

BODY SIZE PREDICTS VOCAL TRACT SIZE IN A MAMMALIAN VOCAL LEARNER

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1. Mechanisms for escaping acoustic allometry

Animals whose call features do not scale with their body size are said to escape acoustic allometry. These animals may thus sound smaller or larger than they are. Recent work (Garcia & Ravignani, 2020; Ravignani & Garcia 2021) found that they can achieve this by evolving vocal tract modifications (e.g., laryngeal descent; Reby & McComb, 2003) or by learning to better control their vocal organs (i.e., vocal learning, Janik & Slater, 1997). To identify which mechanism is used by species to escape acoustic allometry, one could perform an anatomical study to test if vocal tract size scales with body size. Acoustic allometry is escaped by anatomical adaptations if vocal tract size does not scale with body size, and through vocal learning if there is scaling between vocal tract size and body size.

2. Anatomical studies can help find more vocal learners

Studies that test whether animal vocal tracts scale with their body size offer a simple way of testing the hypothesis pitting anatomical adaptations vs. vocal learning (Garcia & Ravignani, 2020; Ravignani & Garcia 2021). Moreover, they can help to identify new species capable of vocal learning, a prerequisite for human speech. Adopting a comparative approach which considers an increasing number of vocal learning species could offer promising insights into the biological underpinnings of communication systems such as spoken language.

3. Harbor seal vocal tracts scale with their body size

Harbor seals' (*Phoca vitulina*) large vocal plasticity allows them to modulate the call frequencies they produce (Ralls et al., 1985; Torres Borda et al., 2021), enabling them to produce sounds with different frequencies than predicted from their body size. The current study tests if the vocal tract of the harbor seal, a known mammalian vocal learner, scales with its body size (de Reus et al., 2022). Vocal tracts, including larynges, of 68 young harbor seals (pups and weaners) were measured using a caliper and tested for allometry with body size using generalized linear mixed models. We find that both body length and body mass predict vocal tract length, vocal fold length, and tracheal dimensions (Table 1). Interestingly, allometry between body size and vocal fold length emerges after puppyhood, suggesting that ontogeny may modulate the anatomy vs. learning distinction. We conclude that the vocal tracts of harbor seals do indeed scale with body size. Consequently, by exclusion, vocal learning is the likely mechanism used in young harbor seals to escape acoustic allometry.

Table 1. Selected models for each vocal tract measurement.

<i>Measurement</i>	<i>Model</i>	<i>Deviance explained</i>
Vocal tract length	<u>BL</u> + <u>BM</u> + <u>A</u> + <u>S</u> + <u>BL*S</u>	59.30%
Vocal fold length	<u>BL</u> +BM+A+ <u>S</u> +A*BM+ <u>A*S</u>	74.89%
Subglottic-tracheal dorsoventral distance 1	<u>BL</u> + <u>BM</u> + <u>A</u> + <u>S</u>	69.99%
Subglottic-tracheal dorsoventral distance 2	BL+ <u>BM</u> + <u>A</u> +S	58.38%

Note. BL = body length, BM = body mass, A = age class, S = sex. Predictor terms joined by an asterisk denote an interaction. Significant predictor terms are underlined.

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References

- de Reus, K., Carlson, D., Lowry, A., Gross, S., Garcia, M., Rubio-Garcia, A., ... & Ravignani, A. (2022). Vocal tract allometry in a mammalian vocal learner. *Journal of Experimental Biology*, 225(8), jeb243766.
- Garcia, M., & Ravignani, A. (2020). Acoustic allometry and vocal learning in mammals. *Biology Letters*, 16(7), 20200081.
- Janik, V. M., & Slater, P. J. (1997). Vocal learning in mammals. In: P. Slater, C. Snowdon, J. Rosenblatt, & M. Milinski (Eds.), *Advances in the Study of Behaviour*, 26, 59-100.
- Ralls, K., Fiorelli, P., & Gish, S. (1985). Vocalizations and vocal mimicry in captive harbor seals, *Phoca vitulina*. *Canadian Journal of Zoology*, 63(5), 1050–1056.
- Ravignani, A., & Garcia, M. (2021). A cross-species framework to identify vocal learning abilities in mammals. *Philosophical Transactions of the Royal Society B*, 377(1841), 20200394.
- Reby, D., & McComb, K. (2003). Anatomical constraints generate honesty: Acoustic cues to age and weight in the roars of red deer stags. *Animal Behaviour*, 65(3), 519–530.
- Torres Borda, L., Jadoul, Y., Rasilo, H., Casals, A. S., & Ravignani, A. (2021). Vocal plasticity in harbour seal pups. *Philosophical Transactions of the Royal Society B: Biological Sciences*. 376, 20200456.