

Nonlinear Respiratory Biomechanics Broadens the Range of Amplified Dynamics During Birdsong

Facundo Fainstein^{1,2}, Franz Goller^{3,4}, and Gabriel B. Mindlin^{1,2,*}

¹*Universidad de Buenos Aires, Facultad de Ciencias Exactas y Naturales, Departamento de Física, Ciudad Universitaria, 1428 Buenos Aires, Argentina*

²*CONICET, Universidad de Buenos Aires, Instituto de Física Interdisciplinaria y Aplicada (INFINA), Ciudad Universitaria, 1428 Buenos Aires, Argentina*

³*Institute of Integrative Cell Biology and Physiology, University of Münster, 48143 Münster, Germany*

⁴*School of Biological Sciences, University of Utah, Salt Lake City, Utah 84112, USA*



(Received 9 June 2025; accepted 17 June 2026; published 6 August 2026)

Evolution has shaped animal bodies, yet to what extent biomechanical systems impose constraints and provide opportunities across different behaviors remains unclear. In birds, quiet breathing operates at a resonance of the respiratory biomechanics, but song, a behavior thought to be shaped by strong sexual selection, requires much higher breathing rates. Combining physiological recordings with a nonlinear biomechanical model, we show in canaries (*Serinus canaria*) that song production drives the system into a nonlinear regime that broadens the frequency range of amplified responses. This enhancement encompasses the full range of syllabic rates, with an average magnification of $\sim 94\%$ of the theoretical maximum. Thus, song exploits a broadened regime of high amplification, extending biomechanical support beyond the narrow resonance observed during quiet breathing. Our results illustrate a shared optimization strategy across behavioral states, reveal a deep connection between neural and biomechanical dynamical parameters, and show that sexually selected displays may still rely on optimization strategies.

DOI: [10.1103/k495-q611](https://doi.org/10.1103/k495-q611)

I. INTRODUCTION

Physical properties of animal bodies are shaped by evolution. A classic example is the modification of energy-harvesting traits such as jaws and beaks [1]. Natural selection has also resulted in efficient execution of fundamental cyclical movements, including locomotion [2–8] and respiration [9–12]. However, performance of biomechanical systems is usually assessed for specific scenarios, which fails to account for the diversity of natural behaviors in which they operate. A broader approach is needed to understand how morphological changes constrain behaviors, and to what degree optimization strategies extend across them.

We investigated avian respiration in canaries (*Serinus canaria*). Besides its life-sustaining function, the respiratory system plays a central role in vocal production. Songs of many bird species, including canaries, are composed of repeated acoustic elements separated by short silent intervals [vocalizations called trills; Fig. 1(a)]. The sound pulses are generated with a high-amplitude expiratory airstream, and the silent intervals are used for short inspirations (mini-breaths) that replenish the air supply [13]. Control of sound frequency

requires coordinated activity of the respiratory and vocal motor systems [14,15], and in canaries, mini-breath trills can reach up to ~ 30 Hz (Fig. 1(b)). Song production therefore demands delicate and rapid vocal-respiratory motor control and is thought to indicate a singer's fitness [16,17].

During quiet breathing, respiratory rates match a resonance of the respiratory biomechanics [11]. This allows an efficient translation of motor instructions into the air pressure responsible for lung ventilation. However, the respiratory frequency increase during song results in a large departure from the resonance of quiet breathing. Song is a behavior thought to be shaped by strong sexual selection [19–22] that occupies a substantial portion of the animal's daily activity and entails a measurable direct energetic cost [23–25]. Thus, understanding this deviation represents an opportunity to investigate key aspects of behavior, including (1) constraints by physics and physical properties of the body, (2) the degree of synergistic interaction between the nervous system and the biomechanics, and (3) the relationship between fitness and optimization strategies in sexually selected displays [26].

II. RESULTS

A. Nonlinear biomechanical model

To address these questions, we first compare respiratory dynamics during quiet breathing and song production. The avian respiratory system consists of a set of air sacs, which are compressed or expanded by expiratory and inspiratory muscles, and these movements ventilate rigid lungs [Fig. 1(c)]

*Contact author: gabo@df.uba.ar

Published by the American Physical Society under the terms of the [Creative Commons Attribution 4.0 International](https://creativecommons.org/licenses/by/4.0/) license. Further distribution of this work must maintain attribution to the author(s) and the published article's title, journal citation, and DOI.

