

Juvenile song learning in regent honeyeaters, *Anthochaera phrygia*, at Taronga Zoo, Australia.



by

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Thesis

Presented to the Faculty of Science, Department of Biological Sciences

Macquarie University, Sydney, NSW Australia

in partial fulfilment of the requirements for the degree of

Master of Research.

9th October 2015

To the examiners,

The style and formatting of this thesis has been written according to the author guidelines for a journal article from the Journal of Avian Biology. Deviations from this journal style are in accordance with the Macquarie University Masters of Research thesis guidelines.

Declaration

I certify that the research presented in this thesis is my original work. However this research could not have been undertaken without the highly appreciated assistance of my supervisor K-lynn Smith. K-lynn Smith assisted with experimental design, data collection, data analysis, interpretation and provided feedback on the introduction, methods, and results sections, but did not have access to the discussion section. Bernard Lohr provided feedback on the discussion section. Drew Allen also assisted with the statistical analysis.

This work has not been presented for a higher degree to any other university or institution, and contains no material previously published or written by any other person except where due reference is made in the text.

A handwritten signature in black ink, appearing to read 'Michelle Vecsei', with a stylized, cursive script.

Michelle Vecsei

Acknowledgments

First and foremost I would like to thank my supervisor, K-lynn Smith, for all her support throughout this project and for her valuable expertise in helping me to complete it. This project would not have been possible without her. I would like to thank all the people in the Bird Department at Taronga Zoo, NSW Australia including Michael Shiels, Nick Boyle, Dave Wilkin, Katy Horsinburgh, Mark Domenici and Sonia Fisher Dobin for their cooperation needed to undertake this project and assistance in accessing aviaries. Also, thank you to Corrine Symons of Taronga Zoo for providing the title page photo.

The statistical analysis of this research would not have been possible without K-lynn Smith and Drew Allen. Thank you to Bernard Lohr for valuable feedback on this project. I would also like to thank my family and friends for their constant support throughout the many stressful hours spread out over this 8 month project, especially Ron Vecsei, Kim Vecsei, James Vecsei, Sue Gumley and Zenta Staley. Lastly I want to thank the Department of Biological Sciences at Macquarie University for providing the funding for my thesis.

Abstract

Songbirds show tremendous variation in when, how and from whom they learn their songs. Song learning may involve directly imitating another bird, known as a tutor, or may involve the recombination of song elements from multiple tutors. This study investigated song learning in a captive population of a critically endangered bird, the regent honeyeater, *Anthochaera phrygia*, at Taronga Zoo, NSW. The aim of this study was to add to the limited body of knowledge of song learning within the honeyeater family and provide valuable information that may assist with the regent honeyeater recovery program. Twenty-nine related and unrelated birds were recorded and the most common song types were selected for song similarity analysis. Song similarity was assessed using dynamic time warping followed by cluster analysis to determine which birds produced similar song types. The results revealed wide variation in tutor selection by juveniles, with 78% singing similar songs to multiple tutors. Song types produced included songs from tutors with which the juveniles had direct social interaction, as well as ones in which they were only able to hear. This suggests that social experience is important but not essential for song learning in this species. This study is the first to investigate song learning in regent honeyeaters.

Key words: birds; regent honeyeater; *Anthochaera phrygia*; song learning; birdsong; tutor

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1. INTRODUCTION

Many species of animals use vocalisations to communicate, but only a subset of these must learn their signals. Of these, songbirds (oscines) are one of the most intensely studied, second only to humans. More than 50 years of research on songbirds has uncovered many parallels between song learning in birds and speech learning in humans (Slater 2003). Parallels include; early sensitive learning periods, learning by imitation of an adult model, a dependence of vocal behaviour on auditory feedback and lateralisation in vocal processing brain regions (Woolley 2012). Many other parallels exist between human and songbird vocal learning, consequently song learning in birds has become the model system for exploring the evolution of vocal learning (Brainard and Doupe 2002). Further exploration into song learning in birds may subsequently expand knowledge regarding the evolution of human vocal learning.

There is tremendous diversity in the song learning programs between species of birds. Differences have been clearly demonstrated in regard to when, how and from whom birds learn their songs (Brenowitz and Beecher 2005). These differences are often related to the life-history traits of the species (e.g. sedentary or migratory, territorial or colonial breeding; Catchpole and Slater 2008) but there is still controversy over the general patterns of song learning programs.

Song learning has also received much attention because of its importance in avian ecology. Male song can serve many functions including individual identification, species recognition, inter-sexual signalling (e.g. female attraction; Bensch and Hasselquist 1992) and intra-sexual signalling (e.g. territorial defence; Nowicki and Searcy 2014). Song types may also vary from region to region within a species (Marler and Tamura 1964; Mundinger 1982), which can affect dispersal, mate choice and male-male interactions (see Baker and Cunningham 1985 for review).

Understanding the song learning program of a specific species is hence relevant for conservation and management programs. It may be particularly important for captive breeding and release programs where the primary goal is to rear and release fully-competent individuals into the wild (Whitehead 2010).

1.1 WHEN DO BIRDS LEARN?

It has long been accepted that timing plays an important role in song learning among birds. This notion arose from the observations that the majority of songbird species do not begin life with the ability to sing perfectly, but rather progress along a development path over time eventually

producing their species specific song (Catchpole and Slater 2008). Male chaffinches (*Fringilla coelebs*), for example, hatch between May and July but do not start to sing their adult song until approximately seven to eight months later when they begin their first breeding season (Riebel et al. 2015). Consequently, early research focused on investigating when exactly young birds were learning their song.

Thorpe (1958) was the first to show that the song an adult chaffinch produced was a clear copy of the song it heard during a particular time during development. This was demonstrated by varying systematically the acoustic environment of young birds, including their exposure and their timing of experience with different recorded adult songs (Thorpe 1958). Based on such work, Marler (1970) proposed the original model of song learning, which involved an adult bird instructing a young bird on how to sing. Fundamental to this instruction-based model was that there is a specific timeline in which birds learn how to sing. This model suggests that soon after hatching young birds begin a process of song learning that can be divided into two distinct phases, sensory acquisition and sensorimotor learning (Marler 1997). The initial sensory acquisition phase occurs in a bird's natal summer and involves listening to and memorising the song of an adult bird, known as a tutor. This model proposes that songbirds have an innate template that biases birds to learn from conspecifics. The following sensorimotor phase is defined by song production, where the young bird attempts to match its vocal output to what was memorised. This phase begins with a period of quiet and highly variable practice vocalisations, known as subsong (Marler 1997). Vocalisations then become louder and more structured, in a period known as plastic song. The final outcome of the sensorimotor phase is the production of a stable adult song, known as song crystallisation (Marler 1997). While comparative studies have revealed the learning timeline of many songbirds do generally fit this model, many species deviate from it in certain aspects (Brenowitz and Beecher, 2005). For example, many species, such as village indigobirds (*Vidua chalybeate*) do not show a stable crystallized song but instead change their song as adults (Payne 1985). In addition, many species overproduce songs in the plastic phase to eventually select a particular song or repertoire of songs (Nelson 1996, 2000). This selection behaviour is explained by the selection-based model which proposes young birds hear and memorise many more songs than they will produce as an adult (Nelson 1996, 2000).

Evidence that learning is occurring at certain times is provided by isolation and deafening experiments. When young birds are acoustically isolated or deafened, thereby denying them access to appropriate tutors, the majority of songbirds will produce abnormal adult song (Konishi 1965; Baptista and Petrinovich 1984). For example, white-crowned sparrows (*Zonotrichia leucophrys*)

isolated or deafened during the sensory phase produce deficient song, whereas birds subjected to these treatments after crystallisation sing normally (Marler 1970).

There are three general types of song learning programs: age-limited, young adult and open-ended (Beecher and Brenowitz 2005). Age-limited or sensitive period learners learn their songs within an early sensitive period (Marler and Peters 1987), which varies from species to species. For example, experimental manipulations revealed that white-crown sparrows only produce a song if it is heard before 100 days of age (Marler 1970) whereas zebra finches (*Taeniopygia guttata*) produce songs heard between 20 and 65 days of age (Eales 1985; Riebel 2009). Alternatively, other species have been shown to learn throughout their entire first year of life, including the chaffinch (Lachlan and Slater 2003), and the indigo bunting, *Passerina cyanea* (Beecher and Brenowitz, 2005; Margoliash et al. 1994). Finally, open-ended learners are capable of song learning throughout their lifetimes (Beecher and Brenowitz 2005). This learning may occur at any time or be restricted to a series of sensitive learning periods throughout a birds life. Examples include the village indigobird (Payne 1985), great tit, *Parus major* (McGregor and Krebs 1989), willow warbler, *Phylloscopus trochilus* (Gil et al. 2001), Canary, *Serinus canaria* (Nottebohm et al. 1987) and European starlings, *Sturnus Vulgaris* (Chaiken et al. 1994). Often open-ended learners do not sing new songs throughout the year, but rather change songs each season, and thus are referred to as seasonal learners (Catchpole and Slater 2008). Canaries, for example, sing highly variable songs in winter and then will produce a stable song each spring that incorporates new song elements (song elements are the smallest units of song and can be defined as a continuous line on a sonogram) (Nottebohm et al. 1987). This seasonal pattern in song learning has been shown to vary with changes in testosterone, indicating sex hormones may influence the timing of song learning (Schlinger 1997). One problematic issue regarding the timing of learning is the difficulty in determining from field studies of life-long learners whether songs are developed from imitating new tutors or involve producing previously memorised songs (Brenowitz and Beecher 2005). Another issue concerns the validity of numerous studies suggesting species are age-limited learners when long-term observation has not occurred and thus production of new songs cannot be ruled out (Beecher and Brenowitz 2005).

Why song learning occurs at different times for different species is not well understood. Research exploring why there is such wide variation in song learning programs is only in its early stages but some suggest that this variation may relate to differences in life-history traits (Catchpole and Slater 2008). For example, age-limited learners may learn songs early because it is adaptive to learn their songs before they disperse from natal territories. Sharing songs between natal neighbours who settle and breed in the same area may be beneficial because it avoids the break-up of co-adapted genes and favours the development of adaptations to the local habitat and social environment (Catchpole

and Slater 2008). Specifically, song learning may occur early because of the important function natal song plays in mate attraction. Danner et al. (2011) showed female rufous-collared sparrows (*Zonotrichia capensis*) prefer males who sing their natal song dialect to the dialect of a foreign population only 25km away. Therefore some species may learn their species specific song before dispersal to facilitate assortative mating based on natal song dialects (Danner et al 2011). Conversely, it may be beneficial for open-ended learners to continuing learning songs after dispersal from natal territories because a preference for natal dialects in mate selection is non-adaptive and/or they benefit more by matching songs with changing non-natal neighbours (Nelson et al. 2001).

1.2 HOW DO BIRDS LEARN?

Songbird species also show wide variation in how they learn to sing. This variation is reflected in the extent to which a song is copied from a tutor and can be separated into three strategies: imitation, improvisation and invention (Janik and Slater 2000; Hughes et al. 2002). Early research suggests that the majority of birds learn their species specific song through a process of imitation whereby a song is closely copied from a tutor (Hughes et al. 2002). Early experimental studies by Thorpe (1958) and Marler (1952) showed that hand-reared chaffinches faithfully imitate the recorded song of a conspecific tutor. Single male zebra finch juveniles raised alone with one adult male tutor will also produce a near perfect copy (Tchernichovski and Nottebohm 1998). Further evidence that imitation is a common song learning strategy comes from the abundance of species that exhibit song dialects (Podos and Warren 2007). Song dialects are characterised by geographically separated neighbourhoods of birds singing more similar songs to each other than to members of different neighbourhoods (Baker and Cunningham 1985). Song dialects can therefore be viewed as a direct consequence of species utilising an imitation strategy. Lemon (1975) suggests species displaying dialects relative to distance is a result of copying errors made after dispersing to new territories. Many songbird species display dialects including white-crowned sparrows (Marler 1970), brown-headed cowbirds, *Molothrus ater* (Rothstein and Fleischer 1987) and bronzed cowbirds, *Molothrus aeneus* (Warren and Nelson 2002).

