The mechanics and behavior of Cliff Swallows during tandem flights

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SUMMARY

Cliff Swallows (Petrochelidon pyrrhonota) are highly maneuverable social birds that often forage and fly in large open spaces. Here we used multi-camera videography to measure the three dimensional kinematics of their natural flight maneuvers in the field. Specifically, we collected data on tandem flights, defined as two birds maneuvering together. These data permit us to evaluate several hypotheses on the high-speed maneuvering flight performance of birds. We found that high speed turns are roll-based, but that the magnitude of the centripetal force created in typical maneuvers varied only slightly with flight speed, typically reaching a peak of ~2 body weights. Turning maneuvers typically involved active flapping rather than gliding. In tandem flights the following bird copied the flight path and wingbeat frequency (~12.3 Hz) of the lead bird while maintaining position slightly above the leader. The lead bird turned in a direction away from the lateral position of the following bird 65% of the time on average. Tandem flights vary widely in instantaneous speed (1.0 to 15.6 m s⁻¹) and duration (0.72 to 4.71 s), and no single tracking strategy appeared to explain the course taken by the following bird.
INTRODUCTION
Behaviors in bird, bat, and flying insect species range in complexity from migratory cruising to high- and low-speed maneuvering during courtship, territory defense, and predator-prey interactions. Our understanding of the maneuverability of bats (Iriarte-Díaz and Swartz, 2008; Riskin et al., 2008) and insects (Card and Dickinson, 2008; Combes et al., 2012), along with birds (Tobalske, 2007), has grown rapidly over the last decade with new methodological developments being deployed in studies across flying species. Most research to date on the mechanics of vertebrate flight have taken place in laboratories with wind tunnels (e.g. Tobalske and Dial, 1996; Ward et al., 2001; Spedding et al., 2003) or simple obstacle courses navigated at low speed (e.g. Swaddle, 1997; Warrick et al., 1998). The latter is a powerful approach for analyzing a specific maneuver because it allows for repeatable behaviors and optimally placed cameras to capture subtle details of the flight movements (e.g. Hedrick and Biewener, 2007; Iriate-Díaz and Swartz, 2008; Ros et al., 2011). However, the behaviors elicited in laboratory environments may differ from those in natural environments, and are confined in speed and scope by the size of the experimental space. To overcome these difficulties, and to better understand the dynamics of high-speed avian flight maneuvers, we use high speed video cameras to quantify flight maneuvers and conspecific interactions in natural environments.

We chose to study Cliff Swallows (*Petrochelidon pyrrhonota*) because they perform their well-known flight maneuvers in open spaces that permit easy recording with cameras. Cliff Swallows build nests in large colonies each spring in North America and migrate to South America for the winter (Brown and Brown, 1986). They are highly social passerines that perform many activities in groups including feeding, preening, gathering mud for nest-building, and perching (Emlen, 1952). As aerial insectivores, Cliff Swallows have evolved body and wing shapes consistent with changing direction (turning acceleration), and are therefore considered to be highly maneuverable (Brown and Brown, 1998).

Near nesting colonies, Cliff Swallows engage in one-on-one tandem flights, which appear to be aggressive chase sequences of high-speed maneuvers. These flights have been described as
competitive interactions resulting from an intruder approaching a guarded nest (Brown and Brown, 1989). Because Cliff Swallows are conspecific nest parasites, such chases may serve to prevent the investment of energy in the rearing of adopted offspring (Petrie and Møller, 1991). These tandem flights can escalate to in-flight physical altercations including grappling with their feet, falling from flight while grappling, and disentangling just before reaching the water (personal observations, RMS, BEJ, see supplemental video). Therefore, we expect that the birds participating in tandem flights exhibit flight performance at the upper end of their performance envelope; these interactions appear to include the most elaborate maneuvers at relatively high speeds, compared to other flight behaviors near the nest colony (personal observations, RMS, BEJ, TLH).

This study examines several specific questions related to these free-flight behaviors. What is the performance and maneuvering envelope of freely flying Cliff Swallows? What are the turning mechanics of Cliff Swallows in the field? What are the characteristics of these tandem flights? Why do these tandem flights occur? With respect to these questions we predict that we will see similar linear velocities and accelerations to those previously measured in laboratory-based obstacle courses and wind tunnels (Warrick, 1998; Park et al., 2001); that roll angle is the primary variable determining the centripetal force and the rate of change in heading because this is the primary method of turning for both airplanes and dragonflies (Alexander, 1986). With regard to bird-bird interactions we expect that these tandem flights are chases with a simple tracking or intercepting algorithm as exhibited by insects (Collett and Land, 1978; Olberg et al., 2000) because we have seen birds physically fight in midair; and that these tandem flights are competitive interactions, with the lead bird taking action to avoid the following bird because the tandem flights tend to start near the nests in the season of nest guarding (Brown and Brown, 1989).