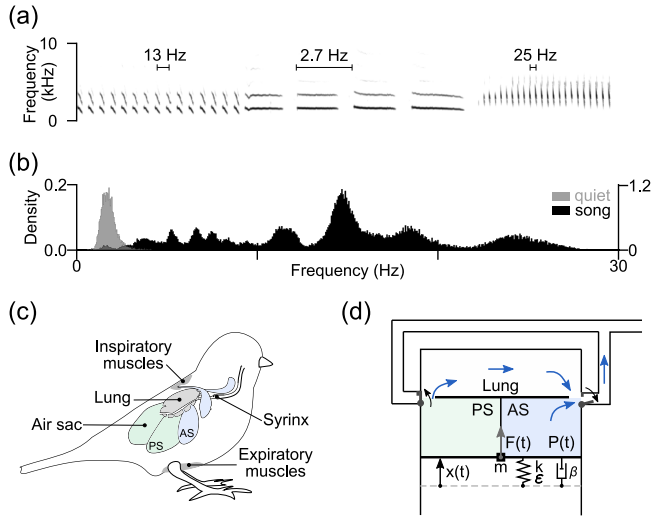


FIG. 1. Avian respiratory system and its timescales across behaviors. (a) Sound spectrogram of a typical canary song composed of trills at different rates, each syllable produced within a respiratory cycle. (b) Distribution of respiratory rates during quiet breathing (in gray, right axis) and song production (in black, left axis). Respiratory frequency during song production expands a broad range, largely departing from quiet breathing rates. Data from five individuals are used (see number of samples in Table S1 in the Supplemental Material (SM) [18]). (c) The respiratory system consists of air sacs and a rigid lung. Muscles force the rib cage in or out, thus compressing or expanding the air sacs that act as bellows and ventilate the lung. (d) Elements of the model. A forced piston changes the volume of the cavities representing the posterior (shaded in green, PS) and anterior (shaded in blue, AS) air sacs. Aerodynamic valves direct the flow.

[27]. During inspiration, the thorax expands, drawing air into the posterior air sacs and through the lungs into the anterior air sacs. During expiration, the air sacs are compressed, such that air from the anterior sacs is exhaled, while air from the posterior sacs passes through the lungs. Aerodynamic valves ensure this unidirectional flow through the lungs, which are perfused with oxygenated air during both respiratory phases.

An avian respiration model was proposed in terms of three cavities and a piston, incorporating aerodynamic valves, an elastic restitution for the piston, and an external forcing [Fig. 1(d)] [11]. For small forcing amplitudes, such as those required to reproduce normal breathing, the model was assumed to be linear. Fitting the model to data recorded during quiet breathing revealed that the average respiratory frequency, which is ~ 2 Hz [Fig. 1(b)], matches the resonance of the model for air pressure, ensuring efficient lung ventilation [11].

During singing, the dynamics departs markedly from the one observed during normal respiration. Whereas in quiet breathing the system operates near its linear resonance, the respiratory rhythm during song displays a strikingly different structure: a multimodal distribution with peaks at frequencies that reflect the complex rhythmic composition of the vocalization [see Figs. 1(a) and 1(b)] [28,29]. Remarkably, the rate of respiratory cycles can increase by up to 15 times relative to resting respiration, which is well beyond the resonance identified in the linear regime. In addition, syringeal oscillations are

induced by expiratory pressures that are at least an order of magnitude greater than during normal respiration [13,29,30].

Song also drives the respiratory system into a regime in which nonlinear biomechanical effects become relevant. First, large forcing amplitudes and the associated pressure and displacement excursions can make the elastic response of the thoracoabdominal system depart from a purely linear description [31,32]. Second, airflow through the respiratory pathway is asymmetric: the syringeal lumen narrows during expiration, facilitating high pressurization, and widens during inspiration [33–35]. This state-dependent airflow conductance constitutes a nonlinear contribution to the respiratory dynamics. Together, these nonlinear features raise the question of whether song production reshapes the frequency response of the respiratory biomechanics, allowing forcing to evoke amplified pressure responses over a broader range of frequencies.

Applying Newton's law to the displacement of the piston $x(t)$ and considering the thermodynamics of a cylinder with an opening and gauge pressure $p(t)$, we derived a simple biomechanical model [11]. Introducing the nonlinearities which are relevant during song production, performing an adiabatic elimination of the inertial term, and nondimensionalizing the dynamical variables, the resulting model reads

$$\tau_x \dot{x} = -(1 + x^2)x - p + F_0 f(t), \quad (1)$$

$$\tau_p \dot{p} = -(1 + x^2)x - [1 + \alpha(p)]p + F_0 f(t), \quad (2)$$

where $\tau_x = \frac{\beta}{k}$, $\tau_p = \frac{V_0 \beta}{P_0 A^2}$, $\alpha_{i,o} = \frac{\tilde{\alpha}_{i,o} \beta}{A^2}$, $F_0 = \frac{f_0 \varepsilon^{1/2}}{k^{3/2}}$. Here k is the elastic restitution constant, β the dissipation coefficient, A the cross-sectional area of the piston, V_0 the total volume, and P_0 the atmospheric pressure. The nonlinear contribution to the elastic restitution is modeled with a cubic term of coefficient ε . The relative change in the conductance of the inlet (α_i) and outlet (α_o) flow can be expressed as $\alpha(p) = \alpha_i - (\alpha_i - \alpha_o)\theta(p)$, with $\theta(p)$ the Heaviside function. The amplitude-normalized function $f(t)$ represents the external forcing, whose amplitude is set by the coefficient F_0 . A more detailed description of the model is given in Sec. I A of the SM [18].

