

Original Article

Koala bellows and their association with the spatial dynamics of free-ranging koalas

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Acoustic communication mediates sociality in a variety of animals. One of the more ubiquitous vocal signals to have evolved is the sexual advertisement call of males. Koala (*Phascolarctos cinereus*) males emit a sonorous bellow call during the breeding season, but no detailed studies of the calling context appear to have been published. We used a novel remote sound detection network to monitor koala bellowing while simultaneously collecting koala behavioral data using collar-mounted GPS units. Our approach enabled us to examine fine scale temporal variation in vocalization and spatial movements of free-ranging koalas without direct behavioral observations. Bellow occurrence was susceptible to weather conditions, with fewer calls occurring when wind speed and temperatures were high. The number of bellow vocalizations recorded during an annual period mirrored breeding activity, with nearly all male bellows recorded during peak mating season. The distance traveled by koalas and the occurrence of koala bellows both peaked around midnight, but only female travel distance during the breeding season was temporally correlated with bellow occurrence. We conclude that environmental factors might trigger male bellowing to launch the breeding season and that these male vocal signals function more to attract females than to repel males. Female mate selection is probably an important component of male reproductive success in koalas, which is partly mediated by male bellow characteristics. *Key words:* GPS collar, koala, mate selection, remote acoustic monitor, vocalizations. [*Behav Ecol* 22:372–377 (2011)]

Animal vocalizations are used in a variety of contexts (Bradbury and Vehrencamp 1998). For example, fallow deer call to attract their fawns (Torriani et al. 2006), many primates utter copulation calls (Hauser 1996), and vocal sexual advertisements are prominent features of male reproductive tactics in a diverse array of taxa (Darwin 1871; Andersson 1996; Frey and Gebler 2010). However, interpretation of animal vocal communication requires not only that the sounds be described but also that the context of the vocalization be known (Lemasson et al. 2004). For example, male birds attract mates and repel competitors from their territory using vocal signals (Catchpole and Slater 2008), but the timing and function of vocalizations varies between species (Staicer et al. 1996; Dalziel and Cockburn 2008). In orangutans, *Pongo pygmaeus* (Mitani 1985; Rodman and Mitani 1987) and Thomas' langurs, *Presbytis thomasi* (Sterck et al. 2005), detailed field studies have revealed that male long calls function as mechanisms mediating male–male competition rather than female choice. In American bison, *Bison bison*, male bellowing also appears to mediate male–male competition and not female mate choice (Berger and Cunningham 1991; Wyman et al. 2008). Although it has often been assumed that song complexity regulates female mate choice, recent studies have revealed that complex vocal repertoires need not be associated with male reproductive benefits (Bernal et al. 2009).

Vocal complexity is common among the arboreal marsupials of Australia but is poorly understood for many of these species (Sharpe and Goldingay 2009). Koalas are seasonal breeders (Lee and Martin 1988; McLean and Handasyde 2006; Allen et al. 2010; Ellis et al. 2010) and males utter a low-pitched bellow, primarily during the breeding season (Smith 1980; Mitchell 1990; Martin and Handasyde 1999), but detailed field studies of bellowing have not been reported. Koalas regularly travel on the ground but spend most of their time in the trees (Martin and Handasyde 1999). When koala males bellow, they tend to sit below the tree canopy while pointing their heads upward (Smith 1980; Mitchell 1990; Martin and Handasyde 1999). Thermoregulatory constraints appear to affect koala movement patterns (Pfeiffer et al. 2005), and a nutrient poor diet restricts activity budgets (Krockenberger 2003). Furthermore, because atmospheric conditions and environmental surroundings influence sound transmission (Wiley and Richards 1978), bellowing could be dependent on temperature. The structure of the koala mating system remains unclear, and whether male bellows function to attract females and/or repel males is unknown. Encounters between male koalas are infrequent and often mediated by ritualized behavioral signals rather than physical contests (Martin and Handasyde 1999).

