Tail Flaring is an Agonistic Signal in Hummingbirds

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Abstract

The tail of birds contributes substantially to flight aerodynamics through lift generation, reduction of pressure drag, and pitch stabilization. Hummingbirds are powerful flyers, able to sustain hovering in still air, generate lift in both the up- and downstroke, and takeoff due to substantial developmental investment in their wings and corresponding musculature. Given the abundance of wing power, it is possible that tails are less essential to the aerodynamics of hummingbird flight than they are in other birds, freeing them for non-locomotor functions. Hummingbird tails are well known for their

morphological elaboration as sexually selected ornaments, including sound generation. Our observations, and brief descriptions in the literature, led us to hypothesize that tail flaring may serve as another form of sexual signaling, used by males during male-male fighting. To test this, we used high-speed video to record agonistic encounters among seven species of hummingbird the field and found 95% of inter- and intra- sexual and specific contests included tail flaring. We measured kinematics of this flaring during male-male fighting of calliope hummingbirds (*Selasphorus calliope*, n = 5) indoors. Consistent with our hypothesis, captive males exhibited greater angles of tail flare when engaged in a fight (26.9 ± 42.9°, mean ± sd) than when performing solitary landing (-12.7 ± 8.6°) and takeoff (-11.1 ± 6.6°) maneuvers. We evaluate these results in the context of signaling during animal contests and propose future tests of whether tail flaring is an honest signal of individual quality and Resource Holding Potential (RHP).

Keywords

Animal behavior, animal contests, flight kinematics, honest signaling, morphology, resource holding potential, signals

Summary Statement

Male-male fighting is common in hummingbirds with competition over food and mates. During these competitions, tail flaring and waggle maneuvers are used as a signal of aggressive intent.

Introduction

Self-propelled flight requires more power output than any other form of animal locomotion (Alexander, 2005). Animals that fly must generate sufficient power to remain airborne (weight support), as well as to overcome drag created by fluid air on both the body and the lift-generating surfaces used in flight. While birds' wings have received the most research attention, the tail also serves as a lift-generating surface. Flight researchers have considered the tail and how its diverse morphology and presentation to the air may contribute to overcoming the challenges of living "on the wing" (Evans, 2003; Gatesy and Dial, 1996; Maybury and Rayner, 2001; Maybury et al., 2001; Schwaner et al., 2021; Song et al., 2022; Thomas, 1997), but there is still much we don't know about its function in different flight conditions across taxa.

Research spanning the last several decades has suggested several ways in which the avian tail aids in flight. To address the demands of weight support, incoming air travels over the tail's surface and generates lift (Tobalske, 2022). The presence of a tail also provides a more fusiform shape to the bird, serving as a splitter plate and thereby reducing pressure drag on the body (Maybury et al., 2001). How well the tail accomplishes these tasks depends on its shape. Viewing tail morphology through delta wing theory suggests that tails whose widest points are at their trailing edges are the best are maximizing lift relative to drag (Thomas, 1997). Selective pressures on tail shape can address performance flight metrics beyond lift. Forked tails, which already maximize lift with their wide trailing edges, increase flight performance through increased maneuverability (Thomas and Balmford, 1995). A single tail shape can modify morphology to address demands within a wingbeat. In the Warbling White-eye (*Zosterops japonicus*), a passerine species, the tail is flared in mid-downstroke and interacts with wing downwash to mitigate downward pitch of the body (Su et al., 2012). In short, there is some evidence that the tail performs diverse aerodynamic roles in volant birds.

Hummingbirds are the only avian species that can sustain hovering in still air, they are extremely agile fliers (Badger et al., 2023; Cheng et al., 2016), and their abilities appear to be due to their small size and specializations of their wings. These specializations include high wingbeat frequencies (20-50 Hz) (Corben, 1983), generation of weight support in both up and down strokes (Warrick et al., 2005), and high mass-specific power output from their proportionally large primary flight muscles (Agrawal et al., 2022) the pectoralis and supracoracoideus, which together account for ~27% of total body mass (Altshuler et al., 2010; Hartman, 1954). Compared to other avian species, hummingbirds are considered to be "hyper-aerial," and this lifestyle is hypothesized to have resulted in an evolutionary tradeoff between developmental investment in the forelimbs versus hindlimbs (Heers and Dial, 2015). This is manifest in hummingbirds having proportionally tiny hindlimbs and using their wings to provide 41% of the initial thrust for takeoff compared to <10% in other birds studied (Earls, 2000; Heppner and Anderson, 1985; Tobalske et al., 2004). Thus, the wings dominate over the hindlimbs for flight in hummingbirds, but whether they dominate over the tail is presently less clear.

The tail may play an aerodynamic role in hummingbird flight, but it is far better known for its role in sexual selection. An aerodynamic study regarding the tail focused on performance in escape, a dramatic maneuver that requires high power output and agility (Cheng et al., 2016). For

the duration of an escape from a looming stimulus, the tail flares constantly; however, Computational Fluid Dynamic Modeling of the tail suggests that generation of torque is brief (8% of total time), and peak magnitude is only a fraction of that provided by the wings (25%) (Haque et al., 2023b). While the tail's role in escape therefore is not nominal, this function seems minor compared to that of mate attraction. Across the hummingbird clade, tails exhibit diverse and fascinating forms, with morphologies including long streamers and spatulate tips, as well as feathers which generate sounds (sonations) in courtship (Clark, 2010). These specialized morphologies may have arisen through decreased evolutionary pressure on the tail for aerodynamic performance (Clark, 2010). This hypothesis has been supported by forward flight studies, wherein hummingbirds flying in a wind tunnel with experimentally shorter or longer tails suffered minimal reductions in top flight speed and only marginal increases in metabolic rates (Clark and Dudley, 2009). Consequently, while the tail of hummingbirds may play a role in flight performance (such as escape), it is likely not evolving strictly for aerodynamic purposes.

There is also evidence that the tail is used in hummingbirds' extremely agile and aggressive territorial defense. Many species of hummingbirds, especially those of the bee clade (McGuire et al., 2014), fiercely defend territories (Dearborn, 1998; Kodric-Brown and Brown, 1978; Nuñez-Rosas et al., 2017; Powers, 1987; Stiles and Wolf, 1970). Descriptions of agonism in several species during territorial defense note the fanning of tails (Hunter, 2008; Hunter and Picman, 2005; Hurly et al., 2001; Williamson, 2020). Territories are worth defending as they provide a source of food and a stage from which to perform impressive courtship dives, shuttles, sonations, and gorget signaling to potential mates (Clark et al., 2018; Hogan and Stoddard, 2018). Defense of the territory from inter- and intraspecific competition can include displacements and chases (Tamm et al., 1989), escalating to feather-pulling or jousting (Rico-Guevara and Araya-Salas, 2015). While competition seems dramatic and extreme, injury and lethality appear to be rare (Baltosser and Russell, 2020; Evens and Harper, 2020); in other groups of fighting animals, this rarity of injury is the result of preliminary signaling or assessment stages in contests (Hardy and Briffa, 2013; Hoem et al., 2007). Aspects of combat have been documented in several hummingbird species (Bribiesca et al., 2019; Ewald, 1985; González-Gómez et al., 2014; López-Segoviano et al., 2018; Márquez-Luna et al., 2022). Yet open questions remain about how these contests escalate, how individuals communicate their quality or ability to win, and whether tail flaring functions as a signal.

