

Effects of tail length on an escape maneuver of the Red-billed Streamertail

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Abstract Sexually selected, elongated tails in birds may not exhibit significantly different kinematics from the impair or alter naturally selected functions related to flight controls, suggesting that the greatly elongated tail stream- The aim of this study was to test whether experimentalers have relatively small effects on the bird's ability to manipulation of tail length affected the kinematics of a maneuver at low speeds. Based on these observations, low-speed escape maneuver. The Red-billed Streamertail greatly elongated tails may not pose a large cost to low- (Trochilus polytmus) has the longest tail of any hum- speed maneuvering flight. mingbird and is highly sexually dimorphic in tail length. I

hypothesized that streamertails with either a long tail or Keywords High-speed video Maneuver with the tail removed would perform maneuvers with Red-billed Streamertail Rotation Tail reduced linear and angular accelerations, relative to Trochilus polytmus maneuvers performed with a short tail. Two high-speed video cameras recorded maneuvers from male and female Red-billed Streamertails under three tail length treatments Introduction short tail, long tail, and no tail. The detailed kinematics of

the maneuvers were highly variable. Whereas the bird's The elongated tails of numerous birds are a classic example always performed rolls (rotation about the bird's axis) of a sexually selected morphological trait (Andersson 1982, during the maneuver, there was variation in the relative 1992; Petrie et al. 1991; Pryke and Andersson 2002). Birds importance of pitching motions (rotation about the x-axis) also use their tails to produce aerodynamic forces in flight or yawing motions (rotation about the z-axis), with yawing (Gatesy and Dial 1993; Maybury and Rayner 2001; rotations playing a small role in pitch-roll turns, and Maybury et al. 2001; Tobalske 2007; Usherwood et al. pitching motions playing a small role in yaw/roll turns 2005). Therefore, sexually selected modifications of tail Birds missing their entire tail exhibited reduced maximum morphology may impair or alter naturally selected func- linear accelerations associated with a curving trajectory tions related to flight.

By contrast, birds maneuvering with an elongated tail did Take, for example, high-speed forward flight, during which tail morphology has multiple influences on the drag generated by a bird's body. By studying a physical model of a Starling (*Sternus vulgaris*) in a wind tunnel, Maybury and Rayner (2001) showed that a short tail streamlines the body, reducing drag. Similarly, Clark and Dudley (2009) showed that attaching the elongated tail-streamers from the Red-billed Streamertail (*Trochilus polytmus*) to the Anna's Hummingbird (*Calypte anna*) resulted in an increase in the metabolic costs of flight and a decrease in the top speed the birds could fly, apparently caused by increased drag. These experiments show that an elongated tail can impair high-

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speed, linear flight. In the rapid flight studied in these when startled. Moreover, escape maneuvers potentially hummingbird experiments, the birds held the tail shut and approach the maximal flight performance that an individual did not appear to use it to actively modulate aerodynamics capable of attaining, whereas maneuvers performed force production. without a startle stimulus may vary greatly according to the

A flight context in which the tail appears to be used to behavioral motivation of the individual. actively modulate force production is maneuvering flight. There are a large number of kinematic variables that are (Hedrick and Biewene 2007; Warrick and Dial 1998). By potentially important to maneuvering flight. During a spreading the tail widely to expose a relatively large surface area, the whole animal can translate the movement in face area, birds generate aerodynamic forces (modeled in three dimensions X, Y, and Z), as well as rotate about the Maybury et al. 2001; Thomas 1993). Additionally, the X (roll), Y (pitch), and Z (yaw) axes (Dudley 2002; Hedrick mass of the rectrices causes the tail to have inertia. Together and Biewene 2007; Warrick et al. 2002). A bird's ability to ther, aerodynamic forces and inertia will impart forces and modulate these kinematic variables will be strongly influenced by its initial flight speed. Therefore, I elected to elicit Modified tail morphology may affect how birds maneuver startles from hovering birds (velocity $> 0 \text{ m s}^{-1}$). I by altering the forces that the tail produces. I hypothesized that, in slow maneuvers, the tail generates

It is unknown how forces generated by the tail may forces that help the bird to rotate and produce a curved trajectory. Because at low speeds, an elongated tail may makes it difficult to use models of force production to increase inertia and possibly drag, I hypothesized that an predict how a maneuver would change with varying tail elongated tail would result in lowered linear accelerations morphologies. An alternative approach to study how tail and angular speeds attained over the course of the maneuver. morphology influences flight is experimental manipulation. Moreover, because the forces produced by a short tail of the tail of live birds, coupled with a measure of potentially assist the bird in maneuvering, I hypothesized behavioral aspects of flight performance (Balmford et al. that removal of the entire tail would reduce the angular speed 2000; Clark and Dudley 2009; Evans et al. 1994; Rowe and linear accelerations attained during the maneuver. et al. 2001). One commonly used assay is a maze of strings:

a released bird flies through the maze, and the number of strings hit and the time required to fly through the maze are measured (Balmford et al. 2000; Evans et al. 1994; Matyjasik et al. 2004). Alternately, Matyjasik et al. 1999; Experiment 2000) measured differences in foraging success of Sand

Martins (*Riparia riparia*) as a function of different tail morphologies, and Evans and colleagues (Buchanan and Evans 2000; Rowe et al. 2001) filmed the curving flight of approximately 1,000 m a.s.l.), in June–August of 2004 and swallows approaching their nests. While these behavioral methods can at times link variation in tail morphology to performance with obvious fitness consequences, such as the ability to catch prey (Matyjasik et al. 1999, 2000), they do not address the functional connection between tail morphology and performance. feathers over the course of the experiment). After habituation

An intermediate between models (physical and mathematical) and behavioral analyses is the detailed analysis of flight arena measuring $2.25 \times 1.5 \text{ m}$ (length \times height one particular flight context in which the tail is thought to generate important forces. The aim of this study was to examine the detailed kinematics of an escape maneuver as a function of tail length. The Red-billed Streamtail of the birds spent most of their time perched at this end of the Jamaica was selected as the study species because female of this species have tails of a normal length whereas males have a pair of greatly elongated tail-streamers that are the longest tail feathers of any hummingbird (Clark 2010), and study of the mechanics of flight. An escape maneuver was selected because in other slow maneuvers, hummingbirds do not spread their tail, whereas they do spread it widely maneuver was filmed to 0.5 m in width (Fig.

