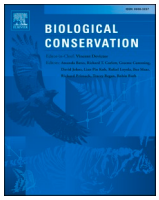
Biological Conservation 284 (2023) 110171

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon



Zoo-bred female birds prefer songs of zoo-bred males: Implications for adaptive management of reintroduction programs

Daniel L. Appleby [a,*], Joy S. Tripovich [b,c], Naomi E. Langmore [d], Robert Heinsohn [a], Benjamin J. Pitcher [b], Ross Crates [a]

[a] Fenner School of Environment and Society, Australian National University, Acton, ACT, Australia
[b] Taronga Institute of Science and Learning, Taronga Conservation Society Australia, Bradleys Head Rd, Mosman, NSW 2088, Australia
[c] Centre for Ecosystem Science, School of Biological, Earth and Environmental Sciences, The University of New South Wales, UNSW Sydney, NSW 2052, Australia
[d] Research School of Biology, Australian National University, Acton, ACT, Australia

ARTICLE INFO

Keywords:
Conservation
Ornithology
Behavioural ecology
Captive breeding
Reintroduction biology
Cultural evolution

ABSTRACT

Understanding the factors affecting the success of animal reintroductions is crucial for facilitating endangered species recovery. Cultural differences between individuals from different animal populations can lead to assortative mating, whereby individuals prefer to breed within their own familiar cultural cohort. Assortative mating can hinder the assimilation of zoo-bred individuals into wild populations, so quantifying this risk becomes important for informing adaptive management strategies in conservation. We conducted mate choice experiments on zoo-bred female regent honeyeaters (*Anthochaera phrygia)* to assess whether they showed stronger behavioural responses to the familiar but abnormal songs of zoo-bred male regent honeyeaters than those of their wild counterparts or an interspecific control song. Female regent honeyeaters were no more likely to enter the playback aviary in response to the songs of zoo-bred males than those of wild males or a different species. However, females that did enter the playback aviary were significantly more likely to respond quickly, approach the speaker closely and remain in the playback aviary for longer in response to the songs of zoo-bred males than wild songs or control songs. Our study is the first to show experimentally that zoo-bred females prefer familiar, but abnormal, zoo-bred songs over unfamiliar wild-type songs. We suggest that assortative mating amongst released birds is a risk in reintroduced regent honeyeaters, given recent evidence that the breeding success of reintroduced pairs is low. Our study demonstrates how small-scale experiments conducted within applied zoo-breeding settings can yield useful information to refine husbandry techniques and reduce cultural divides between wild and reintroduced populations.

1. Introduction

Zoo breeding programs are a widely used conservation strategy to bolster populations of endangered species and to supplement declining wild populations undergoing concurrent in-situ conservation (Rahbek, 1993; Seddon et al., 2014). Although many species readily breed in captivity, the success of reintroduction programs, whereby zoo-bred individuals are released to the wild, is often low or variable (Crates et al., 2022; Fischer and Lindenmayer, 2000; Sheean et al., 2012). Identifying the factors that determine the success or failure of reintroductions is complex, but is a priority to maximise returns on conservation investment (Fischer and Lindenmayer, 2000; Robinson et al., 2020; Sheean et al., 2012). Many studies have assessed common issues, ranging from poor planning (Ewen and Armstrong, 2007) and a failure to address the initial causes of population decline (Kingsford et al., 2009; Sheean et al., 2012) to the effects of the captive environment, including inbreeding (Araki et al., 2009; Frankham, 2008; Fraser, 2008) and adaptations to captivity (Frankham, 2008; McPhee, 2004). More recently, erosion of animal cultures – a lack of socially-transmitted behaviours in captivity – is being recognised as a potential barrier to successful reintroduction to the wild (Brakes et al., 2019; Rutz et al., 2016). Although zoo breeding programs are increasingly being run with more rigorous protocols (Ewen and Armstrong, 2007; Frankham, 2010; Greggor et al., 2018), animal cultures are rarely considered in their planning and implementation (Brakes et al., 2019).

Cultures in animals are behaviours that are acquired through social

* Corresponding author.
E-mail address: daniel.appleby@anu.edu.au (D.L. Appleby).

https://doi.org/10.1016/j.biocon.2023.110171
Received 15 December 2022; Received in revised form 4 May 2023; Accepted 16 June 2023
Available online 7 July 2023

learning between individuals and are shared at a population or sub-population level and maintained through generations (Rendell and Whitehead, 2001; Rutz et al., 2016; Whiten, 2021). Culture is key to kin recognition, social cohesion, and mate attraction, amongst other social factors (Rutz et al., 2016; Whiten, 2021). However, culturally-acquired behaviours such as birdsong can be lost or altered in zoo environments through changes to the social composition and dynamics of zoo-bred populations relative to their wild counterparts (Crates et al., 2022). Devising innovative ways to maintain wild animal cultures in zoo environments through adaptive management is increasingly being recognised as an important conservation consideration (Brakes et al., 2021).

Songbirds learn songs and song preferences from older conspecific tutors, including parents or associated adults (Beecher et al., 2007; Catchpole and Slater, 2008). While copying errors and cultural drift can lead to changes in song culture over time, rapid and drastic changes to population-level song cultures are likely to be an outcome of population decline or fragmentation (Paxton et al., 2019). Songs in birds are used in mate attraction and territory defence (Catchpole and Slater, 2008; Laiolo and Tella, 2007), and assortative mating between individuals that belong to the same song dialect (where either both the male and female sing or only the male sings songs that non-singing females were exposed to during development) is widespread (Wang et al., 2022; Planqué et al., 2014). Therefore, changes to song structure may isolate social groups even if they co-occur (Crates et al., 2021). Assortative mating, whereby individuals preferentially pair within the same cultural cohort based on sexual or social preferences formed through developmental auditory experience (Jiang et al., 2013; Chen et al., 2017), can hinder the assimilation of zoo-bred individuals into wild societies (Slade et al., 2014). Although successful pairing between captive-reared and wild individuals is essential to the success of captive-rearing programmes, no studies have previously investigated whether dialect-based assortative mating occurs in this context (Lewis et al., 2020). As songs are learnt from adults during early development, and typically become fixed before their release, zoo-bred birds may fail to integrate and interbreed with wild populations. This potentially limits the ability of naïve, zoo-bred birds to acquire behaviours socially from wild conspecifics that may be crucial for their long-term survival.

The regent honeyeater (*Anthochaera phrygia*) is a critically endangered Australian songbird with an estimated population of fewer than 300 individuals remaining in the wild (Commonwealth of Australia, 2016; Garnett and Baker, 2021). To mediate the risk of imminent extinction in the wild, zoo breeding to bolster the wild population through reintroductions and provide an insurance against further population decline is a high priority strategy in the species' national recovery plan (Commonwealth of Australia, 2016). However, the ongoing supplementation of the wild population with zoo-bred regent honeyeaters has had limited success in arresting the population decline (Heinsohn et al., 2022; Tripovich et al., 2021), with the majority of zoo-bred birds failing to establish a breeding territory or pair with wild mates (Kvistad et al., 2015; Tripovich et al., 2021). In the past, a failure to pair with wild conspecifics could be explained by the small number of wild birds persisting at the traditional reintroduction site in northern Victoria (Kvistad et al., 2015). However, the reintroduction strategy shifted in 2021 such that zoo-bred birds are now reintroduced into the greater Blue Mountains in New South Wales (NSW), where the vast majority of wild regent Honeyeaters persist (Heinsohn et al., 2022). Despite this shift, zoo-bred birds still show poor breeding success (unpublished release data).