As part of a larger research effort applying animal contest theory to study the evolution of male-male fighting in hummingbirds, we noticed frequent use of the tail in early stages of agonistic interactions. We hypothesized there may be a difference in the posture of the tail during solitary behaviors compared to competitive interactions. We predicted that tails would be flared at greater angles when in competition, with an alternative prediction that if flaring of the tail was a byproduct of maneuvering in hummingbirds, we would see similar angles in solitary maneuvers (take-off and landing) and competition. We tested these predictions in both field and laboratory settings. To place tail flaring in a natural context, we measured the frequency of tail flaring among seven species of wild hummingbirds engaged in fighting outdoors. To measure details of tail kinematics, we also studied calliope hummingbirds (*Selasphorus calliope)* engaged in agonistic encounters in an indoor flight arena. These two datasets would support our predictions if tail flaring was greatest when in competition and tail flaring was regularly seen in naturally occurring interactions. We would then have preliminary evidence that the tail may function in communication role during agonism, much like it does in courtship.

Materials and Methods

Kinematic Analysis

We obtained videos for 3D kinematic analysis using synchronized cameras. In laboratory studies, we used six cameras: two Nova S6, one Mini AX100, and three Mini UX100 (Photron Inc., San Diego, CA, USA), sampling at 2000 frames s^{-1} with a shutter speed of 1/5000 s. In the field we used three video cameras (two Photron Nova S6 and one MiniAX-100), sampling at 1000 frames s^{-1} with a variable shutter speed dependent on ambient light conditions. We used DLTdv8 (Hedrick, 2008) and EasyWand5 (Theriault et al., 2014) in MATLAB (Mathworks, Inc., 2025) to digitize and calibrate the videos via direct linear transformation to resolve global 3D coordinates.

Field observations

As part of a comparative study of hummingbird agonism in the field, we obtained videos for 3D kinematic analysis of free ranging birds. Our field sites were at the Southwestern Research Station (Cochise County, AZ, “SWRS”) and Santa Rita Lodge (Madera Canyon, AZ, “Madera”). During this field season (September 1-7, 2024), we recorded video of contests (n = 185) of adult and immature males and females of seven species of hummingbird fighting in the vicinity of artificial feeders:

148 calliope, black-chinned (*Archilocus alexandri*), rufous (*Selasphorus rufus*), broad-billed (*Cynanthus*
149 *latirostris*), Anna's (*Calypte anna*), Rivoli's (*Eugenes fulgens*) and blue-throated mountain-gem
150 (*Lampornis clemenciae*). Because these were wild and untagged birds, we were unable to estimate
151 total number of individuals within each species or repeat interactions between birds within each of
152 our two sites. Viewing the videos, we noted each species involved in the intra or interspecific
153 interaction as well as absence/presence of tail flaring. For this purpose, we considered the
154 minimum tail angle to qualify as flaring to be approximately 30° and the flaring had to be sustained
155 for at least 5 ms. Because active fighting attracted our attention when triggering video recordings, it
156 is likely our samples were biased towards more dramatic agonism, but we attempted to film any
157 agonistic encounter, regardless of the presence of tail flaring.

158 *Bird Capture and Housing*

159 Male calliope hummingbirds (*Selaphorus calliope*, 2.6±0.1g, mean ± standard deviation, n = 5) were
160 captured upon arrival at a breeding ground (May 14-20, 2024) in Missoula County, MT, USA. We
161 trapped birds on private land using a modified Russell drop trap (Russell and Russell, 2001), then
162 transported them to the Field Research Station at Fort Missoula, Montana, USA. Birds were housed
163 in a 0.6 m^3 cages constructed of 1mm wire mesh, equipped with feeders providing ad libitum a
164 50:50 mix of NektarPlus (NEKTON® Günter Enderle, Pforzheim, BadenWürttemberg, Germany) and
165 20% sucrose (mass: volume). Birds experienced natural lighting and photoperiods during captivity.
166 Capture and housing were permitted by Montana Fish, Wildlife and Parks (2024-019-W) and the US
167 Fish and Wildlife Service (SCCL-771277). Animal procedures were approved by the Institutional
168 Animal Care and Use Committees of the University of Montana (011-23, 055-23). We measured
169 body mass using a digital balance (±0.001g), and projected surface areas of the frontal view of the
170 body and dorsal view of the wings and tail (mm^2) using digital photographs (Apple IPhone 8se, 7
171 megapixel, Apple, Inc, Cupertino, CA, USA). Birds were released unharmed after 4-6 weeks of
172 captivity.

173 *Competition Arena*

174 We constructed a competition arena (1.45m w × 2.9m l × 1.2m h) from aluminum supports and
175 white diffuser fabric. This arena contained a single food source and two perches of differing heights
176 (183.5 cm, 154.4cm) to serve as a resource and elicit aggressive interactions (Gaffney, 2017). To
177 measure activity patterns and body weight, we equipped the perches with load cells (Futek S-Beam
178 Jr Load Cell, Futek Advanced Sensor Technology, Inc., Irvine, CA). Birds were acclimated

individually in the arena. Competition trials only began after birds regularly used perches and regularly fed. During acclimation time, we obtained video recordings of perch landings and takeoffs when birds were calmly completing these maneuvers, without any startle response due to researcher movement. Competition trials occurred between dyads of randomly selected males. Birds were allowed to freely interact for the first 90 minutes of a trial, after which we periodically startled the birds off their perches using hand waving that was visible to the birds via the access door or clear windows in the walls of the arena. This upset the residency (Alcock and Bailey, 1997; Davies, 1978) of a desirable perch, thus birds were more likely to interact while attempting to secure this resource.

3D Kinematic analysis of body positions

The competition arena was surrounded by six synchronized high-speed cameras and was illuminated using LED lights. We digitized ten anatomical landmarks on the birds (beak tip and base and left and right: shoulders, wingtips, tail bases, and tail tips). One out of every 50 frames (2%) were hand-digitized in DLTdv8, and we used these as a training set for Deep Neural Network Learning (DeepLabCut) (Mathis et al., 2018) to digitize remaining points. We inspected the results for variation in a fixed morphological measure (bill length). When error exceeded 5%, we used hand-digitizing to replace the results from DeepLabCut (coefficients of variance for data reported in Table S1).

