Mimicry in Regent Honeyeaters: is it really mimicry after all?

Ross Crates

Fenner School of Environment and Society, Australian National University, Linnaeus Way, Acton, Canberra 2601, Australia Email: Ross.crates@anu.edu.au

Received 4 July 2019; accepted 4 August 2019; published on-line 16 August 2019

The Regent Honeyeater *Anthochaera phrygia* is widely understood to mimic other species. To the best of our knowledge, amongst the Meliphagidae mimicry is unique to the Regent Honeyeater. An obvious question, therefore, is why does the Regent Honeyeater appear to be the only honeyeater to mimic other bird species? After spending 5 years monitoring the Regent Honeyeater throughout its range, here I propose that the incorporation of other species' songs into the repertoires of Regent Honeyeater should not be defined as "mimicry". Instead, I suggest that interspecific singing is maladaptive, confers no fitness advantage and is a consequence of the Regent Honeyeater occurring at population densities far below those in which it evolved. Low population density appears to be compromising the ability of some individuals to learn the species-specific song, probably due to a lack of other Regent Honeyeater demonstrators to learn songs from during a critical song-learning period in early life.

INTRODUCTION

Similar to humans, primates and parrots, many components of the vocal repertoire of songbirds (Passerines) are not innate. Instead, songbirds learn their songs, just as babies learn to speak, during a critical period in early life (Beecher & Brenowitz 2005). The ability to learn to sing 'correctly' is of crucial importance, because vocalisations have evolved to play key roles in social life-history. Just as language helps humans communicate, songs help birds to acquire mates and maintain territories (Arcese 1989), recognise relatives (Sharp *et al.* 2005) and defend against predators (Igic *et al.* 2015).

Many bird species have learned to incorporate the songs of other species into their own songs in a process defined as mimicry. Whilst the Superb Lyrebird *Menura novaehollandiae* is the classic example of a mimic (Dalziell & Magrath 2012), many other Australian birds are excellent mimics, including Olive-backed Oriole *Oriolus sagittatus* (Diamond 1982), Brown Thornbill *Acanthiza pusilla* (Igic *et al.* 2015) and Spotted Bowerbird *Chlamydera maculata* (Kelley & Healy 2010). Birds mimic other species because it provides them with a fitness benefit in some way, for example through mate acquisition, foraging efficiency, competitor deception, or nest defence (Igic *et al.* 2015; Dalziell *et al.* 2015).

The fact that mimicry conveys a selective advantage to the mimic is key to determining exactly which vocalisations can, and which cannot, be considered as mimicry. Dalziell *et al.* (2015) define a vocalisation to be mimetic if 'The behaviour of the receiver changes after perceiving the acoustic resemblance between the mimic and the model' (See **Box 1** for definition of key terms) and that 'the behavioural change of the receiver confers a selective advantage on the mimic.'

Box 1. Definition of key terms

- **Mimic** – an individual that sings the song of other species with a high degree of resemblance. In doing so, the mimic obtains a selective advantage by altering the behaviour of the recipient.
- **Recipient** – the individual receiving and interpreting the song from the mimic or the interspecific singer.
- **Model** – the species which the mimic or the interspecific singer has learned to sing like.
- **Interspecific singer** – an individual that has learned the song of another species with a high degree of resemblance, but receives either no, or negative, fitness costs from doing so.
- **Conspecific** – an individual of the same species.
- **Interspecific / Heterospecific** – an individual of a different species.
- **Fitness benefit** – a means by which an individual can enhance their lifetime breeding success or survival.

METHODS

We searched for Regent Honeyeater in the Capertee Valley in 2015 and throughout their contemporary breeding range between 2016 and 2018 (Crates *et al.* 2019). I recorded the songs of a sample of males and noted the location of any males that sang songs of other species. I also included verified public observations of interspecific singing by Regent Honeyeater during this period. I then compiled a database of historic records of interspecific singing by Regent Honeyeater, through a literature search and from personal communication with other Regent Honeyeater researchers.

RESULTS

In **Table 1** I have summarised known examples of interspecific singing by a male Regent Honeyeater. In those cases where the source of the information was not my own study, I have indicated either where the report was published or the name of the field worker who reported the observation to me.

Table. Records of interspecific singing in male Regent Honeyeater.