We adopted a novel technique for examining the functional significance of male bellowing. We conducted a 12-month study that continuously monitored sounds, koala movement patterns, and weather conditions in a single population of free-ranging koalas. We used a coordinated approach that recorded koala bellows with remote sensor devices and also monitored koala movement with GPS collars, in order to test

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whether bellows were more likely to be produced in the context of male–male competition or female mate choice. Simultaneously, remote weather sensors enabled us to examine the extent to which environmental factors are associated with bellowing. We hypothesized that if male bellows were intended to influence the behavior of other males, for example by establishing or maintaining territorial boundaries, then we would expect to detect changes in male ranging behavior associated with bellowing activity. Alternatively, if male bellows served as a mate attraction mechanism, then we would expect to detect changes in female ranging behavior to coincide with bellow dynamics. We present the first systematic data on vocal seasonality and the role of bellowing in the ecology of this iconic species.

MATERIALS AND METHODS

St Bees Island (lat 21°01'S, long 149°54'E) is a continental island of approximately 1000 ha in size that lies some 30 km off the coast of Queensland, Australia (Figure 1). The vegetation is characterized by *Eucalyptus tereticornis*-dominated woodlands, interspersed with rainforest gullies, open grassy slopes, and steep coastal slopes.

Six adult male (6.5 kg standard error of the mean [SEM] 0.86) and 6 adult female (5.2 kg SEM 0.73) koalas among a study population (ca. 250) on St Bees Island were caught using standard methods (Ellis et al. 1995). These 12 koalas were fitted with collar-mounted GPS loggers (Sirtrack, Havelock North, New Zealand), programmed to continuously record and store positional fixes at 2-hourly intervals.

GPS collars were calibrated by operating them with a clear sky view at a precise location (differential mode GPS; Trimble, Sunnyvale, CA), for 1 month prior to deployment. Each GPS logger recorded highest dilution of precision (HDOP) information for each location fix. Stationary collars at known locations with HDOP values below 2.1 were accurate to 8.58 m (SEM 0.64). These units still reported travel (measured as the distance covered between consecutive 2 h location fixes, each with HDOP value <2.1) unless apparent travel of less than 10 m was rejected, whereupon the stationary units reported no travel events. Hence, the travel distances that we report for koalas are limited to distances greater than 10 m, for consecutive GPS fixes with HDOP values less than 2.1. Travel data indicated that estimates of mean travel distance were affected by rare (<1%) large (>100-fold) excursions made by both male and female koalas during the year, so median (not mean) travel distance was selected to compare travel patterns among koalas.

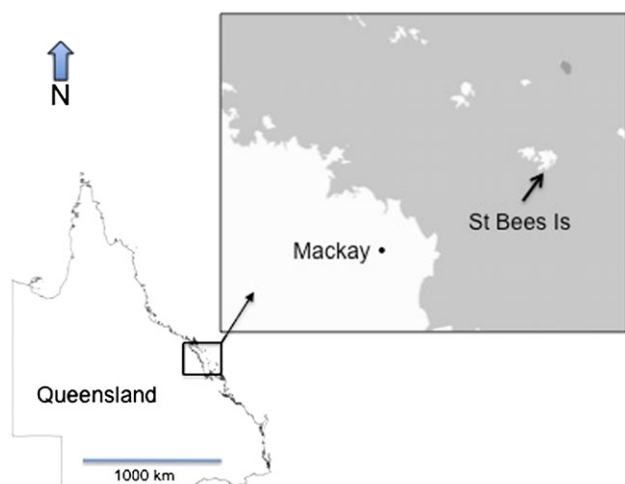


Figure 1
Location of the St Bees Island study site, Queensland, Australia.

Autonomous listening stations (3) consisted of a mobile cell phone (Dopod C730) powered by a deep cycle 12 V battery (model 67; Century, Brisbane, Australia) that was in turn charged by an amorphous solar panel (SS70M, 17.2 V; Shine Solar, Perth, Australia). A charge controller was fixed inside the battery housing, and the mobile phone was sealed within a waterproof case and placed beneath the solar panel (Figure 2). The phone antenna and external microphone were attached to raised aluminum arms at each end of the solar panel. Each phone was programmed to turn on and record sound for 2 min at 30-min intervals each 24 h and immediately upload the data to a central server at The Queensland University of Technology, via the Telstra phone network.

Sound recordings were listened to, visualized, and digitally tagged on a Web site (<http://www.sensor.mquter.qut.edu.au>) to identify koala bellows. Individual bellow components were identified from the audio-spectrogram, and the digital data were delivered in CSV format.

