Tail Flaring as an Agonistic signal in Hummingbirds

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Abstract

Signaling between conspecifics is considered evolutionarily stable when signals communicate honest information about individual quality. Signaling often serves as an initial step of assessment in contests by mitigating escalation. Previous research suggests that hummingbird tails are under relaxed selection for aerodynamic function, which may explain diversification of tail morphology in the clade via sexual selection. Our observations, and brief descriptions in the literature, led us to hypothesize that tail flaring may function as an agonistic signal during male-male fighting. To test this, we studied male-male fighting in dyads of calliope hummingbirds (*Selasphorus calliope*, n = 5) in an indoor contest arena, and we studied seven species of free-living hummingbirds. Consistent with our hypothesis, captive males exhibited greater angles of tail flare when engaged in a fight than when performing solitary landing and takeoff maneuvers (Δ36.5±0.7°). Tail flaring angles were greater in contest winners than losers (Δ17.2±0.9°) with an effect of dominance rank. In the field, 90% of inter- and intra- sexual and specific contests included tail flaring. Our results quantify the use of the tail in agonistic signaling in the context of dominance in hummingbirds, and we outline predictions for future tests of whether the tail is an honest signal.

Keywords

Animal behavior, animal contests, dominance hierarchy, flight kinematics, male-male agonism, morphology, resource holding potential

Introduction

Signaling is a key step in mediating escalation of animal contests and serves to advertise individual quality (Husak et al., 2015; Smith and Harper, 2003; Zehavi and Zahavi, 1997). Agonistic contests in animals typically occur over resources such as food, territories and mates (Hardy and Briffa, 2013; Painting and Holwell, 2014; Schuett et al., 2023). The quality of certain phenotypes may improve Resource Holding Potential (RHP) (Parker, 1974), which is the capacity to obtain and maintain resources. A recognizable signal of this phenotype may establish an individual's relative RHP, disincentivizing potential challengers. Signals of quality can have on-off states (i.e. flaring of a peafowl tail, *Pavo spp*.) to communicate RHP to rivals during contests and render asymmetries between rivals more visible (Hardy and Briffa, 2013). The size and movement of the signal may impact RHP. For example, fiddler crabs (*Uca spp.*), a model taxa for studies of signaling RHP, exhibit substantial variance in weapon (claw or chela) size and signaling movements (Crane, 1958; Crane, 1997). Male fiddler crabs use claws to wrestle over ideal burrows for mating, but these contests are often preceded by signaling behaviors, such as claw raising and waving to compare size prior to physical engagement. This allows males with lower RHP (smaller claws) to retreat before engaging in a costly fight that could accrue metabolic costs or physical injury (Arnott and Elwood, 2009; McLain et al., 2019; Taylor and Elwood, 2003). These signals may present functional tradeoffs with other aspects of performance. Male sand fiddler crabs (*Uca pugilator*) that use enlarged claws for signaling experience a tradeoff with increased metabolic cost and reduced endurance during locomotion (Allen and Levinton, 2007). However, other species like *U. terpsichores* and *U. beebei* maintain fighting strength through slight changes in morphologies allowing their large claws to serve as both effective signals and weapons (Dennenmoser and Christy, 2013). Signals as mediators of animal contests have been well studied in arthropods (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 less is known about signaling RHP in vertebrates.

Agonism over territories is widely exhibited by hummingbirds, but the use of signaling in relation to resource holding potential (RHP) is presently unclear. In many species, males hold territories and females travel across 'dispersed leks' (Frith, 2024; Hutto, 2014) of these territories to observe courtship displays and choose a mate. Competition amongst males over territories can include behaviors such as chasing (Tamm et al., 1989), perch displacements, feather pulling, and jousting (Rico-Guevara and Araya-Salas, 2015). Previous research provides extensive insight into male-male fighting (Bribiesca et al., 2019; Ewald, 1985; González-Gómez et al., 2014; López-Segoviano et al., 2018; Márquez-Luna et al., 2022), but does not explore signaling in relation to RHP. Signaling may precede fighting and function to reduce the metabolic cost of escalated contests—an important consideration given that hummingbirds in flight have the highest mass-specific metabolic rates among vertebrates (Shankar et al., 2019; Suarez, 1992).

Compared to other avian species, hummingbirds are considered to be "hyper-aerial", which means they spend a lot of time in the air and they exhibit robust wings and reduced legs (Heers and Dial, 2015). In hummingbirds, wings account for 41% of the thrust in takeoff, compared to 1-10% provided by the wings of other bird species that use leg-dominated takeoff (Earls, 2000; Heppner and Anderson, 1985; Tobalske et al., 2004). Hummingbirds have proportionally enormous pectoralis and supracoracoideus muscles which function as the primary motor for their wings (~27% body mass) (Altshuler et al., 2010; Hartman, 1954). They are the only taxa that can sustain hovering in still air. This is facilitated by their high mass-specific power output (Agrawal et al., 2022) associated with high wingbeat frequencies (20-50 Hz) (Corben, 1983). Also, while hovering, they move their wings in a manner that provides weight support during the up and down stroke (Warrick et al., 2005).