Regent honeyeaters sing a soft, metallic-sounding song that is locally variable and forms loose geographic dialects (Crates et al., 2021). Over the past 25 years their songs have gradually changed within all populations (Powys, 2010; Crates et al., 2021). Now, the vast majority of recorded birds sing the dialect, referred to in Crates et al. (2021) as the "Blue Mountains typical" dialect. Zoo-bred male regent honeyeaters sing an abnormal song that is distinct from any wild population (Crates et al., 2021). Their songs are simpler, shorter and contain fewer distinct syllables, none of which overlap with the wild population (Crates et al., 2021). The founding population of zoo-bred regent honeyeaters were hand-reared from wild nestlings that never had the opportunity to learn the wild song. This simplified song has persisted for nine generations (assuming three years per generations per Heinsohn et al., 2022) in the zoo population. Post-release, interbreeding between zoo-bred and wild regent honeyeaters of either sex has rarely been observed (Ingwersen, 2014; Kvistad et al., 2015). This may be because females of many bird species exhibit preferences for familiar song dialects when selecting a mate (Beecher et al., 2007). This assortative mating strategy may occur if wild females show lower levels of attraction to the simplified, unusual songs of zoo-bred males. Conversely, most zoo-bred females are typically only exposed to zoo-bred song dialects prior to release, meaning they may show a preference for the familiar songs of zoo-bred males over wild conspecifics based on their developmental auditory experience (Chen et al., 2017). The observation that zoo-bred regent honeyeaters have lower breeding success than their wild counterparts (Taylor et al., 2018) means that quantifying the risk of assortative mating based on differences in song dialects is a conservation priority.

We adopted an experimental approach within the regent honeyeater zoo-breeding facilities to test the hypothesis that zoo-bred female regent honeyeaters show a behavioural preference for the song dialect of zoo-bred male regent honeyeaters, with which they are familiar, over the culturally dominant song dialect of wild male regent honeyeaters occupying future release sites within the greater Blue Mountains.

2. Methods

2.1. Study populations

Female regent honeyeaters ($n = 18$) were raised at Taronga Zoo, Sydney, and/or Taronga Western Plains Zoo, Dubbo in NSW, Australia. All birds spent a minimum of one year in the Taronga Western Plains Zoo population, which was founded from part of the Taronga Zoo population in 2019.

We conducted our experiments within the breeding season, when we expect females would be naturally most receptive to males' songs. So as not to interfere with the breeding effort, we did not implement subcutaneous oestradiol implants, as has been conducted in similar experiments in other species (Dunning et al., 2014). We implemented two of the three trials at the beginning of the breeding season, within one week of the regular pairing of birds for the breeding program in June 2021 ($n = 6$ females) and June 2022 ($n = 6$). The third trial took place later in the breeding season in January 2022 ($n = 6$), but still within the known regent honeyeater breeding period (Geering and French, 1998).

2.2. Selection of playback songs

We selected zoo-bred regent honeyeater songs from recordings of contemporary males recorded at Taronga Zoo between 2018 and 2021. Each female received unique wild and zoo-bred songs. Male song at the Taronga Western Plains Zoo closely resembles these recordings, as the population was largely founded from Taronga Zoo. To ensure previous experience of a male's song did not bias female responses, we vetted the identity of the recorded males to ensure that females were not presented with songs of previous mates, or of their own fathers. The zoo breeding aviaries are in multiple blocks of four individual aviaries, so while it is possible to isolate juvenile females from the songs of males in other blocks, it is not possible to totally isolate them from the songs of males in neighbouring aviaries within their own block. As future releases are planned for areas within the greater Blue Mountains, NSW, we selected wild songs from recordings categorised as 'Typical Blue Mountains' in Crates et al. (2021), which is the cultural norm within this part of the species' range. We selected songs with the highest fidelity and signal to noise ratios from Crates et al. (2021) field recordings, which we assigned to females randomly. We used an interspecific song as a neutral control

to test whether females respond to a vocal stimulus simply out of curiosity. For the interspecific song we selected superb fairy-wren (*Malurus cyaneus*) song as this species is abundant around the zoo-breeding facilities and are presumed not to threaten regent honeyeaters in any way. We acquired the superb fairy-wren songs from xeno-canto (https://xeno-canto.org/) recorded within NSW to maximise familiarity. We selected the highest possible fidelity recordings of similar lengths to those of the regent honeyeater songs (range = 1.0–1.3 s), which we presented at the natural superb fairy wren frequency range. Example songs of wild and zoo-bred regent honeyeaters and the control songs of superb fairy-wrens are shown in Fig. 1. A list of songs is provided in the Supplementary Information Table S1.

2.3. Song preference testing

We implemented song preference experiments in a bank of aviaries ordinarily used for breeding. The experimental area consisted of three 4 × 4 × 6 m aviaries with opaque Perspex dividers between them and a metre wide, floor to ceiling door linking each aviary (Fig. 2). The aviaries are vegetated with a combination of live trees and shrubs, and trimmed browse affixed to the walls. We provided food, water, and flowers in the central aviary and installed four speakers on the wall 1.7 m from the ground at the front and rear corners of the outer two aviaries (i.e. aviaries b and d in Fig. 2).

For the description of the experimental design, we use the following definitions:

- Song bout: One song (as shown in a panel in Fig. 1) from each of three different males singing the same song type, played successively in a random order, with randomized intervals of between three and fifteen seconds between the three individual songs. We chose this interval range to represent the males' natural singing frequency during the breeding season.
- Presentation: the three-minute period during which we played a female a single song bout and measured her responses to it.
- Treatment: Five presentations of each of the three different song types: zoo-bred regent honeyeater, wild regent honeyeater and interspecific superb fairy-wren control.

To minimise stress, we undertook the experiment when females were due to be moved between free-flight and breeding aviaries. We introduced 18 females, one at a time, from the free-flight aviary to the experimental area (aviary block b, c & d in Fig. 2) and gave each a minimum of two hours to acclimatise. After experimentation on each female was complete, they were moved from the experimental area to neighbouring individual breeding aviaries (e.g. aviaries e and f in Fig. 2).

For the experiments, aviary 'c' was always the neutral aviary and contained the feed station. We used aviaries 'b' and 'd' for playback and they were deemed 'occupied by a male' when we played song bouts from speakers in that aviary or 'unoccupied' when we played songs from the opposite treatment aviary. We alternated the 'occupied' and 'unoccupied' aviaries within treatments, ensuring song bouts in each treatment were played from both outer aviaries b and d. We also randomized (i) whether song bouts were played from the front of back speakers in the occupied aviary; and (ii) the order in which we presented the three treatments to females.

We tested female responses to three 15-min treatments; unfamiliar wild-type regent honeyeater song, familiar zoo-type regent honeyeater song, and familiar but heterospecific superb fairy-wren song. During each presentation, we measured female responses to songs for three minutes, from the moment the first song within a bout was broadcast. Treatments were separated by 20 min of silence.

