The uses and implications of avian vocalizations for conservation planning

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Abstract: There is a growing recognition that animal behavior can affect wildlife conservation, but there have been few direct studies of animal behavior in conservation programs. However, a great deal of existing behavioral research can be applied in the context of conservation. Research on avian vocalizations provides an excellent example. The conspicuous nature of the vocal behavior of birds makes it a useful tool for monitoring populations and measuring biodiversity, but the importance of vocalizations in conservation goes beyond monitoring. Geographic song variants with population-specific signatures, or dialects, can affect territory formation and mate choice. Dialects are influenced by cultural evolution and natural selection and changes can accumulate even during the timescale of conservation interventions, such as translocations, reintroductions, and ex situ breeding. Information from existing research into avian vocalizations can be used to improve conservation planning and increase the success of interventions. Vocalizations can confer a number of benefits for conservation practitioners through monitoring, providing baseline data on populations and individuals. However, the influence of cultural variation on territory formation, mate choice, and gene flow should be taken into account because cultural differences could create obstacles for conservation programs that bring birds from multiple populations together and so reduce the success of interventions.

Keywords: behavior, bioacoustics, birdsong, conservation interventions, cultural evolution, monitoring

Resumen: Hay un creciente reconocimiento de que el comportamiento animal puede afectar a la conservación de la fauna, pero ha habido pocos estudios directos del comportamiento animal en los programas de conservación. Sin embargo, una gran cantidad de la investigación existente sobre el comportamiento puede aplicarse en el contexto de la conservación. Las investigaciones sobre las vocalizaciones de aves son un excelente ejemplo. La naturaleza conspicua del comportamiento vocal de las aves hace que sea una herramienta útil para el monitoreo de las poblaciones y las medidas de la biodiversidad, pero la importancia de las vocalizaciones en la conservación va más allá del monitoreo. Las variantes geográficas de canto con firmas específicas para cada población, también conocidas como dialectos, pueden afectar a la formación del territorio y a la elección de pareja. Los dialectos están influenciados por la evolución cultural y la selección natural y los cambios pueden acumularse incluso durante la escala de tiempo de las intervenciones de conservación, como las reubicaciones, las reintroducciones y la reproducción ex situ. La información disponible a partir de las investigaciones existentes sobre las vocalizaciones de aves puede usarse para mejorar la planeación de la conservación e incrementar el éxito de las intervenciones. Las vocalizaciones pueden otorgar un número de beneficios para quienes practican la conservación a través del monitoreo, proporcionando información de la línea base de las poblaciones y los individuos. Sin embargo, la influencia de la variación cultural sobre la formación del territorio, la elección de pareja y el flujo genético deberían considerarse ya que las diferencias culturales podrían crear obstáculos para los programas de conservación que agrupan a aves de diferentes poblaciones y con ello reducen el éxito de las intervenciones.

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Article impact statement: Avian vocalizations are well studied but should be considered more both as a tool and potential hindrance in conservation interventions.

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**Palabras Clave:** bioacústica, canto de aves, comportamiento, evolución cultural, intervenciones de conservación, monitoreo

**Abstract:** Currently, people are increasingly recognizing animal behavior as a means to understand wildlife conservation, but in many projects, the study of animal behavior is largely absent. Many conservation projects are inherently linked to behavior, with many more are in decline. Many conservation measures have been attempted to help reverse declines; intensive interventions, such as ex situ breeding, reintroductions, and translocations, have proven valuable (e.g., Cade & Jones 1993; Miskelly & Powlesland 2013). When planning these types of interventions, it is important to consider how animal behaviors may affect success.

Although attention to animal behavior in conservation has increased in recent years, there is still a broad consensus that information on animal behavior is underutilized (Angeloni et al. 2008; Berger-Tal et al. 2016). Thus, future research should examine behavior and conservation in tandem. However, there is already considerable behavioral research available that has implications for conservation and can be used to guide management strategies. Vocal communication is an easily detected, conspicuous behavior and is well described for many species (Lovette & Fitzpatrick 2016). We summarized the relevant background information on variation in avian vocalizations, considered how vocalizations influence key processes of conservation interest, and explored the potential roles of vocalizations in conservation applications.

**Introduction**

A recent assessment by BirdLife International (2018) showed that around 13% of all extant bird species are globally threatened and many more are in decline. Many conservation measures have been attempted to help reverse declines; intensive interventions, such as ex situ breeding, reintroductions, and translocations, have proven valuable (e.g., Cade & Jones 1993; Miskelly & Powlesland 2013). When planning these types of interventions, it is important to consider how animal behaviors may affect success.

Although attention to animal behavior in conservation has increased in recent years, there is still a broad consensus that information on animal behavior is underutilized (Angeloni et al. 2008; Berger-Tal et al. 2016). Thus, future research should examine behavior and conservation in tandem. However, there is already considerable behavioral research available that has implications for conservation and can be used to guide management strategies. Vocal communication is an easily detected, conspicuous behavior and is well described for many species (Lovette & Fitzpatrick 2016). We summarized the relevant background information on variation in avian vocalizations, considered how vocalizations influence key processes of conservation interest, and explored the potential roles of vocalizations in conservation applications.