Because of the dominance of wings for flight in hummingbirds, their tails are candidates for signaling during agonistic encounters. The evolution of diverse tail morphology in response to sexual selection—including long streamers, spatulate shapes, vane asymmetry and notched tips to generate sounds (sonations) during courtship—is hypothesized to have been facilitated by relaxed selection on the aerodynamic function of the tail in hummingbirds (Clark, 2010). Experimental addition of streamers induces only minimal costs to metabolic rate (max: 11%), especially at slow flight speeds, and only marginally decreases maximal flight speed (3.4%) (Clark and Dudley, 2009). Also, even though escape is the most dramatic maneuver presently known in hummingbirds (Cheng et al., 2016), the tail only provides a minor function. Escape involves extreme agility and power output, and is composed of a stereotypic sequence of pitch and roll maneuvers that lasts ~120 ms (Cheng et al., 2016). In response to a looming stimulus, tail flaring occurs at the start of the escape, and the tail remains flared throughout. Regardless of this flaring, results from models of Computational Fluid Dynamics (CFD) suggest that the tail is only aerodynamically active in brief moments at the start and end of the maneuvering (8% of total time). Peak instantaneous torque that the tail exerts on the body is only 25% of the magnitude of peak torque contributed by the wings (Haque et al., 2023).

As part of a larger research effort applying animal contest theory to study the evolution of contests in hummingbirds, we noticed an overwhelming use of tail flaring in early stages of interactions. This tail flaring during fighting has been briefly mentioned in previous work investigating hummingbird agonism (Hunter, 2008; Hunter and Picman, 2005; Hurly et al., 2001), though never quantified. Here, we hypothesize that relaxed selection on aerodynamic function allows the tail to serve as an agonistic signal in addition to its established role as a sexually-selected ornament (Clark, 2010). To test this, we measured tail kinematics of calliope hummingbirds (*Selasphorus calliope)* during agonistic encounters in a flight arena. In the field, we measured the frequency of use of tail flaring among seven species of wild hummingbirds engaged in fighting. We predicted that if the tail is being used as a signal, there would be more frequent tail flaring with greater intensity (flare angle) and duration during agonistic encounters than during flight maneuvers in the absence of a competitor.

Methods

Bird Capture and Housing

Male calliope hummingbirds (*Selaphorus calliope,* 2.5±0.2 g, n = 5) were captured upon arrival at a breeding ground (May 14-20, 2024). Birds were trapped on private land using a modified Russell drop trap (Russell and Russell, 2001), then transported to the Field Research Station at Fort Missoula, Montana, USA. Birds were housed in a 0.6 m^3 cage constructed of 1mm wire mesh, equipped with feeders providing *ad libitum* a 50:50 mix of NektarPlus (NEKTON® Günter Enderle, Pforzheim, BadenWürttemberg, Germany) and 20% sucrose (mass: volume). Birds experienced natural lighting and photoperiods during captivity. Capture and housing were permitted by Montana Fish, Wildlife and Parks (2024-019-W) and the US Fish and Wildlife Service (SCCL-771277). Animal procedures were approved by the Institutional Animal Care and Use Committees of the University of Montana (011-23, 055-23). We measured body mass using a digital balance (±0.001g), and projected surface areas of the frontal view of the body and dorsal view of the wings and tail (mm^2) using digital photographs. Birds were released unharmed after 4-6 weeks of captivity.

Trial arena

We constructed a trial arena (1.45m w × 2.9m l × 1.2m h) from aluminum supports and white diffuser fabric. This arena contained a single feeder and two perches of differing heights (183.5 cm, 154.4cm) to serve as a resource and elicit aggressive interactions (Gaffney, 2017). To measure activity patterns and body weight, we equipped the perches with load cells (Futek S-Beam Jr Load Cell, Futek Advanced Sensor Technology, Inc., Irvine, CA). Birds were acclimated individually in the arena. Contest trials only began after birds were regularly using perches and feeding. During acclimation time, perch landings and takeoffs were recorded when birds were calmly completing these maneuvers, without any startle response due to researcher movement. Contest 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 contest arena was surrounded by six synchronized high-speed 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. The arena was illuminated using LED lights. We used DLTdv8 (Hedrick, 2008) and EasyWand5 (Theriault et al., 2014) in MATLAB to digitize and calibrate the videos *via* direct linear transformation to resolve global 3D coordinates. We used a right-hand coordinate system with axes X+ forward, Y+ left and Z+ upward.

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 (θ) of tail flare using the dot product of these vectors. Negative values of θ 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 in 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). To measure bird-centered body rotations (yaw, pitch and roll, 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 contest arena, we watched all contest videos (n=103) to characterize flight trajectories and whether either individual exhibited visible tail flaring. For this purpose, we considered the minimum tail angle to qualify as flaring was approximately 30° and the flaring had to be sustained for at least 5 ms.

