Testing the maintenance of natural responses to survival-relevant calls in the conservation breeding population of a critically endangered corvid (*Corvus hawaiiensis*)

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Abstract:

Vocal communication serves an important role in driving animals' social interactions and ultimately their survival. However, natural vocal behavior can erode in human care. Determining if animals in conservation breeding programs exhibit and respond appropriately to species-specific vocalizations is therefore important for ensuring their survival post-release. We tested whether endangered 'alalā (*Corvus hawaiiensis*), which are extinct in nature, have retained their natural responses to survival-relevant vocal calls. We conducted our studies on breeding populations derived from a small number of founding 'alalā maintained in human care since their extinction in the wild in 2002. We presented pairs of 'alalā with alarm, territorial intrusion, and two types of control playback calls (a non-threatening territorial maintenance call and a novel heterospecific call). 'Alalā were significantly more likely to approach the speaker following alarm call playback than other call types, and were more likely to respond to territorial intrusion calls with the same aggressive territorial calls. Males were more likely to make these aggressive calls than females, mirroring their roles in territory defense. We also found individual consistency in the level of vocal behavior response across all call types, indicating that some individuals are more vocal than others. These results are encouraging, showing that 'alalā exhibit relevant, species-specific behaviors despite generations under human care. It does illustrate, however, that all individuals do not respond uniformly, so vocal response may be an important factor to consider in determining the release suitability of individuals.

Keywords: anti-predator, captive breeding, communication, corvid, translocation, territory defense, vocalization

Introduction

Animals have evolved mechanisms for communication that facilitate survival and reproduction. For primarily vocal species, how individuals respond to conspecific vocal cues and signals can have survival-relevant consequences. For instance, failing to respond to an alarm call could result in predation, or failing to adequately broadcast territorial calls could cause a loss of territory, mates, or offspring. Whether or not animals exhibit appropriate species-specific communication is particularly important in conservation breeding programs. Animals that have spent generations in human care need to retain their natural behaviors for successful return to the wild (Rabin 2003; McPhee 2004 a, b). However, the loss of survival-relevant behaviors (McPhee & Carlstead, 2010; Shier 2016), including losses in vocal diversity (Corfield et al., 2008, Digby et al 2013) and dialect drift (Lewis et al., 2021), are a common byproduct of conservation breeding settings. A combination of forces from evolution, culture (Brakes et al., 2019), and direct experience interact to shape animals' vocal behaviors (Bradbury & Vehrencamp, 2011; Hollén & Radford, 2009), all of which may be impacted by the altered environment in conservation breeding facilities. Management of animals in human care, therefore, faces the challenge of providing opportunities for animals to maintain and express these behaviors (Greggor et al., 2018).

Among the vocal signals that animals need to retain, anti-predator signals (alarm calls) are particularly important because they are a component of an animal's defense against predators (Hollen & Radford, 2009). Developmentally, they may be more canalized, with alarm call production and responses emerging in development without direct experience with predators. While learning is undoubtedly important to fine-tune production and responses to antipredator calls (Griffin et al., 2000), selection should favor individuals that respond appropriately to alarm calls without direct experience associating alarm calls with predation. However, some antipredator behavior responsiveness can be lost over an individual's lifetime in the absence of predator exposure (Muralidhar et al., 2019). The importance of antipredator alarm calling for conservation breeding and translocation programs is underscored by the finding that predation is one of the primary causes of mortality for animals after release to the wild (Fischer & Lindenmayer, 2000, Moseby et al., 2011, Berger-tal et al., 2020).

Another important set of signals helps animals avoid conspecific conflict by alerting others to their shared or defended resources. Territorial species, for instance, have evolved multiple forms

of communication that broadcast an intent to defend their territory. From ornamental displays, to physical demonstrations (e.g., Decourcy & Jenssen, 1994), or auditory signals (Greenfield & Minckley, 1993), there are a variety of ways that animals communicate territory occupancy to avoid unnecessary conflict. These calls often serve to communicate motivation and a level of severity of the territorial threat (Mager et al., 2012), ranging from maintenance calls to aggressive intrusion calls. The ability to efficiently set up and defend a territory can be critical to breeding and later reproductive success (Hiebert et al., 1989). Therefore, for territorial species that rely on vocal communication, having an ability to understand and respond to different territorial calls may be crucial for survival and reproduction in the wild. Any divergence in the production or perception of these important calls from wild phenotypes may challenge social integration and the success of translocation outcomes (Lewis et al., 2021).

Here we examine the communication system of the endangered ‘alalā (*Corvus hawaiiensis*) within conservation breeding facilities, with the goal of evaluating their responses to major categories of conspecific vocal signals. Ultimately, we aim to determine if they have retained important components of natural behaviors that will facilitate successful reintroduction. The ‘alalā, or Hawaiian crow, is the last remaining corvid species of the Hawaiian islands (Banko et al., 2002). They are keystone species for the Hawaiian wet and mesic forests, and the only known seed disperser for a number of native plants (Culliney et al., 2012). They went extinct in the wild in 2002, after decades of rapid decline, surviving only in conservation breeding facilities (USFWS, 2009). Efforts are ongoing to reintroduce ‘alalā back into the wild, yet the birds still face a long road to recovery and have not yet demonstrated successful breeding in the wild.