Species	Location	Year	Observer / reference
Red Wattlebird	Melbourne, VIC	1974	Veerman 1991
Anthochaera carunculata	Bundarra, NSW	1998	S. Debus
	Canberra, ACT	1992	Veerman 1994
	Chiltern, VIC	1988	R. Webster / Veerman 1994
	Capertee Valley, NSW	2008	Powys 2010
Little Wattlebird	Adelaide, SA	1977	H. Crouch / Veerman 1991
Anthochaera chrysoptera	Melbourne, VIC	1984	F. Smith / Veerman 1991
	Wyong, NSW	1991	Morris & Chafer 1991
	Dunbogan, NSW	2019	L. Murphy
	Guerilla Bay, NSW	2019	J. Morgan
	Coffs Harbour, NSW	2017	L. Murphy
	Lake Macquarie, NSW	2014	Roderick 2014*
	St Albans, NSW	2016 & 17	B. Hensen
Pied Currawong	Chiltern, VIC	2015	R. Crates
Strepera graculina	Kurri Kurri, NSW	2018	M. Roderick
New Holland Honeyeater	Chiltern, VIC	2015	R. Crates
Phylidonyris novaehollandiae			
Spiny-cheeked Honeyeater	Capertee Valley, NSW	2015	R. Crates
Acanthagenys rufogularis	Capertee Valley, NSW	2000	D. Geering
	Capertee Valley, NSW	2008	Powys 2010
	Barraba, NSW	2019	S. Debus
Noisy Friarbird	Barraba, NSW	2017	R. Crates
Philemon corniculatus	Capertee Valley, NSW	2018	
	Armidale, NSW	1991	A. Ley / Veerman 1991
	Chiltern, VIC	2018	D. Ingwersen
Little Friarbird	Capertee Valley, NSW	2016	R. Crates
Philemon citreogularis	Deniliquin, NSW	1992	P. Maher / Veerman 1994
Olive-backed Oriole	Capertee Valley, NSW	2015	R. Crates
Oriolus sagittatus			
Eastern Rosella	Emmaville, NSW	2016	R. Crates
Platycercus eximius	Armidale, NSW	1998	S. Debus
Black-faced Cuckoo-shrike	Wollongong, NSW	2018	R. Crates
Coracina novaehollandiae			
Noisy Pitta	Sydney, NSW**	2012	M. Roderick
Pitta versicolor			
Australasian Figbird	Sydney, NSW**	2008	S. Debus
Sphecotheres vieilloti			
Cockatiel	Sydney, NSW**	2008	Powys 2010
Nymphicus hollandicus			
Bush stone-curlew	Sydney, NSW**	2008	Powys 2010
Burhinus grallarius			

* This bird was also heard to include some 'snippets' of typical Regent Honeyeater song in its repertoire. See video at https://www.youtube.com/watch?v=55IQwd_ynH0.

** Denotes captive origin bird

DISCUSSION

Batesian vocal mimicry hypothesis

Given the need for mimicry to change the behaviour of the receiver to the benefit of the mimic, how might a Regent Honeyeater that sings the songs of other species benefit by changing the behaviour of another Regent Honeyeater or other bird species to their advantage? Veerman (1994) and Roderick (2014) suggest that singing like other, larger species such as Red *Anthochaera carunculata* or Little Wattlebird *A. chrysoptera* may reduce interspecific aggression from co-occurring honeyeaters during foraging. This theory, known as 'Batesian vocal mimicry' implies that a Regent Honeyeater singing like a larger, more dominant species can deceive other honeyeaters into thinking that a Regent Honeyeater *is* an individual of that other larger species, thereby reducing the rate at which it is chased off from nectar resources.

The Batesian hypothesis does at first seem plausible, especially given the struggles of Regent Honeyeater to compete for nectar against larger honeyeater species in unnaturally small flocks (Ford *et al.* 1993; Crates *et al.* 2017). Indeed, almost all records of interspecific singing in Regent Honeyeater (i.e. putative mimicry) involve larger model species (**Table 1**), suggesting that there may be a selective advantage to 'sounding bigger than one actually is.'