The adaptive significance of song learning through imitation can be explained by the sharing hypothesis (Beecher and Brenowitz 2005). The sharing hypothesis suggests that the goal of an imitation based strategy is song sharing, as it is believed to increase reproductive success by facilitating communicative interactions between songbirds within a particular neighbourhood (Lachlan et al. 2004). Research by Payne and Payne (1997) revealed that young indigo buntings that

share more similar songs with older neighbours were more successful in gaining a territory, finding a mate and producing offspring, than birds that sang different songs.

While it is undisputed that imitation plays a large role in song learning, further research has revealed that the majority of species rarely produce perfect imitations in the wild (Goodwin 2008). Instead many species use improvisation strategies in combination with imitation to learn their song (Tchernichoski and Marcus 2014). Improvisation can be defined as the production of a song that resembles a tutor song, rather than being an exact copy (Beecher and Brenowitz 2005). Specifically improvisation can arise by copying song themes from a tutor and adding new features, or rearranging the acoustic elements of a tutor/s song to create a unique song (Marler and Peters 1982). For example, Marler (1981) reported that song sparrows (*Melospiza melodia*) tutored by multiple models often produced a song that appeared as a collage of repeating small song units (syllables) from different birds.

The use of improvisation in song learning is thought to be adaptive as it provides birds with the flexibility to change songs with changes in their social environment (Tchernichoski and Marcus 2014). However, the combination and degree to which different species use imitation and improvisation strategies is complex and poorly understood. As mentioned above, further research into life history traits may reveal certain selection pressures which could also explain interspecific variations in song learning strategies (Catchpole and Slater 2008). For example, sedentary species tend to rely more on imitation than closely related migratory/nomadic species; which tend to improvise more of their songs (Nelson et al. 1996). This pattern suggests it may be more adaptive for migratory species to utilise more of an improvisation strategy as it allows birds to communicate with a variety of changing neighbours. Alternatively, the adaptive function for combining imitation and improvisation may involve finding the balance between song conformity and individuality (Nelson and Poesel 2009). Nordby et al. (2007) showed male song sparrows overproduce many songs in the plastic phase to eventually select a smaller subset of songs once they settle on a territory. Sparrows were found to retain songs that were most similar to the majority of neighbours, only later to modify them so that shared songs became less similar. These findings led to the suggestion that song learning development in some species may include two opposing forces: a tendency to retain songs that will be shared with neighbours and a tendency to change some aspects of shared songs so individuality can be recognised (Nordby et al. 2007). Nelson and Poesel (2009) work with white-crown sparrows reported a similar finding. A noteworthy complication involved in song learning research is the possible difficulty in differentiating between improvisation and copying error. Copying error and improvisation can both be defined as deviations from a tutor song resulting in an imperfect imitation (Goodwin 2008). However copying errors imply that the changes

are inadvertent and potentially reduce fitness, whereas improvisation may be functionally advantageous. If copying errors were disadvantageous then they would be expected to occur at low levels within a population (Goodwin 2008). In contrast if improvisation is advantageous, it could potentially explain high levels of novel vocalisations within a population (Goodwin 2008).

The final strategy birds may use to develop song is invention. Invention can be characterised as a song that bears no resemblance to the song of any tutor heard in development (Beecher and Brenowitz 2005). Marler and Peters (1982) revealed evidence of invention in laboratory bred swamp sparrow (*Melospiza georgiana*) song wherein a large proportion of song syllables bore no resemblance to any tutor song. Invention has also been reported in numerous other species including grey catbirds, *Dumetella carolinensis* (Kroodsma et al. 1997), nightingales, *Luscinia megarhynchos* (Hultsch and Kopp 1989), indigo buntings, (Payne 1996) and sedge wrens, *Cistothorus platensis* (Kroodsma et al. 1999). While clear cases of invention have been reported within highly controlled experiments, separating invention from improvisation is a difficult task in observational field studies (Goodwin 2008). Without complete experimental control it is impossible to document every song a bird has heard in development, thus invention and improvisation often cannot be confidently separated (Goodwin 2008).

Invention may be adaptive as a song learning strategy because it may facilitate the creation of large song repertoires (Searcy 1992). While for some species song sharing between territories members appears to be a primary goal of selection, the primary goal for other species appears to be the production of numerous and varied song types (Beecher and Brenowitz 2005). Kroodsma et al. (1997) work with catbirds supported this idea by showing that high levels of song invention are not displayed by species with dialects. Further support for this idea comes from studies involving the sedge warbler, a species known to use invention to produce some of the longest most complicated of all birds songs (Catchpole and Slater 2008). Firstly, several studies have found females will pair with males earlier in the breeding season that produce larger repertoires (Catchpole 1980; Buchanan 1997; Catchpole et al. 1984). Secondly, males with larger repertoires are shown to have larger territories and provide more parental care to offspring (Buchanan and Catchpole 1997). This suggests females may be selecting males with larger repertoires because they gain direct fitness benefits. Thus the invention learning strategy and resulting large song repertoires may be under direct control of intersexual selection (Catchpole and Slater 2008).

1.3 FROM WHOM DO BIRDS LEARN?

Fundamental to the process of song learning in the majority of songbirds is the passing of vocal traditions from one group member to another. Thus by definition, song learning is a form of cultural transmission and exploring who juveniles learn their song from is a distinctive feature of a species song learning programme (Heyes 1994). Cavalli-Sforza et al (1982) describes three directions of cultural transmission: (1) vertical; where information is passed from parents to offspring, (2) horizontal; where information is passed between members of the same generation, and (3) oblique; where information is passed from adult group members to younger individuals. Vertical transmission implies genes are being passed along with song, while oblique transmission suggests song transmission may occur between unrelated individuals (Bell et al. 1998). Creating an index of song similarity is the most common method of determining from which individual(s) a juvenile has learned a song (Norby et al. 1999; Liu and Kroodsma 2006). Song similarity can be determined on a fine scale by measuring song elements or on a larger scale by comparing song types (Catchpole and Slater 2008). Vertical transmission is seen in captive bred Bengalese finches (*Lonchura striata domestica*) and white-rumped munias (*Lonchura striata*), where songs between fathers and sons were very similar, with 90% shared elements (Takahasi et al. 2006; Takahasi and Okanoya 2010). Mann and Slater (1995) showed evidence of vertical transmission in zebra finches with male juveniles preferring to copy paternal song types when tutored by their father and an unrelated male. However, if adult tutors are not provided, horizontal transmission is documented between juvenile zebra finch brothers if one brother has already learnt the song from his father (Deregnaucourt and Gahr 2013). While these zebra finch studies suggest both vertical and horizontal learning is possible, little evidence of horizontal transmission has been found in other studies of this species suggesting that members of the same generation do not commonly learn their song from each other when adult tutors are available. Oblique transmission appears to be the most common form, especially in territorial species, with juveniles often producing a stable adult song that is most similar to older adult neighbours (Catchpole and Slater 2008). Liu and Kroodsma's (2006) field study found that each year old male chipping sparrow (*Spizella passerina*) sang a very similar song to only one immediate neighbour on the breeding territory, suggesting that young sparrows learn by oblique transmission. Other examples of young birds sharing similar songs with a particular older adult neighbour include: young indigo buntings (Payne and Payne 1993), song sparrows (Beecher et al. 1994; Wilson et al. 2000), Nuttall's white-crown sparrows, *Zonotrichia leucophrys nuttalli* (Bell et al. 1998), village indigobirds (Payne 1985) and chowchillas, *Orthonyx spaldingii* (Koetz et al. 2007). Wilson et al. (2000) work with song sparrows revealed oblique transmission in species that

display regional dialects can be adaptive because sharing a high proportion of songs with territory neighbours was shown to increase the chance of a male surviving and retaining a territory.

A last alternative is that young birds may copy songs from a range of different tutors, often including various combinations of parents and adult neighbours. Interestingly, some lines of evidence suggest that learning from multiple tutors may be more common in the wild than controlled laboratory experiments suggest (Riebel et al. 2015). Many of the aforementioned studies involve exposing young birds to socially limited tutoring environments resulting in juveniles producing songs similar to one individual. Whereas controlled studies giving birds the option to learn from several tutors, generally found they produced similar songs to multiple tutors (Mann and Slater 1995). Observational studies such as Wheelwright et al. (2008) work on a natural island population of male savannah sparrows (*Passerculus sandwichensis*) provide further support for multiple tutor learning. Using visual and quantitative measures of similarity this study found no evidence of juveniles perfectly imitating a single tutor, instead they exhibited varying similarities with a range of different tutors. While no bird sang a song most like their genetic father, 12% of birds sang songs most like their social fathers, 35% were most similar to natal neighbours, 26% were most similar to older breeding neighbours and 26% were most similar to 1-year old breeding neighbours. None of the assessed factors, including juvenile age, juvenile body condition, tutor morphology or tutor reproductive success, explained the juveniles' choice of tutor. Furthermore, siblings raised in the same early acoustic environment with shared parents produced very different songs to each other revealing clutch membership did not explain tutor choice. Ultimately this study suggests within natural, highly variable social environments certain species may draw upon a wide set of tutors to learn their song, rather copying a single tutors song in its entirety (Wheelwright et al. 2008).

Why a species may select to learn from a particular individual rather than multiple tutors is not well understood. However, there is some evidence that the number of tutors selected may be related to certain life history characteristics (Nelson et al. 1995, 2001). For example, in a sedentary species exhibiting dialects closely imitating the song of one particular neighbour or parent would be adaptive because it facilitates stable communication with the same neighbours (Catchpole and Slater, 2008). Alternatively, a migratory species producing a multiple song types may have to communicate with different neighbours over time in different regions in order to compete for mates and/or territories (Catchpole and Slater 2008). Learning from multiple tutors may benefit such species because it facilitates song flexibility enabling them to match songs with different individuals (Nelson et al. 1995, 2001). Alternatively, the availability of particular tutors may change resulting in juveniles learning from multiple tutors. Böhner (1990) proposed zebra finch juveniles

may first learn from sires before independence but if the sire is not within close proximity after 2 months a new tutor will be chosen. Conversely if the juvenile has continuing social contact with the sire, the juvenile is more likely to continue to only learn from him. This suggests that for some species juveniles during sensitive periods may learn from as many tutors as they are exposed to if previous tutors are unavailable (Roper and Zann 2006).

One of the most significant discoveries within bird song research over the past 50 years is the undeniable impact of the social environment on when, how and from whom birds learn their song (Soma 2011). Some of the first evidence that vocal learning may depend on social interactions came from species differences in ability to learn from taped tutors (Soma 2011). While chaffinches, white-crown sparrows and swamp sparrows readily copy songs from taped tutors, other species such as sedge wrens, do not (Baptista et al. 1997). Furthermore, species that can learn from taped tutors often produce very different results when exposed to socially interactive tutors (Nelson 1997). Exposure to live tutors has also been shown to extend the sensory period in which a bird may learn. For instance, Marler's (1970) tape tutor experiments indicated that the sensory period for sparrows closes around 50 days, while Baptista and Petrinovich (1984) study on the same species using live tutors revealed learning occurred after this period. Moreover, species that rejected heterospecific taped tutors later copied these foreign species, but only when live socially interactive tutors were provided (Baptista and Petrinovich 1984).

