How Hummingbirds Hum: Oscillating Aerodynamic Forces Explain Timbre of the Humming Sound

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Abstract
The source of the hummingbird's distinctive hum is not well understood, but there are clues to its origin in the acoustic nearfield and farfield. To unravel this mystery, we recorded the acoustic nearfield generated by six freely hovering Anna's hummingbirds using a 2176 microphone array. We also directly measured the 3D aerodynamic forces generated by the hummingbird in vivo using a new aerodynamic force platform. To determine the degree to which the aerodynamic forces cause the hum, we developed a simple first-principles model to predict the acoustic field radiated by the 3D oscillating forces. The correspondence between the predicted and measured acoustic field shows the primary acoustic sources of the hum are the lift and drag forces that oscillate as the flapping wings move back and forth. The model also shows how the aerodynamic force profile of the flapping wing determines the hum's timbre and sound pressure level: profiles that support bodyweight with higher harmonics radiate more acoustic power. Further, extending this model across birds and flying insects, we show how the radiated acoustic power scales with body mass to the second power—with allometric deviation making larger birds quieter and elongated flies louder. The model's ability to predict the acoustic signature of flapping wings suggests it can be applied for such diverse uses as differentiating wing and feather sounds in bird display behaviors to interpreting how insects generate courtship songs with their wings to making flapping robot wings more silent.

Significance Statement
Hummingbirds are aptly named for the sound they make as they flap their wings, but the source of their hum is not fully understood. Using new experimental setups, we integrate the absolute and acoustic pressure field combined with wing kinematics to show that the hum's timbre arises from oscillating lift and drag forces on each wing. We developed a first-principles acoustic model that predicts—for a given wing size, wingbeat frequency, stroke amplitude and weight support profile—the acoustic spectrum and power a flapping wing will produce. We modeled the hum generated by flapping animal wings ranging from insects to birds, which clarifies bioacoustic observations. Our model should be extendable to design the acoustic signature of robots with flapping wings.

Main Text
Introduction
Birds, bats and insects flap their wings to generate unsteady aerodynamic forces that lift their body into the air, which enables them to fly. When their flapping wings move through air, they create unsteady pressure fluctuations that radiate outward at the speed of sound. In addition to furnishing flight, pressure waves serve various acoustic communication functions during behavioral displays. Male Drosophila use aerodynamically functional wings to create humming songs near their flapping frequency to increase female receptivity to mating (1). More sophisticatedally, male and female mosquitoes duet at the third harmonic of their wingbeat frequency (2). In contrast, pigeons use modified primary feathers that
sonate around 1 kHz when they start flapping their wings to automatically alert flock members that they are taking off (3–6). Feather sonation during flapping flight may also communicate information like flight speed, location in 3D space, and wingbeat frequency to conspecifics (7). Hence, male broad-tailed hummingbirds generate a whistling sound with modified primary feathers in their flapping wings during displays to defend courting territories (8). Silent fliers like owls, on the other hand, suppress the aerodynamic sound generated by their wings to mitigate interference with their hearing and escape prey detection (9–13). Their flapping wings also generate less structural noise (13) because their feathers lack the noisy directional fastening mechanism that locks adjacent flight feathers during wing extension in other bird species (14). These diverse adaptations illustrate how a wide range of mechanisms can contribute to the sound that flapping wings generate. Consequently, it is not fully understood how flapping wings generate their characteristic sound—from the mosquito’s buzz, the hummingbird’s hum, to the larger bird’s whoosh.

Our physical understanding of how wings generate sound is primarily based on aircraft wing and rotor aeroacoustics (15, 16). In contrast to animals, however, engineered wings do not flap, do not change shape dynamically, are much larger, and operate at much higher speeds (higher Reynolds numbers). They also operate at lower angles of attack to avoid stall, which results in more compact airflow patterns than animals generate in flapping flight (17–19). Despite these marked differences, rotors and flapping wings have one thing in common: they both revolve around a center pivot. Whereas flapping wings reciprocate along the joint, rotors revolve unidirectionally. The revolution of rotors generates loud tonal noise, because the pressure field they generate rotates in space at the same frequency (20, 21). Similarly, when animals flap their wing back and forth along the shoulder joint during each stroke, they create a high-pressure region below their wing and a low-pressure region above. The pressure differences are associated with the wing’s high lift and drag respectively (22, 23). Computational fluid dynamics (CFD) simulations of flapping insect wings suggest that the acoustic field can be characterized as a dipole at the wingbeat frequency (24–26). Further, flapping wing pitch reduction (27) and increased wing flexibility (28) reduces the simulated nearfield sound pressure level. All these findings point to the potential role of oscillating aerodynamic forces in generating wing hum. Indeed, numerical simulation of the Ffowcs Williams and Hawkings aeroacoustic equation showed that the farfield hum of flapping mosquito wings is primarily driven by aerodynamic force fluctuation (26). Despite these important advances, in vivo evidence is lacking. Finally, there is no simple first-principles model that can satisfactorily integrate flapping wing kinematics and aerodynamic forces to predict the acoustic near and far field generated by animals across taxa.

Hummingbirds are an ideal model for developing and testing a minimal, first-principles model of flapping wing hum: their wing kinematics and unsteady aerodynamic forces are very repeatable during hover (29–31). Further, hummingbird wing morphology and flight style share similarities with both birds and insects. In addition to high-frequency feather sonations, hummingbirds produce a prominent hum that is qualitatively similar to an insect’s buzz. Earlier aeroacoustics studies of hummingbirds have resolved the farfield acoustic pressure field, at a distance greater than 10 or more body lengths away from the hummingbird (32–35). While this distance relates to how humans perceive and interact with these animals, hummingbirds frequently interact with conspecifics and other animals at more intimate distances—in the acoustic nearfield. For example, rufous hummingbirds intimidate intruders near a food source by performing cobra-like maneuvers close-up (36). Furthermore, wing hum can announce a hummingbird’s presence, especially to the opposite sex (37). Although their audiogram has yet to be established below 1 kHz (38), this and other behavioral evidence suggests hummingbirds may be able to perceive the wing hum from a conspecific. Finally, the hum may reveal the hummingbird’s presence to predators in plant clutter when vision is obstructed.

To resolve how the oscillating aerodynamic force generated by flapping wings may contribute to wing hum, we developed a new aerodynamic force platform (AFP; (31, 39, 40)) to directly measure the net 3D aerodynamic force generated by freely hovering hummingbirds. We integrated this data in a new first-principles aeroacoustics model to predict the sound radiated due to the oscillating forces from flapping wings. Next, we compared the predicted acoustic field with novel acoustic nearfield recordings for six freely hovering hummingbirds, which corroborates the predictive power of our minimal model. We then used our validated model to determine how flapping wing hum depends on the frequency content in the oscillating forces across mosquitoes, flies, hawkmoths, hummingbirds, and parrotlets in slow hovering flight. Finally, we used these findings to determine how the hum scales with body mass and flapping frequency across 170 insect and bird species.
Results

**In vivo 3D aerodynamic force and acoustic nearfield measurements**

We used a 3D aerodynamic force platform (AFP; Fig. 1A) consisting of six instrumented force plates to record the oscillating aerodynamic forces generated by a hovering hummingbird **in vivo**. Simultaneously, three calibrated stereo high-speed camera pairs captured the wingbeat kinematics through three orthogonal imaging windows (N = 6 birds, each bird made 2 flights, n = 5 wingbeats were fully analyzed per flight for 60 total wingbeats). We combined the 3D forces, 3D wing kinematics and morphology measurements to decompose the oscillating lift and drag forces that each wing contributes throughout the wingbeat (Fig. 1B). This shows the oscillating lift consists primarily of the first and second wingbeat harmonic (whereby the first harmonic mean ± standard deviation is 44.2 ± 1.8 Hz), while the drag is composed primarily of the second and third harmonic (Fig. 1C). We also measured the 3D beak contact force on the artificial flower from which the hummingbird was feeding (5.2 ± 2.3% bodyweight), which is negligible.

To quantitatively reconstruct the 3D acoustic field associated with the bird’s hum, we used broadband nearfield acoustic holography (NAH) computed with measurements from a custom flight arena with four acoustic arrays (Fig. 1D; N = 6 birds, n =18 flights total, see Table S1 for details). Each frequency component of the holograms was regularized independently using a Bayesian evidence method (41) before adding them all together to create the broadband NAH results. To reduce distortions due to frequency leakage, linear predictive border padding (42, 43) was applied to the time signals. The recording of a typical pressure profile by a single microphone in the top array centered above the bird reveals the pressure fluctuations throughout a single wingbeat (Fig. 1E). The many fluctuations explain the rich frequency content revealed in the acoustic spectrum averaged over all microphones (Fig. 1F). These include strong peaks at the fundamental frequencies of the wingbeat as well as its higher harmonics, which rise prominently above the background noise floor and characterize the hummingbird hum.

Aerodynamic force (AFP) and acoustic (array) recordings provide complementary insights into the pressure field generated by flapping wings. Whereas the AFP records the steady and low-frequency unsteady components of the integrated pressure field (for which Fig. 1C is representative) up to three times the wingbeat frequency, the array measures only the unsteady content of the pressure field distribution but up to ~1000 times the wingbeat frequency, of which we studied the first ten harmonics (for which Fig. 1F is representative). Yet these two representations of the pressure fluctuations generated by the bird should relate mechanistically if the aeroacoustic field of the hummingbird’s hum originates primarily from the oscillating aerodynamic lift and drag force generated by the flapping wing.

**Aeroacoustics model of the hum synthesizes in vivo forces and wing kinematics**

To determine if the low frequency oscillating forces generated by the birds’ flapping wings drive the characteristic humming sound spectrum, we develop a simple aeroacoustics model based on the governing acoustics equations that predict the resulting acoustic field. Our minimal model of the acoustic pressure field radiated by the flapping wings (Fig. 1G) depends only on the physical properties of air, the wing stroke kinematics (Fig. 1H), and the oscillating lift and drag forces that we measured **in vivo** (Fig. 1B).

Aerodynamic blade-element theory shows how the radial aerodynamic force distribution can be integrated and represented by the net force at the center of pressure, a characteristic radial location where the net force acts (44). Analogously, using an acoustic blade-element model, we determine that an unsteady aerodynamic force distribution over the wing can also be concentrated into an equivalent point force source at the effective acoustic source radius along the wing, similar to propeller noise theory (21). The effective radius of this point, measured with respect to the shoulder joint, is equal to the point at which the net drag force results in the same net torque on the wing (21). This radius lies at the wing-length-normalized third moment of area for flapping wings, $R_3/R$ (44). For Anna’s hummingbirds $R_3/R$ is equal to 55% wing radius (45). In practice, the effective radius for acoustic calculations can differ somewhat from the effective radius for a point force (21). Therefore, we conduct a dimensional analysis to determine how acoustic pressure scales with radial position (see Supplementary Information for details),
which confirms $R_3$ is the appropriate radius. This acoustic radius agrees with wind turbine acoustics measurements at lower harmonics of the blade passing frequency (46).

