

NEUROMUSCULAR CONTROL AND KINEMATICS OF INTERMITTENT FLIGHT IN BUDGERIGARS (*MELOPSITTACUS UNDULATUS*)

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Summary

Kinematic and electromyographic data were collected from budgerigars (parakeets), *Melopsittacus undulatus*, flying at different speeds in a variable-speed wind tunnel. Birds exhibited flap-gliding at low speeds and flap-bounding at high speeds. The percentage of time spent flapping generally decreased at intermediate speeds. These behavior patterns are consistent with minimizing energy expenditure according to aerodynamic theory. During intermittent glides, the pectoralis exhibited an isometric contraction while the supracoracoideus was inactive. During bounds, both muscles were inactive.

Contrary to earlier work, our studies indicate that budgerigars do not exhibit simultaneous twitch contractions of the pectoralis during each wingbeat, but rather generate typical multiple-spike electromyographic bursts that represent motor unit action potential trains or asynchronous twitch contractions from different motor units. The relative intensity of electromyographic bursts from the primary flight muscles increased with flight speed. This may indicate an increase in force production.

Our observations of isometric contractions during glides, along with patterns of variation in muscle activity and wingbeat frequency, do not support the hypothesis that small birds such as the budgerigar use flap-bounding as their only means of reducing power output during flight.

Introduction

Most species of birds do not flap their wings continuously during flight. Rather, they exhibit one of two intermittent flight styles termed undulating and bounding (Lighthill, 1977; Rayner, 1977, 1985; Alexander, 1982; Ward-Smith, 1984*a,b*). Undulating flight consists of flapping phases alternating with brief glides and is typically exhibited by small- to medium-sized birds such as starlings (Sturnidae), jays and crows (Corvidae) and falcons (Falconidae). Bounding is a flight pattern in which a bird alternates flapping phases with periods in which its wings are folded against its body; it is generally observed in small passerines (Passeriformes), woodpeckers (Piciformes), owls (Strigiformes) and parrots (Psittaciiformes), such as the budgerigar (or parakeet), *Melopsittacus undulatus*.

Key words: budgerigar, *Melopsittacus undulatus*, intermittent flight, electromyography, kinematics.

The terminology of ‘undulating’ and ‘bounding’ flight styles is confusing and non-intuitive because birds exhibiting either intermittent flight style periodically rise and fall in altitude: a pattern which people unfamiliar with the terminology readily interpret as undulation. In an effort to use terms more descriptive of the respective locomotor styles within intermittent flight, taking into account wing kinematics and overall flight path, we will discuss undulating and bounding (*sensu* Lighthill, 1977; Rayner, 1977, 1985; Alexander, 1982; Ward-Smith, 1984*a,b*) as flap-gliding and flap-bounding, respectively.

To date, no empirical study has demonstrated why birds perform these two basic patterns of intermittent flight (but see Csicsáky, 1977; Scholey, 1983). However, several authors have presented mathematical models in an attempt to characterize aspects of mechanical power output during intermittent flight (Lighthill, 1977; Rayner, 1977, 1985; Alexander, 1982; Ward-Smith, 1984*a,b*). These authors predict that flap-bounding, compared with continuous flapping flight, offers an energetic saving at high speeds (i.e. above maximum range speed, V_{mr}). Rayner (1985) further suggested that flap-gliding flight is energetically attractive at most flight speeds, especially those slower than minimum power speed (V_{mp}).

Birds should experience strong selective pressures to minimize energetic costs because flying is an energetically expensive form of locomotion per unit time (Tucker, 1968, 1973; Pennycuik, 1968*b*, 1989; Rayner, 1979; Schmidt-Nielsen, 1984). As flap-bounding and flap-gliding are seldom observed in the same species (Rayner, 1985), the question arises as to why a flap-bounding bird does not flap-glide at slow speeds to reduce the cost of aerial locomotion (Rayner, 1985).

To explain this paradox, Goldspink (1977) and Rayner (1977, 1985) suggested that flap-bounding is a compromise between the need to maintain muscle contractions at an optimal velocity and the need to assume a range of flight speeds. In small birds, including the budgerigar, the pectoralis consists entirely of fast-twitch oxidative-glycolytic fibers (FOG) (Rosser and George, 1986). Specific muscle fiber types have a narrow range of efficient contractile velocities (Goldspink, 1977, 1981), thus limiting the range of useful strain rates.

Rayner (1985) suggested that such homogeneity of fiber types may constrain the pectoralis to function as a ‘fixed gear’ during flapping flight. According to the ‘fixed gear’ hypothesis (Rayner, 1985), a small bird in flight should limit the range of contractile velocity in its muscle fibers either by maintaining constant wingbeat frequency and amplitude or by inversely varying wingbeat frequency with amplitude. Gliding, where muscles are active (e.g. Goldspink *et al.* 1978), but velocity of shortening is zero, should not be used regularly by small birds lacking slow muscle fibers because their faster fibers are relatively uneconomical during isometric contractions (Goldspink, 1977, 1981; Rayner, 1985). Thus, for small birds, the only efficient method of varying power output during flight would be to bound intermittently.

The ‘fixed gear’ hypothesis (Rayner, 1985) relies in part upon Aulie’s (1970) observations of single-spike electromyographic (EMG) bursts from the pectoralis muscles of flying budgerigars. These have been interpreted as synchronous recruitment of motor units or the activation of only one motor unit with each wingbeat (Hagiwara *et al.* 1968; Aulie, 1970). Single-spike action potentials could represent a single rise and fall in

force, as seen for *in situ* ‘twitch’ contractions (McMahon, 1984), which would thereby limit the available range of force production in the flight muscles (Rayner, 1985).

Several studies of flight in budgerigars (Tucker, 1968; Aulie, 1970) and other small birds (Hagiwara *et al.* 1968; Torre-Bueno and LaRochelle, 1978) have demonstrated relatively constant wingbeat frequencies during flapping flight at different speeds (Rayner, 1985). Wingbeat amplitude may be more variable and may be related to the theoretical increase in power costs of flapping flight at low and high speeds (Hagiwara *et al.* 1968; Goldspink, 1981; Torre-Bueno and LaRochelle, 1978).

In this paper, we report on the neuromuscular activity patterns of the pectoralis and supracoracoideus muscles together with some basic kinematics of budgerigars flying in a variable-speed wind tunnel. Using muscle activity patterns to represent force of contraction (Dial and Biewener, 1993) and wing kinematics (wingbeat frequency and wing-tip position) to infer velocity of contraction, we test the ‘fixed-gear’ hypothesis (Rayner, 1985) that small birds such as the budgerigar are physiologically constrained to use flap-bounding as their only means of varying power output during flight at different speeds.

