Acoustic Differences in Loud Calls of Decken's and Crowned Sifakas (Propithecus deckenii and P. coronatus) at Two Sites in Madagascar

Author: Fichtel, Claudia

Source: Primate Conservation, 2014(28) : 85-91

Published By: Conservation International

URL: https://doi.org/10.1896/052.028.0105

Primate Conservation 2014 (28): 85–91

Acoustic Differences in Loud Calls of Decken's and Crowned Sifakas (*Propithecus deckenii* and *P. coronatus*) at Two Sites in Madagascar

Claudia Fichtel

Behavioral Ecology and Sociobiology Unit, German Primate Center, Göttingen, Germany

Abstract: Signals are important for species recognition. In this study, I examined the acoustic structure of loud calls ("Tchi-faks") in two populations of closely related lemur species in Madagascar, the Decken's and crowned sifakas (*Propithecus deckenii* and *P. coronatus*). Both populations exhibited a strong individual signature in the acoustic structure of Tchi-faks. Furthermore, Tchi-faks clearly differed in the acoustic structure between the two populations. Tchi-faks of Decken's sifakas at Bemahara were, on average, longer and have more energy in lower frequency ranges than Tchi-faks of crowned sifakas at Antrema. This variation is most likely due to anatomical differences of the vocal tract between the two species. However, loud calls of further populations need to be studied in order to understand whether the documented variation in loud calls represents species-specific signatures. In addition, to understanding whether these loud calls are important for species recognition, playback experiments are required to examine if sifakas themselves discriminate between calls of different species.

Key Words: vocalizations, acoustic structure, species recognition, *Propithecus coronatus*, *Propithecus deckenii*

Introduction

Signals are essential in species recognition (Bradbury and Vehrencamp 1998). The importance of signals for the evolution and diversification of taxa has been suggested in many species (Mayr 1963; Ryan and Rand 1999; Grant and Grant 2006; Robillard *et al.* 2006). On the one hand, species-specific signals can be considered a result of sexual selection in which they function as a premating isolation mechanism (Mayr 1963; Nevo *et al.* 1987). On the other hand, species-specific vocalizations can be a result of natural selection through adaptations of the acoustic structure of calls according to habitat properties in order to optimize their transmission (Morton 1975; Ryan *et al.* 1990; Brown *et al.* 1995). In particular, acoustic signals are considered to be important parameters in species-level taxonomic analysis, ranging from crickets, anurans and birds to mammals, including primates (Macedonia and Stanger 1994; Ryan and Rand 1999; Gray and Cade 2000; Grant and Grant 2006; Cap *et al.* 2008).

Loud or long distance calls of non-human primates are the most distinctive calls in the vocal repertoire and are common in most primates (Wich and Nunn 2002). They travel over long distances and have been suggested to transmit information pertaining to inter-group spacing and territorial behavior (Marler 1967; Waser 1982; Mitani 1985; Brown *et al.* 1995). They typically have a species-specific acoustic structure and have therefore been used to infer phylogenetic relationships (Oates and Trocco 1983; Macedonia and Stanger 1994; Nietsch and Kopp 1998; Zimmermann *et al.* 2000; Konrad and Geissmann 2006; Mendez-Cardenas *et al.* 2008; Merker *et al.* 2009; Thin *et al.* 2010).

In this study, I examined acoustic variation in loud calls, the Tchi-faks, of two populations of closely related lemurs, Decken's sifaka (*Propithecus deckenii*) at Bemahara and crowned sifaka (*P. coronatus*) at Antrema in Madagascar. Tchi-faks belong to the group of loud calls and are given by sifakas during inter-group encounters, for group coordination, and sometimes in response to terrestrial predators (Fichtel and Kappeler 2002, 2011). The Verreaux's sifaka group, inhabiting the west of Madagascar, has traditionally been considered as a single species comprising four subspecies (*P. verreauxi coquereli, P. v. coronatus, P. v. deckenii*, and *P. v. verreauxi*). Recently these taxa have been elevated to species level (Pastorini *et al.* 2001, 2003; Mayor *et al.* 2004; Groves and Helgen 2007; Mittermeier *et al.* 2008, 2010), though neither chromosomal nor molecular data support a separation

of *P. verreauxi*, *P. coronatus*, and *P. deckenii* (Pastorini *et al.* 2001, 2003; Rumpler *et al.* 2011).