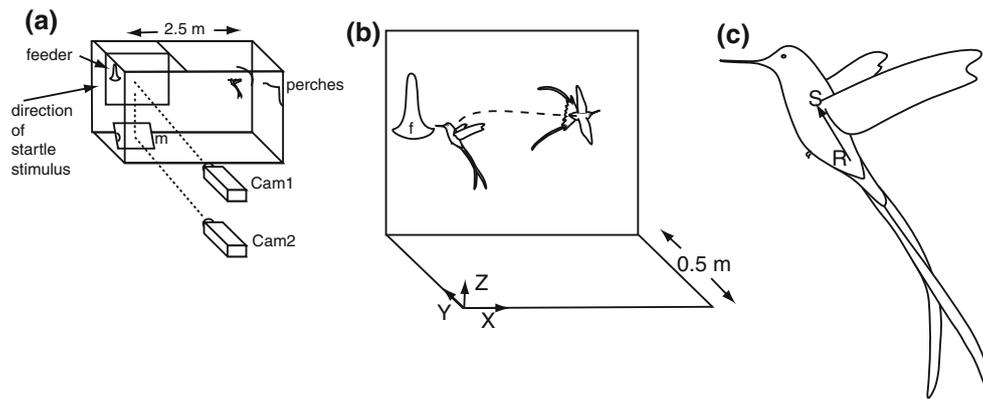


Fig. 1 The experimental setup for eliciting maneuvers from Red-accelerated towards it, causing it to perform an escape maneuver in billed Streamertail (*Trochilus polytmus*) a Flight arena (2.5 × 2.5 × 1.5 m, length × height × width). Perches were placed next to a coordinate system was arrayed such that the plane was horizontal, natural light source at one end of the arena, and a feeder was placed in the Z-axis vertical, and the X-axis was parallel to the direction of the a 0.5-m-wide alcove at the other end of the arena. Two 500-W halogen lights (not shown) illuminated the feeder, and the space by digitized on the birds over the course of the maneuver. The body the feeder was filmed with two high-speed cameras. One camera (Cam 1) obtained a side view, whereas the other camera (Cam 2) obtained a view from below through the use of a mirror. (b) As a bird hovered at the feeder, a startle stimulus was suddenly

The purpose of this experiment was to elicit behaviors. After a few preliminary startles, the birds tended to from a hovering bird that were near to \hat{O} maximal \hat{O} turning approach the feeder with increased wariness. Over the and linear accelerational performance. To elicit a turn of course of the experiment, the birds were observed to ensure nominally 180, the birds were startled as they hovered at that they did not discontinue visiting the feeder altogether or close to the feeder. Due to the shape of the arena, to which risked depriving the bird of food), damage their escape, the birds had to turn around in order to linearly wing-feathers, or show signs of being unduly stressed (e.g., accelerate away from the feeder (Fig).

Multiple stimuli to elicit the maneuver were tested; the arena, rather than using the provided perches). In the rare birds exhibited the strongest response to large objects as in which any of these events occurred, the experimenter that suddenly, rapidly accelerated directly towards themment was terminated prematurely.

Use of a mechanical scare in which the experimenter was out-of-sight did not work well because the birds tended to flee in a random direction. The startle stimulus that

resulted in the most consistent and repeatable flight trajectories (both within and between birds) entailed the utilized (Fig. 2). Males and females were put through experimenter standing as still as possible, in plain sight complementarily manipulations. The first treatment was no approximately 0.8 m behind the feeder, outside of the manipulation: males retained their long tail, and females, a flight arena. This meant that as a bird approached the short tail. The second manipulation was the reverse of their feeder, it could see a human standing near the feeder respectively natural tail-lengths: in males, the streamers were through the mesh wall of the arena. After a bird replaced with the fourth rectrices from a female, and approached and hovered at the feeder, a bright red cloth the males were given a pair of the elongated fourth rectrices (a handkerchief) was abruptly accelerated directly from a male. In the third manipulation, which was a second towards the bird. Effort was made to accelerate the cloth control, the feathers from the second treatment were in as repeatable a fashion as possible, such that in all removed, and the individual \hat{O} s original tail-feathers were re-startles the cloth followed a similar trajectory. The cloth attached, resulting in long-tailed males and short-tailed was not in danger of actually hitting the bird, for its females. Finally, in the fourth treatment, all ten rectrices rapid motion was arrested by the mesh side of the flight chamber (but not the tail-coverts) were plucked.

chamber. Because the birds tended to approach the feeder To splice the feathers into the tail, a bird was restrained warily, it appeared that the visible presence of the human and the distal portions of the birds \hat{O} fourth rectrices were standing behind the feeder caused the birds establish a predetermined direction in which to escape. (diameter 0.10 or 0.15 mm, length 6 mm) was dipped in

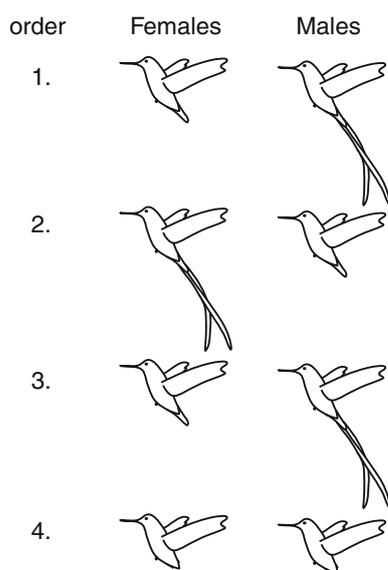


Fig. 2 Experimental manipulations used in this study. The elongated tail-feathers of male streamertails are the fourth rectrices, which is the second-to-outermost tail feather. No manipulation, 2 tail morphology was manipulated, in which the fourth rectrices of males were spliced onto females, and *visa versa*, an individual's original rectrices were spliced back on as a second control. In all of the rectrices were removed, rendering an individual with no tail