The direct social relationship between a juvenile and an adult may influence tutor selection (Beecher and Burt 2004). For example, zebra finches, which do not learn from taped tutors, have been shown to more readily learn from tutors with whom they can have some form of interaction; either visual or physical interaction (Pecking, grooming etc.) was found to facilitate song learning in zebra finches (Eales 1989; Slater et al. 1988). Specifically, the behavioural response of tutors to juveniles during direct social interaction may influence tutor selection. For example, zebra finches when given a choice of tutors have been shown to prefer to learn from tutors who were more aggressive towards them (Clayton 1987). Social behaviours, like aggression may indicate a males' quality and his ability to survive and reproduce. Considering females have been shown to prefer males that produce songs with certain features that indicate male quality, it would also be adaptive for juveniles to select tutors which females prefer (Soma 2011). Soma et al. (2009) showed juvenile Bengalese finches (*Lonchura striata*) preferred male tutors with higher song complexity, a preference which adult females display when choosing a mate. Alternatively the length of time spent in close proximity with an adult, not necessarily the nature of the interactive itself, may influence tutor selection. Mann and Slater (1995) study on zebra finch song tutor choice showed a preference for juveniles to learn from adults with whom they had a longer period of social contact.

Furthermore, if the time with a selected tutor was shortened, juveniles were shown to prefer a second tutor who shared a similar song or morphological traits with the original tutor (Mann and Slater 1995).

Interestingly, some evidence suggests social experience influencing song learning need not be physical or visual in nature. Many species have been shown to learn in the absence of direct physical and visual interaction as long as singing interactions can be heard (Beecher and Burt 2004). The action of a bird listening to the singing interactions of others can be referred to as eavesdropping (Beecher et al. 2007). Evidence suggests male and female songbirds eavesdrop on the singing interactions of others as a means to extract information, including dominance and mating status, and then use this information to make behavioural decisions (Otter et al. 1999). Such findings lead researchers to suggest juveniles may also eavesdrop as a method to make tutor and song selection decisions in the learning process (Beecher and Burt 2004). Templeton et al. (2009) demonstrated that juvenile song sparrows in their sensory phase are attracted to singing interactions between adults rather than an individual adult singing. Their methods involved exposing juveniles to speakers playing recordings of two birds singing compared to recordings of one bird singing solo. Juveniles only approached the speakers broadcasting singing interactions, however they did not approach closely or sing in response, suggesting the approach was to facilitate learning via eavesdropping. Male birds often match songs with each other as a way to compete and communicate aggression or threat (Catchpole and Slater 2008). Eavesdropping as learning strategy may therefore be adaptive because it allows young birds to gain information from tutors while limiting potentially aggressive encounters (Templeton et al. 2009).

For the majority of species the specific social factors that influence tutor selection have yet to be experimentally tested. Beecher and Burt (2004) recommend future studies in this area utilise computer simulated tutoring which manipulates the exposure of singing interactions between a juvenile and a computer simulated bird. This design proposes more naturalistic results by incorporating social factors and facilitating eavesdropping. Utilisation of this design may therefore allow species which fail to learn from taped tutors, to learn from recordings of singing interactions between live or artificial birds (Beecher and Burt 2004).

1.4 SONG LEARNING AND SPECIES CONSERVATION

Understanding the specific song learning program of a species is also relevant for the management of songbirds in captive breeding and release programs. In these programs, it may not be feasible to

provide natural social interactions due to housing constraints (Lui et al. 2014) or due to lack of appropriate tutors, such as when only eggs are collected from the wild (Lieberman and Kuehler 2009). If appropriate tutors are not available during the sensitive period, juveniles may develop songs that are different from wild populations (e.g. Palila, *Oxioides bailleui* Banko and Farmer 2014). This difference in song type may have implications for successful reintroductions because it has been previously demonstrated that differences in song dialect can be a barrier to dispersal for some species (Baker and Mewaldt 1978). For example Marler and Tamura (1962) showed that while populations of white-crowned sparrows may occur only kilometres away from each other, populations display clear differences in song dialect. Considering white crowned sparrows learn their song in the first few weeks of life, a preference for natal dialects may be learned early and act as a barrier to dispersal. Specifically, females may only select to reproduce with males who sing their natal dialects (Marler and Tamura 1962). Thus a zoo bred population of birds singing a particular song dialect may be released into an area with a population of birds singing a different dialect. Zoo bred birds in this situation may fail to attract, mate and/or successfully compete for resources with particular wild populations, thus limiting their successful reintroduction into particular areas.

By drawing on the existing body of literature on song learning, several methods arise that may be potentially beneficial for captive breeding and release programs. These include the use of taped tutors, facilitating eavesdropping on social interactions between pairs and using computer simulated tutoring similar to that recommended by Beecher and Burt (2004). These methods would need to be tested empirically for each species because of the diversity in song learning programmes.

1.5 THE REGENT HONEYEATER

1.5.1 Regent honeyeater ecology

The focus of this thesis is the regent honeyeater (*Anthochaera phrygia*), a medium sized, aggressive, weakly sexual dimorphic, nectarivorous species that is endemic to the dry open forests and woodlands of south eastern Australia (Oliver and Lollback 2010). Regent honeyeaters are generally considered nomadic, following flowering patterns of several eucalypt species in small flocks, however it is possible their movements may involve seasonal migration (Higgins et al. 2001). During the breeding season, males and females form loose aggregations before establishing a defended territory (Higgins et al. 2001). The current main breeding colonies are at three locations: Chiltern, Victoria (Menkhorst et al. 1999), Capertee Valley, New South Wales and Bundarra-

Barraba region near Armidale, New South Wales (Oliver and Lollback 2010). The breeding season extends from May to March with peak egg laying occurring in September (Geering and French, 1998). The female is responsible for nest construction and will lay two to three eggs per clutch, which she will incubate for 14 days. The chicks remain in the nest for a further 14 to 19 days before fledging. Both parents feed the fledglings until independence (approximately 3 weeks). At independence, juveniles leave the natal territory and may join flocks of other juveniles and non-breeding adults (Higgins et al. 2001; Liu et al. 2014).

1.5.2 Recovery programme: captive breeding and release

In the 1800's, regent honeyeaters were reported to occur over a range of 2000km that extended from Adelaide in South Australia, Victoria, up the eastern coast of Australia into Queensland (Higgins et al. 2001). A decline in the population was first noted in the 1920's and over the past 30 years, the population has declined to an estimated 350-400 remaining in the wild (Garnett et al. 2011). Habitat clearing has left the geographic range of this species severely contracted and highly fragmented and is suggested as the primary cause of its rapid population decline (Menkhorst et al. 1999). Regent honeyeaters are today listed as critically endangered (IUCN Red List, 2015). In response to this population decline, a national recovery programme began in 1995 involving collaboration between several zoos, wildlife agencies, local communities and non-government organisations (Liu et al. 2014). The founder population of the Taronga Zoo birds was 10 nestlings collected from New South Wales and Victoria. In 1997, three first-year birds were collected from the Capertee Valley and 4 additional adult males were brought into the breeding colony from New South Wales in 2012. The programme has been very successful in breeding the birds and several cohorts have been released into the wild (Liu et al. 2014).

1.5.3 Regent honeyeater song

Vocalisations of the majority of honeyeaters (Meliphagidea) have been poorly studied, even though they represent the largest radiation of passerines in Australia (Gardner et al. 2010). To date, there have been no studies investigating song learning and development in this species or in any species of honeyeater. The male regent honeyeater's song is short (~1 to 1.5 s), comprising a series of brief, frequency modulated whistles and pulses, and can include bill snaps at the beginning of songs. Elaborate head bobbing movements are often performed during the song (Higgins et al. 2001). The males are most vocal in the non-breeding season. Females sing shorter, less complex versions of the males' songs (C. Smith; unpub data). Based on historical accounts of the regents' songs, research suggests that there is geographical and temporal variation in songs (Powys 2010). Analysis of recorded song phrases from 1977 to 2008 showed that there are regional dialects and that the songs

produced by regent honeyeaters in the same location changed over a period of several years (Powys, 2010). However specific individuals have not been tracked over long periods of time so it is unknown if specific individuals change song over time or if song changes occur over generations. Previous work also revealed greater responsiveness of regent honeyeaters to songs from the same dialect, as well as to current compared to non-current songs (Powys 2010). There are also differences between the songs of wild birds compared to captive reared birds. Birds bred at Taronga zoo were reported by Powys (2010) and Liu et al. (2014) to sing simpler, harsher and less melodious songs that bore little resemblance to the songs of wild birds. This difference in songs between the two populations of birds raised the question of the function of song dialect in this species and its potential effect on the released birds' breeding success (Liu et al. 2014). Overall, different groups of regent honeyeaters appearing to sing different songs points towards evidence of song learning (Powys 2010). Furthermore, considering the vast majority of songbirds learn their songs it would be highly unusual if regent honeyeaters did not. Thus a first step in addressing these questions was to determine how regent honeyeaters learn their songs.

1.6 PROJECT AIMS

The aim of this thesis was to conduct an observational study investigating song learning in juvenile regent honeyeaters at Taronga Zoo. During Taronga Zoo's normal husbandry routine, juveniles experienced different potential tutors during different developmental stages. These potential tutors included 1) their sires and males in neighbouring aviaries, 2) virtual tutors (a live audio from the wild caught birds' enclosures broadcast via a speaker into a crèche enclosure that housed juveniles after independence), and 3) other birds housed with juveniles later in development. Specifically, I tested the similarity of a juvenile's song to these potential tutors. Assessing song similarity between juveniles and adults is a widely used method for determining from whom a bird has learned (Norby et al. 1999; Liu & Kroodsma, 2006). Based on a similar study by Wheelwright et al. (2008), which found wild migratory male sparrow juveniles learn from a variety of tutors, I predicted juvenile regent honeyeaters would also learn from a variety of tutors. The degree of similarity between songs of juveniles and adults could also suggest whether imitation alone or imitation combined with improvisation/invention was used to learn songs. In addition, because juveniles were housed with known adults at different times inferences about the timing of song learning could be drawn.

Ultimately, very little is known regarding the possible functions of regent honeyeater songs and even less is known about their song learning development. In addition, limited information can be extrapolated from other related species as the majority of song learning research has focused on

North American and European species or model species, such as the zebra finch. To the best of my knowledge, this is the first study of song learning in any Australasian species of honeyeater.

2. METHODS

2.1 STUDY SITE AND EQUIPMENT SETUP

This study was conducted at Taronga Zoo, NSW, Australia (33.8433° S, 151.2411° E). Subjects were housed off-exhibit in free flight aviaries. Each adult breeding pair was housed in a separate aviary (sizes ranged from 1.5 x 6.6 x 3.5 to 8.2 x 3.8 x 3.5 (length x width x height in meters) that was part of one of three banks of adjacent aviaries (Figure 1). Juveniles were reared by their parents in these aviaries and then transferred to the crèche aviary (10 x 20 x 4 m; l x w x h) once independent (Figure 1). Birds were later moved to a large, mixed-species free-flight aviary (Figure 1 outset; see figure 2 for details of transfers between aviaries). Every aviary contained food, water and natural cover. Breeding aviaries contained nesting materials.