Materials and methods

Wind tunnel and training

The variable-speed wind tunnel contained a 76 cm×76 cm×91 cm clear acrylic section through which air was drawn by a Buffalo 36-b-vanaxial-asymmetric fan, coupled with a 15 000 W d.c. motor. Airflow was straightened at all airspeeds by 5-mm honeycomb baffling (10 cm thick) placed upwind from the flight chamber. By placing a smoke bomb at the intake funnel and filming the 25-cm diameter stream of smoke moving through the wind tunnel, we examined turbulence of the airstream within the flight chamber. In addition, we placed a Davis TurboMeter electronic wind speed indicator (accurate to ±3 %) in 12 locations around the test section of the wind tunnel to measure the velocity of the airflow. These data demonstrated that airflow was laminar in all areas of the working section more than 2.5 cm from the walls and that the velocity of airflow varied by no more than 4.2 %. Wind velocities were monitored with a pitot tube and an airspeed indicator calibrated with the Davis Turbometer.

Budgerigars (mean body mass 34.5±0.5 g, range 29.0–40.0 g, $N=8$) were trained for approximately 30 min per day (one bird flew continuously for more than 1 h in the tunnel) to fly in the wind tunnel for several minutes at each of the speeds selected for filming and for electromyographic experiments: 7, 9, 11, 13 and 16 m s⁻¹. Eight birds were used during this study, although sample sizes for specific tests were always less than eight. We followed the methods of Torre-Bueno and LaRochelle (1978) for training the birds to fly in the tunnel. For each bird, training required a minimum of 4 weeks. Up to four birds were trained in the tunnel simultaneously.

Electromyography

Electromyographic data were recorded ($N=4$ birds) using surgically implanted bipolar electrodes similar to those previously described (Dial *et al.* 1987, 1988, 1991; Dial,

1992a,b; Dial and Biewener, 1993). Birds were administered methoxyflurane inhalant and intramuscular doses of ketamine (25 mg kg^{-1}) to induce deep anesthesia during all surgical procedures. During surgery, body temperature was monitored with a YSI telethermometer and YSE series 400 probe. Body temperature was maintained at $41 \pm 0.5^\circ \text{C}$ using a heating pad and infrared lamp. Target muscles (left side, pectoralis major pars sternobrachialis and supracoracoideus) were exposed by skin incisions and blunt dissection and then implanted with electrodes (twisted pairs of $100 \mu\text{m}$ 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 De Luca, 1985; Loeb and Gans, 1986). We used low-voltage electrical stimulation and visual inspection of wing movements to verify that electrodes were placed in the middle of each muscle.

Each electrode was sutured to adjacent fascia approximately 5 mm from its exit from the pectoralis pars sternobrachialis and at two points on the sternal carina. 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 trailing electrodes were approximately 75 cm long, 0.3 mm in diameter and 1 g in mass, and ran from the carinal sutures to a female miniature connector (Microtech FG-6) placed at the bottom of the flight chamber in the wind tunnel.

EMG recordings started 1 h after the bird recovered from surgery. A lightweight four-lead shielded cable (Cooner Wire Co.) with a male miniature connector was used for carrying electrical signals from the female connector at the bottom of the flight chamber to the recording equipment. Thus, the budgerigars only had to carry the electrodes during flight. EMG signals were amplified and filtered (Grass P511J, gain $1000\times$, filter $100\text{--}3000 \text{ Hz}$ bandpass) and recorded directly to a computer (Zenith 386SX) via a Keithley 5000 series analog-to-digital (A/D) 12-bit converter. Digital sampling rates were 5 kHz .

In an effort to replicate Aulie's (1970) EMG experiments on budgerigars, we subcutaneously implanted a unipolar electrode with a 3-cm exposed tip over the pectoralis major pars sternobrachialis of one bird and also implanted a conventional bipolar electrode (Basmajian and De Luca, 1985; Loeb and Gans, 1986) into the muscle as described above.

Cinematography

Budgerigars ($N=5$) were filmed while flying at various speeds in the wind tunnel using a Red Lakes 16-mm camera at either 100 or $200 \text{ frames s}^{-1}$. Simultaneous lateral and dorsal views were provided by placing the camera lateral to the flight chamber and using a mirror mounted at 45° on top of the flight chamber. During filming, each bird flew either alone or with up to two other birds. High-speed films were also made of approximately half of the EMG sequences. An electrical pulse synchronized with each frame of film (Kodak 7250 Ektachrome) was recorded on computer to permit correlation of kinematic and EMG data.

Data analysis

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.). 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 analyzed for both muscles during different flight speeds.

We calculated duration of burst (ms) and relative intensity (the area of the rectified and integrated EMG burst, divided by the value for the maximum intensity burst observed for that electrode). The data were approximately normally distributed (Sokal and Rohlf, 1981); thus, we quantified variance using univariate mixed-model, two-way analysis of variance (ANOVA) (SPSS Inc., 1990). We considered speeds ($N=4$, the birds would not fly at 16 m s^{-1} during EMG experiments) to be a fixed effect and birds ($N=4$) a random effect. Variance among bursts ($N=10$ for each bird and speed) provided the within-individual error term for each ANOVA. Variance components for factors in the analysis were determined following Sokal and Rohlf (1981).

Film was viewed using an L-W motion analyzer projector (model 224-S) with a frame counter to analyze wing-flapping and non-flapping intervals along with wingbeat frequency. We divided flights into cycles. Each cycle began with the onset of flapping following a non-flapping interval and lasted until the end of the next non-flapping interval (number of cycles = 234). Continuous flapping during an entire filming period (approximately 5 s each) was counted as one cycle, and all flights lasted at least 4 s. Wingbeat frequency was calculated from all of the wingbeats in the flapping portion of each cycle divided by the duration of the flapping phase.