B. Measurement of the variables and parameter fitting

We collected physiological data from five naturally behaving individuals to measure the dynamic variables and determine the parameters of the model. In these experiments, we recorded air sac pressure and electromyographic activity (EMG) of expiratory muscles (see Sec. IV A for details). In three other birds, thoracic displacement, a proxy of the displacement of the air sacs, was measured [11]. During singing, the calibrated thoracic displacement amplitude increases relative to quiet respiration, indicating that the system samples a wider region of the nonlinear elastic restitution curve [31,32]. Using the measured EMG signal as input, we fitted the model parameters to reproduce the morphology of the pressure gestures (see Sec. IV B for details). This procedure yielded the bird- and regime-specific parameter sets used below to compute the corresponding frequency responses.

The first three panels of Fig. 2 show simultaneous recordings of sound, EMG activity, and air sac pressure during singing. The fourth panel shows the output of the fitted model.

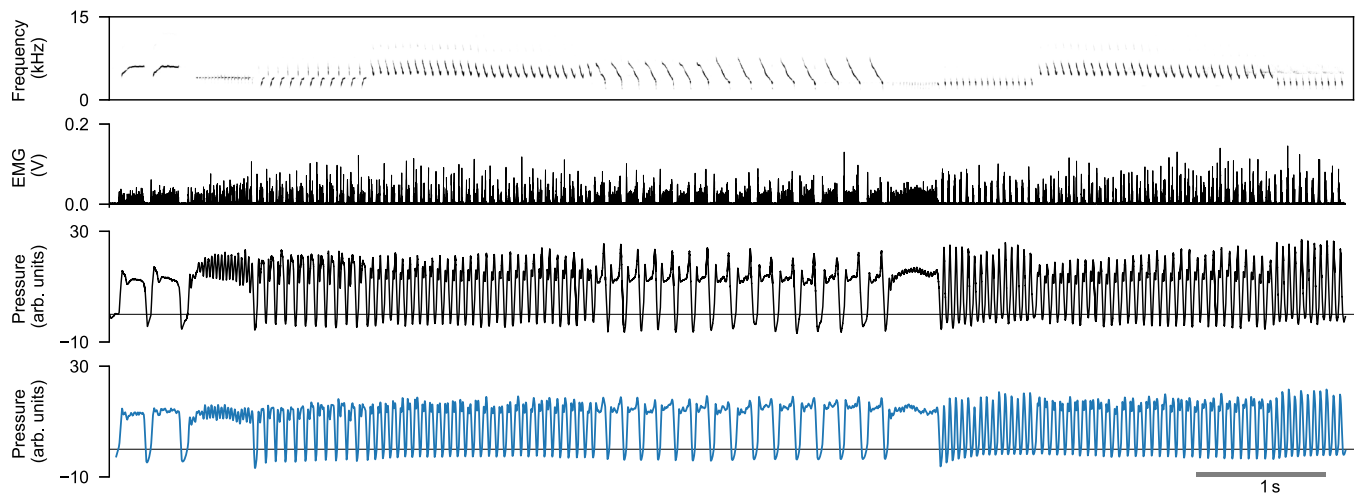


FIG. 2. Respiratory dynamics during song production. Model prediction (blue line) of measured air sac pressure patterns (black line) using recorded expiratory electromyographic activity (EMG) as input. Pressure units are in terms of quiet respiration amplitude, which is normalized to $[-1, 1]$. Top panel shows the spectrogram of the recorded sound.

The fitted model reproduces the temporal structure of the pressure signal, including both the syllabic rhythm and the morphology of individual pressure gestures. Fits for the other individuals are shown in Fig. S1 of the SM [18]. For each bird, a single song parameter set accounted for the diversity of sung syllables, and no separate parameters were fitted for individual syllable types.

C. Resonances and magnification curves

The frequency response of a linear system is obtained by computing the output amplitude in response to harmonic forcing at different frequencies. The resulting frequency-response curve, normalized by its maximum value, defines the normalized magnification curve [36,37]; details on this normalization are provided in Sec. IB of the SM [18]. In a nonlinear system, the situation is more subtle, because the response depends on the amplitude of the driving force. In our case, this amplitude is constrained by fits to the experimental data and determines the contribution of the nonlinearity due to tissue restitution. During song, the state-dependent airflow conductance associated with the inspiration-expiration asymmetry introduces an additional nonlinearity into the model. Once the parameters and forcing amplitude are fixed, there exists a range of frequencies within which entrainment occurs and for which magnification can be high.