Seven of the breeding aviaries (B2-4 and B39-42) were each equipped with a Berhinger® C-2 studio condenser, cardioid pickup pattern microphones. Microphones were connected via XLR cables (Canare cable, Nuetrak Connector) to an analogue-to-digital converter (Presonus® FireStudio, frequency response: 20 Hz to 20 kHz). The audio was recorded by the multi-channel audio recording software (Boom Recorder, VosGames V8; 48kHz/16bit) running on a computer (Mac Mini) connected to the analogue-to-digital converter within the equipment room. The crèche aviary was equipped with a Bose Freespace 51® environmental speaker that was connected via speaker cable to a Denon® amplifier (DN-A300M 3U, 100w @ 4Ohms). Audio from one of the breeding aviaries (B41) was fed to the amplifier from the analogue-to digital converter.

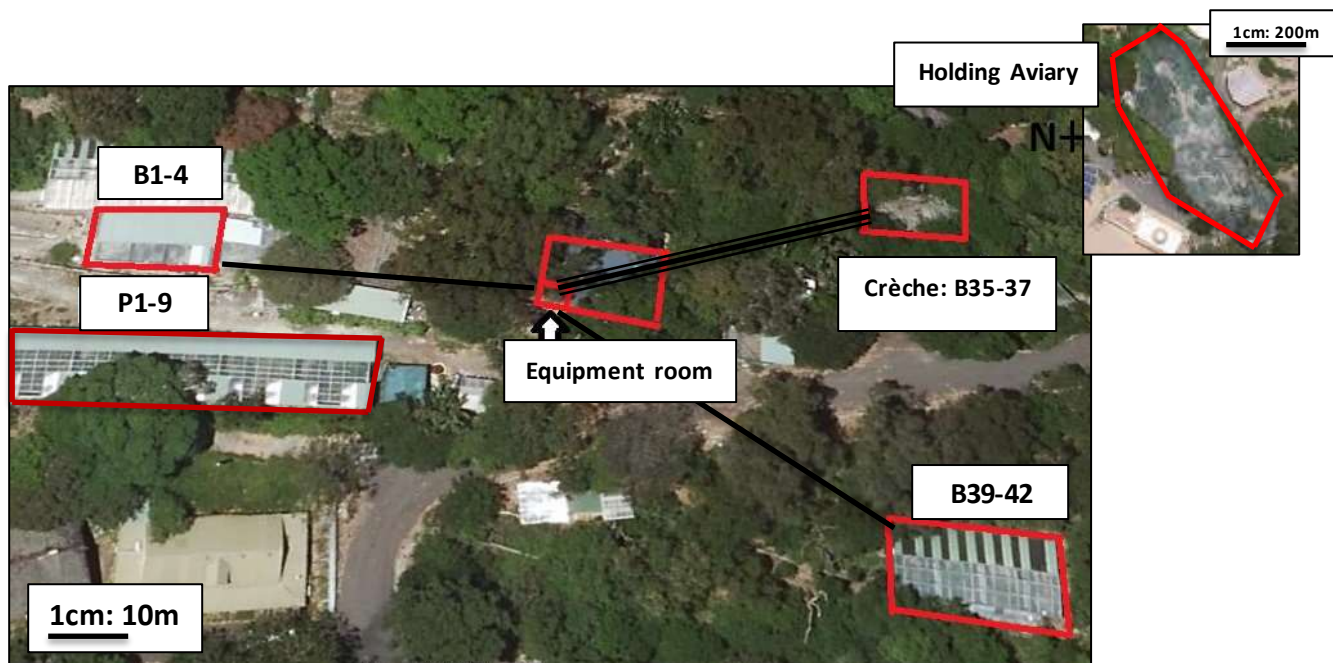


Figure 1. Satellite image of regent honeyeater (*Anthochaera phrygia*) enclosures at Taronga Zoo, NSW Australia. Breeding aviaries: Bank A (B1-4), Bank B (B39-42) and Bank C (P1-9). Juvenile housing: Crèche (B35-37). Holding aviary: mixed-species aviary ~ 300 m from main aviaries (smaller outset image). Equipment room: location of recording and computer equipment. Single black line indicates microphone cables running from breeding aviaries to equipment room. Triple black line indicates speaker cable running from banding room to crèche. Image from Google Earth 1/8/2015.

2.2 SUBJECTS

Twenty-nine male regent honeyeaters were recorded for this study, 9 adults and 20 juveniles. Of the 9 adults, 7 were sires of juveniles used in this study and two had not sired chicks (Table 1). The adults were from different locations: four were caught in the wild (Capertee Valley and locations in NSW), four were reared in Taronga Zoo and one was reared at Adelaide Zoo. All of the juveniles in this study were reared by their parents at Taronga Zoo as part of the species recovery program (Table 2). The juveniles used in this study hatched between August and December, 2014. All of the birds were individually identified by combinations of coloured leg bands and a metal leg band with the bird's ARC number. All birds that were released into the wild in April 2015 and recorded in pre-release aviaries are referred to by their release band colour ID's (Table 1, 2). Sires that were not released are referred to by their aviary letter/number combination (Table 1).

Table 1. Adult regent honeyeaters (*Anthochaera phrygia*) recorded for analysis.

Release band ID	Age (yrs)	Aviary/ Sire ID	Aviary bank	Sire* (Y/N)	Origin
-	3.5	B2	A	Y	Adelaide Zoo
PNKORG	2.4	B3	A	Y	Taronga Zoo
REDYEL	2.4	B4	A	Y	Taronga Zoo
-	3.4	B39	B	Y	Capertee Valley
-	4.4	B40	B	Y	Capertee Valley
-	4.4	B41	B	Y	New South Wales
-	5.9	B42	B	Y	New South Wales
GRNBLK	1.4	P5	C ⁺	N	Taronga Zoo
YELPNK	1.3	P9	C ⁺	N	Taronga Zoo

* Sire of one or more of the juveniles listed in Table 2.

⁺ birds were not in the aviary at the same time as the juveniles

- Sires that did not have release band IDs'

Age = age at time of pre-release recording of juveniles (12/4/2015)

Table 2. Juvenile regent honeyeaters (*Anthochaera phrygia*) recorded for analysis.

Release band ID	Age at recording (dph)	Hatch aviary	Aviary bank	Sire origin	Dam origin	Sire's songs recorded? *
ORGWHT	157	B2	A	Adelaide Zoo	Taronga Zoo	yes
YELWHT	157	B2	A	Adelaide Zoo	Taronga Zoo	yes
MAUBLK	101	B4	A	Taronga Zoo	Taronga Zoo	yes
WHTBLK	101	B4	A	Taronga Zoo	Taronga Zoo	yes
REDBLK	139	B4	A	Taronga Zoo	Taronga Zoo	yes
GRNYEL	215	B39	B	Capertee Valley	Taronga Zoo	yes
WHTORG	138	B39	B	Capertee Valley	Taronga Zoo	yes
YELMAU	210	B40	B	New South Wales	Adelaide Zoo	yes
REDRED	120	B40	B	New South Wales	Adelaide Zoo	yes
WHTMAU	120	B40	B	New South Wales	Adelaide Zoo	yes
BLKMAU	168	B40	B	New South Wales	Adelaide Zoo	yes
REDMAU	136	B42	B	New South Wales	New South Wales	yes
BLKYEL	155	P1	C	Taronga Zoo	Taronga Zoo	No
REDGRN	155	P1	C	Taronga Zoo	Taronga Zoo	No
REDWHT	145	P1	C	Taronga Zoo	Taronga Zoo	No
BLKGRN	227	P5	C	Taronga Zoo	Melbourne Zoo	No
REDPNK	144	P5	C	Taronga Zoo	Melbourne Zoo	No
BLUPNK	144	P5	C	Taronga Zoo	Melbourne Zoo	No
WHTGRN	182	P5	C	Taronga Zoo	Melbourne Zoo	No

* recordings of sire's songs during nestling and fledgling stages. dph = days post hatch.

Timeline of bird relocations and the juveniles' acoustic environment

Juvenile birds were housed with their parents in their natal aviaries until they were independent (i.e. approximately 35 days post hatching; range: 30 to 39 dph). Juveniles were then moved to the crèche aviary until they were on average 90 days post-hatch (age range: 38 to 153 dph, B35-37, Figure 1). They were then moved into a large, mixed species holding aviary on public display within the Zoo where they remained for an average of 44 days (range: 17 to 57). Once the juveniles had left, the adults from Banks A and B were moved to the crèche aviary. Bank C adults were moved into aviaries elsewhere in the Zoo. From February 16th to March 26th 2014, the juveniles were moved into Bank A aviaries, which were reconfigured to allow the birds to move freely between the four aviaries. The juveniles and the adults to be released remained in this aviary bank for approximately 2 months until their release into the wild in Victoria, Australia (Figure 2). All bird movements

between aviaries were under complete control of zoo keepers and performed in response to space restrictions, according to optimal animal welfare.

Birds within a bank of aviaries could hear the vocalisations from the other birds within that bank. Bank A, Bank B and the crèche aviary were sufficiently distant from each other that the birds were acoustically isolated (i.e. could not hear the birds from the other banks). The proximity of a Bank A and C was such that the birds could potentially have faintly heard each other (Figure 1).

When the juveniles were in the crèche aviary, they were provided with a “virtual tutor”, which allowed them to hear singing between a wild caught male, its breeding partner and the breeding pairs in the surrounding three aviaries, using a Bose Freespace 51[®] environmental speaker that broadcast a live audio feed from a microphone in B41. The feed was live 24hrs/day, 7 days/week for the duration of the time that the juveniles were in the crèche. During this time, the juveniles had no visual contact with any adults and were only able to hear Bank B birds (virtual tutors). Bank B birds were not able to hear the juveniles. Two juveniles from Bank C (BLUPNK and REDPNK) were not housed in the crèche aviary and thus never heard the virtual tutors.

When the juveniles were in the holding and pre-release aviaries, they had the potential for direct visual and auditory contact with four adult birds (the sires from B3 and B4 and yearlings GRNBLK and YELPNK) as well as other juveniles that did not sing during the recording sessions.

This timeline of bird relocations facilitates several predictions: (1) If juveniles from bank A only produce song types from bank B adults/ the virtual tutor, juveniles may not be learning songs from their sires (i.e. no vertical transmission of song). This prediction also suggests learning occurs between 35 to 90 dph. (2) If only juveniles from bank B produce the virtual tutor song type it may be concluded that direct social interaction is required to learn songs. This conclusion could be made because bank B juveniles are the only subjects so have direct social interaction with the virtual tutors (B41/B42). This result would also suggest learning occurs from 0 to 35 dph.