For statistical analysis of kinematic variables, we included only non-EMG implanted flights because synchronized EMG–kinematic data were not collected for all birds and speeds. We grouped wing extension during non-flapping intervals into three categories on the basis of our visual estimate of wing extension (glide, wings fully extended at least to the wingspan at mid-downstroke during the two flaps immediately before and after the glide; intermediate, wing extension anywhere between a glide and a bound – the birds usually held their wings in a ‘horseshoe-shaped’ posture; bound, wings fully flexed and wingtips against the body as during perching) and tallied these data for each flapping/non-flapping cycle observed. We tested for non-random association between flight speed ($N=5$) and the proportion of intermittent non-flapping phases in each category of wing extension ($N=3$) using a χ^2 -test (SPSS Inc., 1990). Variance in wingbeat frequency and percentage of time spent flapping within a cycle were examined using univariate two-way ANOVA (SPSS Inc., 1990) as described previously for EMG variables. Data for these two kinematic variables satisfied the assumptions for parametric analysis (Sokal and Rohlf, 1981).

Kinematics during EMG sequences were examined by projecting each frame of 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 a grid against the walls of the flight chamber (Digitize and Analysis software for the Macintosh, courtesy of Dr Stephen M. Gatesy). Kinematic variables included body angle (acute angle formed by a line between the center of the head and the base of the tail and a horizontal

line through the base of the tail), altitude (relative to a fixed point within the flight chamber), distance between wingtips (wing span) and perpendicular distance of the wingtip above or below the midline of the body (wingtip elevation). Values are presented as mean \pm S.E.M.

Results

Muscle activity

Electromyographic signals using conventional bipolar electrodes in the pectoralis major pars sternobrachialis and supracoracoideus muscles of flying budgerigars clearly showed multiple positive and negative spikes in each burst rather than one bi-directional spike of electrical activity per wingbeat as previously reported for budgerigars by Aulie (1970) (Figs 1, 2A, 6, 7). Our replication of Aulie's (1970) EMG methods (unipolar electrodes) produced both low-amplitude and occasional high-amplitude single-spike signals similar to the 'twitch' contractions he reported.

The average relative intensity and average duration of EMG bursts ($N=4$ birds) showed a trend to increase with flight speed in both the pectoralis and supracoracoideus (Table 1). Overall, relative intensity of pectoralis activity averaged 0.57 ± 0.01 (range 0.25–1.0); for the supracoracoideus, the mean was 0.42 ± 0.01 (range 0.1–1.0). Pectoralis burst duration

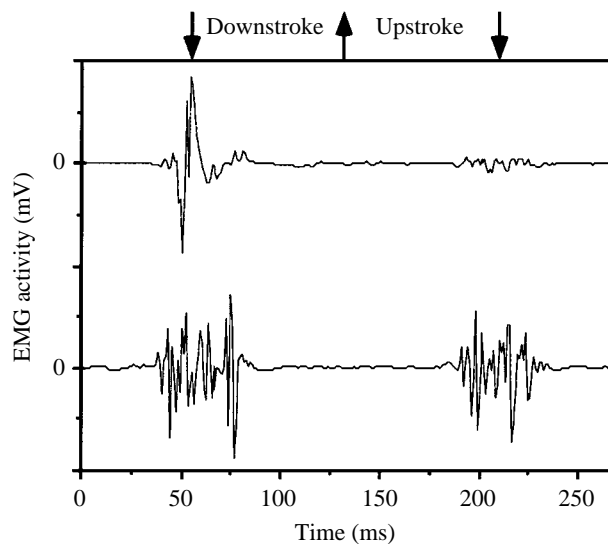


Fig. 1. Electromyographic signals from the pectoralis muscle of a flying budgerigar. The lower EMG, recorded using intramuscular bipolar electrodes (0.5 mm exposed tip), shows multiple-spike bursts that represent 'tetanic' contractions during two successive wingbeats. The upper EMG, recorded from the same wingbeats, was a replication of Aulie's (1970) method using a subcutaneous unipolar (3 cm exposed tip) electrode. This EMG appears similar to the 'twitch' contractions Aulie reported, but was probably due to movement of the electrode under the skin.

Table 1. *Relative intensity and duration of EMG bursts for the pectoralis and supracoracoideus muscles of budgerigars (N=4) during flapping flight at different speeds*

Speed (m s ⁻¹)	Pectoralis		Supracoracoideus	
	Relative intensity	Duration (ms)	Relative intensity	Duration (ms)
7	0.47±0.05	24.8±2.4	0.38±0.03	21.4±1.2
9	0.57±0.02	27.6±2.1	0.37±0.05	22.6±0.9
11	0.65±0.03	27.5±1.5	0.41±0.07	23.1±1.9
13	0.64±0.09	27.3±2.1	0.51±0.03	24.7±2.0

Values are mean ± S.E.M.

averaged 27.2±0.5 ms (range 12.2–45.8 ms), and supracoracoideus bursts averaged 23.1±0.5 ms (range 11.6–52.0 ms) during flapping flight.

For both muscles, relative intensity and duration varied greatly within individuals (Fig. 2A,B), which accounted for 28–53 % of the total variance for each variable (error terms, Table 2). Relative intensity was significantly different among speeds ($P \leq 0.01$ for both muscles). In the pectoralis, speed accounted for 49 % of the total variance. In contrast, duration was significantly different ($P \leq 0.01$) among birds (approximately 33 % of the total variance for each muscle, Table 2).

The EMGs recorded during flapping flight always showed fluctuations in peak amplitude (Fig. 2A), and these fluctuations were reflected in both relative intensity and duration (Fig. 2B). Pooling data from all birds and speeds, the duration and relative intensity of EMG bursts were positively correlated for both the pectoralis (Pearson product moment correlation, $r=0.22$, $P \leq 0.01$, $N=160$) and supracoracoideus ($r=0.41$, $P \leq 0.01$, $N=160$). However, these correlations were not consistent for individual birds, often being positive at some speeds and negative at other speeds. Moreover, correlations

Table 2. *Variance components for electromyographic and kinematic variables from flight at different speeds in budgerigars, expressed as percentages of total variance observed for each variable (Sokal and Rohlf, 1981)*

Variable	Speed	Bird	Speed × bird	Error
Pectoralis relative intensity	49.0*	14.8*	11.5*	24.6
Pectoralis duration	12.6*	32.8*	27.1*	27.5
Supracoracoideus relative intensity	13.4*	8.4	43.5*	34.2
Supracoracoideus duration	12.0	33.9*	11.2*	42.8
Wingbeat frequency	34.9*	16.1	5.5	43.5
Percentage of time spent flapping	17.6*	47.6*	2.0	32.8

* P -value ≤ 0.01 for F statistic, two-way ANOVA (SPSS Inc. 1990).

Note that error (within-individual variance) was not tested for statistical significance (Sokal and Rohlf, 1981).

