NEUROMUSCULAR CONTROL AND KINEMATICS OF INTERMITTENT FLIGHT IN THE EUROPEAN STARLING (STURNUS VULGARIS)

BRET W. TOBALSKE
Division of Biological Sciences, University of Montana, Missoula, MT 59812, USA

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Summary

Electromyographic (EMG) and kinematic data were collected from European starlings (Sturnus vulgaris) flying at a range of speeds from 8 to 18 m s⁻¹ in a variable-speed windtunnel. Their flight at all speeds consisted of alternating flapping and non-flapping phases. Wing postures during non-flapping phases included glides, partial-bounds and bounds. Glides were performed proportionally more often within each speed and were longer in duration than either of the other two non-flapping postures, but the percentage of bounds increased markedly with increasing flight speed. The shift from flap-gliding at slow speeds towards flap-bounding at fast speeds was consistent with reducing mean power output relative to continuous flapping.

The starlings often combined more than one non-flapping posture within a single non-flapping period. Transitions between non-flapping postures, as well as transitions between bounds and subsequent flapping, were classified as ‘pull-outs’. Pull-outs consisted of an increase in wingspan but no change in wingtip elevation. The pectoralis and supracoracoideus exhibited electrical activity during glides but not during bounds. The scapulohumeralis caudalis was not active during glides, but this muscle and the supracoracoideus were typically active during partial-bounds and pull-out phases. The scapulohumeralis caudalis occasionally showed activity during bounds, which may reflect its role as a humeral retractor. The frequency and duration of non-flapping intervals in starlings were less during EMG experiments than during non-implanted flights.

During flapping phases, relative intensity and duration of EMG signal and wingbeat frequency increased with flight speed, whereas flapping or non-flapping cycle duration, the percentage of a cycle spent flapping and the number of wingbeats in a cycle were all greatest at 8 m s⁻¹. Wingbeat amplitude was smaller at intermediate speeds, but differences among speeds were not significant. These variables allowed indirect estimates of power output and suggested that minimum power speed for starlings was near 12 m s⁻¹ and that power output increased at both slower and faster speeds. Within windtunnel speeds, muscle activity changed in relation to wingspan at mid-upstroke, wingtip excursion, wingbeat frequency, acceleration, velocity, altitude and horizontal position.

Key words: European starling, Sturnus vulgaris, intermittent flight, flight, electromyography, muscle, kinematics, flap-glide, flap-bound, partial-bound, power output.

Introduction

Many species of birds exhibit intermittent flight in which flapping phases are regularly interrupted by phases of gliding (wings extended) or bounding (wings flexed). Flapping flight, per unit time, has the highest metabolic cost of any form of vertebrate locomotion (Tucker, 1968, 1973; Torre-Bueno and LaRochelle, 1978; Pennycuick, 1989; Schmidt-Nielsen, 1984). Is intermittent flight performed in order to reduce energy expenditure during flight? Several mathematical models based upon aerodynamic theory predict that, at fast speeds (generally at or faster than maximum range velocity, \(V_{mp}\)), flapping flight should offer a reduction in power output in comparison with continuous flapping flight (Lighthill, 1977; Rayner, 1977, 1985; Alexander, 1982; Ward-Smith, 1984a,b), whereas the model of DeJong (1983) predicts that savings should be greatest at minimum power velocity (\(V_{mp}\)). In contrast, flap-gliding should be less costly at slower speeds. Ward-Smith’s (1984b) model for flap-gliding flight predicts that a lower power output compared with continuous flapping may only be achieved during flight at \(V_{mp}\), whereas Rayner’s (1985) model predicts a significant saving at, or slower than, \(V_{mp}\). Thus, if intermittent flight is a method of reducing energetic costs, birds should tend to flap-gliding when flying at slower speeds and shift to flap-bounding at faster speeds (Rayner, 1985).

In general, intermittent flight patterns appear stereotypic for bird species and frequently serve as a characteristic for field identification. The ‘heavy’ flap-bounding flight style of woodpeckers (Picidae) is an example of this (Tobalske 1994a,b), as is the flap-gliding of falcons (Falconidae).
Moreover, most of the published mathematical models that pertain to intermittent flight behavior treat the two forms independently (Lighthill, 1977; Rayner, 1977, 1985; Alexander, 1982; Ward-Smith, 1984a,b). These models either imply or explicitly state that a bird species exhibits either flapping or flap-bounding, but not both, in order to fly over a range of speeds. DeJong (1983) developed a model for flap-bounding flight that includes a ‘pull-out’ phase of wing extension that occurs each time flapping resumes after a bound. The pull-out phase consists of an increase in wingspan without wingtip elevation and, according to DeJong (1983), should be aerodynamically similar to a glide but very brief in duration. Kinematic variation during the pull-out phase dramatically affects flap-bounding efficiency in DeJong’s (1983) model.

Empirical evidence regarding what form of intermittent flight a bird exhibits across a range of flight speeds is relatively scarce. Consistent with the hypothesis that intermittent flight patterns are fixed for a species, zebra finches (Taenopygia guttata) intermittently bound during slow-speed flight when intermittent gliding would, according to theory, be less costly (Rayner, 1985). However, the finches did not fly across a full range of flight speeds (Schloery, 1983; Rayner, 1985). By comparison, budgerigars (Melopsittacus undulatus) flying in a variable-speed windtunnel tend to decrease wing extension during non-flapping intervals as flight speed increases, from glides at slow speeds to partial-bounds at intermediate speeds and to bounds at fast speeds (Tobalske and Dial, 1994). During flapping phases, wingbeat frequency and patterns of motor-unit recruitment in their primary flight muscles also vary considerably, both within and among flight speeds.

