

Phylogenetic and kinematic constraints of the vocal-flight-respiratory axis.

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Background.- The Motor Theory for Vocal Learning Origin posits that vocal imitation, the substrate for human speech, is a specialization of an ancestral neural pathway in the forebrain that controls locomotor activities¹. Birds have been the main model for understanding the biology of human speech, however, evolutionary explanations remain contentious and the Motor Theory has not been tested using phylogenetic comparative analysis, a cornerstone of evolutionary biology.

Justification.- High Performance Computing (HPC) resources at the Texas Advanced Computing Center (TACC) were accessed remotely from the Biology Department at UT Rio Grande Valley in Brownsville, Texas. We used Lonestar5 to discover novel evolutionary relationships between a fundamental aspect of avian locomotion, vocal signal duration and body mass in 150 species spanning 12 (of 34) extant taxonomic orders of birds². Hypothetically, wingbeat period and flight call duration should be positively related because both are constrained by respiratory periods, which vary positively with body mass (Fig. 1)².

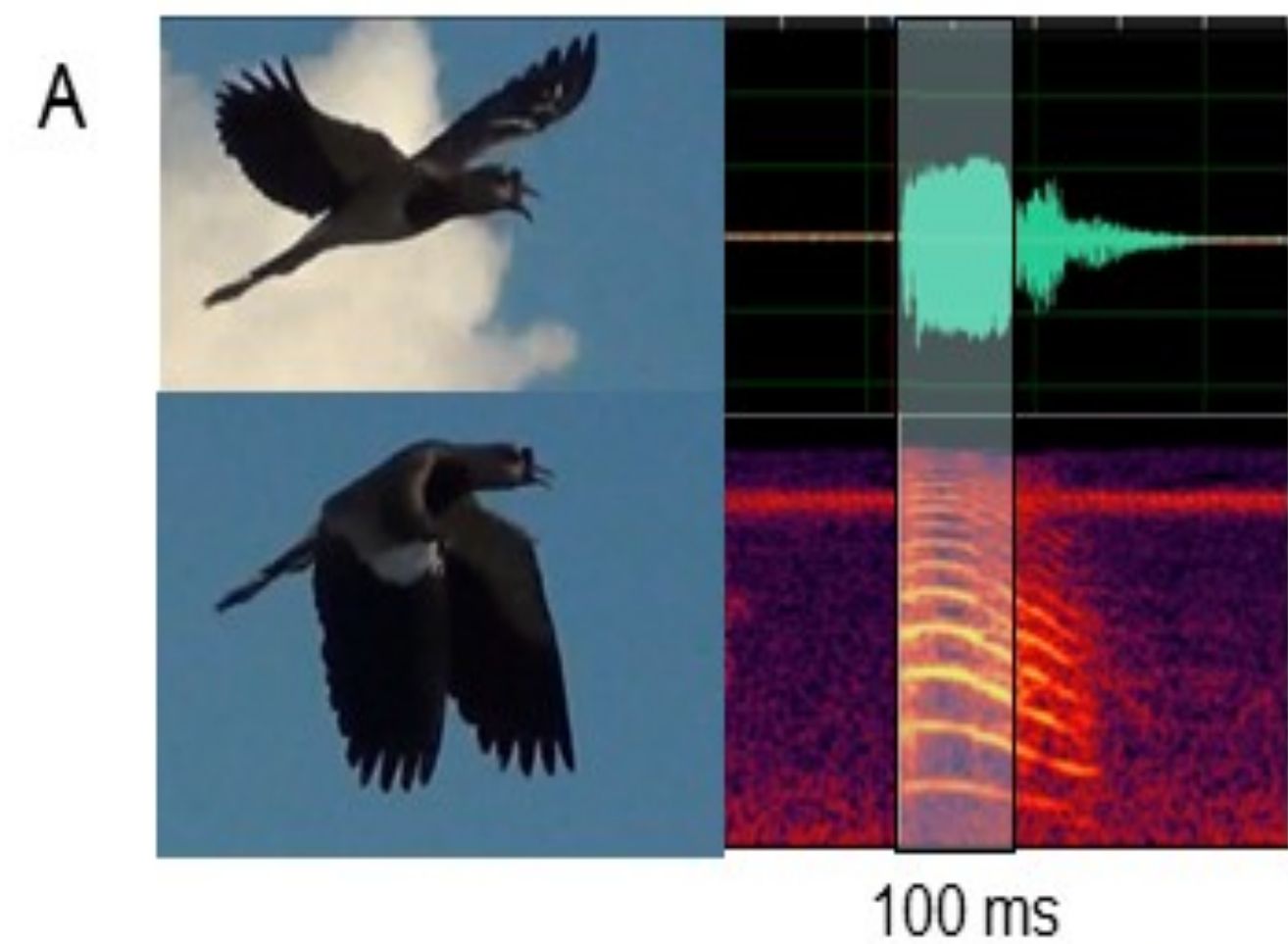
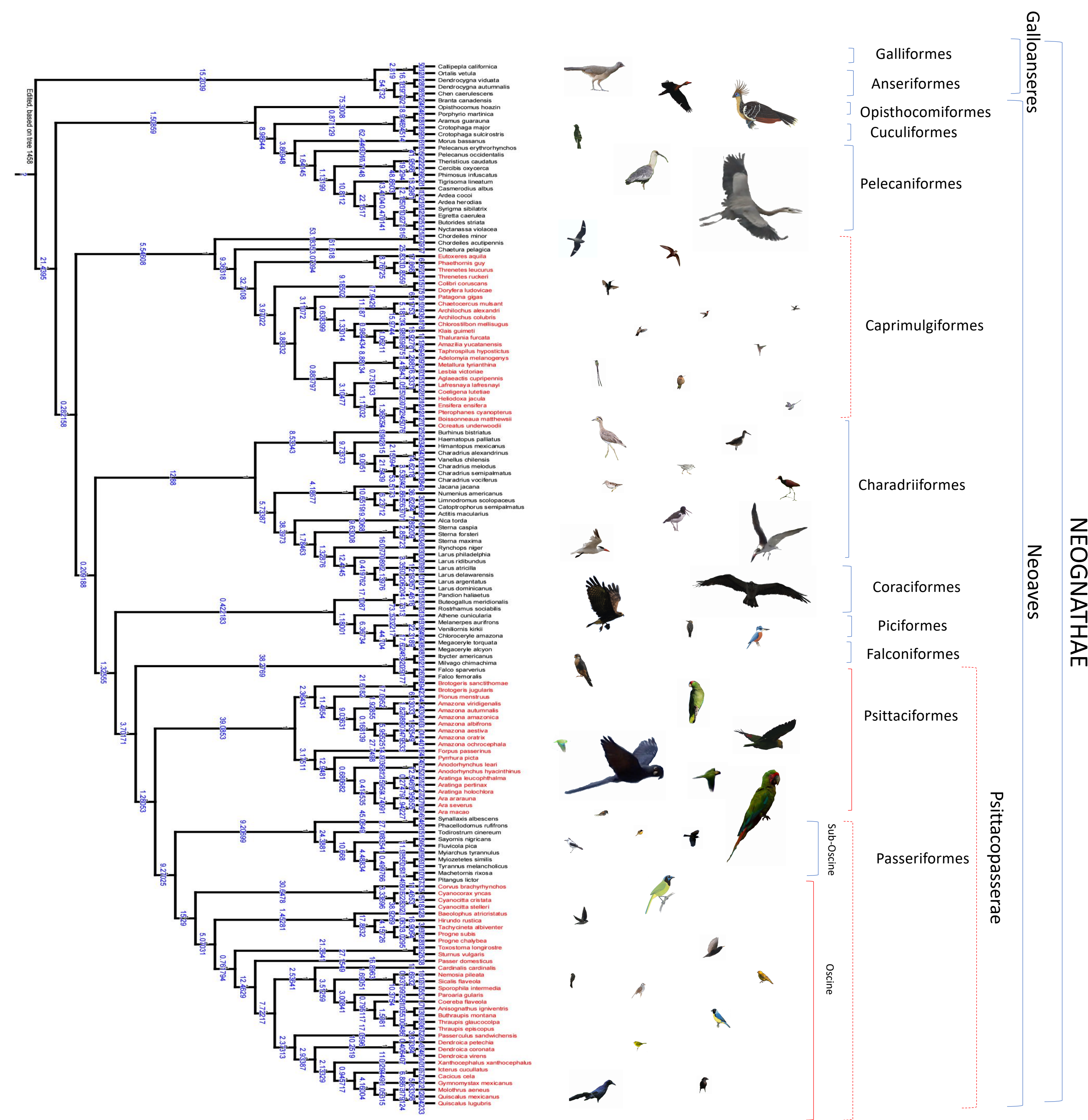