Geographically, the *P. verreauxi*-complex occurs through much of western Madagascar with Coquerel's sifaka (*P. coquereli*) occurring north of the Betsiboka River and Verreaux's sifaka (*P. verreauxi*) occurring south of the Tsiribihina River (Tattersall 1986; Wilmé and Callmander 2006; Wilmé *et al.* 2006). The two other species, crowned sifaka and Decken's sifaka, occur in the region between these two rivers, mostly in allopatric or parapatric populations, but with several populations showing melanistic or possibly hybrid forms (Tattersall 1986; Curtis *et al.* 1998; Pastorini *et al.* 2001; Thalmann *et al.* 2002; King *et al.* 2012, 2014; Rakotonirina *et al.* 2014), and some isolated reports of possible co-occurrence of the two species (Tattersall 1982, 1988; Thalmann and Rakotoarison 1994; but see Rakotonirina *et al.* 2014 and King *et al.* 2014). It is, therefore, of particular interest to study whether these two species differ in the acoustic structure of their loud call to understand if these calls are used for species recognition, and whether they may function as a premating isolation mechanism preventing hybridization (Ryan and Rand 1999; Höbel and Gerhardt 2003; Grant and Grant 2006).

Methods

Study sites and acoustic analysis

Vocalizations (Fig. 1) were recorded of 12 adult crowned sifakas at Antrema, Katsepy, northwest Madagascar, and of nine adult Decken's sifakas at Tsingy Bemahara, western central Madagascar. The two sites are 370 km apart, and each currently supports only one of the sifaka species. Vocalizations were recorded using a Marantz PMD 670 CF-Recorder and a Sennheiser ME 80 directional microphone. Tchi-faks were elicited by presenting species-specific Tchi-faks given during group encounters via a loudspeaker (Davidactve, Visonik) hidden in the vegetation.

In order to obtain a balanced sample size, I selected 10–12 calls from each of nine Decken's sifakas and 12 crowned sifakas, resulting in 246 calls in total. Vocalizations were digitized using AVISOFT-SASLab pro 5.0.07 (R. Specht, Berlin, Germany). I visually inspected and sampled only calls of good quality and low background noise at a sampling frequency of 44.1 kHz. Next, I conducted a fast Fourier transformation (1024-pt FFT; time step: 5 ms; frequency range: 22.05 kHz; frequency resolution: 21 Hz) with AVISOFT-SASLab pro. Frequency-time spectra were analyzed with LMA 9.2, a custom software tool to extract different sets of variables from acoustic signals (Schrader and Hammerschmidt 1997). I focused on acoustic variables that characterize the general call structure and are comparable with acoustic variables that were measured in other studies characterizing the structure of mammalian vocalizations (Manser *et al.* 2001; Fichtel and Hammerschmidt 2002; Fichtel *et al.* 2005; Gros-Louis *et al.* 2008). Also, I briefly describe the acoustic variables that were used for the analysis (Fig. 1). I measured the mean duration, the mean frequency range, the mean peak frequency, and several variables of the central frequency (DFA2). The frequency range is the difference between the maximum and minimum frequency of a call. The peak frequency is the frequency with the highest amplitude. In order to characterize the frequency distribution of the call, I measured the statistical distribution of the frequency amplitudes across the spectrum. The frequency at which the cumulative sum of the frequency amplitudes (starting with the lowest frequency in the spectrum) reaches the median of the total distribution is the central frequency. Here, I measured the maximum, minimum and median of the central frequency. Acoustic variables entered in the analysis were revealed by Pearson's correlation analysis. I excluded variables exhibiting a correlation coefficient higher than 0.8; the remainder were kept and entered into the analysis.

Statistical analysis

I used a permuted discriminant function analysis (pDFA, Mundry and Sommer 2007) to identify acoustic differences of Tchi-faks. The discriminant function analysis provides a classification procedure that, based on the discriminant function, assigns each call to its appropriate group (correct assignment) or the other group (incorrect assignment). In order to cross-validate the discriminant functions that were generated for contexts, I used up to eight calls of each individual to create the discriminant function and up to four calls of each individual for the cross-validation of the original discriminant function. Since the discriminant function analysis is sensitive to number of variables entered in the analysis and to unbalanced sample sizes, I used a permuted discriminant function analysis to statistically evaluate the classification result. The permuted discriminant function analysis first creates 100 random selections of calls of the original data set to control for any possible random effects of call selection. In the next step 1000 randomized data sets are created. The