The conflicting evidence from the studies of finches and budgerigars makes it worthwhile to conduct additional experimental studies of intermittent flight in birds. A prediction that follows from the study of budgerigars is that most birds that use intermittent flight will exhibit flapping-gliding at slow speeds and flap-bounding at fast speeds (Tobalske and Dial, 1994). In the present study, I begin to test this prediction by repeating the experiments performed upon budgerigars in Tobalske and Dial (1994) using European starlings (Sturnus vulgaris) (hereafter referred to as starlings). In addition, I report the effect of airspeed upon the wing kinematics and muscle activity patterns that starlings exhibit during flapping and non-flapping phases of intermittent flight. Starlings represent a species that commonly engages in flapping-gliding flight in the wild: Rayner (1985) presents a model for flapping-gliding flight based upon this species, and Torre-Bueno and LaRochelle (1978) describe well-trained starlings to be those that fly in a windtunnel with intermittent, ‘brief glides as is typical of starlings in the wild’. There is also some evidence that starlings flap-bound in nature, at least during migratory flights (Danielson, 1988).

Materials and methods

Windtunnel and training

The variable-speed windtunnel used in this study was the same as that used by Tobalske and Dial (1994). The flight chamber in which the starlings flew was walled with clear acrylic and measured 76 cm × 76 cm × 91 cm. Air was drawn through the flight chamber by a Buffalo 36-b-vanaxial-asymmetric fan, coupled with a 15 000 W d.c. motor. Airflow was straightened at all airspeeds by a 5 mm honeycomb baffling (10 cm thick) placed upwind from the flight chamber. Airflow was laminar in all areas of the flight chamber more than 2.5 cm from the walls, and airflow velocity varied by no more than 4.2% (Tobalske and Dial, 1994). Wind velocities were monitored with a pitot tube and an airspeed indicator calibrated with a Davis TurboMeter electronic airspeed indicator.

From a total of 11 starlings trapped from wild populations near Missoula, MT, USA, six were willing to fly in the windtunnel and were therefore used in this study [mean body mass 79.2±2.7 g (s.e.m.), mean wingspan 35.4±0.5 cm, N=6]. To encourage the birds to fly in the windtunnel, I used the methods of Torre-Bueno and LaRochelle (1978). Over a period of 4–6 weeks, I trained each starling for approximately 30 min per day to fly at 8, 10, 12, 14, 16 and 18 m s⁻¹. These speeds were selected as they represented the full range of speeds at which all of the birds would sustain flight for at least 1 min. Various combinations of five starlings were used for each experiment.

Kinematic analysis

Starlings (N=5) were filmed and video-taped while flying at various speeds in the windtunnel using a Red Lakes 16 mm camera at 200 frames s⁻¹, and a Panasonic Hi-8 video recorder at 60 frames s⁻¹ with an electronic shutter set at 4000 s⁻¹. Simultaneous lateral and dorsal views of the starlings were provided by placing the camera or video recorder lateral to the flight chamber and using a mirror mounted at 45° on top of the flight chamber. Posterior views were obtained by video-recording through the fan section behind the flight chamber. All electromyography (EMG) experiments were recorded on video tape and simultaneous high-speed films were made of approximately half of these sequences. An electrical pulse synchronized with each frame of film (Kodak 7250 Ektachrome) was recorded on computer to permit synchronization of kinematic data recorded on film (but not video tape) and EMG data.

Film and video tape were used to study flapping and non-flapping intervals. Film was viewed using an L-W motion analyzer projector (224-S) with a frame counter. Video tapes were viewed using a Panasonic AG-1960 video player with a shuttle advance and a television monitor. I identified non-flapping intervals as phases of no wing movement lasting at least 15 ms on filmed runs (three frames at 200 Hz) and 33.3 ms on video-taped flights (two frames at 60 Hz). These phases were classified into three categories on the basis of my visual estimate of wingspan (glide, wings extended greater than 30 cm; partial-bound, wingspan 5–20 cm; bound, wingspan less than 2.5 cm). Intervals during a non-flapping phase in which wingspan increased but wingtip elevation remained constant were considered ‘pull-outs’ (DeJong, 1983). I categorized wingspan for a total of 1093 non-flapping intervals among five starlings. The percentage of non-flapping phases in...
each category of wing extension \((N=3)\) was calculated for each bird \((N=5)\) at each speed \((N=6)\). Averages among birds were then computed for each speed.

I divided flights into cycles, which began with the onset of flapping following a non-flapping interval and lasted until the end of the subsequent non-flapping interval(s). Two non-flapping postures in immediate succession (i.e. without a wing-flap between them) were considered to be part of the same cycle, with the portion of time during which wing movement resulting in the transition between postures (pull-out) occurred counting as part of the second non-flapping posture. Continuous flapping for more than 5s was considered a complete cycle. Using up to ten cycles per bird \((N=5)\) and speed \((N=6)\), I recorded the number of wingbeats within the flapping phase, the duration of the flapping phase (ms) and the duration of the non-flapping phase(s) (ms). Average values for these variables and for the proportion of time spent flapping during a flight cycle were calculated for each bird and speed.

Kinematics during EMG sequences were examined by projecting each frame of high-speed film onto a graphics tablet (Summagraphics Bit Pad Plus) and digitizing anatomical landmarks (center of head, base of tail and distal tips of wings) along with reference points on the flight chamber (Digitizing and Analysis software, courtesy of Dr Stephen M. Gatesy). Kinematic variables included altitude (relative to the bottom of the flight chamber), horizontal position (relative to the back of the flight chamber), wingspan (distance between wingtips) and wingtip elevation (perpendicular distance of the wingtip above or below an imaginary line connecting the eye and the lateral base of the tail). I calculated flight velocity using changes in the altitude and horizontal position of the starling’s eye during 50 ms intervals. Acceleration was calculated as the rate of change in flight velocity within the 50 ms intervals. To reduce erratic fluctuations in the data, flight velocity and acceleration values were smoothed as a running average over five points using the formulae in Alexander (1983).