We used solar powered autonomous weather stations (Hastings, Ballina, Australia) to record and store data on temperature, wind speed, light intensity, and rainfall at our site.

Data sets generated from the digital tagging of recorded koala bellows, the GPS recordings of koala travel, and information from the environmental monitors were combined in Microsoft Excel and analyzed using the StatPlus package 1 (version Mac 2009; AnalystSoft Inc., Vancouver, Canada). The time, location, and duration of each bellow were recorded, and these data were collated into 2-hourly time intervals, which corresponded to the data generated by the GPS collars for koala travel. Bellow data were compared with environmental data using Spearman's rho to investigate relationships between weather variables and bellow characteristics, and the results for the bellowing and travel were similarly compared with detect associations between koala travel and bellowing at our site. Temporal patterns of travel were analyzed using paired *t*-tests for individuals between months (using individual median per 2-h time period) and using single factor analysis of variance (ANOVA) (again using median accounts of travel of individual males and females) for each time period. Incomplete data sets were available for the month of July, so 11 months of travel data were analyzed for general koala movement. Home range analysis was conducted using the Ranges 8 software package (Kenward and Hodder 1995).



Figure 2
Remote acoustic sensor system for detecting koala bellows at St Bees Island. The solar panel has a microphone extension attached to right, a battery on the ground beneath, and the cell phone is contained in a small waterproof housing under the solar panel.

Measures of central tendency report the mean and SEM. We used two-tailed statistical tests for all analyses and set the significance level at $P < 0.05$.

RESULTS

Home range and koala travel

Monthly home range size (adaptive kernel) averaged 1.47 ha (SEM 0.34, max 3.0 ha October, min 0.4 ha February) for females ($n = 6$) and 2.01 ha (SEM 0.28, max 3.2 ha September, min 0.9 ha April) for males ($n = 6$). The average number of travel records collected per month was 74 (SEM 0.85) for females and 68 (SEM 1.4) for males. For July, less than 30 travel observations were collected for any individual koala, so data for this month were excluded. There was a significant circadian effect on travel distance of koalas (data consisting of median travel distance per 2-h period for each koala: males $F_{1,11} = 2.83$, $P = 0.002$; females $F_{1,11} = 3.02$, $P = 0.002$) confirming that koalas are largely nocturnal.

Male travel distances appeared to be greater during the breeding season than at other times of the year (Figure 3), but whereas male travel was not correlated with month ($F_{1,10} = 1.6$, $P = 0.11$), female travel was ($F_{1,10} = 3.34$, $P = 0.0008$). However, for some individual males, travel distance during breeding season months was significantly greater than for non-breeding season months (e.g., Male 1: September vs. April $t_{12} = 3.82$, $P < 0.005$; September vs. March $t_{12} = 2.47$, $P < 0.05$). Analysis of the combined monthly data for all koalas revealed that there was no effect of gender on median distance of travel (single factor ANOVA $F_{1,20} = 1.49$, $P = 0.23$); for males, August was the month of greatest distance of travel and June the month of least distance of travel, and for females, the corresponding months were October and March (Figure 3).

Acoustic signals

Bellows were detected between 4 PM and 8 AM during the study (Figure 4), clustered between September and December, indicating a circadian and a seasonal effect. Koala bellows were generally recorded during the months of August–December, with very occasional outliers in other months. The bellows recorded for the free-ranging koalas at St Bees Island averaged 35.6 s ($n = 263$, SEM = 1.39), with a maximum broadcast duration of 2 min, which is similar in length to those recorded in captivity by Smith (1980). Koala bellows consist of inhale and exhale components (Smith 1980); at the height of bellowing activity, the average duration of each was 1.6 and 0.46 s, respectively. The frequency range of inhalation at the height of bellowing activity was approximately 80–750 Hz. Frequency range for exhalation at the height of bellowing was approximately 90–400 Hz.

There was an insignificant decrease in average bellow duration over the course of the study, from a peak of 37.9 s in

September to a low of 31.6 s in December ($t_{143} = 1.55$, $P = 0.06$).

Daily bellow occurrence was positively associated with the previous day's minimum humidity ($r^2 = 0.46$, $n = 122$, $P = 0.0472$) and negatively related to maximum nocturnal temperature ($r^2 = -0.52$, $n = 122$, $P = 0.027$). Bellow occurrence was also negatively associated with average nocturnal wind speed ($r^2 = -0.52$, $n = 122$, $P = 0.028$).