We began each song bout only when the female was settled in the central (neutral) aviary. For each song bout, we measured four female response metrics on separate stopwatches:

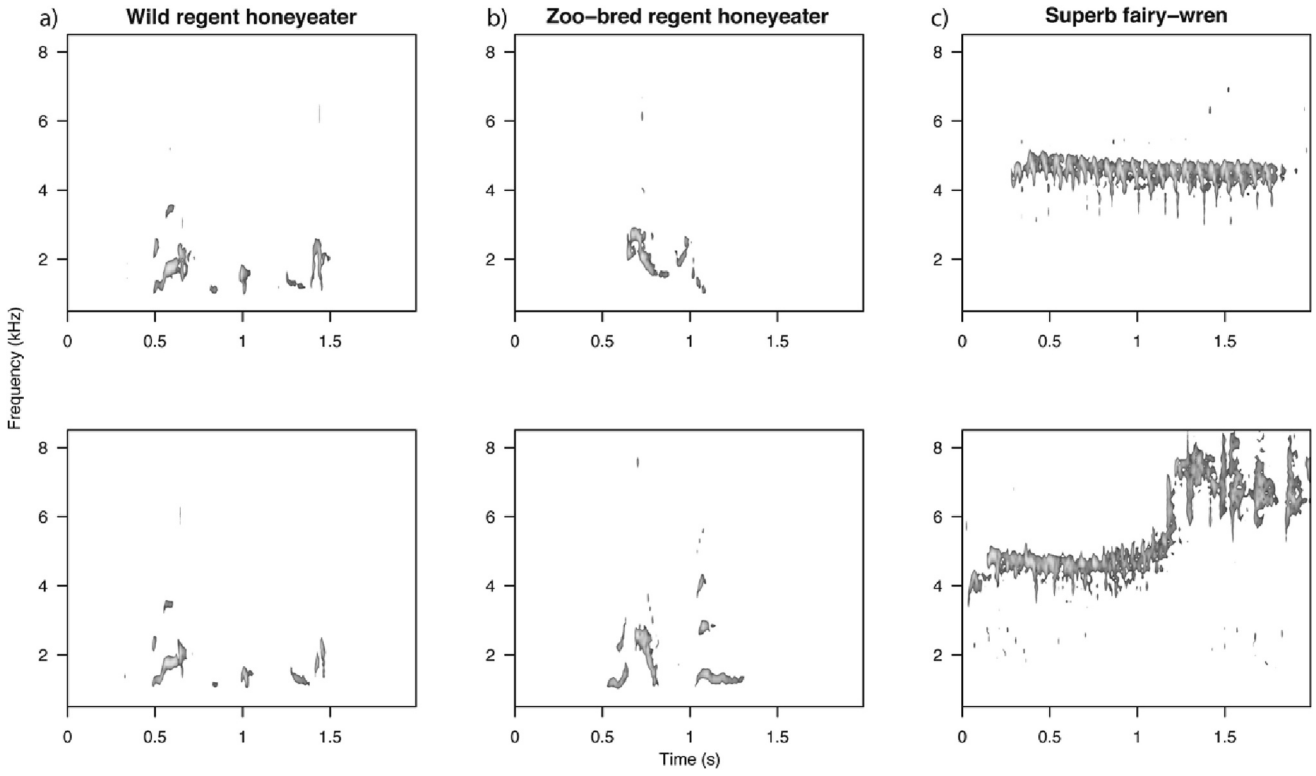


Fig. 1. Example spectrograms of: column a) typical Blue Mountains wild regent honeyeater; column b) zoo-bred regent honeyeater and column c) superb fairy-wren; songs used in female regent honeyeater song preference experiments. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

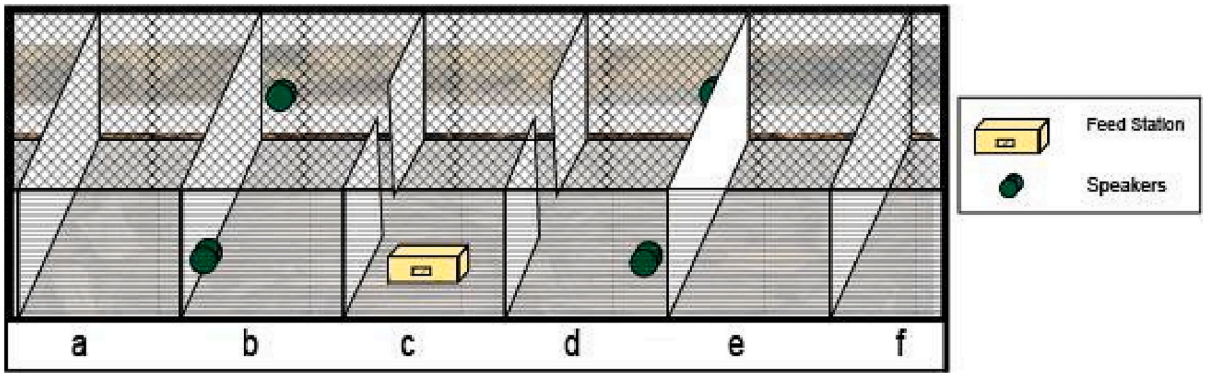


Fig. 2. Floor plan of aviaries used to explore song preference in zoo-bred female regent honeyeaters. Aviaries were in a bank of 10. We selected 3 aviaries to use for the experiments at least 2 aviaries away from the edge to reduce bias toward one side. Aviaries 'a', 'e' and' 'f' were not used in the experiment.

- Association time: The total amount of time during each presentation the female spent within the playback aviary.
- Close association time: The total amount of time during each presentation the female spent within 1 m of the playback speaker.
- Latency: The time interval between the commencement of the first song in a song bout and the female entering the playback aviary.
- Negative association time: The total amount of time spent during each presentation in the outer aviary not broadcasting song.

A list of the randomized experimental protocol is provided in Supplementary Table S2.

2.4. Sample sizes

We considered each presentation as a separate response measure as females had to return and settle in the central aviary prior to commencement of the next song bout. As each treatment had five presentations (i.e. five three-minute periods containing one song about each), there are 20 data points for each of the 18 females, equating to 360 data points in total (90 each for zoo-bred and wild type regent honeyeater songs and 180 for control superb fairy-wren songs).

2.5. Statistical analysis

We used RStudio version 4.0.3 for all data analysis (R Core Team, 2020). We first checked the distribution of each of the four response measures. Because association, close association, and negative association times had zero-inflated distributions, we implemented two complementary hierarchical approaches for the response measures.