At the retarded time $t$ (the time when the acoustic field began to propagate from the point where it was emitted to the observer location), we numerically solve the acoustic wave equation for point forces to predict how the 3D oscillating point force radiates pressure waves outward from the left and right flapping wings. An unsteady aerodynamic point force, $F_{\text{wing}}$, in arbitrary motion generates an air pressure fluctuation, $p$, in the stationary atmosphere at the retarded time that radiates outward at the speed of sound, $a_o$, as follows (21):

$$p = \left[ \frac{1}{4\pi a_o|\mathbf{r}|^2(1 - M_r)^2} \left( \mathbf{r} \cdot \frac{\partial F_{\text{wing}}}{\partial t} + \frac{1}{1 - M_r} \frac{\partial M_r}{\partial t} (\mathbf{r} \cdot F_{\text{wing}}) \right) + \frac{1}{4\pi|\mathbf{r}|^2(1 - M_r)^2} \left( \frac{1}{|\mathbf{r}|} (1 - M_r^2) \frac{(1 - M_r)}{(1 - M_r^2)} (\mathbf{r} \cdot F_{\text{wing}}) - (F_{\text{wing}} \cdot \mathbf{M}) \right) \right]. \quad (1)$$

Brackets represent values that are evaluated at the retarded time; $\mathbf{r}$ are the Cartesian coordinates measured from the inertial observer, the location of a microphone in our experiment, with respect to the non-inertial point force location on the flapping wing. Further, the Mach vector, $\mathbf{M}$, is defined as $\mathbf{M} \equiv \mathbf{v}_{\text{R3}}/a_o$ where $\mathbf{v}_{\text{R3}}$ is the velocity of the wing at $R_3$ and $a_o$ is the speed of sound. Finally, we define the Mach number as $M \equiv |\mathbf{M}|$ and the convective Mach number as $M_r \equiv |\mathbf{M} \cdot \mathbf{r}|/|\mathbf{r}|$. The acoustic pressure fluctuation consists of two contributions: The first term (Eqn. 1) is the farfield quadrupole term that radiates sound along four primary directions proportional to the point force unsteadiness and the radial acceleration of its position in space. The second term is the nearfield pressure term that radiates sound like a dipole source along two primary directions proportional to the point force and Mach vector. The nearfield term is dominant near the sound source. In the case of a hummingbird, the nearfield term decays exponentially with distance since the hummingbird acts as a compact acoustic source (47). Because the wavelength of the first radiated acoustic harmonic ($a_o/f_1$) is much larger than the source length scale: $R f_1/a_o < 0.01$ in which $f_1$ overlaps with the wingbeat frequency (44.2 Hz, $N = 6$, $n = 2$), and $R$ is approximated by the wing radius $R = 0.058 \pm 0.003$ m. Consequently, a hummingbird acts as an approximate compact acoustic source up to its tenth wingbeat harmonic ($10 \cdot f_1$).

Using Eqn. 5, we calculate the resulting pressure fluctuation at each of the 2176 microphones in our acoustic arena to directly compare the simulated and measured humming sound up to the tenth harmonic (after which the ambient noise floor of the experiment is approached). We find excellent frequency agreement between the model and in vivo spectra for the first ten harmonics (Fig. 2A), good spatial agreement throughout a wingbeat (Fig. 2B), and good agreement in the magnitude of the sound pressure for the first four harmonics (Fig. 2A and Table 1). The first four harmonics represent most of the radiated harmonic power: ~99% of the simulated power and ~67% of the measured power for +/-2.5 Hz bands around each wingbeat harmonic up to 180 Hz. The percentage difference is due to at least three factors: (i) harmonics beyond the fourth contribute more power in the measured than in the simulated spectrum (Table 2), (ii) the experiment’s ambient noise floor is substantially higher than the computational noise floor (Fig. 1F), and (iii) some low amplitude tonal noise sources observed between harmonics cannot be attributed to humming (Fig. 2A).

**Dipole acoustic directivity patterns align with gravitational and anatomical axes**

The directivity of the acoustic pressure field varies between harmonics. Odd harmonics are associated with a rotational pressure fluctuation mode while even harmonics are associated with a vertical pressure fluctuation mode. To assess the near and farfield directivity, we reconstruct 3D broadband pressure fields (across 3–500 Hz) over an entire wingbeat during stationary hovering flight using spherical NAH (48). The reconstructed pressure fields start out at a radius of 8 cm centered on the body such that the inner spherical surface encloses the hummingbird (the wing radius with respect to the body center is 5.8 ± 0.3 cm) and the outer spherical surface ends at a radius of 10 m (Fig. 3A). To evaluate acoustic pressure directivity in the nearfield (1 m distance, ~8.6 wingspans, Fig. 3B) and farfield (10 m distance, ~86 wingspans, Fig. 3C), we calculate the cross sections of the pressure field in the sagittal (side) and coronal (frontal) anatomical planes. Averaging directivity plots across all birds and flights, we find the 3D broadband pressure surface is roughly spherical in the nearfield and farfield.
The mass, wingspan, and flapping frequency change across all individual animals in each group. Throughout the wingbeat change each of the four groups, the instantaneous weight support, stroke amplitude, and frequency content the simplified model matches the original model for a hummingbird well (Fig. S1, Table S2). Between exact same approximations for hummingbirds as we field for each animal

Rationale for asymmetric wings

To simplify the comparison further elongated flies and compact flies (Lepidoptera), compact flies (Cyclorrhapha), and elongated flies (Nematocera), which fly with marked shallower stroke amplitudes than compact flies. Since 3D aerodynamic force and wing kinematics data are not available for all these species, and most of the radiated acoustic sound is directed vertically (Fig. 3B-K), we simplified the model. We chose a well-studied animal for which a wingbeat-resolved vertically-oriented force component has been reported previously to act as a paradigm for each group. Respectively, the vertical force of pacific parrots (Forpus coelestis (49)) for generalist birds, the vertical force of Anna’s hummingbird (Calypte anna; (31)) for hummingbirds, the lift force of hawkmoths (Manduca sexta (50)) for moths and butterflies, the lift force of mosquitoes (Culex quinquefasciatus; (51)) for elongated flies and the net force of Drosophilid flies (Drosophila hydei; (52)) for compact flies (Table S4).

To simplify the comparison further, we approximate the stroke plane as horizontal and the normalized lift profile to have the same shape as the reported vertically oriented force profile, so that the lift generated during a wingbeat sums up to body weight for all associated species in the same way. To calculate the associated drag profile, we used previously reported quasi-steady lift/drag ratio data for Anna’s hummingbirds (31, 45) and assume it is representative for all animals. Finally, to compute the acoustic field for each animal’s wing, we locate the lift and drag force at the third moment of area of a hummingbird wing, 55% of the wing radius (which compares to 58% for parrots (49)). In our comparison we make the exact same approximations for hummingbirds as we do for the other animals. Despite these assumptions, the simplified model matches the original model for a hummingbird well (Fig. S1, Table S2). Between each of the four groups, the instantaneous weight support, stroke amplitude, and frequency content throughout the wingbeat change based on the associated paradigm animal (Fig. 4A and B). In contrast, the mass, wingspan, and flapping frequency change across all individual animals in each group.

Calculating the ratio of the wing length scale and the wavelength of the first radiated acoustic harmonic (based on wingbeat frequency) across all species, we find $R_{wm}/a_0 \leq 0.01$ (Fig. S9). Thus, the flapping wings of all these animals act as compact acoustic sources from the first to tenth harmonic in the

Extension of the acoustic model across animals that flap their wings

Using our model, we predict the acoustic sound generated by flapping wings for a wide range of insects and birds that hover or perform slow flapping flight during takeoff and landing across seven orders of magnitude in body mass, $m$, and three orders of magnitude in wing flapping frequency, $f_w$. We generalize the flapping animals we consider here into five distinct groups for which we found data: generalist birds (Aves except Trochilidae), hummingbirds (Trochilidae), moths and butterflies (Lepidoptera), compact flies (Cyclorrhapha), and elongated flies (Nematocera), which fly with marked shallower stroke amplitudes than compact flies. Since 3D aerodynamic force and wing kinematics data are not available for all these species, and most of the radiated acoustic sound is directed vertically (Fig. 3B-K), we simplified the model. We chose a well-studied animal for which a wingbeat-resolved vertically-oriented force component has been reported previously to act as a paradigm for each group.

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hummingbird. Indeed, synchronized acoustic and video recordings show that the measured first acoustic harmonic overlaps with the wingbeat frequency across insects (2, 53), hummingbirds (Fig. 1), and other birds and bats (54).

The weight support profiles of each of the five paradigm animals has distinct harmonic content (Fig. 4B). To understand how this drives acoustic power and timbre, we use our acoustic model to assign each of the five paradigm animals all five weight support profiles. For example, we variously assign the weight support profile of a mosquito, fly, hawkmoth, hummingbird, and parrotlet to our hummingbird model. This allows us to investigate the weight support profile’s effects on differences in radiated acoustic power (Fig. 4C) and the acoustic spectrum (Fig. 4D). The weight support profiles of the mosquito and fly consistently generate more acoustic power and sound pressure than the other weight support profiles. Lastly, we extend the acoustic model from the five paradigm animals to 170 animals across the five groups. Body mass and flapping frequency for hummingbirds, compact flies, elongated flies, and moths and butterflies were obtained from Greenewalt (55), while the values for larger birds were obtained from Pennycuick (56) (Fig. 4E,F). Comparing the model simulation results with the isometric scaling relation we derived based on the model (Eqn. S25-50) shows that radiated acoustic power scales allometrically with body mass (Fig. 4E) except for compact flies and moths and butterflies, which scale isometrically. Considering flapping wing parameters are known to scale allometrically with body mass, we test the scaling law itself (Fig. 4F), which collapses the data well on average across species (average slope = 0.9; ideal slope = 1), confirming the scaling law represents our model.