Movement and bellows

Median daily distance traveled by females, but not males, was positively correlated with daily bellow occurrence during the period between September and December (e.g., October: $r^2 = 0.789$, $P = 0.028$; Figure 5).

DISCUSSION

Our novel approach to studying the behavioral ecology of koalas revealed an association between female, but not male, travel distances and the incidence of bellowing, supporting the suggestion that bellows mediate mate choice by females more than competition among males. Research in captive koalas indicates that females in estrus are more active than nonestrous females (Johnston et al. 2000; Takahashi et al. 2009). At St Bees, the seasonal distribution of bellows corresponds with the seasonal patterns of female movement, suggesting that estrus females are probably searching for bellowing males. Only one of our female subjects with a GPS unit provided sufficient information to compare movement patterns with reproductive state. Based on her capture records, this female conceived in October, gave birth in November, and was carrying a pouch young when recaptured in May. Although sample size is only one koala, the evidence aligns with the more extensive data indicating that females travel more when searching for mates. In red deer, male roars hasten the onset of estrus (McComb 1987), and a more pronounced pattern might occur among koalas, given that they are induced ovulators (Johnston et al. 2000).

Our data confirm other studies that bellows are generally restricted to the mating season but extend our knowledge of context by revealing that bellow frequency is associated with specific weather conditions. Hot nights and strong winds are linked to a reduction in the occurrence of bellows, but the mechanism linking these environmental variables to call occurrence remains to be examined further. Although costs of bellowing are unknown, in both fallow deer (Vannoni and McElligott 2009) and bison (Wyman et al. 2008), male sexual advertisements decline in frequency over the course of the rutting season. Given nutritional constraints on koalas (Ellis et al. 1995; Krockenberger 2003), our finding that bellows are emitted less often toward the end of the mating season, and are reduced in frequency during hot nights, suggests that bellowing might exert an energetic cost on males. Furthermore, although koala fur is a better insulator against wind

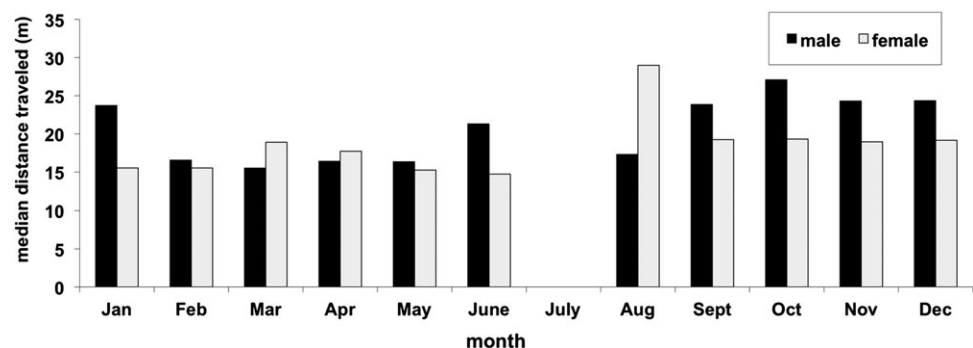


Figure 3
Monthly median distance moved (meter per 2-h sampling period) by koalas at St Bees Island, Queensland.

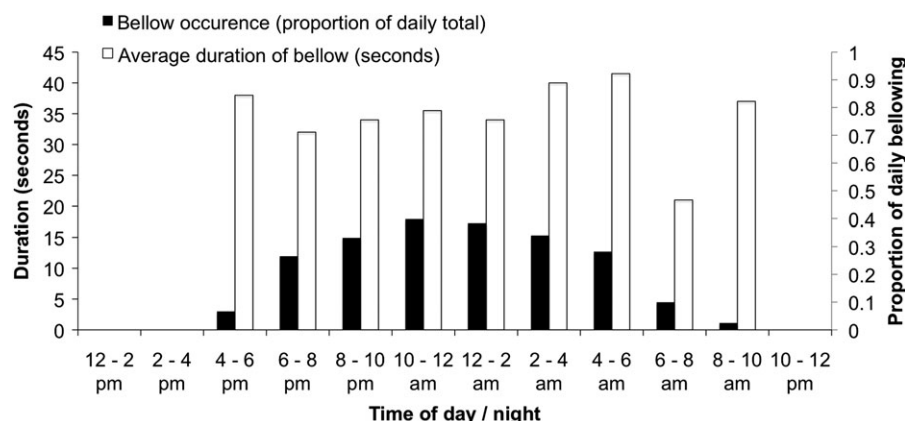


Figure 4
Diurnal variation in bellow duration (seconds) and proportion of bellows recorded at St Bees Island plotted against the time of day at St Bees Island, Queensland.