RESULTS

General results
In each recorded tandem flight the following bird copied the movements of the lead bird in three dimensional (3D) space and in the x, y, and z position components independently (e.g. Fig. 1). Copying behavior appeared to be independent of variation in distance travelled, interaction time, elevation change, and turning rate among tandem flights. We recorded the mean and maximum
speed, acceleration, rate of change in heading (here the direction of the 3D velocity vector), and flight time of our trials (Table 1). The mean of the trial mean speeds (7.0 m s\(^{-1}\)) is less than half the maximum observed instantaneous speed (15.6 m s\(^{-1}\)) showing that these interactions often occur below peak linear speed performance. The mean power of the 10 trials with the highest mass specific power (±SD) was 21.2 ± 4.5 W kg\(^{-1}\) (see Eqn 1). These tandem flights were short, lasting 2.28 s on average.

**Turning performance**

We measured or calculated the roll angle relative to the gravity adjusted centripetal force (\(\theta'\)), flight speed (\(u\)), rate of change in heading (\(w\)), and gravity adjusted centripetal force (\(F'\)) of 42 lead bird turns, and we found strong and significant correlations between \(\theta\) and \(w\) (\(r^2 = 0.727, p < 0.001\), Fig. 2A), \(\theta\) and \(F\) (\(r^2 = 0.876, p < 0.001\), Fig. 2B), and \(F\) and \(w\) (\(r^2 = 0.746, p < 0.001\), Fig. 2C). We did not find a significant correlation between \(u\) and \(F\) (\(r^2 = 0.085, p = 0.065\), Fig. 2D), and found only a weak association between \(u\) and \(w\) (\(r^2 = 0.111, p = 0.031\)). There was one turn with an apparent \(F'\) outlier producing 7.8 body weights of force, more than twice the force of any other observed turn, which was not included in the above statistics – see further examination of this result below. The extended mixed-effects analysis of these results (Table A1) confirmed the findings of the linear regressions; a linear model relating \(F'\) to \(\theta'\) produced the lowest AIC of all models without random effects (84.08); the overall best model added a random effect of trial but only reduced the AIC to 82.04; the linear coefficient for \(\theta'\) was highly significant and nearly identical in the two cases.

**Leader – follower comparisons**

We observed a variety of following positions with respect to the lead bird, but there was a tendency to avoid following directly behind the leader (Fig. 3A), and a statistically significant trend of aiming above the leader (Fig. 3B, using a generalized estimating equation, \(p = 0.03\)). The mean wingbeat frequencies of the lead bird (12.3 ± 1.7 Hz) and following bird (12.4 ± 1.6 Hz) were statistically indistinguishable. The following bird, on average, started its downstroke less than \(\frac{1}{4}\) wingbeat after the lead bird (Fig. 4). The outer circle represents the full wingbeat cycle of the following bird and each point is the mean timing of the start of the downstroke of the lead bird. Perfect synchronization would be represented by all points positioned at 0\(^\circ\). The non-random distribution (Rayleigh Test; \(r = 0.38, p = 0.021, n = 26\)) averaged 332\(^\circ\) (95% CI: 292\(^\circ\) to 11\(^\circ\)).
On average, the lead bird turned away from the following bird 65% of the tandem flight (Fig. 5A, t-test, p < 0.001). The following bird had a longer flight path and flew 6% faster on average than the lead bird (t-test, p = <0.001, Fig. 5B).

**High force outlier**

We estimated a centripetal force of 7.8 body weights in one turn, more than double any other turn we observed (Fig. 6). This sequence included a number of factors that may have contributed to the high force measurement: a large $\theta$ of 78°, a fast speed of 14.6 m s$^{-1}$ immediately preceding the turn, a quick reduction in speed by 4.5 m s$^{-1}$ during the time of the turn, and the possibility of ground effect enhancing aerodynamic forces since the entire tandem flight occurred just above the water surface.

**DISCUSSION**

**Flight performance envelope**

Compared to the single turn produced by 7.8 times body weight force, most trials included performance well within the known flight envelope for Cliff Swallows and related species. While Cliff Swallow flight has not been examined in a wind tunnel to the best of our knowledge, we can compare our data to previous research on Barn Swallows (*Hirundo rustica*). Flight speeds of two Barn Swallows ranged from 3.4 to 14.0 m s$^{-1}$ in a wind tunnel (Park et al, 2001). We found that the time averaged flight speeds of Cliff Swallows had a similar range and identical maximums (2.8 to 14.0 m s$^{-1}$) despite differences in wing shape and body size between the two species. Since we measured open-area flights, and birds were free to fly at self-chosen varying speeds, we can also look at the maximum instantaneous flight speeds over 0.01 second intervals. Cliff Swallows flew at instantaneous speeds up to 15.6 m s$^{-1}$.