Discussion

Oscillating lift and drag forces explain wing hum timbre

Our minimal, first-principles aeroacoustic model shows the hummingbird’s hum originates from the oscillating lift and drag forces generated by their flapping wings. Remarkably, the low frequency content in the aerodynamic forces also drives higher frequency harmonics in the acoustic spectrum of the wing hum. The higher harmonics originate from nonlinear frequency mixing in the aeroacoustic pressure equation between the frequency content in the wing’s aerodynamic forces and kinematics. The predicted humming harmonics of the wingbeat frequency overlap with the measured acoustic spectrum (averaged over all microphones). In addition to the good frequency match, the sound pressure level magnitudes of the first four harmonics match with a difference of 0.5–6 dB (Table 1). This agreement is similar or better compared to more detailed aeroacoustic models of drone and wind turbine rotors, that predict noise due to blade-wake interactions and boundary layer turbulence (57–59). Further, comparing the measured and predicted spatial acoustic-pressure holograms for the top and front arrays (reconstructed holograms at a plane 8 cm from the bird; Fig. 2B), we find that the hologram phase, shape, and magnitude correspond throughout the stroke. The regions of high and low pressure in the hologram are associated with wing stroke reversals, similar to the pressure extrema observed at stroke reversal in computational fluid dynamics simulations of flapping insect wings (25–27).

Even though the input forces were lowpass filtered beyond the fourth harmonic, the amplitudes of higher harmonics are predicted. This is due to two distinct stages of nonlinear frequency mixing in our wing hum model: (i) the calculation of the resulting aerodynamic force vector generated by each flapping wing and its oscillatory trajectory in space, and (ii) the calculation of the resulting acoustic pressure waves (see Supplementary Information for details).

Our acoustic model predicts hum harmonics that lie in an intermediate frequency range between the wingbeat frequency (~40 Hz) and the lower bound of feather sonations (typically >300 Hz;60, 61)). Hence our model allows for an objective contrast between wing hum noise and other possible aerodynamic noise generation mechanisms. Indeed, we observe small tonal peaks between the prominent harmonics in Fig. 2A that are not radiated by the oscillating aerodynamic forces generated by the flapping wing, according to our first-principle hum model. Consequently, these low amplitude peaks must radiate from another acoustic source such as aeroelastic feather flutter (62) or vortex dynamics (17).

In the under-studied frequency regime of the hum, the first two harmonics are paired as they have similar sound pressure levels (Fig. 2A). For the hummingbird, the pairing of the first and second harmonics is due to the dominance of the pressure differential generated twice per wingbeat during the downstroke and upstroke. The associated substantial weight support during the upstroke (Fig. 1B; 31) has been found across hummingbird species (31), which generalizes our findings. The sound pressure level pairing also mirrors the harmonic content in the lift and drag forces (Fig. 1C) as well as the stroke and deviation kinematics (Fig. 1I). Given that the first and second harmonics dominate both the forces...
and kinematics spectra, the harmonic content of the resulting acoustics is a mixture of these two. The third harmonic and beyond resemble the first paired harmonic because they are associated with the noise generation mechanisms of the first two harmonics (47). In concert, the first four harmonics constitute most of the acoustic radiated power of the hum timbre—the distinct sound quality that differentiates sounds from distinct types of sources even at the same pitch and volume—which is determined by the number and relative prominence of the higher harmonics present in a continuous acoustic wave (63).

Wing hum acoustic directivity and orientation depends on harmonic parity

Acoustic directivity is consistent from near to farfield, but changes based on the harmonic. In the 3D holograms, the dipole structures are associated with the high vertical forces to offset weight (31). These dipole orientations are not evident in the broadband holograms (Fig. 3B-C) because slight variations between the flights are averaged and smear out the dominant dipole lobes (individual flights for each directivity plot shown in Fig. S3). The first and third harmonics resemble dipoles that are tilted aft. For example, for the first harmonic in the sagittal plane in both the nearfield and farfield, the dipole is tilted aft (Fig. 3D-E; Table 2), which is associated with the pressure generated during the downstroke once per wingbeat. In contrast, second and fourth harmonics are more vertically oriented. The second harmonic is directed upwards in the nearfield and farfield (Fig. 3F-G; Table 2) and is associated with the pressure generation for the vertical weight support that occurs twice per wingbeat. The third and fourth harmonics have more complex shapes (Fig. 3H-K) that bear resemblances to the first two because they are associated with the first two harmonics (47). The acoustic model also shows these directionality effects over the first two harmonics in the sagittal and coronal near and farfield. In contrast, the simulation has more symmetry between the upstroke and downstroke, resulting in a symmetric and better-defined dipole structure. Finally, the simulation agrees well with the dipole shapes and orientations reported in CFD simulations of flapping insect wings along sagittal and coronal planes (25).

Acoustic model explains perceived hum loudness and timbre of birds and insects

The sound magnitude that flapping wings produce depends heavily on the weight the flapping wings must support, and the timbre depends on the unique frequency content of each weight support profile (Fig. 4B). Flies and mosquitoes are orders of magnitude lighter than our three other paradigm animals and produce less acoustic power accordingly (Fig. 4C). Yet the fly and mosquito weight support profiles have the highest harmonic content (Fig. 4B) and therefore, when all else is equal, consistently radiate the most power (Fig. 4C). In contrast, the parrotlet weight support profile has the lowest harmonic content (Fig. 4B); with most of the force being generated once per wingbeat during the downstroke, hence it radiates the least power when all else is equal (Fig. 4C). For hummingbirds and hawkmoths, the proportion of weight support in upstroke versus downstroke is similar (25, 31); this gives them roughly similar vertical force profiles and leads to similar acoustic power (Fig. 4C). The effect of altering the weight support profile is also visible in the acoustic spectrum. At the scale of a hummingbird (Fig. 4C, inset), the prescribed weight support profiles distinguish the distribution of the overall decibel level for the first four harmonics (Fig. 4D). This explains why flies and mosquitoes may seem loud relative to their small size: while they have little mass, it is partially offset by the high harmonics in their weight support profiles. Furthermore, it is the higher harmonics present in the weight support profile that directly affect the perceived quality of the sound—the timbre.

Radiated acoustic power scales allometrically in birds, and elongated flies

Body mass is a strong predictor of radiated acoustic power because the aerodynamic forces needed to sustain slow hovering flight must be proportionally larger for heavier animals (44, 64, 65). The associated increase in aerodynamic force amplitude drives acoustic pressure (Eqn. 1). The resulting radiated acoustic power, $P_s$, scales with the square of the acoustic pressure, $P$ (Eqn. S25). Increasing flapping frequency also increases the radiated acoustic power; flapping faster requires more power from the animal and injects more acoustic energy into the air. Applying scaling analysis to Eqn. 1 (derived in Supplementary Information; Eqn. S25-50), we can predict the order of magnitude of the radiated acoustic power in the farfield (66):

$$P_s = \frac{4\rho f^2 \Phi^2 f_0^2}{\pi \rho_0 \rho_{0,1}^2} \approx 2.5 \cdot 10^{-6} \Phi_0^2 m^2 f_0^2,$$  
(2)
where the subscript "o" corresponds to the reference value and $F_o = mg$ is the aerodynamic force magnitude required to maintain hover. The resulting acoustic power law scales with the product of wing stroke amplitude, $\Phi_o$, body mass, $m$, and wingbeat frequency, $f_w$, squared. Further, since $\Phi_o$ is dimensionless, it has order of magnitude one, measured in radians, across flapping birds (67) and insects (68). The remaining terms, $4/\pi$, the gravitational constant $g = 9.81 \text{ m s}^{-2}$, the air density $\rho_o = 1.23 \text{ kg m}^{-3}$, and speed of sound in air, $a_o \approx 343 \text{ m s}^{-1}$ are constants that determine the factor $2.5 \cdot 10^{-6} \text{ kg}^{-1} \text{s}^{-1}$ between the radiated acoustic power and its scaling variables.

When acoustic power is plotted as a function of mass (Fig. 4E), the predicted exponent of 2.0 is higher than the observed average exponent of 1.3. Among the five groups, compact flies and moths and butterflies do match the scaling law prediction, showing their acoustic power scales isometrically with body mass. The other groups scale allometrically with either higher, elongated flies, or lower, hummingbirds and other birds, exponents of body mass. Allometric divergence can more readily explain why larger hummingbirds are quieter, because they have disproportionately larger wings combined with an approximately constant wing velocity across an order of magnitude variation in body mass, which is thought to maintain constant burst flight capacity (65). Conversely, for insects, the gracile bodies and larger wings of moths and butterflies are compensated by the higher flapping frequency of compact flies. Therefore, flies use asynchronous flight muscles to achieve these high flapping frequencies (69). Large elongated flies are unusually noisy for their body mass, with radiated acoustic power values well above the average scaling law (Fig. 4E). The disproportional noise generated by elongated flies is due to two combined effects: the higher harmonic content of their weight support profile (Fig. 4A,B) and their consistent allometric acoustic power scaling (Fig. 4E).

The difference between the scaling exponents for mass is primarily due to allometric scaling of wingbeat frequency with body mass because the simulated acoustic power scales with the right-hand side of scaling Eqn. 2 with an exponent of 0.9 (on average), close to 1 (Fig. 4F). Scaling Eqn. 2 is precise for birds, compact flies, and moths and butterflies, but the two other groups scale allometrically: larger birds get more silent (slope = 0.9) while elongated flies (1.1) get louder than predicted by isometric scaling incorporating the allometric body mass and wing frequency relationship. The deviation may be partially explained by variation in wing stroke amplitude (51, 67, 68). Further, body size and wingspan in insects are highly variable amongst individuals of even the same species (70), which may explain the larger variation. Finally, the assumptions underpinning our scaling analysis may explain some deviation.

**New tool to interpret complex bioacoustics behavior**

The extension of our simple model to predict flapping wing hum across a wide range of species (Fig. 4) makes it a useful tool to study insects, birds, and bats performing a variety of complex behaviors. Like the acoustic power scaling law (Eqn. 2), Equation 1 can be simplified further (Fig. S8,9) for comparative biomechanical and neuroethological studies:

$$p = \frac{1}{4\pi \alpha_o |r|^2} \left( \frac{\partial F_{\text{wing}}}{\partial t} + \frac{4 \Phi_o R F_w^2}{a_o} (r \cdot F_{\text{wing}}) \right)_{\text{farfield}} + \frac{1}{4\pi |r|^2} (r \cdot F_{\text{wing}})_{\text{nearfield}}$$

Our study shows how this model can elucidate the mechanistic origin of wing hum timbre (and modulation) in vivo by integrating acoustic recordings with high-speed videography and aerodynamic force recordings. Likewise, we showed it can be used to make predictions or interpret acoustic measurements by integrating a simplified wing kinematics and aerodynamic force model. It can also be used to estimate the auditory detection distance of wing hum by combining it with an audiogram. Finally, the ability to distinguish between the nearfield versus farfield provides an additional lens for behavioral inquiry.