**Variation in Avian Vocalizations**

Avian vocalizations can vary in a number of ways based on temporal factors (Table 1), spectral characters, and the elements, syllables, and phrases vocalizations are composed of. Variation among species, often used for conspecific recognition, and the role of among-species variation in territory defense (e.g., North Island Saddlebacks [*Ptilostoma rubisater*] [Parker et al. 2010]) and mate choice (e.g., Medium Ground Finches [*Geospiza fortis*] and Cactus Finches [*G. scandens*] [Grant & Grant 1996]) are well understood (Catchpole & Slater 2008). However, variation can occur at smaller scales within and among populations.

Within populations, individual variation is common. Such variation may be affected by intrinsic factors, such as morphology: body size affects spectral characters and beak shape affects temporal factors (Derryberry et al. 2018; García & Tubaro 2018). Vocal repertoire and repertoire size can also vary widely between individuals of the same species (Krebs & Kroodsma 1980).

Among populations, cultural variation in vocalizations, known as dialect, has been reported in many species (e.g., Wright et al. 2008; Robin et al. 2011). There are a number of suggested mechanisms for dialect formation and evolution (Catchpole & Slater 2008), and understanding these is essential to predicting the possible impacts of dialects on conservation programs.

Cultural drift describes the random accumulation of song mutations due to copying errors and improvisation (Mundinger 1980). The action of drift is more severe in smaller populations, especially in fragmented environments, which are commonplace in conservation (Laiolo & Tella 2007). Over 19 years, calls of the Yellow-naped Amazon (Amazona auropalliata) showed a lower degree of stability in the smaller northern population relative to the larger southern population (Wright et al. 2008). The rate of drift may also be influenced by song traits. In White-bellied Shortwings (*Sicionala major*), simple songs are still similar in populations that have been separate for thousands of years, but differences in complex song clusters are apparent in populations separated for a comparably shorter time (100–150 years) (Purushotham & Robin 2016).

Cultural traits like song diversity can be lost during population bottlenecks, such as the colonization of new habitats (e.g., Baker 1996) or population reductions following habitat loss or fragmentation (Laiolo & Tella 2007). Hill et al. (2013) reported reduced syllable diversity and a lower percentage of trills in the threatened Chatham Island Tui (*Prosthemadera novaeseelandiae chathamensis*) relative to its mainland counterpart (*P. n. novaeseelandiae*). However, it is often impossible
Table 1. Glossary of specialist terms pertaining to bioacoustics and song learning.

| Term                      | Definition                                                                                                                                 |
|---------------------------|-------------------------------------------------------------------------------------------------------------------------------------------|
| Amplitude                 | volume of sound, measured as height of sound waves in vocalization                                                                     |
| Call                      | short, simple vocalizations used for social cohesion, parent–offspring communication, aggression, and signaling danger                   |
| Closed-ended learner      | bird in which song learning is restricted to a short period, usually the first year of life (Beecher & Brenowitz 2005)                   |
| Cultural variation        | variation among populations in information or behaviors shared by individuals and acquired from conspecifics by social learning (Whitehead & Rendell 2015) |
| Dialect                   | sets of geographic vocalization variants with distinct, population-specific vocal features                                              |
| Elements                  | smallest divisions of birdsong, also referred to as notes                                                                               |
| Frequency                 | wavelength of sound; shorter wavelengths produce higher frequencies; frequency of a call can be measured as the maximum (highest frequency), minimum (lowest frequency), mean (across the song or individual elements), and peak (frequency with the highest amplitude) |
| Open-ended learner        | bird in which song learning can occur throughout life (Beecher & Brenowitz 2005)                                                      |
| Phrases                   | series of units (usually syllables) occurring together in a particular pattern                                                            |
| Repertoire                | full set of vocalizations that a single individual produces                                                                            |
| Repertoire size           | total number of different vocalizations an individual produces, usually measured as the number of different song types                 |
| Song                      | loud, long, and usually complex vocalizations most often used in courtship and territory defense                                            |
| Song complexity           | variously, song repertoire size, note repertoire, versatility, nonlinearity, and standard deviation of frequencies have been proposed as definitions of complexity and all may act as honest signals of fitness (Soma et al. 2006; Pearse et al. 2018) |
| Song rate                 | number of songs produced by an individual per unit time                                                                               |
| Spectral factors          | factors relating to the frequency of vocalizations                                                                                     |
| Syllables                 | building blocks of phrases, can be complex (containing multiple elements) or simple (containing only 1 or 2 elements)                   |
| Temporal factors          | factors relating to the timing of vocalizations                                                                                         |
| Withdrawal of learning    | rapid song innovation following colonization by founders that dispersed before song crystallization (i.e., before they produce stereotyped, adult songs) (Thielcke 1973) |

*Unless otherwise stated, definitions are based on Catchpole and Slater (2008) and Lovette and Fitzpatrick (2016).*

to detect bottleneck events from song diversity due to the continued action of drift or withdrawal of learning (Potvin & Clegg 2015). In such cases, past bottlenecks may be evidenced by low shared syllables between populations (e.g., Lang & Barlow 1997).

