Literature Review 3: Topic summary

As a solitary and nocturnal animal, koalas rely more heavily on vocal signaling than other cues to coordinate mating behavior (Ellis et al., 2011). Koala bellows consist of repeated inhalation/exhalation phases and increase during the breeding season (Charlton, Ellis, McKinnon, Brumm, et al., 2011). Current research on koala vocal communication suggests that the vocalizations of males and females contain information about the callers (Charlton, Ellis, McKinnon, Cowin, et al., 2011; Charlton, 2015), and receivers of these vocalizations may modify their behaviour depending on this information (Charlton, Ellis, et al., 2012; Charlton et al., 2013; Charlton et al., 2017)

Most studies have focused on the information content of male koala bellows and their function in a reproductive context. Charlton, Ellis, McKinnon, and Cowin et al. (2011) investigated whether there was a correlation between male koala bellows and the body size of the caller. Through statistical analyses of the head length of male koalas and formant spacing of their bellows, researchers found that lower and closely spaced formants corresponded to larger body sizes (Charlton, Ellis, McKinnon, Cowin, et al., 2011). Through measurements of the acoustic characteristics of male koala vocalizations at varying distances, Charlton and Reby et al. (2012) found that male koala bellows retained individually unique acoustic features over distances up to 150 m, a distance similar to that of the radius of a koala's home range, 145 m (Charlton, Reby, et al., 2012). These studies suggest that male koala vocalizations contain honest information about the caller's body size (Charlton, Ellis, McKinnon, Cowin, et al., 2011) and are intended to send information about the caller to other koalas within their home range (Charlton, Reby, et al 2012).

The response of females to male koala bellows provides information about the mating preferences of female koalas. In a study done by Charlton and Ellis et al. (2012), female koalas were presented with recordings of male koala bellows corresponding to different body sizes. The results of this study showed that females stayed close by and looked longer towards speakers playing bellows of larger male koalas (Charlton, Ellis, et al., 2012). This suggests that females prefer to mate with males that have larger body sizes as they likely possess higher individual fitness and have a greater chance for reproductive success (Charlton, Ellis, et al., 2012).

The response of rival males to male koala bellows provides information about intrasexual competition (Charlton et al., 2013). In a study done by Charlton et al. (2013), male koalas were presented with playbacks of rival bellows corresponding to small, medium, and large body sizes. It was found that when presented with bellows indicative of large body sizes, subjects would pause for longer before bellowing in response (Charlton et al., 2013). This suggests that koalas use the body size related information in the bellows of rival males to decide whether to engage with them and are more hesitant to engage in confrontation with a larger male than small or medium males (Charlton et al., 2013).

The information content and role of female koala vocalizations have also been researched. A study by Charlton (2015), recorded then analyzed vocalizations of female koalas and found that female bellows differed from male bellows (Charlton, 2015). Female vocalizations also consist of rejection calls that sound like squawks, wails, and screams produced by females when rejecting copulation attempts (Charlton, 2021). In a study by Charlton et al. (2017), male koalas were presented with recordings of male bellows and female rejection calls. The researchers found that the subject koalas looked longer towards speakers playing male bellows followed by female rejection calls (Charlton et al., 2017). These studies suggest that

female koala vocalizations function to notify receivers of their sex (Charlton, 2015) and grab attention from nearby rival males (Charlton et al., 2017).

Overall, koala vocalizations play important roles in reproductive behaviour. Existing research explores the information content of these vocalizations and how they influence mating behaviour. Future research should investigate the role of hormones in the development of koala vocalizations (Charlton, 2015). Additional studies should be conducted on whether koalas have neural control over vocalizations (Charlton, 2021) and whether male koalas can consciously alter bellows during vocalization (Charlton, Ellis, McKinnon, Cowin, et al., 2011).

Bibliography

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

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

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

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

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

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

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

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

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