glue (cyanoacrylate) and inserted approximately 3 mm into the hollow shaft of the feather to be attached, such that the remaining 3 mm of the pin remained exposed. This free tail-coverts insert into the body (Fig. c). Each point was digitized twice and averaged to reduce digitization error. External markers were not placed on the birds because both the birds' rotations and the wings inevitably occluded the external markers for a significant period in all of the videos. The object space for the trials was calibrated by digitizing the corners of a cube measuring 0.186 × 0.136 × 0.136 m, which filled approximately 30–50% of the image of each camera. Using a Direct Linear Transformation in the program Peak Motus ver. 8.4, three-dimensional (3D) object-space was established for each trial. The coordinate system was arrayed so that the XY plane was horizontal and the Z-axis was vertical; the X-axis was oriented parallel to and away from the feeder and startle stimulus (Fig. 1b). Linear velocities and accelerations of the shoulder point (which was close to the center of mass) were calculated. The shoulder and rump points were digitized from the silhouette, and it was impossible to digitize a third point on the bird's body. Because only the bird's body axis (as the bird flew backwards (rather than turning) or those indicated by the vector between the rump and shoulder points; Fig. 1c) was available, it was possible to calculate Euler angles corresponding to the body's pitch and yaw (Haslwanter 1995), but not roll. Because roll was unavailable, it was not possible to measure the angular velocity of the bird's angular speed was calculated at each instant in

On occasion, hummingbirds simultaneously lose their entire tail (i.e., all 10 rectrices) during molt (Stiles 1995) or when attacked by predators (Spofford 1976). Therefore, the manipulation of plucking all the tail-feathers falls within the natural range of variation of tail morphology naturally experienced by wild hummingbirds. Multiple subjects from these experiments were recaptured or observed in the wild to be behaving normally up to 3 weeks after release.

High-speed video analyses

The maneuvers were illuminated by two 500-W halogen lights (V-light; Lowel, Hauppauge, NY) and recorded by two synchronized high-speed cameras (Redlake Motion-Meter, 292 × 210 pixel resolution; Eastman Kodak, Rochester, NY) at 500 frames/s. One camera filmed a side view of the maneuver; the second camera obtained images from below, at 90° to the first camera, through use of a mirror directly below the feeder (Fig. 1a).

The synchronized videos were digitized in the program Peak Motus ver. 8.4 (Vicon Motion Systems, Centennial, CO). Two points were digitized on bird silhouettes in the videos: (1) the shoulder (S), which was a point internal to the bird's surface, between the wing bases, on the animal's midline, and close to the center of mass (Fig. 1); (2) the

rump (R), which was a point on the bird's dorsal surface, on this midline, and at the base of the tail, where the rectrices and remaining 3 mm of the pin remained exposed. This free tail-coverts insert into the body (Fig. c). Each point was digitized twice and averaged to reduce digitization error. External markers were not placed on the birds because both the birds' rotations and the wings inevitably occluded the external markers for a significant period in all of the videos.

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Linear velocities and accelerations of the shoulder point (which was close to the center of mass) were calculated. The shoulder and rump points were digitized from the silhouette, and it was impossible to digitize a third point on the bird's body. Because only the bird's body axis (as the bird flew backwards (rather than turning) or those indicated by the vector between the rump and shoulder points; Fig. 1c) was available, it was possible to calculate Euler angles corresponding to the body's pitch and yaw (Haslwanter 1995), but not roll. Because roll was unavailable, it was not possible to measure the angular velocity of the bird's angular speed was calculated at each instant in

time by measuring the angular displacement of the bird's body angle relative to the instant (0.002 s) preceding it. A scalar index of angular acceleration was computed from the derivative of the angular speed. As these scalars exclude rotational contributions from the roll, these computed values will at times underestimate the magnitude of the bird's true angular velocity and acceleration.

The linear and angular positions, velocities, and accelerations were calculated using a quintic spline in Peak Motus ver. 8.4. The parameter representing the error variance (Walker 1998; Woltring 1985) used to smooth the spline will affect the estimated accelerations, especially the angular accelerations. As the purpose of this study was to compare different experimental manipulations to each other, I used the same error variance for all trials across all birds. Peak Motus's default method tended to underestimate the error variance, as determined by digitizing an object known to be accelerating under the force of gravity. Consequently, I selected an appropriate error variance by varying this parameter over three orders of magnitude and examining the fit between the spline and the raw data, for three randomly selected trials. The value 0.0008 was selected because it resulted in the best average velocity data. Use of a different smoothing parameter would change the magnitude of the linear and angular accelerations that are presented here, but as it would affect all trials similarly, it appeared unlikely that a different smoothing parameter would affect the statistical results presented.

Kinematic variables

It was not possible to determine precisely when the bird began to react to the startle stimulus; therefore, the start of each maneuver (time = 0) was operationally defined as the instant in which the bird's linear velocity exceeded 0.20 m s⁻¹. Seven additional variables were obtained from the trials: (1) the time (after the start of the maneuver) that it took the bird to travel 20 cm (resultant distance); (2) the magnitude of the bird's maximal resultant linear acceleration (a scalar); (3) the time (after the start of the maneuver) of the maximal linear acceleration; (4) the time at which the bird spread its tail (excluded in the no-tail treatment); (5) the time (after the start of the maneuver) that it took the bird to rotate through 120° in yaw; (6) the timing and (7) magnitude of the bird's maximal angular speed. Velocities and accelerations were not recorded from the final ten samples from a trace in order to avoid 'edge' effects of the spline.

Angular speed was log-transformed to achieve a normal distribution, and four variables (time to travel 20 cm, maximum linear acceleration, time taken to yaw 120°, and log maximum angular speed) were placed into a principal components analysis (PCA), without respect to bird identity or experimental manipulation. Based on the PCA, PC1

Table 1 Factor loadings from a PCA of maneuvers, and the percentage of variation attributable to the first two principal components

Factors/variation	PC1	PC2
Variables in PCA		
Time to travel 20 cm	0.697	-0.141
Maximum linear acceleration	0.064	0.731
Time to yaw 120°	0.714	0.097
Log (max. angular speed)	-0.027	0.660
Percentage of variation	35.5	29.6

PCA principal component analysis

loaded strongly on the time to travel 20 cm and the time to yaw 120°, and weakly on the other two variables (Table 1). PC2 loaded heavily on the bird's ability to accelerate (i.e., angular speed and linear acceleration). The purpose of this experiment was to measure the bird's 'maximal' performance, whereas multiple maneuvers had been obtained for each experimental treatment. Because PC2 was an overall index of the bird's ability to accelerate, the trial with the highest PC2 score for each bird-treatment combination was kept for statistical analysis, and the remaining trials were dropped from the analysis.