Wingbeat amplitude was estimated using video tapes of posterior-view flight. Hi-8 video master tapes were recorded to Super VHS using a Panasonic AG-1960 video player. Video frames were then imported to a Macintosh Quadra 950 computer using Macintosh Screenplay software. I digitized the dorsal wing near the wrist and shoulder using Image software (N.I.H.). Wingbeat amplitude was calculated as the angle described by the pivoting of the shoulder—wrist line during the time between the beginning of the downstroke and the beginning of the upstroke. I calculated wingbeat amplitude for both wings and averaged the result per wingbeat. Ten wingbeats were measured for each bird and speed.

Electromyography

EMG data were recorded using surgically implanted bipolar electrodes, as in Tobalske and Dial (1994). Birds were deeply anesthetized using intramuscular doses of ketamine \((25\text{mg kg}^{-1})\) during all surgical procedures. During surgery, body temperature was monitored with a YSI telethermometer and YSE series 400 probe. Body temperature was maintained at 41±0.5 °C using a heating pad and infrared lamp. Target muscles [left side, pectoralis major pars sternobrachialis (PECT), supracoracoideus (SUPRA) and scapulo-humeralis caudalis (SHC)] were exposed by skin incisions and blunt dissection and then implanted with electrodes (twisted pairs of 100 μm diameter silver wire with 0.5 mm insulation removed at each recording tip and the tips separated by a distance of 1 mm) using a 23 gauge hypodermic needle (Basmajian and DeLuca, 1985; Loeb and Gans, 1986). I used low-voltage electrical stimulation and visual inspection of wing movements to verify that electrodes were placed in the mid-region of each muscle.

Each electrode was sutured to adjacent fascia approximately 5 mm from its exit from the muscle. A short loop of wire was left between the exit point and fascial suture to allow the electrode tips to move freely with the contracting muscle, thus reducing low-frequency movement artifacts from the EMG signals. The electrodes were channeled subcutaneously to a female miniature connector (Microtech FG-6) which was sutured to the intervertebral ligaments and opened superficially between the scapulae on the dorsal surface of the bird.

EMG recordings started the day after an evening surgery. A lightweight, six-lead cable (Cooner Wire Co.) with a male miniature connector was used for carrying electrical signals from the female connector on the dorsal surface of the bird to the recording equipment. EMG signals were amplified and filtered (Grass P511J, 1000× gain, bandpass filter 100–3000 Hz) and recorded directly onto a computer (Zenith 386SX) via a Keithley 5000 series analog-to-digital (A/D) 12-bit converter. Digital sampling rates were 5 kHz.

For analysis of motor patterns of the recorded muscles, EMG signals were displayed from stored digital data using custom-built programs (DMAN and DAD, Dr Garr Updegraff, Data Crunch Inc., San Clemente, CA, USA). EMG bursts were identified as spikes with rectified amplitude at least two times greater than the baseline electrical noise. Timing was measured at a resolution of 0.5 ms. For each bird, ten consecutive wingbeats within a flight (disregarding intermittent non-flapping intervals) were measured for the three muscles at each flight speed. I calculated duration of burst (ms), relative intensity (the area of the rectified and integrated EMG burst divided by the value for the maximum intensity burst observed for that electrode) and wingbeat frequency (the reciprocal of the time interval from the onset of pectoralis muscle activity during one wingbeat to the onset of pectoralis activity for the subsequent wingbeat; Dial, 1992).

Statistical analysis

Values are presented as means ± s.e.m. \((N=5)\) starlings). For each of the variables examined in this study, I computed an average within each bird at each speed \((N=6)\). The distributions of these mean values did not violate the assumptions associated with parametric statistical analysis; thus, I tested for a significant effect of flight speed upon each variable by using univariate repeated-measures analysis of variance (von Ende, 1993; MANOVA procedure, SPSS Inc. 1990). The variables tested
were: relative intensity of EMG, EMG duration, wingbeat frequency, wingbeat amplitude, cycle duration, the percentage of time spent flapping within a flapping or non-flapping cycle and the number of wingbeats within a cycle.

Results

Starlings exhibited glide and partial-bound postures during non-flapping intervals at all flight speeds from 8 to 18 m s\(^{-1}\), whereas bound postures were only observed for speeds from 10 to 18 m s\(^{-1}\) (Fig. 1). At all speeds, glides made up over 50% of the total non-flapping intervals observed, but starlings decreased the percentage of glides and increased the percentage of bounds as flight speed increased from 8 to 18 m s\(^{-1}\) (Fig. 1). A trend with flight speed was not evident for partial-bounds, which were always less than 10% of the total non-flapping intervals within a speed. Non-flapping phases often consisted of more than one wing posture. Of the 751 glides recorded, 24.9% were preceded by a bound or a partial-bound, 51% of 272 bounds were followed immediately by a partial-bound or glide, and 61% of 70 partial-bounds were followed immediately by a glide. Glides were always followed by flapping flight, and bounds were always preceded by flapping flight. Pull-out phases, when wingspan increased but wingtip elevation remained near 0 cm (DeJong, 1983), always occurred between two non-flapping postures within a single non-flapping phase and between a bound and subsequent flapping flight.

Among five starlings, glides lasted 284.1±16.4 ms (S.E.M.), whereas the average duration for partial-bounds was 66.7±6.6 ms and for bounds was 57.0±3.6 ms. Pull-out phases lasted on average 43.8±2.4 ms. There was a significant effect of flight speed upon the average duration of a flapping or non-flapping cycle (P<0.0005), the percentage of time spent flapping during a cycle (P=0.049) and the number of wingbeats within a cycle (P<0.0005; Figs 2A, 3). At 8 m s\(^{-1}\), the average cycle duration was 5806±936 ms, the percentage of the cycle time spent flapping was 95.3±0.8% and the number of wingbeats in a cycle was 61.2±12.1. Average cycle duration and the number of wingbeats within a cycle both decreased with increasing flight speed to reach a minimum at 16 m s\(^{-1}\), where cycles lasted 1451.82±187 ms (Fig. 2A) and the number of wingbeats in a cycle was 14.5±2.0 (Fig. 3). At 18 m s\(^{-1}\), cycle duration increased to 1719±307.6 ms and the number of wingbeats in a cycle increased to 17.6±3.9. The percentage of time spent flapping within a cycle was 96.2±1.6%

Fig. 1. Starlings (Sturnus vulgaris) performed glides (black areas) more frequently than bounds (white areas) or partial-bounds (hatched areas) at any flight speed. As flight speed increased from 8 to 18 m s\(^{-1}\), the average percentage of bounds increased while the percentage of glides remained relatively constant. The trend of an increasing percentage of bounds and a decreasing percentage of glides at higher speeds was similar to that observed in budgerigars (Tobalske and Dial, 1994).