The acoustic adaptation hypothesis predicts that habitat-dependent selection shapes song evolution. Different habitats have different sound transmission properties: complex vegetation causes greater attenuation, particularly of high-frequency sounds, than more open habitats (Brumm & Naguib 2009). A meta-analysis of studies examining acoustic adaptation showed a small overall effect of habitat on frequency across oscine and suboscine species; lower frequencies (minimum, maximum, and peak) and smaller frequency bandwidths occur in closed habitats (Boncoraglio & Saino 2007).

Biotic noise is highly variable and may be hard for birds to avoid. There are increasing examples of spectral and temporal partitioning in the acoustic signals of wild birds, both in response to other birds (Ficken et al. 1974; Planque & Slabbekeorn 2007; Luther 2009) and other taxa (Sueur 2002; Hart et al. 2015). Grant and Grant (2010) detail song changes of G. fortis and G. scandens after the arrival of G. magnirostris on Daphne Major in 1983. Over the study period (1983–2010), the song traits of G. fortis and G. scandens dispersed away from those of G. magnirostris; changes included shorter songs and increased trill rate, which could not be explained by other changes in the environment.

It is likely that dialect formation is influenced by a combination of the mechanisms mentioned above. Given the number of possible influences, it is difficult to disentangle the driving factors, and factors may change in importance over time (Potvin & Clegg 2015; Purushotham & Robin 2016).

**Importance of Variation in Vocalizations to Processes of Conservation Interest**

Variation in vocalizations among populations can play an important role in a number of processes important for population persistence, such as territory maintenance, mate choice, and gene flow.

**Teritory Formation and Defense**

In many species, holding territories is essential for resource acquisition and the formation and maintenance of pair bonds and so improves mating success (Hinde
Successful territory maintenance relies on the ability to identify conspecifics and respond by defending the territory. However, birds respond more strongly to unfamiliar songs of their own dialect and to songs that are more similar to their own than to foreign dialects (e.g., Searcy 1997). As a result, birds may fail to adequately defend their territories from conspecifics with foreign dialects. Irwin et al. (2001) examined responses of the Greenish Warbler (Phylloscopus trochiloides), a species where songs vary clinally in a ring. Along the cline, males respond to playback from recordings taken 1000–1500 km away but no further. When the 2 terminal subspecies, which have come into secondary contact and exhibit large differences in dialect, were tested, neither responded to the other regardless of distance between the male and the recording. The combined evidence from territory studies suggests birds may find it difficult to defend territories where foreign dialects are prevalent (Slabbekoorn & Smith 2002), which could reduce access to food, nest sites, and mates. This may cause problems if birds with different dialects are brought together during conservation interventions (Parker et al. 2010; Bradley et al. 2013; Valderrama et al. 2013).

**Mate Choice**

Birdsong plays an important role in female mate choice. There is evidence that performance-related factors, such as amplitude and rate (e.g., Ballentine et al. 2004 but see Kroodsma 2017 for critique), song complexity, and repertoire size (Searcy 1992; Byers & Kroodsma 2009) may influence female preference and could act as honest signals of male quality (Gil & Gahr 2002). Dialect can also influence female mate choice. Female preference for local dialects can promote assortative mating, where animals select mates genetically or phenotypically similar to themselves (Jiang et al. 2013). Searcy et al. (2002) found that female Song Sparrows (Melospiza melodia) showed similar responses to local and nearby (18 km) foreign dialects, but discriminated against dialects from greater distances (34, 68, and 135 km).

Selectiveness in mating can lead to an increased probability of mate rejection, reducing overall mating rates. Where mating opportunities are limited, as in some small, endangered populations, this may result in fewer individuals finding mates and breeding, potentially contributing to population declines and extinction (Bessa-Gomes et al. 2003). Assortative mating plays a key role in premating reproductive isolation, possibly resulting in speciation (Kirkpatrick 2000; Verzijden et al. 2012), and can promote reproductive isolation at secondary contact (Grant & Grant 2002)—including during conservation interventions when previously separated populations are brought together. This has been reported following multiple conservation interventions in the North Island Kokako (Callaeas wilsoni) (Bradley et al. 2014).

Female preference for local dialects could be adaptive; females may gain fitness advantages by choosing males from their natal region (Slabbekoorn & Smith 2002; Podos & Warren 2007). Although singing a local dialect should not be inherently more costly than singing a foreign dialect (Nowicki & Searcy 2005), dialects could act as behavioral markers for other traits. In the Red Crossbill (Loxia curvirostra), song and bill morphology are strongly correlated. Mating within the local population, signaled by dialect, prevents the production of offspring with intermediate, less fit phenotypes (Snowberg & Benkman 2007). Local dialect may also signal males with local experience (Searcy 1982) who may be better able to secure resources for females and their offspring, thus providing direct benefits to choosy females.