To measure tail movement, we defined two position vectors, one on the left and the other on the right, each originating at the base of the tail and moving to the outermost visible rectrix. We obtained the angle of tail flare using the dot product of these vectors. Negative angles represented a tail which was folded, where the distance between the tips of the two rectrices was less than the distance between the rump points (Fig. 1). For each hummingbird (n=5) we measured flaring throughout one takeoff, landing, contest win, and contest loss. To standardize digitized contests, we chose those in which the incoming bird was visible to their competitor (frontal approach). Fights ranged from 0.3 to 3.6 seconds, with an average duration of 0.9 ± 0.7 seconds. To avoid bias due to interval duration, we downsampled measurements of the tail in each individual per flight event in longer events to 623 samples (311.5 ms) via systematic decimation, selecting every nth point based on each flight's total duration. To measure bird-centered body rotations (yaw, pitch and roll, using a right-hand coordinate system, Fig. S1), we defined the center of the caudal spine as the average x, y, z coordinates of the base of the tail (rump). The body plane was then defined by two

position vectors originating at the rump and moving to the left and right shoulders. We defined the z axis as the cross-product of these two vectors. The bird-centered x axis was from the origin to the center of the spine between the shoulders, and the y axis was the cross product of the x and z axes. We measured yaw about the z axis, pitch about y axis and roll about the x axis.

Qualitative description of contests

For fights in the competition arena, we watched all contest videos (n=103) to characterize flight trajectories and whether either individual exhibited tail flaring with flaring defined as in our field recordings: the flaring was approximately 30° and the flaring had to be sustained for at least 5 ms. Our qualitative visual assessment was informed by our prior 3D measures of tail flaring, described above.

We also noted when a bird successfully displaced their competitor from the high perch (win) and when a bird retreated (loss). When an incoming bird intimidated their competitor, we noted if the bird approached from caudal or from the lateral side of the receiving bird, as opposed to the front. From this we analyzed if signaling (tail flaring) effort varied across these approach angles.

Statistical analysis

The distributions of tail flare angles were heavily skewed with peak values centered around zero. Because these data were not normally distributed, we used a series of non-parametric tests to test for differences in tail angles across treatment (takeoff, landing, competition) and to test for relationships between tail flaring and approach angle. We used R for all tests (R core team, 2025):

A **Wilcoxon Signed-Rank Test** (*wilcox.test*) was used to compare differences in mean angle of tail flare between treatments (i.e. flight circumstances), paired for each individual (n=5) (Statistical methods in laboratory medicine, 2020). When we had an *a priori* hypothesis, a single-tailed test was used. From this test a V statistic was generated, which represented how many of the paired individuals have a greater value of tail flaring from the first to the second treatment (sum of the rank differences). We tested if tail angles were different between 1) takeoff and competition (one-tailed, *a priori* prediction of greater angles in competition than takeoff), 2) takeoff and landing (two-tailed, no prior prediction) and 3) between contest winners and losers (two-tailed, no prior prediction). We also used this to test for differences in projected frontal area with and without the tail flared in morphometric photos.

We obtained an effect size for all treatment combinations tested in Wilcoxson Signed-Rank Tests using a **Rank-Biserial Correlation** (*wilcox_effsize)* (Kassambara, 2023)*,* which measured the magnitude of differences between groups from Wilcoxon Signed-Rank tests using Z-scored data. This correlation ranges from 0 (no correlation) to 1 (strongest correlation).

Our second test was a **Kolmogorov-Smirnov Test** (*ks.test*), a non-parametric test to compare distributions (Berger and Zhou, 2014). We chose this test given a high inflation of near-zero values paired with a large variance of angles, and low counts of great (<100°) tail angles. This test measured the cumulative distribution for each step in tail angles (n=311 points for each flight condition per bird). A steeper curve to the cumulative distribution meant most data were at low tail angles, while a shallow curve represented a broader distribution across tail angles. Comparisons were made between 1) takeoff and landing, 2) solitary (takeoff and landing pooled) and competition and 3) winners and losers of a competition. This test produces a D statistic, which represents the maximum distance (as a ratio) measured between the two distributions, as well as a p-value.

We tested whether approach angles affected the use of tail flaring by measuring a proportion of each approach angle (front, side, caudal) where the tail was flared. To do this we used a **Friedman Test** *(friedman.test)*, this is a non-parametric alternative to a repeated-measures ANOVA, run on the ranks of treatments instead of their mean values (Sheldon et al., 1996). To control for pseudo replication where some birds approach many times or always from one angle, we calculated a proportion of signaling for each approach angle per individual. The statistical test was then run on a summary of each bird. One bird never approached caudally, so this individual was omitted from the analysis. For this test we report df and p-values.

We tested which pairwise comparisons of approach angle produced significant differences in the Friedman test using a **Conover-Iman test** with a Benjamini-Hochberg correction (Conover and Iman, 1981). This test is appropriate for small sample sizes and few groups. We report pairs of approach angles that accounted for the statistical differences in tail flaring. We did this using *frdAllPairsConoverTest* (Pohlert, 2024).

Finally, to test the correlation between body mass and the size of a flared tail in morphometric photos, we used a **Spearman Rank correlation** test *(cor.test, method= "spearman")* (Zar, 2005). This test produces an S value, which corresponds to the sum of squared differences in rank of the two variables. A rho value is also reported, which ranges from -1 to +1, with zero corresponding to

no association and 1 corresponding to a perfect negative (-1) or positive (+1) association. We report p-values from this test.

AI Statement

Machine learning AI was used to digitize anatomical points videos from a training set of points selected by authors (DeepLabCut) (Mathis et al., 2018). These points were quality controlled to ensure coefficients of variance were within acceptable threshold (5%). AI-assisted technologies were used as templates for analysis and visualization code, then further modified and ensured for accuracy of data representation by authors.

Results

During field study in Arizona, seven species of hummingbirds (males and females, adults and immatures) in two different locations frequently exhibited agonistic interspecific and intraspecific interactions (Table 1; Fig. 2). We recorded 370 instances of a bird engaged in a fight (note 2 birds per fight), tail flaring was present in 352 (95%) of the instances. The species with the least prevalence of flaring was the broad-billed hummingbird, who flared their tails in 84% of interactions. Our results indicate that tail flaring was routinely used during the behavioral context of inter- and intraspecific agonistic encounters.

Table 1. **Tail flaring activity in seven species of free-ranging hummingbirds in Arizona (Madera Canyon and Southwestern Research Station).** Intra- and interspecific competitions are pooled, and percentages are species specific.

Species	**Sites**	**Total Contests**	**Contests with Flaring (%)**
Anna's (*Calypte anna)*	Madera	8	100%
Blue-throated mountain-gem (*Lampornis clemenciae*)	Madera, SWRS	58	98.3%
Rufous (*Selasphorus rufus*)	Madera, SWRS	106	98.1%
Black-chinned (*Archilochus alexandri*)	Madera, SWRS	159	93.7%
Calliope (*Selasphorus calliope*)	SWRS	11	90.9%
Rivoli's (*Eugenes fulgens*)	Madera, SWRS	9	88.9%
Broad-billed (*Cynanthus latirostris*)	Madera, SWRS	19	84.2%

Tail flaring angles among *S. calliope* during lab trials were different between take-off (-11.1 ± 6.6°), and landing (-12.7 ± 8.6°) versus during competition (when birds won or secured the high perch after a contest: 29.0 ± 41.5°, and when losing 24.1 ± 39.1°, example: Video S1). The differences between tail angles during takeoff and competition was significant (Fig. 3, Wilcoxson signed rank test, V = 0, n =5, p=0.031) with a strong effect size (rank-biserial correlation, r=0.905). There was no statistical difference between mean tail angles during takeoff and landing (Wilcoxson signed rank test, V = 9, n =5, p=0.181). While there was a medium effect size of winning (secured the high perch) or losing on tail flaring angles (rank-biserial correlation, r=0.543), it was not statistically significant (Wilcoxson signed rank test, V=12, n =5, p=0.3125).