than the fur of other marsupials (Degabriele and Dawson 1979), it seems improbable that koalas would be attempting to limit heat loss at our study location during the breeding season, but perhaps ambient noise associated with wind discourages the broadcasting of bellows in this species. Low-pitched roaring vocalizations by males seem to incur more metabolic costs than often assumed (Frey and Gebler 2010), especially if male reproductive strategies are affected by time budget limitations that include reduced feeding during the mating season. Given that male-male physical confrontations among koalas are rare, bellowing traits could reveal aspects of male quality that are indicative of endurance rivalry (Andersson 1996) and have an impact on female mate choice.

Our study was not designed to assess bellow traits that might influence female mate choice, but our data reveal that male bellows probably function as mate attraction mechanisms. Vocal attributes mediating mate choice among animals differ across taxa, and no information is available that elucidates which components of the male bellow might be most attractive to females. For example, among red deer, the rate of roaring has an impact on female mate choice (McComb 1991), whereas bellow rate does not influence mating decisions among bison (Wyman et al. 2008). Although it is often assumed that specific call features regulate female mate choice in mammals, research linking sexual advertisements to fitness and female choice are sparse to nonexistent (McComb and Reby 2005; Charlton et al. 2007). Roaring is a common sexual selection advertisement emitted by a male and is character-

ized by a very low fundamental frequency, which can be influenced by a variety of factors, such as a lowered vocal tract, elongated throat, extension of the head, lengthened proboscis, or extra vocal mass (Frey and Gebler 2010). Koala males adopt a posture in the tree canopy when uttering the bellow roar that lengthens the vocal tract by tilting the head upward. Therefore, the positional behavior of the male koala, the low-frequency sound of the bellow, the near restriction of the bellow to the mating season, and the outbursts occurring more often when weather conditions favor sound transmission and reduction of metabolic costs, all indicate the likelihood that koala male bellows are an outcome of sexual selection.

Although koalas are solitary, the structure of their mating system remains unresolved. Paternity analysis at a different research site has shown that males who adopt alternative reproductive strategies can sire comparable numbers of joeys (Ellis et al. 2002). We have no data on bellow frequency from that site, and our remote sound detection system could not identify which male was bellowing, but genetic data from St Bees has revealed a strong male reproductive skew (Ellis and Bercovitch 2011). Future research has been designed to investigate potential links between paternity and male traits, including aspects related to sound transmission.

We found that bellows peak in occurrence prior to the peak of breeding activity and comparison of our data for bellowing with previous studies of breeding at this site confirm this (Figure 6), so bellowing may be a prebreeding behavior that influences male spacing. In koalas (Martin and Handasyde 1999) as well as other Australian marsupials (Tyndale-Biscoe and Renfree 1987; Hesterman and Jones 2009), testosterone concentrations in males follow an annual rhythm with peak levels appearing shortly before the onset of signs of estrus in females. Hence, the onset of spring in Australia, that is, September, could trigger androgen output in male koalas that stimulates bellowing activity. Although we cannot dismiss male bellowing as a spacing mechanism among males, our data on koala travel patterns are equivocal in this regard. Males had nonsignificant seasonal variation in their travel distance, and we found no significant relationship between bellow occurrence and patterns of male movement. On a month-to-month basis, some significant variation in male travel distance was observed for individual males, and males had the greatest range areas in August or the prebreeding season. Across the year, females show less site fidelity than males, suggesting that males may guard a smaller range to which they hope to attract a female. This could also indicate that male home range size is related to resource quality, explaining previous findings of no relationship between male body size and home range size (Ellis et al. 2009). Therefore, our data are more parsimoniously explained as an outcome of male sexual advertisements