Dialect preferences could also be a nonadaptive result of familiarity (Slabbekoorn & Smith 2002). Female White-crowned Sparrows (Zonotrichia leucophrys) in mixed-dialect populations show neither preference for their fathers’ dialects nor consistent preference for any dialect across successive breeding seasons (Chilton et al. 1990). In captivity, females do not respond differently to 2 dialects they commonly hear within their population, but show reduced responses to a dialect from a different population (Chilton et al. 1996). These results suggest that females from mixed-dialect populations can distinguish between dialects, but show no difference in preference among songs they commonly hear. Females exhibiting a preference (for father’s dialect or otherwise) would be expected to mate with birds of the same dialect across seasons. However, if preferences do not align with mate choice in the field, dialect may not have a profound effect on mating during conservation.

**Gene Flow**

If dialects contribute to mate choice, they may reduce gene flow by reducing breeding between populations. Such inbreeding can affect fitness and affect both individual and population performance (Keller & Waller 2002). For example, inbreeding reduced hatching success, fledgling survival, and recruitment in the Red-cockaded Woodpecker (Picoides borealis) (Daniels & Walters 2000).

A number of studies report substantial genetic mixing between populations despite dialect differences (e.g., Orange-tufted Sunbirds [Cinnyris bouvieri] [Leader et al. 2008] and Puget Sound White-crowned Sparrow [Zonotrichia leucophrys pugetensis] [Poesel et al. 2017]). Other studies show some genetic structuring related to dialect differences (e.g., Mountain White-crowned Sparrows [Zonotrichia leucophrys oriantba] [MacDougall-Shackleton & MacDougall-Shackleton 2001]). Even small reductions in gene flow
can reduce the effective population size, potentially contributing to reduced heterozygosity and Allee effects (Chesser et al. 1993).

Although dialects could limit gene flow between populations and increase genetic differentiation, other factors may also contribute. In particular, dialect differences are often related to distance between populations. In the White-bellied Shortwing, song and genetic differences appear highly correlated. However, when controlling for geographic distance and dispersal barriers, spectral and syntax differences are not correlated with genetics (Purushotham & Robin 2016).

There is little consensus on the impact of dialects on gene flow, and some studies even show conflicting results for the same species and populations (e.g., Nuttall’s White-crowned Sparrow [Zonotrichia leucophrys nuttali] [Baker & Mewaldt 1978; Petrinovich et al. 1981; Baker et al. 1982; Zink & Barrowclough 1984; Hafner & Petersen 1985; Soha et al. 2004]). This is likely due to methodological differences (e.g., marker used, scale of study, and populations or subspecies chosen). The significance of dialect for gene flow is likely to vary by species due to life-history traits (e.g., dispersal rates and mating systems) and vocal learning: birds learning song before dispersal are more likely to be affected than those learning throughout life (Podsi & Warren 2007). Overall, there is little evidence to suggest that dialect alone could completely prevent gene flow between populations: even a few cross-dialect pairs per generation would be sufficient to prevent divergence (Potvin et al. 2013). More information is required to provide useful evidence for conservation practitioners. Monitoring gene flow and dispersal events across a range of species, particularly endangered species during conservation interventions, should be a priority for researchers examining genetics in avian conservation.

Uses and Implications of Avian Vocalizations for Conservation

Understanding the biology of avian vocalizations and their impact on population processes can help one appreciate the role of vocal behavior during conservation. We considered potential applications for the use of avian vocalizations (summarized in Table 2) and the potential negative effects of variation in vocalizations and how they might be overcome (summarized in Table 3).

Monitoring

The conspicuous nature of vocalizations means they are easy to measure, even in complex environments, making them a useful noninvasive tool for monitoring (Teixeira et al. 2019). With recent advances in recording technologies and analysis, such as autonomous recording units, it has become possible to collect large amounts of acoustic data with comparatively little effort through passive acoustic monitoring (PAM) (Brandes 2008). Bioacoustic methods perform as well as traditional point counts in a number of cases (Alquezar & Machado 2015; Darras et al. 2018). There remains a need to create standardized practices for acoustic detection surveys (Darras et al. 2018), but a wealth of data with conservation relevance can be collected using these methods.

Acoustic monitoring can provide useful baseline data by examining the spatial and temporal variation of sound (e.g., Pieretti et al. 2011; Rodriguez et al. 2014; Sebastian et al. 2016). Vocalizations extracted from recordings can be used for a number of purposes, including detecting species presence or absence, identifying preferred habitats, detecting juveniles, and determining predator abundance from alarm calls (Teixeira et al. 2019).

Interindividual variation within species allows conservation practitioners to improve the resolution of baseline data (Terry et al. 2005). The ability to discriminate between vocalizations of different individuals can be useful for population censuses (Terry et al. 2005). However, this requires that all birds in a given area vocalize during the sampling period or that researchers have some knowledge of the proportion of birds singing (e.g., if males sing and females do not). If not all birds vocalize, or if vocalizations are biased toward certain demographics or areas (e.g., Legare et al. 1999), population sizes may be underestimated or habitat use may be misinterpreted. The ability to identify individuals by assigning vocalizations to known birds is considerably harder but, when possible, provides useful, high-resolution data. For example, this can allow researchers to assess how life-history traits, such as survival, vary among individuals (Terry et al. 2005).