Each of the kinematic variables was individually analyzed using repeated measures analysis of variance (ANOVA), with experimental treatment as a factor, bird as the repeated measure, and sex as a cofactor. Because males and females underwent a different time-series of experimental treatments (Fig. 2), two analyses were run. First, the four trials per bird were analyzed with respect to their

temporal order, and without respect to the tail length. This was to test for time-dependent effects, such as effects caused by learning. Second, for each bird, the slower trial of treatments 1 and 3 was discarded (based on PC2), and the data were analyzed across the three tail-length treatments in a repeated measures ANOVA, with sex as a cofactor and a sex-treatment interaction term. The interaction term was included expressly to test whether there was a difference between males and females in their response to the experimental treatments. This could hypothetically occur, for example, if there were behavioral responses to tail manipulations of abnormal length, such as if females had lowered performance with a long tail, whereas males had lowered performance with a short tail.

Results

Description of the maneuver

Seven male and ten female Red-billed Streamertails were subjected to the experiments, although one male and two

females did not complete all four treatments. Overall, the maneuvers had several features in common. The birds initially hovered stationary while facing the feeder (yaw = 0), with a pitch angle of roughly 50° and usually held the tail completely shut. Upon being startled, they immediately spread their tails widely in 100% of the trials (n = 52; no-tail trials excluded), while simultaneously initiating a rapid body rotation with bilaterally asymmetric wingbeat kinematics. The time at which their velocity reached 0.20 m s⁻¹ was highly correlated with the time at which they spread their tail, with the birds spreading their tails on average 13.7 ± 0.17 ms before their velocity (Fig. 4), which appear to be similar to the banked turns analyzed in previous studies of flying birds (Hedrick and Biewener 2007; Hedrick et al. 2009; Warrick et al. 1998).

At the other end of the continuum were yaw/roll turns, in which the birds rolled and yawed to one side (tracings 2D9 of Fig. 3). In contrast to pitch-roll turns, it may be possible for the pitch angle to vary little through the course of yaw/roll turns (compare Figs 3d, e), although towards the end of the turn, the pitch angle typically declined as the bird accelerated horizontally. To perform this type of maneuver, the birds simultaneously rolled and yawed to one side (tracings 2D9 of Fig. 3).

Once the maneuver was initiated, the bulk of the rotation resulting in smooth variation in the yaw angle through the course of the maneuver (Fig. 4). In contrast to pitch-roll turns, it may be possible for the pitch angle to vary little through the course of yaw/roll turns (compare Figs 3d, e), although towards the end of the turn, the pitch angle typically declined as the bird accelerated horizontally. To perform this type of maneuver, the birds simultaneously rolled and yawed to one side (tracings 2D9 of Fig. 3).

Outside of these common features, the birds exhibited considerable variation in the exact kinematics used to perform the turn. A main aspect of this variation appeared to be individual changes in pitch and yaw could vary greatly, with the bird nevertheless attaining high linear and angular velocities and accelerations in the course of executing a 180° turn. I name the two extremes of this continuum as pitch-roll turns (the hyphen indicates the rotations are approximately sequential), and yaw/roll turns (in which the slash indicates the rotations about these axes are simultaneous). Two trials typifying the two extremes of the continuum are presented in Figs. 3 and 4 and explained below.

Pitch-roll turns

In pitch-roll turns, linear accelerations rose while the bird initiated the pitching motion (Fig. 3d) and then peaked during the rolling motion, when the bird was oriented away from the startle stimulus. Notably, acceleration in the Y remained low throughout the maneuver. For example, in Fig. 3c, the trace depicting resultant speed almost completely occludes the line depicting velocity. In yaw/roll turns, linear accelerations were initially low while the bird initiated the start of the rotation (Fig. 4). Y-acceleration initially rose faster than X-acceleration as the bird began translating in the X and Y axes (trials with significant motion in Z were not included in the analyses). The operationally defined start of the maneuver (speed 0.20 m s⁻¹) is indicated with a gray line in Figs. 3d, e and 4d, e.

Pitch-roll turns

At one end of the continuum, the birds occasionally performed a pitch-roll turn (Fig. 3). A bird initiated the maneuver by first rotating purely in pitch, nose-up (tracings 1D4 in Fig. 3c), until the shoulder point passed over the rump point (frame 3 in Fig. 3), so that the yaw orientation remained low throughout the maneuver. For example, in Fig. 3c, the trace depicting resultant speed almost completely occludes the line depicting velocity. In yaw/roll turns, linear accelerations were initially low while the bird initiated the start of the rotation (Fig. 4). Y-acceleration initially rose faster than X-acceleration as the bird began translating in the X and Y axes (trials with significant motion in Z were not included in the analyses). The operationally defined start of the maneuver (speed 0.20 m s⁻¹) is indicated with a gray line in Figs. 3d, e and 4d, e.