We also noted when a bird successfully displaced their competitor from the high perch (wins) and when a bird retreated (loses). We used time on high perch in dyadic interactions to inform a dominance hierarchy. We found that this hierarchy held across all contests, and therefore we assigned males a rank from 1 (most time on high perch) to 5 (least). 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. This was key, as hummingbirds have a small band of binocular vision (22-38°), a lateral view of monocular vision (145-162°, where “side approaches” are visible) and a dorsal blind spot (15-27° where “caudal approaches” are located and invisible to a bird) (Altshuler and Wylie, 2020; Tyrrell et al., 2018). From this we analyzed if signaling (tail flaring) effort varied across these approach angles.

Statistical analysis

We tested for significant differences in mean angle of tail flare during solo maneuvers (takeoff and landing) versus during agonism using a linear mixed-effect model with individuals as a random effect (*lmer* function in lme4 package) (R Core Team, 2023). We used a second linear mixed-effect model to test for significant differences in tail angles between losers and winners of a single interaction (win measured as obtaining high perch after interaction), also with individual as random effect. We assigned birds to a dominance hierarchy using cumulative time spent on the high perch (the desired resource). Individual and dominance rank were co-linear, thus we used the interaction of dominance rank with competition outcome (win/loss) in a linear model (*lm* function, R stats) to explore individual differences in tail angle when winning or losing. We used Chi-square tests of independence (*chisq.test* function, R stats) to test for a relationship between approach angle (frontal/lateral/caudal to the receiver) and (1) signaling (tail flaring absent/present) and (2) fight outcome (win/loss). We first generated contingency tables to confirm all frequencies were >5% and appropriate for this statistical test. We used Fisher's Exact Test (*fisher.test* function, R stats) to test for a relationship between dominance rank and approach angle. A Chi-square was not appropriate because some birds never used a caudal or side approach. We report mean ± SD.

Field observations

As part of a comparative study of hummingbird agonism in the field, we obtained videos for 3D kinematic analysis in a manner generally like our methods of videography in the laboratory, but we used only three video cameras (two Photron Nova S6 and one MiniAX-100) and the birds were free ranging. Our field sites were at the Southwestern Research Station (Cochise County, AZ, "SWRS") and Santa Rita Lodge (Madera Canyon, AZ, "Madera"). We recorded video contests (n = 185) of adult and immature males and females of seven species of hummingbird fighting in the vicinity of artificial feeders: calliope, black-chinned (*Archilocus alexandri*), rufous (*Selasphorus rufus*), broad-billed (*Cynanthus latirostris*), Anna's (*Calypte anna*), Rivoli's (*Eugenes fulgens*) and blue-throated mountain-gem (*Lampornis clemenciae*). Viewing the videos, we noted each species involved in the intra or interspecific interaction as well as absence/presence of tail flaring using the same criteria of angle and durations as stated above. Because active fighting attracted our attention when triggering video recordings, it is likely our samples were biased towards more dramatic agonism, but in both lab and field trials, we attempted to film any agonistic encounter, regardless of the presence of tail flaring.

Results

Tail angles (θ) were smaller (the tail was less flared) during solitary take-offs and landings when compared to those during agonistic contests (Fig. 2). Tail angles were slightly less during take-off (-11.1 ± 6.9 °) compared with landing (-13.8 ±0.78°), but the difference was not statistically significant (Chi-square, t = -3.4). The increase in tail flaring during agonistic encounters (Δ36.5±0.67 °) was statistically significant (Chi-square, t=54.5) (Fig. 2). There was a large amount of variation among individuals (model residual = 234.8).

The competing males appeared to exhibit "call and response" of tail flaring. For example, Figure 3 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).

Overall, the magnitude of tail flaring was related to the outcome of the contests. Winners exhibited tail angles 17.2±0.9° greater than those of losers (Chi-square, t=18.7). The individual residual of this result was large (760.7). Differences in intensity of tail flaring were most strongly impacted by dominance rank (Fig. 4). All birds, regardless of rank, frequently exhibited small tail angles with primary modes of their frequency distributions < 10°, but the more dominant birds exhibited secondary modes > 50° and the secondary mode for the most dominant bird was greatest of all and centered at 100°.

There was a significant interaction between contest outcome (win or loss) and dominance ranking (1-5) (linear model, p <0.001). This interaction was most pronounced in losses. High-ranking birds exhibited similar tail flare angles between winning and losing, however low-ranking birds exhibited dramatically smaller tail flare angles when they lost compared to when they won (Fig. 5).

Tail flaring increased the projected ventral area of the birds. As measured from our photos for morphometrics, the frontal projected area the combined body relaxed tail (wings not included) was 719.6±48.4 mm^2. With the tail flared at 110°, this combined area increased to 994.0±54.1 mm^2, an increase of 38.6±10.6%. This difference in projected area was statistically significant (Fig. 6A,B; Chi-square, t= 9.7).

