

Literature Review 3: Annotated Bibliography

This annotated bibliography is organized according to the information content of male and female koala bellows, how males respond to male and female koala bellows, and how females respond to male koala bellows. Each section is ordered chronologically.

Information content of male and female koala bellows

Charlton, B. D., Ellis, W. A. H., McKinnon, A. J., Brumm, J., Nilsson, K., & Fitch, W. T. (2011). Perception of male caller identity in koalas (*Phascolarctos cinereus*): Acoustic analysis and playback experiments. *PLoS ONE*, 6(5), e20329. <https://doi.org/10.1371/journal.pone.0020329>

Article Summary

This article investigated whether male koala vocalizations are unique to individuals and provide information about the caller's phenotype. Previous studies suggest a strong association between male koala bellows and reproductive activity, which includes intra-sexual competition and securing a mate. The main objectives of this study were to find out if male koala bellows are individually distinctive and whether male and female koalas have the ability to differentiate between male callers based on their bellows.

To carry out this study, recordings of male koala bellows were analyzed based on the source-filter theory of vocal production, where it is suggested that mammalian vocal signals are produced by the filtering of acoustic energy generated by the larynx (source) by the vocal tract (filter). The results of this study confirmed that male koala bellows are individually distinctive, suggesting that filter-related characteristics of male koala bellows are mainly responsible for producing identity cues within vocalizations. To determine whether koalas are able to differentiate between callers, playback experiments were carried out where six male and six female koalas were subject to hearing recordings of different koalas. The results of this portion showed that both male and female koalas exhibited reactions to changes in the identity of the caller koala in the recordings.

The authors suggest that future research should investigate the extent to which distance affects the information content of koala vocalizations. Furthermore, additional studies should be conducted on the filter-related characteristics of male koala bellows to determine their significance and role in vocal communication and recognition of koalas.

Article Contribution

This article was included in the literature review as it highlights the ability of both male and female koalas to distinguish between different male callers, which leads to further questions about how male koala vocalizations influence the reproductive behaviour of koalas. This study advances knowledge in the field of koala vocal communication by providing a foundation upon which future studies can build and add more information.

Charlton, B. D., Ellis, W. A. H., McKinnon, A. J., Cowin, G. J., Brumm, J., Nilsson, K., & Fitch, W. T. (2011). Cues to body size in the formant spacing of male koala (*Phascolarctos cinereus*) bellows: Honesty in an exaggerated trait. *Journal of Experimental Biology*, 214(20), 3414–3422. <https://doi.org/10.1242/jeb.061358>

Article Summary

This article examined how formants in male koala bellows represent body size. Previous studies suggest that male koala bellows function to repel rival males and mark territory and that

koalas can distinguish between calls of different males. The objectives of this study were to determine whether koala bellows possessed formants (differing frequencies of the source signal produced by the vocal tract) at all, if formant spacing is a reliable indicator of body size, and whether male koalas possess anatomical adaptations that allow them to modify vocalizations during call production.

In this study, Charlton et al. recorded the bellows of 20 male koalas and analyzed them through spectrograms. The head length of each koala was measured, as male koala body size is correlated to head length. The prominent frequency bands from the spectrograms were independent of the fundamental vocal frequency, or F0, bands indicating that koala vocalizations did in fact contain formants. Lower and closely spaced of formant frequency corresponded to longer head length, which suggests that formant spacing is indicative of body size. Furthermore, researchers discovered that male koalas had a permanently descended larynx and well-anchored sternothyroid muscle. This suggests that male koalas use these structures to modify the vocal tract during bellow production and produce lower formants, exaggerating their body size.

From these findings, the authors suggest further research must be conducted on whether the exaggeration of body size is mainly targeted for the determent of rival males or attraction of female koalas for mating.

Article Contribution

This article identifies the previously unknown information that is conveyed by male koala bellows. This information contributes to the study of koala social and mating behavior by highlighting the role of vocal communication in a predominantly solitary species. This generates ideas for future research based on koala vocalizations such as female koala bellows and their function.