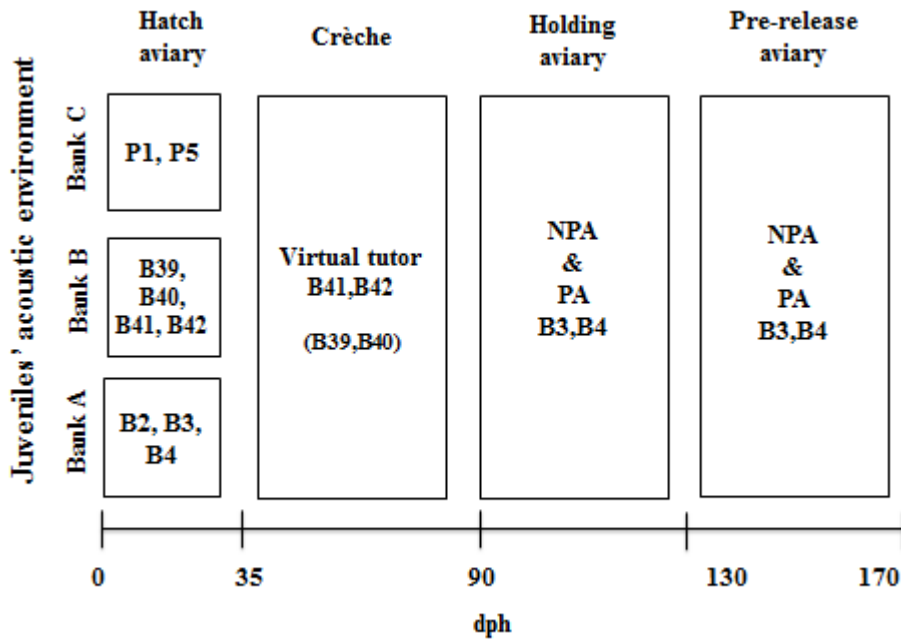


Figure 2. Timeline of juvenile regent honeyeater (*Anthochaera phrygia*) location and acoustic environment. Birds listed within the rectangles indicate the birds that the juveniles could hear during those times. Juveniles within each rectangle could also always hear each other. Note: Two juveniles from Bank C were not housed in the crèche but were housed in the holding and pre-release aviary. Within the crèche juveniles could primarily hear singing interactions between B41 and B42 as the microphone was set up within B41 aviary; however B39 and B40 are included in brackets because juveniles may also have heard the singing of these adults.

2.3 DATA COLLECTION

Juvenile song recordings

Juvenile songs were recorded from March 6th to April 12th, 2015, between 0700 and 1500 (GMT +10). All recordings were taken with a MKH816T Sennheiser directional microphone fitted with a Rycote windshield and handle. The microphone was powered by an external 48V phantom power supply and recordings were stored on an SD card in a Zoom (H4n) handheld recorder (Figure 3). Birds were opportunistically recorded when singing and then verbally identified on the recording following the song using the unique leg band colour combinations. All recordings were made in Bank A aviaries.



Figure 3. Regent honeyeater (*Anthochaera phrygia*) pre-release enclosure equipment set up. Sennheiser directional microphone fitted with windshield and 48V phantom power supply connected to Zoom (4Hn) handheld recorder.

Adult song collection

A custom written Automator (Apple Inc, V2.5) script was used to automatically trigger Boom Recorder on the Mac Mini computer to begin audio recording of the breeding aviaries at 0600 and stop recording at 0800 (GMT +10). Recordings were made every day from 15 July 2014 to 15 January 2015. This period covered the start of the breeding season to the move out of the final fledglings. Recordings were 48kHz, 16bit. Each audio file contained a separate channel for each aviary. For the songs from the sires, files were selected for days during the nestling and fledgling stages of juvenile development for each aviary.

2.4 DATA ANALYSIS

The audio files were imported into Audacity (version 2.1.1, 48 kHz, 16 bit; FFT: 1024, Hamming window) and songs were identified by visual inspection of the spectrogram and by playing the recordings. The most common song types per bird were identified from the recordings. A subset of these songs (3 to 5 per song type per individual) was selected based on the quality of the recordings (e.g. low background noise) for the song learning analysis. Each song then exported as a separate file (WAV 16 bit signed) and imported into Luscinia acoustic analysis software (version 2.14.05.15.01) (<http://luscinia.sourceforge.net>). Within Luscinia, song elements were marked to

allow analysis of the similarity between the song types of adult and juvenile regent honeyeaters. Song elements were defined as continuous marks on the spectrograms (Catchpole and Slater 2008). Luscinia uses dynamic time warping (DTW), a distance based measure that compares two time series that was initially developed for speech recognition and has since been adapted to analyse bird song (Ito et al. 1996; Kogan and Margoliash 1998), to create a dissimilarity score between each song pair. Scores range from zero, indicating that the signals are identical, to 1. Scores are calculated by scaling 15 song parameters (e.g. peak frequency), in a metric manner in order to produce the optimal alignment for two songs, which are then averaged along that alignment. The dissimilarity matrix scores were then imported into R (<https://www.r-project.org/>; R Studio Version 0.98.501) and hierarchical cluster analysis was performed using the hclust function (Vegan and cluster packages) using the Ward method (Ward 1963; Murragh et al. 2014). The cuttree function was used to create clusters at different levels and then silhouette plots (Rousseeuw 1987) were created to determine the similarity of each set of clusters. The hierarchical cluster that created the highest Global Silhouette Index was used to determine which juveniles' song types were most similar to which adults' song types.

3. RESULTS

A total of 332 songs were extracted from approximately 50 hours of recordings. Visual and acoustic inspection of the songs revealed that the juvenile and adult regent honeyeaters sang between 1-4 common song types. The juveniles did not produce exact copies of any adult song. However, the juvenile songs frequently contained similar elements that occurred in similar relative positions and were of similar lengths to specific adults' songs. Like the adult songs, juvenile songs often contained one or more introductory bill snaps followed by a series of elements (mean = 3, range = 2 – 12), including whistles and frequency modulated sweeps which were not typically repeated within a song.

For the hierarchical cluster analysis, the Global Silhouette Index was highest (0.23) for the tree that clustered the songs into 6 groups (Figure 4). Thus, this cluster structure was used to determine which juveniles shared similar songs with which adults.

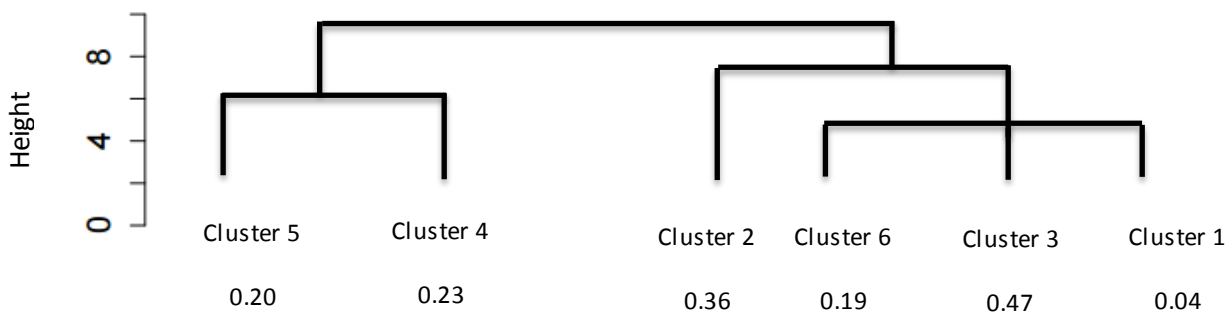


Figure 4. Dendrogram and silhouette scores for regent honeyeater (*Anthochaera phrygia*) song clusters. Silhouette scores for each cluster are displayed under each cluster and represent how well songs fit within their cluster. Height represents distance between clusters.

Cluster 1 reported a silhouette score of 0.04, which suggests that the songs within this group should not be considered a true grouping of a particular song type. Visual and auditory inspection of the songs within this cluster confirmed the low similarity of songs placed within this group. Cluster 1 contains songs from 7 of the 19 juveniles and thus has individuals from all aviary banks, and includes songs from sires B2-4, B4², B41-B42 as well as songs from the non-parental adults (NPA; Table 3). Figure 5 shows examples of two song types from cluster 1; including two songs from adults and two from juveniles. The two song types were chosen to represent the diversity of songs within cluster 1. Figure 5b, the adult song, consists of multiple bill snaps followed by two frequency modulated descending whistles. Figure 5a, the juvenile song, consists of two bill snaps followed by one frequency modulated whistle, which rises and then falls. Figure 5d, the second adult song, consists of an initial bill snap followed by three long sweeping whistles, the last two whistles beginning and ending at higher frequencies than the first element. Figure 5c, the second juvenile song, consists of an initial bill snap followed by one sweeping whistle. While these songs were selected to represent cluster 1 all songs within this grouping are highly variable and will therefore not be included in the result summary displayed in Table 4.

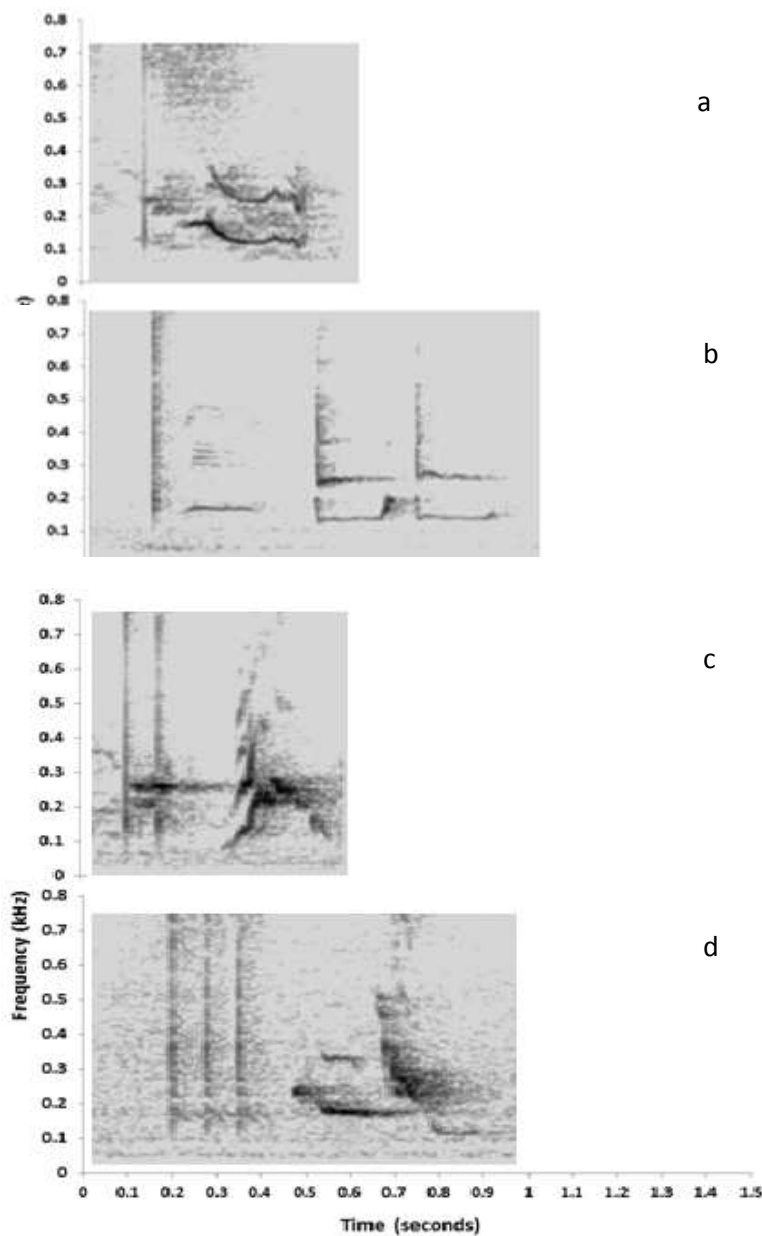


Figure 5. Representative songs of regent honeyeaters (*Anthochaera phrygia*) from cluster one. (a) represents a juvenile song, (b) represents an adults song. (c) represents a different juvenile song, (d) represents a different adults song.

Cluster 2 reported a relatively higher silhouette score of 0.36 suggesting songs within this grouping share a higher degree of similarity and fit well within the cluster. This cluster includes juvenile songs from all banks, songs from parental adults produced within the hatch aviary (B3¹,B4¹) and parental songs produced with juveniles in pre-release aviary (B3²,B4²). More than half of the juveniles (53%) produce a cluster 2 song type. Figure 6 represents this cluster 2 song type. Figure 6b, the adult song, consists of a one frequency modulated whistle, rising at start and falling at the end, followed by a short unmodulated pure tone whistle or pulse. Figure 6a, the juvenile song,

consists of a slightly more modulated whistle with a similar pattern to the adult song, followed by a more broadband, slightly frequency modulated pulse. The majority of songs within this grouping follow a very similar structure however some include an additional element.