Bioacoustic data can be used to measure responses to environmental perturbations or human disturbance. Anthropogenic noise can affect birds in a number of ways, including altering habitat use and influencing the characteristics of vocal signals (Ortega 2012). Deichmann et al. (2017) used PAM to examine the impacts of natural gas exploration on avian biodiversity and found diversity increases as distance from the drilling site increases. Such information can be used to minimize the impacts of future disturbances and advise conservation programs. Acoustic monitoring can also be employed to evaluate the success of conservation interventions, providing useful evidence for future efforts. Buxton and Jones (2012) used acoustic monitoring to confirm breeding and document population increases of seabirds after the eradication of introduced Arctic foxes (Alopex lagopus) in the Aleutian Archipelago. Similarly, individual identification could be useful in postrelease monitoring to determine the fate of specific individuals.
| Conservation activity | Use of bioacoustics | Possible taxa | Potential problem | Proposed solution | Reference |
|-----------------------|---------------------|---------------|-------------------|------------------|-----------|
| Collecting baseline data | detecting species presence or absence, identifying preferred habitats, etc. | species producing vocalizations | lack of standardized methods for acoustic detection surveys | produce standard protocols so studies are comparable | Teixeira et al. 2019 |
| Conducting censuses | individual discrimination to improve resolution | all vocally active species (Terry et al. 2005) | requires all birds to vocalize during census period or for researchers to understand the proportion and demographics vocalizing | research species' vocalizations prior to census where possible | reviewed by Terry et al. 2005 |
| Assessing life history traits/fitness | recognition of individual animals | all vocally active species (Terry et al. 2005) | assigning vocalizations to individuals can be challenging | investigate vocal individuality prior to study onset | reviewed by Terry et al. 2005 |
| Assessing responses to perturbations | detecting presence or absence, changes in activity, differences in biodiversity | species producing vocalizations | e.g. Deichmann et al. 2017 |
| Assessing success of conservation interventions | (as above) | species producing vocalizations | e.g. Buxton & Jones 2012; Metcalf et al. 2019 |
| Attraction of single taxa to new habitats | playback of conspecifics to replicate conspecific attraction | e.g. territorial songbirds, colonial seabirds | unsuccessful attraction of target species | understanding of species' biology and ecology - especially habitat, carrying capacity, and community structure | e.g. Reed & Dobson 1993; Ward & Schlossberg 2004; Hahn & Silverman 2007; Bayard & Elphick 2012 |
| Attraction of multiple taxa to new habitats | (as above) | (as above) | (as above) | (as above) | e.g. DeJong et al. 2015 |
Table 3. A summary of the implications of avian vocalizations in conservation.

| Conservation problem                        | Acoustic implications                                                                 | Taxa to consider                                                                 | Proposed solution                                                                 | Reference                        |
|--------------------------------------------|--------------------------------------------------------------------------------------|----------------------------------------------------------------------------------|-----------------------------------------------------------------------------------|----------------------------------|
| **In situ conservation**                   |                                                                                      |                                                                                  |                                                                                  |                                  |
| Habitat fragmentation                      | vocal divergence through differential drift and acoustic adaptation in separated populations | vocal learners – parrots, hummingbirds, songbirds, corvids (Catchpole & Slater 2008; Bluff et al. 2010) | conserve species as contiguous populations or maintain or improve connectivity | Laiolo & Tella 2005              |
| Land use and habitat change               | vocal change through acoustic adaptation, vocalizations poorly adapted to transmission in the new environment | species producing vocalizations closed-ended learners e.g. estrildid finches and sparrows (Brenowitz & Beecher 2005) | minimize land-use change where possible or maintain and improve connectivity | Boncoraglio & Saino 2007; Brumm & Naguib 2009 |
| Invasive species                          | competition in the acoustic landscape resulting in signal masking                     | native species producing vocalizations                                          | prevent future invasions and manage current invasive species                     | Grant & Grant 2010; Farina et al. 2013 |
| **Translocations**                         |                                                                                      |                                                                                  |                                                                                  |                                  |
| Small founder populations                  | formation of cultural bottlenecks, accelerated by serial translocations               | populations/species with multiple vocalization types                            | increase founding population size where possible select representative sample of vocal diversity when choosing birds to translocate use adult birds (or birds with crystallized song) in translocations | Parker et al. 2012; Valderrama et al. 2012, 2013 |
| Translocation of juveniles                 | withdrawal of learning resulting in rapid vocal divergence                             | juvenile birds                                                                  |                                                                                  | Potvin & Clegg 2015              |
| Founding populations from multiple sources | reduced success of territory formation and maintenance assortative mating in translocated populations | birds with vocal dialects (mainly vocal learners, as described above)            | increase founding population size to counteract increased mate selectiveness use individuals from the same source where possible select source populations with similar dialects to reduce variation in founding population monitor populations over multiple generations to determine the full extent of assortative mating following the translocation explore the potential of familiarizing birds with other dialects pre-release | Rowe & Bell 2007; Bradley et al. 2013, 2014; Valderrama et al. 2013 |