Even though tests of paired means (Wilcoxon signed-rank test) did not show significant differences in tail flare between winning or losing, there were significant differences in frequency distributions of tail flare angles through a contest (Fig. 4). There was strong statistical support that tail angle distributions differed between take-off and landing (Kolmogorov-Smirnov test, D=0.190, p < 0.001), between solitary (take-off and landing pooled) and competition conditions (Kolmogorov-Smirnov test, D= 0.49, p <0.001), and between winners and losers of competitions (Kolmogorov-Smirnov test, D=0.226 p < 0.001). The distributions that had the greatest pairwise differences were solitary and competitive conditions (D=0.49, or a maximum of 49% divergence between the distributions).

Competing males appeared to exhibit “call and response” of tail flaring. For example, Figure 5 presents tail angles during a fight (595 ms in duration) between a winning bird (green line) who was initially in the air and a bird (yellow line) on the high (desirable) perch who was ultimately displaced. At 63 ms into the encounter, the winning bird flared its tail from 2.6 deg to 120 deg (i in Fig. 3). There was a 50 ms lag before the losing bird started to flair its tail from 1 to 66 deg (ii). The losing bird takes off from the perch at 280 ms (iii) and maintained a tail angle averaging 68 deg, much greater than mean tail angles during solitary takeoff (see above). At 400 ms when the losing bird began to retreat in the air (iv), it reduced its tail angle from 71 to 9 deg. Throughout the interval from 235 ms (v) to the end of the fight, the winning bird maintained a tail angle of 95 to 124 deg. We considered the fight to end when the losing bird retreated outside the interrogation volume of our cameras (vi).

Our qualitative analysis of tail flaring during approaches toward a bird on the high perch in the flight arena provided further support that tail flaring by the approaching bird was directed toward

the perched competitor. There was a significant association between the angle from which a bird was approaching and whether their tail was flared (Friedman test (df=2), p-value = 0.0381). Post hoc tests revealed significant differences in tail flaring between caudal approaches and front approaches (Conover test with a Bejamini-Hochberg correction, p=0.01) and between caudal approaches and side approaches (p=0.009). In other words, birds flared their tail significantly less often when approaching from behind their opponent.

Tail flaring appeared to increase projected frontal surface area of a competitive male (Fig. 6A,B), assuming a fixed angle of tail spread of 110° and a vertical upright orientation of the body and tail, our morphometrics revealed that total projected frontal area was significantly greater 38.6±10.7%, than when tails were not flared (Wilcoxson signed-rank test V=0, p-value = 0.03125, r = 0.905). This increase in tail area was not accounted for by the birds' body mass as there was a weak and insignificant correlation between total projected area and body mass (Spearman rank correlation, S =14, rho = 0.3, p =0.683).

In addition to the spread of the tail, hummingbirds exhibited body movements with tail flaring in what we here describe as a "waggle" (Fig. 6C) (Hurly et al., 2001). This waggle occurred in ~39% of encounters that involved tail flaring. One bird who spent the least time on the high perch never performed this behavior and thus this analysis was for n=4 birds. The body movements included linear translations and rotations about all three axes (pitch, roll and yaw, Fig. S1). Among the four birds who exhibited waggles, average tail angle was 67.1 ± 16.5° and average pitch angle of the body was 98.3 ±14.0°, meaning the bird was tilted dorsally slightly beyond vertical. Linear translations were 6.7 ± 3.8 cm and 1.4 ± 0.9 cm in the horizontal and vertical directions, respectively. Range of angles about each body axis were 67.7 ± 33.3° for pitch, 61.2 ± 25.1° for yaw and 79.6 ± 41.6° for roll.

We present an example of a bird engaged in tail flaring with waggle display (Fig. 6). Throughout this display, average tail angle was 89.1° and average pitch angle of the body was 80.3°. The bird translated 2.81 cm horizontally and 1.96 cm vertically. He rotated through an approximately symmetrical yaw of 93.1°. Roll angles occupied a 41.3° range and pitch changed angle by 37.8° (Fig. 6D). The waggle maneuver increased the projected area swept by the tail to be 6.43 cm^2 (Fig. 6C). The equivalent projected areas for his unflared and flared tail were 1.32 cm^2 and 1.516 cm^2, respectively (Fig. 6A,B).

Discussion

We found greater tail flaring angles in male calliope hummingbirds during competition trials than in other contexts. These results support our hypothesis that the posture of hummingbirds' tails varies between locomotor actions (takeoff and landing) and agonistic competition, suggesting that this flaring is used most often in a social contest. Moreover, hummingbirds did not flare their tails as frequently when out of the view of their competitor. The maximum angles of tail flaring during competition appeared similar to those during rapid escape performance in calliope hummingbirds (Anwar et al., 2024) and four other species of hummingbirds (Haque et al., 2023b). However, the duration of tail flaring during agonism lasted much longer (often over 1 second compared to 120ms, for example 600 ms in Fig. 5).

Our results suggest that flaring of the tail is used for communication with other hummingbirds and this form of communication is consistent with the hummingbird visual system. Tail flaring and waggling (Fig. 6) can be easily perceived by other hummingbirds based on current understanding of the hummingbird visual system. Hummingbirds are near-sighted (equivalent of ~20/100) (Altshuler and Wylie, 2020) with a region of binocular vision (~29°) by the bill tip, monocular vision on the sides of the head, and a blind spot at the back of the head (~22°) (Tyrrell et al., 2018). This blind spot probably accounts for the observation that birds infrequently flared their tail in caudal approaches, given this is outside of the visual field and communication with a visual signal is not effective here.

We propose that the use of tail flaring with a waggle display may be attempts to intimidate opponents via a looming stimulus. Flaring by itself increased the projected body size presented to a competitor, but the addition of waggling increased this size further (Fig. 6). These two behaviors together present a looming stimulus to a competitor, and looming in many taxa elicits an evasive response (Peek and Card, 2016). Waggling specifically causes an individual to spend time in both the monocular and binocular visual field of their opponent. Looming stimuli depend on the fractional rate of change of an approaching item on the retina, and the efficacy of looming depends on estimates of time-to-contact (TTC) (Peek and Card, 2016). TTC is best discriminated when an opponent is in the binocular visual field (Gray and Regan, 2004), but the increased ganglion cell density and invagination of the central retina (fovea centralis) in hummingbirds (Tyrrell et al., 2018) allow for spatial acuity, and probably accurate TTC estimates, even in the monocular region. That said, in humans, the addition of horizontal motion to a stimulus reduces TTC accuracy (Calabro et

al., 2011). Tail flaring with added waggling during approaches from the front or side (Fig. 6) may introduce uncertainty in TTC estimates and may augment the intimidation effect.