The Batesian mimicry hypothesis has limitations however (**Table 2**). Firstly, there is no evidence that a Regent Honeyeater singing like a larger species experiences less aggression when foraging than a Regent Honeyeater that sings like a Regent Honeyeater. Second, any selective advantage that a mimic may obtain by sounding like a larger species will immediately be lost at the point the recipient sees the mimic. Considering how active and abundant honeyeaters are during feeding bouts at rich blossom patches (Ford 1979; Ford *et al.* 1993), the length of time that a Regent Honeyeater could 'acoustically conceal' its identity by mimicking a larger honeyeater before being seen must surely be very short. Third, observation data shows that in many honeyeaters, most aggression is directed towards conspecifics (Ford 1979; Ford *et al.* 1993), in which case a Regent Honeyeater would still be subject to high levels of aggression even if it mimicked a different species. If there are advantages to sounding bigger, we might also expect acoustic mimicry to occur in a range of other small, co-occurring honeyeater species yet, to the best of my knowledge, no such evidence exists. Finally, one may suppose that the best way to avoid detection, and hence minimise aggressive displacement when feeding, would be to not sing at all; and this is exactly the strategy that male Regent Honeyeater employ to minimise predation risk when nesting (Ley & Williams 1994; R. Crates, pers. obs.).

Table 2. Evidence for and against the Batesian vocal mimicry and interspecific singing hypotheses for the Regent Honeyeater.

Batesian Vocal mimicry		**Interspecific singing**	
For	Against	For	Against
- Models invariably larger species	- Model species does not always co-occur with interspecific singer.	- More frequent in birds occurring at low population density.	?
	- No records of mimicry in any other Meliphagidae.	- Young captive-bred birds learned to sing like other, co-occurring species.	
	- Is relatively rare. Should be more common (selected for) if it confers a fitness advantage.	- Appears to be increasing in frequency concurrent with ongoing decline in population size and density. (Very rare in the Capertee Valley in 1990s).	
	- Interspecific singers never heard to sing any 'typical' Regent Honeyeater song. - Any benefits of vocal mimicry immediately lost when competitor sights the mimic.	- Anecdotal evidence of interspecific singing in other species e.g. starlings (Hindmarsh 1984), Prairie Warbler (Byers *et al.* 2013), Florida Grasshopper Sparrow (Ragheb *et al.* 2015).	

An alternative potential benefit of interspecific song learning in Regent Honeyeater is to improve chances of mate acquisition. Song appears to be a key component of courtship and territory acquisition for the Regent Honeyeater, as males sing directly 'at' both females and rival males with characteristic head bobbing behaviour (Ley & Williams 1994, Figure 1). In contrast to the observations of Veerman (1994), I can confirm that interspecific singing does occur in the Regent Honeyeater during the breeding season, though mostly only prior to nesting. Despite this new evidence, and despite further evidence that interspecific singers can successfully obtain a partner female and initiate nesting, I consider it unlikely that interspecific song learning improves the breeding success of a male Regent Honeyeater. Unlike mimicking species that increase the complexity of their species-specific song with songs of other species (Hindmarsh 1984), I have never observed an interspecific singing Regent Honeyeater also vocalise songs typical of Regent Honeyeater, despite monitoring some interspecific singers for many weeks during the breeding season. I have sometimes heard Regent Honeyeater-type calls in interspecific singers, but unlike songs, calls are innate rather than learned. In this instance, interspecific singing represents a replacement song rather than an enhancement of a species-specific song. It is hard to imagine a female being impressed by a male singing exclusively like a Black-faced Cuckoo-shrike *Coracina novaehollandiae* or a Pied Currawong *Strepera graculina*! (**Table 1**). In addition, we find that, although interspecific singers can be paired and initiate nesting, more often than random they are located away from the core breeding range, often in isolation (Veerman 1991). It is hard to determine cause and effect in this relationship. In other words, are interspecific singers less likely to find a mate because of their interspecific songs, or is the very reason they have interspecific songs because of a lack of co-occurring male Regent Honeyeater to learn from, and hence a lack of co-occurring females to mate with?

Erroneous interspecific song learning?

If interspecific singing provides a male Regent Honeyeater with no obvious fitness benefit, then why do they do it and why does it appear to be increasing in frequency? As Veerman (1991) suggests, the explanation is likely linked to the decline in population status of the Regent Honeyeater. Like most songbirds (Mennill *et al.* 2018), the Regent Honeyeater almost certainly learns to sing by replicating the songs of other male Regent Honeyeater that they co-occur with between the ages of 2 to 8 months (Vescei 2015). By one year of age, their songs are likely to be fixed for life (Beecher & Brenowitz 2005). Young male Regent Honeyeater are unlikely to learn songs from their fathers because, to avoid attracting predators, male Regent Honeyeater do not sing at all when raising young (R. Crates pers. obs.). Young birds also disperse away from their parents before they enter their song-learning phase, meaning young males must find 'another' singing male to learn their song from.

