻAlalā have been seen throughout much of the Northern Western region of the NARS (higher elevation areas of the NARS; State of Hawaiʻi 2020).
Figure 2. Overall vocal repertoire diversity by life stage and paired status. These categories indicate birds that died before adulthood (juvenile), birds that never paired with another bird during the course of this study (unpaired), and birds that paired with another bird at some point during this study (paired). The boxplots show the median and interquartile range for each pair status of the `Alalā.
Figure 3. The repertoire size (left) and repertoire diversity (right) of `Alalā that paired with another bird or remained unpaired during different stages of their life. The boxplots show the median and interquartile range for each life stage of the `Alalā.
Figure 4. Percent of total calls of each behavior type for individual `Alalā separated by their final status. SU- Submissive calls, SC- Social contact calls, AL- Alarm calls, AG- Aggressive calls, TB- Territorial Broadcast calls.
Figure 5. Social network measures (list three measures here) compared at the different final life stages for each `Alalā included in the study. A higher affiliative score indicates a bird that affiliates with more individuals, a higher pair bonding score indicates pair bonding interactions with more birds, and outward aggression scores are directly related to the amount of aggression shown to a larger number of birds. The boxplots show the median and interquartile range for each pair status of the `Alalā.
References


https://doi.org/10.1016/j.tree.2016.09.001


https://www.nature.com/scitable/knowledge/library/the-diversity-of-behavior-15129167/