We computed the magnification curves using the experimentally inferred parameter sets for each bird and behavioral regime, including the fitted amplitude of the driving force. For song, the parameters were obtained from the measured pressure gestures driven by the EMG-derived input. For quiet respiration, the parameters not expected to vary between regimes, τ_x and τ_p , were held fixed at the values obtained from the song fit, whereas only the forcing amplitude and effective airflow conductance were adjusted to the quiet-breathing regime (see Sec. IV B). For each fixed parameter set, we then drove the model [Eqs. (1) and (2)] with harmonic forcing of the fitted amplitude and computed the corresponding magnification curve as a function of frequency. The curves are shown

for one bird in Fig. 3; those for the remaining individuals are shown in Fig. S4 of the SM [18].

The dashed gray curve in Fig. 3 shows the frequency response of the fitted nonlinear model in the quiet-breathing regime. Its agreement with the analytic response of the corresponding linearized model (solid gray curve) confirms that quiet breathing is well described by the linear approximation (see the derivation in Sec. IB of the SM [18]) [11]. In contrast, song explores a nonlinear regime, and its frequency

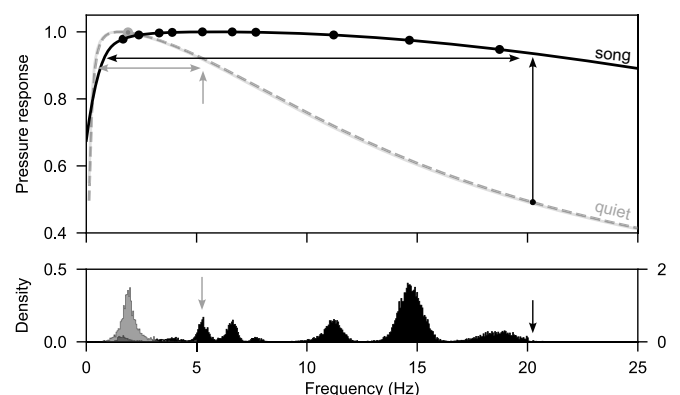


FIG. 3. Birdsong engages nonlinear respiratory dynamics that broadens biomechanical magnification beyond the quiet breathing resonance. Top: Normalized air sac pressure magnification curves. The dashed gray curve shows the numerical response of the fitted nonlinear model in the quiet-breathing regime; the solid gray curve shows the analytic response of the corresponding linearized model with the same parameters (see Sec. IB of the SM [18]). The solid black curve shows the numerical response of the fitted nonlinear model in the singing regime. Black dots indicate the modal production rate of each syllable type (see Sec. IV C and Fig. S3 of the SM [18]). Bottom: marginal distributions of syllable rates during singing (black, left axis) and quiet-breathing rates (gray, right axis). Sample sizes are given in Table S1 of the SM [18]. Black arrows in the lower panel indicate the highest syllabic rate observed, which defines a magnification level (marked by a black arrow in the top panel). This magnification level sets the bandwidth, shown by horizontal arrows.

response (solid black curve) displays a substantially broader range of amplified frequencies. We find that the bandwidth increases by a factor of approximately 5 (5.4 ± 1.5), averaged across five birds, as defined by the amplification threshold encompassing all sung syllables (indicated with arrows in Fig. 3). This nonlinear enhancement enables the syllables to be produced, on average, at $\sim 94\%$ (94.22 ± 0.03) of the theoretically maximal magnification. In contrast, under linear response conditions (dashed gray curves in Fig. 3 and Fig. S4 of the SM [18]), the system would reach only $\sim 55\%$ (55.3 ± 0.1), averaged across individuals. We also quantified the quality factors of the magnification curves for each behavioral regime; the estimates are reported in Table S4, and the procedure is described in Sec. IB of the SM [18]. Together, these findings indicate that the system operates at a biomechanical resonance during normal breathing, and that the nonlinear response engaged during singing allows all syllables to be produced with a high level of magnification.

III. DISCUSSION

In this work, we studied the avian respiratory system as a biomechanical device operating under two markedly different behavioral demands: quiet breathing and song production. Quiet breathing consists of slow, regular cycles required for ventilation, whereas song requires rapid and diverse respiratory gestures that support a behavior involved in territorial defense and mate attraction [13,33,38]. This contrast allowed us to ask whether a single biomechanical system can maintain mechanically favorable operating conditions across behavioral states.

Combining physiological recordings with a nonlinear model, we found that quiet respiration and song correspond to different dynamical regimes. During quiet breathing, the system operates near a well-defined biomechanical resonance [11]. During song, respiratory rates depart from this narrow resonance, but the effective transformation of motor commands into air sac pressure is not lost. Instead, the nonlinear response of the system broadens the range of frequencies over which pressure responses are highly magnified. This broadened regime encompasses the syllabic rates used during song, allowing respiratory gestures to be produced close to maximal magnification.