For example, some hummingbirds perform a "Cobra" maneuver, where an antagonist hummingbird rears up in a vertical body position to rebuff other hummingbirds near a food source; a displaying bird also flaps 30% faster for a burst of 1-2 seconds, making its hum louder (36). Our model predicts this increase in flapping frequency will increase the acoustic pressure by ~3 dB, which makes a large difference in the directionality of the sound in the nearfield. By rearing up, the displaying bird tilts its directivity dipole further aft, directing more sound towards the intruding bird. Although hummingbird audiograms are not available at these lower frequencies, hummingbirds have a peak sensitivity to sound
between 2000 Hz and 2500 Hz (38), similar to audiograms for similar-sized birds (71). Using the low end of the audiogram for *Passeriformes* as a proxy for hummingbirds, we can estimate the combined effects of increased flapping frequency and directivity during a Cobra maneuver: the third harmonic of a Cobra maneuver can be perceived by another hummingbird from 1.4 wing radii away instead of 1.0 wing radius. Thus, the increased flapping frequency, proximity, and strong directivity of the Cobra maneuver improve the likelihood of its acoustic perception, which in vivo play back experiments could test.

The predicted range over which wing hum can be perceived is even larger in homing pigeons; approximately four meters or ~12 wing radii (*Columba livia*: flapping frequency 7 Hz, mass 400 g, wing length 32 cm; (72)). The perception distance scales up with body mass (Fig. 4E) and the auditory threshold of pigeons is exquisitely sensitive to the wingbeat frequency (73), which can thus potentially inform flocking behavior (7). Conversely, while the low frequency oscillating aerodynamic forces also radiate high frequency humming harmonics up to the tenth wingbeat harmonic (Fig. 2A and Table 1) and beyond, the corresponding decibel amplitudes are insignificant compared to harmonics close to the wingbeat frequency (Fig. 1F). This helps explain why some birds rely on specialized flight feathers that sonicate loudly at high frequency to signal over longer distances how they are flapping their wings during flock takeoff (4–6), mating displays (34) and displays to defend courting territories (8). Perception of wing hum also has implications for bird-insect predation, because moths have been shown to respond to the wingbeat hum of birds in playback experiments (74).

Finally, an acoustic model analogous to the one we present here has recently been used to simulate mosquito buzz (26) in conjunction with computational fluid dynamics to predict how aerodynamic forces (51) color the mosquito’s aerial courtship song (2). Intriguingly, whereas mosquitoes fly with a shallow wing stroke to generate high harmonic content, fruit flies do not (51). When fruit flies use their wing as an aeroacoustic instrument during terrestrial courtship serenades, however, they reduce their stroke amplitude to a similar degree (1, 75), which likely colors their timbre as in mosquitoes (Fig. 4A-D).

**Conclusion**

Our acoustic model explains how the oscillating lift and drag forces generated by each wing of a hovering hummingbird radiate the distinctive humming timbre. It integrates in vivo 3D aerodynamic force and wing kinematics measurements and is corroborated spatially and temporally through in vivo nearfield acoustic holography. The measurements and model show that hovering hummingbirds generate a highly directional hum. The broadband acoustic pressure is primarily oriented downward opposing gravity, while the acoustic directivity and orientation of the harmonic components depend on harmonic parity. The model explains how perceived differences in hum loudness and timbre across birds and insects stem primarily from the harmonic content in the aerodynamic weight support profile. Higher harmonic content throughout the wing stroke makes flies and mosquitoes buzz, equivalent first and second harmonic content makes hummingbirds hum, while dominant first harmonic content gives birds their softer whoosh. The associated scaling relation for radiated acoustic power shows how it is proportional to the product of stroke amplitude, body mass and wingbeat frequency squared. Our scaling analysis across 170 different animals in slow hovering flight reveals how the radiated acoustic power scaled with mass. Allometric deviation explains why larger birds radiate less acoustic power than expected and why elongated flies have a remarkably loud buzz as perceived by a casual observer. Finally, our acoustic model and scaling equation can help neuroethologists and bioacousticians interpret the loudness and timbre of the hum generated by flapping winged animals performing complex behaviors as well as guide bioinspired engineers how to design more silent flapping robots (76, 77).

**Materials and Methods**

**3D AFP experimental setup**

The 3D AFP flight arena consisted of a 0.5 × 0.5 × 0.5 m (height, width, depth) chamber, each side consisted out of a carbon fiber force plate that mechanically integrates pressure and shear forces generated by the freely flying hummingbird (31, 39, 40). Three of the plates have acrylic windows to enable optical access into the flight arena. Each plate is statically determined and attached to three vee blocks (VB-375-SM, Bal-tec), each instrumented by a Nano 43 6-axis force/torque sensor (4000 Hz sampling rate, lowpass filtered with an eighth order digital lowpass Butterworth filter at 180 Hz, silicon strain gage based, with SI-9-0.125 calibration, 2 mN resolution, ATI Industrial Automation). There are also two force sensors instrumenting a beam attached to the artificial flower to measure hummingbird contact.
forces and body weight. For detailed analysis, we selected 3D force traces over five consecutive wingbeats per flight \((N = 6 \text{ birds, each bird did 2 flights, } n = 5 \text{ wingbeats per flight for 60 wingbeats total})\) for which we manually tracked the 3D wing kinematics of four points on the bird (right shoulder, distal end of the leading-edge covert, wingtip, and tip of the fifth primary feather). We recorded wingbeat kinematics through three orthogonal acrylic access ports using stereo high-speed videography at 2000 Hz using three pairs of DLT calibrated (78) cameras (four Phantom Micro M310s, one R-311, and one LC310: Vision Research). We filtered the kinematics with a fourth order digital lowpass Butterworth filter with a cutoff frequency of 400 Hz (~10 times the wingbeat frequency).

**Acoustic experimental setup**
The NAH setup consisted of a chamber that is \(0.3 \times 0.9 \times 0.9 \text{ m (height, width, depth)}\). The sides of the chamber were made of IR transparent acrylic (Plexiglass 3143) to allow visual access into the chamber while controlling what the hummingbird views from inside the chamber. Two battery-powered LED lights (Neewer CN126) sustained a constant light level of 3000 lux at the flower. Combined, the arrays surrounded the hummingbird with 2176 microphones (of which 25 ± 7 were disabled during each measurement; see Supplementary Information for details) while it freely hovered in front of a flower to feed. The top and bottom arrays (Sorama CAM1Ks) each consist of 1024 microelectromechanical (MEMS) microphones, while the two frontal arrays (Sorama CAM64s) feature 64 microphones each with a sampling frequency of 46,875 Hz sampling frequency. During the actual flight these arrays were covered by an acoustically transparent cloth (Acoustone speaker grille cloth) to protect both the bird and the microphones. To limit wall effects encountered in flight arenas (40), the feeder was centered 15 cm horizontally from the edge and 15 cm above the bottom array. Finally, the sides of the acoustic arena featured optically accessible panels in the infrared range, which were used to film the hummingbirds with 4 direct linear transformation calibrated high-speed infrared cameras at 500 fps.

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**Author Contributions**
B.J.H., R.S., R.I., D.D.C., and D.L. developed and performed the acoustic experiment. B.J.H. and P.W.A.W. processed the acoustic data and made simulations. B.J.H. and D.L. developed the acoustic model. B.J.H., R.I., D.S., and D.L. developed the aerodynamic force experiment, and B.J.H. performed the experiment. B.J.H. and J.N. processed the force data. B.J.H., P.W.A.W. and D.L. made figures. B.J.H., P.W.A.W. and D.L. wrote the manuscript. All authors interpreted the data and edited the manuscript.

