Vocal Distinctiveness in the Harsh Coughs of Southern Hairy-Nosed Wombats (<italic>Lasiorhinus latifrons</italic>), Benjamin D. Charlton,
Acta Acustica **vol. 100** (Number 4), 2014, pp. 719-723

DOI
https://doi.org/10.3813/AAA.918750

ACTA ACUSTICA UNITED WITH ACUSTICA
Vol. 100 (2014) 719 – 723

DOI 10.3813/AAA.918750

Vocal Distinctiveness in the Harsh Coughs of Southern Hairy-Nosed Wombats (*Lasiorhinus latifrons*)

Benjamin D. Charlton
School of Psychology, University of Sussex, Brighton, East Sussex, U.K. b.d.charlton@sussex.ac.uk

Summary
Individual differences in vocal signals are documented in numerous mammals, yet little is known about marsupial vocalisations. In this study acoustic analysis based on source-filter theory was used to document the structure of Southern hairy-nosed wombat harsh coughs, and then to examine the potential for these calls to encode individual identity. The results show that harsh coughs are highly individualised and indicate that the formant structure of these calls provides potentially important information about the identity of callers. The ecological relevance of individual distinctiveness in this endangered species is discussed.

PACS no. 43.80.-n

1. Introduction

Empirical evidence for individual acoustic variation in vocal signals exists in a wide range of mammals [1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11]. Although few detailed acoustic studies have been conducted on marsupials (but see: [11, 12]), the presence of individual characteristics in marsupial vocalisations are also predicted to occur because individual differences in vocal production anatomy affect the acoustic structure of vocal signals [13, 14]. In addition, vocal distinctiveness is adaptive for animals that live in social groups, where selection to maximize differences between individual's vocalisations and for receivers to differentiate between callers would generally be expected [15, 16, 17, 18].

Southern hairy-nosed (SHN) wombats are herbivorous marsupials that inhabit the semi-arid grassland regions of Southern Australia [19, 20]. The predominantly nocturnal nature of the SHN wombat means that visual communication is likely to be restricted to infrequent associations. As a result, vocal communication could be important for coordinating this species' social behaviour. Furthermore, because SHN wombats live in complex burrows (or "warrens") that are shared by up to 10 individuals [21], they should have the opportunity to familiarize themselves with the calls of other group members and acoustically identify individuals that they have previously encountered. The SHN wombat's most conspicuous vocalisation is a short "harsh cough" that is characterized by deterministic chaos (episodes of non-random noise generated by chaotic vocal fold vibration) and is often produced when individuals come into close contact [19]. The information content and precise functions of these calls is unknown; however, predictions about which acoustic characteristics could provide receivers with reliable information about the caller's identity can be made [14, 22].

The source filter theory states that vocal signal production is generated by the conversion of airflow from the lungs to acoustic energy by the larynx, the source, which is then filtered by the vocal tract [23]. The rate the vocal folds in the larynx open and close determines the fundamental frequency (F0) of the vocalisation and the supralaryngeal vocal tract acts as a spectral filter, selectively transmitting certain frequencies called vocal tract resonances or 'formants' [24]. The length and shape of the vocal tract determines the frequency values and spacing of the formants, with longer vocal tracts producing lower, more closely spaced formants. Harsh or "noisy" calls are particularly good for revealing formants because the sound source has a very broad frequency spectrum and no harmonics (multiple integers of F0) that could potentially be confused with formants. Thus, the broadband noisy quality of SHN wombat harsh coughs makes them well suited for highlighting an individual's formant pattern [25, 26]. Furthermore, because inter-individual differences in vocal tract morphology are likely to exist, the formant structure of SHN wombat harsh coughs could yield information on a given caller's identity [3, 8, 11, 27, 28].

The goal of this study was to document the acoustic structure of SHN wombat harsh coughs and determine the importance of different acoustic components for coding individuality. To this end, I performed an acoustic analysis on the vocalisations of seven female SHN wombats before using a discriminant functions analysis to objectively categorise vocalisations to different individuals based solely

---

Received 11 November 2013,
accepted 7 February 2014.

on their acoustic structure. My findings will shed light on whether SHN wombat coughs could be used to acoustically signal information on caller identify, and add to a growing body of literature on the potential importance of source and filter-related acoustic cues in nonhuman mammals.

2. Methods

2.1. Study site and subjects

Harsh coughs were recorded from seven adult female SHN wombats ranging from 6–21 years at Australian Animal Care and Education's Project Kial, Malborough, QLD, Australia. To minimize the effect of individual variability in arousal levels, harsh coughs were recorded on at least two different days for each subject.