Flaring of the tail during competition and its potential role for intimidation align with current definitions of signals used for animal communication. An incoming bird who initiated a contest (Figs. 5 and 6) flared its tail, which may communicate an intention of attack with force if its opponent does not retreat (Bradbury and Vehrencamp, 2011). The continued use of tail flaring throughout the interaction could also mean this is a signal that directly communicates some aspect of the quality of the opponent. If body size is an important quality to signal, as it is in other taxa (Brown et al., 2005; Guilford and Dawkins, 1995; Umbers et al., 2012; Vieira and Peixoto, 2013), we might expect the use of a signal that is constrained by a physical property of the signaler where only the largest individuals have the largest signals (i.e., an index signal) (Bradbury and Vehrencamp, 2011). If true, then we would expect large individuals to flare their tails the most widely. This was not supported by our data, as body mass was not correlated with projected frontal area when the body was flared. In fact, our results suggest that there is a unique distribution of maximal tail flare angles in individuals that win the high perch (Fig. 4), but maximal angles are not correlated with body mass. Of the highest quantile (80TH) of tail flare angles that we measured, over 30% of maximal angles were exhibited by the bird with the *smallest* body mass. This individual also spent the most time on the desirable high perch (Gaffney, 2017) via successful displacements.

If the hummingbird tail is a signal of individual fighting ability, or resource holding potential (RHP), then flaring for communication would help explain the rarity of lethality and injury in field-observations of hummingbird fighting (Baltosser and Russell, 2020; Evens and Harper, 2020). When opponents can estimate the RHP of a rival from the quality of a signal, it often pays the weaker competitor to cede the contest before it escalates to dangerous battle (Smith and Harper, 2003; Zahavi, 1975). Agonistic signals have been well studied in a diversity of animal contests (Brown et al., 2005; Emlen et al., 2012; Green and Patek, 2018; Vieira and Peixoto, 2013; Yasuda et al., 2011; Yasuda et al., 2011), but little is known about this sort of signaling in hummingbirds. Tail flaring has been described in fights of other hummingbirds (Hurly et al., 2001; Williamson, 2020) and we show here that it is used extensively during fighting in seven species in the field, and in male calliope hummingbirds in our competition arena.

If flaring does signal individual quality, we predict that this is due to the metabolic cost of flaring the tail, not the cost of growing or carrying it. The energetic cost for developing tail feathers

415 in minimal (Buttemer et al., 2020) and the tail only contributes marginally to body mass and
416 aerodynamic drag (Clark and Dudley, 2009). These costs are energetically inexpensive when
417 compared with signals of male quality in other taxa (e.g. horns, antlers, overall body size (Emlen,
418 2008)). Tail feathers are molted seasonally and are easily shed in response to predatory attack
419 (Farner and King, 2013). The ability of tail flaring to communicate individual quality may instead rely
420 on the energy used by muscles to flare the tail. Overall muscle quality is important in combat,
421 allowing for an individual to chase faster (Sholtis et al., 2015) or be more agile in fighting. Muscular
422 contractions by the *bulbi retricium* muscle (Gatesy and Dial, 1996) are responsible for the flaring of
423 the tail. Tail flaring during contests can last up to several seconds, and the energetic cost of muscle
424 contraction should be proportional to the duration of contraction and the number of motor units
425 recruited (Taylor et al., 1980). If individuals with the highest RHP also flare their tails at the greatest
426 angles or for the longest periods of time, this could be signaling an individual's overall muscle
427 quality. If flaring adversely affects the aerodynamics of hovering through wake interactions, (Su et
428 al., 2012), alteration of body pitch, or changes in wing trajectories, perhaps this can only be
429 accomplished by individuals with the highest RHP. Tail flaring that is accompanied by waggles may
430 further accentuate RHP if waggling increases metabolic costs beyond steady hovering (Groom et
431 al., 2018).

432 Flaring of the tail thus seemed important for signaling during agonism, but this role must of
433 course coexist alongside any aerodynamic function during flight. Tails that were flared during
434 competition exhibited small oscillations (~15°) in angle approximately in phase with the wingbeat
435 cycle (faint lines in Fig. 5). In-phase flaring in the passerine species, the warbling white-eye
436 (*Zosterops japonicus*), is used to mitigate excess body pitch (Su et al., 2012). The wingbeat
437 kinematics of this passerine varies significantly from those of hummingbirds; an asymmetric
438 flexed-wing upstroke of the passerine provides minimal aerodynamic function (Crandell and
439 Tobalske, 2015), while the active upstroke of the hummingbirds' fully-extended wing generates lift
440 (Warrick et al., 2005). In hummingbirds, the wings dominate the aerodynamics (Haque et al.,
441 2023a), but high-frequency of modulation of the tail in our work suggests the tail could be providing
442 minor pitch stabilization via aerodynamic forces. In addition, it is possible that the inertia of the
443 tails of hummingbirds could function as vibration absorbers and dampers to suppress the body
444 oscillations induced by wing flapping (Haque et al., 2023b). Even during the dramatic maneuvers of
445 escape flight from a looming threat, the tail contribution to overall torque is minimal compared to
446 the contribution of the wings (Nasirul Haque et al., 2023). One species of hummingbird (black-

chinned hummingbird, *Archilocus alexandri*) is known for their exaggerated and diagnostic (Sibley, 2014) "pumping" of the tail during slow flight. Females and males of this species modulate tail flare angles and angle of the tail plane relative to the body plane. This species additionally flared their tail in ~94% of interactions in our field study (Table 1). Further study of this species would be a promising direction to test for an evolutionary tradeoff between slow flight dynamics versus tail flaring for communication in hummingbirds.

To understand signaling of the tail, whether it communicates quality and functions to modulate contest escalation within hummingbird agonism, it will be necessary to study tail flaring in relation to other phenotypic traits including morphology, behavior, and physiology. Traits that are already understood to improve flight performance in hummingbirds include marginal power availability which correlates with agility (Altshuler et al., 2004; Dakin et al., 2018; Segre et al., 2015). In other bird species, individual aggression and overall body condition (Careau et al., 2008; Dolnik and Hoi, 2010), including bilateral symmetry (Møller, 1992) have explained differences in male competitive and reproductive success. Variable time budgets may be associated with aggression (Ewald and Bransfield, 1987), and if muscular activity from flaring of the tail comes at a metabolic cost it could be important to consider daily energy expenditure on these tasks (Shankar et al., 2019). To rigorously test whether tail flaring correlates with individual quality, it will be necessary to carefully investigate phenotypes at the individual level in behavioral experiments that control for residency effects (Alcock and Bailey, 1997; Mendiola-Islas et al., 2016) and repeat interactions. Together, these would further our understanding of the evolution of dominance in contests, phenotypes associated with competition success and tail flaring as a signal in hummingbird agonism.