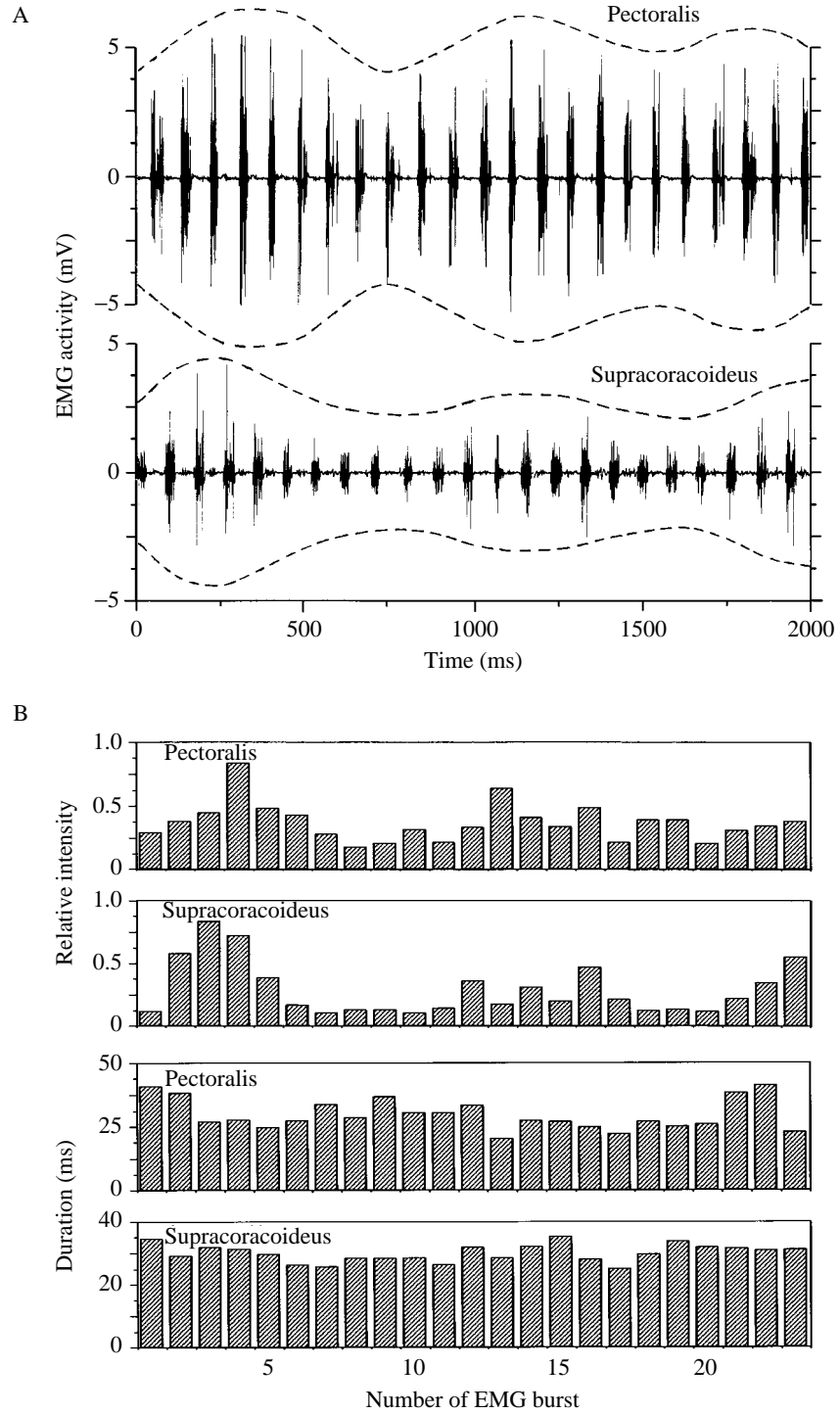


Fig. 2

Fig. 2. During flapping flight at all flight speeds (this sequence was from flight at 11 m s^{-1}), the EMG signals from the pectoralis and supracoracoideus muscles of budgerigars exhibited periodic fluctuations in amplitude with each wingbeat (A), as first noted by Aulie (1970). These fluctuations are reflected in the relative intensity and duration of bursts (B). The variability among bursts indicates differences in temporal or spatial recruitment of motor units within the major flight muscles.

between duration, relative intensity and flapping flight kinematics were either inconsistent or statistically insignificant.

Kinematics

Wingbeat frequency, calculated from all of the flight cycles ($N=234$), averaged $13.2 \pm 0.2 \text{ Hz}$ (range $5.3\text{--}20.0 \text{ Hz}$) (Fig. 3). Wingbeat frequency was most variable within birds; the error term accounted for 43.5 % of the total variance observed (Table 2). Also, there was a significant difference in wingbeat frequency among speeds ($P \leq 0.01$) that accounted for 34.9 % of the total variance (Table 2). A general trend relating average wingbeat frequency with speed was not evident among birds (Fig. 3). Also, differences in wingbeat frequency among birds and the speed \times bird interaction effect were not statistically significant (Table 2).

The mean percentage of time spent flapping within a cycle was $85.3 \pm 1.1 \%$ (range $23.5\text{--}100 \%$). Average flapping phase duration was $727.8 \pm 64.1 \text{ ms}$ (range $50\text{--}5570 \text{ ms}$); average non-flapping duration was $60.7 \pm 3.3 \text{ ms}$ (range $0\text{--}219 \text{ ms}$). Additionally, the mean number of wingbeats uninterrupted by non-flapping phases was 10.0 ± 0.9 (range $1\text{--}86$). The percentage of time spent flapping within a flapping/non-flapping cycle varied considerably among birds (47.6 % of the total variance, $P \leq 0.01$ for F -statistic) and within birds (32.8 % of the total variance) (Table 2, Fig. 4). The differences among

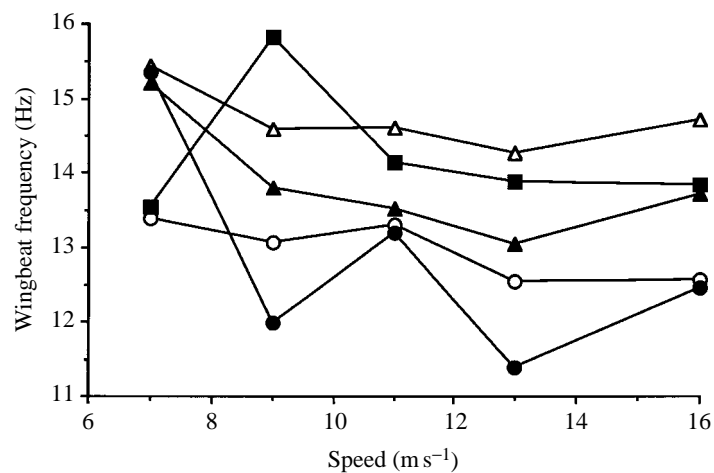


Fig. 3. Wingbeat frequency for five budgerigars during wind-tunnel flight at five speeds. There was statistically significant variance among flight speeds, although a correlation with flight speed was not apparent.