2.2. Recordings

Recordings were captured using a RØDE NTG-2 directional microphone and a H4N portable solid-state digital recorder (sampling rate: 48 kHz, amplitude resolution: 16 bits) at distances ranging from 2 -10 meters. The recordings were transferred to a laptop computer, normalized to 100% peak amplitude and saved as WAV files (48 kHz sampling rate and 16 bits amplitude resolution). The overall spectral structure of each harsh cough was initially investigated using narrow band spectrograms (see Figure 1: FFT method; window length 0.03 s; time steps = 250; frequency steps = 1000; Gaussian window shape; dynamic range = 45 dB) and recordings with high levels of background noise were discarded. This left a total of 134 harsh coughs from 7 individuals for the acoustic analysis.

2.3. Acoustic analyses

Acoustic features were extracted and measured using custom-built programs in Praat 5.0.29 DSP package (www.praat.org). Initial inspection of spectrograms confirmed that five frequency bands exist below 8000 Hz that could represent formants (Figure 1). Accordingly, I set the analysis in Praat to track and measure five formants in the frequency range 0–8000 Hz. Linear Predictive Coding (LPC; 'To Formants (Burg)' command in Praat) was used to measure the frequency values of the first five formant candidates using the following analysis parameters: time step: 0.01 seconds; window analysis: 0.03 seconds; maximum formant value: 6000–8000 Hz; maximum number of formants: 5; pre-emphasis: 50 Hz. To check if Praat was accurately tracking the formants the outputs were compared with visual inspections of relevant spectrograms and power spectrums (using cepstral smoothing: 500 Hz). The average formant spacing (ΔF) was then estimated using a regression method in which each formant value is plotted against its expected value (this method is covered in more detail in [29]). The intensity contour of each harsh cough was also extracted (To intensity command in Praat) to measure the minimum and maximum amplitude across the call in dB. Mean amplitude variation (Ampvar) was then calculated as maximum minus minimum amplitude.

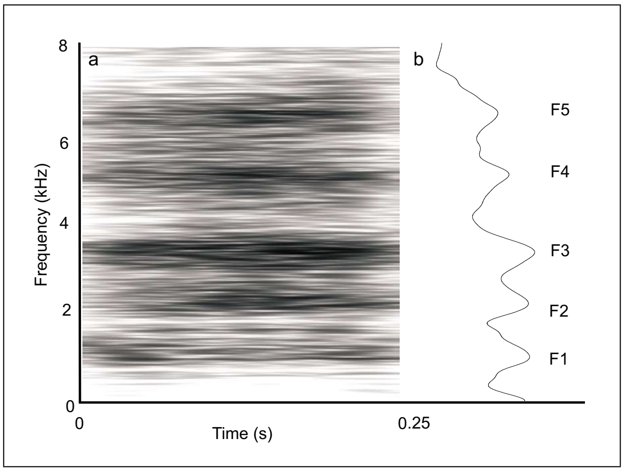

Figure 1. Spectrogram (a) and LPC spectrum (b) to show the acoustic structure of SHN wombat harsh coughs. The formants are labelled $F1$–$F5$. Spectrogram settings: FFT method, window length = 0.05 s, Gaussian window shape, dynamic range = 45 dB. The LPC spectrum is 500 Hz cepstral smoothed.

To verify whether the spectral peaks derived from the LPC analysis were formants I obtained a radiograph for one of the individuals in the analysis to measure the length of the supra-laryngeal vocal tract (glottis to lips), and then estimated vocal tract length (VTL) from the formant spacing of this individual's calls using the following equation: $\mathrm{VTL} = c/2\Delta F$ where c is the approximate speed of sound in the mammalian vocal tract (350 m/s) and the vocal tract is modelled as an idealised uniform-tube open at one end and closed at the other [24]. The measured VTL on the radiograph was 19.0 cm and the estimated VTL derived from the formant spacing was 19.1 cm. The close correspondence between the anatomically verified and estimated VTL confirm that the frequency components of harsh coughs are very likely to be formants.