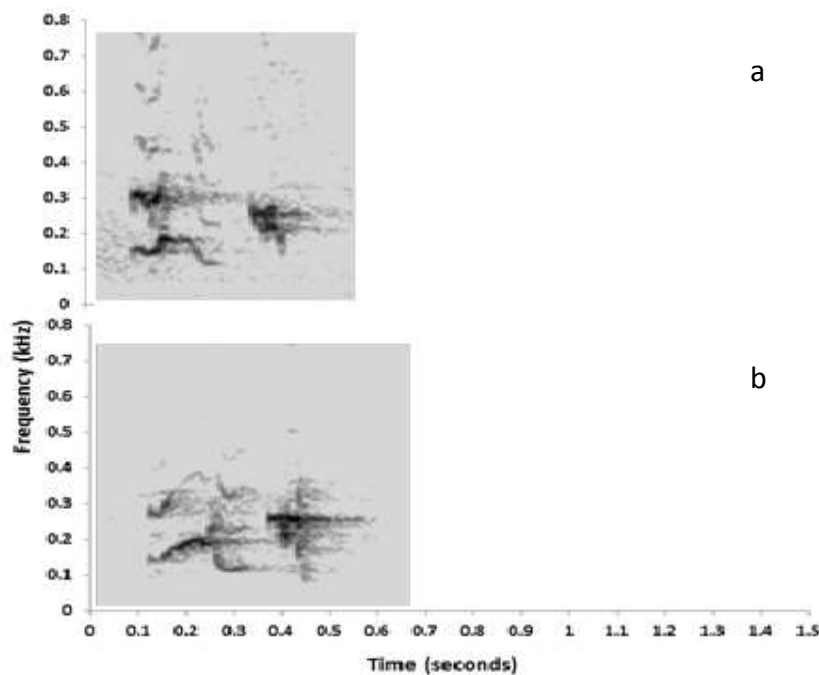


Figure 6. Representative songs of regent honeyeaters (*Anthochaera phrygia*) from cluster two. (a) represents a juvenile song, (b) represents an adult song.

Cluster 3 reported the highest silhouette score of 0.47 indicating a strong grouping. This cluster includes only songs of sires from B39 and B40. Figure 7 illustrates the typical song type from this cluster consisting of a sweeping whistle between two bill snaps followed by two more similar sweeping whistles with frequency modulation. Each whistle has harmonics. This song type represents the longest of all the six song types with some including a fourth sweeping whistle with a broadband buzz.

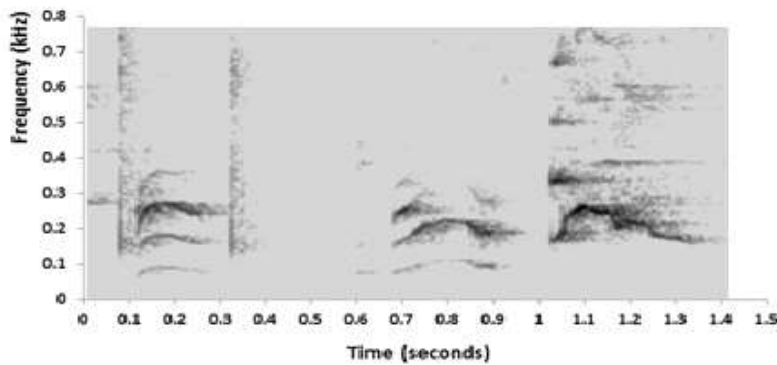


Figure 7. Representative songs of regent honeyeaters (*Anthochaera phrygia*) from cluster three. This cluster only consisted of adult songs and consequently does not include a juvenile song comparison.

Cluster 4 had a silhouette score of 0.23, suggesting the songs fit moderately well within the cluster. Sires B41-42 (the virtual tutors) and juveniles from all banks are included within this grouping. Figure 8 shows representatives of this song type, including both an adult and juvenile song. Figure 8b, the adult song, consists of two bill snaps followed by five short whistles, or pulses, with narrow bandwidth that alternate in relatively higher and lower frequencies. Figure 8a, the juvenile song, also consists of five alternating high and low short whistles, however it has only one bill snap and the whistles have some frequency modulation involving a rapid rise and fall in structure. Songs within this cluster generally consist of between 1 to 4 bill snaps with 4 to 10 short whistles that alternate in frequency.

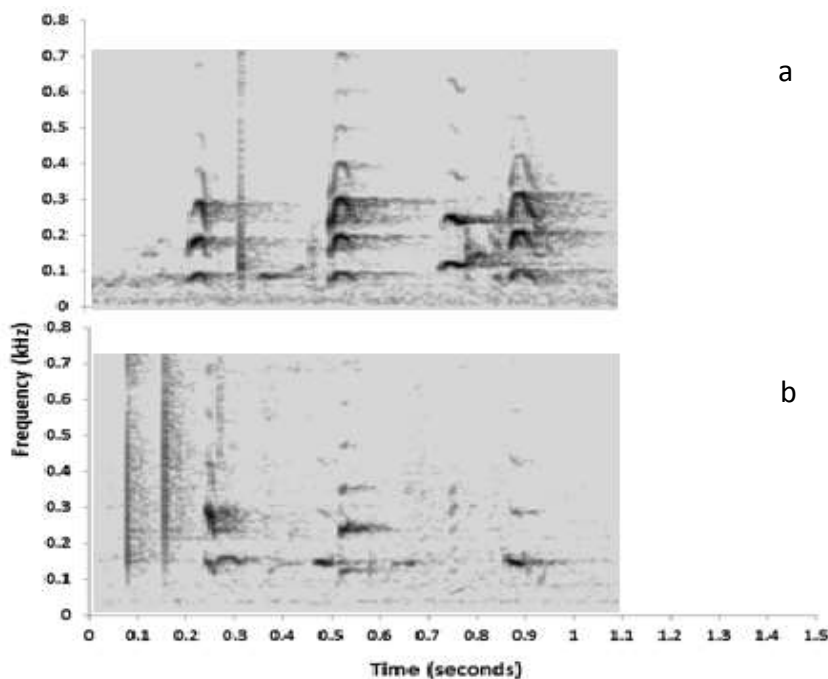


Figure 8. Representative songs of regent honeyeaters (*Anthochaera phrygia*) from cluster four. (a) represents a juvenile song, (b) represents an adult song.

Cluster 5 reported a silhouette score of 0.20, indicating moderate similarity between song types. This cluster includes juveniles from all banks, non-parental adults and sire songs only produced with juveniles in the pre-release aviary (B3²). Figure 9 displays representatives of this song type. Figure 9b, the adult song, consists of a bill snap followed by a soft ascending whistle, then a loud short pure tone pulse, a descending soft whistle and ending with a loud relatively longer whistle which descends at the end. Figure 9a, the juvenile song, is very similar in structure to the adult's song, however the third element is a more broadband short whistle and the last whistle does not finish with a prominent fall in frequency. Some songs within this cluster differ from these representative songs by either beginning with two bill snaps or by lacking bill snaps completely.

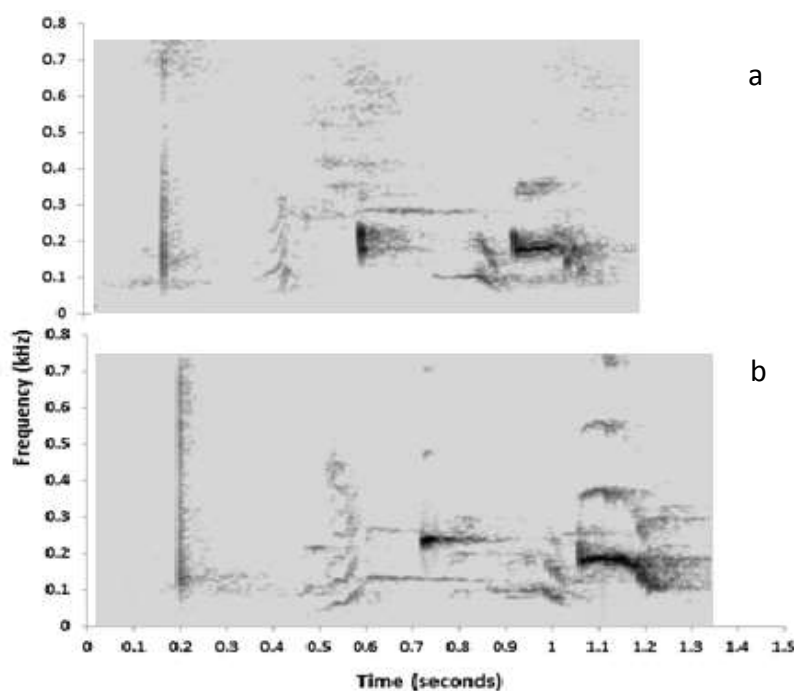


Figure 9. Representative songs of regent honeyeaters (*Anthochaera phrygia*) from cluster five. (a) represents a juvenile song, (b) represents an adult song.

Cluster 6 had a silhouette score of 0.19, again indicating a moderately good fit for the songs in this cluster. This cluster includes juveniles from all banks and sire (B3²) song recorded with juveniles within the pre-release aviary. Figure 10b displays a representative of the adult song type consisting of a bill snap followed by a sweeping whistle which has an initial rise and then ends with a drop in frequency, followed by a short narrowband pulse. Figure 10a shows juveniles sing a similar song

however two initial bill snaps are included and the last pulse has frequency modulation. This song type is similar to song type two, however it differs as all songs within this grouping include 1-3 bill snaps.

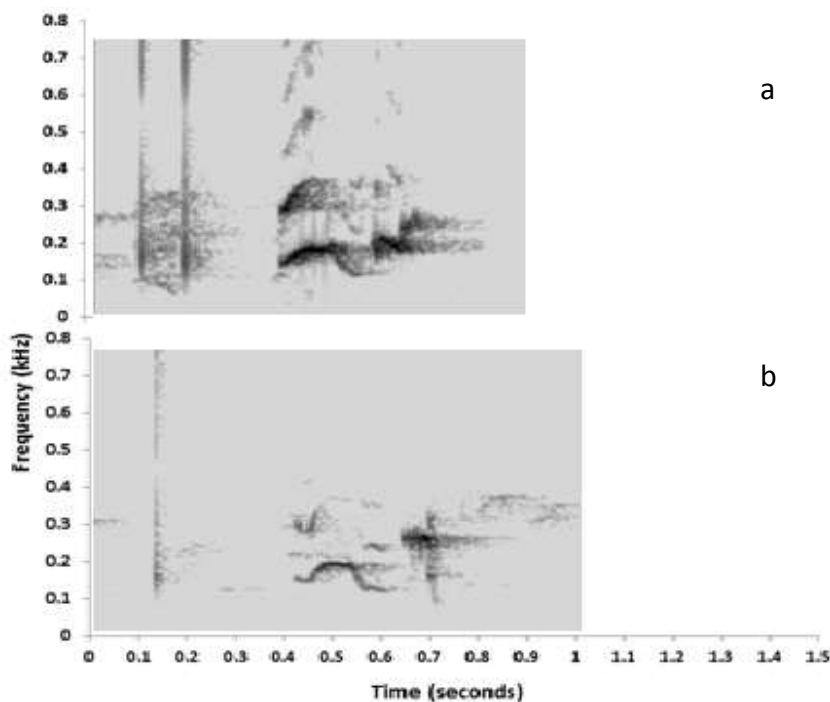


Figure 10. Representative songs of regent honeyeaters (*Anthochaera phrygia*) from cluster six. (a) represents a juvenile song, (b) represents an adult song.