Fig. 2. (A) Flight speed had a significant effect upon the average duration of a flapping or non-flapping cycle (P<0.0005) and the average percentage of the cycle time spent flapping (P=0.049) for five starlings (Sturnus vulgaris) flying at speeds from 8 to 18 m s\(^{-1}\) in the windtunnel. Values are means±S.E.M. (B) The percentage of time spent flapping within a cycle for five individual starlings. The pattern observed for starlings S6 and S9 was considered most likely to represent behavior in the wild.
flapping decreased from 8 m s\(^{-1}\) to a minimum value at 12 m s\(^{-1}\) when the starlings flapped, on average, 78.7±4.9 % of the cycle time (Fig. 2A). From 12 to 18 m s\(^{-1}\), the average percentage of the cycle spent flapping was between 82 and 84 %.

Trends for all of the variables I examined showed considerable variation within individuals in comparison to the mean values among birds within a speed. For example, in starlings S6 and S9, the pattern for the percentage of time spent flapping within a cycle described an approximately U-shaped curve (i.e. lowest values at either 10 or 12 m s\(^{-1}\) and higher values at slower and faster speeds), whereas the three other starlings I used in this experiment (starlings S2, S5 and S8) decreased the percentage of time spent flapping as speed increased from 8 to 18 m s\(^{-1}\) (Fig. 2B). In general, starlings S6 and S9 appeared more acclimated than the other birds when flying in the windtunnel and they consistently performed longer-duration flights (with less external encouragement) at all flight speeds.

Flight speed did not have a significant effect upon wingbeat amplitude (\(P=0.617\)), although average amplitude was lowest at 10 m s\(^{-1}\) (92.9±4.1°) and somewhat greater (between 99.6 and 102.5°) at 8, 16 and 18 m s\(^{-1}\) (Fig. 4). Wingbeat frequency did vary significantly with flight speed (\(P=0.001\)), increasing from an average of 13.3±0.4 Hz at 8 m s\(^{-1}\) to 16.2±0.2 Hz at 18 m s\(^{-1}\) (Fig. 4).

In the PECT and SUPRA muscles, the general trend for both relative intensity and duration of EMG bursts during flapping was an increase from minimum values at 8 m s\(^{-1}\) through intermediate values at 10 and 12 m s\(^{-1}\) to maximum values at

Fig. 3. The average number of wingbeats within a flapping or non-flapping cycle varied with flight speed (\(P<0.0005\)) for five starlings (*Sturnus vulgaris*) flying in a windtunnel. The number of wingbeats in a cycle was considerably larger at 8 m s\(^{-1}\) than at other speeds. Values are means±S.E.M.

Fig. 4. The average wingbeat frequency increased with flight speed in five starlings (*Sturnus vulgaris*) (\(P=0.001\)). Average wingbeat amplitude was smaller at intermediate speeds but this was not significant (\(P=0.617\)). Values are means±S.E.M.

Fig. 5. The average relative intensity of EMG signal in five starlings (*Sturnus vulgaris*) during flapping flight tended to increase with flight speed. Flight speed had a significant effect on the relative intensity of EMG bursts in the supracoracoideus (SUPRA; \(P=0.001\)), a marginally non-significant effect for the relative intensity of the pectoralis (PECT; \(P=0.055\)) and the effect on the relative intensity of the supracoracoideus (SHC) was not significant (\(P=0.334\)). Values are means ± S.E.M.

Fig. 6. The average duration of EMG signal from the pectoralis (PECT), supracoracoideus (SUPRA) and scapulohumeralis caudalis (SHC) during flapping flight in five starlings increased with flight speed from a minimum at 8 m s\(^{-1}\) to a maximum at 18 m s\(^{-1}\). Differences among speeds were significant for the duration of EMG burst in the pectoralis (PECT; \(P=0.019\)) and in the supracoracoideus (SUPRA; \(P=0.008\)) but marginally non-significant in the scapulohumeralis caudalis (SHC; \(P=0.079\)). Values are means ± S.E.M.
higher speeds (Figs 5, 6). An example of this pattern is the average relative intensity of the PECT EMG, which was least at 8 \text{ m s}^{-1} (0.54\pm0.06) and greatest at 14 \text{ m s}^{-1} (0.75\pm0.03) and 16 \text{ m s}^{-1} (0.75\pm0.05). The duration of the SUPRA EMG was 44.5\pm3.0 ms at 8 \text{ m s}^{-1} and 66.9\pm5.3 ms at 18 \text{ m s}^{-1}. Differences among flight speeds were statistically significant for PECT EMG duration \((P=0.019)\) and for SUPRA EMG relative intensity \((P=0.001)\) and duration \((P=0.008)\). Variation with flight speed was evident but marginally non-significant in PECT relative intensity \((P=0.055)\) and SHC duration \((P=0.079)\), and variation in SHC relative intensity \((P=0.334)\) was not significant.