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**Data and materials availability:** All data needed to evaluate the conclusions present in the paper and/or the supplementary materials. Additional data related to this paper may be requested from the authors.
Fig. 1. Oscillating aerodynamic force and acoustic field measurements to determine how hummingbirds hum. (A) 3D aerodynamic force platform (AFP) setup to measure the forces generated by a hovering hummingbird. Each of the flight arena's walls comprises a force plate (fp) instrumented by three force sensors (fs), two additional force sensors instrument the perch. The six DLT calibrated cameras imaging through three orthogonal ports in pairs are not shown. (B) The lift and drag force generated by hovering hummingbirds during a wingbeat (gray area, downstroke; mean ± std based on $N = 6$ birds, each bird made 2 flights, $n = 5$ wingbeats were fully analyzed per flight for 60 total wingbeats). Lift is negative during the upstroke since the direction of the lift vector is perpendicular to the wing velocity while the drag vector is parallel and opposite to the wing velocity direction, resulting in the lift vector being defined as the cross product of the wing velocity direction and the drag direction (inset). (C) Whereas most of the frequency content in the lift profile is contained in the first and second harmonic (first harmonic mean ± standard deviation is $44.2 ± 1.8$ Hz across all birds and flights), the content in the drag profile is contained primarily in the second and third harmonics. (D) Acoustic flight arena in which hovering hummingbirds ($N = 6$ birds, $n = 2$ flights per bird) were surrounded by 4 acoustic arrays (labeled aa; $2 \times 1024$ and $2 \times 64$ microphones) and four high-speed cameras (hs) while feeding from a stationary horizontal flower (separate experiment with six other individuals). (E) Throughout a wingbeat, each microphone records the local acoustic field generated by the hovering hummingbird (microphone located at the center above bird #1). (F) To generate a representative spectrum of a single bird, the signals of all microphones in all arrays around the bird were summed (green line: $N = 1$, $n = 1$) and plotted up to the tenth harmonic. The background spectrum of the lab (range over all trials) is plotted in gray, showing the hum consists primarily of tonal noise higher than the background at wingbeat harmonics (dark green line, 3 dB above maximum background noise). In addition, several smaller non-harmonic tonal peaks can be
observed between the first and fourth harmonic with a dB level equivalent to the sixth - seventh harmonic. (G) To determine the acoustic source of the hum, we constructed a simple model that predicts the acoustic field. The acoustic waves radiate outwards from the overall oscillating force ($F_{wing}$) generated by each wing, which can be decomposed into the lift ($L$) and drag ($D$) forces generated by each wing (recorded in vivo, Fig. 1B). To predict the aeroacoustics, these forces are positioned at the third moment of inertia of the wing ($R_3$) and oscillate back and forth due to the periodic flapping wing stroke ($\phi$) and deviation angle ($\theta$) (recorded in vivo, Fig. 1H). Angle of attack $\alpha$ is defined for modelling flapping wing hum across flying species (Fig. 4). (I) Hummingbird wing kinematics ($\phi$, $\theta$) measured in vivo from the 3D AFP experiment (gray area, downstroke; mean ± std based on $N = 6$ birds, $n = 2$ flights). (I) Whereas most of the frequency content in the stroke profile is contained in the first harmonic, the content in the deviation profile extends to the second and third harmonics.
Fig. 2. The measured spectra and holograms match those predicted by the simple aeroacoustics model. (A) A representative acoustic spectrum measured from all arrays for hummingbird #1 in hover is shown in dark green ($n = 1$), while the range for $N = 6$ hummingbirds is shown in light green. The variation in the frequency and sound pressure level (SPL) peak value associated with each harmonic is shown with orange circles (mean) and ellipsoids (width and height, 68% confidence intervals; their asymmetric shape stems from computing the covariance in Pascals while the spectrum is in dB). The peak sound pressure levels predicted by our acoustic model (purple line) match those of the measured spectrum up to higher harmonics. In addition, several smaller non-harmonic tonal peaks can be observed between the first and fourth harmonic with a dB level equivalent to the sixth - seventh harmonic. The predicted spectrum starts at the numerical noise floor, of which the amplitude ($< -10$ dB) is physically irrelevant. (B) Acoustic holograms throughout the example wingbeat for hummingbird #1 (Fig. 1E and F) are presented side-by-side as measured (left) and modeled (right) for the top and front array microphone positions. There is reasonable spatial and temporal agreement between the measured and predicted acoustic nearfield centered around stroke transition (30–70%) where the pressure transitions from minimal (blue) to maximal (red).
Fig. 3. Nearfield versus farfield measured radial sound pressure level generated by a hovering hummingbird. (A) The full 3D broadband (from 3 to 500 Hz) pressure field measured over a wingbeat from bird #1 (oriented as the 3D view avatar) is shown across the spherical circumference at 1 m radius, the acoustic nearfield (outside the wing radius of the bird, 8 cm) and at 10 m radius, the acoustic farfield (wavelength of first wingbeat harmonic is 7.8 m). These 3D acoustic field reconstructions are based on the measurements from all arrays (Fig. 1 D). (B) At a nearfield distance of 1 m, the 3D broadband pressure surfaces can be represented with cross sections along the two key anatomical planes, the side/sagittal and front/coronal plane respectively, to visualize the broadband pressure directivity over the entire wingbeat. The mean pressure directivity trace for all birds is colored dark with color coding referring to the anatomical plane, the quantiles for each of the six birds are shaded light, and model prediction are shown in black. The overall pressure shape in 3D is plotted in the middle in black, which has a roughly spherical shape in the broadband holograms. (C) The 3D broadband pressure directivity at a farfield distance of 10 m. The waists of the individual lobes in each flight are smeared out due to small variations between the birds and their flights, obscuring the directivity in the average plots (individual traces shown in Fig. S3). To show where the principle axes of the individual pressure lobes fall, we calculated the waistline pressure level between the minimum lobes and plot the directivity axis as the line perpendicular to the waistline (grey line, light grey arc ± 1SD; D, E). The broadband hologram can be further decomposed into contributions from the first harmonic. The measurement and simulations match better for the nearfield (computationally backpropagated) than for the farfield (computationally propagated). In the sagittal plane, the dipoles for both the measurement and model are tilted aft. This tilt can also be observed as a rotational mode associated with the wingbeat frequency in the longitudinal direction in the 3D animation for the first harmonic for bird #1. In contrast, the associated coronal dipoles are oriented vertical. The 3D pressure shape is also more oblong, as viewed by the ovoid black shape in the middle. (F, G) The sagittal and coronal dipoles of the second harmonic are oriented vertically in both the nearfield and farfield. This vertical orientation is associated with the vertical force generation occurring twice per wingbeat and is also visible in the 3D animation for the second harmonic. (H, I) We observed a rotational mode in the 3D animation for the third harmonic. (J, K) Both the sagittal and coronal dipoles of the fourth harmonic are oriented vertical in both the nearfield and farfield, which is also visible in the animation. The third and fourth harmonic are decompositions of the first two modes; therefore, they share directivity similarities. Finally, the data driven model prediction in B-K (black contours) match the in vivo data reasonably well in amplitude considering the differences in peak spectrum amplitude noted in Table 1. There is also good agreement in the directivity of the predicted angles for the first two harmonics for both sagittal and coronal planes and for the first four harmonics for the coronal plane (Table 2), which matches the agreement in amplitude.
Fig. 4. Distinct aerodynamic weight support profiles and non-allometric flapping wing scaling differentiates the acoustic spectrum and radiated power of flapping wing hum. (A) Representative aerodynamic weight support profiles of paradigm animals representing elongated flies, compact flies, butterflies and moths, hummingbirds, and generalist birds. The representative weight support profile was used to simulate the hum across animals in each group, with body mass varying over seven orders of magnitude and flapping frequency over three orders of magnitude. (B) The frequency content of these weight support profiles is distinct. Elongated flies and compact flies concentrate energy at the second harmonic and have substantial frequency content at higher harmonics compared to hummingbirds and hawkmoths, which have high first and second harmonics. In contrast, parrotlets concentrate most of their energy at the first harmonic. (C) Using our aeroacoustics model, we prescribed each of the five animals (grey avatars) all five weight support profiles (red, orange, blue, green, and purple datapoints match avatars in A) to determine how this affected the total radiated acoustic power of the wing hum (e.g. a fly was prescribed the respective weight support profiles of a mosquito, fly, hawkmoth, hummingbird, and parrotlet). The weight support profiles of the mosquito and fly consistently generate more radiated power than the profiles of the other animals. Differences between the paradigm animal groups across the different scales are primarily governed by nonlinear interactions between the acoustic parameters. The inset zooms in on the model results at hummingbird scale, which reveals the marked influence of weight support profile on radiated power over one order of magnitude. (D) At the hummingbird scale, the weight support profiles (A and B) differentiate between the overall decibel level and distribution across the first four harmonics (to enhance readability we slightly shifted each spectrum from the harmonic to the left). (E) We find these effects across the seven orders of magnitude across which body mass ranges for the 170 flying animals that perform flapping flight. The model is based on body mass, wing length, and flapping frequency of each individual species combined with the weight support profile of the associated paradigm animal (A). The computational results across all species (black line, best-fit scaling across all groups) show the simplified scaling law derived from the acoustic equations used in the model (grey line, predicted scaling result) closely matches the computational outcome for moths and butterflies (blue line).
Other groups deviate appreciably from the acoustic scaling law prediction (colored lines, best-fit scaling per group), because their wing length and flapping frequency scale allometrically with body mass. (F) To test if the acoustic scaling law is reasonably accurate for all groups when allometric scaling is incorporated, we plot the simulated radiated acoustic power versus the scaling law: the product of force, stroke amplitude and flapping frequency squared (divided by the constant product of air density and speed of sound). On average this shows good agreement between the computational model (black line) and scaling law prediction (gray line) across all groups.
Table 1. The measured and predicted sound pressure level peaks across the first ten harmonics.
The measurement and model are close up to the fourth harmonic. The over-prediction for the seventh
harmonic and up may be attributed to frequency mixing. Past the tenth harmonic, we approach the
ambient noise floor for the measurements.

| Harmonic | 1<sup>st</sup> | 2<sup>nd</sup> | 3<sup>rd</sup> | 4<sup>th</sup> | 5<sup>th</sup> | 6<sup>th</sup> | 7<sup>th</sup> | 8<sup>th</sup> | 9<sup>th</sup> | 10<sup>th</sup> |
|----------|---------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|
| Measurement [dB] | 60.8 | 60.0 | 47.9 | 46.4 | 42.7 | 41.7 | 34.0 | 28.8 | 23.6 | 25.2 |
| ± SD [dB] | ± 1.2 | ± 1.2 | ± 2.6 | ± 3.4 | ± 3.2 | ± 3.2 | ± 2.6 | ± 3.7 | ± 3.1 | ± 2.3 |
| Model [dB] | 55.3 | 57.0 | 48.4 | 40.5 | 33.4 | 30.9 | 32.9 | 28.1 | 31.5 | 23.1 |
Table 2. The measured and predicted broadband pressure directivity angles match. Aft tilt is evident in the sagittal planes, whereas the coronal planes show vertical directionality associated with vertical force generation. Harmonic modes 1-4 match well in the coronal plane and modes 1 and 2 match well in the sagittal plane.

| Broadband | Sag Near | Cor Near | Sag Far | Cor Far |
|-----------|---------|---------|--------|--------|
| Measurement [°] | 99.4 ± 3.1 | 88.0 ± 3.4 | 97.4 ± 3.2 | 89.1 ± 4.6 |
| Model [°] | 102.3 | 90.2 | 97.8 | 90.0 |

Sagittal Nearfield

| Measurement [°] | 119.7 ± 3.4 | 86.3 ± 1.9 | 126.9 ± 13.7 | 69.6 ± 5.0 |
| Model [°] | 125.8 | 99.8 | 82.7 | 44.3 |

Sagittal Farfield

| Measurement [°] | 120.4 ± 4.4 | 85.4 ± 2.2 | 116.6 ± 24.4 | 70.8 ± 5.1 |
| Model [°] | 125.6 | 99.8 | 78.9 | 44.6 |

Coronal Nearfield

| Measurement [°] | 86.7 ± 8.8 | 89.7 ± 2.7 | 88.7 ± 9.3 | 89.8 ± 4.1 |
| Model [°] | 89.9 | 90.2 | 89.9 | 90.0 |

Coronal Farfield

| Measurement [°] | 89.4 ± 6.6 | 90.2 ± 2.8 | 90.5 ± 10.3 | 90.9 ± 7.2 |
| Model [°] | 90.1 | 90.0 | 90.0 | 90.0 |
Supplementary Information

Birds
For both of the 3D AFP and acoustic experiments, six male Anna’s hummingbirds (*Calypte anna*, N = 6 birds, n = 2 flights each) were captured using drop-door traps and released again on the same day at the location of capture. Hummingbirds were housed in individual cages before and after the experiment. Birds were deemed trained once they acclimated to their flight chamber and fed *ad libitum* on sugar solution from the artificial flower. All bird training and experimental procedures were approved by Stanford’s Administrative Panel on Laboratory Animal Care.

Acoustic microphone performance
The microphones used are Akustica AKU242 MEMS sensors which are sensitive to stiction: liquid, dust or other particulate matter can enter the acoustic port and cause the microphone membrane to become temporarily or permanently stuck. This can trigger the self-reset mechanism of the microphone which causes erroneous spikes in the output signal. Since the microphone captures only the dynamic pressure, the mean output value of a microphone in normal operation should always be close to zero (with a small and fixed offset due to the sensor’s internal analog-digital converter). Based on this, the heuristic we use to flag microphones that may have experienced stiction during the measurement is when the average of the raw microphone data was greater than 15% of the digital full scale.