There have been but a few studies on ‘alalā vocal behavior, yet we know they have a diverse vocal repertoire (Tanimoto et al., 2017a). Based on the complexity of vocal communication in other corvids and the role it plays in their social lives (Clayton & Emery, 2007), we would expect ‘alalā calls to vary in meaning, with important fitness consequences. ‘Alalā are fiercely territorial as adults, but as juveniles they form flocks, and associate with members of both sexes. Historically, breeding pairs, and especially males, would make a number of different, frequent territorial broadcast calls on the edges of their large territories (Banko et al., 2002); however, the use of some of these calls appears to have declined in breeding facilities (Tanimoto et al., 2017b). Additionally, like many species, ‘alalā are known to employ a range of alarm calls to warn others of danger

(Tanimoto et al., 2017a, Greggor et al., in review). While comparatively little was known about ‘alalā calls when the species became extinct in the wild, evidence suggests that the frequency and type of calls they make in the conservation breeding centers differ from their historical vocal behavior in the wild (Tanimoto et al., 2017b). It is unclear whether these changes are due to the erosion of natural behavior in the conservation breeding facilities, or due to a lack of context for expressing wild-type calls. Additionally, given that they are housed a much higher densities than wild ‘alalā and suffer reproductive consequences from close proximity of conspecifics (Flanagan et al., 2020), it is possible individuals in the conservation breeding population have become desensitized to their social surroundings, and no longer respond appropriately to these important signals. Thus far there have been no studies examining behavioral responses to experimental playbacks of vocal calls in ‘alalā.

To address this important knowledge gap in the behavioral biology of this near-extinct species, we conducted an investigation of ‘alalā responses to vocal signals. Specifically, we examined whether ‘alalā still respond appropriately to species-specific calls, despite their generations removed from nature, or whether their responses to conspecific call playbacks are indicative of behavioral erosion in human care, a call for concern that portends poor social integration and antipredator defense upon release. We presented birds with recorded playbacks of alarm and aggressive territory intrusion calls, alongside relevant control calls and sounds, and measured how likely birds were to approach the calling sound and to respond to it with the same call type or a different call type (Table 1). We chose these two call types in the context of preparing birds for survival alongside predators and the maintenance of social skills necessary for setting up and defending territories from conspecifics. We also presented ‘alalā with two control calls to rule out the effect of the social novelty and auditory novelty of hearing a call outside of their aviary. Namely, we played a non-threatening ‘alalā territorial maintenance call, which birds routinely make from their existing territories, and should therefore not broadcast any threat, and a call from a novel species that ‘alalā have never heard. If the environment of the conservation breeding facility has dulled birds’ responses to auditory stimuli generally, we would expect that ‘alalā produce no response to any of the call types (neither approaching nor making calls of their own), suggesting that the birds are over-stimulated. In contrast, if birds have retained their natural responses, we would expect to see differences between the recorded playbacks of aggressive territory intrusion calls and control call types. Specifically, birds should respond to territorial

intrusion calls with their own aggressive territorial intrusion calls (Bradbury & Vehrencamp, 2011) , and this effect should be most pronounced in males, due to the larger role males historically played in territorial defense (Banko et al.,, 2002). For alarm calls, the natural response is more complicated. We would expect birds to approach the source of the call to investigate the potential source of danger, and may respond with alarm calls (Manser et al., 2002, Hill 1986). Meanwhile the birds should ignore the general territorial maintenance call, since it does not denote a threat, and may show signs of neophobia, or a hesitancy to approach, the novel call, since ‘alalā are highly neophobic in other contexts (Greggor et al., 2020).

Methods

We conducted the experiment on 28 breeding pairs, i.e. 62% of the entire ‘alalā breeding population, at the Keauhou Bird Conservation Center (KBCC; n = 24 pairs) and the Maui Bird Conservation Center (MBCC; n = 4 pairs) between September and November 2018. The birds at both facilities are currently several generations removed from the wild. Birds were tested in their home enclosure with their breeding partner. Each pair was housed in an outdoor aviary, with covered areas for shelter and feeding, and had daily ad libitum access to food and water. Throughout the facility, interaction with people is minimized to reduce the effects of human care (see Greggor et al., 2018). The birds have auditory access to other breeding pairs and most do not have visual access. For the few buildings with more than one pair in adjacent aviaries we only tested one pair per building to minimize subjects’ prior exposure to the experimental setup. It is possible that birds could see the experimental setup at adjacent aviaries, so we put as much time as possible between trials at neighboring aviaries. Four pairs were physically separated from each other for husbandry reasons but both had visual access to each other during all of their trials.

Experimental design of playback study

We designed the playback study to determine how ‘alalā respond to alarm and other social and non-social acoustic stimuli. We hypothesized that responses to different call types will vary according to the context in which they are used and putative call meaning (Tanimoto et al., 2017a). The experiment entailed playback of four distinct acoustic stimuli: (1) conspecific alarm call, (2)

conspecific territorial intrusion call, (3) conspecific non-threatening territorial maintenance call, and (4) heterospecific call from a novel bird species (Table 1). Alarm calls are high-pitched calls given to warn other birds of danger (Tanimoto et al., 2017a), which are typical of corvid vocal repertoires (e.g. Bila et al., 2016, Marzluff et al., 2010, McIvor et al., 2018). By contrast, territorial intrusion calls are given when birds are actively and aggressively defending their territory, in situations that can escalate into physical aggression. Meanwhile, the non-threatening, territorial maintenance calls that ‘alalā make routinely on the edges of their territories in the absence of any direct threat or aggression were included as a conspecific control stimuli.