2.4. Statistical analyses

A Discriminant Function Analysis (DFA) was used to classify the calls, with subject identity as the group identifier and the eight acoustic variables (duration, ampvar, $F1$, $F2$, $F3$, $F4$, $F5$, ΔF) as discriminant variables. For each classification, both the reclassification and the more conservative leave-one-out cross-validation procedure were applied. Because of uneven subject participation in the dataset the percentage correct classification expected due to chance was calculated according to the group sizes (see Table I). The statistical significance of correct classification of harsh coughs to each individual and across all subjects was obtained using the Chi square statistic. The statistical analyses were conducted using SPSS version 20 and significance levels were set at $P = 0.05$.

3. Results

3.1. Acoustic structure of SNH wombat harsh coughs

The mean ± SD duration of SHN wombat harsh coughs was 0.32±14 s. The duration of harsh coughs ranged between 0.16 and 0.96 s. No discernable $F0$ or harmonic structure was observed. Amplitude range was quantified by subtracting minimum from maximum amplitude in dB. Mean±SD amplitude range was 6.42±3.93 dB, with minimum and maximum values of 0.50 to 21.97 dB, respectively. Finally, there were five observable formants in the frequency range 0–8000 Hz. Mean±SD for $F1$–$F5$ and ΔF are as follows: $F1$ = 1278.22±253.94 Hz; $F2$ = 2382.43±220.85 Hz; $F3$ = 3408.47±253.12 Hz; $F4$ = 4373.19±243.75 Hz; $F5$ = 5323.38±168.48 Hz; ΔF = 1260.48±43.23 Hz. The formants were static across the call, indicating that very little articulation occurs during vocal production.

3.2. Individual differences in the acoustic structure of SNH wombat harsh coughs

The DFA correctly classified 78.4% of 134 harsh coughs to the 7 individuals, falling to 70.9% when a more conservative leave-one-out cross validation was applied. This level of classification was statistically significant for each individual and across all individuals (see Table I: all $P < 0.001$). In addition, the univariate analysis showed that duration, amplitude range, $F1$–$F5$ and ΔF all differed significantly between individuals (see Table II: all $P < 0.001$). The structure matrix generated by the multivariate DFA (Table III) shows that the main contributors to individual vocal distinctiveness were the upper formants and ΔF, which are likely to reflect differences in vocal tract length (see Table III for more information on the variance explained by each of the discriminant factors and the loading of each acoustic variable on these factors).

Table I. Observed % of correct classification against expected levels as calculated from group sizes. *P* values were obtained using the Chi square statistic.

Subject	N	Expected	Observed	*P*
Bella	46	34.3%	89.1%	<0.001
Cody	4	3.0%	50.0%	<0.001
Holly	21	15.7%	61.9%	<0.001
Isa	4	3.0%	100.0%	<0.001
Lolly	24	17.9%	79.2%	<0.001
Tjuka	10	7.5%	50.0%	<0.001
Wiggles	25	18.7%	84.0%	<0.001
Total	134	14.3%	78.4%	<0.001

Table II. Tests of equality of group means between individuals for each of the acoustic features used in the discriminant function analysis.

Measures	Wilks' lambda	*F*	*P*
Duration	0.516	19.856	<0.001
Ampvar	0.694	9.319	<0.001
$F1$	0.746	7.203	<0.001
$F2$	0.782	5.887	<0.001
$F3$	0.525	19.139	<0.001
$F4$	0.487	22.315	<0.001
$F5$	0.711	8.589	<0.001
ΔF	0.581	15.291	<0.001

Table III. DFA structure matrix showing pooled within-groups correlations between discriminating variables and standardized canonical discriminant functions. Largest correlation between each variable and any discriminant function are in bold. Variables ordered by absolute size of correlation within function.

Measures	Discriminant functions			
	1	2	3	4
$F4$	−0.626	0.333	0.273	0.222
$F3$	−0.566	−0.101	0.497	0.324
$F5$	0.545	0.518	0.034	0.323
ΔF	−0.425	0.089	0.718	0.228
$F2$	−0.137	0.194	0.290	0.692
$F1$	0.355	0.131	0.070	0.342
ampvar	0.190	0.515	0.272	−0.433
duration	0.088	−0.160	0.770	−0.331
Eigenvalue	2.263	0.864	0.552	0.318
% of Variance	55.6	21.2	13.5	7.8
Cumulative%	55.6	76.8	90.3	98.1

4. Discussion

4.1. Acoustic structure of SNH wombat harsh coughs

In this study I have provided a quantitative description of the acoustic structure of SHN wombat harsh coughs. Previous work on this species' vocal behaviour reported the social contexts that harsh coughs were delivered in and gave basic data on frequency components [19]. In particular, Gaughwin described the broadband noisy characteristic of these calls, the lack of harmonic structure, and the preponderance of energy at 2–3 kHz. The prominent energy band reported by Gaughwin appears to correspond to $F2$ and $F3$, which were also the highest amplitude frequency components of SHN wombat harsh coughs in the current study (see Figure 1).