Cliff Swallows have been previously examined during linear escape flights. Warrick found the linear acceleration in four different swallow species ranged from 5.45 to 8.92 m s$^{-2}$, with Cliff Swallows averaging 5.98 m s$^{-2}$, when measured starting from rest and flying in a straight horizontal line (Warrick, 1998). Cliff Swallows in tandem flights had an average linear acceleration of 13.6 m s$^{-2}$, but unlike the horizontal flight test experiment, some of the swallows in our study were able to descend, using potential energy as well as muscle work to accelerate, and potentially taking advantage of other environmental factors. Calculating the mass-specific
power output (not including drag, see Eqn 1 in Methods) can account for added acceleration due to gravity and provides a more relevant comparison between the different behaviors. Warrick’s Cliff Swallows started from rest and accelerated to 7.26 m s\(^{-1}\) in 4 m, resulting in a mass specific power of 22.8 W kg\(^{-1}\) (23 g body mass). Swallows in tandem flights, starting from a wide range of speeds, averaged 21.2 ± 4.5 (mean ± SD) W kg\(^{-1}\). These power estimates would increase if we included drag and a full aerodynamic model. Thus, the freely flying swallows exhibited approximately the same mass specific power as was found in the capture and release study of escape accelerations, even though the conditions of these measurements were drastically different. The level acceleration experiment with recently captured wild swallows was designed to elicit maximum performance; the similar results from freely behaving birds suggests that Cliff Swallows may use most, if not all, of their performance envelope on a day to day basis.

The vertical takeoff power outputs of Blue-Breasted Quail (47.0 W kg\(^{-1}\); 43.6 g body mass; Askew et al, 2001) and Gray Jay (27.7 W kg\(^{-1}\); 68.9 g body mass; Jackson and Dial, 2011) are larger than our measured Cliff Swallow free-flight power. Assuming morphological isometry, aerodynamic and allometric theory would predict that the smaller Cliff Swallows should have higher mass specific power outputs than the other, larger, species (Pennycuick 1975), which may suggest that our Cliff Swallow values are not maximal. Alternately, since swallows are not acceleration specialists and can often use potential energy to enhance flight maneuvers and prey capture attempts, Cliff Swallows may simply have a lower maximal capability for muscle powered acceleration.

Based on the flight speed and turning radius in tandem flight turns, we estimated the aerodynamic centripetal forces developed by Cliff Swallows (Table 1, Fig. 2). Similar field measurements during high-speed flight have only been reported for the courtship dives of Anna’s hummingbirds, which experienced a gravity assisted centripetal force of 9 body weights on average while reaching an average maximum flight speed of 27.3 m s\(^{-1}\) (Clark, 2009). This centripetal force is only slightly higher than the 7.8 body weights maximum reported here, but much greater than our median magnitude of centripetal force of 1.0 body weights. The static wingload of adult male Anna’s hummingbirds is 28.8 Pa (converted from 0.294 g cm\(^{-2}\); 4.3 g body mass; Stiles et al., 2005), or roughly 60% larger than that of Cliff Swallows at 18.0 Pa (Warrick, 1998). Thus, Anna’s hummingbirds appear to be producing higher centripetal forces with respect to both body weights and wingloads, albeit at a flight speed approximately twice that of the Cliff Swallows. This difference is not surprising considering the large difference in
ecological niche and typical flight behavior of these birds. It is likely that the number of documented turning kinematics in the literature will rapidly increase over the next 10 years, providing more of a scaling context for these results.

We can also compare these centripetal forces to experiments on pigeons and cockatoos completing 90° turns through L-shaped corridors at low speeds in laboratory maneuvering tests. Pigeons flying at 3.3 m s\(^{-1}\) with a turning radius of \(~1.0\) m produced a maneuver-averaged centripetal force of 10.9 body weights (Ros et al., 2011); Rose-Breasted Cockatoos making similar turns at 3.01 m s\(^{-1}\) with a radius of 0.92 m produced 9.8 body weights (Hedrick and Biewener, 2007). These larger birds are producing larger forces than our Cliff Swallows which produced less than 2.0 body weights at similar speeds and likely reflect the severe spatial constraints the birds were forced to maneuver under in the laboratory studies.

**Turning mechanics**

As we predicted, \(\theta'\) strongly correlated with both \(F'\) and \(w\). Swallows produced about 2.7 body weights of centripetal force at a 90° \(\theta'\) (Fig. 2B), independent of flight speed (Fig. 2D). An ideal fixed-wing glider performing a level turn could transfer all aerodynamic force (lift) into centripetal force and would be able to produce 1.0 body weights of centripetal force at a 90° roll angle, assuming no change in coefficient of lift. These differences are reasonable given the swallows’ expected ability to vary coefficient of lift and their continued wing flapping through most of the turns. We were unable to determine many details of wing flapping kinematics such as wing extension, stroke amplitude and gait changes.