We employed a repeated-measures design in which each subject received playback of each call type in a balanced, random order ensuring that each type of call was played first, second, third, or fourth an equal number of times across all trials. Individual and temporal differences in responsiveness to the experimental setup and acoustic playback can be a source of response variation that adds statistical noise in playback studies. To address this possibility, we included a pre-trial period before call playbacks in which subjects were exposed to ambient forest noise playback (details below). The same forest noise was used as a post-playback stimulus for all trials, so that conditions were constant for comparisons of observed behavior in pre- and post-call playback periods. We used this comparison to evaluate behavioral changes in the aftermath of call playbacks.

Call type	Experimental design function	Predicted behavioral responses
Alarm	Evaluate whether ‘alalā retain anti-predator responsiveness to conspecific calls indicating danger or predation threat	Vigilance, alarm calls, cautious approach (predicted to coordinate social anti-predator response)

Territorial Intrusion	Discriminate between response to an alarming social stimulus versus an alarming antipredator stimulus	Aggressive approach, territorial intrusion calling
Territorial maintenance	Control: non-alarming conspecific stimulus	No specific call response predicted, but ‘alalā could show interest and possible social attraction
Novel Control	Control: non-alarming heterospecific stimulus	No call response predicted; perhaps hesitancy to approach, based on neophobia.

Table 1. Explanation of stimuli types and predicted responses.

Call recording and playback methods

We collected all audio recordings with a Roland R-05 acoustic recorder and directional boom microphone. Conspecific calls and forest noise controls were recorded at the KBCC. We collected calls opportunistically but tried to capture certain situations where we expected birds to make the calls in question. For example, for territorial intrusion calls we recorded when males were being moved between aviaries for husbandry purposes, as this is a time when we would expect these territorial intrusion calls. To address pseudoreplication, one set of calls were collected from three separate males, resulting in three unique sets of conspecific calls. A follow up analysis revealed no difference in birds' responses between the three sets of calls (see Supplementary Materials). We assigned ‘alalā call types initially by social context and subjective perception, then confirmed assignment by examining spectrograms. Calls from unfamiliar species were collected opportunistically at the Panaewa Zoo in Hilo, Hawaii from medium- or large-bodied birds that breeding center ‘alalā would never have experienced (peacock, cockatoo, and toucan). Since

several species of corvids are able to distinguish characteristics of conspecifics from calls (Woods et al, 2018), each pair received all three call exemplars from the same male to avoid individual differences in donor birds influencing responses to call types. As breeding center birds are likely able to hear most conspecifics housed at the same facility, all subjects were likely somewhat familiar with individual calls from nearby conspecifics. However, to minimize familiarity with calls we selected playback calls from individuals that were not housed in adjacent aviaries and did not repeat call playback sets at adjacent aviaries.

We ensured that calls in the same category from different males had similar delta frequency and average power using Raven Pro, version 1.5. In order to standardize the duration and number of calls between call types with different durations and pauses, we ascertained that each 30-second stimulus contained 6-7 seconds of sound and between 6-20 individual calls, ensuring the natural spacing that the bird used between individual sounds to the extent possible. Therefore, we did not edit the calls themselves but did edit the spacing between calls and the number of calls to keep the total sound duration to 6-7 seconds for all kinds of stimuli. We measured sound duration and conducted all audio editing in Audacity. We also checked that all sounds in the same category were played from the speaker (omni jacket ultra, Altec Lansing) at the same minimum and maximum decibel level using the Decibel X app for iphones.

All playback trials were conducted between 9:30am and 11:30am, when morning husbandry-related disturbance had finished. Also, this time window is not within the species-specific period of peak vocal activity that have been historically reported (0600 to 0900 and 1500 to 1800; Banko et al., 2002), to attempt to avoid times where there could be background noise from other aviaries that might otherwise cause a distraction. For each playback trial we placed the speaker on the ground in a standardized location on the side of the aviary, along an opaque wall. While the birds may have known a person was outside the aviary, they were unable to directly see the observer placing the speaker. We allowed the subjects a 5-min habituation period after the observer placed the speaker and moved to the observation location. Each of four trials consisted of three different observation periods: pre-trial (3-min playback of forest noise to control for general response to sound playback), stimulus presentation (0.5-min call playback), and post-trial (3-min forest noise playback repeated). Following a 19-min intermission, we repeated the three-period trial using a different call type. This playback routine was repeated for all four calls in

balanced, randomized order across individuals. This resulted in 30 minutes between stimulus presentations. The observer scored trials live through a small window at the front of the aviary and recorded trials by setting up a video camera at each window. The birds likely heard the observer enter, but once the 5-minute habituation began, the observer stayed quiet and out of view as much as possible. Therefore, it is possible that the birds were aware of the presence of the observer and video camera, but we tried to minimize disturbance as much as possible. We scored trials live but consulted video recordings to improve data accuracy. We recorded the following behaviors across all three trial periods: (1) approach (bird approaches playback speaker); (2) latency to approach (time at which bird first moved in the direction of the stimulus); (3) number and (4) type of all calls made by each bird. Call types were classified into four categories: alarm, territorial intrusion, subordinate begging and other. Territorial maintenance calls were never made in response to the stimuli so they were not included in the models.