This result shows how biomechanical magnification can remain effective when a behavior requires temporal flexibility. Song production moves the respiratory system away from the narrow resonance associated with quiet breathing, a departure that could in principle impose a strong physical constraint on rapid vocal gestures [39,40]. Moreover, birdsong involves syllables produced at specific rates, so a narrow resonance would amplify some gestures while penalizing others. The nonlinear broadening observed here provides a different solution: it preserves high biomechanical magnification while allowing the same respiratory apparatus to support a broad repertoire of syllabic timescales.

More generally, these results show that the biomechanics imposes constraints but also provides dynamical opportunities for behavior. In birdsong, the nonlinear regime engaged during singing results in a bandwidth expansion that allows all syllables to be produced with a high level of magnifica-

tion. These results emphasize that behavioral output cannot be inferred from motor commands alone, but depends on how those commands are transformed by the periphery [4,41–43]. Birds' respiratory biomechanics therefore provides a quantitative example of the close relationship between neural motor activity and the physical properties of animal bodies and their environment across behavioral states.

IV. MATERIALS AND METHODS

A. Experiments

1. Subjects

Experiments were conducted on five male canaries (*Serinus canaria*), according to the regulation of the animal care committee of the University of Buenos Aires. Birds were acquired from local breeders. After 10-d quarantine, birds were housed individually in 27 cm $\times$ 23 cm $\times$ 20 cm wire cages inside an acoustic chamber. The chamber's door was usually opened, and the subjects had intermittent (but daily) auditory and visual contact with other canaries. They were fed with food and water *ad libitum*. The photoperiod was set from 6:00 AM to 8:00 PM and was controlled by an automatic timer. Measurements were done between October and March (South American spring and summer).

2. Surgery

Surgery was performed under general anesthesia using isoflurane. During surgery, a flexible silicone cannula (AM-systems Silicon Tubing 0.76 mm $\times$ 1.65 mm $\times$ 0.450 mm Catalog No. 807000) was inserted right below the last rib, 5 mm into the anterior thoracic air sac. The cannula was sutured to the rib cage, and the incision site was sealed with tissue cement (Vetbond; 3 M Animal Care Products, St. Paul, MN, USA). The free end of the cannula was attached to a piezoresistive pressure transducer (FHM-02 PGR, Fujikura, Tokyo, Japan), positioned in the backpack. In five individuals, differential EMG activity was recorded with a pair of fine (<0.01 cm diameter), custom-built, silver-plated copper wires (44TDQ, Phoenix Wire Inc., South Hero, VT, USA). To record from expiratory abdominal muscles, the bare wire tips (0.2 cm length) of the electrodes were aligned in parallel and inserted into the thin muscle sheet and fixed in place by tissue adhesive (Vetbond) applied to the muscle surface. Insulated leads were routed under the skin to the birds' back and connected to the backpack from which stronger wires led to the recording unit. Methods used to measure thoracic displacement are described in Ref. [11].

3. Experimental recordings

Song was recorded using a directional microphone (Venetian HT-81 A) and audio amplifier (Behringer MIC100). All signals were acquired using a National Instruments acquisition board (NIDAQ-USB-6212 or NIDAQ-USB-6259). Recordings were controlled using a custom MATLAB script at 44.15 kHz sample rate. Pressure signal was connected, before digitization, to a custom-built variable gain analog amplifier ($300\times$ maximum gain). EMG signals were processed with a 150 Hz high-pass RC filter and with an analog differential amplifier ($225\times$), both printed on the backpack. All

custom-built analog devices were powered by external 12-V batteries to avoid line noise.

B. Model fitting

1. Muscle forcing

The external drive was determined from the measured expiratory EMG. A critically damped linear oscillator was used to process the EMG signal and approximate the expiratory force generated by the muscles [44,45], namely,

$$\dot{x}_1 = x_2, \quad (3)$$

$$\dot{x}_2 = -\frac{1}{\tau^2}[x_1 - m(t)] - \frac{2}{\tau}x_2, \quad (4)$$

where $m(t)$ is the absolute value of the EMG. The temporal scale τ is set to 5 ms, consistent with *in vitro* muscle stimulation of these muscles [46]. The normalized expiratory force is obtained as $f_{\text{exp}}(t) = \frac{x_1(t) - P_{10}}{P_{90} - P_{10}}$, with P_{10} and P_{90} the 10th and 90th percentiles of x_1 , respectively. A threshold of three times the standard deviation of x_1 , computed in an interval in which no sound was produced, is used to determine the intervals of nonactivity of the expiratory muscles. A half-wave sinusoidal function approximates the inspiratory force, with nonzero values in each of these intervals ($f_{\text{insp}}(t)$). The amplitude-normalized external force is obtained by the summation $f(t) = f_{\text{exp}}(t) + f_{\text{insp}}(t)$.