Sound and room isolation
Sources of background noise and acoustic reflections were mitigated to achieve accurate force and acoustic recordings. Since force plates of the 3D AFP act as pressure transducers capable of measuring miniscule pressure variations, they are capable of inadvertently measuring infrasonic pressure variations due to air-conditioning systems. Both the 3D AFP and acoustic experiments were thus performed at an isolated field station. The field station has low background noise levels of 36.6 dB because it is remote and has no air conditioning system. We optimized the position of the acoustic flight arena such that it was centered from the walls (by more than 1.5 m), raised 1.5 m from the ground, and 1.5 m below the ceiling to limit the effects of acoustic reflections. Further, acoustic foam (Alphamax anechoic wedge foam, 8 in thick) was placed on the ground to attenuate acoustic reflections. Both the acoustic setup and the 3D AFP were situated on three Mighty Mount M10 rubber supports (Part No. 25-2205, 80/20 Inc) for ground vibration and shock isolation.

Calculation of lift and drag
The *in vivo* shoulder location, the wing chord, velocity distribution and wingtip kinematics determine the motion of $R_3$. We determined the wing velocity vector, $\mathbf{v}$, by taking the (component-wise) time derivative of the wing radius position vector, $\mathbf{r}$, in a world reference frame. Considering the velocity distribution along the radius of the hummingbird wing is linear within good approximation (31, 79), the velocity vector of the acoustic point source $\mathbf{v}_R$ at $R_3/3$ is:

$$\mathbf{v}_{R3} = \frac{r_3}{R} \mathbf{v}_{up}.$$  (S4)

The aerodynamic force generated by each wing is equal to the vector sum of the lift (with magnitude $L$ and direction $\hat{e}_L$) and drag (with magnitude $D$ and direction $\hat{e}_D$) at $R_2$, the second moment of area (80). As the AFP measures net forces, the forces in the longitudinal ($F_x$) and vertical ($F_z$) directions can be measured directly since the contributions from the left and right wings sum together. On the other hand, because each wingbeat is symmetrical about the bird's midline, the lateral force $F_y$ from the left and right wings cancel out when measured by the AFP (80). Thus, we defined the 3D force from each wing as:

$$\mathbf{F}_{wing} \overset{\text{def}}{=} \begin{pmatrix} F_{x,\text{measured}} \\ F_{y,\text{calculated}} \\ F_{z,\text{measured}} \end{pmatrix} = -L \hat{e}_L - D \hat{e}_D.$$  (S5)

The drag unit vector is defined to act in the opposite direction as velocity at the second moment of area $R_2$. 

21
\[
\hat{e}_D = -\frac{v_{R2}}{\|v_{R2}\|} = -\hat{v}_{R2}.
\]

The lift unit vector acts perpendicular to the wing velocity unit vector and the wing radius unit vector (\(\hat{w}\), points from the bird’s right shoulder to its right wingtip) at \(R_2\):

\[
\hat{e}_L = \pm \frac{-\hat{v}_{R2} \times \hat{w}}{\|\hat{v}_{R2} \times \hat{w}\|}.
\]

We designated the negative sign for the left wing and the positive sign for the right wing. Based on the lift and drag unit vectors and force vector, Eqn. S2 yields three coupled equations that solve for the unknown lift \((L)\) and drag \((D)\) magnitudes as well as the instantaneous lateral force \((F_y, \text{calculated})\). The calculated lift, drag, and lateral forces are sensitive to measurement error when the vertical and horizontal components of lift and drag are near zero, which occurs at stroke reversal. To improve the calculated force accuracy at stroke reversal, we smoothed this singularity using a regularization developed by Deetjen et al. (80).

**Regularization of lift and drag at stroke reversal**

The calculated lateral force and aerodynamic power were sensitive to error at stroke reversal, where the vertical and horizontal components of lift and drag are near zero. We incorporated a regularization developed by Deetjen et al. (80). The sensitivities arise because solving Eqn. S2 requires taking the inverse of the matrix:

\[
E = \begin{pmatrix}
\hat{e}_{DX} & \hat{e}_{LX} \\
\hat{e}_{DZ} & \hat{e}_{LZ}
\end{pmatrix}.
\]

When \(E\) is nearly singular, the calculated forces can reach unrealistically high values due to computational limitations. Thus, we regularized the calculated force through multiplication by a weight at each instance in time:

\[
W = 1 - \max\left(0, \min\left(1, \frac{\log|\det(E)| - \log c_0}{\log c_0 - \log c_1}\right)\right),
\]

where \(c_0\) and \(c_1\) are tunable constants that determine the degree of regularization. In the regularization method, when the absolute value of the denominator is below \(c_0\), the weight is zero because the result is too sensitive to be used. When the absolute value of the denominator is between \(c_0\) and \(c_1\), the weights are between zero and one (Fig. S4). Chin and Lentink (81) reported that values of \(c_0 = 0.05\) and \(c_1 = 0.35\) eliminate the spikes in lateral force for parrots with little effect on the mid-downstroke lift and drag values. We found altering these constants had little effect on the calculated lift and drag (Fig. S5), so we used the values reported by Chin and Lentink (81). After applying the regularization, we used Eilers’ perfect smoother (82) to smooth the lift and drag curves so the time derivatives needed to determine the acoustic pressure remain bounded when input into the acoustic model.

**Frequency mixing**

The first frequency mixing stage combines the oscillating lift and drag forces from the 3D AFP measurement (Fig. 1B), which were filtered at 180 Hz to eliminate natural frequencies in the 3D AFP setup, and the wing kinematics, which were filtered at 400 Hz. The second frequency mixing stage comes from the calculation of acoustic pressure (Eqn. 1; spectrum shown in Fig. S2E), specifically the inner product between the aerodynamic force vector \(F_{\text{wing}}\) (spectra shown in Fig. S2A and 2B) and \(r\), the vectorial distance between the flapping wing radius (spectra shown in Fig. S2C and 2D) and the fixed microphone positions. The higher harmonics come from the amplitude of \(F_{\text{wing}}\) being modulated by the nonlinear position in \(r\). The resulting frequency mixer embodied by the wing hum model (Eqn. S2-5; Fig. S2) creates higher harmonics at the sum and difference of the input frequencies (83). Finally, one of the most obvious differences between the model and measurements is the higher noise floor in the measurements due to the background noise, acoustic reflections, and microphone properties (84).
Acoustic model for hovering flight with 3D forces

The acoustics of hummingbird flights can provide valuable insight into how they generate force. The crux of the acoustic model is Eqn. 1, where the bracketed terms indicate evaluation at the emission time $t'$:

$$t' = t - \frac{|r|}{a_0},$$

(S10)

where $r$ represents the Cartesian coordinates $(x, y, z)$ measured from the inertial observer (microphone location) to the non-inertial source (the point force moving with the wing at radius $R$):

$$r = (x - R\sin\phi, y - R\cos\theta\cos\phi, z - R\sin\theta\cos\phi).$$

(S11)

Note that for consistency with Lowson (21), we defined the vertical direction as $x$, the front of the bird as $z$, and the right of the bird as $y$. The rotational Mach number is defined based on both wing stroke and deviation angular velocity:

$$M = \sqrt{\left(\frac{\theta R}{a_0}\right)^2 + \left(\frac{\phi R}{a_0}\right)^2}.$$  

(S12)

Consequently, the 3D components of the Mach number along each Cartesian axis are defined as:

$$M = (M\sin\theta, -M\sin\phi\cos\theta, M\cos\phi\cos\theta),$$

in which $M_r$ is the component of the instantaneous convection Mach number in the direction of the observer:

$$M_r = \frac{M_r}{|r|}.$$  

(S14)

The unsteady aerodynamic forces in the aeroacoustics model are based on direct in vivo measurements using the 3D AFP, as in Eqn. S2, which we used to calculate the acoustic pressure from the right wing. The resultant equation must be solved numerically since it is a function of the emission time $t'$, which is recursively defined as a function of itself. We thus established a time vector $t$ and solved for the emission time using a Newton-Raphson root finder. To obtain the acoustic pressure from the left wing with minimal computational effort, we mirrored the wing and motion across the $xz$ plane.

Simplified acoustic model for hovering flight from vertical forces

Considering that the stroke-resolved aerodynamic forces and kinematics we measured for Anna’s hummingbird are not available for other animals, we made simplifications to apply our model across species. To do this consistently, we applied the same simplifications to all animal groups, including hummingbirds. This enabled us to validate our simplifications for hummingbirds by direct comparison of the simplified and full-fledged model results. For hummingbirds, we obtained the vertical force for *Calypte anna* hummingbirds from Ingersoll and Lentink (31) and approximate the lift force $L$ from the vertical force $F_v$ as:

$$L \approx F_v.$$  

(S15)

In this approximation we assume the vertical velocity of the wing can be ignored compared to the horizontal, which is reasonable based on our validation (Fig. S6). Since the stroke angle of a flapping wing can be represented well by harmonic motion (31), we modeled the wing element to oscillate along an arc of radius $R$ in the $yz$ plane at a constant flapping frequency. The constant wingbeat frequency, $f_w$, drives the periodic wingbeat through the following equation for the angular position of the wing:

$$\phi = \Phi_v \sin ft,$$  

(S16)
\[ \Omega = 2\pi f_w, \]  
\[ \phi = 0 \] is aligned with the \( y \) axis and \( A_\phi \) is the wing stroke amplitude. Through substitution of Eqn. S13 and S14 into the definition of Mach number, the rotational Mach number \( M \) can then be written as

\[ M = \frac{\phi R}{a_0} = \frac{\partial R \Phi \cos \alpha}{a_0}. \]  
and the associated components of the Mach number along each Cartesian axis are:

\[ M = (0, -M \sin \phi, M \cos \phi). \]

The wingbeat-resolved vertical force profile and angle of attack profile were adapted from Ingersoll and Lentink (31). To calculate the associated lift and drag values we applied the quasi-steady hummingbird aerodynamic model that corroborated lift and drag coefficients from spinning wing experiments (45) as a function of angle of attack:

\[
\begin{align*}
C_L &= 0.0028 + 1.1251 \cos(0.0332\alpha + 4.6963) \quad \text{for } \alpha < 0, \\
C_D &= 1.1993 + 1.0938 \cos(0.0281\alpha + 3.1277) \\
C_L &= 0.0031 + 1.5842 \cos(0.0301\alpha + 4.7124) \quad \text{for } \alpha \geq 0, \\
C_D &= 8.3171 + 8.1909 \cos(0.0073\alpha + 3.1416)
\end{align*}
\]

Using the wing lift, \( C_L \), and drag, \( C_D \), coefficient combined with the measured angle of attack, \( \alpha \), the drag can be calculated based on the lift as:

\[ D = L \left( \frac{C_L}{C_D} \right)^{-1}. \]

Since lift acts in the vertical direction and drag acts in the x-y plane, the aerodynamic point force generated instantaneously by the wing is:

\[ F = (-L, -D \sin \phi, D \cos \phi). \]

At stroke reversal, there are sharp peaks that occur in the drag curve. This is due to the extreme angle of attack transition from positive to negative (and vise versa) that occurs at stroke reversal. To mitigate the numerical discontinuity in the quasi-steady model during wingbeat reversal, the quasi-steady lift and drag curves are filtered using Eilers’ perfect smoother so the time derivatives that feed into the acoustic pressure remain bounded (82). Lastly, to calculate the lift and drag on each wing, aerodynamic symmetry was assumed, and we could thus simply divide the lift and drag predicted for the whole bird by two to calculate the force and associated acoustic radiation for each wing.

