

GREAT APE VOCAL REPERTOIRES ARE ALL SIMILAR IN SIZE: NOW WHAT?

Steven Moran^{*1,2}, Marco Maiolini¹, and Adriano Lameira^{*3}

^{*}Corresponding Authors: steven.moran@unine.ch, Adriano.Lameira@warwick.ac.uk

¹Institute of Biology, University of Neuchâtel, Neuchâtel, Switzerland

²Department of Anthropology, University of Miami, Coral Gables, USA

³Department of Psychology, University of Warwick, Coventry, UK

There is an uncanny similarity between the size of nonhuman great ape vocal repertoires and that of the phonological inventories documented in human languages. Great ape repertoires vary from a conservative estimate, and lower-bound, of 18 calls in both species of gorillas (*Gorilla*), to the low-to-mid 20s in chimpanzees and bonobos (*Pan*), to the mid 30s in orangutans (*Pongo*). These numbers are in line with the average number of contrastive speech sounds in modern and in ancient and reconstructed languages. See Table 1 for details.

This observation suggests a common evolutionary pressure for a two digit system repertoire, one that existed before the origin of language, and present at the split with our evolutionary ancestors. The difference between systems is well documented – language combines speech sounds (or signs) into an open-ended communication system that *infinitely* produces new words and meanings. And although we do not yet know what led to the cognitive abilities that gave rise to this system in *Homo*, there are many similarities between the vocal repertoires of great apes and those in languages left to explore.

Like language, great ape calls are produced in non-random combinations (Lameira et al., 2021; Girard-Buttoz et al., 2022). Like speech, orangutan vocal repertoires are composed of consonant- and vowel-like calls (Lameira, 2014; Lameira, Maddieson, & Zuberbühler, 2014; Lameira et al., 2017). Orangutan vocalizations also involve modest airstream and articulatory control (Wich et al., 2008; Lameira et al., 2013, 2015) and experiments done in captivity show precise vocal fold motor control, including voicing (Lameira & Shumaker, 2019). And along with other cognitive skills, e.g., tool making, some great ape vocalizations are arguably learned (Hopkins, Taglialatela, & Leavens, 2007; Taglialatela, Reamer, Schapiro, & Hopkins, 2012; Wich et al., 2012; Russell, McIntyre, Hopkins, & Taglialatela, 2013; Lameira et al., 2015; Lameira, Hardus, Mielke, Wich, & Shumaker, 2016; Lameira & Shumaker, 2019) with some groups in captivity reportedly transmitting raspberries to their young, which they use to get the attention of caretakers (Hopkins et al., 2007; Taglialatela et al., 2012; Russell

et al., 2013). Finally like languages, the call repertoires of great apes are shaped by socio-cultural factors (Lameira et al., 2022), they have dialects (Crockford, Herbinger, Vigilant, & Boesch, 2004; Lameira, Delgado, & Wich, 2010; Lameira et al., 2017), change through contact (Mitani & Gros-Louis, 1998; Watson et al., 2015b, 2015a), and their existence and diversity are under the threat of extinction (Meijaard et al., 2011; Wich et al., 2012, 2016; Estrada et al., 2017).

We conducted an extensive review of the existing literature (66 published articles) and found that call repertoires are similar in size across extant great apes. However, we also discovered that there is little in terms of a comparative articulatory and acoustic analysis of these vocalizations. This is because there is a serious gap in the descriptions of the articulatory features of great apes in the literature, including for both vocal and gestural data.

A step towards a comprehensive comparative phonetic analysis of articulations of all great apes is needed to shed light on the similarities between vocal communication systems and how each evolved in its own right over the last 6-7 million years of divergent evolution. It is crucial for language evolution research that we have articulatory and acoustic phonetic analyses, of the sort conducted by Perlman and Clark (2015) through audio-visual recordings, for all great ape species (and ideally for each community). This would allow, for example, more studies along the lines of Grawunder et al. (2022), who explored the evolution of the vowel space in chimpanzees. The challenge, however, is not trivial because it is difficult to collect the necessary field data – unlike in linguistics, in which fieldworkers have access to speakers and can also ask them questions directly.