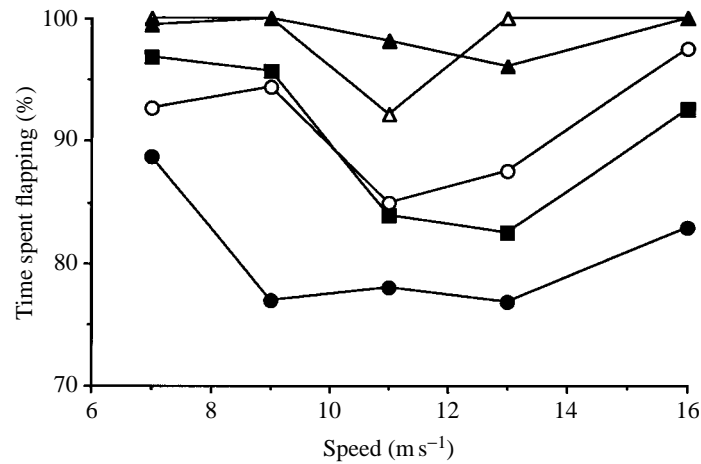


Fig. 4. The percentage of time spent flapping during flapping/non-flapping cycles in five budgerigars flying at various speeds in our wind tunnel. Flapping percentages varied considerably among birds; nonetheless, they tended to flap less at intermediate speeds.

speeds were statistically significant but accounted for only 17.6% of the total variance. In general, the percentage of time spent flapping was less at intermediate flight speeds (11 and 13 m s⁻¹) (Fig. 4).

Among birds that exhibited non-flapping flight at all flight speeds ($N=4$), a striking trend emerges in association with flight speed (Fig. 5). These birds tended to glide intermittently at slower flight speeds, adopt a partially extended intermittent wing posture at intermediate speeds and bound intermittently at faster speeds. The non-random nature of this trend was highly significant ($\chi^2=101.5$, d.f.=10, $P\leq 0.001$). During glides, with wings fully extended, the dorsal surface area of the wings averaged 87.2 ± 1.9 cm² (range 82.1–90.6 cm²). This decreased to 50.2 ± 2.0 cm² (range 45.5–53.6 cm²) for the intermediate postures, and to 38.9 ± 0.5 cm² (range 37.3–39.6 cm²) for bounds, with wings fully flexed.

Neural control and kinematics of a typical glide and bound

We successfully recorded EMG data from the pectoralis and supracoracoideus muscles of budgerigars during more than 50 intervals of non-flapping flight. The basic EMG and kinematic patterns differed between glides and bounds, but were consistent within each category. The neuromuscular control and kinematics during non-flapping ‘intermediate posture’ phases were essentially the same as for bounds. We therefore describe a glide and a bound typical of the intermittent non-flapping intervals we observed in budgerigars.

During a glide observed in one bird flying at 11 m s⁻¹ (Fig. 6), the pectoralis muscle exhibited an isometric contraction and the supracoracoideus was not active. The glide began in mid-downstroke, during continuous pectoralis EMG activity. As the wingtips moved ventrally, they were extended to the glide position. The tips of the wings were held near maximal extension during the glide and, from a lateral perspective, they were held

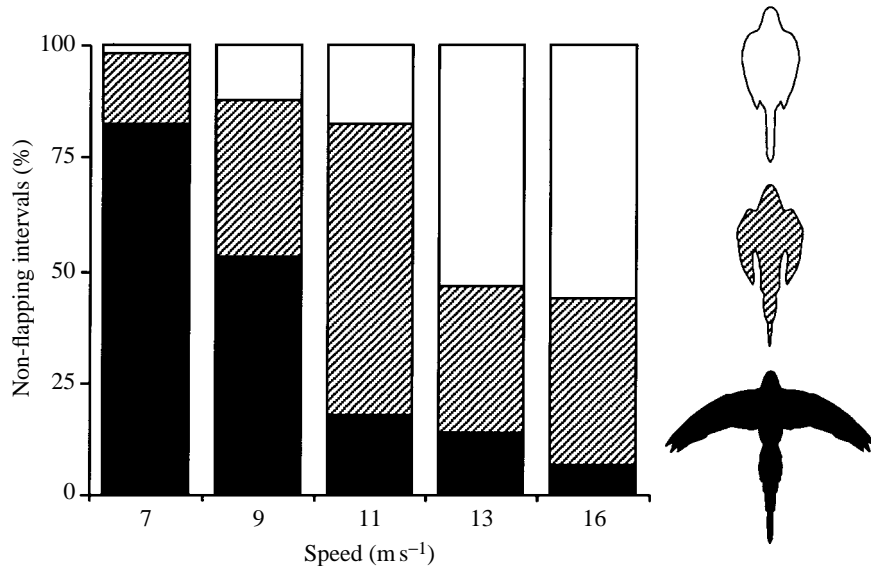


Fig. 5. As flight speed increased in the wind tunnel, budgerigars that exhibited intermittent flight at all speeds ($N=4$) tended to flex their wings during intermittent non-flapping periods. This type of behavior was probably in response to an increase in profile drag with airspeed. Similar flexion was not apparent during flapping periods.

slightly more ventral than the midline of the body with slight vacillations in elevation. The bird's altitude decreased by 10 cm prior to the glide phase. During the glide, body angle relative to the horizontal increased from 9 to 23° and the bird regained altitude. As the glide ended, the supracoracoideus became active and the wingtips were drawn medially and dorsally for an upstroke.