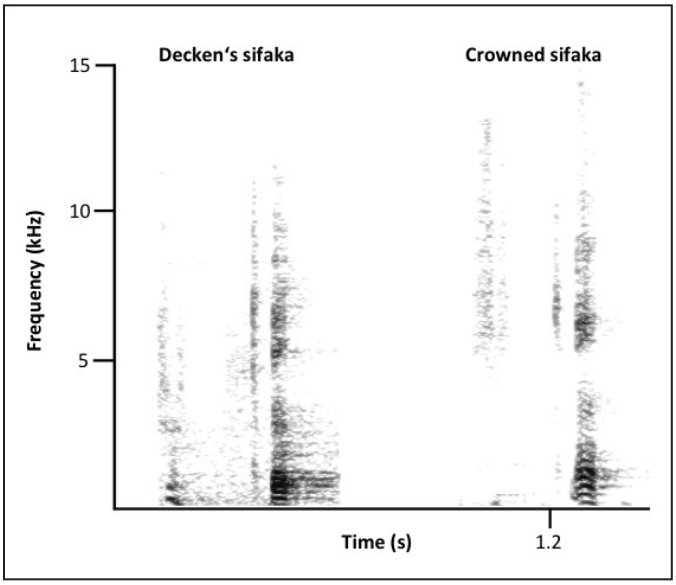

Figure 1. Spectrograms of Tchi-faks of Decken's and crowned sifakas.

permutation algorithm randomizes subjects between contexts, by this means controlling for the factorial (nested) structure of the data with subjects being nested within contexts. In the last step the permuted discriminant function analysis compares the mean correct assignment of the 100 original data sets with the correct assignment of the 1000 randomly created data sets (Mundry and Sommer 2007).

In total, I conducted three different permuted discriminant function analyses. Two permuted discriminant function analyses were conducted to characterize individual differences in the acoustic structure of the Tchi-faks of crowned and Decken's sifakas. The third discriminant function analysis was conducted to characterize differences in the acoustic structure of Tchi-faks between the two sifaka populations. For subsequent analysis of single acoustic variables such as duration and frequency range, I fitted a LMM with species as a fixed factor and ID as a random factor using the R software (R Development Core Team, Vienna, Austria, 2010) with the lme-package (Zuur *et al.* 2009).

Results

Decken's sifaka Tchi-faks: acoustic structure and individuality

Tchi-faks of Decken's sifakas at Bemahara were characterized by a mean duration of 267 ± 52 ms (Fig. 1; Table 1). They had a frequency range of, on average, 3552 ± 1014 Hz, and a central frequency of, on average, 2347 ± 576 Hz. The discriminant function analysis revealed a correct assignment of calls to each of the nine individuals of 85% and a correct assignment of the cross-validation of 78%. The correct assignment of the original data sets differed significantly from the correct assignment of the random data sets (P = 0.001). The correct classification of the remaining calls for the cross-validation of the original data set did not differ from the random data sets (P = 1).

Crowned sifaka Tchi-faks: acoustic structure and individuality

Tchi-faks of crowned sifakas at Antrema were characterized by a mean duration of 219 ± 63 ms (Fig. 1; Table 1). They had a frequency range of, on average, 4698 ± 2131 Hz, and a central frequency of, on average, 4322 ± 1237 Hz. The discriminant function analysis revealed a correct assignment of calls to each of the 12 individuals of 69% and a correct assignment of the cross-validation of 61%. The correct assignment of the original data sets differed significantly from the correct assignment of the random data sets (P = 0.001). The correct classification of the remaining calls for the cross-validation of the original data sets did not differ from the random data sets (P = 1).

Comparison of the acoustic structure of Tchi-faks between the two populations

The discriminant function analysis revealed a correct assignment of calls to the two populations of 96% and a correct assignment of the cross-validation of 99%. The correct assignment of the original data sets differed significantly from the correct assignment of the random data sets (P = 0.001). In addition, the remaining calls withheld for the cross-validation of the original data sets were also better correctly classified than the random data sets (P = 0.001). A subsequent LMM revealed that Tchi-faks between the two populations differed significantly in all acoustic variables, except the mean frequency range (Fig. 2a, 2b; Table 2). Thus, calls clearly differed in their acoustic structure between the species at the two locations sampled. Calls of Decken's sifakas at Bemahara were, on average, longer and had more energy in lower frequency ranges than calls of crowned sifakas at Antrema.

