Vocal mimicry in male lyrebirds

Sound choice and repertoire size as predictors of mating success

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INTRODUCTION

Amid the dense flora of the Australian rainforest, squat, gray-brown colored birds can be seen bowing forward, shimmying their tails—long, modified rectrices dancing about. From beneath a fantastic white veil of tail feathers, these birds deliver a series of melodic whistles and calls, each one borrowed from a species that doesn't quite match the singer. Rarely, even mechanical clicks and machinery from nearby human activity can be heard amongst their imitations. This memorable physical and vocal display is that of the lyrebird, one of the world's most celebrated and cherished mimics.

The lyrebird is considered a member of the more modern group of passerine birds, the Oscines (or songbirds). Unlike their more ancestral relatives, the Suboscines, songbirds must actually learn to sing, rather than being born with a distinct, innate call (Reilly, 1988). Only two representatives of their family (Menuridae) exist today: the Superb Lyrebird, *Menura novaehollandiae*, and Albert's Lyrebird, *Menura alberti*. One should not be misled into believing a large number of lyrebird species have passed into extinction, however, as only one other species exists in the fossil record (Robinson and Curtis, 1996).

At the start of the Tertiary period, the temperate rainforest environment the lyrebirds were accustomed to began to change from an open, cool landscape to one of thick vegetation. Because lyrebirds have limited flight abilities, they were restricted to life on the dense rainforest floor, and needed to increase vocal communication abilities through cultural transmission (Putland, et al., 2006). Employing vocal mimicry was an easy way for the lyrebirds to expand their collective species repertoire (Robinson and Curtis, 1996). Today, that repertoire is regarded as among the most impressive; taken together, the Albert's lyrebird and the Superb lyrebird are reputed to mimic upwards of 20 model songs (Reilly, 1988).

According to a study of vocal mimicry by Robinson (1974) and one of lyrebird mimicry by both Robinson and Curtis (1996), approximately 70-80% of a lyrebird's vocal display consists of mimicry. Why would an animal dedicate so much of its energy allocated for vocalization on sounds borrowed from other species? After all, utilizing mimicry potentially costs Oscine birds; in greater racket-tailed drongos, for example, incorrectly reproducing a sound means losing part of the intended signal (Goodale and

Kotagama, 2006a). Furthermore, choosing sounds in order to be recognized as a lyrebird and not as the model is a striking advertisement to potential predators. These costs lead one to wonder what benefits might justify such extravagant mimicry as seen in the lyrebird. In this paper, I explore the idea that these benefits are reproductively linked.

It is hypothesized herein that the impressive vocal mimicry of lyrebirds is utilized for the primary purpose of attracting mates, and that mimetic repertoire size and sound choice predict mating success in lyrebirds. The larger the repertoire of the male lyrebird, the more likely he is to succeed in mating. I hypothesize further that the male will prefer to mimic sounds which are complex, increasing display impressiveness—improving the ability to compete and leading to successful mating encounters.

The function of vocal mimicry in birds not at all well understood, despite the fact that about 15-20% of the world's bird species exhibit the behavior. There are a number of possible non-mating explanations for avian vocal mimicry, but a single explanation has yet to be developed. Confounding things further is the fact that lyrebirds are not well understood themselves. They are notoriously elusive and "shy" creatures, unless trained otherwise (Robinson and Curtis, 1996). This paper explores the purpose and predictive value of vocal mimicry in lyrebirds with special regard to the elements of interest in the hypothesis.

DISCUSSION

Sexual selection has long been considered the major force acting upon the evolution of birdsong, so the Idea that lyrebird mimicry is related to mating is not a unique one. Charles Darwin proposed intersexual selection as a factor in traits related to mate selection in 1871 (Howard, 1974), and the idea seems to have gone relatively uncontested. As sexual selection (particularly intersexual) is considered such a strong factor in both birdsong and mate selection, it is probable that there is a relationship between the two. The belief that birdsong is utilized primarily for reproductive benefit is widespread and generally accepted amongst the scientific community. While lyrebird mimicry is neither innate nor

comprised of its own species specific sound, it is as important a vocalization as any—particularly when one considers the large portion of other avian vocalizations that are learned rather than instinctual.