So far we have identified the gaps in the literature and created an ontology of the disparate terminology used in great ape studies.¹ Our research suggests that one pertinent area to explore for acoustic analysis is the spectral envelope (Boë et al., 2019; Grawunder et al., 2022), so that we can ask whether prosodic features can be modified to give information to the receiver (Zimmermann, Leliveld, & Schehka, 2013; Pell et al., 2015; Pisanski, Cartei, McGettigan, Raine, & Reby, 2016). Such findings will shed light on whether paralinguistic features are shared across all great apes. Another area ripe for investigation is what effects exist due to sexual dimorphism, e.g., in orangutans and gorillas, and to understand how to categorize these vocalizations.

We know that the size of great ape vocal repertoires are similar across all extant great apes and that we share eight innate vocalizations, e.g., screaming, crying, laughing (Anikin, Bååth, & Persson, 2018). However, there is still much to learn about what we share vocally, and gesturally (Liebal, Slocombe, & Waller, 2022), and how and when we diverged linguistically.

¹https://github.com/bambooforest/great_ape_vocal_repertoires

Table 1. Vocal repertoire sizes (see also McComb and Semple (2005)).

Genus	Species	Mean repertoire size	Main references
<i>Gorilla</i>	<i>beringei</i>	18	Fossey (1972), Hedwig, Robbins, Mundry, Hammerschmidt, and Boesch (2014), Luef, Breuer, and Pika (2016)
	<i>gorilla</i>	18	Salmi, Hammerschmidt, and Doran-Sheehy (2013), Hedwig et al. (2014), Luef et al. (2016)
<i>Pan</i>	<i>troglodytes</i>	21	Marler, Tenaza, and Sebeok (1977), Goodall (1986), Crockford and Boesch (2005), Taglialatela et al. (2012), Dezecache, Zuberbühler, Davila-Ross, and Dahl (2020), Grawunder et al. (2022)
<i>Pongo</i>	<i>paniscus</i>	19	De Waal (1988), Bermejo and Omedes (1999)
	<i>pygmaeus</i>	29	Hardus et al. (2009), Mackinnon (1974)
	<i>abelii</i>	28	Hardus et al. (2009)
<i>Homo</i>	<i>sapiens</i> (modern)	31	Maddieson (1984), Maddieson and Precoda (1990), Moran and McCloy (2019)
	<i>sapiens</i> (ancient)	30	Marsico (1999), Marsico, Flavier, Verkerk, and Moran (2018), Grossman, Eisen, Nikolaev, and Moran (2020)

Acknowledgements

SM & MM were funded by the Swiss National Science Foundation (EVOPHON grant #186841). ARL was funded by the UKRI Future Leaders Fellowship (MR/T04229X/1).

References

- Anikin, A., Bååth, R., & Persson, T. (2018). Human non-linguistic vocal repertoire: Call types and their meaning. *Journal of Nonverbal Behavior*, 42(1), 53–80.
- Bermejo, M., & Omedes, A. (1999). *Preliminary vocal repertoire and vocal communication of wild bonobos (Pan paniscus) at Lilungu (Democratic Republic of Congo)* (No. 6). S. Karger AG.
- Boë, L.-J., Sawallis, T. R., Fagot, J., Badin, P., Barbier, G., Captier, G., Ménard, L., Heim, J.-L., & Schwartz, J.-L. (2019). Which way to the dawn of speech?: Reanalyzing half a century of debates and data in light of speech science. *Science Advances*, 5(12), eaaw3916.
- Crockford, C., & Boesch, C. (2005). Call combinations in wild chimpanzees. *142*(4), 397–421.
- Crockford, C., Herbinger, I., Vigilant, L., & Boesch, C. (2004). Wild chimpanzees produce group-specific calls: a case for vocal learning? *Ethology*, 110(3), 221–243.
- De Waal, F. M. (1988). The communicative repertoire of captive bonobos (*Pan Paniscus*), compared to that of chimpanzees. *Behaviour*, 106(3–4), 183–251.