2.5.1. Binomial association and close association responses

First, we reclassified the association time within each presentation into a binomial response; 0 = no time spent in the playback aviary, 1 = time spent in the playback aviary. We then fitted a logistic regression with the binomial response of association or no association, with song type as a fixed effect and individual identity, song presentation order and aviary side (left or right) as random terms. We also included time within breeding season as an interaction term with song type:

$$\text{Binomial association model} <- \text{glmer}\,(\text{Association or not} \sim \text{Song type} + \text{Song type} : \text{Time within breeding season} + (1|\text{Female ID}) + (1|\text{Presentation order}) + (1|\text{side of aviary})\,, \text{family} = \text{`binomial'}, \text{data} = \text{all data})$$

In cases where the female entered the playback aviary (154 times, 44/90 in response to zoo-bred, 73/180 in response to control, 37/90 in response to wild), we also reclassified close association time into a binomial response; 0 = no time spent within one metre of the playback speaker, 1 = time spent in one metre of the playback speaker. We then fitted the same logistic regression described for the binomial association, but with the binomial response of close association or no close association using only the positive response data:

$$\text{Binomial close association model} <- \text{glmer}\,(\text{Close Association or not} \sim \text{Song type} + \text{Song type} : \text{Time within breeding season} + (1|\text{Female ID}) + (1|\text{Presentation order}) + (1|\text{side of aviary})\,, \text{family} = \text{`binomial'}, \text{data} = \text{positive response data})$$

2.5.2. Association time

We then explored two approaches to analysing the full dataset, including null responses: these were a zero-inflated Poisson general linear mixed effects model (ZIP) using function *glmmTMB* via package 'glmmTMB' v1.14 (Brooks et al., 2017) and a negative binomial generalized linear mixed model in 'lme4' 1.1–27.1 (Bates et al., 2015). Goodness of fit measures including conditional R^2 values, normality of residuals and Akaike Information Criterion (AIC) values indicated the ZIP models were best suited to the data (see results and Supplementary Table 4). We therefore modelled association time as a function of song type, again including an interaction term for time within the breeding season (early versus late), as well as random terms for song presentation

order and the side of aviary from which we broadcast the song during each bout of playback. We also included female identity within the zero-inflated component of the model (ziformula):

Association time model < − glmmTMB (Association time ∼ Song type + Song type : Time within breeding season + (1|Presentation order) + (1|side of aviary) , ziformula =∼ 1 + (1|Female identity) ,family = Poisson,data = all data).

2.5.3. Latency, close association time and negative association time

For these three measures, we focused only on the response data (i.e., positive when the female entered the playback aviary for latency and close association [154 responses] or negative when the female entered the non-playback aviary for negative association[132 responses]). For the close association and negative association models, the data were still zero-inflated, and we maintained the default zero-inflation formula. Latency response data was not zero-inflated, so we removed the zero-inflation term from the latency model formula but kept the female identity random term in the model:

Close association time model < − GlmmTMB (Close association time ∼ Song type + Song type : Time within breeding season + (1|side of aviary) + (1|Presentation order) , family = poisson,ziformula =∼ 1 + (1|Female identity) ,data = positive response data).

Latency model < − GlmmTMB (Latency ∼ Song type + Song type : Time within breeding season + (1|Female identity) + (1|Presentation order) + (1|side of aviary) , family = poisson,data = positive response data).

Negative association model < − GlmmTMB (Negative association time ∼ Song type + Song type : Time within breeding season + (1|Female identity) + (1|Presentation order) + (1|side of aviary) , family = poisson,ziformula =∼ 1 (1|Female identity) ,data = negative response data).

3. Results

3.1. Binomial response for association and close associations

The probability of a female entering the playback aviary in response to zoo-bred song was not significantly higher than in response to either the control playback (relative to zoo-bred songs, control $\beta = -0.40$, se = 028, $p = 0.159$) or to wild playback (wild $\beta = -0.3$, se = 0.32, $p = 0.256$, Fig. 3a, Table S3). During many trial presentations females preferred to stay in the central aviary where food and water were provided. However, of the birds that did enter the playback aviary, the probability of females subsequently approaching within 1 m of the playback speaker was significantly higher in response to zoo-bred song playback than wild songs or control songs (relative to zoo-bred songs, wild song $\beta = -3.10$, se = 0.66, $p \leq 0.001$, control songs $\beta = -3.48$, se = 0.63, p ≤0.001, Fig. 3b, Table S3).

3.2. Association time

Females spent significantly more association time in the aviaries that broadcast zoo-bred songs than in the aviaries that broadcast either the control or the wild song types in both the early breeding season (relative to zoo-bred songs, control songs $\beta = -0.46$, se = 0.04, $p < 0.001$, wild songs $\beta = -0.48$, se = 0.03, $p \leq 0.001$), and the late breeding season (relative to zoo-bred songs, control songs $\beta = -0.25$, se = 0.05, p < 0.001, wild songs $\beta = -0.17$, se = 0.06, $p = 0.03$). Association time was greater in the late season for all song types (Fig. 4a). The interaction between 'time in season' and 'song type' was significant ($\chi^2 = 509.77$, df = 3 $p \leq 0.001$, Table S6). The conditional R^2 value of the model was 0.30.

3.3. Close association time

The ZIP model for close association time revealed that the females that responded to playback spent significantly more time within one metre of the speaker (i.e. close association) in response to zoo-bred song than either wild songs or control songs in the early breeding season (relative to zoo-bred songs, wild songs $\beta = -0.81$, se = 0.10, $p \leq 0.001$, control songs $\beta = -0.43$, se = 0.15, p ≤0.001). In the late breeding season, females associated closely with zoo-bred song playback more than either wild or control songs, but this was only significant for control songs (relative to zoo-bred songs, wild songs $\beta = -0.97$ se = 0.47, $p =$ 0.29, control songs $\beta = -1.28$, se = 0.22, $p \leq 0.001$). A significant interaction between 'time in the season' and 'song type' was revealed by this model ($\chi^2 = 12.09$, df = 3, $p = 0.007$, Table S6).

3.4. Latency

Of the females that responded to playback, the latency to approach the speaker was significantly shorter in response to zoo-bred song playback than control and wild song playbacks in the early breeding

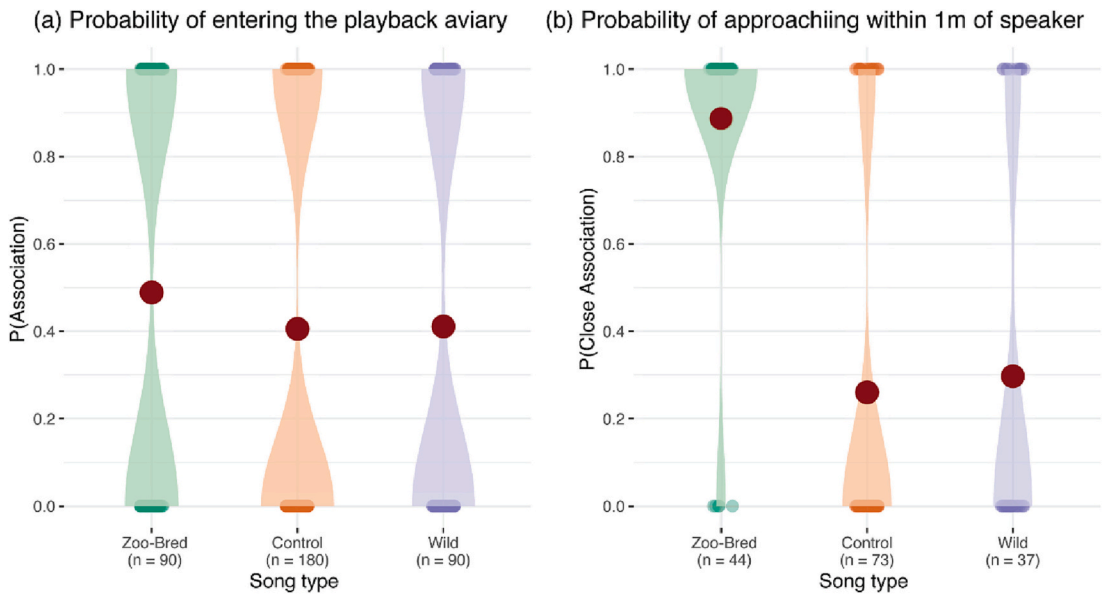


Fig. 3. Logistic regression plots showing the probability of (a) positive association of zoo-bred female regent honeyeaters to playback song type; and (b) of associated birds making a close association within 1 m of the speaker. The red circle represents the estimated probability, the shaded areas represent the kernel density and numbers in parentheses denote the sample sizes (i.e. the number of song bout presentations) included in each analysis. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