Given how sparsely distributed Regent Honeyeater nesting activity now is (Crates *et al.* 2019), it is entirely plausible that, after dispersing from the natal area, some young male Regent Honeyeater fail to locate any other males during their song-learning phase. Instead, these males learn the songs of other species they co-occur with during this period, hence the wide range of model species that interspecific singers have learned to sing like (**Table 1**). Long-distance nomadic wanderings of Regent Honeyeater likely explain why interspecific singers don't always co-occur with their model species when sighted (Franklin *et al.* 1998; Powys 2010). Hence, whilst interspecific singers are often found in association with the species they have learned songs from, we also find males in the Capertee Valley and Chiltern singing like Little Friarbird and New Holland Honeyeater *Phylidonyris novaehollandiae*, respectively, despite both model species being rare at these locations.

Due to their rarity and unpredictable post-breeding movements to largely unknown areas (Commonwealth of Australia 2016), our ability to gather monitoring data to test the interspecific song-learning hypothesis will always be limited. Nevertheless, it appears that the proportion of male Regent Honeyeater that are interspecific singers is increasing as the population decreases. I estimate that around 15% of the current wild male population are interspecific singers. Given that interspecific singers are more likely to occur away from the remaining core range and are therefore less likely to be found, 15 % may well be a conservative estimate. David Geering and Stephen Debus (pers. comm.) both report that incidence of interspecific singing in the Capertee Valley and Bundarra-Barraba, respectively, was rare in the 1990s, at which time the Regent Honeyeater population was around an order of magnitude larger than it is today (Commonwealth of Australia 2016).

There are a small number of published examples of other, isolated wild songbirds learning to sing the wrong songs. Most notably, Ragheb *et al.* (2015) report observing a critically endangered Florida Grasshopper Sparrow *Ammodramus savannarum floridanus* that had learned to sing like a co-occurring Bachmans's Sparrow *Peucaea aestivalis*. Similarly, Byers *et al.* (2013) report a Prairie Warbler *Setophaga discolor* that sang songs of a Field Sparrow *Spizella pusilla.* Perhaps the best available evidence in Regent Honeyeaters comes from the captive population at Taronga Zoo. Young birds housed in crèche aviaries appear to have learned the songs of other species present nearby, including Australasian Figbird *Sphecotheres vieilloti* (S. Debus pers. comm.) and Noisy Pitta *Pitta versicolor* (M. Roderick pers. comm.).

CONCLUSIONS

Interspecific singing in male Regent Honeyeater is a fascinating phenomenon. Similar to loss of languages in indigenous societies, it is sad to think that the severe population decline which the Regent Honeyeater has undergone may now be impacting the ability of the remaining population to maintain their song culture. With the standardised Regent Honeyeater monitoring data we have been gathering over the past 5 years, and with experiments planned to study song learning in captive Regent Honeyeater, we hope to gain a better understanding of this unusual behaviour, as Powys (2010) discusses, in the near future. One intriguing question remains: as Veerman (1991, 1994) noted, the model species that interspecific singing Regent Honeyeater have learned from are almost exclusively larger-bodied species (**Table 1**). Under the interspecific singing hypothesis, I see no reason why the Regent Honeyeater should not learn the songs of smaller species, yet they very rarely appear to do so.

ACKNOWLEDGEMENTS

I thank Hunter Bird Observers Club for funding my research on Regent Honeyeaters through the Wilma Barden Memorial Grant. Phillip Veerman, Mick Roderick, Dean Ingwersen, David Geering, Damon Oliver and Stephen Debus provided insightful discussion on putative mimicry by Regent Honeyeater. I also thank the referee for their helpful suggestions.

REFERENCES

Arcese, P. (1989). Territory acquisition and loss in male song sparrows. *Animal Behaviour* **37**: 45:55.

Beecher, M. D. and Brenowitz, E. A. (2005). Functional aspects of song learning in birds. *Trends in Ecology and Evolution* **20**: 143-149.

Byers, B. E., Kramer, B. A., Akresh, M. E. and King, D. I. (2013). Interspecific song imitation by a prairie warbler. *Journal of Field Ornithology* **84**: 181-186.