Analysis

All analyses were conducted in R version 3.4.1 (R core team, 2017). In order to determine if our pre-trial conditions were consistent for each stimulus, we ran a generalized linear mixed model (GLMM) with a negative binomial distribution and a log link function, using the package glmmTMB (version 0.2.3; Brooks et al., 2017), with the number of all calls made during the pre-trial as the response variable. The initial model included the main effects of stimulus type and order as well as the interactions between stimulus type and order. We also included the random effect of bird ID.

To investigate the degree of individual consistency in call responses, we ran an intraclass correlation using the package irr (version 0.84; Gamer et al., 2012) for the number of calls each individual produced during the stimulus and post-trial combined for each stimulus type.

In order to determine interest in different stimuli, we ran a cox proportional hazards model using the package survival (version 2.38; Therneau 2015) on the likeliness of birds to approach the stimulus for each stimulus type. This model included stimulus type, sex, and order as main effects as well as the interaction between stimulus type and sex and stimulus type and order. We clustered data around bird ID.

To evaluate the circumstances influencing call production, we used generalized linear mixed models (GLMM) with a negative binomial distribution (as data were zero inflated) and a log link function, using the package glmmTMB (version 0.2.3; Brooks et al., 2017) to separately test whether all calls, alarm calls, territorial intrusion calls and begging calls were more likely to occur during the stimulus and post-trial period depending on the playback type. All models initially included the main effects of stimulus type, sex and trial order as well as the interactions between stimulus type and sex and stimulus type and order. We also included the random effect of bird ID. We used the territorial maintenance control call as the reference group when comparing the different stimulus types as this should represent a conspecific call in a new location, so this accounts for any calls or approaches simply due to the social novelty and not the call itself. The GLMM with the number of territorial intrusion calls made during the stimulus and post-trial would not converge properly when the model included interactions, so only main effects were tested.

For all GLMMs except for the model with territorial intrusion calls as the response variable, we first determined if the interaction terms warranted inclusion in the models. Starting with the interaction between stimulus type and order, as this was likely less biologically relevant, and then continuing with the interaction between stimulus type and sex, we removed interaction terms if their inclusion failed to decrease AIC values by > 2.. We did not simplify the model past determining which interactions to include, as all remaining effects were important variables we wanted to consider in the final model. See the supplementary materials for the full process of model selection for each response variable. For all GLMMs we also visually inspected binned plots of the expected versus residual values for the final model.

Ethical note

This work using animal subjects was approved by San Diego Zoo Wildlife Alliance's IACUC committee (No. 16-009). Several permits were issued for the conservation breeding of ʻalalā (USFWS Native Endangered Species Recovery Permit TE060179-5, State of Hawaii Protected Wildlife Permit WL19-16).

Results

Pre-trial call frequency in response to playback of forest noise

As expected, we found no differences in call number among treatments before stimulus exposure during the pre-trial period (alarm trial vs. territorial maintenance: GLMM, b = -1.008, z = -0.942, *P* = 0.346; novel control trial vs. territorial maintenance: b = -0.836, z = -0.804, *P* = 0.421; territorial intrusion trial vs. territorial maintenance: b = -0.677, z = -0.665, *P* = 0.506). Therefore, we have not weighted post-trial data as a function of pre-trial calling rates. However, bird calls significantly increased across trials (b = 0.769, z = 2.179, *P* = 0.029); therefore, we included trial order in all subsequent models.

Approach latency during stimuli presentation

Birds were more likely to approach after the alarm stimulus than the territorial intrusion stimulus (Figure 1B; alarm vs. territorial maintenance: Cox Proportional Hazards Model, coefficient = 1.293, z = 2.293, Pr = 0.0218) whereas the other stimuli had no significant effect on the likelihood of approaching compared to the territorial maintenance stimulus (Figure 1A; novel control compared to territorial maintenance: coefficient = 0.827, z = 1.608, Pr = 0.108; territorial intrusion versus territorial maintenance: coefficient = 0.479, z = 0.892, Pr = 0.372). Trial order was also significant, with birds more likely to approach in later trials (coefficient = 0.242, z = 1.997, Pr = 0.0458). Sex did not have a significant effect on the likelihood of approaching (effect of sex: coefficient = 0.115, z = 0.376, Pr = 0.707)

Individual call consistency during stimuli presentation and post-trial

Birds were individually consistent in the total number of calls they each made during the stimulus and post-trial periods across all different trial treatments (Intraclass correlation coefficient, 0.367, CI = 0.231-0.515, P < 0.001); i,e., birds who made fewer calls in one type of trial also made fewer calls in all trials.