Table 1. Mean (± SD) of the analyzed acoustic variables of the Tchi-faks of Decken's sifakas at Bemahara and crowned sifakas at Antrema, Madagascar.

Acoustic variables	Decken's sifakas	Crowned sifakas
Duration	267 ± 52 ms	218 ± 63 ms
Maximum central frequency	5614 ± 1051 Hz	7051 ± 875 Hz
Minimum central frequency	1055 ± 131 Hz	1154 ± 214 Hz
Median central frequency	2347 ± 576 Hz	4322 ± 1237 Hz
Mean frequency range	3552 ± 1014 Hz	4698 ± 2131 Hz
Mean peak frequency	1097 ± 422 Hz	1672 ± 704 Hz

Table 2. Estimate, Standard errors and p-value for each Linear Mixed Effects Model.

Acoustic variables		Estimate	Std. Error	p-value
Duration	Intercept	216.85	15.41	<0.001
	Species	49.61	23.53	0.048
Maximum central frequency	Intercept	7039.67	211.84	<0.001
	Species	-1423.35	323.41	<0.001
Minimum central frequency	Intercept	216.85	15.41	<0.001
	Species	49.61	23.53	0.048
Median central frequency	Intercept	4297.03	270.61	<0.001
	Species	-1956.18	413.28	<0.001
Mean frequency range	Intercept	4644.17	466.06	<0.001
	Species	-1092.82	711.77	0.14
Mean peak frequency	Intercept	1671.34	124.47	<0.001
	Species	-572.18	189.98	0.007

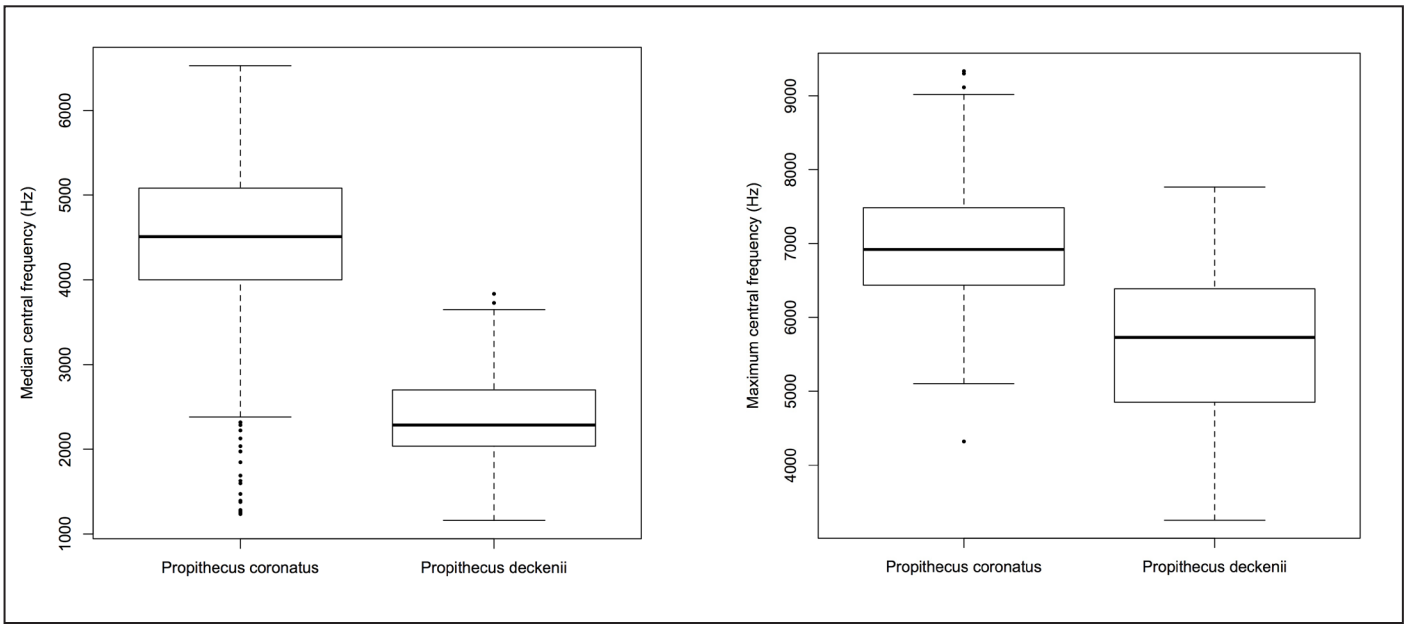

Figure 2. Boxplot of (a) the median central frequency and (b) the maximum frequency of Tchi-faks of crowned sifakas (*Propithecus coronatus*) at Antrema and Decken's sifakas (*Propithecus deckenii*) at Bemahara. Represented are median (black bars), interquartile range (boxes), upper and lower hinge (whiskers) and outliers (circles).