2. Fitting procedure

Model parameters were obtained independently for each bird by minimizing the squared distance between the measured air sac pressure and the pressure obtained by integrating the model [Eqs. (1) and (2)].

Song data were fitted first. For each bird, one song recording that included a broad diversity of the respiratory gestures produced by that individual was selected. The pressure trace was normalized by the quiet-respiration amplitude of the same bird, such that quiet respiration spanned the interval $[-1, 1]$. The same normalization was used for song and quiet respiration, constraining the model to reproduce both the waveform within each regime and the relative pressure amplitudes across regimes. The song pressure trace was resampled onto a uniform temporal grid with time step 0.3 ms using linear interpolation. The time dependence of the forcing function $f(t)$ was prescribed from the measured EMG signal (Sec. IV B 1), while its overall amplitude was set by the fitted parameter F_0 .

For song, the fitted parameters were τ_x , τ_p , α_i , α_o , and F_0 . A grid search with $\geq 4.9 \times 10^4$ parameter combinations was performed over the intervals shown in Table S2 of the SM [18]. This procedure yielded a single song parameter set for each bird. No additional optimization was performed for individual syllable types or clusters. The resulting model integrations are shown in Fig. 2 and Fig. S1 of the SM [18].

Quiet respiration was then fitted using the same normalization. For each bird, a recording containing five

consecutive quiet-respiration cycles was selected. The pressure trace was resampled onto a uniform temporal grid with time step 1 ms. The parameters not expected to change, τ_x and τ_p , were held fixed at the values obtained from the song fit. The forcing amplitude and airflow conductance were allowed to differ between song and quiet respiration. Following Ref. [11], quiet respiration was modeled using a square-wave forcing function with normalized amplitude, and equal conductances were assumed for inspiration and expiration, $\alpha_i = \alpha_o \equiv \alpha$. Thus, only α and F_0 were fitted in the quiet-respiration regime. A grid search with 10^4 points over the (α, F_0) parameter space was performed to minimize the same squared-distance objective. The parameters obtained for each regime and each bird are shown in Fig. S2 and Table S3 of the SM [18]. Dimensional parameter estimates are discussed in Sec. IC and reported in Table S5 of the SM [18].

C. Song syllabic timescales

To analyze syllabic-rate distributions (defined as the inverse of syllable duration), we performed an automatic clustering of all song-related air sac pressure patterns recorded from each individual. The clustering was performed as follows. First, song syllables were segmented from the recordings, resampled to 1000 points, and normalized to the range $[-1, 1]$. For each bird, all resampled and normalized syllables were arranged into an $N_s \times 1000$ matrix, where N_s is the number of syllables for that bird (sample sizes are given in Table S1 of the SM [18]). We then applied a two-dimensional Uniform Manifold Approximation and Projection (UMAP, using `umap-learn` for Python), which embedded each syllable pressure pattern into a two-dimensional space, revealing separated clusters. These clusters were identified algorithmically using Hierarchical Density-Based Spatial Clustering of Applications with Noise (HDBSCAN), with a minimum cluster size set to 2% of the dataset (via `scikit-learn`) [47]. Figure S3 in the SM shows the result of this procedure for bird 1 [18]. For visualization purposes only, black dots in Fig. 3 mark the modes of the syllabic-rate distributions computed separately for each cluster of bird 1.

ACKNOWLEDGMENTS

We are grateful to A. Amador, S. M. Geli, J. F. Döppler, R. Bistel, F. L. Leites, and P. Clark Di Leoni for valuable help and discussions. This work was partially funded by ANPCyT-FONCyT (Argentina) under Grant No. PICT-2018-00619, Universidad de Buenos Aires (UBACyT, Argentina), and Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET, Argentina).

DATA AVAILABILITY

All the data and codes that support the findings of this study are publicly available in Zenodo [48].

[1] P. R. Grant and B. R. Grant, Evolution of character displacement in Darwin's finches, *Science* **313**, 224 (2006).

[2] M. H. Dickinson and J. R. Lighton, Muscle efficiency and elastic storage in the flight motor of *Drosophila*, *Science* **268**, 87 (1995).