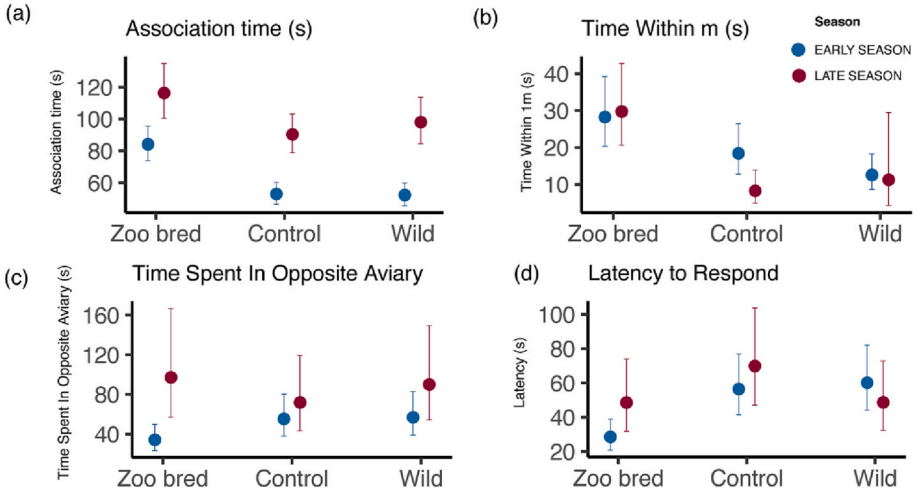


Fig. 4. Prediction plots for linear mixed models showing mean +/− SE amount of time spent by zoo-bred female regent honeyeaters in (a) the playback aviary; (b) within 1 m of the playback speaker (i.e. close association time); (c) in the non-playback outer aviary, and (d) the latency to enter the playback aviary, by song playback type and time within breeding season.

season (relative to zoo-bred song type, control songs $\beta = 0.64$ se $= 0.07$, $p \leq 0.001$, wild songs $\beta = 0.72$, se $= 0.04$, $p \leq 0.001$). In the late breeding season females' latency to approach the speaker was shorter in response to zoo-bred songs than both control and wild songs, however, this was only significant compared with control songs (relative to zoo-bred song type, control songs $\beta = 0.36$, se $= 0.10$, $p \leq 0.001$, wild songs $\beta = 0.003$, se $= 0.10$, $p = 0.10$). Latency did not differ significantly within groups for any song type between early season and late season (Fig. 4d, Table S7). The interaction between 'time in season' and 'song type' was significant ($\chi^2 = 52.96$, df $= 3$, $p \leq 0.001$, Table S6).

3.5. Negative association

Negative time indicates the time spent in the aviary opposite the playback aviary. We include it to show that the bird may move from its initial position in the central aviary to another aviary without being directly influenced by playback. It sets a benchmark to compare females' response to playback with. For females that entered the non-playback outer aviary, song type was a significant predictor of the amount of time spent in the non-playback outer aviary ($\chi^2 = 159.74$, df $= 2$, $p \leq 0.001$). Females that entered the non-playback outer aivary spent significantly less time during the zoo-type playbacks than during the control and wild playbacks in the early season (relative to zoo-bred songs, control songs $\beta = 0.47$, se $= 0.06$, $p \leq 0.001$, wild songs $\beta = 0.51$, se $= 0.04$, $p \leq 0.001$, Fig. 4c). In the late season, there were no significant differences in the amount of time spent in the non-playback outer aviary (relative to zoo-bred songs, control songs $\beta = -0.30$, se $= 0.11$, $p = 0.11$, wild songs $\beta = -0.55$ se $= 0.12$, $p \leq 0.001$). The interaction of time in season and treatment was significant ($\chi^2 = 50.12$, df $= 3$, $p \leq 0.001$).

4. Discussion

Understanding the fitness consequences of captivity on individual animals bred for release into the wild is critical to the success of ex-situ conservation efforts (Baskett and Waples, 2013; Crates et al., 2022). Using a rigorous experimental protocol within an applied zoo breeding environment, we demonstrated that female regent honeyeaters were no more likely to enter an aviary containing playback of the familiar songs of zoo-bred males than the unfamiliar songs of wild regent honeyeaters or an interspecific control. However, of those individuals that did enter the playback aviary, females spent a longer time in the aviary and were more likely to approach to within 1 m of the playback speaker in response to familiar, zoo-bred males' songs than unfamiliar wild males' songs or the songs of an interspecific control. This is the first demonstration that female zoo-bred birds prefer familiar but abnormal songs from the captive environment to those of a wild counterpart. We conclude that assortative mating based on a preference for familiar song dialects is a risk for the regent honeyeater zoo-breeding program, with potentially negative consequences for reintroduction efforts. However further work is required post-release to better quantify these risks. Our study adds to the growing body of literature exploring potential fitness consequences of divergent cultural norms between wild and zoo-bred populations in conservation programs (Lewis et al., 2020; Crates et al., 2022). Here we discuss the implications of our findings for adaptive management of zoo-bred populations.

Playback studies have the difficult task of interpreting the meaning of the female's behaviour (Fujii et al., 2022). Our results showed a significant difference in the probability of females entering the playback aviary in response to the familiar, zoo-bred songs compared with the control but not to the unfamiliar, wild song type. While the individual responses were inconsistent, 16/18 females responded to zoo-bred playback in at least one of the presentations of playback. There are at least two possible explanations for this. First, a female could enter the playback aviary at any time during the trial, not just when the playback was being broadcast. As such, an approach could be misinterpreted as interest in the song when the motivation for entering the aviary could be related to other factors. The probability of entering the non-playback outer aviary was lower but comparable across song types suggesting that bird movements can be independent of broadcasted playback. Second, some females may have had a greater interest in visiting the feeder in the neutral aviary than in responding to playback, thereby weakening any effect of preferences for song types.

Arguably, more meaningful measures of preference than entry to the playback aviary are the amount of time spent in the playback aviary and the probability of approaching the speaker closely. The amount of time spent associating with a potential mate has been shown to be a reliable indicator of mate preference in birds (Witte, 2006). We found that females spent a significantly greater amount of time in the playback aviary, and were more likely to approach the speaker closely, in response to familiar, zoo-bred songs than either wild songs, or those of another species, regardless of the time within the season. We included close association time (time spent within one metre of the speaker) as a clearer indication of female response due to the separation of the speakers from the vegetated areas elsewhere in the aviary and the direct investigation of the source of sound. Close association time was also significantly greater in response to familiar songs than unfamiliar ones. Latency to respond is also a consistent indicator of behavioural response in passerine birds (Freeman and Montgomery, 2017; Vargas-Puentes et al., 2021). Our results showed that the latency to approach the playback aviary was significantly shorter in response to familiar, zoo-bred songs than unfamiliar ones. We included negative association time, not as a direct measure of interest but to demonstrate the nature of movement in the experimental aviary and the amount of time spent in an area with no playback. Our results demonstrated that birds spent a similar overall amount of time in the non-playback outer aviary as in the playback aviary in response to wild and control type songs. In response to familiar songs, birds spent less time in the non-playback outer aviary than when they were exposed to the unfamiliar song types.