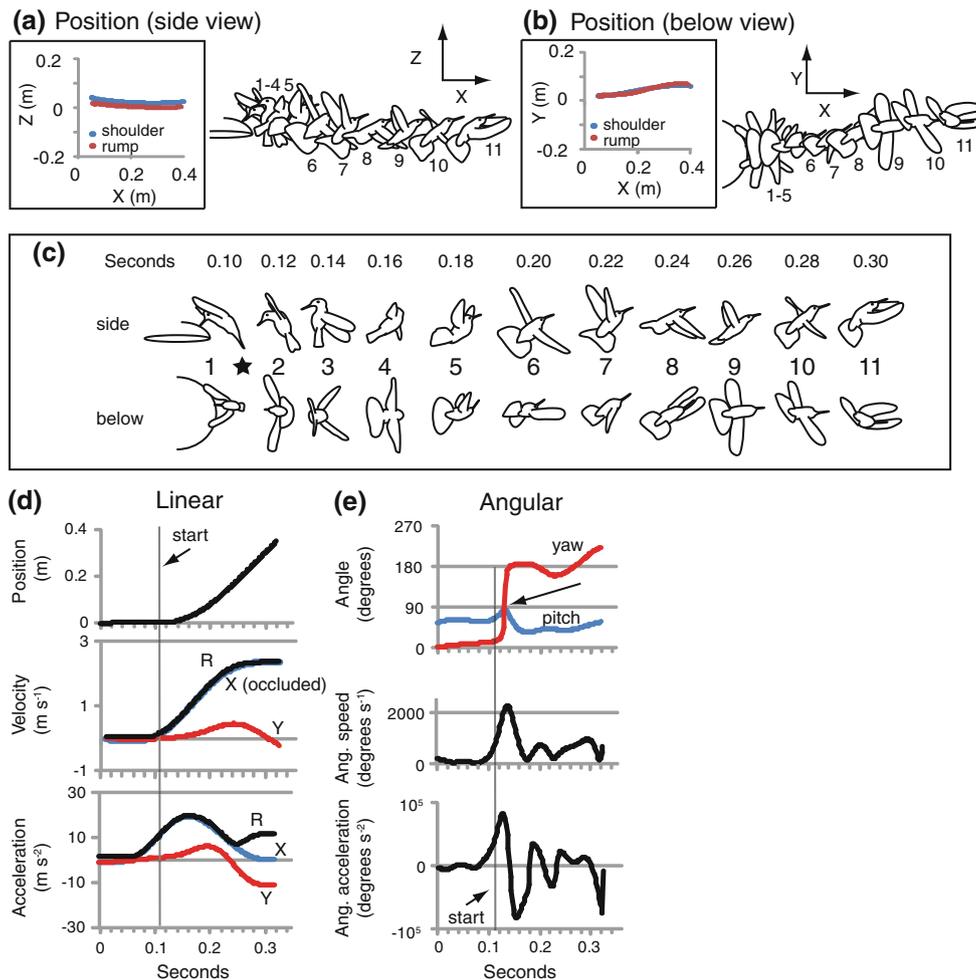


Fig. 3 A typical pitch-roll maneuver, performed by an unmanipulated female Red-billed Streamertail (which lacks elongated R4). Graph indicates the X and Z position of the shoulder and rump points. A series of 11 tracings (each 0.02 s apart) from a high-speed video are superimposed to reflect the actual position of the bird over time. **a** Side perspective of the maneuvering hummingbird. **b** Perspective from below of the maneuvering hummingbird. **c** The same tracings as in **a** and **b** arrayed so that the body posture of the bird is visible. The start of the maneuver (occurs between tracings 1 and 2) is indicated by a gray line. During the maneuver, the bird pitches nose-up (tracings 2 and 3) followed by a roll (tracings 4–6). As a result, the bird executes a 180° rotation in orientation with little translation in the Y axis. **d** Linear kinematics of the shoulder point during the pitch-roll maneuver, with motion in X, Y, and the resultant R. Z components of motion (not shown) were small. The resultant velocity exceeded 0.2 m s^{-1} at time = 0.11 s (gray line), which was operationally defined as the start of the maneuver. The resultant velocity is almost entirely occluded by the resultant velocity. **e** Angular kinematics of the pitch-roll maneuver. Pitch and yaw have been calculated from the Euler angles of the body vector (see Fig. 4). Angular velocities and accelerations (i.e., vectors) could not be calculated because roll data were unavailable. The start of the maneuver is indicated by a gray line. Arrow indicates the instant in which pitch $\approx 90^\circ$, and yaw jumps from 0 to 180°. This occurs because the Euler convention has been used to define the body angles (Haslwanter 1995) and not because the bird has initiated a rotation in yaw (i.e., it has not begun to rotate about its yaw axis).

angle passed through 90° (Fig. 4e), the X-acceleration rose. The bird continued to rotate, and X-acceleration continued to rise as the yaw angle passed 90° and approached 180° . As yaw approached 180° , the bird was both translating in +X and +Y. To avoid colliding with the wall of the arena, the bird began to negatively accelerate in Y, while positive X acceleration remained high. As a result, the maximum resultant linear acceleration in this type of maneuver perfectly to linear X acceleration (Fig. 3d), meaning that

tended to correspond to high positive Y acceleration and high Y deceleration (Fig. 4d). Re-stated, the maximal acceleration was often associated with a curved portion of the bird's trajectory, in which the bird's acceleration corresponded to both to increases in speed and also changes in direction. This is in direct contrast to pitch-roll turns, in which resultant linear accelerations corresponded almost perfectly to linear X acceleration (Fig. 3d), meaning that