Continued
| Conservation problem | Acoustic implications | Taxa to consider | Proposed solution | Reference |
|----------------------|-----------------------|------------------|------------------|-----------|
| **Ex situ conservation**  
Small, isolated populations | cultural drift may be accelerated in small, isolated populations | vocal learners particular concern for species with complex songs | manage species in larger groups where possible, or retain greater levels of connectivity by moving birds between populations more frequently | Laiolo & Tella 2007; Purushotham & Robin 2016 |
| Differences between wild and ex situ habitats | acoustic adaptation to ex situ habitats different acoustic landscapes due to non-native species assemblages | species producing vocalizations | reduce number of generations birds are kept in captivity increase similarity between in situ and ex situ environments (e.g., denseness of planting, reduce anthropogenic noise, and reproduce native species composition) | Potvin & Clegg 2015 |
| Adaptation to captivity | release from selection pressure resulting in large scale vocal divergence from wild-type | species held in captivity for many generations | reduce number of generations birds are kept in captivity minimize differences between in situ and ex situ habitats breeding management to ensure that individual ancestors do not become over-represented | Honda & Okanoya 1999; Tanimoto et al. 2017 |
| **Reintroductions**  
Ex situ breeding  
Release from ex situ populations | discussed above vocalizations poorly adapted to new environments | discussed above species producing vocalizations particular concern for closed-ended learners | discussed above reduce differences between in situ and ex situ environment reduce number of generations in captivity increase founding population size to counteract increased mate selectiveness select source populations with similar dialects to each other or to in situ population to reduce variation in newly formed populations explore potential of familiarizing birds with other dialects pre-release | discussed above Rowe & Bell 2007; Bradley et al. 2013, 2014; Valderrama et al. 2013 |
Artificial Playback for Conspecific Attraction

The presence of conspecifics can attract birds to a habitat, but natural conspecific attraction can be unreliable when conspecifics are rare or absent in new habitats (Crates et al. 2017). Artificial playback of vocalizations can be used in place of conspecifics to reinforce existing populations or encourage animals to colonize new areas (Reed & Dobson 1993). This technique has been used to increase local populations of a number of species (e.g., Ward & Schlossberg 2004; Hahn & Silverman 2007), but is not always successful. Bayard and Elphick (2012) found no evidence of a response to broadcast in Saltmarsh Sparrows (Ammodramus caudacutus), possibly due to insufficient cues, already saturated habitats, or broadcast in unsuitable areas.

Conspecific attraction could be used to create communities by attracting multiple species simultaneously to a single site (e.g., DeJong et al. 2015). This would be especially useful for colonizing newly restored habitats or replenishing protected areas. However, past attempts highlight the need to consider the effects of community change on both target and non-target species. DeJong et al. (2015) found that populations of focal species increased near playback speakers, but populations of some non-target species declined and suggest that differences in response between species could relate to interspecific competition.

Although artificial playback for conspecific attraction is a simple and cost-effective method, we believe that current evidence shows a need for understanding species’ biology and ecology to accurately predict outcomes. Where communities contain multiple endangered species, it is essential to consider the risks associated with conspecific attraction—an increase of one species of conservation concern could lead to the decline of another.

In Situ Conservation

Large- and small-scale changes in land use can isolate previously contiguous populations, promoting song divergence through drift in the separate populations and through adaptation to changed habitat structure (both for improved acoustic transmission and due to changes in morphological features). Closed-ended learners may be particularly vulnerable to habitat change because they would be unable to alter their song to transmit well in the new environment. We suggest that preventing land-use change and protecting species as contiguous populations in the same habitat would help prevent vocal change. Where this is not possible, maintaining or improving connectivity between populations may reduce divergence in song characteristics.

Although limiting the impact of invasive species is a key goal of many conservation efforts, the impact of invasive species on vocalizations is rarely considered. When new species enter the acoustic landscape, resident species may alter song characteristics (Grant & Grant 2010) or become masked by the new vocalizations. Acoustic monitoring of Mediterranean shrubland revealed that the invasive Red-billed Leiothrix (Leiothrix lutea) is acoustically dominant in the landscape, competing with and potentially lowering the density of native species (Farina et al. 2013). If native species cannot compete with invaders in the acoustic landscape, they may not be able to adequately communicate and breed. Preventing future invasions is important to maintain acoustic landscapes for conservation of native species.