Conclusions

Tail flaring was regularly used by free-ranging hummingbirds in seven species at two different field sites, as well as among male calliope hummingbirds during competition trials in an indoor competition arena. The angles of tail flaring were different between solitary maneuvers and during competition, with differences in frequency distributions between birds that won a desired territory (high perch) and those that did not. The use of tail flaring was variable and did not associate with body size, therefore we propose that it and concurrent waggle maneuvers may serve as signals of aggressive intent in male-male fighting in hummingbirds. Our field observations indicate such

signaling is also performed by females. Testing for correlations between tail flaring and an individual's quality (Resource Holding Potential, RHP) may be revealed through further study of the metabolic energy requirements and aerodynamics of aerial competition that includes tail flaring.

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Competing Interests

The authors declare no competing interests. This research is original and not submitted for consideration of publication at any other journals.

Author Contributions

RLE: project conceptualization, data curation, investigation, methodology, formal analysis, visualization, writing-original draft. MZA: data curation, investigation, formal analysis, writing-review and editing. DRP: data curation, investigation, methodology, writing-review and editing. BC: project conceptualization, funding acquisition, writing-review and editing. HL: project conceptualization, funding acquisition, writing-review and editing. BWT: project conceptualization, funding acquisition, data curation, investigation, methodology, formal analysis, supervision, writing-review and editing.

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Data and resource availability

Raw data associated with this manuscript are published on a dryad digital repository: 10.5061/dryad.dz08kpsbj. R scripts for data analysis will be available on GitHub upon acceptance.

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Figures

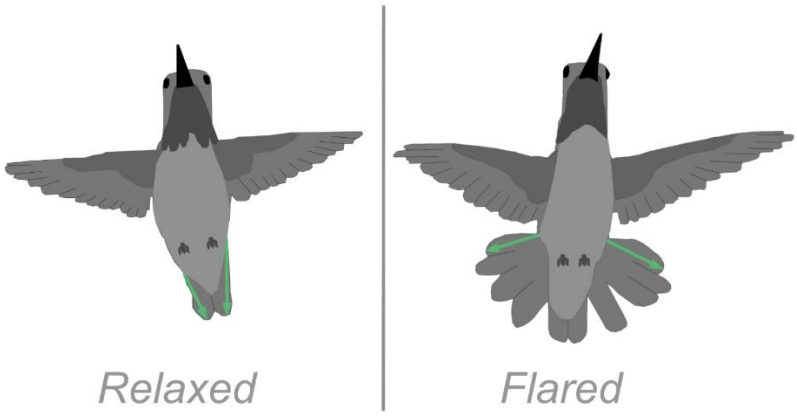

Figure 1. Two tail states in male calliope hummingbirds (*Selasphorus calliope*): relaxed and flared. Tail angle was the acute angle between left and right position vectors (green arrows) originating where the outer margin of the tail met the body and going to the tip of each outer rectrix (R5). In these examples drawn from frames of high-speed video, the relaxed tail angle was -26° and flared angle was 136°.

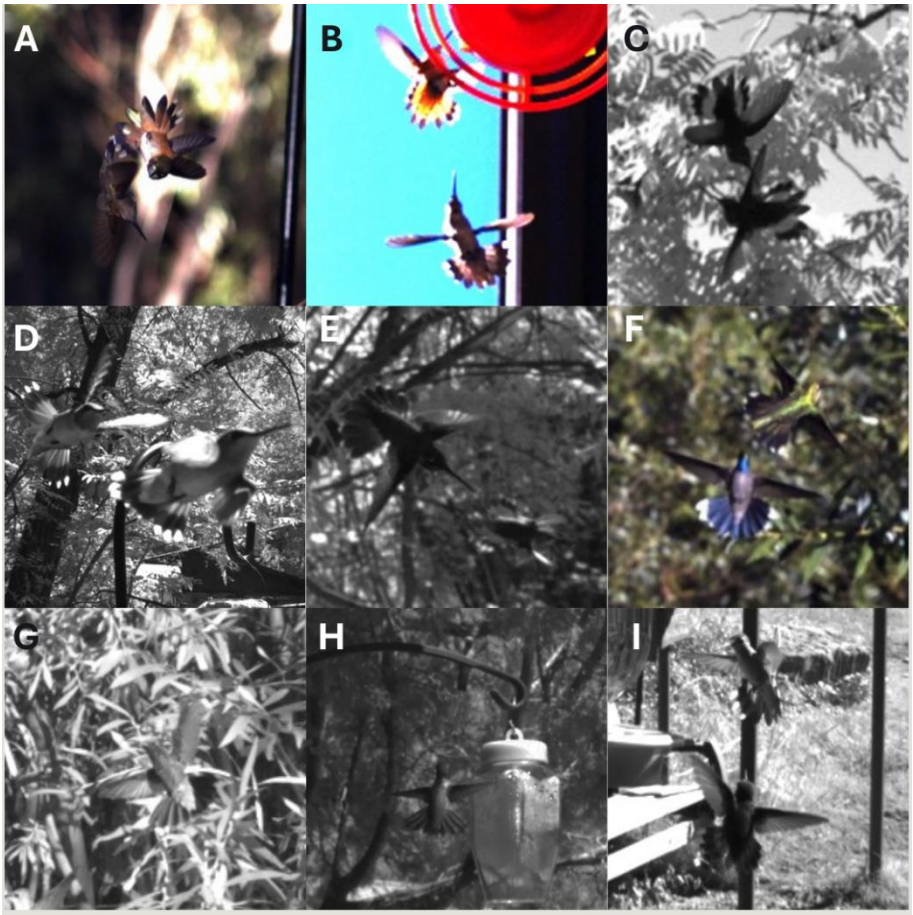

Figure 2. Compilation of flared tails in wild hummingbirds engaged in agonistic encounters in Arizona, USA. A) rufous (*Selasphorus rufus*, right), chasing black-chinned (*Archilochus alexandri*, left), B) rufous (top) and black-chinned in contest at feeder (red disc), C) two rufous in ascending fight, D) black-chinned (left) chasing conspecific, E) Rivoli's (*Eugenes fulgens*) chasing a rufous, F) blue-throated mountain-gem (*Lampornis clemenciae*) intimidating a black-chinned, G) Broad-billed (*Cynanthus latirostris*) with flared tail directed at a bird out of frame, H) dorsal view of Anna's (*Calypte anna)* facing conspecific, I) Calliope (*Selasphorus calliope*) in the foreground flaring tail towards a black-chinned at a feeder.