- Dezecache, G., Zuberbühler, K., Davila-Ross, M., & Dahl, C. D. (2020). Flexibility in wild infant chimpanzee vocal behavior. *bioRxiv*, 1–17.
- Estrada, A., Garber, P. A., Rylands, A. B., Roos, C., Fernandez-Duque, E., Di Fiore, A., Nekar, K. A.-I., Nijman, V., Heymann, E. W., Lambert, J. E., et al. (2017). Impending extinction crisis of the world's primates: Why primates matter. *Science Advances*, 3(1), e1600946.
- Fossey, D. (1972). Vocalizations of the mountain Gorilla (*Gorilla gorilla beringei*). *Animal Behaviour*, 20(1), 36–53.
- Girard-Buttoz, C., Zaccarella, E., Bortolato, T., Friederici, A. D., Wittig, R. M., & Crockford, C. (2022). Chimpanzees produce diverse vocal sequences with ordered and recombinatorial properties. *Communications Biology*, 5(1), 1–15.
- Goodall, J. (1986). Social rejection, exclusion, and shunning among the Gombe chimpanzees. *Ethology and Sociobiology*, 7(3-4), 227–236.
- Grawunder, S., Uomini, N., Samuni, L., Bortolato, T., Girard-Buttoz, C., Wittig, R. M., & Crockford, C. (2022). Chimpanzee vowel-like sounds and voice quality suggest formant space expansion through the hominoid lineage. *Philosophical Transactions of the Royal Society B*, 377(1841), 20200455.
- Grossman, E., Eisen, E., Nikolaev, D., & Moran, S. (2020). Revisiting the uniformitarian hypothesis: Can we detect recent changes in the typological frequencies of speech sounds? In A. Ravignani, C. Barbieri, M. Martins, M. Flaherty, Y. Jadoul, E. Lattenkamp, H. Little, K. Mudd, & T. Verhoef (Eds.), *The evolution of language: Proceedings of the 13th international conference (EvoLang13)*. Brussels, Belgium.
- Hardus, M. E., Lameira, A. R., Singleton, I., Morrogh-Bernard, H. C., Knott, C. D., Ancrenaz, M., Utami Atmoko, S. S., & Wich, S. A. (2009). A description of the orangutan's vocal and sound repertoire, with a focus on geographic variation. In S. A. Wich, S. S. U. Atmoko, T. M. Setia, & C. P. van Schaik (Eds.), *Orangutans: Geographic variation in behavioral ecology and conservation*.
- Hedwig, D., Robbins, M. M., Mundry, R., Hammerschmidt, K., & Boesch, C. (2014). Acoustic structure and variation in mountain and western gorilla close calls: A syntactic approach. *Behaviour*, 151(8), 1091–1120.
- Hopkins, W. D., Taglialatela, J. P., & Leavens, D. A. (2007). Chimpanzees differentially produce novel vocalizations to capture the attention of a human. *Animal Behaviour*, 73(2), 281–286.
- Lameira, A. R. (2014). The forgotten role of consonant-like calls in theories of speech evolution. *Behavioral and Brain Sciences*, 37(6), 559–560.
- Lameira, A. R., Alexandre, A., Gamba, M., Nowak, M. G., Vicente, R., & Wich, S. (2021). Orangutan information broadcast via consonant-like and vowel-like calls breaches mathematical models of linguistic evolution. *Biology Letters*, 17(9), 20210302.