Translocations

Translocations often involve small founder populations, so the formation of cultural bottlenecks is a concern. Serial translocations, where populations from successful translocations are used as source populations for future translocations, may increase the rate of song differentiation among populations, resulting in population divergence, isolation, and reduced retention of animals near release sites. In the North Island Kokako, in translocated populations, songs are shorter and of higher frequency and phrase repertoires are lower than in source populations (Valderrama et al. 2012, 2013). Vocal activity is also markedly reduced, potentially reducing immigration and retention of birds in already small populations (Valderrama et al. 2012). When examining serial translocations in North Island Saddlebacks, Parker et al. (2012) reported reduced song type sharing between translocated and ancestral populations in successive interventions (9.8% shared after the first translocation, 9.2% after the second, and 3.3% after the third). Withdrawal of learning could also cause rapid divergence of songs in recently translocated populations. Moving adult birds with crystallized songs would be preferable to moving juveniles when aiming to limit changes in vocalizations. The withdrawal of learning effect is poorly understood in many species, so monitoring vocalizations after interventions would provide vital information for future conservation programs.

To improve genetic diversity during interventions, multiple source populations may be used for translocations. However, if source populations have different dialects, this may affect territory formation and mate choice. In the North Island Kokako, which is the subject of intensive conservation management, local songs elicit stronger responses from territory-holding pairs than foreign songs (Bradley et al. 2013), although this result is not consistent among sites (Valderrama et al. 2013). Further examination of responses to dialects across populations is necessary to determine the nuances of differential discrimination. Populations (or individuals) that respond similarly to local and foreign dialects would more easily integrate into new mixed-dialect populations.
making them potential targets for conservation interventions. However, choosing birds based on response may result in inadvertent selection for response and associated traits. Similarly, assortative mating with respect to dialect is common in Kokako; across 10 multisource translocations over 18 years (1993–2011), Kokako mated assortatively in most seasons at all 5 sites. Very few mixed-dialect pairs formed (Bradley et al. 2014), and mixed-dialect pairs took considerably longer to form than matched pairs (Rowe & Bell 2007). The long-term impact of mate selection based on dialect is not clear. First-generation Kokako hatched at translocation sites do not appear to show preferences for their fathers’ dialects, lending support to theories on familiarity. However, sample sizes are too small to draw clear conclusions. Two first-generation females paired, one with a male of dialect similar to her father’s and the other with a male of a different dialect (Rowe & Bell 2007). Monitoring of mate choice in populations over multiple generations would help determine the overall impact of selection based on dialect over time.

Where dialects are a conservation concern, several mitigation methods could be used: increase starting population size to counteract increased selectiveness; use individuals from the same source population where possible; and select populations with similar dialects to reduce dialect differences in the new group. It is possible that familiarizing birds (either adults or juveniles) with different dialects using playback before translocations could alter preferences and reduce selectiveness in mate choice. MacDougall-Shackleton et al. (2001) report that preference for natal-dialect song attenuated in birds exposed to foreign-dialect song when they were 1 year old. More research is required into the feasibility of this technique. However, if familiarity with dialects reduces aversion to foreign-dialect mates, conservation practitioners may be able to familiarize birds with all dialects in their new population before the interventions take place, thus improving mating success.

Ex Situ Conservation

Populations in ex situ management are often small and isolated, which may accelerate the rate of cultural drift (Laiolo & Tella 2007). Housing species in larger groups ex situ where possible or retaining greater levels of group connectivity, for example, by moving birds between populations more frequently, could help to combat the effects of drift. Reducing the number of generations birds are held in ex situ populations would also reduce the likelihood of building up large song differences. These mitigations are particularly important for species with complex songs because these may undergo accelerated rates of drift compared with simple songs (Purushotham & Robin 2016).

Breeding birds ex situ may promote song divergence from the wild-type through acoustic adaptation, meaning birds will be poorly adapted when reintroduced. Although captive environments are necessarily different from those in situ, matching the environments as closely as possible would limit song evolution. Small changes could be made to increase similarities, such as matching the denseness of vegetation in wild habitats and reducing the presence of anthropogenic noise, such as air-conditioning units. Again, reducing the number of generations birds spend in unfamiliar environments during conservation interventions may also reduce adaptation because acoustic adaptation can increase with time (Potvin & Clegg 2015).

Captive environments may also differ from those in situ due to species compositions. Mixed-species enclosures often hold a range of species that would not overlap in the wild, creating an unnatural acoustic landscape. As with invasive species, birds may alter their vocalizations, but if signals become masked, then breeding success in these aviaries may be reduced. Although there is currently little research in this area, potential issues could be avoided by housing species in natural assemblages from the same geographic location.

In captive populations, breeding pairs are usually assigned rather than allowed to form naturally to maximize genetic variability. However, animals limited in mate choice often show reduced reproductive success (Martin & Shepherdson 2012). We hypothesize that a lack of acoustic separation from males with high-quality or local-dialect songs may alter females’ perceived mate availability, resulting in females reducing reproductive efforts with their assigned mates. Allowing mate choice or providing appropriate acoustic separation could help alleviate this problem and increase breeding success.

Although reducing the number of generations in captivity could act to reduce divergence in vocal communication, this may not always be possible, and some birds have already been conserved ex situ for many generations (e.g., the ‘Alalā [Corvus bauvatiensis] [Tanimoto et al. 2017]).