**Location of point force along wing radius**

While the theoretical location of the force is at \( R_3 \), its location as the effective acoustic point source should be verified in practice. To determine the appropriate radial distance of the effective acoustic source, we performed a scaling analysis on Eqn. 1. This shows the dependence of the acoustic pressure distribution on wing velocity distribution, and combined with knowledge of hummingbird morphology this validates our choice of placing the effective acoustic point source, the net aerodynamic force generated by the right wing, at \( R_3 \):

\[ p \propto \frac{\rho u^3}{(1-M)^2 r^2} \left( \frac{u^3}{a_0} + \frac{4u^4}{(1-M) a_0^2} + \frac{2u^2}{r} \right). \]

Thus, the acoustic pressure depends on the second, third, and fourth powers of velocity. This is equivalent to how point forces that depend on these powers of velocity are applied at the respective moment of area in blade-element models of flapping flight. Based on our analogous distributed acoustic
source model for a hummingbird wing, the second, third, and fourth moments of area \((R_2, R_3, \text{and } R_4)\) respectively) for calculating the associated effective acoustic point source locations are:

\[
R_2/R = \frac{\int_0^R r^2 c(r)r^2dr}{\int_0^R c(r)r^2dr} \approx 0.50R, \tag{S25}
\]

\[
R_3/R = \frac{\int_0^R r^3 c(r)r^3dr}{\int_0^R c(r)r^3dr} \approx 0.55R, \tag{S26}
\]

\[
R_4/R = \frac{\int_0^R r^4 c(r)r^4dr}{\int_0^R c(r)r^4dr} \approx 0.60R, \tag{S27}
\]

where \(c(r)\) is the chord length of the wing element at radius \(r\). Thus, the point of application of the force on the wing occurs at some combination of \(R_2, R_3, \text{and } R_4\). At the nearfield distances of the microphones in our \textit{in vivo} aeroacoustics measurements, we found a distance of 0.55\(R\) fits the data well (Fig. S7, Table S3). This effective acoustic point source distance agrees with wind turbine acoustics at low frequencies (46).

**Dimensional analysis and scaling of radiated acoustic power**

We performed dimensional and scaling analysis to gain a better understanding of the importance of parameters like mass, wingspan, and flapping frequency in the production of sound. We investigated radiated acoustic power \(P\), which encompasses the total sound energy radiated by a source in all directions, by integrating it over an enclosing spherical surface that includes all sources. Because of the integration, the radiated acoustic power is independent of parameters like source size. For the flapping animals we study here, the total acoustic power is acoustic intensity \(I\) integrated over the surface of a sphere \(S\) of a given radius that encloses them (and their unsteady aerodynamic wake) entirely:

\[
P = \int_S IdS = \int_S \frac{p^2}{\rho_o c_o} dS. \tag{S28}
\]

In flapping flight, the time-averaged speed of the wingtip scales as (85):

\[
U \approx 4\Phi_o R f_w. \tag{S29}
\]

This allowed us to obtain the Mach number for flapping flight:

\[
M_f = \frac{U}{a_o} \approx \frac{4\Phi_o R f_w}{a_o}. \tag{S30}
\]

The Mach vector \(M_f\) contains the components of the flapping Mach number along each Cartesian coordinate and thus depends on wing stroke and deviation:

\[
M = (M_f \sin \theta, -M_f \sin \phi \cos \theta, M_f \cos \phi \cos \theta) = M_f (\sin \theta, -\sin \phi \cos \theta, \cos \phi \cos \theta). \tag{S31}
\]

Since trigonometric functions are bounded by -1 and 1, \(M_f\) has the same order of magnitude scaling as \(M_f\). If there is no deviation, \(\theta = 0\), meaning \(M_z = 0\). However, \(M_y\) and \(M_z\) will be maximized and only depend on the stroke angle since the cosine of zero is one.

Similarly, the instantaneous convective Mach number is the Mach vector in the direction of the observer:

\[
M_v = \frac{M_r}{|\textbf{r}|}. \tag{S32}
\]

The vector \(\textbf{r}/|\textbf{r}|\) has a magnitude of unity, so \(M_v\) scales as \(M\). The distance to the observer \(\textbf{r}\) is defined as:
\[ \mathbf{r} = (x - R \sin \theta, y - R \cos \phi \cos \theta, z - R \sin \phi \cos \theta). \] (S33)

Thus, when \( \mathbf{M} \) is dotted with \( \mathbf{r} \) and integrated over the surface of the sphere, if one term is maximized in \( \mathbf{M} \), it will be compensated for by a commensurate change in \( \mathbf{r} \).

Small animals tend to have higher flapping frequencies but smaller wingspans (86). We plotted the flapping Mach number for all 170 animals and, as expected, found it is small compared to unity (Fig. S8):

\[ M_f \leq 0.1. \] (S34)

Since the flapping Mach number is less than 0.3, it is subsonic. Substituting the representative scales for a flapping wing, we derived

\[ \frac{\partial M_f}{\partial t} \approx \frac{uf_{w}}{a_o} = \frac{4 \Phi_0 R_f^2}{a_o}. \] (S35)

Next, we nondimensionalized Eqn. 1 by creating the following nondimensional variables (denoted by *):

\[ r^* = \frac{r}{r_o}; F^* = \frac{F}{F_o}; t^* = \frac{u t}{R}; \Phi^* = \frac{\Phi}{\Phi_o}; P^* = \frac{p}{P_o}, \] (S36)

where \( r^* \) is the nondimensional distance from the observer (normalized by a distance \( r_o \)) and \( F^* \) is the nondimensional force (normalized by a force scale \( F_o \)). Further, \( t^* \) is the nondimensional time (normalized by \( U \), the absolute time-averaged speed of the flapping wing at the wingtip and by \( R \), the wing radius), \( \Phi^* \) is the nondimensional sound pressure (normalized by a small pressure amplitude \( \Delta p \) such that \( \Delta p \ll p \)), and \( P^* \) is the nondimensional total acoustic power (normalized by a reference power \( P_o \)). After which we plugged Eqn. 1 into the equation for acoustic power Eqn. S25 to nondimensionalize the terms in Eqn. S33:

\[ P_o P^* = \int_S \frac{\Delta pp^*}{\rho_o a_o} dS, \] (S37)

where:

\[ \Delta pp^* = \left[ \frac{r_o a_o^2}{4 \pi a_o^2} \left( \frac{F_o U}{R} \frac{\partial F^*}{\partial t^*} + \frac{F_o U f_{w}}{a_o} \right) \right] + \left[ \frac{F_o F^*}{4 \pi r_o^2} \right]^2. \] (S38)

We algebraically simplified the above equation to separate most of the dimensional terms from the nondimensional terms:

\[ \Delta pp^* = \left[ \frac{1}{4 \pi a_o^2} \left( \frac{F_o U}{R} \frac{\partial F^*}{\partial t^*} + \frac{F_o U f_{w}}{a_o} \right) \right] + \left[ \frac{F_o F^*}{4 \pi r_o^2} \right]^2. \] (S39)

\[ \Delta pp^* = \frac{F_o}{4 \pi r_o^2} \left[ \frac{U}{a_o} \left( \frac{1}{R} \frac{\partial F^*}{\partial t^*} + \frac{f_{w}}{a_o} \right) + \frac{F^*}{r_o} \right]. \] (S40)

\[ \Delta pp^* = \frac{F_o}{4 \pi r_o^2} \left[ \frac{U}{a_o} \frac{1}{R} \frac{\partial F^*}{\partial t^*} + \frac{F_o}{a_o} \frac{f_{w}}{a_o} \right] + \frac{F_o}{4 \pi r_o^2} \frac{F^*}{r_o}, \] (S41)

\[ \Delta pp^* \left( \frac{F_o}{4 \pi r_o^2} \frac{U}{a_o} \frac{1}{R} \right)^{-1} = \frac{\partial F^*}{\partial t^*} + \frac{f_{w}}{a_o} \frac{F^*}{R} + \left( \frac{U}{a_o} \right) \frac{1}{R} \frac{F^*}{r_o}. \] (S42)

\[ \Delta pp^* = \left( \frac{F_o}{4 \pi r_o^2} \frac{U}{a_o} \frac{1}{R} \right) \left[ \frac{\partial F^*}{\partial t^*} + \frac{f_{w}}{a_o} \frac{F^*}{R} + \frac{a_o R F^*}{U R_o} \right]. \] (S43)
We plugged this nondimensional representation of sound pressure into Eqn. S25 to solve for the nondimensional radiated acoustic power:

\[
P_o P^* = \left( \frac{\rho_o U}{4\pi r_o R r^*} \right)^2 \int_S \left[ \frac{\partial F^*}{\partial t^*} + \frac{R f_w}{a_o} F^* + \frac{a_o R}{u r_o^2} F^* \right]^2 dS.
\] (S44)

We made the substitution \( U \cong 4 \Phi_o R f_w \) (85) and simplified algebraically:

\[
P_o P^* = \left( \frac{f_o \Phi_o f_w}{\pi r_o^2} \right)^2 \int_S \left[ \frac{\partial F^*}{\partial t^*} + \frac{R f_w}{a_o} F^* + \frac{a_o}{4 \Phi_o f_w r_o^2} F^* \right]^2 dS.
\] (S45)