**Periodic fluctuation in muscle activity and kinematics during flapping phases**

Within a windtunnel speed, all of the starlings exhibited periodic fluctuation in EMG relative intensity and duration, which was visible in the EMG recordings (Fig. 7). This variation was concurrent with changes in wingbeat frequency (Fig. 8) and wingbeat kinematics, including wingspan at mid-upstroke and wingtip excursion in a parasagittal plane (Fig. 9). During peak accelerations, generally when a starling was gaining in altitude prior to a non-flapping phase and exceeding the windtunnel airspeed, wingbeat frequency and the distance the wingtip moved in a lateral plane during a wingbeat were increased, whereas wingspan at mid-upstroke was decreased (i.e. the wingtips were drawn in closer to the midline of the body). Also, EMG relative intensity increased and EMG duration decreased for the PECT, SUPRA and SHC muscles. Immediately preceding, or following, non-flapping phases, the starlings tended to decelerate or remain at a constant velocity. Relative intensity of EMG, wingtip excursion and wingbeat frequency were decreased, and duration of EMG burst and wingspan at mid-upstroke were increased. Peak negative acceleration of the starling usually occurred during the non-flapping phase.

![Graph showing EMG patterns](Image)

Fig. 7. Typical periodic fluctuations in EMG patterns from the pectoralis (PECT), supracoracoideus (SUPRA) and scapulohumeralis caudalis (SHC) during the flapping phases of intermittent flight in starling S9 with windtunnel airspeed at 16 \text{ m s}^{-1} (corresponds with Figs 8, 9). Similar patterns were seen for all starlings at all speeds. This sequence shows the final six wingbeats from flapping phase 1, a non-flapping phase (a partial-bound followed by a pull-out and then a glide) and then flapping phase 2, consisting of 17 wingbeats. Flapping phase 2 was followed by a partial-bound (not shown). Fluctuations in the peak positive and negative amplitudes of the EMG signals occurred during the flapping phases. In particular, wingbeats 7–14 of flapping phase 2 show increased EMG amplitude for all three muscles.
Measurements from 2 s of intermittent flight in starling S9 with the windtunnel airspeed at 16 m s\(^{-1}\) provide an example of the extent of these changes in EMG and kinematic variables (Figs 7–9). The sequence consisted of the last six wingbeats from a flapping phase (1) lasting 410 ms followed by a non-flapping phase lasting 310 ms (a partial-bound followed by a pull-out and then a glide), and then an entire flapping phase (2) including 17 wingbeats and lasting 1280 ms. During the two flapping phases, wingspan was always near 35 cm at mid-downstroke but varied between 2 and 8 cm at mid-upstroke (Fig. 9). Wingtip elevation varied between 7 and 16 cm at the beginning of downstroke and between -6 and -17 cm at the beginning of upstroke. In the PECT, relative intensity of the EMG signal ranged from 0.2 to 1.0 and duration of the EMG signal ranged from 22 to 41 ms (Fig. 8). Similar variation was observed in the SUPRA and SHC. Wingbeat frequency varied between 11.5 and 16.3 Hz (Fig. 8).

Wingbeats immediately preceding or following the non-flapping phase were most different from those in the middle of a flapping phase. For example, between wingbeat 1 of flapping phase 2, just after the non-flapping phase, to wingbeat 11 of flapping phase 2, during the middle of the flapping phase, wingspan at mid-upstroke decreased from 10 to 2 cm, the difference in wingtip elevation between the start and end of downstroke increased from 25 to 34 cm, the relative intensity of the EMG signal in the PECT increased from 0.28 to 0.36, the duration of EMG signal in the PECT decreased from 41 to 28 ms, and wingbeat frequency increased from 11.5 to 16.0 Hz.

During the non-flapping phase, wingspan fluctuated slightly but remained less than 10 cm during the partial-bound, which lasted 115 ms (Fig. 9). The subsequent glide lasted 210 ms, during which wingspan first increased to 32.5 cm with a pull-out, decreased slightly to 30 cm during the next 45 ms and remained near 30 cm for 120 ms until the end of the glide. The wingtip was held approximately 1 cm above the lateral midline of the body during the partial-bound and first half of the pull-out and at 0 cm during the rest of the pull-out and glide.

During the final six wingbeats of flapping phase 1, the starling’s altitude increased by 26 cm and its horizontal position (distance from the back of the flight chamber)
increased by 15 cm (Fig. 9). Also during this time, flight velocity was approximately 17.2 m s$^{-1}$, 1.2 m s$^{-1}$ faster than the windtunnel airspeed, and acceleration was near 0 m s$^{-2}$. During wingbeat 20, the final wingbeat of flapping phase 1, flight velocity began to decrease and acceleration therefore became negative. 20 ms into the non-flapping phase, vertical position began to decrease and a peak deceleration of $-7.5$ m s$^{-2}$ occurred. Velocity continued to decline throughout the non-flapping phase, reaching 15 m s$^{-1}$ by the end of the glide. 200 ms into the non-flapping phase,
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Horizontal position reached a maximum of 84 cm, whereupon it began to decrease. Acceleration increased from negative values to $0 \text{m s}^{-2}$ by wingbeat 3 of flapping phase 2. At this time, flight velocity reached a minimum of approximately $14.8 \text{m s}^{-1}$, and both horizontal and vertical positions continued to decrease. During wingbeats 9 and 10 of flapping phase 2, horizontal and vertical positions began to increase, flight velocity exceeded $16 \text{m s}^{-1}$ and acceleration reached a maximum of $4.5 \text{m s}^{-2}$. During the final wingbeats of flapping phase 2, prior to the next non-flapping phase (which was a partial-bound), acceleration began to decrease, flight velocity reached approximately $17 \text{m s}^{-1}$, and both horizontal and vertical positions had increased to values similar to those before the previous non-flapping phase.