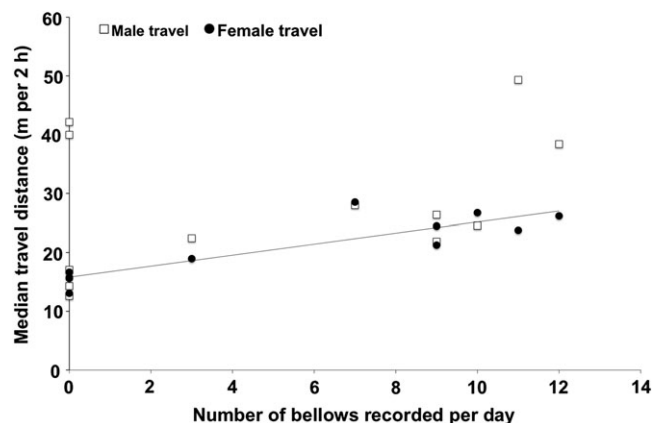


Figure 5
Number of bellows recorded per 24 h and median distance moved (meter) by male and female koalas during each sampling period (2 h) at St Bees Island, Queensland. Line displays linear regression of bellows on female travel ($R^2 = 0.79$, $P = 0.028$).

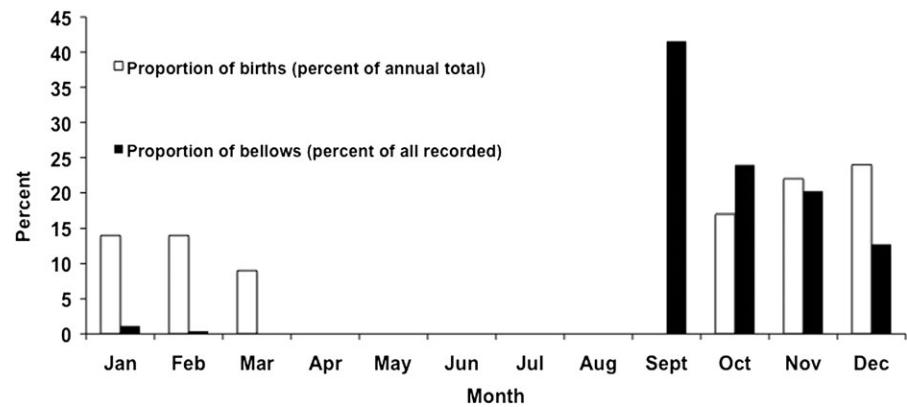


Figure 6

Comparison of monthly recordings of koala bellows at St Bees Island with published records of monthly koala births at the same location (Ellis et al. 2010).

aimed at influencing female mate choice more than repelling male competitors.

If bellowing were designed to attract a mate, we would expect most bellowing to occur at the time when most pairings are also predicted to occur because koalas are thought not to have a prolonged period of courtship. Alternatively, the peak could be an estrous-induction mechanism that primes females, who then search for males when estrus has been triggered, which is why they show less site fidelity than males. Hence, the onset of bellowing seems to be associated with environmental variables; the broadcast of bellows seems to not only attract females but might induce estrus; and the decline over the breeding season in bellows, combined with their greatest frequency during the night (Figure 4), suggests that bellowing has a metabolic cost to males.

Our report provides additional evidence of how sexual selection mediates koala reproduction. Among mammals, both acoustic and olfactory signals tend to be more pronounced among males than females and have been associated with sexual selection (Darwin 1871; Andersson 1996). Although not the subject of the current study, koala males have a sternal scent gland that is absent in females (Martin and Handasyde 1999). The chemical cocktail exuded by the male scent gland is much more complex during the mating, than nonmating, season, with initial production of scent output coinciding with maturation into adulthood (Tobey et al. 2009). The combined impact of male koala sound displays and scent output have been reasoned to mediate female mate choice (Bercovitch et al. 2006; Bercovitch 2007).

In conclusion, our use of novel technologies has provided insights into the koala mating system. Male bellow occurrence peaks immediately prior to the maximum breeding period but continues throughout the breeding months, a time when female koalas are maximizing the distance that they move. We propose that male bellows are a sexual advertisement broadcast to stimulate and attract females and that attributes of the bellow will be shown to be important mediators of female mate choice.