The two clearest indicators of response, close association time and latency, were the same or stronger in the early breeding season, while association time was greater in the late breeding season (Fig. 4). The early breeding season represented experiments undertaken in late June. At this time zoo-bred birds are observed attempting to form pairs and collecting nesting material (pers comm.). The late season represented the experiments undertaken in January, a time when birds may be underway with a second or third clutch, potentially with a new partner (Geering and French, 1998). At this time wild regent honeyeaters may also have finished breeding and be gathering in post breeding flocks. Thus, some females may have been less motivated to seek out mates at this time, either because of the limited time remaining for breeding and/or because of hormonal changes as breeding winds down (Maney et al., 2008). Further, although females spent longer in the playback aviary than the non-playback outer aviary during the late breeding season, they did not necessarily investigate the speaker. This may have been a function of the increased temperature at this time of year, leading to a trade-off between activity and temperature regulation (Pattinson et al., 2020). Although familiar songs resulted in significantly less negative association time than unfamiliar songs in the early season, this was the not the case in the late season. Combined with the fact that negative time was lower in the early breeding season for all song types suggests if interest in the playback stimulus is lower in the late breeding season then bird movements may be independent of the playback stimulus. Alternatively, this may reflect the smaller sample size of females assayed later in the breeding season.

In tandem with the wider regent honeyeater literature, our study suggests that variations in song dialects and associated differences in female familiarity with these dialects could contribute to assortative mating based on song type in this species. The results from our study are consistent with Crates et al. (2021) who demonstrated that wild males that sang songs different to the regional cultural norm were less likely to be paired with a female, and those that did pair were significantly less likely to build nests that reached the egg stage. Further, both sexes showed a higher propensity to survive post-release when exposed to song-tutoring (Tripovich et al., 2021). Our results may also help to explain the rarity of pairings between released zoo-bred birds and wild birds, despite releases taking place within known breeding areas (Ingwersen, 2014; Kvistad et al., 2015). None of these observations show that song differences alone are responsible for the lack of breeding success. Birds with non-locally conforming songs in Crates' study were often isolated from other birds, and as such may have had limited opportunities to attract females. Likewise, the lack of zoo-bred male – wild female pairs after release may be due to a paucity of females at release sites or be influenced by differences between zoo-bred and wild males in other sexual signals such as plumage, ornamentation or physical condition (Burley, 1981; Candolin, 2003; Wang et al., 2022). However, even amongst paired males, those with an abnormal song were significantly less likely to initiate nesting, suggesting that song abnormalities could carry a fitness cost (Crates et al., 2021).

Similar to other studies (Fujii et al., 2022; O'Loghlen and Beecher, 1997; Vargas-Puentes et al., 2021), our results show that female responses to male vocal stimuli were not limited exclusively to familiar songs but were significantly stronger than to unfamiliar ones. The evidence of wild females pairing with males who sing non-local songs, and zoo-bred birds pairing with wild birds suggests that abnormal song is not an absolute barrier to pairing. Despite this, aberrant song may still have fitness consequences for released birds. Females constrained to non-preferred partners by a lack of choice due to small population size or low population density may experience deleterious effects to both their physical condition and to the success of the breeding effort (Griffith et al., 2011). This appears to be consistent with Crates et al. (2021) who

showed that aberrant song was not an absolute barrier to pairing, but it did result in significantly lower likelihood of producing a nest that reached the egg stage.

Our study provides evidence that females prefer to associate with males that sing familiar songs, suggesting that they may be more likely to pair with these males than those that sing unfamiliar songs. Assortative mating is likely to inhibit gene flow that is pivotal in the conservation of critically endangered species (Slade et al., 2014) and has the potential to reduce the overall number of birds forming pairs and hence the number of offspring produced. If dialect differences inhibit released birds from integrating into established flocks, the experience of wild birds is unlikely to be conferred to re-introduced birds (Kleiman, 1989), which models show will compromise the capacity of zoo-bred birds to population recovery post-release (Heinsohn et al., 2022).

Considering the song differences between wild and zoo-bred birds, we have now implemented a song tutoring program at Taronga Zoo that exposes young birds to the songs of wild males with the aim of improving post-release outcomes. Our study has important implications for adaptive management of the zoo-breeding program, highlighting the importance of exposing not only males, but also females, to wild-type songs given the evidence that courtship preferences in birds can be shaped by juvenile auditory experiences (Chen et al., 2017). Secondly, it reinforces the need to release females in places and at times they can gain rapid exposure to wild males and their songs prior to the breeding season. More broadly, our study shows the importance of the potential, but often-overlooked fitness consequences of cultural isolation in zoo-breeding settings (Brakes et al., 2019). The initial implementation of the regent honeyeater breeding program aimed to understand husbandry requirements and consequently began with a small number of nestling wild founders and implemented hand-rearing (Liu et al., 2014). This prevented crucial social learning of wild song dialects from the commencement of the breeding program, which has influenced the song culture of all successive generations. The selection of founders for ex-situ conservation programs must consider not only their life-stage but also their behavioural competency/diversity. Programs must also be designed to maintain these traits across generations and facilities. Conservation breeding programs must strive to consider socially learned behaviours in their management of species.

Small scale behavioural experiments are rarely a priority in zoo-breeding programs (Kemp et al., 2015) as limited resources are often directed toward husbandry and breeding outcomes. However, it is increasingly acknowledged that the phenotypic quality of zoo-bred animals is as important as their quantity in determining the success of reintroductions (Crates et al., 2022). Despite the limitations of working on critically endangered species amongst a raft of research and conservation priorities, our study demonstrates that carefully planned experiments can be incorporated into husbandry practices with minimal inconvenience. We suggest such experiments should be considered an essential part of reintroduction programs, as they can inform the adaptive management of husbandry and release protocols to increase the fitness of zoo-bred animals and thereby the success of ex-situ conservation more broadly.

CRediT authorship contribution statement

DA-Experimental design (lead), experiments (lead), data curation (equal), formal analysis (equal), first draft (lead), final manuscript (equal.

RC – experiments (supporting), data curation (equal), formal Analysis (equal), final manuscript (equal) NL – Experimental design (equal), final manuscript (equal).

RH- Final manuscript (equal), supervision.

JT. Experimental design (supporting), final manuscript (supporting) BP. Experimental design (supporting), final Manuscript (supporting).

Funding

DA received funding from Holsworth Wildlife Research Endowment 2021, and the Cumberland Bird Observers Club. JT and BP received funding from Winifred Violet Scott Charitable Trust. Regent Honeyeater research at Taronga Conservation Society is supported by the Commonwealth of Australia Department of Climate Change, Energy, the Environment and Water grant "Expansion and Capacity Building in Recovery of Critically Endangered Regent Honeyeater and Bellinger River Snapping Turtle (ERF-WRR2-017-018).

Declaration of competing interest

The authors declare no competing interests.

Data availability

Data will be made available on request.