The hummingbirds exhibited body movements with tail flaring in what we here describe as a “waggle” (Fig. 6C) (Hurly et al., 2001). This occurred in ~39% of encounters that involved tail flaring. The body movements included linear translations and rotations, particularly about the yaw axis. As an example, in Figure 6C, a bird engaged in tail flaring (average tail angle = 89.1 deg, average pitch angle of the body 80.3 deg) and translated 1.96 cm vertically and 2.81 cm horizontally. During this interval, it rotated through an approximately symmetrical yaw of 93.1 deg. 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 the unflared and flared tails were 1.32 cm^2 and 1.516 cm^2, respectively (Fig. 6A,B).

Approaches from the caudal or lateral side of a competitor were infrequent but were accompanied by less tail flaring. Our qualitative analysis of signaling and approach angles during fights yielded 199 instances of distinct behaviors among the five calliope hummingbirds. Most approaches were from the front (67%), 19% were lateral and 14% were caudal. There was a statistically significant relationship between approach angle and use of signaling only when the birds used a caudal approach (Chi-square, p = 0.02), not when approaching from the lateral side (p= 0.33) or front (p = 0.85). Similarly, there was a significant effect of approach angle on fight outcome wherein birds that used a caudal approach tended to win (Chi-square, p=0.02). There were significant differences in within-individual variance for approach (Fisher exact test, p = <0.001), meaning a given bird tended to favor a general approach strategy.

During field study in Arizona, seven species of hummingbirds (males and females, adults and immatures) frequently exhibited agonistic interspecific and intraspecific interactions (Table 1). 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.

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%

Discussion

Our results were consistent with our hypothesis that tail flaring is an agonistic signal among hummingbirds. Previous researchers suggested that tail flaring is part of agonistic displays in several hummingbird species. Hunter and Picman (2005) described an “agonistic position with a flared tail and bill pointed towards the intruder”. Our results quantify the magnitude, duration and frequency of this signaling and place it within the context of dominance. Not only was tail flaring greater during competitive trials in the lab compared with solitary takeoff and landing maneuvers (Fig. 1), but the magnitude of flaring was significantly greater in dominant males and winners. The maximum angles of tail flaring appeared similar to those during rapid escape performance in calliope hummingbirds (Anwar et al., 2024) and four other species of hummingbirds (Haque et al., 2023). However, during agonism tail flaring lasted much longer (Fig. 3). In the field, extreme prevalence of tail flaring among seven species, including juveniles and females, suggests this signal is widely understood and reciprocated among individuals (Table 1, Fig. S2).

Hummingbird visual system and looming

Tail flaring and waggling can easily be perceived by other hummingbirds based on current understanding of the visual system of these birds if a competitor is in front of or lateral to a receiver. Hummingbirds are near-sighted (equivalent of ~20/100) (Altshuler and Wylie, 2020) with a region of binocular vision (~29°) by the bill tip, a blind spot at the back of the head (~22°), and monocular vision on the sides of the head (Tyrrell et al., 2018). This likely explains why the hummingbirds exhibited less tail flaring with caudal approaches.

Tail flaring and waggling are likely to intimidate a competitor. Flaring by itself likely increases a competitor's perception of body size (Fig. 6) and may explain call and response behavior even in perched birds (Fig. 3). Flaring and body motion contribute to looming, and looming is perceived as a threat that merits evasive response in a diverse array of taxa (Peek and Card, 2016). For a hummingbird, the ability to assess a looming threat varies with the direction of approach. Increased ganglion cell density as well as invagination in the central region of the retina (termed the fovea centralis) allows for spatial acuity in the lateral, monocular region of hummingbird sight (Tyrrell et al., 2018). Monocular vision provides a receiver with information on the rate of approach of a competitor with time-to-contact (TTC) estimated from fractional rate of change of the projection of the approacher upon on the retina (Peek and Card, 2016). The capacity to discriminate TTC is significantly enhanced by binocular vision (Gray and Regan, 2004). Humans exhibit a drop in accuracy of TTC estimation when horizontal motion is added to an approaching stimulus (Calabro et al., 2011). Collectively, these observations lead us to propose that tail flaring may reduce estimated TTC in a receiving bird and waggle movements may introduce uncertainty in this estimate (Fig. 6). This may augment the intimidation effect in frontal and side approaches.

Variation in flare angle with wingbeats

Calliope hummingbirds exhibited slight variation in tail angle (~15°) approximately in phase with their wingbeat cycle (faint lines in Fig. 3), which may indicate a minor aerodynamic function distinct from signaling. In other species of birds, it is hypothesized that tail flaring in phase with the wingbeat cycle functions in stabilization of body pitch during momentary hovering and slow flight (Su et al., 2012). In the warbling white-eye (*Zosterops japonicus*), a passerine species, the tail is flared in mid-downstroke and interacts with downwash in the wake generated by the wings to mitigate downward pitch of the body (Su et al., 2012). This species uses a more asymmetric flapping pattern than hummingbirds, i.e., a flexed-wing upstroke with minimal aerodynamic function (Crandell and Tobalske, 2015) and the tail is flexed during this half cycle. We interpret that the high-frequency modulation of tail angle in hummingbirds (Fig. 3) could provide a similar function, but the magnitude of the flaring in hummingbirds is minimal because they have an aerodynamically active upstroke and instantaneous weight support is distributed throughout their entire wingbeat cycle (Warrick et al., 2005). In addition, it is possible that the tails of hummingbirds could function as vibration absorbers and dampers to suppress the body oscillations induced by wing flapping. Black-chinned hummingbirds (*Archilocus alexandri*) were an exception to the general pattern of tail movement in hummingbirds as both sexes routinely exhibited exaggerated “pumping” of their tails during hovering and slow flight. This pumping included modulation of tail flaring and angle of the tail plane relative to the body plane. This pumping is diagnostic in identifying this species in the field (Sibley, 2014). Thus, to explore a potential evolutionary tradeoff between hovering and slow flight aerodynamics and tail signaling in hummingbirds, the relative aerodynamic versus signaling function of the tail in the black-chinned hummingbird merits further study.