Ellis, W., Bercovitch, F., FitzGibbon, S., Roe, P., Wimmer, J., Melzer, A., & Wilson, R. (2011). Koala bellows and their association with the spatial dynamics of free-ranging koalas. *Behavioral Ecology*, 22(2), 372–377. <https://doi.org/10.1093/beheco/arq216>

Article Summary

This article examined the function of male koala vocalizations and environmental influences on koala vocal communication. Previous studies have found that koalas are seasonal breeders that spend most of their time in trees, suggesting the importance of vocal communication in the organization of social structure in this species. The objectives of this study were to determine whether male koala bellows function mainly for intrasexual competition or female mate choice and if environmental factors have an influence over bellows.

To explore these objectives, the authors monitored koala vocalizations, movement patterns, and weather conditions in a population of free-ranging koalas over a time period of 12 months using GPS collars for tracking movement and remote sensor devices for recording bellows. The results of this study showed an association between female koala travel distances and male koala bellows, which suggests that although they also play a role in intrasexual competition, male koala bellows mainly function to attract female koalas for mating. The results also showed that the frequency of male koala bellows decreased during strong winds and hot nights, which suggests that bellowing is energetically costly for male koalas and environmental factors influence koala vocalization. The authors suggest that future research should investigate possible connections between paternity and male traits such as vocal signal transmission.

Article Contribution

This article supports previous findings that male koala bellows occur mostly during the breeding season. It advances knowledge in koala vocal communication as it suggests that bellow frequency is influenced by environmental factors and that male koala bellows function mostly for attracting mates.

Charlton, B. D. (2015). The acoustic structure and information content of female koala vocal signals. *PLoS ONE*, 10(10), e0138670. <https://doi.org/10.1371/journal.pone.0138670>

Article Summary

Previous studies on koala vocalizations have been focussed on the information content and function of male koala vocalizations while there had been little research on female koala vocalizations. Female koalas typically have one mate during an oestrous cycle and due to the relatively low reproductive potential of male koalas, it is likely that females must be selective of their partners. Furthermore, a previous study suggested that males and females that had mated in the past were more likely to mate during future breeding seasons. These findings indicate that female vocalizations may contain information about age and identity of the caller. This research article explored different types of female koala vocalizations and aimed to determine the information content within them. The objectives of this study were to classify different types of female koala vocalizations based on their acoustic structure and determine the information contained within these vocalizations.

For this study, vocalizations from 23 adult female koalas were recorded and analyzed. From the recordings, six types of vocalizations were identified: bellows, snarls, squeaks, squawks, wails, and screams. The last four types of vocalizations had overlapping acoustic features and were therefore grouped together and categorized as rejection calls that female koalas produce when rejecting copulation attempts by male koalas. Female koala bellows were found to be different from male koala bellows, suggesting that female vocalizations contain information about the sex of the caller. The results of the study indicate that female koala vocalizations contain information about age and sex of the koala, allowing them to be individually distinguished.

The author suggests that future research should investigate whether male koalas will use the information contained in female koala vocalizations to determine whether or not to approach a possible mate.

Article Contribution

This article advances knowledge of koala vocal communication by examining the vocal qualities of female koalas, which had previously not been as extensively studied as male koala vocalizations. The article builds on previous findings and generates possibilities for future areas of research centered around the role of female koala vocalizations in koala vocal communication. The article allows for the literature review to be more well-rounded, as the roles of both female and male koala vocalizations can be considered.

Charlton, B. D. (2021). Chapter 18 - Marsupial vocal communication: A review of vocal signal production, form, and function. In C. S. Rosenfeld & F. Hoffmann (Eds.), *Neuroendocrine Regulation of Animal Vocalization* (pp. 297–312). Academic Press.
<https://doi.org/10.1016/B978-0-12-815160-0.00002-5>

Article Summary

This book chapter reviews research that has been conducted on marsupial vocal anatomy, signal production, and communication. Marsupial vocalization is produced by a two-stage

process where the opening and closing of the vocal tract creates a source signal which is then modified by a structure called the supra-laryngeal tract, which is like a filter. This allows for the production of different frequencies, or formants, of the initial source signal. This two-stage process is referred to as the source-filter theory of mammal vocal signal production. There are anatomical limitations of koala and marsupial vocal signal production, where a decreased elasticity and musculature of the vocal tract results in a smaller range of vocal frequencies as well as tonal (pitched) sound.