The basic mechanics of the Cliff Swallow turns were different from those expected for a fixed-wing glider. In the methods we derived a simple linearized expression for a simple fixed-wing banked turn to \(F' \propto \theta'\) (Eqn 9 in methods). Stepping back two equations in our model to \(F' \propto u^2 \sin(\theta')\) (Eqn 7 in methods), we expected to see our correlations increase. Instead, when we substituted any combination of \(u\), \(u^2\), \(\sin(\theta')\) or \(\tan(\theta')\) for \(\theta'\), our correlations decreased in strength (see Table A1). When we tried substituting the horizontal component of centripetal force (\(F' \cos(\theta')\)) for \(F'\) we also saw a decrease in correlations. Essentially, the lateral force produced by swallows is proportional to roll angle, indicating a banked turn, but nearly independent of forward velocity. This indicates that swallows rarely use large lift coefficients when turning while flying fast, despite their apparent ability to do so as demonstrated by the 7.8 g turn discussed earlier. In that maneuver the bird also slowed rapidly, presumably due to the
induced drag associated with the large lift coefficient, demonstrating the costs of high force
turns. Furthermore, flapping provides another avenue for producing larger forces than expected
from forward speed alone and could also account for the absence of a forward speed relationship,
especially at slow speeds. The majority of turns recorded here were flapping maneuvers. The
absence of improvement when using \( \sin(\theta') \) or \( \tan(\theta') \) to examine a specific lift-based turn
model, either one where the bird produces no additional force or produces additional force
adequate to maintain perfect weight support suggests that swallows may compromise between
the two, producing some additional force but not enough for weight support at larger \( \theta' \), a result
also supported by the magnitude of the linear coefficient relating \( \theta' \) to \( F' \). Finally, our large
filming volume precluded us from being able to discern detailed wingbeat kinematics; higher
resolution or closer image captures of swallows turning in high speed free flight will be
necessary to detail the exact motions of the swallow wings and body that produce \( F' \).

**Tandem flights**

Our initial hypothesis that all of these tandem flights were chases including a simple tracking or
intercepting strategy was not supported. Instead of aiming at the lead bird or in front of the lead,
the follower tends to fly parallel to the lead bird while offset to one side or the other, with the
result that the following bird generally copies the flight path of the lead bird. These data do not
support the assumption that the following bird had the ‘goal’ of making contact with the lead
bird, although we occasionally did see contact between two birds (e.g. movie S1). However, the
tendency of the lead bird to turn away from the follower and for the follower to fly faster than
the leader (Fig. 5) does support the hypothesis that these flights are competitive interactions.
Cliff Swallows are highly cooperative populations but they also have high intraspecific brood
parasitism (Brown and Brown, 1989), which could invoke competitive interactions. The flights
we recorded mostly occurred in May and early June, coinciding with nest building and egg
laying. Additionally, while we could not determine the location of the birds relative to the home
nest, most of the flights began close to nests (personal observation RMS, BEJ), further
suggesting that these tandem flights were acts of nest defense from conspecifics. The large
variation in speed, length, bird position, and turning behaviors among trials may represent
varying degrees of relative competitiveness of the two birds involved, with some birds being
driven away more easily and other birds requiring more aggressive pursuit. The offset position of
the follower may provide an aerodynamic advantage of reducing flight cost (Portugal et al.,
2014), or a behavioral advantage of allowing the follower to be seen or to cut off turns towards the nest. These tandem flights might be a graded display with the threat of escalation to physical combat. If so, the birds would attempt to send signals to resolve the conflict with minimal energy loss which would explain why most turns are well below the maximum observed turning force since producing that maximal force appears to have imposed a substantial cost in induced drag, reflected as a decrease in speed during the turn (Fig. 6).

Wingbeat frequency and the timing of wingbeat cycles were unexpectedly synchronized, with a slight phase shift, in lead and following birds. Since the following bird is copying the lead bird’s maneuvers and flight path, it makes sense that the follower would delay its wingbeat in order to first observe the leader’s maneuver. On average, our data show the lead bird starting its downstroke 332° into the follower’s wingbeat cycle (Fig. 4). In other words, the follower’s wingbeat starts 28°, or approximately 6 ms, after the leader’s wingbeat cycle. This response time is fast in comparison to dragonflies (29 ms; Olberg et al., 2007), hoverflies (~20 ms; Collett and Land, 1978), houseflies (~30 ms; Land and Collett, 1974), dolichopodid flies (~15 ms; Land, 1993), and bats (120 ms; Ghose et al., 2006). Thus, it is unlikely that the following birds were simply responding to the timing of the lead birds’ downstroke with each wingbeat cycle. Alternatively, the follower may be reacting to whole-body movements of the lead bird, and may require slightly more than the duration of a wingbeat cycle (81 ms total for wingbeat plus 6 ms delay) to receive, interpret, and react to the input. In other words, the follower’s latency of reaction may mean that what we see as a phase shift of ~30° may actually be a phase shift of ~390°. If the follower exhibited a consistent tracking strategy we would be able to distinguish between the two phase offset possibilities by extracting the response latency between the leader and follower. However, since the swallows appear to use different tracking strategies depending on context, we cannot use this information to conclusively separate the two possibilities, although a 390° offset is more consistent with typical sensory response times as noted above.