The stable, flat formants of harsh coughs indicate that SHN wombats do not actively change the length or shape of their vocal tract during call production. This is consistent with observations of vocalising animals (B Charlton Pers. Obs.). In addition, unlike its close relative the koala (Phascolarctos cinereus) [30], SHN wombats do not appear to possess a descended larynx i.e. a larynx that is positioned low in the throat (B Charlton, Unpublished data). It has been suggested that a descended larynx may represent a mechanism for callers to lower formants in order to increase the impression of their body size to receivers [31]. Therefore, because the wombat's larynx appears to be positioned high in the throat, I suggest that selection pressures for SHN wombats to elongate their vocal tracts and maximize the acoustic impression of their body size conveyed to receivers do not exist. The lack of formant modulation in SHN wombat harsh coughs, however, does make these frequency components particularly well suited for identity cueing. Accordingly, it seems that the relatively stereotyped calling posture and lack of formant modulation in this species may actually facilitate the signalling of caller identity.

4.2. Individual differences in the acoustic structure of SNH wombat harsh coughs

These results show that SHN wombat harsh coughs are individually distinctive, with almost 71% of calls correctly assigned to individual callers using the more conservative "leave-one-out" cross-validated approach. Previous work on acoustic individuality in mammals, in which the biomechanical modes of production were considered, found source-related features (i.e. those produced by the larynx) to be the most highly distinctive [1, 4, 9] whereas other studies on humans and nonhuman mammals have emphasised the importance of formants as cues to individual identity [3, 8, 11, 27, 28]. The results of the current study show that the formants of SHN wombat harsh coughs are individually distinctive components of these vocalisations.

Because formant frequencies and spacing are explicitly linked to the shape and size of the vocal tract, which should vary between individuals, they are expected to be individually distinctive. In particular, the upper formants and overall spacing are expected to contribute to individual vocal distinctiveness because they are largely determined by the length of the vocal tract, and less affected by changes in its shape. Consistent with this, I found that the upper formants and ΔF of SHN wombat harsh coughs were the most individualised acoustic features. Vocal tract length is likely to be correlated to overall skull and body size [14, 32], this also indicates that inter-individual differences in formant structure are mainly generated by size-related differences between individuals. In addition, because harsh coughs are atonal calls that contain broadband energy they should emphasise formants, increasing their salience to receivers [25, 26, 32].

Accordingly, the atonal, noisy quality of SHN wombat harsh coughs may have evolved to facilitate vocal recognition by highlighting a caller's distinctive formant pattern. More generally, marsupial vocalisations often appear to be atonal, harsh or "noisy" (grunts, growls, squeals, snorts, hisses barks) [33, 34, 35, 36, 37], possibly reflecting the more primitive nature of the marsupial larynx [38] and a concomitant lack of sophisticated control over vocal fold vibration. The fused thyroid and cricoid cartilages of the marsupial larynx and the lack of striated muscle fibres in the vocal folds [38] are both likely to limit any fine adjustments to vocal fold length and, ultimately, the control of $F0$. Formants could, therefore, have particular relevance as cues in marsupial vocal communication systems.

The ability to signal individual identity may be important in SHN wombats for resolving disputes between dominant and subordinate individuals without resorting to direct physical confrontation. In addition, interactions between SHN wombats are likely to increase considerably during the breeding season when vocal distinctiveness may even have fitness benefits for female wombats in mate choice the contexts [39, 40]. The current study did not consider male harsh coughs because they are rarely produced (B Charlton, Pers. Obs). Nevertheless, females may prefer to mate with more familiar males, and information on caller identity could, therefore, be important in this context [41]. Future work should use playback experiments to investigate whether male and female wombats can recognise the calls of familiar versus unfamiliar individuals, and also to determine whether they perceive formant shifts in re-synthesized harsh coughs.

In conclusion, these results show that SHN wombat harsh coughs are individually distinctive vocalisations and point the way for further research. SHN wombats live in social systems where selection for vocal individuality may be strong [15, 16, 17, 18]. Whether they can recognize specific individuals using harsh coughs or even distinguish between the calls of different individuals would have to be proved unequivocally, however, the high degree of individual distinctiveness I have found in the acoustic structure of harsh coughs would make this a strong possibility.