Fig. 1 Left: two video frames showing onset and offset of power stroke in Southern Lapwing (*Vanellus chilensis*). Right: Audio waveform and spectrogram of flight call showing that 80% of signal energy occurred during the power stroke.



Non-vocal learner — blue line
Vocal learner gain — red line
Vocal learner gain/loss — orange line

Fig. 2. Example from one of 100 phylogenetic trees of 150 bird species used to model the evolutionary nexus between body mass, wingbeat period and flight signal duration².

However, testing for differences between vocal learners (parrots, songbirds and hummingbirds) and vocal non-learners requires estimating ancestral relationships of each of the traits separately, as well as during phylogenetically controlled comparisons of multiple traits and alternative hypotheses. This can become computationally challenging for large numbers of species and requires manually coding hundreds of model runs.

Methods

- We ran BayesTraits (v.3.0.1), free phylogenetic software, on Lonestar5 using Linux operating system to conduct over one billion phylogenetically controlled regressions.
- To control for effects of ancestry, one hundred phylogenetic trees were produced using birdtree.org (Fig. 2).
- Phylogenetic signal (Pagel's lambda) of the three traits were estimated, given the tree topologies, and compared to lambda estimated from runs of correlations.
- Markov Chain Monte Carlo (MCMC) estimations across trees was used to compare to distributions where no correlation was assumed (burn-in period of 1,000,000 and 5,000,000 MCMC iterations).
- Each run was replicated six times for each of the models ($n=24,000,000$ regressions each).
- Using every thousandth likelihood ratio was to calculate Log Bayes Factors in each run and averaged over six runs.

Results

- Evolutionary transitions to shorter wingbeat periods, controlling for ancestry and body mass, were correlated with transitions to shorter flight signal durations.
- Species from vocal non-learner lineages had vocal signal periods approximately equal to their powerstroke period, while vocal learners had vocal signal periods that exceeded several wingbeat phases (Fig. 3c).
- Akaike Information Criteria, indicated that the best model predicting flight call duration included body mass, wingbeat period and vocal learner covariate².
- MCMC runs were very stable across replicate runs
- Use of Lonestar5 resulted in a reduction in CPU and coding time from an estimated 80 hours down to 2-3 hours.