During a bound demonstrated by the same bird flying at 11 m s^{-1} , both the pectoralis and the supracoracoideus were inactive (Fig. 7). The final flap prior to the bound concluded with a passive upstroke (i.e. the supracoracoideus was inactive and the wingtip was elevated). During the bound, the wings were flexed so that the wingtips were much more medial than at any moment during flapping flight and were virtually on the midline of the body. Flapping resumed with EMG activity in the supracoracoideus concurrent with elevation and extension of the wings. Momentum generated during the flap just prior to the bound contributed to maintenance of altitude during the bound, but the bird's altitude decreased by 9 cm following the bound and was only regained 11 wingbeats later. Body angle relative to the horizontal increased from 12 to 18° immediately before the bound, decreased to 3° during the bound, and returned to 12° after three wingbeats.

Discussion

Birds that exhibit intermittent flight have traditionally been categorized as either flap-gliders or flap-bonders; only a few species of Coraciiformes have previously been

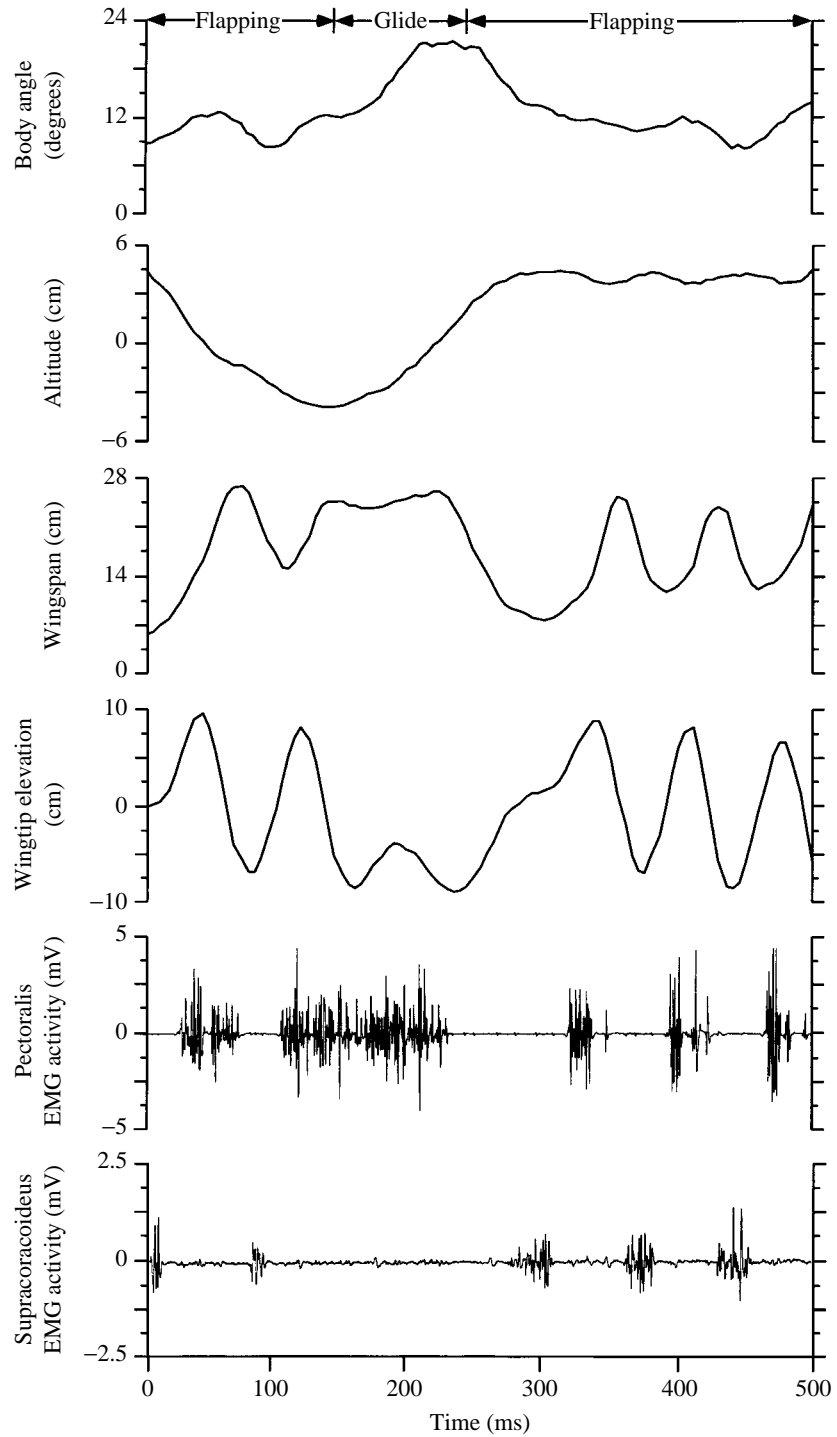


Fig. 6. For legend see p. 14.