Call responses

Even though birds differed individually in the number of calls they made across all stimuli, no patterns emerged in how many calls birds made between stimuli types during the playback and post-trial period combined (Figure 2; alarm vs. territorial maintenance: GLMM, b = 0.497, z =

0.737, P = 0.461; novel control vs. territorial maintenance: b = 0.271, z = 0.408, P = 0.683; territorial intrusion vs. territorial maintenance: b = 1.007, z = 1.471, P = 0.141). There was also no effect of sex (b = -0.598, z = -1.211, P = 0.226) or order (b = 0.099, z = 0.394, P = 0.693) on the total number of calls birds made during the stimulus and post-trial.

When we looked at the production of specific calls, we found that the number of alarm calls birds made during the stimulus and post-trial combined did not significantly vary between any of the different stimuli (Figure 3; alarm stimulus vs. territorial maintenance: b = -1.584, z = -1.093, P = 0.275; novel control stimulus vs. territorial maintenance: b = 0.169, z = 0.097, P = 0.923; territorial stimulus vs. territorial maintenance: b = 0.390, z = 0.312, P = 0.755). All other terms were not significant. There was also no difference in the number of begging calls birds made during the stimulus and post-trial between any of the stimuli (alarm stimulus vs. territorial maintenance: b = 0.820, z = 0.665, P = 0.506; novel control vs. territorial maintenance: b = -0.193, z = -0.170, P = 0.865; territorial intrusion stimulus vs. territorial maintenance: b = -0.441, z = -0.409, P = 0.683). Birds never made the territorial maintenance call in response to any stimuli.

Overall, birds made significantly more territorial intrusion calls during the stimulus and post-trial in response to the territorial intrusion stimulus than the territorial maintenance stimulus (Figure 4; b = 3.825, z = 2.298, P = 0.022) whereas they did not make a significantly different amount of territorial calls during the stimulus and post-trial in response to any other kind of stimulus (Figure 4; alarm stimulus vs. territorial maintenance: b = 2.033, z = 1.064, P = 0.287; novel control vs. territorial maintenance: b = -19.797, z = -0.002, P = 0.999). Males made significantly more territorial intrusion calls during the stimulus and post-trial than females (Figure 5; b = 5.087, z = 3.106, P = 0.002).

Discussion

Species raised in human care have the potential to lose some of their survival-relevant behaviors (Shier, 2016, McPhee & Carlstead, 2010), including responses to species-specific vocalizations (Corfield et al., 2008, Digby et al., 2013, Tanimoto et al., 2017b). Conservation breeding programs or managed care may also change selective forces operating across generations

or developmental processes operating during individuals' lifetimes, creating new cultural vocal variants and response patterns (Lewis et al., 2021). Disrupting the normal signaler-receiver interplay may result in a breakdown in the communication system, with fitness consequences challenging conservation goals. To address these possibilities, we tested whether pairs of 'alalā have maintained responses to survival-relevant classes of vocalizations. Although the conservation breeding history of the species may have dulled some of their responses, we still saw encouraging signs that 'alalā were able to distinguish between natural call types and demonstrate survival-appropriate responses. Specifically, we found that 'alalā were more likely to approach in response to alarm calls, indicating they may have been investigating a potential threat or seeking to coordinate a defensive response with conspecifics. Also, we found that males in particular were more likely to respond to territorial intrusion calls with territorial intrusion calls of their own, suggesting they were willing to defend their breeding aviary. Finally, our results illustrate that there is some individual consistency in the amount of calling over all treatments, but that individual characteristics (e.g. personality or specific rearing history) does not fully explain the variation in call response to the different treatments. A note of caution in interpreting these results is warranted due to the absence of any quantitative and limited qualitative observations of 'alalā vocal behavior before they went extinct in the wild, so we have few reference points other than comparisons with and generalizations from other species.

As a corvid, flexible learning is expected throughout their life (Emery & Clayton, 2004), but vocalizations often require exposure during times of parental care or sensitive periods, which may be limited in human care (Corfield et al., 2008, Digby et al 2013, Tanimoto et al., 2017b). Most 'alalā in this study were puppet-reared by human caretakers (Gregor et al. 2018), removing any opportunities for learning vocal behavior from parents. Of known call types, alarm calls are more likely to be preserved since they potentially share some innate characteristics that make them harder for predators to locate (Maynard Smith & Harper 2003). In the case of 'alalā, we found that birds were more likely to approach alarm call playbacks than other auditory stimuli. However, they were not more likely to make alarm calls in response to alarm playbacks. This lack of vocal response is consistent with what was reported in some pilot work on 'alalā anti-predator behavior (Greggor et al., in review), suggesting that alarm calls may function to alert birds to the need to gather additional information. It is also possible that because we presented alarm calls without other stimuli that could indicate danger, they investigated but did not respond with their own alarm

calls when they saw no clear threat. Further testing of alarm calls with and without presenting a dangerous context would be necessary to tease this apart. However, ‘alalā’s approach of the source of the playback alone may still have had a social function. Animals, including corvids, will often make alarm calls to elicit assistance from conspecifics in investigating or confronting a predator (Coomes et al., 2019, Curio 1978). The fact that birds approached the alarm calls (and not just conspecific playbacks in general) suggests they may still have a similar function in ‘alalā: approach of the caller may precede mobbing or other group antipredator defense. Although mobbing-like behavior has been anecdotally reported in ‘alalā (Greggor et al., in review), this study provides some empirical support that the birds responded appropriately to alarm calls in the absence of other signs of danger and have not become completely desensitized to them.