- [3] M. H. Dickinson, C. T. Farley, R. J. Full, M. Koehl, R. Kram, and S. Lehman, How animals move: An integrative view, *Science* **288**, 100 (2000).
- [4] E. Tytell, P. Holmes, and A. H. Cohen, Spikes alone do not behavior make: Why neuroscience needs biomechanics, *Curr. Opin. Neurobiol.* **21**, 816 (2011).
- [5] S. Kohannim and T. Iwasaki, Analytical insights into optimality and resonance in fish swimming, *J. R. Soc. Interface* **11**, 20131073 (2014).
- [6] E. D. Tytell, C.-Y. Hsu, and L. J. Fauci, The role of mechanical resonance in the neural control of swimming in fishes, *Zoology* **117**, 48 (2014).
- [7] Q. Zhong, J. Zhu, F. E. Fish, S. J. Kerr, A. Downs, H. Bart-Smith, and D. Quinn, Tunable stiffness enables fast and efficient swimming in fish-like robots, *Sci. Robot.* **6**, eabe4088 (2021).
- [8] C. Nguyen and O. Peleg, Where physics meets behavior in animal groups, *PRX Life* **3**, 037001 (2025).
- [9] E. C. Crawford Jr. and G. Kampe, Resonant panting in pigeons, *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* **40**, 549 (1971).
- [10] G. Kampe and E. C. Crawford Jr., Oscillatory mechanics of the respiratory system of pigeons, *Resp. Physiol.* **18**, 188 (1973).
- [11] F. Fainstein, S. M. Geli, A. Amador, F. Goller, and G. B. Mindlin, Birds breathe at an aerodynamic resonance, *Chaos* **31**, 123132 (2021).
- [12] J. H. Bates, C. G. Irvin, R. Farré, and Z. Hantos, Oscillation mechanics of the respiratory system, *Compr. Physiol.* **1**, 1233 (2011).
- [13] R. S. Hartley and R. A. Suthers, Airflow and pressure during canary song: Direct evidence for mini-breaths, *J. Comp. Physiol. A* **165**, 15 (1989).
- [14] A. Amador, F. Goller, and G. B. Mindlin, Frequency modulation during song in a suboscine does not require vocal muscles, *J. Neurophysiol.* **99**, 2383 (2008).
- [15] R. Alonso, F. Goller, and G. B. Mindlin, Motor control of sound frequency in birdsong involves the interaction between air sac pressure and labial tension, *Phys. Rev. E* **89**, 032706 (2014).
- [16] M. F. Schmidt and F. Goller, Breathtaking songs: Coordinating the neural circuits for breathing and singing, *Physiology* **31**, 442 (2016).
- [17] F. Goller, Vocal athletics—from birdsong production mechanisms to sexy songs, *Anim. Behav.* **184**, 173 (2022).
- [18] See Supplemental Material at <http://link.aps.org/supplemental/10.1103/k495-q611> for additional text, figures and tables, which includes Refs. [49–51].
- [19] T. I. Drăgănoiu, L. Nagle, and M. Kreutzer, Directional female preference for an exaggerated male trait in canary (*Serinus canaria*) song, *Proc. R. Soc. Lond. B* **269**, 2525 (2002).
- [20] B. Ballentine, J. Hyman, and S. Nowicki, Vocal performance influences female response to male bird song: An experimental test, *Behav. Ecol.* **15**, 163 (2004).
- [21] S. Nowicki and W. A. Searcy, Song function and the evolution of female preferences: Why birds sing, why brains matter, *Ann. N. Y. Acad. Sci.* **1016**, 704 (2004).
- [22] S. P. Caro, K. B. Sewall, K. G. Salvante, and K. W. Sockman, Female Lincoln's sparrows modulate their behavior in response to variation in male song quality, *Behav. Ecol.* **21**, 562 (2010).
- [23] K. Oberweger and F. Goller, The metabolic cost of birdsong production, *J. Exp. Biol.* **204**, 3379 (2001).
- [24] M. Franz and F. Goller, Respiratory patterns and oxygen consumption in singing zebra finches, *J. Exp. Biol.* **206**, 967 (2003).
- [25] S. Ward, J. R. Speakman, and P. J. Slater, The energy cost of song in the canary, *Serinus canaria*, *Anim. Behav.* **66**, 893 (2003).
- [26] A. Zahavi and A. Zahavi, *The Handicap Principle: A Missing Piece of Darwin's Puzzle* (Oxford University Press, Oxford, 1999).
- [27] J. N. Maina and E. R. Schachner, Biology of the avian respiratory system: Development, evolutionary morphology, function and clinical considerations, *Philos. Trans. R. Soc. B* **380**, 20230419 (2025).
- [28] M. A. Trevisan, G. B. Mindlin, and F. Goller, Nonlinear model predicts diverse respiratory patterns of birdsong, *Phys. Rev. Lett.* **96**, 058103 (2006).
- [29] F. Fainstein, F. Goller, and G. B. Mindlin, Song-like activation of syringeal and respiratory muscles during sleep in canaries, *J. Comp. Physiol. A* **211**, 135 (2025).
- [30] T. Gardner, G. Cecchi, M. Magnasco, R. Laje, and G. B. Mindlin, Simple motor gestures for birdsongs, *Phys. Rev. Lett.* **87**, 208101 (2001).
- [31] P. Scheid and J. Piiper, Volume, ventilation and compliance of the respiratory system in the domestic fowl, *Respir. Physiol.* **6**, 298 (1969).
- [32] J. M. York, B. A. Chua, C. M. Ivy, L. Alza, R. Cheek, G. R. Scott, K. G. McCracken, P. B. Frappell, N. J. Dawson, S. L. Laguë, *et al.*, Respiratory mechanics of eleven avian species resident at high and low altitude, *J. Exp. Biol.* **220**, 1079 (2017).
- [33] R. Suthers, F. Goller, and C. Pytte, The neuromuscular control of birdsong, *Phil. Trans. R. Soc. Lond. B* **354**, 927 (1999).
- [34] F. Goller and R. A. Suthers, Role of syringeal muscles in gating airflow and sound production in singing brown thrashers, *J. Neurophysiol.* **75**, 867 (1996).
- [35] F. Goller and R. A. Suthers, Role of syringeal muscles in controlling the phonology of bird song, *J. Neurophysiol.* **76**, 287 (1996).
- [36] R. P. Feynman, R. B. Leighton, and M. Sands, *The Feynman Lectures on Physics* (Addison-Wesley, Reading, MA, 1966), Vol. 1.
- [37] F. S. Crawford, Jr., *Waves*, Berkeley Physics Course, Vol. 3 (McGraw-Hill, New York, 1968).
- [38] C. K. Catchpole and P. J. Slater, *Bird Song: Biological Themes and Variations* (Cambridge University Press, Cambridge, 2003).
- [39] J. Podos, A performance constraint on the evolution of trilled vocalizations in a songbird family (Passeriformes: Emberizidae), *Evolution* **51**, 537 (1997).
- [40] J. Podos and H.-C. Sung, Vocal performance in songbirds: From mechanisms to evolution, in *The Neuroethology of Birdsong*, edited by J. T. Sakata, S. C. Woolley, R. R. Fay, and A. N. Popper (Springer International Publishing, Cham, 2020), pp. 245–268.
- [41] H. J. Chiel and R. D. Beer, The brain has a body: Adaptive behavior emerges from interactions of nervous system, body and environment, *TINS* **20**, 553 (1997).
- [42] K. Nishikawa, A. A. Biewener, P. Aerts, A. N. Ahn, H. J. Chiel, M. A. Daley, T. L. Daniel, R. J. Full, M. E. Hale, T. L. Hedrick, *et al.*, Neuromechanics: An integrative approach