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REFERENCES

- Allen CD, de Villiers D, Manning B, Dique DS, Burrindge M, Chafer ML, Nicolson VN, Jago SC, McKinnon AJ, Booth RJ, et al. 2010. Seasonal reproduction in wild and captive male koala (*Phascolarctos cinereus*) populations in south-east Queensland. *Reprod Fertil Dev.* 22:695–709.
- Andersson M. 1996. Sexual selection. Princeton (NJ): Princeton University Press.
- Bercovitch FB. 2007. Connecting conservation biology with evolutionary ecology: the case of the koala. *Biodiversity.* 8:33–37.
- Bercovitch FB, Tobey JR, Andrus CH, Doyle L. 2006. Mating patterns and reproductive success in captive koalas (*Phascolarctos cinereus*). *J Zool.* 270:512–516.
- Berger J, Cunningham C. 1991. Bellows, copulations, and sexual selection in bison (*Bison bison*). *Behav Ecol.* 2:1–6.
- Bernal XE, Akre KL, Baugh AT, Rand AS, Ryan MJ. 2009. Female and male behavioral response to advertisement calls of greater complexity in tungara frogs, *Physalaemus pustulosus*. *Behav Ecol Sociobiol.* 63:1269–1279.
- Bradbury JW, Vehrencamp SL. 1998. Principles of animal communication. Sunderland (MA): Sinauer.
- Catchpole CK, Slater PJB. 2008. Bird song. Cambridge (UK): Cambridge University Press.
- Charlton BD, Reby D, McComb K. 2007. Female red deer prefer the roars of larger males. *Biol Lett.* 3:382–385.
- Dalziel AH, Cockburn A. 2008. Dawn song in superb fairy-wrens: a bird that seeks extrapair copulations during the dawn chorus. *Anim Behav.* 75:489–500.
- Darwin CR. 1871. The descent of man and selection in relation to sex. London: John Murray.
- Degabriele R, Dawson TJ. 1979. Metabolism and heat balance in an arboreal marsupial the koala (*Phascolarctos cinereus*). *J Comp Physiol.* 134:293–301.
- Ellis W, Bercovitch F. 2011. Body size and sexual selection in the koala. *Behav Ecol Sociobiol.* doi: 10.1007/s00265-010-1136-4.
- Ellis W, Bercovitch FB, FitzGibbon S, Melzer A, de Villiers D, Dique D. 2010. Koala birth seasonality and sex ratios across multiple sites in Queensland, Australia. *J Mammal.* 90:177–182.
- Ellis WA, Hale PT, Carrick F. 2002. Breeding dynamics of koalas in open woodlands. *Wildl Res.* 29:19–25.
- Ellis WAH, Melzer A, Bercovitch FB. 2009. Spatiotemporal dynamics of habitat use by koalas: the checkerboard model. *Behav Ecol Sociobiol.* 63:1181–1188.
- Ellis WAH, Melzer A, Green B, Newgrain K, Hindell MA, Carrick FN. 1995. Seasonal variation in water flux, field metabolic rate and food