Acknowledgement

Special thanks go to Peter Brooks and Tina Janssen (Australian Animal Care and Education) for allowing B. D. C. to record the SHN wombats. I would also like to thank Mackenzie Smith for help capturing the recordings and Dr. Stephen Johnston for helping to facilitate the research. This work was supported in part by a grant from the Wombat Foundation. B. D. C. was financially supported by a Leverhulme Trust Early Career Fellowship.

References

[1] B. D. Charlton, Z. Zhihe, R. J. Snyder: Vocal cues to identity and relatedness in giant pandas (Ailuropoda melanoleuca). J. Acoust. Soc. Am. **126** (2009) 2721–2732.

[2] D. Reby, J. Joachim, J. Lauga, S. Lek, S. Aulagnier: Individuality in the groans of fallow deer (Dama dama) bucks. J. Zool. **245** (1998) 79–84.

[3] D. Rendall: Acoustic correlates of caller identity and affect intensity in the vowel-like grunt vocalizations of baboons. J. Acoust. Soc. Am. **113** (2003) 3390–3402.

[4] E. Vannoni, A. G. McElligott: Individual acoustic variation in fallow deer (Dama dama) common and harsh groans: A source-filter theory perspective. Ethology **113** (2006) 1–12.

[5] D. Reby, B. Cargnelutti, J. Joachim, S. Aulagnier: Spectral acoustic structure of barking in roe deer (Capreolus capreolus). Sex-, age- and individual-related variations. C. R. Acad. Sci. III **322** (1999) 271–279.

[6] J. Soltis, K. M. Leong, A. Savage: African elephant vocal communication II: rumble variation reflects the individual identity and emotional state of callers. Anim. Behav. **70** (2005) 589–599.

[7] S. Semple: Individuality and male discrimination of female copulation calls in the yellow baboon. Anim. Behav. **61** (2001) 1023–1028.

[8] D. Reby, R. Andre-Obrecht, A. Galinier, J. Farinas, B. Cargnelutti: Cepstral coefficients and hidden markov models reveal idiosyncratic voice characteristics in red deer (Cervus elaphus) stags. J. Acoust. Soc. Am. **120** (2006) 4080–4089.

[9] K. McComb, D. Reby, L. Baker, C. Moss, S. Sayialel: Long-distance communication of acoustic cues to social identity in African elephants. Anim. Behav. **66** (2003) 317–329.

[10] D. T. Blumstein, O. Munos: Individual, age and sex-specific information is contained in yellow-bellied marmot alarm calls. Anim. Behav. **69** (2005) 353–361.

[11] B. D. Charlton, W. A. H. Ellis, A. J. McKinnon, J. Brumm, K. Nilsson, W. T. Fitch: Perception of male caller identity in koalas (Phascolarctos cinereus): acoustic analysis and playback experiments. PLoS ONE **6** (2011) e20329.

[12] M. Baker, D. Croft: Vocal communication between the mother and young of the Eastern gray kangaroo Macropusgiganteus, and the Red kangaroo, M-rufus (Marsupialia, Macropodidae). Aust. J. Zool. **41** (1993) 257–272.

[13] W. T. Fitch, M. D. Hauser: Vocal production in nonhuman-primates – acoustics, physiology, and functional constraints on honest advertisement. Am. J. Primatol. **37** (1995) 191–219.

[14] W. T. Fitch, M. D. Hauser: Unpacking “Honesty”: Generating and extracting information from acoustic signals. – In: Acoustic Communication. A. M. Simmons, R. F. Fay, A. N. Popper (eds.). Springer, New York, 2002, 65–137.

[15] I. Charrier, N. Mathevon, P. Jouventin: Mother’s voice recognition by seal pups – Newborns need to learn their mother’s call before she can take off on a fishing trip. Nature **412** (2001) 873–873.

[16] K. McComb, C. Moss, S. Sayialel, L. Baker: Unusually extensive networks of vocal recognition in African elephants. Anim. Behav. **59** (2000) 1103–1109.

[17] S. J. Insley: Long-term vocal recognition in the northern fur seal. Nature **406** (2000) 404–405.

[18] N. Mathevon, A. Koralek, M. Weldele, S. E. Glickman, F. E. Theunissen: What the hyena’s laugh tells: Sex, age, dominance and individual signature in the giggling call of Crocuta crocuta. BMC Ecology **10** (2010).