- for understanding motor control, *Integr. Comp. Biol.* **47**, 16 (2007).
- [43] A. Gomez-Marin and A. A. Ghazanfar, The life of behavior, *Neuron* **104**, 25 (2019).
- [44] M. B. Shapiro and R. V. Kenyon, Control variables in mechanical muscle models: A mini-review and a new model, *Motor Control* **4**, 329 (2000).
- [45] J. F. Döppler, A. Bush, F. Goller, and G. B. Mindlin, From electromyographic activity to frequency modulation in zebra finch song, *J. Comp. Physiol. A* **204**, 209 (2018).
- [46] K. H. Srivastava, C. M. Holmes, M. Vellema, A. R. Pack, C. P. Elemans, I. Nemenman, and S. J. Sober, Motor control by precisely timed spike patterns, *Proc. Natl. Acad. Sci. USA* **114**, 1171 (2017).
- [47] R. J. Campello, D. Moulavi, and J. Sander, Density-based clustering based on hierarchical density estimates, in *Pacific-Asia Conference on Knowledge Discovery and Data Mining* (Springer, 2013), pp. 160–172.
- [48] F. Fainstein, F. Goller, and G. B. Mindlin, Data and code for “Nonlinear respiratory biomechanics broadens the range of amplified dynamics during birdsong”, Zenodo, 2026, doi: [10.5281/zenodo.20645165](https://doi.org/10.5281/zenodo.20645165).
- [49] J. M. L. Miller, A. Ansari, D. B. Heinz, Y. Chen, I. B. Flader, D. D. Shin, L. G. Villanueva, and T. W. Kenny, Effective quality factor tuning mechanisms in micromechanical resonators, *Appl. Phys. Rev.* **5**, 041307 (2018).
- [50] L. P. Claessens, The skeletal kinematics of lung ventilation in three basal bird taxa (emu, tinamou, and guinea fowl), *J. Exp. Zool.* **311A**, 586 (2009).
- [51] R. J. Brocklehurst, S. Moritz, J. Codd, W. I. Sellers, and E. L. Brainerd, XROMM kinematics of ventilation in wild turkeys (*Meleagris gallopavo*), *J. Exp. Biol.* **222**, jeb.209783 (2019).