Commonwealth of Australia (2016). National recovery plan for the Regent Honeyeater. Available at http://www.environment.gov.au/biodiversity/threatened/recovery-plans/ national-recovery-plan-regent-honeyeater *anthochaera- phrygia*-2016.

Crates, R. A., Rayner, L., Stojanovic, D., Webb, M. H. and Heinsohn, R. (2017). Undetected Allee effects in Australia's threatened birds: implications for conservation. *Emu* **117**: 1-15.

Crates, R. A., Rayner, L., Stojanovic, D., Webb, M. H., Terauds, A. and Heinsohn, R. (2019). Contemporary breeding biology of critically endangered Regent Honeyeaters: implications for conservation. *Ibis* **161**: 521-532. doi: 10.1111/ibi.12659.

Dalziell, A. H. and Magrath, R. D. (2012). Fooling the experts: accurate vocal mimicry in the song of the superb lyrebird *Menura novaehollandiae*. *Animal Behaviour* **83**: 1401-1410.

Dalziell, A. H., Welbergen, J. A., Igic, B. and Magrath, R. D. (2015). Avian vocal mimicry: a unified conceptual framework. *Biological Reviews* **90**: 643-668.

Diamond, J. M. (1982). Mimicry of friarbirds by orioles. *The Auk* **99**: 187-196.

Ford, H. A. (1979). Interspecific competition in Australian honeyeaters: depletion of common resources. *Australian Journal of Ecology* **4**: 145-164.

Ford, H. A., Davis, W. E., Debus, S., Ley, A., Recher, H. and Williams, B. (1993). Foraging and aggressive behaviour of the Regent Honeyeater in northern New South Wales. *Emu* **93**: 277-281.

Franklin, D. C., Menkhorst, P. and Robinson, J. L. (1998). Ecology of the Regent Honeyeater *Xanthomyza phrygia*. *Emu* **89**: 140-154.

Hindmarsh, A. M. (1984). The functional significance of vocal mimicry in song. *Behaviour* **90**: 302-324.

Igic, B., McLachlan, J., Lehtinen, I. and Magrath, R. (2015). Crying wolf to a predator: deceptive vocal mimicry in a bird protecting young. *Proceedings of the Royal Society series B* **282**: doi: 10.1098/rspb.2015.0798.

Kelley, L. A. and Healy, S. D. (2010). Vocal mimicry in male bowerbirds: who learns from whom? *Biology Letters* **6**: 626-629.

Ley, A. J. and Williams, M. B. (1994). Breeding behaviour and morphology of the Regent Honeyeater *Xanthomyza phrygia*. *Australian Birdwatcher* **15**: 366-7.

Mennill, D., Doucet, S., Newman, A. E. M., Williams, H., Moran, I. G., Thomas, I. P., Woodworth, B. K.

and Norris, D. R. (2018). Wild birds learn songs from experimental vocal tutors. *Current Biology*. doi: 10.1016/j.cub.2018.08.011.

Morris, A. and Chafer, C. (1991). Unusual records for July and August 1991. *NSW Field Ornithologists Club Newsletter* **127**: 8-10.

Powys, V. (2010). Regent honeyeaters - mapping their movements through song. *Corella* **34**: 92-102.

Ragheb, E. L. H., Mezebish, C., and Lohr, E. (2015). Probable interspecific song learning in a Florida Grasshopper Sparrow (*Ammodramus savannarum floridanus*). The *Wilson Journal of Ornithology* **127**: 277-280.

Roderick, M. (2014). Observations of a Regent Honeyeater performing mimicry of a Little Wattlebird. *The Whistler* **8**: 58-59.

Sharp, S., McGowan, A., Wood, M. J. and Hatchwell, B. J. (2005). Learned kin recognition cues in a social bird. *Nature* **434**: 1127-1130.

Veerman, P. (1991). Vocal mimicry of larger honeyeaters by the Regent Honeyeater. *Australian Bird Watcher* **14**: 180-189.

Veerman, P. (1994). Batesian acoustic mimicry by the Regent Honeyeater *Xanthomyza phrygia*. *Australian Bird Watcher* **15**: 250-259.

Vescei, M. (2015). 'Juvenile song learning in Regent Honeyeaters *Anthochaera phrygia* at Taronga Zoo, Australia'. Unpublished Masters Thesis, Macquarie University, New South Wales.