Discussion

This study shows that the Tchi-faks of both Decken's and crowned sifakas are highly individually distinctive. Individual distinctiveness in vocalizations has also been shown in other lemur species (Macedonia 1986; Oda 2002; Gamba *et al.* 2012). In addition, the acoustic structure of the Tchi-faks clearly differs between the two locations sampled. They differed in duration but also in four of the five measured frequency-related variables—Tchi-faks of Decken's sifakas at Bemahara are, on average, longer and have a lower pitch as measured by lower frequency values of the maximum, minimum and the median of central frequency and peak frequency than those of crowned sifakas at Antrema. This variation might be the result of ecological factors, genetic differences and/or anatomical differences.

As habitat type affects sound transmission (e.g., Wiley and Richards 1978), animals are expected to adapt their vocal behavior to the structural and acoustic properties of the environment they inhabit ("The habitat adaption hypothesis," Morton 1975). Some studies have found support for this hypothesis (Ryan and Brennowitz 1985; Ey *et al.* 2009), whereas others have not (Brown *et al.* 1995; Daniel and Blumstein 1998). Since the habitat at both sample locations for this study is characterized by dry deciduous forest, it is unlikely that ecological factors will explain diversification of the Tchi-fak calls between the two sifaka populations.

In some primates, acoustic differences in vocalizations have been shown to be in concordance with genetic differences (Merker *et al.* 2009; Thin *et al.* 2010; Markolf *et al.* 2013). Since Decken's and crowned sifakas do not exhibit large differences in mitochondrial DNA (Pastorini *et al.* 2001, 2003; Rumpler *et al.* 2011), a genetic basis underlying structural differences in Tchi-faks is rather unlikely. However, more research combining analyses of molecular and acoustic data are required to understand whether the described acoustic differences may have a genetic base.

The anatomy of the vocal tract influences the acoustic structure of vocalizations in a variety of species (Fitch 1997; Reby *et al.* 2005; Gamba and Giacoma 2006; Charlton *et al.* 2009). For example, in rhesus macaques (*Macaca mulatta*) formant frequency dispersion is correlated with vocal tract length and body size (Fitch 1997). Analysis of sifaka museum specimens show that crowned and Decken's sifakas differ in several cranio-dental measurements as for example bicanine and biorbital breadth or skull length measured as the condylobasal length: crowned sifakas have a more deepened and much broader snout than Decken's sifakas (Groves and Helgen 2007). Thus, acoustic differences in call structure might be due to different shapes of the vocal tract.

However, to understand if these calls are important for species recognition, further populations need to be studied to analyze potential geographical variation within species. For example, in Verreaux's sifakas the acoustic structure of Tchi-faks clearly differed in three geographically separated populations, suggesting that there is strong geographical variation in this closely related species (Fichtel, unpubl. data). Divergence in acoustic signals between populations can lead to species recognition failure, reproductive isolation, and speciation. In some species individuals diverge more in call structure in sympatry than in allopatry (Höbel and Gerhardt 2003; Kirschel *et al.* 2009). Such character displacement occurs where the ranges of two closely related species overlap, and morphological, ecological, or behavioral traits

diverge in sympatry, facilitating coexistence of species in natural communities (Brown and Wilson 1956; Grant and Grant 2006).

Finally, to understand whether sifaka calls may function as a premating isolation mechanism, playback experiments are required to demonstrate whether sifakas discriminate between calls of different species, and use these calls for species recognition to avoid hybridization. These results would have important implications for future conservation management plans.

Acknowledgments

I thank Prof. Dr. Daniel Rakotondravony at the University of Antananarivo, the Commission Tripartite de Direction des Eaux et Forêts, ANGAP, and Prof. Dr. Hladik for their authorization and support of this study. I am very grateful to Mamy Razafindrasamba, Jean-Pierre Tolojanahary and Rodin Rasoloarison for their invaluable support in the field. I also thank two anonymous referees and Tony King for constructive comments on the manuscript. Finally, I am grateful to Josia Razafindramanana for inviting me to contribute to this special issue.