One thing scientist have noted in regard to lyrebird mimicry is that a male will tend to choose mimic models that do not have a breeding season which overlaps with his own (Robinson, 1974). It is unlikely, however, that this is done out of altruism. Robinson and Curtis (1996) suggest that by choosing models with non-overlapping breeding seasons, the mimic ensures that its vocalizations will be recognized as lyrebird mimicry rather than authentic song. This distinction is important to females, who would—in the absence of authentic model calls—understand these mimicked calls to be the lure of a potential mate. This choice of models with non-overlapping breeding seasons highlights the probability that lyrebird mimicry is a product of intersexual selection, and therefore a trait associated with mate attraction.

It has also been found that immediately prior to copulation, mimicry becomes less important with the male opting to vocalize in quieter, more specific sounds (Robinson, 1974). This is not terribly surprising, since loud, resonant mimicry has the potential to attract predators, and this single reproductive act is not one to be taken lightly. More importantly, however, this replacement of complex mimicry with simpler sounds may suggest that mimicry has more to do with initial mate attraction, and less to do with stimulating a physiological breeding response in the female.

There are, of course, alternative hypotheses which suggest that mimicry is utilized for species identification (in the case of brood parasites), or that it is used in mobbing or territorial behavior (Gooding and Kotagama, 2006b). In the case of the lyrebird, these explanations for mimicry are unlikely. Because lyrebirds are generally neither sources nor victims of brood parasitism, the first hypothesis is not likely to have any bearing in this case. With regard to territorial and mobbing behaviors, the resonant calls of a male lyrebird can certainly be recognized by other males. By moving around as he mimics, the singer gives other males an idea of the size and range of his territory. Mobbing behavior, however, is quite unlikely to be incited by lyrebird mimicry, considering the solitary nature of the animal (Reilly, 1988).

Now that the link between lyrebird mimicry and mating has been established, the focus can shift to repertoire size. According to Howard (1974), because natural selection tends to lean toward optimality in a system, the costs of mimicry (in time and energy) must be outweighed by the benefits of successful reproduction. Accumulating a large repertoire, then, may be one way of maximizing these benefits. There are 14 common models known to be mimicked by the Superb lyrebird and 9 mimicked by the Albert's. Additionally, there have been reports of 7-9 other calls mimicked by the Superb and a single Albert's hen mimicking a Nolay Pitta. Lyrebirds are also capable of mimicking non-bird sounds, such as those of nearby mammals or human machinery (Reilly, 1988). Clearly this creature spares no expense when it comes to expanding its repertoire.

Coleman, et al. (2007) state that in species such as the northern mockingbird and the marsh warbler, males have extremely large repertoires of over 100 models , and studies of these birds' mating success have shown a strong positive correlation between repertoire size and successful reproductive encounters. Coleman, et al. (2007) also mention that—as one might expect—lyrebirds show variation in the accuracy of their sound reproductions, and females tend to prefer the most accurate mimics. This mimetic accuracy gives females a measure of the male's physical fitness by expressing his capability to learn and imitate a wide range of sounds at potentially high energetic and temporal costs.

Coleman, et al. (2007) explored the relationship between mimetic repertoire size and mating success in satin bowerbirds (a common mimic model for Albert's lyrebirds) at Wallaby Creek in New South Wales, Australia. They hypothesized, as I do for lyrebirds, that the larger the number of species mimicked by the bowerbird, the greater the mating success. As expected, display information from 29 bower locations indicated a statistically significant positive correlation between the number of species mimicked and the number of successful mating encounters.