Territorial calls are also an important part of vocal communication, including in the historical vocal repertoire of ‘alalā (Banko et al., 2002, Tanimoto et al., 2017a). We played two types of territorial calls, a neutral territorial maintenance call and an aggressive territorial intrusion call. ‘Alalā did not significantly differ in their response to the territorial maintenance call from other call types. However, we found that ‘alalā responded to a simulated territorial intrusion with territorial intrusion calls significantly more than they did to any other playback stimuli. A vocal territorial response is the natural reaction we would expect to a territorial challenge (Maynard Smith & Harper 2003; Bradbury & Vehrencamp 2011), considering we presented the birds with this stimulus in their home aviaries. We did not test any of the birds in a new location outside of their artificial “territory” so we do not know if their responses are flexible and adaptive to context, i.e. defending only their occupied territory. However, given that ‘alalā exhibit fewer territorial calls than their wild counterparts (Tanimoto et al., 2017b), we find it encouraging that ‘alalā displayed this behavioral response suggesting some normal signaler-receiver exchange. Additionally, we found that males were more likely to make territorial intrusion calls, which mirrors patterns noted previously in the wild (Banko et al., 2002). As a sexually dimorphic species with respect to size, males are the larger and more aggressive sex, and thus their greater role in territorial defense is expected (Archer, 1988).

While we found encouraging signs that some birds exhibited natural responses to our playbacks in the absence of any other context or stimuli, many of the birds did not respond vocally when faced with any type of conspecific call. Given that the birds are living in social densities that

are far higher than observed in the wild (Flanagan et al., 2020), the high levels of individual variation we found suggest that some ‘alalā may have become desensitized to the calls of conspecifics vocalizations, perhaps a result of repeated exposure without consequence. While ‘alalā in the conservation breeding facilities may not necessarily be less vocal than wild birds (Tanimoto et al., 2017b), the lack of vocal behavior we saw in many individuals in response to social cues suggests a potential decoupling of the meaning or relevance of conspecific calls. Alternatively, perhaps there is additional context we did not adequately capture in our recordings (e.g. individual caller ID, social status, etc.), that could have differentially influenced some individuals more than others. Corvids are known to respond to individual qualities of callers, such as their dominance status (Massen et al., 2014), and membership in the breeding colony (Woods et al., 2018). Additionally, since calls were recorded opportunistically, there may be subtle differences to the different calls (for example, the particular stimulus causing the alarm calls) that we are unaware of. Therefore, we may have inadvertently been broadcasting information beyond the content of the calls. However, we saw no differences in the number of calls birds made in response to the three different call sets, suggesting that the identity of the caller was not a major cause of variation. Regardless of the cause of the low responses of many individuals, there were still other birds that clearly demonstrated survival-relevant responses.

Although we found no evidence of widespread erosion of vocal communication behavior under human care, the individual differences that we saw in how birds responded to the playbacks could indicate that not all individuals are equally as well equipped for release into the wild. Many factors go into determining fitness for release, and these results suggest that we may need to consider whether birds demonstrate adequate responses to conspecific calls as a criterion for release. Additionally, future research could investigate how likely birds are to regain survival-relevant responses to vocalizations if they are exposed to training that encourages associations between conspecific calls and relevant responses. Given the critical conservation status of the species, any technique that could limit the impact of the conservation breeding environment on survival-relevant behavior is warranted.

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Data accessibility

Data and code will be available at an online repository upon acceptance.

Figures

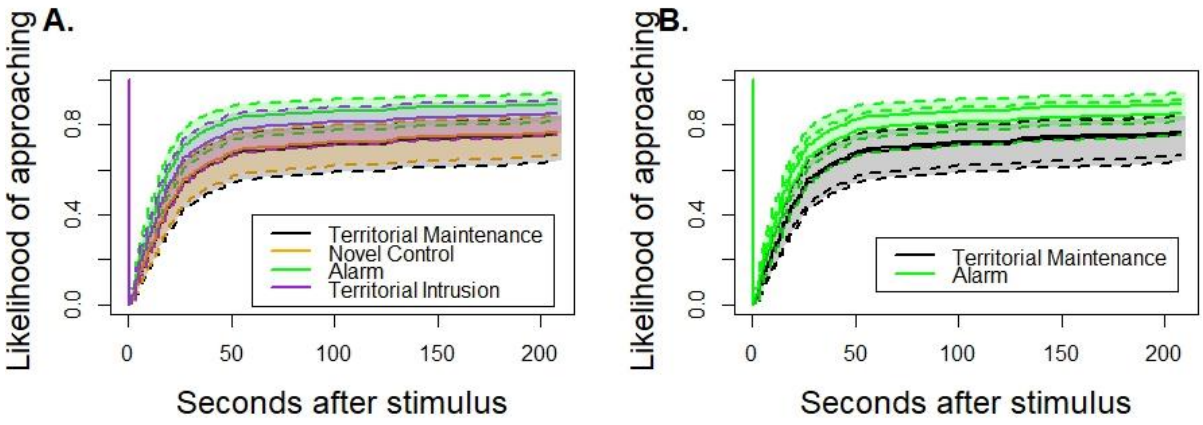

Figure 1. A. Inverted survival curves showing the likelihood that birds approach each stimulus type. B. Inverted survival curves showing the likelihood that birds approach in response to only the two significantly different stimuli, territorial maintenance and alarm.