Prolonged captive breeding could result in species becoming adapted to captivity. Surprisingly, very few studies examine song differences between wild and captive individuals. Tanimoto et al. (2017) compared vocalizations of the ‘Alalā between past wild and current captive populations, finding similar numbers of call types, but significantly different repertoires. Because dialects change over time, it is not possible to say how much of a role captivity played in these changes. All ‘Alalā were brought into captivity, so it is not possible to conduct a contemporary comparison.

The song of the domestic Bengalese Finch (Lonchura striata domestica) is more syntactically complex than that of its wild counterpart, the White-rumped Munia (L. striata) (Honda & Okano 1999). Several possible
explanations for these differences have been proposed, including the lack of predation pressure in captivity for Bengalese Finches (Honda & Okanoya 1999); need for species identification by White-rumped Munia in mixed-species flocks (Kagawa et al. 2012); lower levels of corticosterone in Bengalese Finches (Suzuki et al. 2012); and selective breeding for traits correlated with song complexity, such as reproductive output and parental care, in Bengalese Finches (Suzuki et al. 2013). Domestication exerts far stronger selection pressures on populations than captive breeding. However, this example highlights some potential mechanisms of change during long-term ex situ management.

Many of the situations that give rise to song divergence, such as release from predation and reduced stress, are unavoidable in captivity. However, the steps outlined above, such as minimizing differences in environment and enabling mate choice, may slow or reduce overall change. Breeding management strategies are already commonplace in zoological collections for maintaining genetic and demographic viability (Ballou et al. 2010). These same techniques, such as ensuring individual lineages do not become overrepresented in the breeding pool, may also limit song changes during captive breeding.

Reintroductions

Many issues facing reintroduction efforts stem from breeding ex situ. The negative effects of adaptation to captivity are highlighted by the relative success rates of translocations and reintroductions. Fischer and Lindenmayer (2000) report that 31% of translocations of wild animals have been successful, but only 13% of translocations with captive animals have been successful. Birds with vocalizations adapted to captive environments may signal less efficiently on release to the wild (Tanimoto et al. 2017). We expect this would be more detrimental to closed-ended learners, which would not be able to alter songs for their new environment.

Divergence from wild-type vocalizations may cause problems similar to those seen in translocations with multiple sources if reintroductions aim to supplement preexisting populations. Reintroductions use multiple source populations, or multiple reintroductions to a single site are planned. If dialects have diverged, all of these scenarios may affect territory formation or result in increased mate selectiveness and possibly reduced gene flow. Although dialect-based assortative mating between wild and captive birds has not been studied, it may be expected based on previous studies of female preference (e.g., Searcy et al. 2002) and evidence from translocations (Rowe & Bell 2007; Bradley et al. 2014). We speculate that if reintroduced birds are unable to breed with wild populations or to persist as stable populations themselves and if reintroduced birds compete with native populations, then competition created by reintroductions may hasten rather than prevent extinctions.

Improving the success of reintroductions will involve steps in captivity to reduce song divergence, as outlined above (reduce habitat differences and reduce number of generations in captivity). Recommendations for reintroductions are similar to those for translocations: increase the size of release groups, choose birds with similar dialects to each other and to the source population where possible, and use adult birds to prevent rapid change after release. Moreover, exposing birds both in situ and ex situ to the dialects of other populations may improve integration and mating success, although further research is needed to determine the feasibility of this approach.

Conclusion

Considerable progress has been made in the use of vocalizations to aid conservation, particularly with bioacoustics used to monitor populations and survey biodiversity. Although research into acoustic monitoring continues to grow, research examining the adverse effects of variation in vocalizations during conservation programs is lacking. There are a number of important questions that should be addressed in order to build a better evidence base for conservation practitioners. First, little is known about the actual effect of dialects on mating. Although females often show preference for local songs, this may not reflect how they mate in conservation settings. Although some evidence for assortative mating in the wild exists (e.g., the Kokako), evidence from mixed-dialect populations suggests that dialect-based assortative mating may be due only to familiarity. If this is true, it may be possible to mitigate the problem by familiarizing young birds with the dialects they may encounter during conservation efforts. Similarly, additional research is needed into the long-term effects of dialect-based assortative mating; assortative mating may not be maintained over multiple generations. Long-term population monitoring after intervention would be necessary to determine this. Furthermore, understanding of the interplay between dialects and gene flow remains limited. Individuals are often closely monitored during conservation to examine breeding success. Thus, it may be possible to determine how dialects affect gene flow by constructing pedigrees within populations. If gene flow persists during interventions in spite of dialects, this knowledge would be extremely beneficial to practitioners. Finally, the evolution of birdsong during ex situ management is poorly understood. Understanding the drivers and extent of acoustic change during conservation breeding is essential for planning of breeding programs and reintroductions. Future research should focus on these knowledge gaps to help practitioners and scientists properly plan for and mitigate potential adverse effects of variation in vocalizations during conservation.
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