- consumption of free-ranging koalas (*Phascolarctos cinereus*). *Aust J Zool.* 43:59–68.
- Frey R, Gebler A. 2010. Mechanisms and evolution of roaring-like vocalization in mammals. In: Brudzynski S, editor. *A handbook of mammalian vocalization*. London: Academic Press. p. 439–450.
- Hauser MD. 1996. *The evolution of communication*. Cambridge (MA): MIT Press.
- Hesterman H, Jones SM. 2009. Longitudinal monitoring of plasma and fecal androgens in the Tasmanian devil (*Sarcophilus harrisii*) and the spotted-tailed quoll (*Dasyurus maculatus*). *Anim Reprod Sci.* 112:334–346.
- Johnston SD, McGowan MR, O'Callaghan P, Cox R, Nicolson V. 2000. Studies of the oestrous cycle, oestrus and pregnancy in the koala (*Phascolarctos cinereus*). *J Reprod Fertil.* 120:49–57.
- Kenward RE, Hodder KH. 1995. *Ranges V—an analysis system for biological location data*. Version V. Dorset (UK): Institute of Terrestrial Ecology—Furzebrook research station.
- Krockenberger A. 2003. Meeting the energy demands of reproduction in female koalas, *Phascolarctos cinereus*: evidence for energetic compensation. *J Comp Physiol B Biochem Syst Environ Physiol.* 173:531–540.
- Lee A, Martin R. 1988. *The koala, a natural history*. Sydney (Australia): New South Wales University Press.
- Lemasson A, Richard J-P, Hausberger M. 2004. A new methodological approach to context analysis of call production. *Bioacoustics.* 14: 111–125.
- Martin R, Handasyde KA. 1999. *The Koala: natural history, conservation and management*. Sydney (Australia): UNSW Press.
- McComb K. 1987. Roaring by red deer stags advances the date of estrus in hinds. *Nature.* 330:648–649.
- McComb K. 1991. Female choice for high roaring rate in red deer, *Cervus elaphus*. *Anim Behav.* 41:79–88.
- McComb K, Reby D. 2005. Vocal communication networks in large terrestrial mammals. In: McGregor P, editor. *Animal communication networks*. Cambridge: Cambridge University Press. p. 372–389.
- McLean N, Handasyde K. 2006. Sexual maturity, factors affecting the breeding season and breeding in consecutive seasons in populations of overabundant Victorian koalas (*Phascolarctos cinereus*). *Aust J Zool.* 54:385–392.
- Mitani JC. 1985. Sexual selection and adult male orangutan long calls. *Anim Behav.* 33:272–283.
- Mitchell P. 1990. Social behaviour and communication of koalas. In: Lee AK, Handasyde KA, Sanson GD, editors. *Biology of the koala*. Chipping Norton (Australia): Surrey Beatty. p. 151–170.
- Pfeiffer A, Melzer A, Tucker G, Clifton D, Ellis W. 2005. Tree use by koalas (*Phascolarctos cinereus*) on St Bees Island, Queensland—report of a pilot study. *Proc R Soc Queensl.* 112:47–51.
- Rodman PS, Mitani JC. 1987. Orangutans: sexual dimorphism in a solitary species. In: Smuts BS, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. *Primate societies*. Chicago (IL): University of Chicago Press. p. 146–154.
- Sharpe DJ, Goldingay RL. 2009. Vocal behaviour of the squirrel glider (*Petaurus norfolkensis*). *Aust J Zool.* 57:55–64.
- Smith M. 1980. Behaviour of the koala, *Phascolarctos cinereus* (Goldfuss), in captivity. 3. Vocalizations. *Aust Wildl Res.* 7:13–24.
- Staicer CA, Spector DA, Horn AG. 1996. The dawn chorus and other diel patterns in acoustic signalling. In: Miller D, editor. *Ecology and evolution of acoustic communication in birds*. Ithaca (NY): Cornell University Press.
- Sterck EHM, Williams EP, van Hooft JARAM, Wich SA. 2005. Female dispersal, inbreeding avoidance and mate choice in Thomas' langurs (*Presbytis thomasi*). *Behaviour.* 142:845–868.
- Takahashi M, Tobey JR, Pisacane CB, Hamlin-Andrus C. 2009. Evaluating the utility of an accelerometer and urinary hormone analysis as indicators of estrus in a Zoo-housed koala (*Phascolarctos cinereus*). *Zoo Biol.* 28:59–68.
- Tobey JR, Nute TR, Bercovitch FB. 2009. Age and seasonal changes in the semiochemicals of the sternal gland secretions of male koalas (*Phascolarctos cinereus*). *Aust J Zool.* 57:111–118.
- Torriani MVG, Vannoni E, McElligott AG. 2006. Mother-young recognition in an ungulate hider species: a unidirectional process. *Am Nat.* 168:412–420.
- Tyndale-Biscoe C, Renfree M. 1987. *Reproductive physiology of marsupials*. Cambridge: Cambridge University Press.
- Vannoni E, McElligott AG. 2009. Fallow bucks get hoarse: vocal fatigue as a possible signal to conspecifics. *Anim Behav.* 78:3–10.
- Wiley RH, Richards DG. 1978. Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalizations. *Behav Ecol Sociobiol.* 3:69–94.
- Wyman MT, Mooring MS, McCowan B, Penedos MCT, Hart LA. 2008. Amplitude of bison bellows reflects male quality, physical condition and motivation. *Anim Behav.* 76:1625–1639.