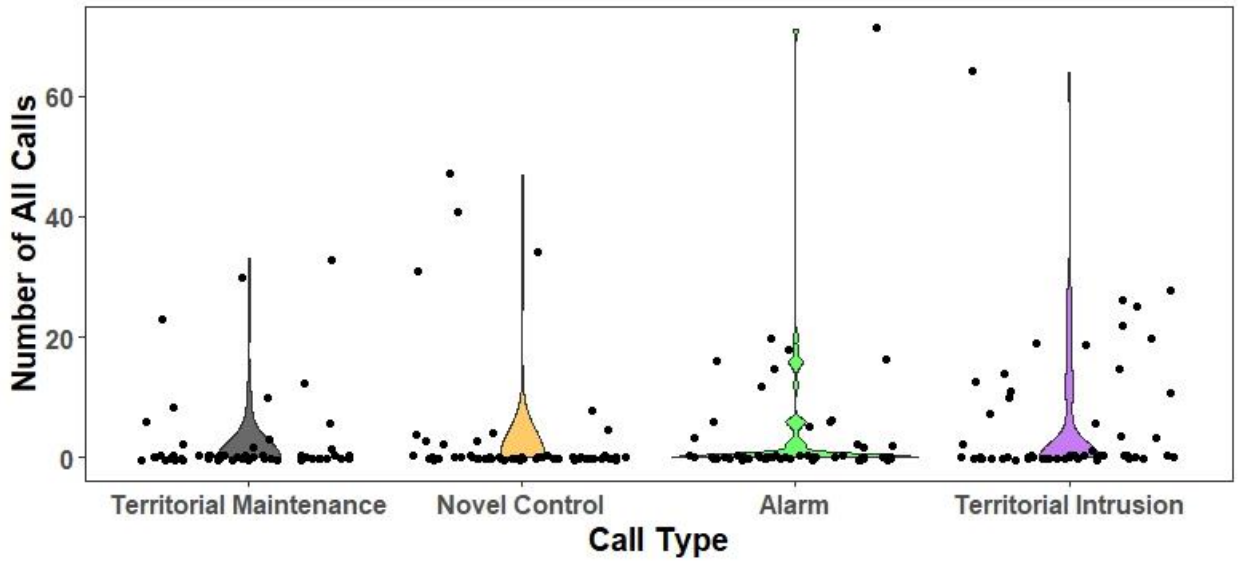

Figure 2. Violin plots and raw data showing the distribution of the number of all calls birds made during the stimulus and post-trial period after each type of stimulus. The points are the raw data.

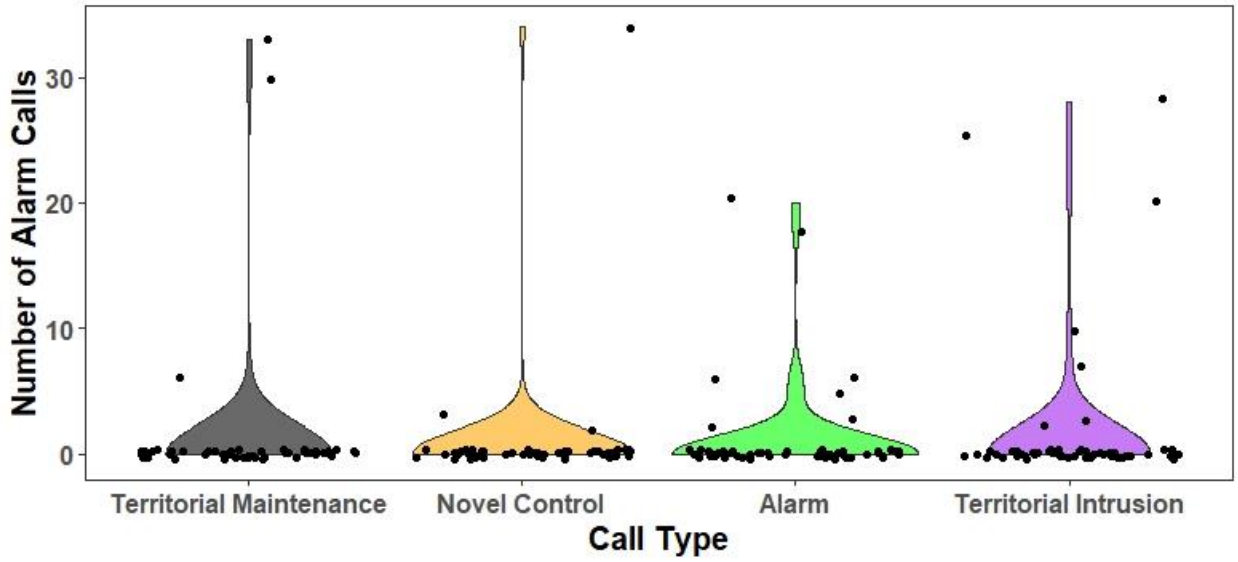

Figure 3. Violin plots and raw data showing the distribution of the number of alarm calls birds made during the stimulus and post-trial period after each type of stimulus. The points are the raw data.