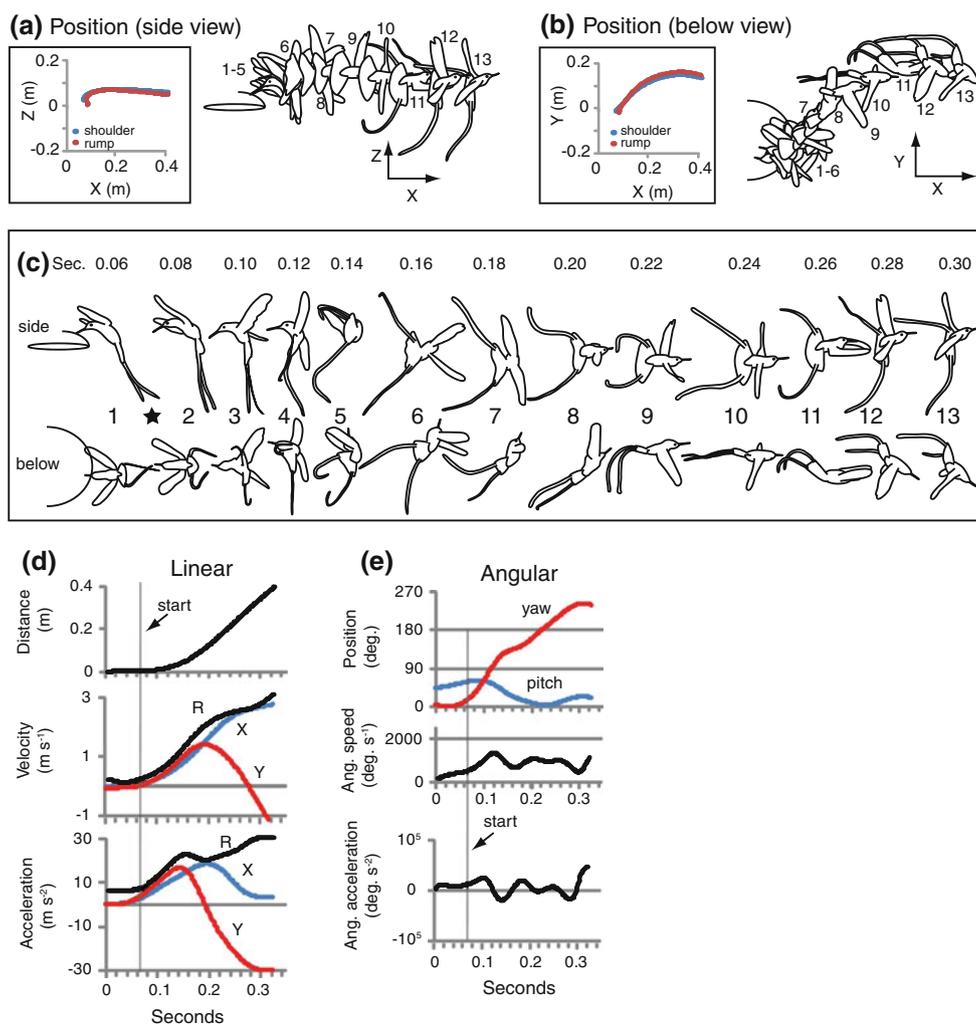


Fig. 4 A yaw/roll maneuver, performed by an unmanipulated male Red-billed Streamertail (with elongated 4th rectrices intact) during the maneuver. The bird simultaneously yaws and rolls, which is especially evident in tracings 3–7 d. Linear kinematics of the shoulder point during the yaw/roll maneuver, including X, Y, and resultant R. Z components of motion (not shown) were small. The resultant velocity exceeded 0.2 m s⁻¹ at the start of the maneuver (0.068 s, gray line), which was operationally defined as the start of the maneuver. Angular kinematics of the yaw/roll maneuver. Pitch and yaw have been calculated from the Euler angles of the body vector, where the body vector is the line between the shoulder and rump points (Fig. 1c). Angular speed and acceleration are both scalar values calculated from the scalar, angular change in body orientation in pitch and yaw. Angular velocities and accelerations (i.e., vectors) could not be calculated because roll data were unavailable. The start of the maneuver is indicated

the maximum acceleration corresponded primarily to changes in speed.

Notable differences between pitch-roll and yaw/roll turns

In addition to the differences in maximal linear acceleration just described, there were additional differences between the maneuvers depicted in Figs 3 and 4. In the

pitch-roll turn (Fig. 3), there are two somewhat distinct rotations: first a pitching motion, followed by a roll. In the yaw/roll turns, rolling and yawing movements appear to be synchronized, such that they are difficult to distinguish. In pitch-roll turns, it is possible for the bird to exhibit a little translation in either the Y or Z dimensions (Fig. 3a, b) while turning completely around. By contrast, yaw/roll turns are characterized by distinct translation in X (Fig. 4a, b). Because the birds

had a choice in how to perform the maneuver, these differences resulted in substantial variation between individual maneuvers.

Results of tail-length manipulations

The PCA of the maneuvers is presented in Table 1. In the PCA, PC1 loaded highly on both the time taken to travel 20 cm and the time taken to yaw 120° and little on maximum linear acceleration or log of maximum angular velocity. PC2 loaded highly on both maximum linear acceleration and log of maximum angular velocity. PC1 therefore was an

index of how quickly the bird performed the maneuver, whereas PC2 represented a measure of the modulation of linear and angular accelerations during the maneuver.

Because the ability of a bird to muster linear accelerations (including the production of a curved trajectory) may be

important components of a maneuver that could be affected by tail morphology, PC2 was used to select which represented a bird's "maximal" performance.

Repeated measures ANOVAs of the maneuver variables with respect to the chronological order of the trials indicated that maximal linear acceleration exhibited significant variation between the chronological treatments ($F_{3,44} = 7.98, P = 0.0002$). The individual treatment effects indicated that, of the four chronological treatments, the fourth treatment (which was also always the no-tail treatment) was significantly lower than the first, second, and third treatments ($t = -3.35, P = 0.002$), whereas the other three treatments were not significantly different (all $t < 1.56, P > 0.12$). Because there were no differences between the first three treatments, the statistical significance of the final treatment is interpreted as indicating that it is removal of the tail that reduces maximal linear acceleration, rather than it being due to a chronological effect. None of the other maneuver variables exhibited significant variation over the chronological order of treatments (all $F < 1.91, P > 0.14$).

The statistical analyses of the effects of tail length on the measured performance variables are presented in Table 2. Of the variables considered, only the maximum linear acceleration varied with experimental treatment (repeated measures ANOVA, $n = 51$ measures over 18 birds, by shifting from tending to use yaw/roll turns, towards pitch-roll turns. This possibility does not seem to be well-varied with experimental treatment (all $F < 2.21, P > 0.14$). The statistical significance of maximum linear acceleration was driven by the significant difference between the short-tail treatment and the no-rectrices treatment ($t = -4.26, P < 0.001$), whereas the difference between the short-tail treatment and the long-tail treatment was not significant ($t = 0.67, P = 0.511$). Moreover, there were no significant sex treatment interactions for any of the variables (all $F < 2.28, P > 0.120$).

Because maximal linear acceleration was found to vary between experimental treatments, a post-hoc analysis of the maximal linear acceleration X and Y was performed. A repeated measures ANOVA of the maximum acceleration indicated that the maximum X -acceleration was not significantly different between the experimental treatments ($n = 51$ measures over 18 birds, $F_{2,29} = 0.16, P = 0.85$), whereas the maximum Y -accelerations were significantly different between treatments ($F_{2,29} = 4.22, P = 0.025$). As indicated in Fig. 4, maximum Y -acceleration was primarily associated with curving trajectories.

Discussion

The tail's role during maneuvers

Overall, the maneuvers performed by male and female Red-billed Streamertails were sufficient to rotate and rapidly propel the birds away from the startling stimulus.