[19] M. D. Gaughwin: Socio-ecology of the southern hairy-nosed wombat (Lasiorhinus latifrons) in the Blanche Town region of South Australia. Ph. D. Thesis, University of Adelaide, 1981.

[20] R. T. Wells: Vombatidae. – In: Fauna of Australia Mammalia. D. W. Walton, B. J. Richardson (eds.). Australian Government Publishing Service, Canberra, 1989.

[21] B. Triggs: Wombats. Csiro Publishing, Collingwood, 2009.

[22] A. Taylor, D. Reby: The contribution of source-filter theory to mammal vocal communication research. J. Zool. **280** (2010) 221–236.

[23] G. Fant: Acoustic theory of speech production. Mouton, The Hague, 1960.

[24] I. R. Titze: Principles of voice production. Prentice Hall, Englewood Cliffs, New Jersey, 1994.

[25] M. J. Owren, D. Rendall: Sound on the rebound: bringing form and function back to the forefront in understanding nonhuman primate vocal signaling. Evol. Anthro. **10** (2001) 58–71.

[26] W. T. Fitch: Primate vocal production and its implications for auditory research. – In: Primate Audition: Ethology and Neurobiology. A. A. Ghazanfar (ed.). CRC press, Boca Raton, FL, 2002, 87–108.

[27] M. J. Owren, R. M. Seyfarth, D. L. Cheney: The acoustic features of vowel-like grunt calls in chacma baboons (Papio cyncephalus ursinus): Implications for production processes and functions. J. Acoust. Soc. Am. **101** (1997) 2951–2963.

[28] J. A. Bachorowski, M. J. Owren: Acoustic correlates of talker sex and individual talker identity are present in a short vowel segment produced in running speech. J. Acoust. Soc. Am. **106** (1999) 1054–1063.

[29] D. Reby, K. McComb: Anatomical constraints generate honesty: acoustic cues to age and weight in the roars of red deer stags. Anim. Behav. **65** (2003) 519–530.

[30] B. D. Charlton, W. A. H. Ellis, A. J. McKinnon, G. J. Cowin, J. Brumm, W. T. Fitch: Cues to body size in the formant spacing of male koala (Phascolarctos cinereus) bellows: honesty in an exaggerated trait. J. Exp. Biol. **214** (2011) 3414–3422.

[31] W. T. Fitch, D. Reby: The descended larynx is not uniquely human. Proc. Roy. Soc. Lond. B **268** (2001) 1669–1675.

[32] W. T. Fitch: Vocal tract length and formant frequency dispersion correlate with body size in rhesus macaques. J. Acoust. Soc. Am. **102** (1997) 1213–1222.

[33] J. F. Eisenberg, L. Collins, C. Wemmer: Communication in the Tasmanian devil (Sarcophilus harrisii) and a survey of auditory communication in the Marsupialia. Zeit. Tierpsychol. **37** (1975) 379–399.

[34] R. L. Goldingay: Loud calls of the yellow-bellied glider, Petaurus Australis – Territorial behavior by an arboreal marsupial. Aust. J. Zool. **42** (1994) 279–293.

[35] D. Pemberton, D. Renouf: A field-study of communication and social behavior of the Tasmanian Devil at feeding sites. Aust. J. Zool. **41** (1993) 507–526.

[36] D. J. Sharpe, R. L. Goldingay: Vocal behaviour of the squirrel glider (Petaurus norfolcensis). Aust. J. Zool. **57** (2009) 55–64.

[37] T. Soderquist, L. Ealey: Social interactions and mating strategies of a solitary carnivorous marsupial, Phascogale tapoatafa, in the wild. Wild. Res. **21** (1994) 527–541.

[38] J. Symington: The marsupial larynx. J. Anat. Physiol. **33** (1898) 31–49.

[39] M. L. East, H. Hofer: Loud calling in a female-dominated mammalian society. 2. Behavioral contexts and functions of whooping of spotted hyaenas, Crocuta-crocuta. Anim. Behav. **42** (1991) 651–669.

[40] D. Reby, M. Hewison, M. Izquierdo, D. Pepin: Red deer (Cervus elaphus) hinds discriminate between the roars of their current haremer stag and those of neighbouring stags. Ethology **107** (2001) 951–959.

[41] B. D. Charlton, Y. Huang, R. R. Swaisgood: Vocal discrimination of potential mates by female giant pandas (Ailuropoda melanoleuca). Biol. Lett. **5** (2009) 597–599.