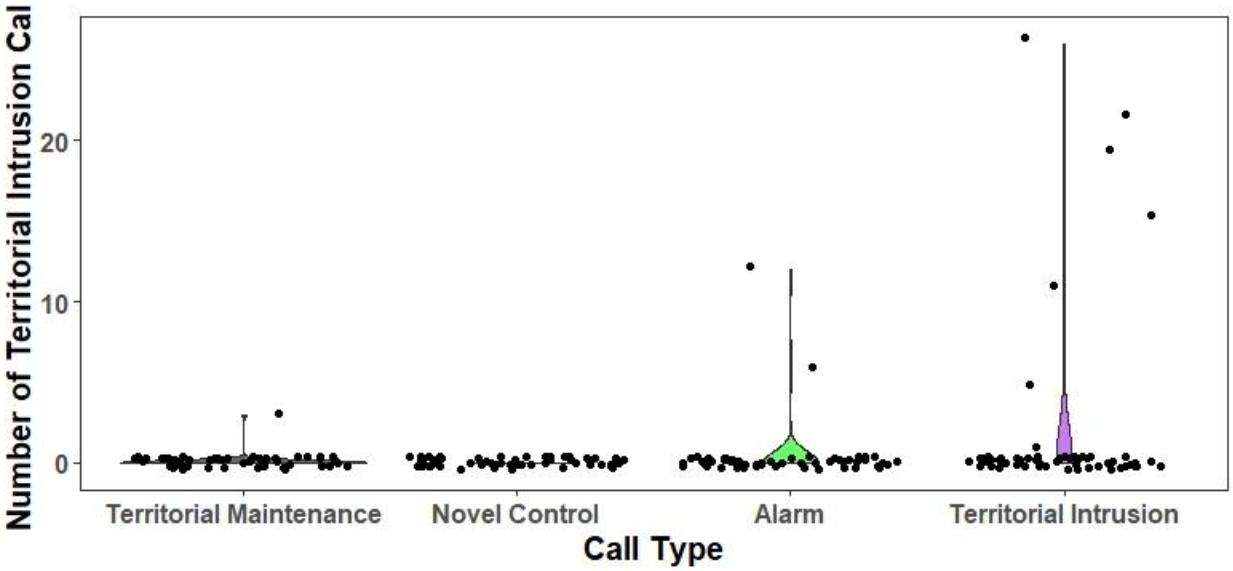

Figure 4. Violin plots and raw data showing the distribution of the number of territorial intrusion calls birds made during the stimulus and post-trial period after each type of stimulus. The points are the raw data.

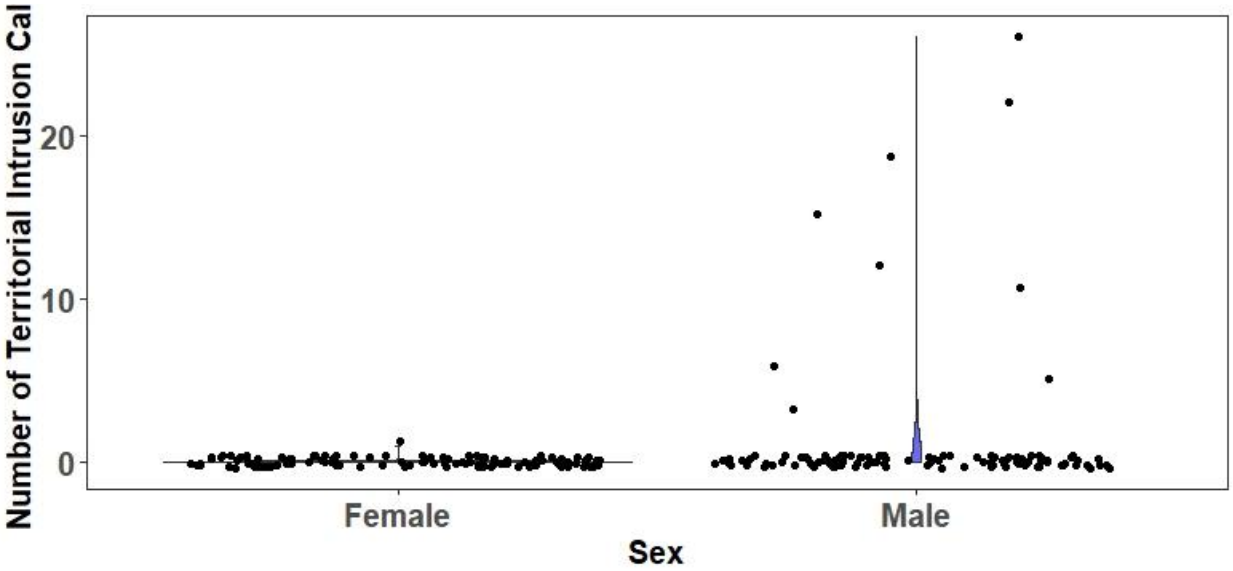

Figure 5. Violin plots and raw data showing the distribution of the number of territorial intrusion calls males and females made during the stimulus and post-trial period after each type of stimulus. The points are the raw data.

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