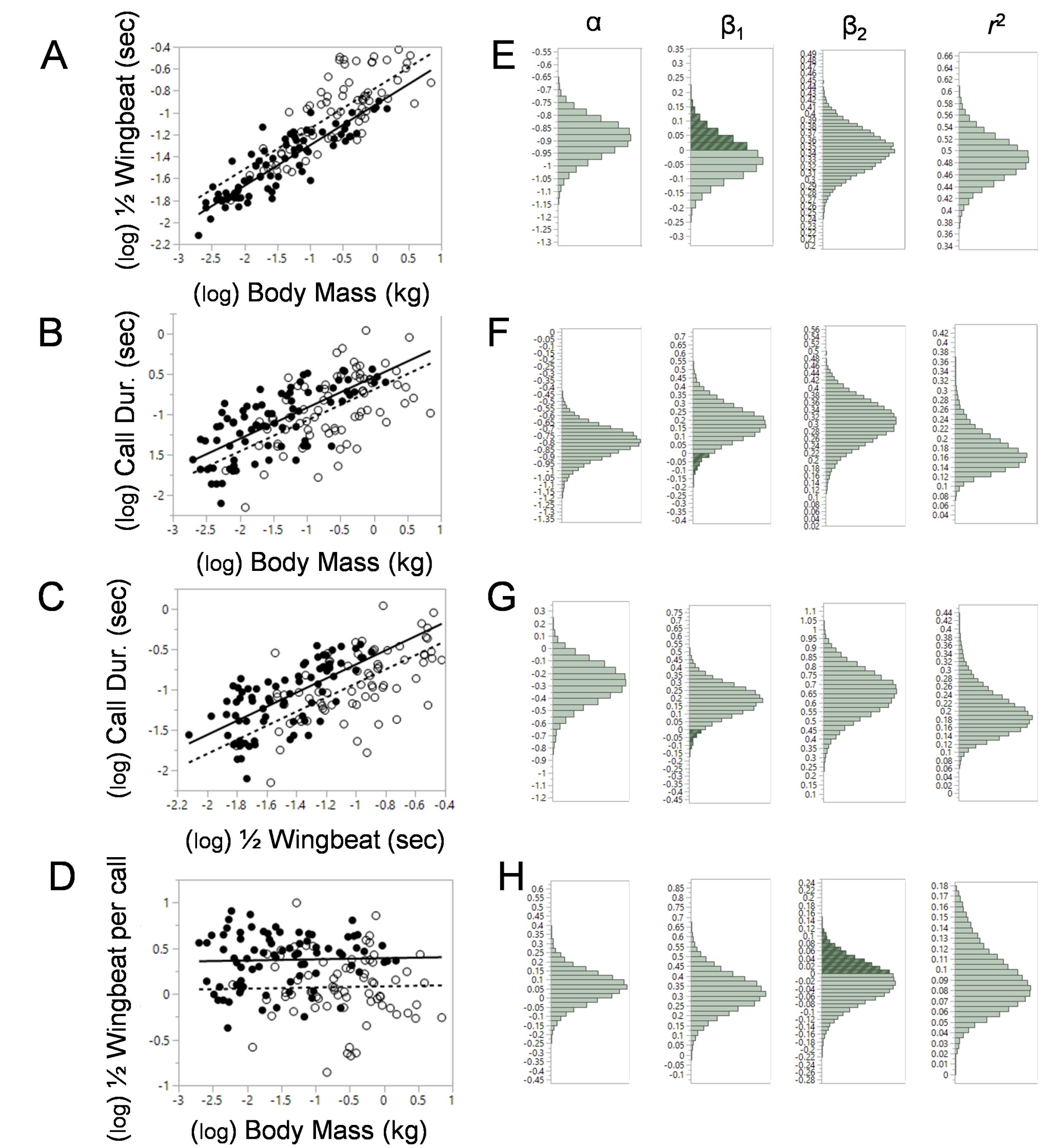


Fig. 3. A-D Scatter plots of species' traits showing differences between vocal learners (black regression lines) and vocal non-learners (hashed lines). E-H Bayesian posterior parameter estimates for each model in A-D. Each histogram contains every thousandth estimate from 24 million estimates ($n=24,000$). Large, dark-colored portions in β_1 (slope of vocal learner covariate) in E and β_2 H (slope of body mass) indicate no significant differences (slopes did not differ from zero). Other estimates of β coefficients showed no evidence of sign reversal, indicating a strong likelihood of correlated evolution².

Discussion

- Vocal learners integrated vocal production with locomotor in ways that differed markedly from vocal non-learners, providing phylogenetic comparative support for the Motor Theory^{1,2}.
- While the biomechanics of avian flight calls remains unknown, one possibility is that neural oscillators controlling flapping, calling and breathing, phase-locked in ancestors, became uncoupled early in the evolution of avian vocal learning².
- Phylogenetic and bioinformatic approaches using HPC can provide efficient means to understanding the diversity of form and function in complex biological systems.

Acknowledgements

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References

1. Feenders et al. 2008. Molecular mapping of movement-associated areas in the avian brain: a motor theory for vocal learning origin. *PLoS ONE* 3, e1768.
2. Berg, K.S., Delgado, S. & Mata-Betancourt, A. 2019. Phylogenetic and kinematic constraints on avian flight signals. *Proc. R. Soc. B.* 286