Acknowledgments

We thank Taronga Zoo, and Taronga Western Plains Zoo for accommodating the study. We thank all husbandry staff for their assistance leading up to and during experiments. Thanks go to Richard Matkovics for information on the background of the zoo breeding program, to Emily Schmelitshek for help in determining suitable individuals for the experiment and to Kara Stevens and Greig Tonkins for help in delivering the experiments. We thank Liam Murphy and Alistair Wells for assistance in conducting the experiments.

Ethics statement

All experiments were conducted in accordance with Taronga Zoo Ethics approval #4a/02/20.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2023.110171.

References

Araki, H., Cooper, B., Blouin, M.S., 2009. Carry-over effect of captive breeding reduces reproductive fitness of wild-born descendants in the wild. Biol. Lett. 5 (5), 621–624. https://doi.org/10.1098/rsbl.2009.0315.

Baskett, M.L., Waples, R.S., 2013. Evaluating alternative strategies for minimizing unintended fitness consequences of cultured individuals on wild populations. Conserv. Biol. 27 (1), 83–94. https://doi.org/10.1111/j.1523-1739.2012.01949.x.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67 (1), 1–48. https://doi.org/10.18637/jss.v067.i01.

Beecher, M.D., Burt, J.M., O'Loghlen, A.L., Templeton, C.N., Campbell, S.E., 2007. Bird song learning in an eavesdropping context. Anim. Behav. 73 (6), 929–935. https://doi.org/10.1016/j.anbehav.2006.10.013.

Brakes, P., Dall, S.R.X., Aplin, L.M., Bearhop, S., Carroll, E.L., Ciucci, P., Fishlock, V., Ford, J.K.B., Garland, E.C., Keith, S.A., McGregor, P.K., Mesnick, S.L., Noad, M.J., Notarbartolo di Sciara, G., Robbins, M.M., Simmonds, M.P., Spina, F., Thornton, A., Wade, P.R., Rutz, C., 2019. Animal cultures matter for conservation. Science 363 (6431), 1032–1034. https://doi.org/10.1126/science.aaw3557.

Brakes, P., Carroll, E.L., Dall, S.R., Keith, S.A., McGregor, P.K., Mesnick, S.L., Garland, E. C., 2021. A deepening understanding of animal culture suggests lessons for conservation. Proc. R. Soc. B 288 (1949), 20202718.

Brooks, M.E., Kristensen, K., Van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Maechler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J. 2017; 9: 378–400. R Journal 9 (2), 378–400 (doi:doi: 10.32614).

Burley, N., 1981. Mate choice by multiple criteria in a monogamous species. Am. Nat. 117, 515–528. https://doi.org/10.1086/283732.

Candolin, U., 2003. The use of multiple cues in mate choice. Biol. Rev. 78 (4), 575–595. https://doi.org/10.1017/S1464793103006158.

Catchpole, C.K., Slater, P.J.B., 2008. Bird Song: Biological Themes and Variations, second edition. Cambridge University Press. https://doi.org/10.1017/CBO9780511754791.