Because the tail (when present) was always widely spread at the onset of the maneuver, the kinematics suggest that the tail produced aerodynamic forces during the maneuver. This is supported by the finding that the bird's maximal linear accelerations were significantly reduced when the tail was removed. The point of maximal linear acceleration often coincided with the production of centripetal accelerations associated with a curving trajectory (i.e., changes in direction), suggesting that it was the ability to produce centripetal acceleration that was specifically reduced in tail-less birds. Consistent with this, the post-hoc analysis detected treatment differences in maximum acceleration and not X -acceleration. In this experiment, high decelerations occurred late in the yaw/roll turns (Fig. 4), as the birds adjusted their trajectory to avoid colliding with the flight arena. Therefore, it would appear that removing the tail from the Red-billed Streamertail decreased either the tendency or ability of the birds to

change direction (i.e., produce a curved trajectory).

This reduction in maximal acceleration could be due to two effects. The birds may have adjusted the type of rotation performed to accommodate the absent tail, for example by shifting from tending to use yaw/roll turns, towards pitch-roll turns. This possibility does not seem to be well-supported by the data, however; none of the other kinematic variables (such as angular speed) were statistically significantly different between the no-tail trails and the other treatments, and a clear shift in the style of maneuver performed was not clearly evident in visual inspection of the videos. The second possible explanation for the reduction in the maximal linear acceleration is that the birds utilized the widely spread tail to generate forces (aerodynamic and/or inertial) during the maneuver, and thus the bird's flight

Table 2 F statistics from repeated measures ANOVAs examining the effects of tail length on maneuver performance (repeated measures over 18 birds)

Variable	Sex	Bird ID	Tail length	Sex × tail-length interaction
Time to travel 20 cm	0.70 (1)	0.91 (16)	1.18 (3)	1.63 (3)
Maximum linear acceleration	13.05* (1)	9.98* (16)	21.90* (3)	1.53 (3)
Time of max. linear acceleration	0.04 (1)	2.00 (16)	2.12 (3)	0.20 (3)
Time to yaw 120	0.59 (1)	2.25 (16)	1.02 (3)	2.28 (3)
Log max. angular speed	1.08 (1)	0.54 (16)	0.04 (3)	0.79 (3)
Time of max. angular speed	0.01 (1)	1.27 (16)	0.66 (3)	0.73 (3)
PC1	0.65 (1)	1.46 (16)	1.00 (3)	2.14 (3)
PC2	6.14 (1)	1.41 (16)	3.18 (3)	1.38 (3)

Degrees of freedom are given in parentheses

ANOVA analysis of variance

^a For maximum linear acceleration, the no-tail treatment (which was also always the last treatment) was significantly different from the short-tail and long-tail treatments ($t = -4.26$, $P = 0.001$), whereas short-tail and long-tail treatments were not significantly different ($t = 0.67$, $P = 0.511$)

^b PC2 was marginally statistically significant across experimental treatments ($P = 0.056$); this result was driven by the no-tail treatment ($t = -2.29$, $P = 0.030$) and not by differences between the long-tail and short-tail treatments ($t = 0.11$, $P = 0.92$). Notably, PC2 loaded highly on maximum linear acceleration (Table 1)

* F values are statistically significant using a Bonferroni-corrected P value of 0.006

performance was altered when missing the tail. Aerodynamic forces and torques produced by it could serve two functions. First, torques generated by the tail could serve to control pitching and/or yawing motions of the body. According to this hypothesis, when missing the tail, the bird would need to sacrifice some thrust from the wings to instead produce a functionally equivalent torque (if it did not do so, presumably it would lose control of flight). Second, the tail may simply function as an additional lifting surface, elevating the total average aerodynamic force the bird can produce (Thomas 1993). In the absence of a tail, the total aerodynamic force generated by the bird would be reduced. Inspection of the high-speed videos suggested that the tail served to control pitching and/or yawing motions in the low-speed maneuvers investigated here. Aerodynamic forces scale as velocity squared (Norberg 1990), thus the forces developed by the tail will vary substantially with airspeed. Therefore, drag from the streamers in a small fraction (<5%) of trials, the birds appeared to be unstable in pitch and/or yaw, as evidenced by strong oscillations in body pitch or yaw. A potential topic of future empirical research would be further investigation of these two potential functions of tail-generated forces.

Whereas removing the entire tail resulted in a decrease in maximum linear acceleration attained by the birds, no statistically significant differences between maneuvers with short or long tail were detected. This suggests that the great differences in roll between the experimental treatments went

Effects of a long tail on maneuvers

Whereas removing the entire tail resulted in a decrease in maximum linear acceleration attained by the birds, no statistically significant differences between maneuvers with short or long tail were detected. This suggests that the great differences in roll between the experimental treatments went

un-measured. Second, the birds studied here exhibited high angular accelerations [$6.23.0 \times 10^5 \text{ s}^{-2}$ ($n \pm$ standard deviation); compare Fig. 4e] with all other species of birds, such that detecting statistically significant effects of tail morphology would necessitate either large sample sizes or pronounced experimental effects. Third, there are reasons to think that the effects of tail morphology on inertia would be subtle. For simplicity, previous estimates of the inertia of the tail have treated the tail as a stiff plate (Evans and Thomas 1992). However, the kinematics of the tail-streamers during the maneuver (Fig. 4) show that the streamers are extremely flexible and bend dynamically during the maneuvers. This bending may be widespread in long-tailed taxa, for it is qualitatively similar to the bending of Barn Swallow tail-streamers observed by Norberg (1994), and it would appear to decrease the effective moment of inertia; in this study, as a bird began to rotate, its streamers would bend, rather than imparting a large moment arm on the rotation. It seems likely that this effect reduces the effects a long tail may have on body rotations.

It is possible that small changes in flight performance present between the long- and short-tail treatments were rendered undetectable by the variation present in the kinematics of the maneuver. Flying organisms have six degrees of freedom (three translational and three rotational; Dudley 2000) and can utilize multiple combinations of these degrees of freedom in the course of maneuvering. The maneuvers studied here were not stereotyped, illustrating the extremes depicted in Figs. 3 and 4. When rotating, the birds could incorporate either pitch, or alternatively, yaw, without significant incorporation of the other type of rotation. This high degree of potential variation in kinematics would appear to benefit an animal performing an escape maneuver. For example, if an escape maneuver were stereotyped, it may be possible for predators or conspecifics to anticipate the target individual's trajectory, thereby impairing its utility as an escape tactic. Despite this variation, the experiment performed here produced significant differences between the maneuvers performed with and without a tail. Therefore, it would appear that if the tail-streamers impair flight, it is to a relatively small degree.