Muscle activity and wing kinematics during non-flapping phases

I successfully recorded simultaneous EMG and kinematic data from the PECT, SUPRA and SHC muscles during 84 non-flapping wing postures and 15 pull-outs in four starlings. The

![Graph showing bird flight and EMG data](image)

**Fig. 10.** An example of the wing kinematics and EMG patterns recorded from starling S9 during a partial-bound followed by a pull-out and then a glide at a windtunnel speed of $16 \text{m s}^{-1}$. Flapping ended on the upstroke before the partial-bound and resumed on a downstroke after the glide.
non-flapping postures included 53 glides, 23 partial-bounds and eight bounds. Eighty-one of these non-flapping postures were from two starlings (starling S6, \( N = 22 \); starling S9, \( N = 59 \)); and all 15 of the pull-outs were from these two birds (starling S6, \( N = 5 \); starling S9, \( N = 10 \)). During EMG experiments, partial-bounds were only performed by starlings S6 and S9 and bounds were only performed by starling S9. As starling S9 performed all of the non-flapping postures while implanted with EMG electrodes, I will describe the neuromuscular control and kinematics of non-flapping intervals in starlings using two typical examples of intermittent flight in this bird.

During flight at 16 m s\(^{-1}\), starling S9 performed a 200 ms non-flapping period consisting of a 20 ms partial-bound followed by a 40 ms pull-out and then a 140 ms glide (Fig. 10). The starling entered the partial-bound during upstroke with very low-amplitude EMG activity present in the SUPRA. During the partial-bound, the wingspan was approximately 10 cm and wingtip elevation was 0 cm. The PECT and SHC were inactive and the SUPRA continued to exhibit low-level spikes of electrical activity. The partial-bound ended and the pull-out began as the wingspan began to increase and the PECT exhibited EMG activity. Throughout the pull-out, the PECT

Fig. 11. An example of a bound followed by a pull-out phase in starling S9 during flight at a windtunnel airspeed of 18 m s\(^{-1}\). Flapping ended on the upstroke before the bound and resumed with an upstroke after the pull-out.
...and SUPRA were active, the SHC inactive and wingtip elevation remained close to 0 cm. For most of the glide, the wingspan was approximately 30 cm, wingtip elevation was near 0 cm, the PECT was continuously active, the SUPRA occasionally exhibited spikes of electrical activity and the SHC was inactive. 20 ms before the end of the glide, EMG activity in the SUPRA ceased; 10 ms later the PECT became inactive and 5 ms before the end of the glide the SHC became active. Flapping resumed with a 25 ms downstroke as wingspan and wingtip elevation decreased. The SHC exhibited electrical activity during the downstroke, and 5 ms after the downstroke commenced the SUPRA also showed a burst of EMG activity. Although the PECT remained inactive during this particular downstroke, in other instances where flapping resumed with a downstroke after a glide, the pectoralis was active (see Figs 7–9).

During a 15 ms bound in starling S9 flying with the windtunnel set at 18 m s\(^{-1}\), wingspan was less than 2 cm, wingtip elevation was approximately 0 cm and the PECT, SUPRA and SHC were inactive (Fig. 11). The starling entered the bound from an upstroke as the PECT and SUPRA were inactive but while the SHC was exhibiting EMG activity. During the bound, wingspan and wingtip elevation were constant. The bound was followed by a pull-out phase which lasted 25 ms. During the pull-out, the PECT remained inactive, the SUPRA and SHC exhibited bursts of EMG activity, wingspan increased and wingtip elevation remained near 0 cm. Activity in the SHC ceased after 15 ms of the pull-out, whereas activity in the SUPRA continued for 10 ms into the subsequent flapping phase. Flapping resumed during this period of SUPRA activity on an upstroke as wingspan increased and wingtip elevation increased.

**Discussion**

Starlings, representing a typical flap-gliding species, tended to flap-glide at slow speeds and flap-bound at fast speeds (Fig. 1). Compared with continuous flapping at all flight speeds, average mechanical power output should be lower if a bird flap-glides at slower speeds and flap-bounds at faster speeds (Lighthill, 1977; Rayner, 1977, 1985; Alexander, 1982; Ward-Smith, 1984a,b). Thus, starlings, like budgerigars (Tobalske and Dial, 1994), used intermittent flight in a manner that was consistent with reducing average mechanical power output during flight across a full range of speeds. DeJong (1983) suggests that the use of pull-out phases after bounds would make flap-bounding flight less costly than continuous flapping at most flight speeds, rather than only at fast speeds. Thus, the use of pull-outs after bounds in starlings (Fig. 11) may explain why I observed some intermittent bounds at all speeds except 8 m s\(^{-1}\).

Mechanical power output was obviously higher during flapping than during glides, partial-bounds and bounds because periods of no wing movement (Figs 7–11) represent no power output (i.e. distance of muscle contraction = 0 cm). Periods of muscle inactivity and isometric contractions during non-flapping phases (Figs 7–11) probably represent substantial savings in metabolic power output relative to isotonic contractions during flapping (Goldspink, 1981).

Models of mechanical power output during level flapping flight predict a U-shaped curve with a minimum power required to fly at an intermediate speed (\(V_{\text{mp}}\)) and greater values at both slower and faster speeds (Pennycuick, 1968b, 1975, 1989; Tucker, 1973; Rayner, 1979). Contrary to these models, the rate of metabolic energy expenditure is relatively constant across measured flight speeds in most of the species of flying animals that have been studied, suggesting a flattened or J-shaped curve (Ellington, 1991). A flat metabolic power curve is particularly evident in starlings (Torre-Bueno and LaRochelle, 1978), but a classic U-shaped curve is evident in budgerigars (Tucker, 1968). The trend in the starlings to use flap-gliding at slow speeds and flap-bounding at fast speeds (Fig. 1) may explain some of the discrepancies between the predictions of mechanical power models and observations of relatively constant metabolic power output for birds that use intermittent flight, if the birds on which metabolic power was measured exhibited such intermittent flight behaviors during the experiments.

The U-shaped metabolic power curve exhibited by budgerigars (Tucker, 1968) seems at first to undermine this argument, but it is probable that the additional payload of a mask and a sampling tube used in measuring oxygen consumption (Tucker, 1968) would severely limit their use of non-flapping phases. The presence of trailing EMG wires appeared to constrain the performance of non-flapping phases in starlings in the present study, and in previous experiments with budgerigars, which have approximately half the body mass of starlings, using trailing EMG wires much greater than 1 g in mass has eliminated their performance of non-flapping phases altogether (Tobalske and Dial, 1994). Significantly, the flat metabolic curve for starlings was obtained using a closed-circuit windtunnel so that the starlings had no increased payload or drag (Torre-Bueno and LaRochelle, 1978).