Honest signaling

More broadly, to improve understanding of the evolution of agonism in hummingbirds, it will be vital to test whether tail signaling honestly conveys information on individual quality (Smith and Harper, 2003; Zahavi, 1975). We propose two scenarios: either 1) the metabolic cost of flaring the tail, not the cost of growing or carrying it, is a signal of individual quality, or 2) the tail serves as a general agonistic signal, and honesty is assessed using other traits. It is unlikely that tail feathers alone can signal quality. The energetic cost for developing tail feathers in minimal (Buttemer et al., 2020) and the tail only contributes marginally to body mass and aerodynamic drag (Clark and Dudley, 2009). Thus the tail seems energetically inexpensive when compared with other signals of male quality (e.g. horns, antlers, overall body size (Emlen, 2008)). Tail feathers are molted seasonally and are easily shed in response to predatory attack (Farner and King, 2013). Nonetheless, in other clades of birds besides hummingbirds, feather color has been associated with individual quality (Hagelin, 2002; Laubach et al., 2013).

The energetic costs associated with tail flaring provide multiple avenues through which honest communication of RHP may be conveyed. Overall muscle quality is important in contest, allowing for an individual to chase faster (Sholtis et al., 2015) or be more agile in fighting. Tail flaring during contests can last up to several seconds. Flaring of the tail is accomplished by contraction of the *bulbi retricium* muscle (Gatesy and Dial, 1996). Energetic cost for this muscle should be proportional to the duration of contraction and the number of motor units recruited (Taylor et al., 1980). If winning birds utilize greater angles of tail flaring for longer periods of time, this flaring could serve as an honest signal of overall muscle quality and higher RHP. Coupling waggle maneuvers with tail flaring (Fig. 6) may accentuate this RHP if the waggle requires more metabolic energy compared to steady hovering (Groom et al., 2018). If a flared tail adversely affects the aerodynamics of hovering through wake interactions (Su et al., 2012), alteration of angle of body pitch, or changes in wing trajectories, perhaps only individuals with the highest RHP have enough available power to sustain hovering *and* signaling.

Tail flaring may be correlated with other phenotypic traits that are honest signals of RHP (Stuart-Fox et al., 2006). Such multi-modal signaling helps ensure a signal of individual quality is clearly received, but any one signal may not be under current selective pressure to communicate RHP (Stuart-Fox et al., 2006). In courtship, males use multimodal signaling (flight maneuvers, sonation and plumage display) to signal quality to females (Hogan and Stoddard, 2018). Phenotypic traits to consider include marginal power availability which is understood to correlate with agility in hummingbirds (Altshuler et al., 2004; Dakin et al., 2018; Segre et al., 2015), individual aggression and overall body condition (Careau et al., 2008; Dolnik and Hoi, 2010), including bilateral symmetry (Møller, 1992).

Tail flaring across behavioral contexts

Tail flaring behavior in male-male fighting may be reinforced evolutionarily if it is homologous with courtship behaviors. At the inflection of the U- or J-dives of courtship behavior of many bee hummingbirds (Clark et al., 2018), the tail is briefly flared and select rectrices generate sonation due to aeroelastic flutter, often well-timed with a flaring of the gorget and deceleration in front of a female (Hogan and Stoddard, 2018). These dive displays in Anna's hummingbirds may also be directed towards conspecific males or birds of other species within a male's territory (Powers, 1987). Rufous hummingbird males at the end of a courtship dives may display a waggle similar to what we report for male-male fighting (Fig. 6, (Hurly et al., 2001)). In some aspects, waggle movements resemble "shuttle" courtship displays performed by male hummingbirds immediately in front of females (Simpson and McGraw, 2019; Stiles, 1982; Wilcox and Clark, 2025).