Zusammenfassung
 Der Einfluss der Schwanzlänge auf ein Fluchtmannöver beim Wimpelschwanz

Zusammenfassung

Der Einfluss der Schwanzlänge auf ein Fluchtmannöver beim Wimpelschwanz

Sexuell selektierte, verlängerte Schwanzfedern bei Vögeln könnten natürlich selektierte Funktionen, die mit Flug in Zusammenhang stehen, behindern oder verbessern. Das Ziel dieser Studie war zu testen, ob eine experimentelle Manipulation der Schwanzlänge die Kinematik eines

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References

Andersson M (1982) Female choice selects for extreme tail length in a widowbird. *Nature* 299:818-820

- Andersson S (1992) Female preference for long tails in lekking Os widowbirds: experimental evidence. *Anim Behav* 43:379D388
- Balmford A, Lewis MJ, Brooke MDL, Thomas ALR, Johnson CN (2000) Experimental analyses of sexual and natural selection on short tails in a polygynous warbler. *Proc R Soc Lond B* 267:1121D1128
- Buchanan KL, Evans MR (2000) The effect of tail streamer length on aerodynamic performance in the barn swallow. *Behav Ecol* 11:228D238
- Clark CJ (2010) The evolution of tail shape in hummingbirds. *Auk* 127:44D56
- Clark CJ, Dudley R (2009) Flight costs of long, sexually selected tails in hummingbirds. *Proc R Soc Lond B* 276:2109D2115
- Dudley R (2000) The biomechanics of insect flight: form, function, evolution. Princeton University Press, Princeton
- Dudley R (2002) Mechanisms and implications of animal flight maneuverability. *Int Comp Biol* 42:135D140
- Evans MR, Thomas ALR (1992) The aerodynamic and mechanical effects of elongated tails in the scarlet-tufted malachite sunbird: measuring the cost of a handicap. *Anim Behav* 43:337D347
- Evans MR, Martins TLF, Haley M (1994) The asymmetrical cost of tail elongation in red-billed streamertails. *Proc R Soc Lond B* 256:97D103
- Gatesy SM, Dial KP (1993) Tail muscle activity patterns in walking and flying pigeons (*Columba livia*). *J Exp Biol* 176:55D76
- Haslwanter T (1995) Mathematics of three-dimensional eye rotations. *Vis Res* 35:1727D1739
- Hedrick TL, Biewener AA (2007) Low speed maneuvering flight of the rose-breasted cockatoo (*Cacatophus roseicapillus*). Kinematic and neuromuscular control of turning. *J Exp Biol* 210:1897D1911
- Hedrick TL, Cheng B, Deng X (2009) Wingbeat time and the scaling of passive rotational damping in flapping flight. *Science* 324:252D255
- Matyjasiak P, Jaborski PG, Olejniczak I, Boniecki P, Lee S-D (1999) Foraging cost of a long tail ornament: an experiment with sand martin females. *Ethology* 105:521D530
- Matyjasiak P, Jaborski PG, Olejniczak I, Boniecki P (2000) Imitating the initial evolutionary stage of a tail ornament. *Evolution* 54:704D711
- Matyjasiak P, Matyjasiak J, de Lope F, Müller AP (2004) Vane emargination of outer tail feathers improves flight manoeuvrability in streamerless hirundines, Hirundinidae. *Proc R Soc Lond B* 271:1831D1838
- Maybury WJ, Rayner JMV (2001) The avian tail reduces body parasite drag by controlling flow separation and vortex shedding. *Proc R Soc Lond B* 268:1405D1410
- Maybury WJ, Rayner JMV, Couldrick LB (2001) Lift generation by the avian tail. *Proc R Soc Lond B* 268:1443D1448
- Norberg U (1990) Vertebrate flight. Springer, Berlin
- Norberg RA (1994) Swallow tail streamer is a mechanical device for self-deflection of tail leading edge, enhancing aerodynamic efficiency and flight manoeuvrability. *Proc R Soc Lond B* 257:227D233
- Park KJ, Evans MR, Buchanan KL (2000) Assessing the aerodynamic effects of tail elongations in the house martin (*Hirundo urbica*): implications for the initial selection pressures in hirundines. *Behav Ecol Sociobiol* 48:364D372
- Petrie M, Halliday T, Sanders C (1991) Peahens prefer peacocks with elaborate trains. *Anim Behav* 41:323D331
- Pryke SR, Andersson S (2002) A generalized female bias for long tails in a short-tailed widowbird. *Proc R Soc Lond B* 269:2141D2146
- Rowe LV, Evans MR, Buchanan KL (2001) The function and evolution of the tail streamer in hirundines. *Behav Ecol* 12:157D163
- Spofford SH (1976) Roadrunner catches hummingbird in flight. *Condor* 78:142
- Stiles FG (1995) Intraspecific and interspecific variation in moult patterns of some tropical hummingbirds. *Auk* 112:118D132
- Thomas ALR (1993) On the aerodynamics of birds' tails. *Phil Trans R Soc Lond B* 340:361D380
- Tobalske BW (2007) Biomechanics of bird flight. *J Exp Biol* 210:3135D3146
- Usherwood JR, Hedrick TL, McGowan CP, Biewener AA (2005) Dynamic pressure maps for wings and tails of pigeons in slow, flapping flight, and their energetic implications. *J Exp Biol* 208:355D369
- Walker JA (1998) Estimating velocities and accelerations of animal locomotion: a simulation experiment comparing numerical differentiation algorithms. *J Exp Biol* 201:981D995
- Warrick DR, Dial KP (1998) Kinematic, aerodynamic and anatomical mechanisms in the slow, maneuvering flight of pigeons. *J Exp Biol* 201:655D672
- Warrick DR, Dial KP, Biewener AA (1998) Asymmetrical force production in the maneuvering flight of pigeons. *Auk* 115:916D928
- Warrick DR, Bundle MW, Dial KP (2002) Bird maneuvering flight: blurred bodies, clear heads. *Int Comp Biol* 42:141D148
- Woltring HJ (1985) On optimal smoothing and derivative estimation from noisy displacement data in biomechanics. *Hum Mov Sci* 4:229D245