Literature Cited

Bradbury, J. W. and S. L. Vehrencamp. 1998. *Principles of Animal Communication.* Sinauer Associates, Inc., Sunderland, MA.

Brown, C., R. Gomez and P. Waser. 1995. Old world monkey vocalizations: adaptation to the local habitat? *Anim. Behav.* 50: 945–961.

Brown Jr., W. L. and E. O. Wilson. 1956. Character displacement. *Syst. Zool.* 5: 49–64.

Cap, H., P. Deleporte, J. Joachim and D. Reby. 2008. Male vocal behavior and phylogeny in deer. *Cladistics* 24: 1–15.

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

Curtis, D., A. Velo, E.-O. Raheliarisoa, A. Zaramody and P. Müller. 1998. Surveys on *Propithecus verreauxi deckeni*, a melanistic variant, and *P. v. coronatus* in northwest Madagascar. *Oryx* 32: 157–164.

Daniel, J. C. and D. T. Blumstein. 1998. A test of the acoustic adaptation hypothesis in four species of marmots. *Anim. Behav.* 56: 1517–1528.

Ey, E., C. Rahn, K. Hammerschmidt and K. Fischer. 2009. Wild female olive baboons adapt their grunt vocalizations to environmental conditions. *Ethology* 115: 493–503.

Fichtel, C. and K. Hammerschmidt. 2002. Responses of redfronted lemurs (*Eulemur fulvus rufus)* to experimentally modified alarm calls: evidence for urgency-based changes in call structure. *Ethology* 108: 763–777.

Fichtel, C. and P. M. Kappeler. 2002. Anti-predator behavior of group-living Malagasy primates: mixed evidence for a referential alarm call system. *Behav. Ecol. Sociobiol.* 51: 262–275.

Fichtel, C. and P. M. Kappeler. 2011. Variation in the meaning of alarm calls in Verreaux's and Coquerel's sifakas (*Propithecus verreauxi*, *P. coquereli*). *Int. J. Primatol.* 32: 346–361.

Fichtel, C., S. Perry and J. Gros-Louis. 2005. Alarm calls of white-faced capuchin monkeys: an acoustic analysis. *Anim. Behav.* 70: 165–176.

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

Gamba, M. and C. Giacoma. 2006. Vocal tract modeling in a prosimian primate: the black and white ruffed lemur. *Acta Acustica* 92: 749–755.

Gamba, M., C. Colombo and C. Giacoma. 2012. Acoustic cues to caller identity in lemurs: a case study. *J. Ethol.* 30: 191–196.

Grant, P. R. and R. Grant. 2006. Evolution of character displacement in Darwin's finches. *Science* 313: 224–226.

Gray, R. and W. H. Cade. 2000. Sexual selection and speciation in field crickets. *Proc. Natl. Acad. Sci.* 97: 1449–14454.

Gros-Louis, J., S. Perry, C. Fichtel, E. Wikberg, H. Gilkenson, S. Wofsy and A. Fuentes. 2008. Vocal repertoire of white-faced capuchin monkeys (*Cebus capucinus*)*:* acoustic structure, context and usage. *Int. J. Primatol.* 29: 641–670.

Groves, C. P. and K. M. Helgen. 2007. Craniodental characters in the taxonomy of *Propithecus*. *Int. J. Primatol.* 28: 1363–1383.

Höbel, G. and Gerhardt, H. C. 2003. Reproductive character displacement in the acoustic communication system of green tree frogs (*Hyla cinerea*). *Evolution* 57: 894–904.

King, T., L. H. F. Rakotonirina, A. H. Rakotoarisoa, M. Ravaloharimanitra and C. Chamberlan. 2012. Projet Tsibahaka: conserving the crowned sifaka *Propithecus coronatus*. *Lemur News* 16: 32–34.

King, T., L. H. F. Rakotonirina, A. H. Rakotoarisoa, J. Razafindramanana and J. Ratsimbazafy. 2014 Distributional limits and melanism in the south-west of the range of the crowned sifaka (*Propithecus coronatus*), Madagascar. *Primate Conserv*. (28): 55−64.

Kirschel, A. N. G., D. T. Blumstein and T. B. Smith. 2009. Character displacement of song and morphology in African tinkerbirds. *Proc. Natl. Acad. Sci.* 106: 8256–8261

Konrad, R. and T. Geissmann. 2006. Vocal diversity and taxonomy of *Nomascus* in Cambodia. *Int. J. Primatol.* 27: 713–745.