Overall, cluster analysis reveals juveniles produce similar song types with a wide range of adult birds. No cluster includes a juvenile and adult song that is a precise match, as assessed by visual or auditory inspection. The majority (15/19) of juveniles sing multiple song types but none of the juveniles produce the B39 or B40 song type (Table 3). The virtual tutor song type (B41, B42) is the most common song type produced, being sung by 13 out of 19 juveniles (2 out of 5 juveniles from Bank A, 7 of 7 juveniles from Bank B and 4 of 7 juveniles from Bank C). The two juveniles never exposed to the virtual tutor did not produce the virtual tutor song type (BLUPNK, REDPNK). The results show that juveniles are possibly capable of sharing similar song types with adults they heard in each enclosure, from hatch to 35 dph up until pre-release at 130-170 dph (Table 4). However, songs produced by juveniles which were heard in hatch aviaries (0-35 dph) and the pre-release aviary (130-170dph) were also heard in the crèche and holding aviary (35-130 dph). Therefore juveniles may only produce songs heard between 35 to 130 dph. The majority (13/19) of juveniles also produced song types they heard in holding/pre-release aviaries and these were enclosures in

which they had direct physical contact with adults. Differences in song types produced by juveniles had no relationship to aviary bank membership, age or parent id/ clutch id/ birth aviary (Table 3).

Table 3. Song types produced by juvenile regent honeyeaters (*Anthochaera phrygia*) at Taronga Zoo.

		Song type by cluster					
		1	2	3	4	5	6
		B2, B3, B4 ^{1,2} , B41, B42, NPA,*	B3 ^{1,2} , B4 ^{1,2}	B39, B40	B41, B42 (VT)	B3 ² , NPA	B3 ²
Bird ID	Parent ID						
Bank A							
ORGWHT	B2				x		
YELWHT	B2	x					x
MAUBLK	B4	x	x				x
REDBLK	B4	x				x	
WHITBLK	B4	x	x		x		x
Bank B							
GRNYEL	B39				x		
WHTORG	B39				x	x	x
BLKMAU	B40				x	x	
REDRED	B40		x		x	x	
WHTMAU	B40		x		x		
YELMAU	B40	x			x		x
REDMAU	B42				x		
Bank C							
BLKYEL	P1		x		x	x	x
REDGRN	P1	x	x		x		x
REDWHT	P1		x		x		x
BLKGRN	P5	x	x				
REDPNK	P5		x			x	x
BLUPNK	P5		x				x
WHTGRN	P5				x		

Juveniles are separated by blocks corresponding to which tutors juveniles were able to hear at certain times, within particular enclosures. * represent poor clusters which were not included in results summary table 4. VT= virtual tutor, NPA = non-parental adults, ¹= songs types produced in hatch aviary. ² = song type from same bird produced with juveniles in pre-release aviary.

Table 4. Stage at which regent honeyeater (*Anthochaera phrygia*) song types produced by the tutors were heard by the juvenile.

Juvenile ID	Parent ID	AGE (DAYS POST HATCH)				ID of ADULT(S)' song type(s) produced by juvenile
		0-35	35-90	80-130	130-170	
		Parent and Neighbours	Virtual Tutors	B3 ² , B4 ² , NPA	B3 ² , B4 ² , NPA	
Bank A						
ORGWHT	B2					VT
YELWHT	B2					B3 ²
MAUBLK	B4					B3 ^{1,2} , B4 ^{1,2}
REDBLK	B4					NPA, B3 ²
WHTBLK	B4					B3 ^{1,2} , B4 ^{1,2} , VT
Bank B						
GRNYEL	B39					VT
WHTORG	B39					NPA, VT, B3 ²
BLKMAU	B40					NPA, VT, B3 ²
REDRED	B40					NPA, VT, B3 ^{1,2}
WHTMAU	B40					VT, B3 ^{1,2}
YELMAU	B40					VT, B3 ²
REDMAU	B42					VT
Bank C						
BLKYEL	P1					VT, NPA, B3 ^{1,2} , B4 ^{1,2}
REDGRN	P1					VT, B3 ^{1,2} , B4 ^{1,2}
REDWHT	P1					VT, B3 ^{1,2} , B4 ^{1,2}
BLKGRN	P5					B3 ^{1,2} , B4 ^{1,2}
REDPNK	P5		-			NPA, B3 ^{1,2} , B4 ^{1,2}
BLUPNK	P5		-			B3 ^{1,2} , B4 ^{1,2}
WHTGRN	P5					VT

Juveniles are separated by blocks corresponding to which adults juveniles were able to hear at certain times, within particular enclosures. Grey coloured boxes indicate the time at which a juvenile heard the song it produced. Dashed lines (-) represent juveniles that were never housed in the crèche and therefore never heard the virtual tutor. Age (dph) = average days post hatch. VT= virtual tutor, NPA = non-parental adults, ¹= songs types produced in hatch aviary. ² = song type from same bird produced with juveniles in pre-release aviary.

4. DISCUSSION

4.1 FROM WHOM DO REGENT HONEY EATERS LEARN?

4.1.1. Learning from different tutors

My results suggest juvenile regent honeyeaters at Taronga Zoo learn their songs from a variety of adult tutors. Consequently, regent honeyeaters share some similarities in their song learning programme with Savannah sparrows as reported by Wheelwright et al. (2008). Regent honeyeaters, like Savannah sparrows, are capable of learning from various tutors including parents and older unrelated adults (Wheelwright et al. 2008). Specifically, the current findings indicate juvenile regent honeyeaters are capable of learning from: parents and neighbours heard within the hatch aviary, a virtual tutor and his neighbours broadcasted live over a speaker system and adults birds housed with juveniles later in development. Thus, cultural transmission of song in juvenile regent honeyeaters appears to occur through multiple pathways. Some juveniles produce the song type of their sire suggesting the possibility of genetic transmission of song features as well. However, while juveniles in their hatch aviary would have predominantly heard their sire, it is also possible they could have heard and learned from neighbouring adults in the same aviary bank. Most sires within the same aviary bank shared similar song types. Therefore juveniles might have instead copied the song of a neighbouring male in the next aviary. The current study was unable to avoid this potentially confounding outcome because bird housing and movements were under complete control of Taronga Zoo husbandry practices. Husbandry practices are designed according to space restrictions and optimal animal welfare. In order to test if juveniles are truly learning from sires, a future study would need to isolate juveniles and their sires from all other birds. A future study could also involve cross fostering to assess if there is any genetic transmission of song types.

Findings suggest the majority of juveniles shared similar songs with older unrelated adults. Therefore oblique transmission may be the dominant mode of song transfer. Older unrelated adults within the zoo environment most likely share similarities with older territory neighbours in the wild. Considering regent honeyeaters are nomadic/ migratory birds that disperse from natal territories, establish territories elsewhere, and (possibly) adopt the dialects of their new region, it may be adaptive to share songs with older territory neighbours (Powys, 2010). Wilson et al. (2000) showed song sparrows learn from older territory neighbours after they disperse from natal territories, a pattern which results in group members of the same area sharing more similar songs to each other

than to birds in other areas (i.e. dialects). Furthermore, Wilson et al. (2000) revealed that the probability of a male surviving and staying on his territory increased with the amount of songs he shared with adjacent neighbours. Regent honeyeaters may also learn from older unrelated males because, in the wild, learning from such tutors may promote song sharing and increase competitive ability when defending territories and attracting mates.

Deregnaucourt and Gahr (2013) showed juvenile zebra finches are capable of learning songs from each other, however they will only do so when adult tutors are not provided. Thus if regent honeyeaters are similar to zebra finches in this respect, regent honeyeaters may be capable of horizontal learning. However, as many other songbird species including Savannah sparrows (Wheelwright et al. 2008) show very little evidence of horizontal learning, and adult tutors were continuously available from hatching up to release into the wild, horizontal learning in regent honeyeaters is unlikely. Also, juvenile regent honeyeaters in this study did not cluster by themselves without an adult, suggesting horizontal learning is either not occurring or is not a primary direction of transmission. Furthermore, the majority of juveniles that heard the virtual tutor song did produce the virtual tutor song type, whereas the two juveniles that were never exposed to the virtual tutor did not produce its song. If horizontal transmission was occurring it is likely that these two juveniles would have learnt the virtual tutor song type from other juveniles, because of the high exposure to that song type.

4.1.2. Learning from multiple tutors

Findings also indicate the majority of juvenile regent honeyeaters at Taronga Zoo learn songs from more than one tutor. While only three juveniles produced a single song type (the virtual tutor song type), the majority of juveniles learned songs from the virtual tutor and various non-parental adults. Specifically, the majority of Bank A juveniles appear to have learnt from parents/neighbours; B3 and B4, and the virtual tutor. The majority of Bank B juveniles appear to have learnt from the virtual tutor and combinations of unrelated adults including the parents of Bank A juveniles (B3, B4). Due to the inability to obtain recordings of Bank C sires we cannot speculate on whether Bank C juveniles learnt from parents. However Bank C juveniles do appear to commonly learn from the virtual tutor and various unrelated adults (B3, B4, NPA). Again, our findings are similar to those of Wheelwright et al. (2008) who found within environments where juveniles are exposed to a variety of adults songs they will often draw from a wide set of tutors when learning their song, rather than copying a single tutors song in its entirety. Juvenile regent honeyeaters may benefit by learning from multiple tutors because as a nomadic/ migratory species they need to communicate with a

variety of changing neighbours. Producing various song types copied from multiple tutors may provide them with the song flexibility to quickly share song types with new neighbours, resulting in successful territory acquisition and mating events (Nelson 1996, 1997, 2000).

4.1.3. Why select particular tutors?

The majority of juveniles shared songs with adults they had direct social contact with suggesting that social factors may have an important influence on tutor selection in regent honeyeaters. Social interaction with adults may allow juveniles to extract information regarding dominance or mating status; status that may reflect an adult's ability to survive and/or reproduce (Soma, 2011). As regent honeyeaters are an aggressive species it is possible they may select tutors that display aggression towards them, as shown by Clayton (1987) in a study with zebra finches. Alternatively, it is possible juveniles simply selected tutors with whom they had more social interaction and/or were exposed to for a greater amount of time (Beecher and Burt 2004). The majority of juveniles produced the songs of adults they had been exposed to for greater amounts time. Specifically, all of the juveniles producing their sire's song type not only had interaction with their sire as nestlings, they were also exposed to him and/or his neighbours later in development. Specifically, Bank A juveniles could have heard sires B3 and/or B4 in hatch aviaries and again later in the holding and pre-release aviaries. Bank B juveniles could have heard sires B39, B40, B41, B42 in hatch aviaries and again later in the crèche via the virtual tutor. Thus, like zebra finches as reported by Mann and Slater (1995), juveniles may select to learn from adults they have had more social and/or auditory exposure to. The greater amount of social interaction/exposure may allow juveniles to observe which males sing songs that are most attractive to females, for example. As Soma et al. (2009) showed with Bengalese finches females prefer males with particular song characteristics when choosing a mate, a preference which juveniles also have when selecting a tutor. Therefore, juvenile regent honeyeaters may select a tutor whom they observe to successfully attract and mate with more/higher quality females. This possible tutor selection process would give juveniles direct fitness advantages by producing songs which may increase their chances of attracting and reproducing with a female.