In terms of marsupial vocal communication, research shows that male koala bellows increase during the breeding season and their formant frequencies are indicative of body size, suggesting that this allows females to choose larger males as mates. Female rejection calls have also been identified and studied, and it has been found that rejection calls are individually distinctive and play a role in stimulating the approach of rival males. The effect of hormones on vocal behavior and communication is not yet well known, as there has not been any research conducted. However, studies done on placental mammals suggest that F0 (fundamental frequency) characteristics of marsupials may vary according to testosterone levels. The author suggests that there may be a rise in estrogen levels during the reproductive period of female koalas, allowing them to produce lower frequency bellows.

The author highlights areas that need further research such as the extent of neural control over laryngeal muscles, the role of hormones in marsupial vocal behavior, and male koala responses to female koala distress calls.

Article Contribution

This book chapter provides a well-rounded and in-depth explanation of the mechanisms of koala vocalizations as well as the role vocal communication plays in mating behavior. The chapter also provides suggestions on further areas of research that are needed for a more complete understanding of the complexities of koala vocal signalling and behavior. This is a useful article to include in a literature review as it gives a good overview of what has and has not been researched in koala vocal behavior.

Male response to male or female koala bellows

Charlton, B. D., Reby, D., Ellis, W. A. H., Brumm, J., & Fitch, W. T. (2012). Estimating the active space of male koala bellows: Propagation of cues to size and identity in a eucalyptus forest. *PLoS ONE*, 7(9), e45420. <https://doi.org/10.1371/journal.pone.0045420>

Article Summary

This article investigated the effect of distance on the perception of male koala vocalizations. Previous studies suggest that male koala bellows occur mainly during the breeding season and contain information about body size and identity. This indicates that male koala vocalizations are important in relaying information to other males or females in the caller's habitat. The purposes of this study were to determine the distances at which male koala bellows could reliably and accurately represent the callers body size and identity as well as examine how different acoustic features in male koala vocalizations degrade with increasing distances.

To carry out this study, recordings of male koala bellows were played at various distances and the acoustic features of each recording at specific distances were analyzed. The results showed that male koala bellows remained individually distinct over distances of up to 150 m, which suggests that 150 m is the maximum distance at which other male or female koalas will be able to recognize different individuals based on their vocalizations. Koala home ranges

typically have a radius of 145 m, indicating that according to the results of this study, both male and female koalas will be able to interpret different vocalizations within their home range. Furthermore, this allows male koalas to determine whether or not to enter home ranges of rival males based on the bellows of the rival male koalas within their own home range.

The authors suggest more extensive research should be conducted on the ability of koalas to recognise other individuals solely based on vocal signaling in order to determine whether koalas possess true vocal recognition.

Article Contribution

This article advances knowledge in koala vocal communication as it provides information on the effect of distance on koala vocal signaling, an area of research that had not been previously studied. It supplements previous findings that male koala bellows function to relay honest information about the caller's body size and identity to other koalas. The article also places findings from previous research in the context of the natural environment of koalas, providing a more well-rounded understanding of the subject.

Charlton, B. D., Whisson, D. A., & Reby, D. (2013). Free-ranging male koalas use size-related variation in formant frequencies to assess rival males. *PLoS ONE*, 8(7), e70279.

<https://doi.org/10.1371/journal.pone.0070279>

Article Summary

In this study, the role of male koala vocalizations in intrasexual competition was examined. Previous studies have confirmed that formants of male koala bellows are indicative of body size and that these vocalizations have influence over reproductive interactions. Formants are the different frequencies produced by the modification of an initial source signal (which is produced by the opening and closing of the vocal tract) by the supra-laryngeal tract. It has also been confirmed that other male koalas are able to differentiate between different callers and can interpret whether a rival koala is large or small based on the formants their bellows. The objective of this study was to determine whether male koalas modified their behavioural response to various male koala bellows with formants indicating different body sizes.

To investigate, the researchers studied the response of 12 sexually mature male koalas in their natural environment to male koala bellows with formants indicative of large or small body sizes. The results showed that the subject koalas responded with longer bellows, bellowed for longer overall, and had a longer pause before bellowing in response when presented with a male koala bellow with formants corresponding to a large body size. These findings suggest that male koalas will adjust vocalization responses depending on the formants of other male koalas. The longer pause before responding to large koala vocalizations suggest that koalas are less willing to engage with larger, more dangerous rivals. Furthermore, longer bellows and overall duration of bellows in response to larger koalas may be indicative of a greater competitive potential of the responding koala.