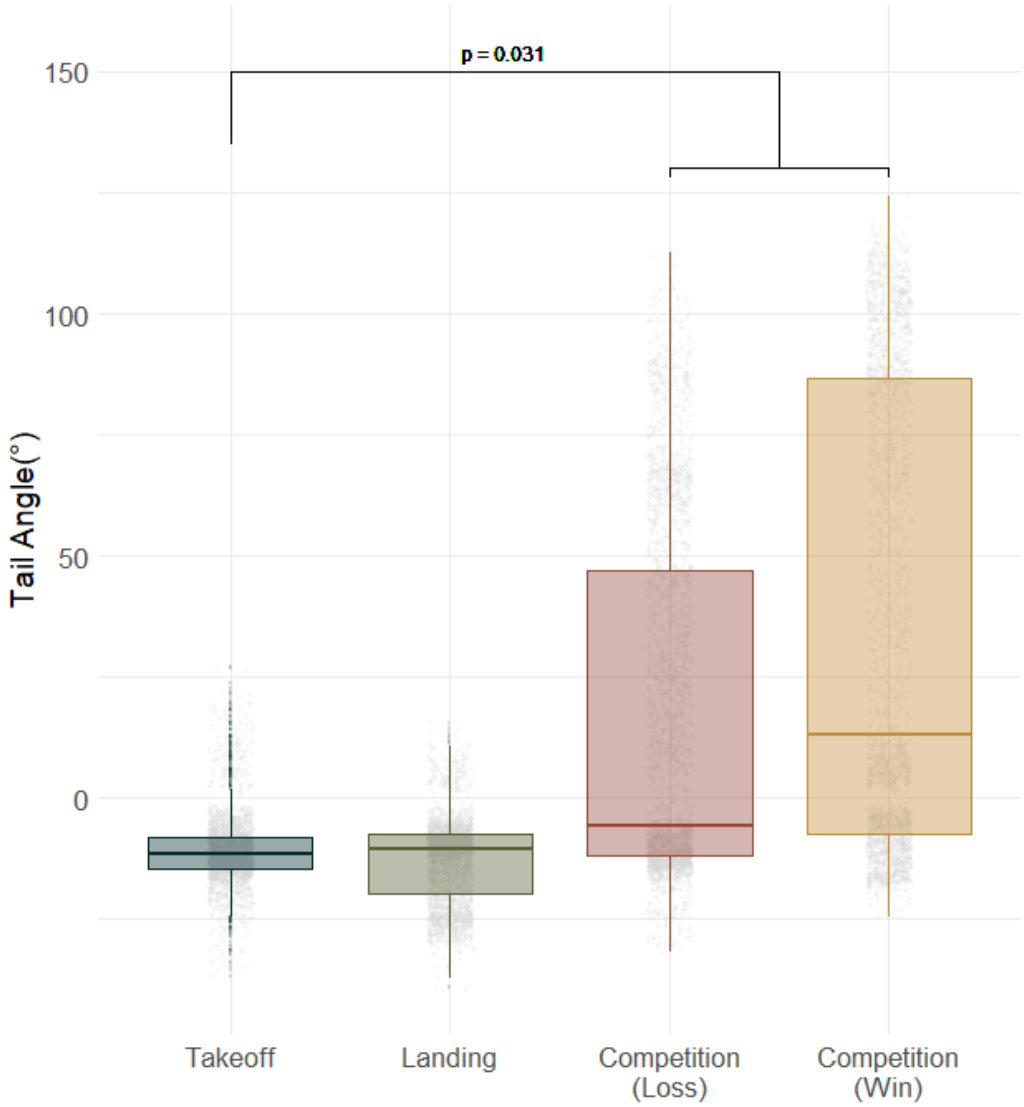

Figure 3. Tail flare angles of calliope hummingbird, *Selasphorus calliope* (n=5) during agonistic encounters were greatest during competition in a laboratory setting. Data from individuals pooled based on condition: solitary takeoffs or landings, compared to contests, which have been split based on contest outcome (win: secured high perch, lose: retreat). Box plots are interquartile range and median values, while vertical lines are minimum and maximum values. Jitter points include 2552 samples (i.e. video frames) per condition, but the p-value from Wilcoxson Signed-Rank test was performed using n=5.

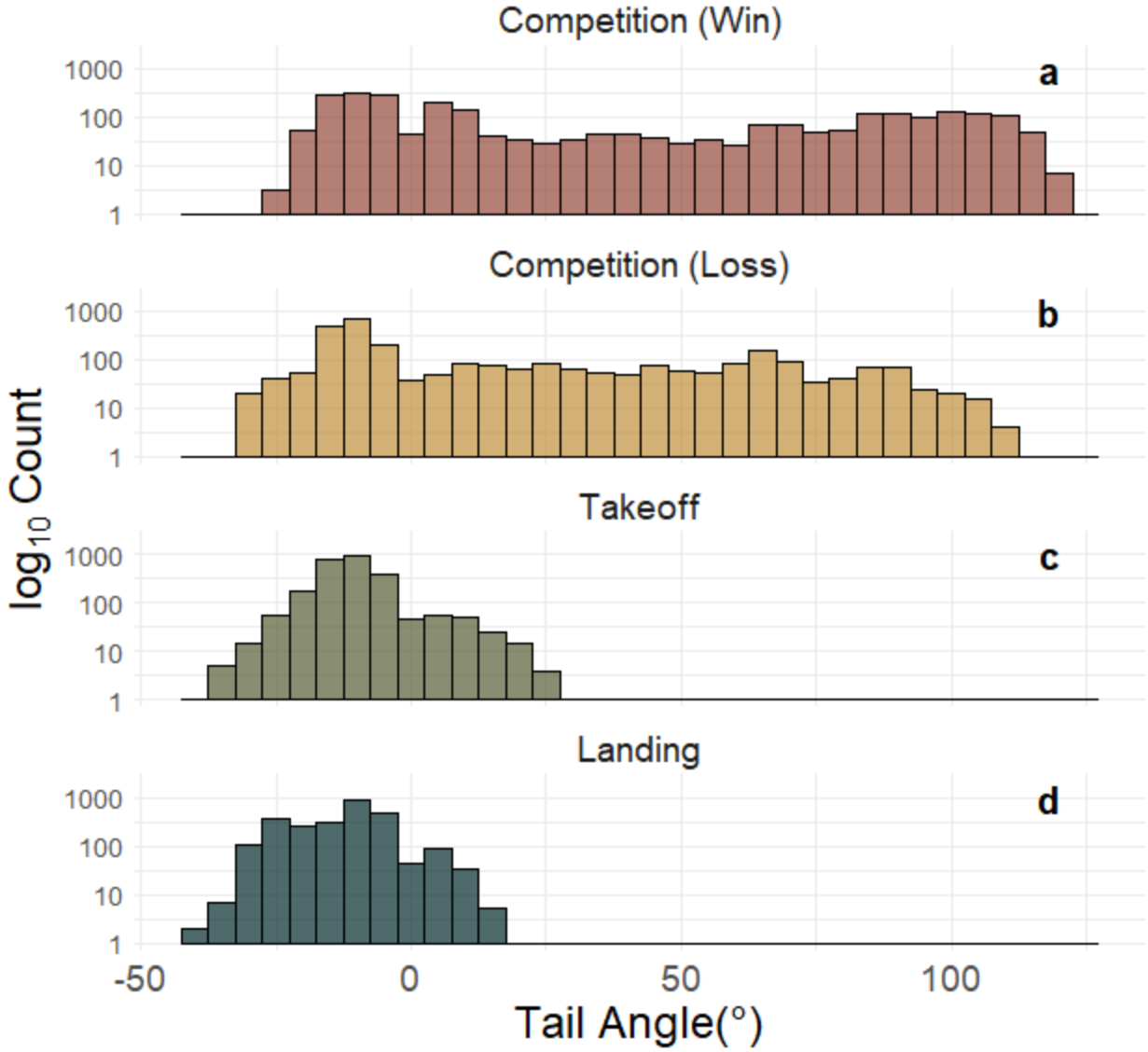

Figure 4. Frequency distributions of tail angles for male calliope hummingbirds (*Selasphorus calliope, n = 5 birds, pooled data with n = 623 samples from video per bird*) during landing, takeoff, and winning or losing of a contest. For ease of visualization in this figure, data were log-transformed along the y-axes to reduce skew. Letters on the right side denote statistically significant differences among non-transformed distributions (Kolmogorov-Smirnov Test).