We set all dimensionless variables equal to their order of magnitude one:

\[
P_o = \left( \frac{f_o \Phi_o f_w}{\pi r_o^2} \right)^2 \int_S \left[ 1 + \frac{R f_w}{a_o} + \frac{a_o}{4 \Phi_o f_w r_o^2} \right]^2 dS.
\] (S46)

The first term in Eqn. S43 dominates the second term in the scaling analysis because they differ by the following multiplicative factor much smaller than one:

\[
\frac{R f_w}{a_o}
\] (S47)

This factor is small because flapping wing animals act as compact acoustic sources. Plotting this factor for the 170 animals we selected shows it is small compared to unity: \( R f_w / a_o \lesssim 0.01 \) (Fig. S9). Note that at higher harmonics, this factor is no longer small compared to unity, limiting our analysis to the first 10 harmonics. Since the Mach numbers for flapping flight were small compared to unity as demonstrated earlier, this multiplicative factor was also small compared to unity when considering the fundamental flapping frequency and can thus be neglected:

\[
P_o = \int_S \frac{f_o \Phi_o f_w}{\pi r_o^2} \left[ \frac{1}{\rho_o a_o^2} + \frac{1}{\rho_o a_o^2} \right]^2 dS,
\] (S48)

\[
P_o = \left( \frac{f_o}{\pi \rho_o a_o^2} \right)^2 \int_S \left[ \frac{\Phi_o f_w}{r_o} \right]^2 dS.
\] (S49)

In the limit of large \( r_o \) the second term in the integrand is negligible, yielding:

\[
P_o = \left( \frac{f_o}{\pi \rho_o a_o^2} \right)^2 \int_S \left[ \frac{\Phi_o f_w}{r_o} \right]^2 dS.
\] (S50)

For a sphere of radius \( r_o \), the integrand can be evaluated as:

\[
P_o = \left( \frac{f_o}{\pi \rho_o a_o^2} \right)^2 \left[ \frac{\Phi_o f_w}{r_o} \right]^2 (4\pi r_o^2),
\] (S51)
and simplified as:

\[ P_o = \left( \frac{2F_o \Phi_0 f_w}{\sqrt{\pi \rho_o a_0^3}} \right)^2 = \frac{4F_o^2 \Phi_0^2 f_0^2}{\pi \rho_o a_0^3}. \]  

(S52)

For an animal hovering in equilibrium, the sum of the vertical aerodynamic force (as in Fig. 4A) generated by both wings should equal the animal's weight, \( mg \), stroke-averaged. To investigate how the radiated acoustic power scales with mass, we can thus substitute \( F_o = mg \):

\[ P_o \propto \frac{4m^2 g^2 \Phi_o^2 f_0^2}{\pi \rho_o a_0^3}. \]  

(S53)

Consequently, \( P_o \propto m^2 \), which shows logarithmic plots of radiated acoustic power as a function of mass have an ideal slope of 2.0 if all assumptions are met (Fig. 4E).

We also plotted \( P_o \) versus \( \frac{4F_o^2 \Phi_0^2 f_0^2}{\pi \rho_o a_0^3} \), which yielded an ideal slope of 1.0, corroborating our simulation results over the 170 different animals (Fig. 4F).
Fig. S1. Spectra shows good agreement between full model and simplified model. The full acoustic model (purple) uses 3D kinematics and lift and drag forces calculated from *in vivo* measurements of the hummingbird. The simplified model (grey) uses the vertical weight support and lift to drag ratio (45) to calculate lift and drag forces. The magnitudes of the first four harmonics agree reasonably well as observed in Table S2.
Fig. S2. Spectra of all inputs into the acoustic model reveal the source of humming harmonics and evidence of frequency mixing. (A and B) The lift and drag profiles were obtained from the kinematic (filtered at 400 Hz) and force (filtered at 180 Hz) data. The synthesis of these data results in the first stage of frequency mixing, whereby there is relatively high power even into higher harmonics. (C and D) The stroke and deviation define the position of the acoustic source and were obtained from the kinematic data. These spectra decay faster at higher harmonics. (E) The simulation spectra exhibit a mixture of the behavior of the inputs, with prominent peaks similar to the lift and drag forces (A and B), and a decay similar to the kinematics (C and D).
Fig. S3. Individual directivity traces show waistlines. The principal axis of each dipole is oriented perpendicular to the waistline (narrow region). The waistlines of individual lobes in each flight are smeared out due to small variations (in orientation, wingbeat, position, etc.) between birds and between flights of the same bird. Individual directivity measurements are shown in grey, and the averages are shown in red for sagittal and orange for coronal planes.
Fig. S4. Illustration of regularization for lift and drag. The lift and drag computations (Eqn. S2) are sensitive when \( \det(E) \) (red) is near zero, which occurs near stroke reversal. To temper the effects of these spikes, we apply a weight (blue) defined by Eqn. S6. When \( \det(E) \) is in the dark green region, it is assigned a weight of zero. When \( \det(E) \) is in the light green region, it is assigned a weight between zero and one. All other data in the white region are assigned a weight of one.
Fig. S5. Choice of regularization constants does not appreciably affect smoothing. The lift and drag forces are inputs to the full acoustic model, but need to be regularized due to sensitivities near stroke reversal. We varied the regularization constants of $c_5$ from 0.01 to 0.1 and $c_*$ from 0.2 to 0.5 (light purple), and we did not find substantial differences in the resultant spectra. We used the reported values of $c_5 = 0.05$ and $c_* = 0.35$ (dark purple) from Chin and Lentink (81).
Fig. S6. Agreement between calculated lift and weight support in the vertical direction. The calculated lift (purple) for both wings in the vertical direction agrees well with the vertical weight support in the vertical direction (grey) as measured by Ingersoll and Lentink (31).
Fig. S7. Sensitivity of the spectrum to the location of the acoustic point force along the wing radius. The spectrum for the full acoustic model does not change appreciably when the source is located at $R_3$ (chosen value; purple), $R_2$ (grey), or $R_4$ (grey). Note that the plots overlap, so differences at the different harmonics can be viewed in Table S3.
Fig. S8. The flapping Mach number $M_f \leq 0.1$ is small for all 170 animals. This value is below 0.3, so the flow can be treated as subsonic.
Fig. S9. The multiplicative factor $Rf_w/a_o \lesssim 0.01$ is much smaller than one for all 170 animals. At the wingbeat frequency, all of these animals act as compact acoustic sources.
Table S1. Summary of the number of acoustic measurements made for each bird. To obtain frequency resolution ≤ 2 Hz, we selected feeding flights of 0.5 s or longer.

| Hummingbird | #1 | #2 | #3 | #4 | #5 | #6 |
|--------------|----|----|----|----|----|----|
| # feedings recorded | 4  | 3  | 4  | 10 | 4  | 3  |
| # feedings > 0.5 s | 3  | 1  | 2  | 6  | 3  | 3  |
Table S2. Comparison between the full and simplified acoustic models. There is reasonable agreement in magnitude for the first four harmonics.

| Harmonic | 1<sup>st</sup> | 2<sup>nd</sup> | 3<sup>rd</sup> | 4<sup>th</sup> | 5<sup>th</sup> | 6<sup>th</sup> | 7<sup>th</sup> | 8<sup>th</sup> | 9<sup>th</sup> | 10<sup>th</sup> |
|----------|----------------|--------------|-------------|--------------|--------------|--------------|-------------|-------------|-------------|--------------|
| Full Model [dB] | 55.3          | 57.0         | 48.4        | 40.5         | 33.4         | 30.9         | 32.9        | 28.1        | 31.5        | 23.1         |
| Simplified Model [dB] | 56.3          | 58.0         | 41.8        | 40.4         | 27.3         | 25.0         | 12.1        | -2.9        | -6.2        | -8.1         |
Table S3. Comparison between the different acoustic source locations. When the acoustic source is located at $R_3$ (chosen) $R_2$, or $R_4$, the resultant spectra have similar peak magnitudes.

| Harmonic | 1$^{\text{st}}$ | 2$^{\text{nd}}$ | 3$^{\text{rd}}$ | 4$^{\text{th}}$ | 5$^{\text{th}}$ | 6$^{\text{th}}$ | 7$^{\text{th}}$ | 8$^{\text{th}}$ | 9$^{\text{th}}$ | 10$^{\text{th}}$ |
|----------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|---------------|
| $R_3$ [dB] | 55.3 | 57.0 | 48.4 | 40.5 | 33.4 | 30.9 | 32.9 | 28.1 | 31.5 | 23.1 |
| $R_2$ [dB] | 55.4 | 57.1 | 48.4 | 40.5 | 33.4 | 30.9 | 32.9 | 28.1 | 31.6 | 23.0 |
| $R_4$ [dB] | 55.1 | 56.9 | 48.3 | 40.5 | 33.4 | 30.9 | 32.9 | 28.1 | 31.5 | 23.1 |
Table S4. Summary of values used for paradigm animals in acoustic models. *Culex quinquefasciatus* was adapted from Bomphrey et al. (51). *Drosophila hydei* mass was adapted from Greenewalt (55), while the other parameters were adapted from Muijres et al. (52). *Manduca sexta* parameters were adapted from Zheng et al. (50). *Calypte anna* values were obtained from the present experiment. *Forpus coelestis* values were adapted from Chin and Lentink (49). To simplify the comparison between the five paradigm animals, we approximated the stroke plane as horizontal and the normalized lift profile to have the same shape as the reported vertically oriented force profile (“Normalized Lift Profile Proxy”), so that the lift generated during a wingbeat summed up to body weight for all associated species in the same way.

| Paradigm Animal | Representative Group | Wingbeat Freq. [Hz] | Mass [g] | Wing Length [mm] | Stroke Amplitude [*] | Normalized Lift Profile Proxy [-] |
|-----------------|----------------------|---------------------|---------|------------------|---------------------|----------------------------------|
| *Culex quinquefasciatus* | Elongated Flies | 717 | 0.0012 | 2.8 | 39 | Lift Force * |
| *Drosophila hydei* | True Flies | 189 | 0.001 | 3 | 70 | Net Force *** |
| *Manduca sexta* | Butterflies and Moths | 29 | 1.4 | 51 | 45 | Lift Force * |
| *Calypte anna* | Hummingbirds | 44 | 4.8 | 53 | 72 | Vertical Force ** |
| *Forpus coelestis* | Generalist Birds | 20 | 28 | 100 | 66 | Vertical Force ** |

** & ***: these forces do not equate to lift, but we used the normalized profile as an approximation for the lift profile.
* & ***: these forces do not necessarily equate to body weight when integrated over a wingbeat in hover.
**: these forces do equate to body weight when integrated over a wingbeat in hover.
* & ** & ***: the normalized profiles of these forces were used and either equate to or are a proxy for the lift profiles.
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