- Lameira, A. R., Delgado, R. A., & Wich, S. A. (2010). Review of geographic variation in terrestrial mammalian acoustic signals: Human speech variation in a comparative perspective. *Journal of Evolutionary Psychology*, 8(4), 309–332.
- Lameira, A. R., Hardus, M. E., Bartlett, A. M., Shumaker, R. W., Wich, S. A., & Menken, S. B. J. (2015). Speech-like rhythm in a voiced and voiceless orangutan call. *PLOS ONE*, 10(1), 1–12.
- Lameira, A. R., Hardus, M. E., Kowalsky, B., Vries, H. de, Spruijt, B. M., Sterck, E. H. M., Shumaker, R. W., & Wich, S. A. (2013). Orangutan (*Pongo* spp.) whistling and implications for the emergence of an open-ended call repertoire: A replication and extension. *The Journal of the Acoustical Society of America*, 134(3), 2326–2335.
- Lameira, A. R., Hardus, M. E., Mielke, A., Wich, S. A., & Shumaker, R. W. (2016). Vocal fold control beyond the species-specific repertoire in an orang-utan. *Scientific Reports*, 6(1), 1–10.
- Lameira, A. R., Maddieson, I., & Zuberbühler, K. (2014). Primate feedstock for the evolution of consonants. *Trends in Cognitive Sciences*, 18(2), 60–62.
- Lameira, A. R., Santamaría-Bonfil, G., Galeone, D., Gamba, M., Hardus, M. E., Knott, C. D., Morrogh-Bernard, H., Nowak, M. G., Campbell-Smith, G., & Wich, S. A. (2022). Sociality predicts orangutan vocal phenotype. *Nature Ecology & Evolution*, 6(5), 644–652.
- Lameira, A. R., & Shumaker, R. W. (2019). Orangutans show active voicing through a membranophone. *Scientific Reports*, 9(1), 1–6.
- Lameira, A. R., Vicente, R., Alexandre, A., Campbell-Smith, G., Knott, C., Wich, S., & Hardus, M. E. (2017). Proto-consonants were information-dense via identical bioacoustic tags to proto-vowels. *Nature Human Behaviour*, 1(2), 1–5.
- Liebal, K., Slocombe, K. E., & Waller, B. M. (2022). The language void 10 years on: multimodal primate communication research is still uncommon. *Ethology Ecology & Evolution*, 34(3), 274–287.
- Luef, E. M., Breuer, T., & Pika, S. (2016). Food-associated calling in gorillas (*Gorilla g. gorilla*) in the wild. *PLOS ONE*, 11(2), 1–16.
- Mackinnon, J. (1974). The behaviour and ecology of wild orang-utans (*Pongo pygmaeus*). *Animal Behaviour*, 22(1), 3–74.
- Maddieson, I. (1984). *Pattern of Sounds*. Cambridge, UK: Cambridge University Press.
- Maddieson, I., & Precoda, K. (1990). Updating UPSID. In *UCLA working papers in phonetics* (Vol. 74, pp. 104–111). Department of Linguistics, UCLA.
- Marler, P., Tenaza, R., & Sebeok, T. (1977). *How animals communicate*. Indiana University Press.
- Marsico, E. (1999). What can a database of proto-languages tell us about the last 10,000 years of sound changes? In *Proceedings of the XIVth international*