Macedonia, J. 1986. Individuality in the contact call of the ring-tailed lemur (*Lemur catta*). *Am. J. Primatol.* 11: 163–179.

Macedonia, J. and K. Stanger. 1994. Phylogeny of the Lemuridae revisited: evidence from communication signals. *Folia Primatol.* 63: 1–43.

Manser, M. B., M. B. Bell and L. B. Fletcher. 2001. The information that receivers extract from alarm calls in suricates. *Proc. Roy. Soc. Lond. B* 268: 2485–2491.

Markolf, M., R. Rakotonirina, C. Fichtel, P. Grumbkow, M. Brameier and P. M. Kappeler. 2013. True lemurs... true species? – Species delimitation using multiple data sources in the brown lemur complex. *BMC Evol. Biol*. 13: 233.

Marler, P. 1967. Animal communication signals. *Science* 157: 769–774.

Mayor, M., J. A. Sommer, M. L. Houck, J. R. Zaonarivelo, P. C. Wright, C. Ingram, S. R. Engel and E. J. Louis. 2004. Specific status of *Propithecus* spp. *Int. J. Primatol.* 25: 875–900.

Mayr, E. 1963. *Animal Species and Evolution*. Harvard University Press, Cambridge, MA.

Mendez-Cardenas, M., B. Randrianambinina, A. Rabesandratana, S. Rasoloharijaona and E. Zimmermann. 2008. Geographic variation in loud calls of sportive lemurs (*Lepilemur* ssp.) and their implications for conservation. *Am. J. Primatol.* 70: 828–838.

Merker, S., C. Driller and D. Perwitasari-Farajallah. 2009. Elucidating geological and biological processes underlying the diversification of Sulawesi tarsiers. *Proc. Natl. Acad. Sci.* 106: 8459–8464.

Mitani, J. C. 1985. Responses of gibbons (*Hylobates muelleri*) to self, neighbor, and stranger song duets. *Int. J. Primatol.* 6: 193–200.

Mittermeier, R. A., J. U. Ganzhorn, W. R. Konstant, K. E. Glander, I. Tattersall, C. P. Groves, A. B. Rylands, A. Hapke, J. Ratsimbazafy, M. Mayor, E. E. Louis Jr., Y. Rumpler, C. Schwitzer and R. M. Rasoloarison. 2008. Lemur diversity in Madagascar. *Int. J. Primatol.* 29: 1607–1656.

Mittermeier, R. A., E. E. Louis Jr, M. Richardson, C. Schwitzer, O. Langrand, A. B. Rylands, F. Hawkins, S. Rajaobelina, J. Ratsimbazafy, R. M. Rasoloarison, C. Roos, P. M. Kappeler and J. Mackinnon. 2010. *Lemurs of Madagascar*. Conservation International, Arlington, VA.

Morton, E. S. 1975. Ecological sources of selection on avian sounds. *Am. Nat.* 109: 17–34.

Mundry, R. and C. Sommer. 2007. Discriminant function analysis with nonintependent data:consequences and an alternative. *Anim. Behav.* 74: 965–976.

Nevo, E., G. Heth, A. Beiles and E. Frankenberg. 1987. Geographic dialects in blind mole rats. role of vocal communication in active speciation. *Proc. Natl. Acad. Sci.* 84: 3312.

Nietsch, A. and M.-L. Kopp. 1998. Role of vocalization in species differentiation of Sulawesi tarsiers. *Fol Primatol* 69: 371–378.

Oates, J. F. and T. F. Trocco. 1983. Taxonomy and phylogeny of black-and-white colobus monkeys: inferences from an analysis of loud call variation. *Folia Primatol.* 40: 83–113.

Oda, R. 2002. Individual distinctiveness of the contact calls of ring-tailed lemurs. *Folia Primatol.* 73: 132–136.

Pastorini, J., M. Forstner and R. D. Martin. 2001. Phylogenetic history of sifakas (*Propithecus*: Lemuriformes) derived from mtDNA sequences. *Am. J. Primatol.* 53: 1–17.

Pastorini, J., U. Thalmann and R. D. Martin. 2003. A molecular approach to comparative phylogeography of extant Malagasy lemurs. *Proc. Natl. Acad. Sci.* 100: 5879–5884.

Rakotonirina, L. H. F., F. Randriantsara, A. H. Rakotoarisoa, R. Rakotondrabe, J. Razafindramanana, J. Ratsimbazafy and T. King. 2014. A preliminary assessment of sifaka (*Propithecus*) distribution, chromatic variation and conservation in western central Madagascar. *Primate Conserv*. (28): 43−53.