MATERIALS AND METHODS

Swallow recordings
We recorded Cliff Swallow interactions from the birds in a colony of 30 to 60 birds at the NC highway 751 bridge over Jordan Lake, Chatham County, North Carolina, USA (35° 49' 42" N, 78° 57' 51" W). We recorded on 26 separate mornings in the months of May and June of 2012.
and May of 2013 collecting 100 Hz three-dimensional (3D) kinematic data for 31 tandem flights totaling 71 seconds. Each day we had a slightly different camera setup and recorded 1 to 3 good trials. We are unable to confirm that each trial involved different individuals since we could not identify individual birds. However, we chose to treat each tandem flight as an independent event given the number of birds present at the colony and the elapsed time between trials.

To collect 3D field flight data in large outdoor volumes we developed a structure-from-motion camera calibration routine which used a wand of known length to set the scale of the scene and provide an initial calibration; this was implemented as a custom MATLAB (The Mathworks, Natick, MA, USA) routine (Therialt et al., 2014). This preliminary calibration was then refined by adding individual swallows from calibration recordings as points of optical correspondence and applying a bundle adjustment optimization (Lourakis and Argyros, 2009) to the data and camera coefficients. The scene was then aligned to gravity by measuring the acceleration of a rock tossed through the scene, transforming the coefficients to place this acceleration vector on the z axis, and converted to a set of direct linear transformation coefficients (DLT) for 3D analysis of bird trajectories (Hedrick, 2008). Camera recording positions varied slightly among trials, but typically set a recording volume of ~7,000 m$^3$. Video data were collected using three synchronized high-speed cameras (N5r, Integrated Design Tools, Inc., Tallahassee, Florida, USA) recording 2336 x 1728 pixel images at 100 Hz. The calibrations had a median DLT residual of 1.23 pixels and the bird trajectories had a median 95% confidence interval of 0.057 m with a range of 0.010 m to 0.412 m, where recordings closer to the cameras are more precisely quantified (Therialt et al, 2014).

We minimized the influence of wind by recording on days with little or no wind (< 1.5 m s$^{-1}$). We measured the wind by placing a digital anemometer (HHF142, OMEGA Engineering, Inc, Stamford, Connecticut, USA) on the shoreline near the camera locations elevated between 2 and 6 meters above the water level. The anemometer was mounted on a gimbal allowing free rotation about the vertical axis; wind velocity was recorded at 1 Hz using a custom data logger which sampled the anemometer output, compass direction via a digital magnetometer and Global Positioning System location and time.
**Kinematic analysis**

We manually digitized the head of each bird in each frame of each camera to determine the 3D bird positions with respect to time for each trial (Fig. 7) using the MATLAB package DLTdv5 (Hedrick 2008). Each trial includes two birds flying as a pair with one bird leading and the other bird following. We designate these birds as the lead bird and following bird, respectively, throughout the paper. These raw data were first processed by iteratively increasing the error tolerances of a quintic smoothing spline to affect a low pass filter at 1.0, 1.5, and 2.5 Hz to remove digitizing errors and within-wingbeat fluctuations in velocity and acceleration. The error variance was extracted from the 3D reconstruction uncertainty for each data point. Varying the filter did not impact any of our statistical conclusions and introduced only small variations in the data. Results in this paper are from the 1.5 Hz low pass filter unless otherwise noted. Derivatives of position with respect to time were calculated from the quintic spline polynomial; we examined the first and second derivatives – velocity ($v$) and acceleration ($a$).

We used the filtered position, $v$, and $a$ data for all further calculations. We recorded the maximum instantaneous values from all of the data of speed, $a$, and magnitude of rate of change in heading to document the maximum observed performance (Table 1). We calculated the mass specific power (not including drag) by

$$\frac{\text{power}}{\text{mass}} = \frac{\Delta(\text{kinetic + potential energy})}{\text{time} \times \text{mass}}.$$  \hspace{1cm} (1)

Mass on the right side of this equation will cancel allowing us to complete the calculation without knowing the mass of the birds. Since our swallows were not always maximizing power, we measured power over each possible 1 s interval for all of our trials and selected the largest mass specific power from each trial. We then focused on the 10 trials with the largest power for further analysis.

We calculated the instantaneous radius of curvature ($r$) directly from $v$ and $a$ by

$$r = \frac{|v|^3}{\sqrt{|v|^2|a|^2 - (v' a')^2}}$$  \hspace{1cm} (2)

where $a'$ is the transpose of $a$. We then calculated rate of change in heading ($w$) by

$$w = \frac{u}{r}$$  \hspace{1cm} (3)

with $u$ defined as flight speed. We extracted the frame and trial number of each local maxima in the graph of $w$ with respect to time of the lead birds (number of peaks = 144) and tried to digitize the location of the extended wingtips in that frame ($\pm$ 2 frames) to calculate roll angle ($\theta$). We calculated $\theta$ as the angle between the line connecting the two wingtips and the line from one
wingtip in the direction of the other wingtip but parallel to the horizontal plane. We could only
clearly identify the wingtip locations for 42 of the 144 turns. For these 42 turns we calculated
centripetal force \( F \) in body weights by

\[
F = \frac{u^2}{9.81r}
\]

We added a directional sign (positive = right, negative = left) for \( w \), \( \theta \), and \( F \).