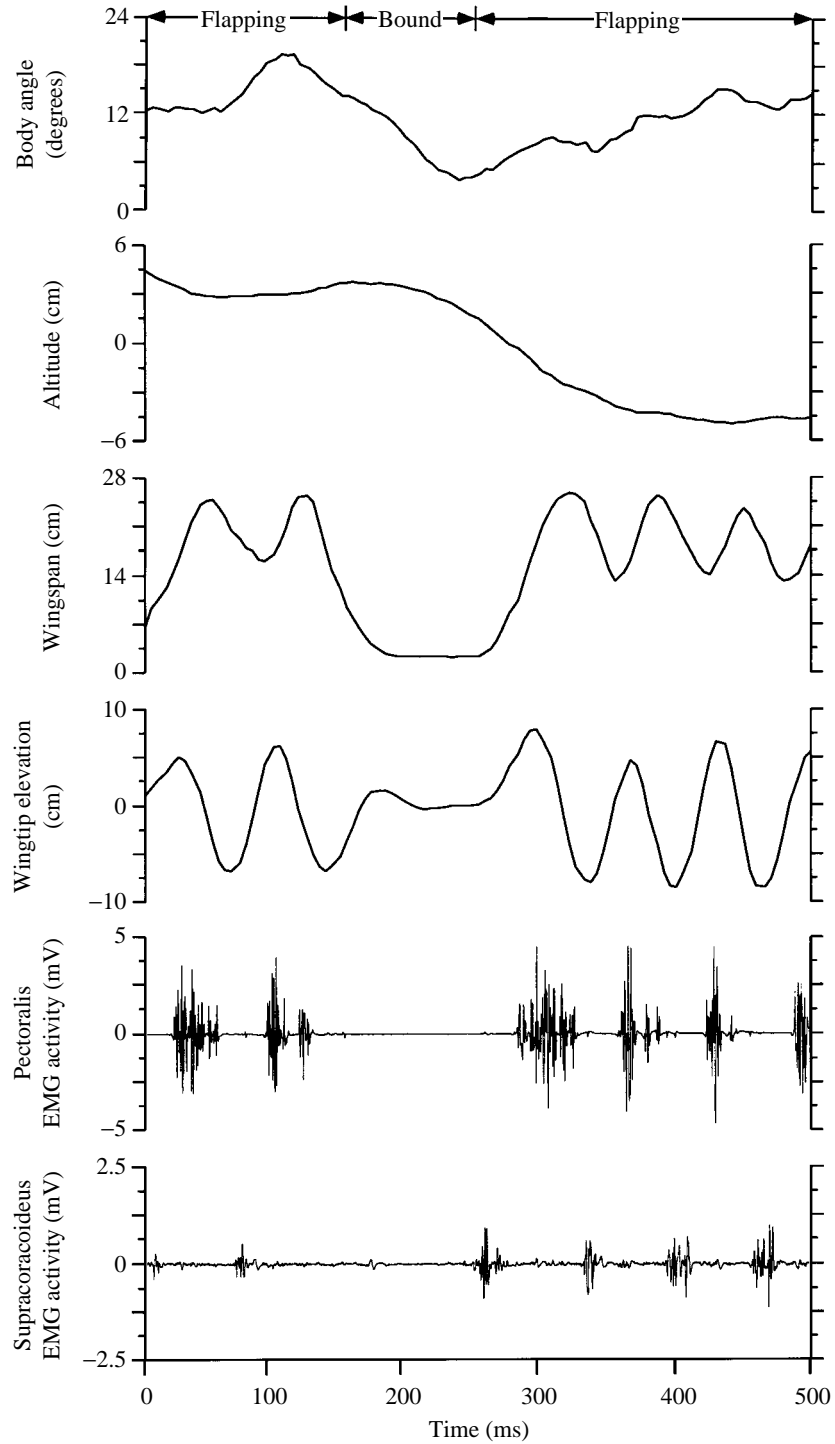


Fig. 7. For legend see p. 14.

Fig. 6. Electromyographic and kinematic data from flap-gliding flight exhibited by a budgerigar flying at 11 m s^{-1} in our wind tunnel. The flapping period, prior to the glide, ended with a downstroke and continuous pectoralis muscle activity. Flapping resumed with activity in the supracoracoideus and elevation of the wing. During the glide, which lasted approximately 100 ms, the pectoralis muscle appeared to exhibit an isometric contraction, while the supracoracoideus was inactive. The wings were fully extended, with the wingtips held as distal as during maximal extension in the downstroke phase of flapping. The left wingtip was held slightly below the mid-coronal plane of the body with a slight dorsal movement apparent during mid-glide. This movement was probably due to the buffeting action of the airstream on the wingtip rather than to movement of the humerus. Altitude decreased by 10 cm prior to the glide and was regained concurrently with an increase in body angle relative to the horizontal prior to the return to flapping flight.

Fig. 7. Electromyographic and kinematic data from flap-bounding flight in a budgerigar flying at 11 m s^{-1} in our wind tunnel. Flapping flight ended with a passive upstroke (i.e. the supracoracoideus was inactive) and resumed after the bound with contraction of the supracoracoideus, and elevation and extension of the wing. During the bound phase, which lasted approximately 95 ms, both the pectoralis and supracoracoideus muscles were inactive. The wings were fully flexed, with the wingtips nearly 10 cm more medial than at any point during flapping flight. Body angle relative to the horizontal increased just prior to the bound, and then decreased. The altitude of the bird decreased by 10 cm during the latter half of the bound. This drop in altitude was regained in subsequent wingbeats, which are not shown.

reported to do both (Rayner, 1985). Budgerigars are small, with homogeneous populations of FOG fibres in their pectoralis muscles (Rosser and George, 1986). Thus, the 'fixed-gear' hypothesis predicts that they should be constrained by muscle physiology (i.e. a restricted range of force production due to twitch contractions and a restricted range of efficient contractile velocities for uniform fiber types) to bound at all flight speeds where power output for flapping flight is less than the maximum sustainable aerobic power that their muscles can achieve (Rayner, 1985).

It is important to note that the fixed-gear hypothesis predicts that gliding, with isometric contractions in the pectoralis muscles, should be relatively inefficient for small birds with pectoralis muscles of uniform fast fiber types (Goldspink, 1977, 1981; Rayner, 1977, 1985) because slow fibers are more economical than fast fibers when the velocity of contraction is 0 m s^{-1} (Goldspink, 1977, 1981).

Our empirical observations, therefore, demonstrate that budgerigars violate the fixed-gear hypothesis (Rayner, 1985) because they routinely glide intermittently, using isometric contractions, at low speeds (Figs 5, 6). Additionally, our EMG and wingbeat frequency data lead us to infer that force production and contractile velocity in the flight muscles during flapping may be highly variable (Tables 1, 2; Figs 2A,B, 3) and therefore less of a constraint than previously supposed (Rayner, 1985).

Rather than being prevented from gliding by their physiology, during non-flapping periods budgerigars demonstrated a continuum of progressively more extended wing postures with decreasing air speeds (Fig. 5). This type of behavior was probably in response to a decrease in profile drag (i.e. form and friction drag on the wings). Profile drag is relatively low for fixed-wing postures at low speeds and increases dramatically with airspeed (Pennycuik, 1968*a,b*, 1975, 1989; Rayner, 1977, 1979, 1985). Intermittent non-flapping phases were of proportionally longer duration at intermediate speeds, where

power requirements might be least (i.e. minimum power speed, V_{mp}) (Tucker, 1968, 1973; Pennycuik, 1968*a*, 1975, 1989; Rayner, 1977, 1979, 1985). By comparison, Csicsáky (1977) observed that the duration of bounds increased with flight speed in zebra finches (*Taenopygia guttata*). For the past two decades, the muscle activity patterns in the pectoralis muscles of budgerigars (Aulie, 1970) have been interpreted to represent twitch contractions with relatively little variation in the temporal pattern of motor-unit recruitment and, by inference, relatively little variation in force production (Rayner, 1985). However, our replication of Aulie's (1970) EMG methods (Fig. 1) suggests that his observations of twitch contractions during level flight were primarily the result of methodological constraints. His unipolar recordings probably represent motion artifacts associated with wing-cycle kinematics.