Reby, D., K. McComb, B. Cargnelutti, C. Darwin, W. T. Fitch and T. H. Clutton-Brock. 2005. Red deer stags use formants as assessment cues during intrasexual agonistic interactions. *Proc. Roy. Soc. Lond. B* 272: 941–947.

Robillard, T., G. Höbel and H. C. Gerhardt. 2006. Evolution of advertisement signals in North American hylid frogs: vocalizations as end-products of calling behavior. *Cladistics* 22: 533–545.

Ryan, M. J. and E. A. Brenowitz. 1985. The role of body size, phylogeny, and ambient noise in the evolution of bird song. *Am. Nat.* 126: 87–100.

Ryan, M. J. and A. S. Rand. 1999. Phylogenetic inference and the evolution of communication in Túngara frogs. In: *The Design of Animal Communication*, M. D. Hauser and M. Konishi (eds.), pp.535–557. A Bradford Book, MIT Press, Cambridge, MA.

Ryan, M. J., R. B. Cocroft and W. Wilczynski. 1990. The role of environmental selection in intraspecific divergence of mate recognition of signals in the cricket frog, *Acris crepitans*. *Evolution* 44: 1869–1872.

Rumpler, Y., M. Hauwy, J.-L. Fausser, C. Roos, A. Zaramody, N. Andriaholinirina and D. Zinner. 2011. Comparing chromosomal and mitochondrial phylogenies of the Indriidae (Primates, Lemuriformes). *Chromsome Res.* 19: 209–224.

Schrader, L. and K. Hammerschmidt. 1997. Computer-aided analysis of acoustic parameters in animal vocalisations: a multi-parametric approach. *Bioacoustics* 7: 247–265.

Tattersall, I. 1982. *The Primates of Madagascar*. Columbia University Press, New York.

Tattersall, I. 1986. Notes on the distribution and the taxonomic status of some subspecies of *Propithecus* in Madagascar. *Folia Primatol*. 46: 51–63.

Tattersall, I. 1988. Distribution survey of the Malagasy lemurs: request for information and initial report. *Primate Conserv.* (9): 116–117.

Thalmann, U. and N. Rakotoarison. 1994. Distribution of lemurs in central western Madagascar, with a distribution hypothesis. *Folia. Primatol.* 63: 156–161.

Thalmann, U., R. Kümmerli and A. Zaramody. 2002. Why *Propithecus verreauxi deckeni* and *P. v. coronatus* are

valid taxa—quantitative and qualitative arguments. *Lemur News* 7: 11–16.

Thin, V. N., C. Hallam, C. Roos and K. Hammerschmidt. 2010. Concordance between vocal and genetic diversity in crested gibbons. *BMC Evol. Biol.* 11: 36.

Waser, P. M. 1982. The evolution of male loud calls among mangabeys and baboons. In: *Primate Communication*, C. T. Snowdon, C. H. Brown and M. R. Petersen (eds.), pp. 117–143. Cambridge University Press, Cambridge, UK.

Wich, S. A. and C. L. Nunn. 2002. Do male "long-distance calls" function in mate defense? A comparative study of long-distance calls in primates. *Behav. Ecol. Sociobiol.* 52: 474–484.

Wiley, R. H. and D. G. Richards. 1978. Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalization. *Behav. Ecol. Sociobiol.* 3: 69–94.

Wilmé, L. and M. W. Calmander. 2006. Les populations reliques de primates: les Propithèques. *Lemur News* 11: 24–31.

Wilmé, L., S. M. Goodman and J. U. Ganzhorn. 2006. Biogeographic evolution of Madagascar's microendemic biota. *Science* 312: 1063–1065.

Zimmermann, E., E. Vorobieva, D. Wrogemann and T. Hafen. 2000. Use of vocal fingerprinting for specific discrimination of gray (*Microcebus murinus*) and rufous mouse lemurs (*Microcebus rufus*). *Int. J. Primatol.* 21: 837–852.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev and G. M. Smith. 2009. *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York.

Author's address:
Claudia Fichtel, Behavioral Ecology and Sociobiology Unit, German Primate Center, Kellnerweg 4, 37077 Göttingen, Germany, E-mail: <Claudia.fichtel@gwdg.de>.

Received for publication: *July 2011*
Revised: 14 October 2014