To evaluate the relative body positions of the lead bird with respect to the following bird
we defined a second non-inertial coordinate system \((x_b, y_b, z_b)\) that rotates with each frame with
\( x_b \) remaining perpendicular to gravity. We rotated and shifted the original coordinate axes \((x, y, z)\) to place the following bird at the origin flying up the \( y_b \)-axis for each video frame. This
allowed us to use the lead bird’s coordinates to define the forward distance as the \( y_b \)-coordinate,
the vertical distance as the \( z_b \)-coordinate, and the lateral distance as the perpendicular distance
from the \( y_b \)-axis to the lead bird position (Fig. 8).

We calculated the average wingbeat frequency by visually determining the frame number
that each bird had its wingtips at their highest point for each wingbeat cycle. Of our 31 tandem
flights, only 26 recordings clearly showed at least four consecutive wingbeats for both birds. To
evaluate the relative timing of wingbeats of the lead bird and following bird we first evaluated
each wingbeat separately. For each following bird wingbeat we calculated the number of frames
until the next wingbeat started, set this wingbeat length equal to 360˚, and noted the timing of the
start of the lead bird’s downstroke relative to the following bird’s 360˚ wingbeat. For each trial
we took the average timing of the lead bird’s downstroke and treated the means from the 26 trials
as independent data points.

**Flight model**

To test if roll angle was the primary variable determining the centripetal force and the rate of
change in heading we tested our measurements of \( F \) against simplified force models for simple
fixed-wing banked turns. We made progressively simplifying assumptions to isolate individual
mechanisms. We started with

\[
\text{Lift} = \frac{1}{2} C_L S u^2
\]

with \( C_L \) = lift coefficient and \( S \) = wing area. This gives the lateral force \( F \) as

\[
F = \frac{1}{2} C_L S u^2 \sin(\theta)
\]
If we drop \( \frac{1}{2} C_L S \) from the equation by assuming that swallows use similar lift coefficient and wing area among all maneuvers, we are left with

\[
F \propto u^2 \sin(\theta)
\]

(7)

Alternatively, if Cliff Swallows modulate wing area and lift coefficient to match Lift (i.e. vertical force) to body weight and maneuver only by redirecting Lift, we expect:

\[
F \propto \sin(\theta)
\]

(8)

and thus lift proportional to \( \theta \) after further linearization:

\[
F \propto \theta
\]

(9)

As a third alternative, Cliff Swallows may turn by redirecting their Lift inward but also modulate coefficient of lift and wing area to maintain a vertical component equal to body weight. In this circumstance,

\[
F \propto \tan(\theta)
\]

(10)

which also linearizes to equation 9 for small \( \theta \). Thus, in our simplest model we would expect to see a correlation for \( F \) with respect to \( \theta \). We would also expect this correlation to increase when we substitute some combination of \( u, u^2, \) and \( \sin(\theta) \) or \( \tan(\theta) \) for \( \theta \), moving toward the more complete models. Also, we would expect an improved correlation from substituting the horizontal component of centripetal force (by \( F\cos(\theta) \)) for \( F \).

These simplified equations only characterize turns in the 2D plane perpendicular to gravity and do not include the 3D complexity of the observed turns, which may not be level and may have a gravitational contribution to or against \( F \). These factors were accommodated by subtracting the gravitational contribution from the observed centripetal force vector, resulting in an aerodynamic centripetal force vector \( F' \), and measuring the adjusted roll angle \( \theta' \) relative to the plane defined \( F' \). If Cliff Swallows are using roll based turns, we would expect to see a correlation between \( F' \) and \( \theta' \). If the swallows do not change overall lift production during maneuvers, we would expect the coefficient relating \( \theta' \) to \( F' \) to be approximately 1.0. The expectations in the above paragraph are still valid after we plug in \( \theta' \) to \( F' \) for \( \theta \) to \( F \).

**Statistical analysis**

We used several different statistical methods to evaluate our data. To measure the correlations between each paired combination of \( F' \), \( \theta' \), \( w \), and \( u \) (Fig. 2) we calculated a linear regression, a correlation coefficient \( (r^2) \), and a p-value. We used a t-test to evaluate the null hypotheses that
the lead bird turns toward and away from the following bird in equal portions of time. A t-test was also used to evaluate the null hypothesis that the lead bird and following bird have equal mean velocities. We used MATLAB for these statistics treating each tandem flight as a single independent trial. We further examined the effect of recording date and trial on the results and additive linear models containing several of the terms from equations 7-10 using linear mixed effect models compared by Akaike’s Information Criterion (AIC). This analysis was performed in R using the nlme package of R 2.12 (Pinheiro et al., 2010; R Development Core Team 2010). A single outlier point with centripetal force more than twice that of the next largest value recorded was excluded from the data for the AIC analysis but not in the initial linear regressions.