Intermittent flight is unlikely to result in a flat power curve, however, because flight speed had a significant effect upon other kinematic and EMG variables in starlings, suggesting, at least qualitatively, that mechanical power output should describe a concave curve in approximate agreement with a U- or J-shape. The average percentage of time spent flapping in a cycle was least at 12 m s\(^{-1}\) (Fig. 2A), which probably reflects \(V_{\text{mp}}\) for starlings. Average cycle duration, the percentage of cycle time spent flapping and the number of wingbeats in a cycle were all greater at 8 m s\(^{-1}\) than at other flight speeds (Figs 2, 3). Thus, average power output is likely to be relatively large at the lowest speed for which the starlings would sustain flight. During flapping phases, however, the relative intensity and duration of EMG signals in the PECT, SUPRA and SHC muscles along with wingbeat frequency generally increased with flight speed (Figs 4–6), which is similar to the pattern seen in budgerigars (Tobalske and Dial, 1994). The changes in relative intensity and duration of EMG signals directly represent changes in the spatial and/or temporal
recruitment of motor units in the muscles (Hagiwara et al. 1968; Burke, 1981; Basmajian and DeLuca, 1985) and also are correlated with force production in muscle (Dial and Biewener, 1993). These trends therefore suggest an increase in power output per wingbeat as flight speed increases because the starlings were likely to be using more forceful contractions with each wingbeat (Dial and Biewener, 1993), the muscles were active for a greater percentage of the wingbeat cycle (Dial et al. 1991; Dial, 1992) and there were more wingbeats per unit time within a flapping phase. Although wingbeat amplitude did not change significantly with flight speed, the average wingbeat amplitude was smaller at intermediate speeds (Fig. 4). This was approximately similar to the pattern Torre-Bueno and LaRochelle (1978) report for starlings, and indicated slightly less contractile range in the muscle fibers, and thus lower power output, during the flapping phases at intermediate speeds (Dial and Biewener, 1993).

Across the full range of flight speeds, it was clear that there was a general increase in relative intensity and duration of EMG signals with flight speed (Figs 5, 6), but the large standard errors and, in certain cases, the lack of statistical significance, make detailed comparisons between close speeds rather tenuous. For example, there was a decrease in the mean relative intensity of EMG signal in the PECT between 16 and 18 m s$^{-1}$ (Fig. 5), which may have represented a reduction in recruitment of motor units and a reduction in peak force during non-flapping intervals in starlings appeared to represent random fluctuation about the mean: between 16 and 18 m s$^{-1}$, the mean values among five starlings flying in the windtunnel were higher for all these variables at all flight speeds, particularly at 8 m s$^{-1}$ (Figs 2–4). Multiplying average cycle time during migratory flights by the average percentage of the cycle spent non-flapping gives an average duration of 200.6 ms for bound phases (Danielson, 1988), whereas the average duration of bounds for starlings in the windtunnel was only 57.0 ms.

Thus, the starlings were probably affected to some extent by the artificial nature of flight in the windtunnel. This is not a surprising result and shows the importance of field studies for evaluating the results of laboratory experiments. Power output during flight can be reduced for animals flying in confined spaces or above smooth surfaces, such as in a flight chamber, because of recirculation of lift vortices (Rayner, 1991; Rayner and Thomas, 1991). With decreased power costs, the starlings presumably would have flapped less during a cycle in the windtunnel in comparison with migratory flight, but this was not the case. Some of the discrepancy between my windtunnel data and Danielson’s (1988) migratory flight data may therefore be explained by the stress that the starlings experienced under experimental conditions in the laboratory or the restriction in changes of altitude caused by the ceiling and floor of the flight chamber. The effect of airspeed upon the average percentage of the cycle spent flapping differed in relation to the apparent willingness with which individual starlings flew (Fig. 2B). For the two starlings (S6 and S9) that I judged to be the most acclimated in the flight chamber, the average percentage of time spent flapping during flight at 12 m s$^{-1}$ was near Danielson’s (1988) reported value of 67.7 % and, in starling 9, this value decreased to 61 % during flight at 10 m s$^{-1}$.
both increased, and both the frequency and duration of non-flapping intervals decreased. Virtually all of the non-flapping phases recorded during EMG experiments were from the two most able fliers (starlings S6 and S9), and only starling S9 performed bounds while implanted with EMG electrodes. Also, the average duration of a bound during non-implanted flight was 57 ms, whereas bounds during EMG experiments generally lasted less than 20 ms (Fig. 11). Rayner (1985) predicts that the percentage of time spent flapping in a cycle should be greater when the fat load of a bird, and thus body mass, is greater. My observations support this prediction if the added payload of EMG recording equipment can be substituted for an increase in mass due to body fat. However, because I lacked control treatments in this study, it was not possible to discriminate between the effects of surgery, EMG electrode implantation and added weight or drag due to EMG electrodes and electrode connections.

The periodic changes in relative intensity and duration of EMG signals in the PECT, SUPRA and SHC, which starlings exhibited during flapping phases at all flight speeds (Figs 7, 8), are also evident in budgerigars (Aulie, 1970; Tobalske and Dial, 1994) and black-billed magpies (Pica pica; Olson, 1993). They may represent a common pattern of motor-unit recruitment (Hagiwara et al. 1968; Burke, 1981; Basmajian and DeLuca, 1985) during the flapping phases of intermittent flight. EMG bursts of higher relative intensity and of shorter duration were coincident with peak positive acceleration, increasing altitude and flight velocity exceeding the airspeed in the windtunnel (Figs 7–9). Wingbeat frequency was higher at these times, as was the difference between wingtip elevation at the beginning of the downstroke and the beginning of the upstroke (wingtip excursion), which Scholey (1983) showed to be related to wingbeat amplitude. The changes in relative intensity of EMG signal, wingbeat frequency and wingbeat amplitude indicate that mechanical power output was greater during the peak positive acceleration phases (Dial and Biewener, 1993).