R.D. Howard (1974) studied the repertoire size hypothesis in mockingbirds, another famous mimic. In a study of ten central Texas mockingbirds and four west Texas mockingbirds, Howard found that larger repertoires led to a higher territorial rank, which in turn positively influenced mating success. He concluded that mockingbird repertoire size is a result of sexual selection, and that large repertoires

predict successful territory acquisition and mate attraction. References to similar predictive ability abound in the relevant literature, including in song sparrows. With such common results across such widely differing passerine birds, it would be reasonable to expect a similar predictive relationship in male lyrebirds.

The second area of interest is sound complexity, which is expected to have a positive correlation with mating success—like that of repertoire size. Song complexity broadcasts valuable information to the females regarding the condition of the male, his ability to learn and reproduce difficult sounds, and even the maturity of the caller. In Indian peafowl, the number of notes in a given peacock call is positively correlated with the sender's age, and females tend to prefer calls with greater than five notes (Yasmin and Yahya, 1996). This again relates to sexual selection, with peahens choosing more impressive males on the basis of song notes, and therefore maturity and reproductive ability. Since large repertoires in lyrebirds are likely to be preferential due to sexual selection, it is also very likely that sound complexity is selected for, as in Indian peafowl.

When simply examining the songs of the birds commonly mimicked by the lyrebird, it becomes obvious that these are not effortless sounds to reproduce—many of the models chosen by the lyrebird are excellent singers on their own. In fact, one of the most commonly mimicked models, the satin bowerbird, is itself considered one of the world's master mimics (Reilly, 1988). Naturally, a male lyrebird will learn to mimic species that occupy the habitat around him due to the fact that these are the only creatures he is exposed to, and because mimetic vocalizations are culturally transmitted. Because these mimic models do inhabit the same dense rainforest environment, they too must have fairly complex vocalizations which carry long distances and can potentially attract mates.

Some would argue that simpler sounds carry a lesser learning cost, and therefore allow a lyrebird to expand his repertoire more quickly. While simplicity may lend itself to quick learning, this would deprive the lyrebird of an important element of attractiveness to females—the fact that he is in good condition and *capable* of learning and accurately reproducing complex sounds. Replacing complex

models with simpler ones presents a cost-benefit trade-off: save time and energy, but lose perceived fitness (and potentially mating encounters).

Other supporters of song simplicity would say that simple sounds are more resonant, allowing mimicked calls to carry more easily throughout a territory. However, simple sounds are shorter and less elaborate in nature, and it is simply unlikely that such sounds could resonate through the dense vegetation of an Australian rainforest enough to attract females any more efficiently than complex sounds. As the fantastic learners and vocalists the lyrebirds are, choosing sounds with a greater complexity would be well worth the slight learning cost and result in a large net reproductive benefit, considering the female preference for complexity observed by Yasmin and Yahya (1996).

The heuristic value of this research to my personal development in the field of animal behavior has been severalfold. Through a thorough study of a topic somewhat narrow in focus, I have gained extensive proximal and theoretical knowledge of sexual selection, birdsong, vocal mimicry, and lyrebird natural history. By casting a wide net for relevant literature and digesting the contents of each paper in search of usable information, I was able to learn from not only the pieces relevant to my question, but from the seemingly extraneous knowledge presented in the literature as well. There was also heuristic value with regard to the field of study itself, in attempting to answer a question from all angles as opposed to tackling it directly.

Further research into lyrebird behavior might explore new means of documenting lyrebird displays for future studies, possible functions for mimicking non-natural sounds such as machinery, or what mimicry (if any) might occur if the bird is removed from its usual habitat and raised around an unusual set of neighboring birds. In a different vein of study, future vocal mimicry research might look deeper into the vocal learning abilities of bottlenose dolphins, which have been reputed so mimic computer generated sounds with surprising bird-like accuracy. This kind of research may help us draw evolutionary linkages between different classes of animals, especially considering the lack of vocal mimicry in terrestrial mammals (Richards, et al., 1984).

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