In all of our experiments (Figs 1, 2A, 6, 7), the pectoralis and supracoracoideus muscles in flapping flight of budgerigars demonstrated multiple-spike EMG bursts representing repeated stimulation of a single motor unit (a motor unit action potential train as in a tetanic contraction) or asynchronous twitch contractions in different motor units (Hagiwara *et al.* 1968; Burke, 1981; McMahan, 1984; Basmajian and De Luca, 1985). The relative intensity of an EMG burst is related to the amplitude and number of spikes, and recent evidence shows, at least qualitatively, that the intensity of EMG bursts is positively correlated with force production in avian pectoralis muscles (Dial and Biewener, 1993).

Upon visual inspection (Fig. 2A,B) it is evident that the EMG signals from both the pectoralis and supracoracoideus vary among bursts during flapping flight. The variation in burst characteristics is reflected by the large within-individual (error) variance components, which range from 24.6 to 42.8 % for relative intensity and duration of EMG bursts for both the flight muscles (Table 2). It is of interest that almost half of the explained variance in the relative intensity of pectoralis bursts was accounted for by the speed factor, whereas the speed factor was the smallest variance component for duration (Table 2). Furthermore, within a given flight, intensity appeared to vary more than duration for both the pectoralis and the supracoracoideus (Fig. 2). These data seem to be consistent with the results of Dial (1992*a*), which showed that intensity of muscle activity varied among flight modes in pigeons, but that temporal patterns were relatively fixed.

The periodic rise and fall in peak amplitude of EMG bursts (Fig. 2A,B) was first described by Aulie (1970). This irregularity is quite unlike the muscle activity patterns observed during the level flapping flight of pigeons (*Columba livia*) or European starlings (*Sturnus vulgaris*) (Dial *et al.* 1987, 1988, 1991; Dial, 1992*a,b*). In general, we observed intermittent non-flapping phases during periods of low-amplitude EMG bursts. Aulie (1970) suggested the rise and fall in amplitude of signals reflected changes in the vertical position of the bird during flight but, from our analysis, we were unable to obtain such a correlation.

In addition to changing recruitment patterns in the muscle, power output may also be varied by altering the time course of force production and/or the distance through which force is applied (McMahan, 1984). For the pectoralis and supracoracoideus, both time and distance of contraction may be reflected in wingbeat frequency and wingbeat amplitude. In contrast to previous studies of budgerigars (Tucker, 1968; Aulie, 1970) as

well as studies of other taxa (Hagiwara *et al.* 1968; Torre-Bueno and LaRochelle, 1978; Dial, 1992a), we observed variable wingbeat frequencies for individual birds at different flight speeds (Table 2, Fig. 3). Also, the within-individual variance component (error term in Table 2) for wingbeat frequency accounted for 43.5% of the total variance observed. This variance component provides further evidence that a given budgerigar is not constrained to flap its wings with fixed frequency.

We were unable to obtain rigorous measurements of wingbeat amplitude using lateral and dorsal views because a bird's wingtip goes through a different arc than its humerus during flapping flight (Scholey, 1983). Amplitude of wingbeat may have varied inversely with frequency, thus maintaining constant contractile velocity during flapping, in agreement with the fixed-gear hypothesis (Rayner, 1985). However, in kinematic terms, a glide is a modified long-duration flap with an amplitude of 0° and a velocity of contraction of 0 ms^{-1} . We inferred the presence of isometric contractions of the pectoralis during glides in budgerigars by comparing simultaneous EMGs with wingtip position in lateral perspective (Fig. 6) (see also Goldspink *et al.* 1978). Whereas the progressive wing flexion during intermittent non-flapping phases reflects a continuum (Fig. 5), neuromuscular activity patterns clearly distinguish flap-gliding and flap-bounding flight. During glides (Fig. 6), the pectoralis was active, undergoing an isometric contraction. During bounds, (Fig. 7) the pectoralis was inactive. We consider intermediate-posture non-flapping periods to be modified bounds because the pectoralis muscle was always inactive during these phases. For glides, similar EMG patterns have been reported in herring gulls (*Larus argentatus*) (Goldspink *et al.* 1978) and American kestrels (*Falco sparverius*) (Meyers, 1991); however, our data provide the first insight into neuromuscular control during a bound.

Csicsáky (1977) showed that the angle of attack (body angle relative to the airstream) assumed by a bounding bird affects the trajectory curve of the bound. If a bird rises and then falls in altitude during a non-flapping phase, the distance covered by the bound should be maximized by minimizing the angle of attack during the ascent and increasing the angle of attack during the descent (Csicsáky, 1977). Our measurements of body angle were relative to the horizontal; thus, body angle must be compared with changes in altitude to estimate the angle of attack (Figs 6, 7). During the glide we describe in Fig. 6, altitude and body angle both increased throughout the glide, thus holding the angle of attack relative to the airstream approximately constant. By comparison, midway through the bound shown in Fig. 7, altitude decreased and body angle relative to the horizontal began to increase. This combination midway through the bound increased the angle of attack in rough agreement with Csicsáky's (1977) predictions for maximizing range during the bound phase.

Our results suggest several directions for future research on intermittent flight in birds. More rigorous field observations of flight behavior (e.g. Scholey, 1983; Pennycuik, 1990; Videler and Groenwold, 1991) would doubtless help clarify whether birds are obligatory or facultative in their intermittent flight behavior. From preliminary field observations (B. W. Tobalske, unpublished results), it appears that birds of several species commonly alternate between flap-gliding and flap-bounding during flight, e.g. pileated woodpeckers (*Dryocopus pileatus*), tree swallows (*Tachycineta bicolor*) and

black-billed magpies (*Pica pica*). It is likely that birds typically observed flap-gliding in the wild are simply flying at speeds for which such behavior is aerodynamically effective (i.e. relatively slowly). Likewise, birds that commonly flap-bound may just tend to fly faster and to fold their wings during rest phases because of the savings in profile drag.

In addition to field observations, wind-tunnel experiments would reveal the behavioral plasticity as well as the preferred flight behavior of the species in question. Given that our empirical evidence suggests that budgerigars are facultatively flap-gliding and flap-bounding according to aerodynamic demands, we predict that all other birds that use intermittent flight will behave in a similar manner when compelled to fly at different speeds. Certainly, larger birds would be useful for investigating the effect of body size on intermittent flight behavior as well as for evaluating the neuromuscular control of more distally located wing muscles during intermittent non-flapping phases.

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