According to Rayner (1985), if a starling fluctuates between high-speed flapping and slow-speed glides, it should obtain increased savings in mechanical power output in comparison with maintaining a constant airspeed during the entire flapping or non-flapping cycle. Starlings typically performed intermittent glides in this manner (Fig. 9). Flight velocity varied around the average incident airspeed in the windtunnel, with slower speeds recorded during and shortly after a non-flapping phase and faster flight speeds recorded prior to a non-flapping phase.

Wingbeat gait is a function of whether the wings produce lift during the upstroke, and increased wingspan during the upstroke is a correlate of lift production (Scholay, 1983; Rayner, 1988). My observations indicate that starlings gradually changed gait within the flapping phases of intermittent flight. Immediately before, and for some time after, a non-flapping phase, wingspan at mid-upstroke was higher than that observed during peak positive accelerations (Fig. 9), when the starlings were gaining in altitude and exceeding the incident airspeed in the windtunnel. This kinematic pattern, with the wings more extended during the upstroke, is more similar to a continuous-vortex gait with lift production during the upstroke, whereas the decreased wingspan at mid-upstroke that the starlings exhibited during peak positive accelerations was more similar to the vortex-ring gait with no lift production during the upstroke (Rayner, 1988). Wingspan in starlings did not vary as much among mid-downstrokes as among mid-upstrokes, and starlings always entered non-flapping phases during the upstroke and resumed flapping with an upstroke after partial-bounds and pull-outs (following a bound; Fig. 11). This behavior is generally consistent with the variable nature of upstroke in lift production (Rayner, 1985, 1988). However, brief downstrokes usually occurred after glides (Figs 9, 10).

The patterns of muscle activity during glides in starlings (Figs 7, 10) closely resembled those of American kestrels Falco sparverius (Meyers, 1993), in which the sternobrachial portion of the PECT and the SUPRA exhibits EMG bursts. The EMG activity in the PECT, with no change in wing movement, indicated an isometric contraction functioning to support the body relative to the wing during the glide (Meyers, 1993), and the SUPRA was presumably functioning as an antagonist to the PECT in order to resist wing depression (Meyers, 1992a, 1993). Herring gulls (Larus argentatus) and budgerigars also exhibit isometric contractions in the PECT during glides (Goldspink et al. 1978; Tobalske and Dial, 1994), but during glides in budgerigars, the SUPRA does not exhibit EMG activity.

It is unlikely that starlings were generating lift with their wings during bounds, because the wings were flexed against the body and wingspan was minimal (Figs 1, 11), but it is not obvious whether lift was produced from the wings during partial-bounds and pull-out phases. Vortex visualization techniques would help to clarify whether these phases were more aerodynamically similar to bounds or to glides (e.g. Speeding, 1987), but some insight is nonetheless available from the EMG results (Figs 7, 9–11).

Because the PECT was inactive during some partial-bounds (Fig. 10) and pull-out phases (Fig. 11), it is unlikely that lift was always being produced. If lift were being produced, the PECT should have been resisting upward wing movement and exhibiting an isometric contraction similar to that recorded during glides (Figs 7, 9, 10) (Goldspink et al. 1978; Meyers, 1993; Tobalske and Dial, 1994). An alternative explanation is that, in the regionally complex PECT, distant motor units were active but occasionally went unrecorded (Boggs and Dial, 1993; Meyers, 1992a, 1993). During the relatively brief partial-bounds, pull-out phases and bounds, the functions of the flight muscles may also have been masked by a delay between the timing of EMG activity and force production on the proximal humerus and subsequent kinematic changes at the wingtip (Biewener et al. 1992; Dial and Biewener, 1993). Any of these alternatives may also explain why the PECT exhibited EMG activity during the initiation of the downstroke after certain glides (Figs 7, 9) and not others (Fig. 10).

During partial-bounds and pull-out phases, the SUPRA and the SHC usually exhibited EMG activity (Figs 7, 9, 11;
compare with Fig. 10 where the SHC was inactive), which may have represented isometric contractions functioning to maintain the posture of the wing (Salt, 1963) or, especially in the case of pull-outs when wingspan increased, isotonic contractions involved in humeral movement. It is difficult to assess precisely the function of these muscles without more detailed data on the kinematics of the humerus (e.g. Jenkins et al. 1988), the electrical activity in more distal wing muscles (e.g. Dial et al. 1991; Dial, 1992) and the aerodynamics of the wing (e.g. Spedding, 1987).

During bounds in starlings, as in budgerigars (Tobalske and Dial, 1994), both the PECT and the SUPRA were inactive (Fig. 11). These two muscles constitute up to 35% of the body mass of flying birds (George and Berger, 1966); thus, their lack of activity during bounds could represent significant savings in metabolic energy during migratory flights, when bounds in starlings last approximately 200 ms (Danielson, 1988). The lack of EMG activity in the SUPRA during bound phases was different from the sporadic EMG activity exhibited during partial-bounds and pull-outs (Figs 7, 9–11). Salt (1963), on the basis of histological study, suggested that the SUPRA functions in wing-fixation during bounds, but my results do not support this hypothesis. The SHC did not exhibit EMG activity during the bound shown in Fig. 11, but in other bounds I recorded bursts of activity similar to the burst observed during the bound shown in Fig. 11, but in other bounds I assessed precisely the function of these muscles without more detailed data on the kinematics of the humerus (e.g. Jenkins et al. 1988), the electrical activity in more distal wing muscles (e.g. Dial et al. 1991; Dial, 1992) and the aerodynamics of the wing (e.g. Spedding, 1987).

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References


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