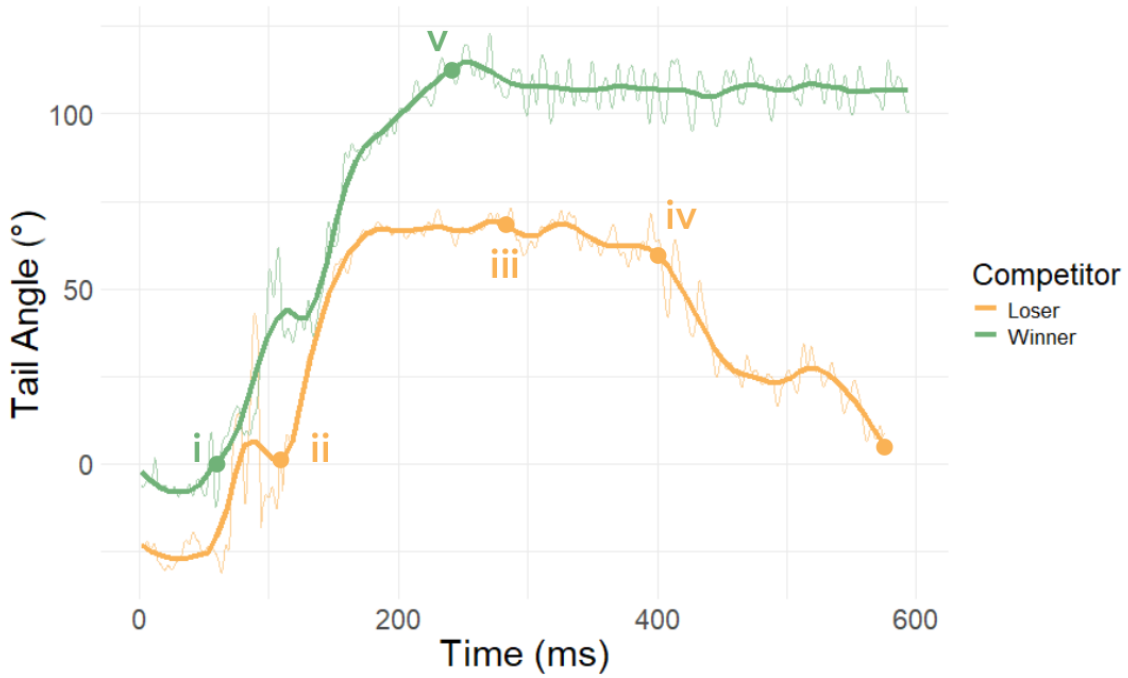

Figure 5. Time series revealing "call-and-response" of angles of tail flaring of two male calliope hummingbirds (*Selasphorus calliope*) fighting over a desired resource (high perch). The winning bird (green) initiates the displacement by flaring its tail starting at (i), and the occupant of the perch (yellow) responds after lag of 50 ms (ii). The losing bird leaves the perch (iii) and eventually retreats (iv). The winning bird maintains tail flare from (v) to the end of the fight when the loser flies out of the interrogation volume of the video cameras (vi). Fine lines represent raw data smoothed over 5 points (2.5 ms) and bold lines represent these data further smoothed using a LOESS formula.

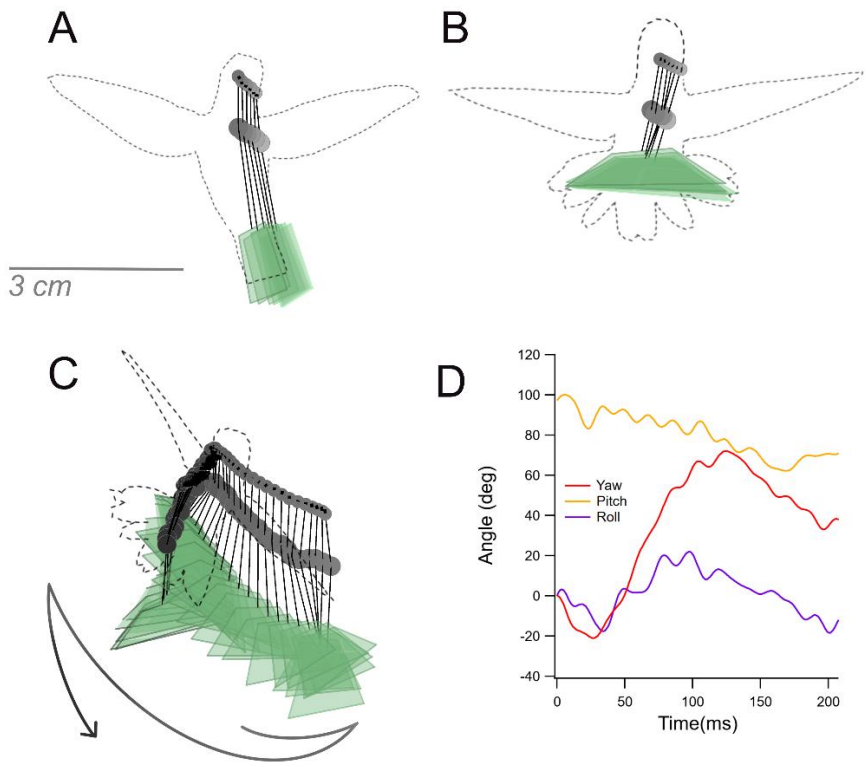

Figure 6. Projected area of the combined body and tail increased when birds flared their tails and was further augmented by "waggle" body movement. Three phases of a display performed by a male calliope hummingbird (*Selasphorus calliope*) in flight while approaching and intimidating a perched bird. A) tail not flared B) tail flared and C) during a "waggle" where tail flaring was paired with linear translations and body rotations. Positions in A-C sampled every 200 ms. Dashed lines represent body outline at end of display. Solid black lines = beak, green = plane of tail, filled circles = head and center of anterior spine, with shading intensity increasing with time during the display. D) plots of angles of yaw, pitch and roll during the waggle in C (continuously sampled at 2000 Hz).