While social factors may influence tutor selection in this population of regent honeyeaters, social interaction does not appear to be essential for song learning. The majority of juveniles from all banks produced the virtual tutor song type, a song that they were exposed to via live broadcast transmission through a speaker. However it should be noted that Bank B juveniles were also exposed to the virtual tutor song in their hatch aviary bank because the virtual tutor and his neighbours were also sires' to Bank B juveniles. All Bank B juveniles produced the virtual tutor

song type, possibly due to the long duration of exposure. Furthermore, almost all of the juveniles who were only exposed to the virtual tutor song in the crèche via a speaker (Bank A and Bank C) also produced the virtual tutor song type. These findings strongly suggest regent honeyeaters may only need to hear singing interactions in order to learn song. The work of Beecher et al. (2007) with song sparrows suggest eavesdropping on the singing interactions of adults may be important for young birds during song development because it is less threatening than direct interactions with adults. For regent honeyeaters, like many species, song matching is a way to communicate aggression (Higgins et al. 2001). Juveniles attempting to practice a song by repeating it back to an adult tutor may be interpreted by the adult as a threat, potentially putting the juvenile in danger. Therefore it may be an adaptive strategy for juvenile regent honeyeaters to only listen to a tutor singing as a way to learn, at least initially, when the bird is young and more vulnerable. Ultimately, my findings suggest regent honeyeaters are capable of learning song by listening to singing interactions broadcasted through a speaker. Therefore, in accordance with a suggestion by Beecher and Burt (2004), future studies could explore which social factors influence song learning in juvenile regent honeyeaters by using a computer simulated tutoring method.

4.2 HOW DO REGENT HONEYEATERS LEARN?

Findings suggest juvenile regent honeyeaters use imitation and improvisation/invention strategies to learn their song. Both visual analysis of song spectrograms and auditory assessment of songs indicate the majority of juvenile songs are similar enough to be copied from the songs of various adults. However very few songs were precise matches indicating the likely use of improvisation as well as imitation. While some deviations from tutor songs are possible copying errors, almost all songs produced by every juvenile clearly deviates from tutor songs in some way, suggesting deviations are adaptive rather than mistakes. Many juvenile songs share similar song characteristics with adults including; song length (1-1.5 seconds) order of song elements, spacing between elements and peak frequency. Bill snaps were highly variable between and within individuals. Visual and auditory assessments were supported by cluster analysis which placed the majority of juvenile songs within adult clusters suggesting the majority of juveniles likely learn their songs by imitating the songs of tutors. Silhouette plots indicated five out of the six clusters included songs which fit well within their respective cluster. Only cluster one received a very low silhouette score, suggesting songs within this cluster were not necessarily more similar to each other than to songs in other clusters. It is possible during data collection an adult which was a tutor to one or several juveniles may not have been recorded and included in this study. Such a tutor may have fitted well

within cluster one. It should also be noted that silhouette plot scores were relatively lower than recommended (Rousseeuw 1987). However this was expected due to high song variation within individuals, specifically, high variation in the number of bill snaps and the addition of one or more elements within songs for many individuals. High within-individual variation and occurrence of low silhouette scores also suggests that the birds are using improvisation in addition to imitation. Because very few juvenile songs bore no resemblance to an adult's song this species may not use invention as a primary song learning strategy. Ultimately, due to the purely observational nature of this study there was a small possibility that juveniles may have learnt from tutors which were not recorded. In order to test if regent honeyeaters are utilising only improvisation, as opposed to invention, in non-imitated portions of song, a highly controlled study would be needed and the recording of all songs heard throughout development would be essential. Also breaking down and comparing smaller song units (elements) would be more appropriate than comparing song types for such a study, as many species improvise and invent songs by recombining small song units (Catchpole and Slater 2008).

The use of imitation in regent honeyeater song learning may be adaptive because it promotes song sharing. This idea is supported by Powys (2008) who suggested regent honeyeaters may display regional dialects. By using imitation as a song learning strategy regent honeyeaters can pass on similar song types between group members within the same area. Regent honeyeaters may therefore benefit by sharing songs between members of the same area because it facilitates the communication necessary to compete for mates and defend territories. Furthermore, Powys (2008) revealed regent honeyeaters may change their songs over time and that birds (male and female) do not respond to non-current songs or other dialects. Thus imitative song learning may ensure birds sing recognisable dialects which females may use to select mates, for example. Future studies should investigate female responses to local verses foreign dialects and current verses non-current song types to determine if these play a role in mate choice.

Like many species, regent honeyeaters do not appear to imitate songs perfectly, but instead change songs in various ways (Goodwin 2008). Regent honeyeaters may combine imitation and improvisation/invention to learn songs because including both strategies facilitates two simultaneous adaptive functions: song sharing and encoding individual identity (Nelson and Poesel 2009). Nordby et al. (2007) showed song sparrows may combine imitation with improvisation as a way to share songs within a local dialect and also signal individual identity. Individual identity in song can convey adaptive benefits such as inbreeding avoidance. While imitation may facilitate song sharing in regent honeyeaters, improvising parts of songs may communicate individual identity. An alternative, but not mutually exclusive, idea suggests combining imitation and

improvisation strategies is adaptive for migratory species because it provides song flexibility (Nelson et al. 1995, 1996). Regent honeyeaters, as a migratory/nomadic species may need to alter songs in order to communicate with changing neighbours. Thus the ability to both improvise and invent parts of songs may benefit regent honeyeaters by allowing them to share songs with new neighbours in order to compete for mates and territories.

4.3 WHEN DO REGENT HONEYEATERS LEARN?

Findings suggest juvenile regent honeyeaters have a sensitive period for song learning that lasts from around 35 to 130 days post hatch. While juveniles produce songs they may have heard in the hatch aviary (0-35 dph) or pre-release aviary (130-170) they may have also heard the same songs in the crèche (35-90 dph) or holding aviary (90-130dph). Consequently, results indicate learning may have been limited to 35 to 130 dph. This timing of sensitive period overlaps with many well studied North American and European species such white-crown sparrows and chaffinches (Catchpole and Slater 2008). Considering that many wild juveniles commonly disperse from parents around 40 dph, findings suggest regent honeyeaters may be capable of learning both before and after dispersal from natal territories (Higgins et al. 2001). This possibility is consistent with current findings that juveniles may learn from both sires' and non- parental adults. Therefore non-parent adult males in Taronga Zoo may take the role of breeding territory neighbours in the wild.

Results indicate that regent honeyeaters may be open-ended song learners or age limited (or perhaps intermediate between the two). Data was based on song recordings obtained over short time periods and thus reflect only a snapshot of behaviour. Future long term studies, preferably in the wild, are needed to assess whether regent honeyeaters can learn only in early development or are capable of changing their songs as adults and learning throughout their lives. Like rufous-collared sparrows, if song learning primarily occurs early in development, before dispersal, singing natal dialects may play an important role in mate preference for regent honeyeaters (Danner et al. 2011). Thus future long term studies should also investigate female responses to natal and non-natal songs. One sire in this study (B3) did show some evidence of song change over time. This sire was recorded in July, 2014 (B3¹) and again in March/April, 2015 (B3²) before birds were released into the wild. The songs of this particular bird were recorded around six months apart and vary greatly in relative position of elements and elements types. The songs produced by this sire were different enough to be classified as different song types according to the current study's methods: visual and auditory assessment and cluster analysis. Therefore, adult regent honeyeaters may be open-ended learners.

4.4 IMPLICATIONS

The current study is the first to uncover details of how, when and from whom juvenile regent honeyeaters learn their song. However, findings may only relate to this zoo bred population of Taronga Zoo. Future studies are needed to investigate if wild juvenile regent honeyeaters and other zoo populations display similar song learning characteristics. Ideally long term studies tracking the songs of wild juveniles and their tutors are needed to uncover the song learning programme of wild regent honeyeaters. Tracking over a period of years would indicate who birds learn from in the wild and if this species is capable of changing songs as adults or whether their songs crystallize at a certain age. Alternatively, future studies could extend the current study's methodology by tracking zoo bred birds once they have been released into the wild. Songs which zoo bred birds produce in the wild at breeding territories could suggest if zoo bred males are successfully attracting and reproducing with wild females. Since findings suggest the majority of juveniles did produce the wild bird/virtual tutor song type, I hypothesise these juveniles may be more successful than previous populations which sang only zoo song types. Ultimately, the Taronga Zoo virtual tutor program appears to be a success considering the majority of males produced the virtual tutor song type. Husbandry practices in terms of bird movement between enclosures also appear to successfully correspond with natural juvenile movements and the sensitive period for song learning. Juveniles in the zoo were exposed to sires, the virtual tutor and older unrelated males all within a sensitive period for song learning, as reported in the current study (35 -130 dph). Further collaboration between the program at Taronga Zoo and researchers will undoubtedly lead to more exciting discoveries involving regent honeyeater song learning, discoveries which will lead to continuing successes for the breeding and release program as well as ensuring the rehabilitation of wild regent honeyeater populations.

On a broader scale, this work investigating song learning in regent honeyeaters may help provide new perspectives on comparative song learning research. Studies have revealed a diversity of song learning trajectories in songbirds. After more than 50 years of research, this diversity is still not entirely understood. Comparative data and functional hypotheses need to be analysed in a phylogenetic context to gain further insights into what drives the evolution and ecology of song learning (Beecher and Brenowitz 2005). Out of the 4000 plus songbird species the majority of research is focused on North American and European species, neglecting large groups from regions such as Australia. Interestingly, oscine songbirds originated in the Australo-Papuan region and Meliphagoidea (honeyeaters) represent the largest radiation of Australian songbirds (Gardner et al.

2010). The current study represents the first investigation of juvenile song learning in a species of Australian honeyeater. Ultimately this work takes the first step in uncovering when, how and from whom regent honeyeaters learn their song. Now honeyeaters can now be included in future comparative analyses of songbird learning which will enrich our understanding of the diversity of songbird learning strategies. Furthermore, due to the numerous parallels between bird song learning and human speech learning, information on the evolution and diversity of song learning in birds may also shed light on questions related to human vocal evolution.

CONCLUSION

This is the first study to investigate song learning in regent honeyeaters. Overall, findings suggest male juvenile regent honeyeaters learn from a variety of adults including sires and older unrelated males. While juveniles are able to learn from tutors they can only hear, social interaction may influence song learning in important ways. The strategies these birds use to learn song may include both imitation and improvisation, and possibly also invention. While the current study was unable to assess if they are age-limited, young adult or open-ended learners, they may have a sensitive learning period that extends from 35 to 130 days old. Together these characteristics suggest juvenile regent honeyeaters display a flexible song learning programme that may be adapted to a nomadic/migratory lifestyle. However, future studies are required to assess whether populations both in the wild and at other captive locations show similar song learning programmes. This study represents the first investigation into song learning in an Australian honeyeater. Consequently this work will further comparative analyses designed to advance the understanding of song learning evolution and why it involves such remarkable diversity.

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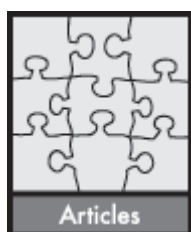
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If more than three authors, in the text:

Lehikoinen et al. (2014) or (Lehikoinen et al. 2014)

Books:

In the text:

Mayr (1963) or (Mayr 1963).

In the reference list:

Mayr, E. 1963. *Animal species and evolution*. Harvard Univ. Press.

Book chapters:

Goodall, D. W. 1972. Building and testing ecosystem models. In: Jeffers, J. N. R. (ed.), *Mathematical models in ecology*. Blackwell, pp. 173-194.

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