For future research, the authors suggest that studies should be done on additional nonhuman mammal species to determine whether formants are indicative of body size for other animals or if it is exclusive to koalas.

Article Contribution

This article advances knowledge of vocal communication in koalas as it studied free-ranging koalas in their natural environment, whereas previous studies focussed on captive koalas, making it more representative of koala behaviour and vocal signaling in nature. The article supports and contributes to previous findings that koalas use the information about body size

contained in the formants of bellows to navigate intra-sexual competition as well as social and reproductive interactions. It is a useful article to include in the literature review as it provides a more in-depth understanding of koala vocal communication.

Charlton, B. D., Watchorn, D. J., & Whisson, D. A. (2017). Subharmonics increase the auditory impact of female koala rejection calls. *Ethology*, 123(8), 571–579.
<https://doi.org/10.1111/eth.12628>

Article Summary

This article explored the behavioural responses of male koalas to female koala rejection calls. Previous studies have suggested that female koalas produce vocalizations (squawks, screams, squeaks, wails, and snarls) when rejecting male koala copulation attempts that are categorized as rejection calls. These rejection calls contain non-linear phenomena, which are irregular vocal fold vibration patterns, that may create unpredictability within the vocalizations as well as increase the auditory impact of the vocal signal. The purpose of this study was to determine whether male koalas paid more attention to a male bellow or a combination of male bellows and female rejection calls. Furthermore, the influence of non-linear phenomena in female rejection calls on male koala response was examined.

To carry out this study, the response of ten free-ranging adult male koalas to single male bellows and single male bellows followed by female rejection calls were observed. The results showed that the male koalas looked for longer durations towards speakers playing the combination of male koala bellows and female rejection calls as well as rejection call sequences that contained more subharmonics. This suggests that the function of female koala rejection calls is to gain the attention of males. Doing so increases the probability for male-male competition, allowing the female to choose the male with the highest individual fitness as a mate.

The authors suggest that future research should focus on whether there are differences in vocal signals and communication across different regional habitats of koalas. Furthermore, they suggest that the significance of non-linear phenomena in other mammals should be examined and compared to that of koalas to determine whether this trait is exclusive to marsupials.

Article Contribution

This article advances knowledge in koala vocal communication by providing information on the function and impact of female koala vocalizations, an area of research that has not yet been extensively studied. Furthermore, because free-ranging koalas were the study subjects, this article provides a more accurate representation of vocal communication and signaling of koalas in their natural environment. This is an effective article to use in the literature review as it highlights the importance of the influence of female koala vocalizations in reproductive behaviour.

Female response to male koala bellows

Charlton, B. D., Ellis, W. A. H., Brumm, J., Nilsson, K., & Fitch, W. T. (2012). Female koalas prefer bellows in which lower formants indicate larger males. *Animal Behaviour*, 84(6), 1565–1571. <https://doi.org/10.1016/j.anbehav.2012.09.034>

Article Summary

This article investigated the response of estrous female koalas to male koala bellows corresponding to different body sizes. Although the amount of influence that vocalizations have over mate choice is undetermined, previous studies suggest that male koala bellows have an

association with reproductive activity due to the increase in the number of male koala bellows during the breeding season. Previous studies also suggest that male koala bellows relay accurate information about the caller's body size due to the presence of formants, or resonance frequencies in the vocal tract, where lower formants are indicative of a larger body size. The purpose of this study was to examine the influence of male koala bellows on the mate choice of female koalas.

To carry out this investigation, 16 estrous female koalas were each presented with male koala bellows that represented small and large body sizes. The researchers found that females would look for longer and more often at speakers presenting male bellows with lower formants and would move towards and stay close to the speakers. This suggests that female koalas prefer males with larger body sizes and will use information about body size contained in male koala bellows to choose larger mates.

The researchers suggest that further studies should be done on whether female koalas have ability to differentiate between medium versus large and medium versus small body sizes based on male koala bellows.

Article Contribution

This article highlights the role that vocal signalling plays in the reproductive behaviour of koalas by suggesting that different male koala bellows will influence female mate choice. It advances knowledge in the field as it was previously unknown whether female koalas used male koala vocalizations to make decisions concerning mates. Furthermore, it supports previous research that male koala vocalizations contain information about body size which affects reproductive behaviour.