Hummingbirds exhibit tail flaring in behavioral contexts aside from male-male fighting and courtship display, including predator response, aggression within and among species, and between males and females. Flaring of the tail is used at the beginning and end of escape maneuvers instigated by a looming threat (Cheng et al., 2016; Haque et al., 2023). In such escapes, the predicted pressure distribution on the tail indicates it functions as a momentary aerodynamic brake (Haque et al., 2023), but it may also serve as a pursuit-deterrence signal towards predators (Hasson, 1991; Murphy, 2006). In the field, we observed hummingbirds of several species flaring their tails and waggling towards praying mantises, a known ambush predator of hummingbirds (Nyffeler et al., 2017). We also observed frequent intraspecific agonism between males and females, especially in blue-throated mountain-gems (*Lampornis clemenciae*) a species lacking dimorphic tail colors. Adult male hummingbirds of many species exhibit substantial modifications of the tail feathers (coloration and shape) relative to adult females and juveniles of both sexes (Clark, 2010). The lack of tail dimorphism in the blue-throated mountain-gems may cause males to mistake the identity of females. To improve understanding of the function of tail signaling, it would be worthwhile to study behavioral responses to experimental manipulation of tail coloration and shape. A robotic model of a hummingbird featuring a tail in which flaring could be actuated on command could be useful (Storms et al., 2022).

Females also need to defend access to resources, so it is not surprising that they also engaged in fights. Females are the sole providers of parental care, so they need to protect their access to food located near their nests. We frequently observed female black-chinned hummingbirds being particularly aggressive towards males and females when defending against access to artificial feeders. The use of tail flaring by females during these fights appeared to be as prevalent as in males. Females are often underrepresented in biological studies (Nunamaker and Turner, 2023; Will et al., 2017), and especially in measurement of animal contests (Stockley and Bro-Jørgensen, 2011; Stockley and Campbell, 2013). Based on our results, female-female fighting compels future study.

Conclusions

Tail flaring was frequently exhibited during fighting between male calliope hummingbirds and was related to dominance rank. Tail flaring was also exhibited by males and females of seven species in the field during fighting and to display toward a predatory threat. As winners flared their tail at greater angles compared to losers in male-male fights, we predict that tail flaring is an honest signal of Resource Holding Potential (RHP) in hummingbirds, but this prediction merits direct study. The frequent use of tail flaring is consistent with our hypothesis that the tail is under relaxed selection for aerodynamic function due to the wing-dominated flight style of hummingbirds. To understand the evolution of tail flaring as a signal, it will be useful to test whether tail flaring and waggle maneuvers in male-male fighting are homologous with seemingly similar behaviors in male courtship displays and female-female fighting.

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Ethics

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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.

Conflict of Interest:

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

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Figures

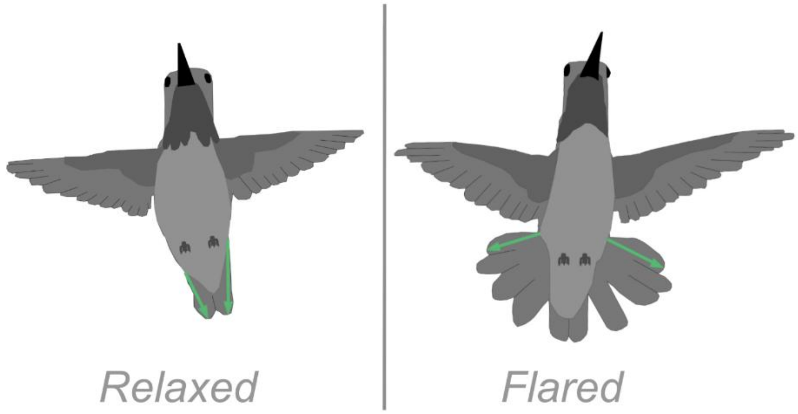

Figure 1. Two tail states in male calliope hummingbirds (*Selasphorus calliope*): relaxed and flared. Tail angle (θ) was the angle between left and right position vectors (green arrows) originating where the tail meets the body and going to the tip of each outer rectrix (R5). In these examples drawn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