To evaluate the relative vertical distance, defined by $Z_b$ in Figure 8, we used a generalized estimating equation to test the null hypothesis that the vertical distance is equal to 0 using R with the geepack library (R Foundation for Statistical Computing, Vienna, Australia; Zeger et al., 1988). We evaluated the relative wingbeat timing for the lead bird and following bird using a Rayleigh Test using Oriana (Kovach Computing Services, Wales, UK; Brazier, 1994).

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**Author contributions**

The overall experimental concept was developed by Hedrick, data recording and analysis was carried out by Shelton and Jackson with contributions from Hedrick, Shelton and Hedrick prepared the manuscript.
List of Symbols

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<th>Symbol</th>
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<td>a</td>
<td>acceleration</td>
<td>m s(^{-2})</td>
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<tr>
<td>(C_L)</td>
<td>coefficient of lift</td>
<td>dimensionless</td>
</tr>
<tr>
<td>(F)</td>
<td>centripetal force</td>
<td>body weights</td>
</tr>
<tr>
<td>(F')</td>
<td>gravity adjusted centripetal force</td>
<td>body weights</td>
</tr>
<tr>
<td>(r)</td>
<td>radius of curvature</td>
<td>m</td>
</tr>
<tr>
<td>(S)</td>
<td>wing area</td>
<td>m(^2)</td>
</tr>
<tr>
<td>(\theta)</td>
<td>roll angle relative to the horizontal plane</td>
<td>degrees</td>
</tr>
<tr>
<td>(\theta')</td>
<td>roll angle relative to the plane defined by (F')</td>
<td>degrees</td>
</tr>
<tr>
<td>(u)</td>
<td>flight speed</td>
<td>m s(^{-1})</td>
</tr>
<tr>
<td>(v)</td>
<td>velocity</td>
<td>m s(^{-1})</td>
</tr>
<tr>
<td>(w)</td>
<td>rate of change in heading</td>
<td>degrees s(^{-1})</td>
</tr>
</tbody>
</table>

References


## Appendix A

Table A1: Mixed-effects model results

<table>
<thead>
<tr>
<th>AIC</th>
<th>Intercept (a)</th>
<th>Coefficient 1 (b)</th>
<th>Coefficient 2 (c)</th>
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<tbody>
<tr>
<td>$F' = a + b \theta'$</td>
<td>-0.08</td>
<td>1.77***</td>
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<tr>
<td>$F' = a + b \sin(\theta')$</td>
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<td>2.16***</td>
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<td>$F' = a + b \tan(\theta')$</td>
<td>-0.15</td>
<td>0.30*</td>
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<tr>
<td>$F' = a + b u$</td>
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<td>0.19***</td>
<td>-</td>
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<tr>
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<td>-0.09</td>
<td>1.91***</td>
<td>-0.02</td>
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<td>0.02***</td>
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<td>$F' = a + b \theta' + c u^2$</td>
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<td>-0.02</td>
<td>2.16***</td>
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<tr>
<td>$F' = a + b \tan(\theta')$, random effect: date</td>
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<td>0.30*</td>
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<td>$F' = a + b \tan(\theta')$, random effect: trial</td>
<td>-0.15</td>
<td>0.30*</td>
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<td>$F' = a + b \tan(\theta')$, random effects: trial nested in date</td>
<td>-0.15</td>
<td>0.30*</td>
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## Tables

Table 1. Flight Performance

<table>
<thead>
<tr>
<th>Variable</th>
<th>Instantaneous maxima</th>
<th>Mean of trial means</th>
<th>Standard deviation of means</th>
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<tr>
<td>Speed (m s(^{-1}))</td>
<td>15.6</td>
<td>7.0</td>
<td>2.4</td>
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<tr>
<td>Acceleration (m s(^{-2}))</td>
<td>78.1</td>
<td>13.6</td>
<td>6.6</td>
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<tr>
<td>Magnitude of rate of change in heading, (w) (deg s(^{-1}))</td>
<td>642</td>
<td>107</td>
<td>37</td>
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<tr>
<td>Tandem flight time (s)</td>
<td>4.71</td>
<td>2.28</td>
<td>1.14</td>
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Figures:

Fig. 1. (A) The 3-dimensional positions of a lead and following bird for a tandem flight starting at the diamonds in the upper left. The z-axis is aligned with gravity. (B) The x, y, and z components of the position with respect to time. The following bird copies the lead bird’s position closely in each component. (C) The speed of the following bird is slightly faster than the lead bird and the speed in this tandem flight ranges from 1.6 to 8.8 m s\(^{-1}\).
Fig. 2. For 42 turns we compared (A) rate of change in heading with respect to the roll angle relative to the gravity adjusted centripetal force, (B) gravity adjusted centripetal force with respect to roll angle relative to the gravity adjusted centripetal force, (C) rate of change in heading with respect to gravity adjusted centripetal force, and (D) flight speed with respect to gravity adjusted centripetal force. For roll angle with respect to gravity adjusted centripetal force, rate of change in heading, and gravity adjusted centripetal force, positive = right and negative = left. A, B, and C have high correlations and significant p-values but D has a near zero correlation and is insignificant. The equations and statistics do not include the centripetal force outlier of 7.8 body weights.
Fig. 3. (A) Each marker represents the mean location of the lead bird with respect to the following bird through one entire tandem flight sequence (n=31). (B) The histogram shows the mean vertical location of the leader for each trial with negative distances defined by the leader being below the follower’s trajectory. The dashed line at zero shows the expected mean if the follower was aiming in line with the leader. This distance is significantly less than zero using a generalized estimating equation (GEE) with p=0.03 meaning the follower tends to aim above the leader.
Fig. 4. Here we show the phase offset of the beginning of downstroke among the follower and leader. The outer circle represents the full wingbeat cycle of the following bird. For each wingbeat cycle we observed the timing in frames of the start of the lead bird’s downstroke relative to the following bird’s wingbeat cycle. Each dot is the mean timing of the start of the lead bird’s downstroke for a single trial. If the top of this graph is defined as zero degrees and numbers increase clockwise, the mean of the trial means is 332 degrees ($r = 0.38$, $p = 0.021$, $n = 26$) with the shaded region showing the 95% confidence interval. This is a significant result supporting a non-random distribution of wingbeat phasing between the two birds with the lead bird tending to flap just before the following bird.
Fig. 5. (A) For each trial we measured the ratio of time that the lead bird is turning away from the following bird and found the leader turning away for the majority of time in 27 of 31 trials. The dashed line at 0.5 shows the expected mean if the turn direction was random. The data mean is significantly different from 0.5 by a t-test (mean = 0.65, SE = 0.03, p < 0.001). (B) The ratio of the mean followers speed to mean leaders speed shows that the lead bird is flying faster than the following bird in only 2 of 31 trials suggesting that the following bird is flying faster to adjust to an unpredictable flight path. The dashed line at 1.0 shows the expected mean if both birds had the same mean velocity. These data are significantly different from 1.0 by a t-test (mean = 1.06, SE = 0.01, p < 0.001).
Fig. 6. This lead bird turn had a centripetal force twice as large as any other observed turn, and rate of change in heading 35% larger than any other turn. (A) These images show the moment of peak rate of change in heading, and the moment 0.05 seconds later. The circle and square markers in the lower right corners are presented in the graphs to show the timing of these images. The contrast in these images has been enhanced. The 3D position (B), velocity with respect to time (C), rate of change in heading (D), centripetal force (E), and mass-specific power (F) are presented with each sequence starting at the diamond. The lead bird starts climbing around 0.5 seconds producing an increase in potential energy which causes the mass-specific power to reach a minimum prior to the minimum speed.
Fig. 7. Example frames from the three synchronized cameras (A, B, C) placed along the shoreline to capture different views of the same volume of space. After completing our camera calibration procedure, we digitized the location of a bird in two or more camera views, shown here with the bird located in one camera (marked by the black circle in A) and the epipolar lines, (in blue in B and C) to find the exact 3D location of the bird at that time. The epipolar line defines the ray where the bird could be located in B and C given its location in A. The zoomed insert in A is contrast enhanced. White dots mark the location of the two digitized birds. The red lines show the flight path of the digitized bird over the preceding 1 second.
Fig. 8. To measure the lateral, vertical, and forward distances between the lead and following birds we made a non-inertial coordinate system that rotates with each frame with $x_b$ remaining perpendicular to gravity. We shifted and rotated the 3D axes of each frame so the following bird was at the origin flying along the $y_b$-axis. The vertical distance is the $z_b$-coordinate of the lead bird (c). The lateral distance is the perpendicular distance from the $y_b$-axis to the lead bird ($\sqrt{a^2 + c^2}$). The forward distance is $y_b$-coordinate of the lead bird (b).
**Movie 1. Cliff swallow aerial contact.** This high-speed movie documents aggressive aerial contact among cliff swallows, behavior occasionally observed during chase sequences.
Table S1. Mixed-effects model results

<table>
<thead>
<tr>
<th>AIC</th>
<th>Intercept (a)</th>
<th>Coefficient 1 (b)</th>
<th>Coefficient 2 (c)</th>
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<tbody>
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<td>$F' = a + b \theta'$</td>
<td>84.08</td>
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<td>$F' = a + b \tan(\theta')$, random effects: trial nested in date</td>
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</table>

* $p < 0.05$ ** $p < 0.001$ *** $p < 0.0001$