- congress of phonetic sciences* (pp. 353–356). San Francisco.
- Marsico, E., Flavier, S., Verkerk, A., & Moran, S. (2018). BDPROTO: A database of phonological inventories from ancient and reconstructed languages. In N. Calzolari, K. Choukri, C. Cieri, T. Declerck, S. Goggi, K. Hasida, H. Isahara, B. Maegaard, J. Mariani, H. Mazo, A. Moreno, J. Odijk, S. Piperidis, & T. Tokunaga (Eds.), *Proceedings of the eleventh international conference on language resources and evaluation (LREC 2018)* (pp. 1654–1658). Paris, France: European Language Resources Association (ELRA).
- McComb, K., & Semple, S. (2005). Coevolution of vocal communication and sociality in primates. *Biology Letters*, 1(4), 381–385.
- Meijaard, E., Buchori, D., Hadiprakarsa, Y., Utami-Atmoko, S. S., Nurcahyo, A., Tjiu, A., Prasetyo, D., Christie, L., Ancrenaz, M., Abadi, F., et al.. (2011). Quantifying killing of orangutans and human-orangutan conflict in Kalimantan, Indonesia. *PLOS ONE*, 6(11), e27491.
- Mitani, J., & Gros-Louis, J. (1998). Chorusing and call convergence in chimpanzees: Tests of three hypotheses. *Behaviour*, 135(8), 1041–1064.
- Moran, S., & McCloy, D. (Eds.). (2019). *PHOIBLE 2.0*. Jena: Max Planck Institute for the Science of Human History.
- Pell, M., Rothermich, K., Liu, P., Paulmann, S., Sethi, S., & Rigoulot, S. (2015). Preferential decoding of emotion from human non-linguistic vocalizations versus speech prosody. *Biological Psychology*, 111, 14–25.
- Perlman, M., & Clark, N. (2015). Learned vocal and breathing behavior in an enculturated gorilla. *Animal Cognition*, 18(5), 1165–1179.
- Pisanski, K., Cartei, V., McGettigan, C., Raine, J., & Reby, D. (2016). Voice modulation: a window into the origins of human vocal control? *Trends in Cognitive Sciences*, 20(4), 304–318.
- Russell, J. L., McIntyre, J. M., Hopkins, W. D., & Taglialatela, J. P. (2013). Vocal learning of a communicative signal in captive chimpanzees, *Pan troglodytes*. *Brain and Language*, 127(3), 520–525.
- Salmi, R., Hammerschmidt, K., & Doran-Sheehy, D. M. (2013). Western gorilla vocal repertoire and contextual use of vocalizations. *Ethology*, 119(10), 831–847.
- Taglialatela, J. P., Reamer, L., Schapiro, S. J., & Hopkins, W. D. (2012). Social learning of a communicative signal in captive chimpanzees. *Biology Letters*, 8(4), 498–501.
- Watson, S. K., Townsend, S. W., Schel, A. M., Wilke, C., Wallace, E. K., Cheng, L., West, V., & Slocombe, K. E. (2015a). Vocal learning in the functionally referential food grunts of chimpanzees. *Current Biology*, 25(4), 495–499.
- Watson, S. K., Townsend, S. W., Schel, A. M., Wilke, C., Wallace, E. K., Cheng, L., West, V., & Slocombe, K. E. (2015b). Reply to Fischer et al. *Current Biology*, 25(21), R1030–R1031.
- Wich, S. A., Gaveau, D., Abram, N., Ancrenaz, M., Baccini, A., Brend, S., Cur-

- ran, L., Delgado, R. A., Erman, A., Fredriksson, G. M., et al.. (2012). Understanding the impacts of land-use policies on a threatened species: is there a future for the Bornean orang-utan? *PLOS ONE*, 7(11), e49142.
- Wich, S. A., Singleton, I., Nowak, M. G., Utami Atmoko, S. S., Nisam, G., Arif, S. M., Putra, R. H., Ardi, R., Fredriksson, G., Usher, G., et al.. (2016). Land-cover changes predict steep declines for the Sumatran orangutan (*Pongo abelii*). *Science Advances*, 2(3), e1500789.
- Wich, S. A., Swartz, K. B., Hardus, M. E., Lameira, A. R., Stromberg, E., & Shumaker, R. W. (2008). A case of spontaneous acquisition of a human sound by an orangutan. *Primates*, 50(1), 56–64.
- Zimmermann, E., Leliveld, L., & Schehka, S. (2013). Toward the evolutionary roots of affective prosody in human acoustic communication: a comparative approach to mammalian voices. In E. Altenmüller, S. Schmidt, & E. Zimmermann (Eds.), *Evolution of emotional communication: From sounds in nonhuman mammals to speech and music in man* (Vol. 116, p. 132). Oxford University Press Oxford, UK.