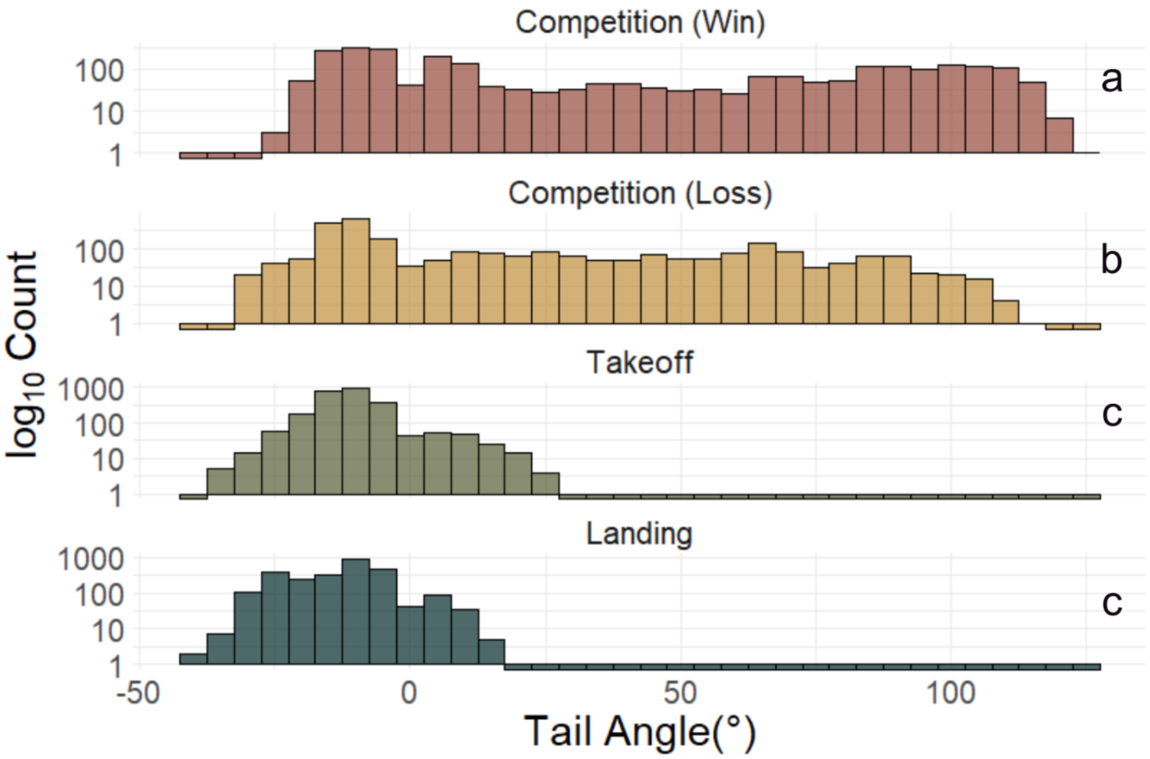

Figure 2. Frequency distributions of tail angles (θ) for male calliope hummingbirds (*Selasphorus calliope*), separated by behavioral events (landing, takeoff, winning or losing of a contest). For ease of visualization in this figure, data were log-transformed along the y-axes to reduce skew. Letters on the right side denote differences in means that that were statistically significant.

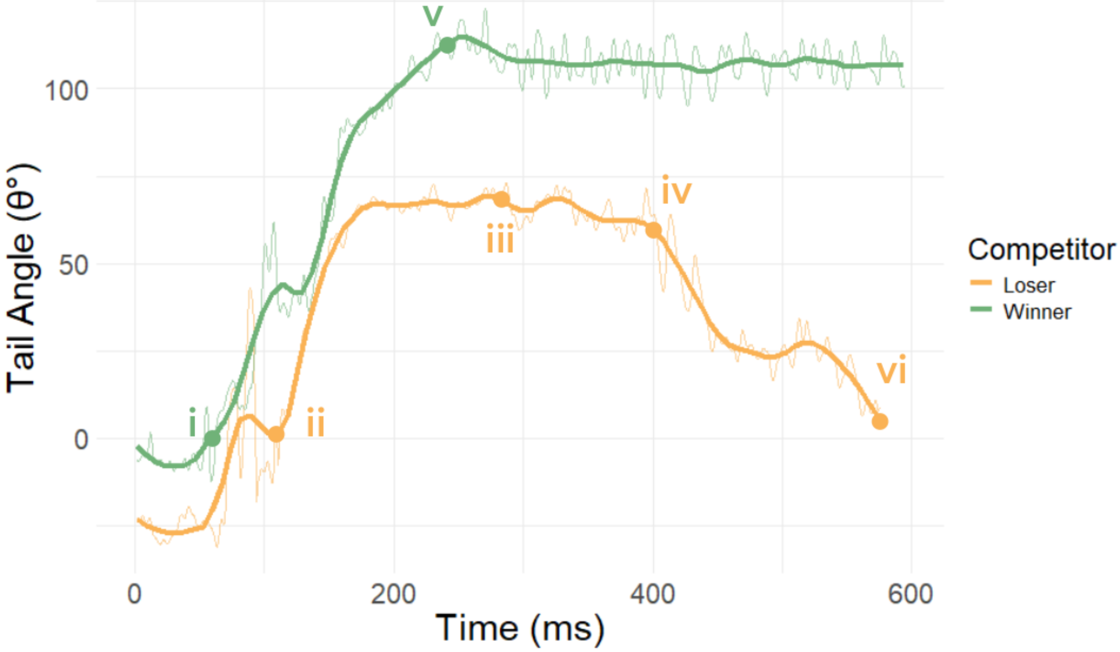

Figure 3. Time series revealing "call-and-response" of angles of tail flaring of two male calliope hummingbirds (*Selasphorus calliope*) fighting over a desired resource (high perch). The winning bird (green) initiates the displacement by flaring its tail starting at (i), and the occupant of the perch (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.