Chen, Y., Clark, O., Woolley, S., 2017. Courtship song preferences in female zebra finches are shaped by developmental auditory experience. Proc. R. Soc. *B*.284 (2017005420170054).
Commonwealth of Australia, 2016. National Recovery Plan for the Regent Honeyeater *(Anthochaera phrygia)*.
Crates, R., Langmore, N.E., Ranjard, L., Stojanovic, D., Rayner, L., Ingwersen, D., Heinsohn, R., 2021. Loss of vocal culture and fitness costs in a critically endangered songbird. Proc. R. Soc. B Biol. Sci. 288 (1947), 20210225. https://doi.org/10.1098/rspb.2021.0225.
Crates, R., Stojanovic, D., Heinsohn, R., 2022. The phenotypic costs of captivity. Biol. Rev. https://doi.org/10.1111/brv.12913.
Dunning, J.L., Pant, S., Bass, A., Coburn, Z., Prather, J.F., 2014. Mate choice in adult female Bengalese finches: females express consistent preferences for individual males and prefer female-directed song performances. PLoS One 9 (2), e89438. https://doi.org/10.1371/journal.pone.0089438.
Ewen, J.G., Armstrong, D.P., 2007. Strategic monitoring of reintroductions in ecological restoration programmes. Ecoscience 14 (4), 401–409. https://doi.org/10.2980/1195-6860(2007)14[401:SMORIE]2.0.CO;2.
Fischer, J., Lindenmayer, D.B., 2000. An assessment of the published results of animal relocations. In: Biological Conservation, Vol. 96, pp. 1–11.
Frankham, R., 2008. Genetic adaptation to captivity in species conservation programs. In: Molecular Ecology, Vol. 17, pp. 325–333.
Frankham, R., 2010. Challenges and opportunities of genetic approaches to biological conservation. Biol. Conserv. 143 (9), 1919–1927. https://doi.org/10.1016/j.biocon.2010.05.011.
Fraser, D.J., 2008. How well can captive breeding programs conserve biodiversity? A review of salmonids. Evol. Appl. 1 (4), 535–586. https://doi.org/10.1111/j.1752-4571.2008.00036.x.
Freeman, B.G., Montgomery, G.A., 2017. Using song playback experiments to measure species recognition between geographically isolated populations: a comparison with acoustic trait analyses. Auk Ornithol. Adv. 134 (4), 857–870.
Fujii, T.G., Coulter, A., Lawley, K.S., Prather, J.F., Okanoya, K., 2022. Song preference in female and juvenile songbirds: proximate and ultimate questions. Front. Physiol. 13, 876205 https://doi.org/10.3389/FPHYS.2022.876205/BIBTEX.
Garnett, S.T., Baker, G.B. (Eds.), 2021. The Action Plan for Australian Birds. CSIRO publishing.
Geering, D., French, K., 1998. Breeding biology of the regent honeyeater Xanthomyza phrygia in the Capertee Valley, New South Wales. Emu - Austral Ornithol. 98 (2), 104–116. https://doi.org/10.1071/MU98011.
Greggor, A.L., Vicino, G.A., Swaisgood, R.R., Fidgett, A., Brenner, D., Kinney, M.E., Farabaugh, S., Masuda, B., Lamberski, N., 2018. Animal welfare in conservation breeding: applications and challenges [perspective]. Front. Vet. Sci. 5 https://doi.org/10.3389/fvets.2018.00323.
Griffith, S.C., Pryke, S.R., Buttemer, W.A., 2011. Constrained mate choice in social monogamy and the stress of having an unattractive partner. Proc. R. Soc. B Biol. Sci. 278 (1719), 2798–2805.
Heinsohn, R., Lacy, R., Elphinstone, A., Ingwersen, D., Pitcher, B.J., Roderick, M., Schmelitschek, E., Van Sluys, M., Stojanovic, D., Tripovich, J., Crates, R., 2022. Population viability in data deficient nomadic species: what it will take to save regent honeyeaters from extinction. Biol. Conserv. 266 https://doi.org/10.1016/j.biocon.2021.109430.
Ingwersen, D., 2014. Regent theatre: on the trail of one of Australia's rarest honeyeaters. Aust. Birdlife 3, 21–23. https://doi.org/10.1121/1.4782590.
Jiang, Y., Bolnick, D.I., Kirkpatrick, M., 2013. Assortative mating in animals. Source Am. Nat. 181 (6), 125–138. https://doi.org/10.1086/670160.
Kemp, L., G, N., R, G., Comer, S., 2015. The Roles of Trials and Experiments in Fauna Reintroduction Programs, pp. 73–89.
Kingsford, R.T., Watson, J.E.M., Lundquist, C.J., Venter, O., Hughes, L., Johnston, E.L., Atherton, J., Gawel, M., Keith, D.A., MacKey, B.G., Morley, C., Possingham, H.P., Raynor, B., Recher, H.F., Wilson, K.A., 2009. Major conservation policy issues for biodiversity in oceania. Conserv. Biol. 23 (4), 834–840. https://doi.org/10.1111/j.1523-1739.2009.01287.x.
Kleiman, D.G., 1989. Reintroduction of captive mammals for conservation: guidelines for reintroducing endangered species into the wild. BioScience 39 (3), 152–161. https://doi.org/10.2307/1311025.
Kvistad, L., Ingwersen, D., Pavlova, A., Bull, J.K., Sunnucks, P., 2015. Very low population structure in a highly mobile and wide-ranging endangered bird species. PLoS One 10 (12). https://doi.org/10.1371/journal.pone.0143746.
Laiolo, P., Tella, J.L., 2007. Erosion of animal cultures in fragmented landscapes. Front. Ecol. Environ. 5 (2), 68–72. https://doi.org/10.1890/1540-9295(2007)5[68:EOACIF]2.0.CO;2.
Lewis, R., Williams, L., Gilman, R., 2020. The uses and implications of avian vocalizations for conservation planning. Conserv. Biol. 35 https://doi.org/10.1111/cobi.13465.
Liu, S.C., Gillespie, J., Atchison, N., Andrew, P., 2014. Australia: regent honeyeater conservation collaboration. Int. Zoo Yb. 48, 83–91. https://doi.org/10.1111/izy.12040.
Maney, D.L., Goode, C.T., Lange, H.S., Sanford, S.E., Solomon, B.L., 2008. Estradiol modulates neural responses to song in a seasonal songbird [doi:10.1002/cne.21830]. J. Comp. Neurol. 511 (2), 173–186. https://doi.org/10.1002/cne.21830.
McPhee, M.E., 2004. Generations in captivity increases behavioral variance: considerations for captive breeding and reintroduction programs. Biol. Conserv. 115 (1), 71–77. https://doi.org/10.1016/S0006-3207(03)00095-8.
O'Loghlen, A.L., Beecher, M.D., 1997. Sexual preferences for mate song types in female song sparrows. Anim. Behav. 53 (4), 835–841. https://doi.org/10.1006/anbe.1996.0348.
Pattinson, N.B., Thompson, M.L., Griego, M., Russell, G., Mitchell, N.J., Martin, R.O., Wolf, B.O., Smit, B., Cunningham, S.J., McKechnie, A.E., Hockey, P.A.R., 2020. Heat dissipation behaviour of birds in seasonally hot arid-zones: are there global patterns? [doi:10.1111/jav.02350]. J. Avian Biol. 51 (2) https://doi.org/10.1111/jav.02350.
Paxton, K.L., Sebastián-González, E., Hite, J.M., Crampton, L.H., Kuhn, D., Hart, P.J., 2019. Loss of cultural song diversity and the convergence of songs in a declining Hawaiian forest bird community. R. Soc. Open Sci. 6 (8) https://doi.org/10.1098/rsos.190719.
Planqué, R., Britton, N.F., Slabbekoorn, H., 2014. On the maintenance of bird song dialects. J. Math. Biol. 68, 505–531. https://doi.org/10.1007/s00285-012-0632-8.
Powys, Vicki., 2010. Regent honeyeaters mapping their movements through song. Corella 34, 92–102.
R Core Team, 2020. R: A Language and Environment for Statistical Computing. In R Foundation for Statistical Computing. https://www.R-project.org/.
Rahbek, C., 1993. Captive breeding-a useful tool in the preservation of biodiversity? Biodivers. Conserv. 2 (4), 426–437. https://doi.org/10.1007/BF00114044.
Rendell, L., Whitehead, H., 2001. Culture in whales and dolphins. Behav. Brain Sci. 24 (2), 309–324. https://doi.org/10.1017/S0140525X0100396X.
Robinson, N. M., Dexter, N., Brewster, R., Maple, D., MacGregor, C., Rose, K., Hall, J., & Lindenmayer, D. B. (2020). Be nimble with threat mitigation: lessons learned from the reintroduction of an endangered species. In *restoration ecology* (Vol. 28, pp. 29-38).
Rutz, C., Klump, B.C., Komarczyk, L., Leighton, R., Kramer, J., Wischnewski, S., Sugasawa, S., Morrissey, M.B., James, R., St Clair, J.J.H., Switzer, R.A., Masuda, B. M., 2016. Discovery of species-wide tool use in the Hawaiian crow. Nature 537 (7620), 403–407. https://doi.org/10.1038/nature19103.
Seddon, P.J., Griffiths, C.J., Soorae, P.S., Armstrong, D.P., 2014. Reversing defaunation: restoring species in a changing world. Science 345 (6195), 406–412. https://doi.org/10.1111/1365-2664.12256.
Sheean, V.A., Manning, A.D., Lindenmayer, D.B., 2012. An assessment of scientific approaches towards species relocations in Australia. Aust. Ecol. 37 (2), 204–215. https://doi.org/10.1111/j.1442-9993.2011.02264.x.
Slade, B., Parrott, M.L., Paproth, A., Magrath, M.J.L., Gillespie, G.R., Jessop, T.S., 2014. Assortative mating among animals of captive and wild origin following experimental conservation releases. Biol. Lett. 10 (11), 20140656. https://doi.org/10.1098/rsbl.2014.0656.
Taylor, G., Ewen, J.G., Clarke, R.H., Blackburn, T.M., Johnson, G., Ingwersen, D., 2018. Video monitoring reveals novel threat to critically endangered captive-bred and released regent honeyeaters. Emu-Austral Ornithol. 118 (3), 304–310.
Tripovich, J.S., Popovic, G., Elphinstone, A., Ingwersen, D., Johnson, G., Schmelitschek, E., Wilkin, D., Taylor, G., Pitcher, B.J., 2021. Born to be wild: evaluating the zoo-based regent honeyeater breed for release program to optimise individual success and conservation outcomes in the wild. Front. Conserv. Sci. 2 https://doi.org/10.3389/fcosc.2021.669563.
Vargas-Puentes, J.A., Arias-Sosa, L.A., Ramos-Montaño, C., 2021. Song divergence indicates an unclear relationship between the Neotropical and Nearctic Horned Larks. Avian Res. 12 (1), 16. https://doi.org/10.1186/s40657-021-00251-y.
Wang, D.P., Forstmeier, W., Farine, D.R., Maldonado-Chaparro, A.A., Martin, K., Pei, Y. F., Alarcon-Nieto, G., Klarevas-Irby, J.A., Ma, S.W., Aplin, L.M., Kempenaers, B., 2022. Machine learning reveals cryptic dialects that explain mate choice in a songbird. Nat. Commun. 13 (1) (doi:ARTN 1630 10.1038/s41467-022-28881-w).
Whiten, A., 2021. The burgeoning reach of animal culture. In: Science, vol. 372. American Association for the Advancement of Science.
Witte, K. (2006). Time spent with a male is a good indicator of mate preference in female zebra finches. *Ethology Ecology & Evolution*, 18(3), 195–204. doi:https://doi.org/10.1080/08927014.2006.9522707.