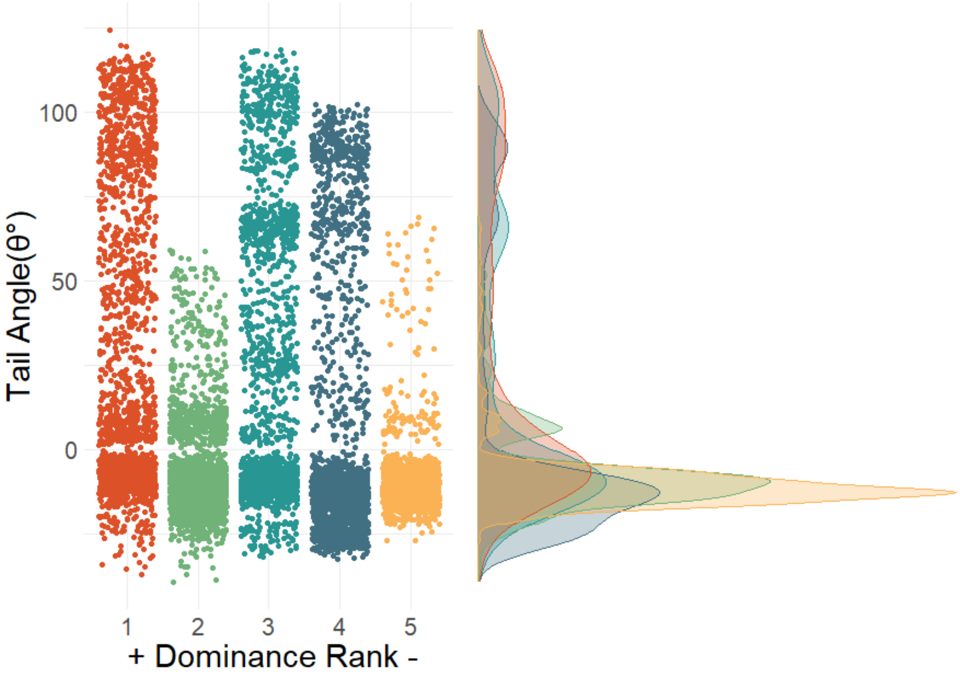

Figure 4. Dominance rank and distribution of tail angles (θ°) in male calliope hummingbirds (*Selasphorus calliope*). Jitter plot on the left reveals the distribution of tail angles during fights from most dominant (red, bird 1) to least dominant (yellow, bird 5). Frequency distributions for these data reveal that angles in all birds were skewed toward lesser values, and the most dominant bird (1, red) exhibited a distribution that was slightly enhanced toward greater tail angles.

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689 **Figure 5.** Statistically significant interaction between fight outcome (win or loss) and dominance 690 rank (1-5) upon tail angle (θ). Regressions for tail angle as a function of rank plotted separately for 691 win and loss outcomes.

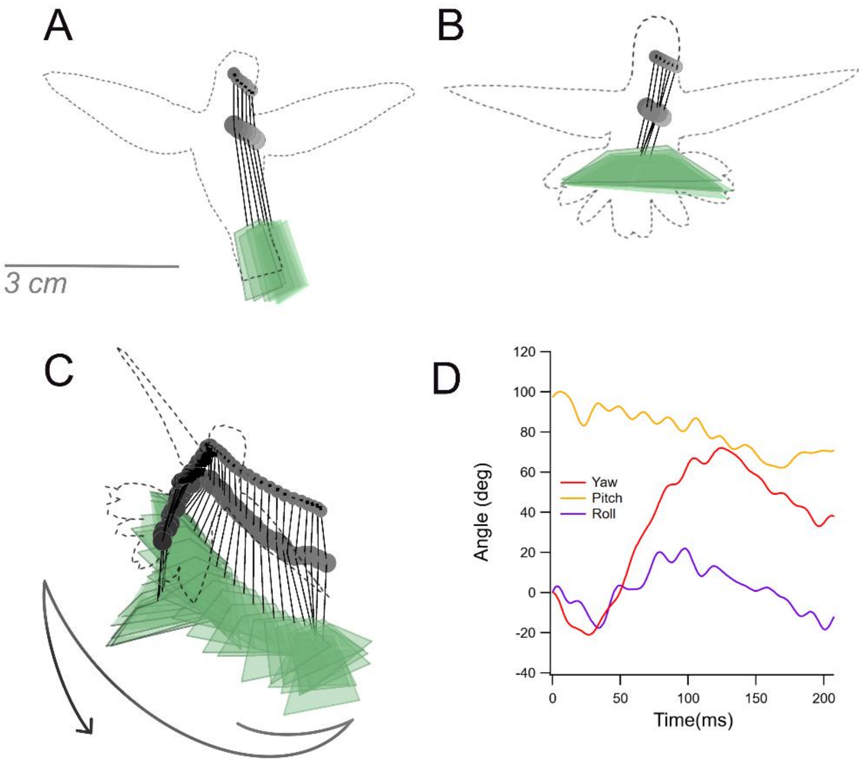

Figure 6. Projected area of the combined body and tail increased when birds flared their tails and was further augmented by body movement. Three phases of an interaction as performed by a male calliope hummingbird (*Selasphorus calliope*) in flight while intimidating a perched bird. A) tail not flared B) tail flared and C) during a "waggle" where tail flaring was paired with linear translations and body rotations. Positions sampled every 200 ms. D) plots of angles of yaw, pitch and roll during waggle in C (415 total frames). Dashed lines represent body outline at end of display. Solid black line = beak, green = plane of tail, filled circles = head and center of anterior spine, with shading intensity increasing with time during the display.