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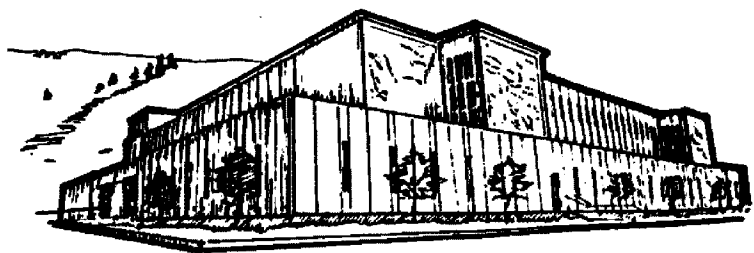
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NEUROMUSCULAR CONTROL OF GAIT MODULATION IN THE BLACK-BILLED
MAGPIE (*Pica pica*)

by

Nathan Eric Olson

B.A. University of Montana, 1990

Presented in partial fulfillment of the requirements

for the degree of

Master of Arts

University of Montana

1993

Approved by


Chairman, Board of Examiners


Dean, Graduate School

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Neuromuscular control of gait modulation in the Black-billed magpie (*Pica pica*)

Director: Kenneth P. Dial, Ph.D. *K.P.D.*

The major objective of this study was to explore the functional basis of the Black-billed magpie's (*Pica pica*) unusual flight style. Laboratory studies were conducted to collect electromyographic (six major flight muscles) and kinematic data from ten magpies flying in a variable-speed wind tunnel over a wide range of flight speeds. Field studies included filming numerous unbanded magpies to document their behavior among different flight modes and to identify the conditions under which they perform their characteristic flight style. The data suggest that magpies are adapted for slow flight and alternate between periods of low and high wingbeat amplitude (i.e. gait modulated flight) as a means of reducing energy expenditure over a range of flight velocities. Differential activity patterns of selected flight muscles between high- and low-amplitude wingbeats provide evidence of the role of these muscles during aerial locomotion. For example, the dorsally positioned scapulohumeralis caudalis appears to ventrally rotate the humerus during downstroke, thus directing the lift vector anteriorly and increasing thrust. The scapulothorax hyper-extends the elbow to increase the wing's total surface area. Working in concert, these two muscles are primarily responsible for changing the wings shape and pitch, thus promoting acceleration.

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INTRODUCTION

All flying birds use one of two general styles of powered flight: 1) constant flapping flight and 2) intermittent flapping flight. Intermittent flight involves flapping phases interrupted either with a gliding phase with wings out-stretched (flap-gliding) or alternatively with wings flexed (flap-bounding) (Rayner, 1985). Medium- to large-sized birds, such as raptors (Falconidae) crows and jays (Corvidae) normally assume flap-gliding flight styles. The smallest reported flap-glider appears to be the European starling (*Sturnus vulgaris*) (Rayner, 1985). Bounding flight is observed in most small birds.

Black-billed Magpies (*Pica pica*) perform an unusual flight behavior compared to most birds as they exhibit a modified form of flap-gliding flight involving a series of alternating high and low wingbeat amplitudes interrupted with occasional gliding phases (Rayner, 1985). The functional significance and the neuromuscular control of this peculiar flight style is unknown and thus forms the basis of this thesis. The modulation in wingbeat frequency and amplitude of magpies may reflect some sort of behavioral display to conspecifics, and/or, their unusual flight style may be a unique method for varying power output in order to fly at different speeds while minimizing energy expenditure.

To better understand the behavior of an organism, one might investigate the internal mechanisms responsible for controlling the actions performed. Understanding the locomotor behavior of animals involves determining the neural basis of this behavior. Electromyography (EMG) has proven to be a valuable tool in studying the neuromuscular patterns produced during bird flight

(Dial et al., 1988, 1991; Dial, 1992 a,b; Schaffer and Lauder, 1985; Jenkins and Goslow, 1983). Rayner (1985) suggested that a fruitful approach to studying intermittent flight would be to investigate muscle activity (e.g.s. EMG's) of flying birds and also to collect field data on flight behavior.

Following these suggestions, I investigated the neuromuscular control of the primary flight muscles (pectoralis, supracoracoideus, scapulohumeralis caudalis, biceps brachii, and humero- and scapulo-triceps) of the Black-billed magpie during level flight at different velocities in a variable-speed wind tunnel. I complemented these studies with field observations of their flight behavior. This represents the first combined field and lab study of flight behavior and neuromuscular control of any bird.

Flying is an energetically expensive form of locomotion per unit time (Tucker, 1968; Butler, 1991; Norberg, 1992; Pennycuick 1968, 1975, 1989; Rayner, 1979, 1985; Alexander, 1982). Butler (1991) has estimated flight to be as much as 2.5 times more expensive per unit time than running or swimming. Thus, species that perform aerial locomotion should experience strong selective pressures to minimize energetic costs. Rayner (1985) predicted that flap-gliding allows a reduction in power costs in comparison to continuous flapping and that this should be especially true at lower flight speeds (i.e., below minimum power speed). Flap-gliding is proposed to be energetically attractive at most flight speeds, allowing for a more efficient form of locomotion compared to constant flapping (Rayner, 1979; 1985; Pennycuick, 1989). Intermittent flight has been compared to what in aeronautical terminology is referred to as chattering flight,

alternating between powered and non-powered flight (Gilbert and Parsons, 1976; Speyer, 1976; Houlihan, Cliff and Kelly, 1982). Studies have shown that chattering flight can conserve considerable amounts of fuel in aircraft (Gilbert and Parsons, 1976; Speyer, 1976; Houlihan, Cliff and Kelly, 1982). Individuals of species that are most efficient (i.e. maximize positive net energy expenditure in their activities) are thought to partition relatively more energy to reproduction and thus improve their fitness (Mugaas and King, 1981). As such, one would expect muscle activity patterns and flight kinematics of the Black-billed magpie to shift in a predictable manner consistent with minimizing the cost of locomotion.

MATERIALS AND METHODS

Birds and Training

Ten Black-billed magpies (mean body mass 182 g, range 148 g to 209 g) were used in my laboratory investigations. Six individuals were used for EMG analysis and all ten were used for kinematic analysis. These birds were captured, using Havahart live traps, from wild populations in western Montana. The birds were housed in large cages (183 cm x 183 cm x 92 cm) permitting brief flight bouts and maintained on a diet of dog food, meal worms, mice and water at libitum. All birds were released back into the wild after fully recovering from post-experimental surgery.

Magpies were trained to fly in a variable speed wind tunnel (test chamber, 91cm X 78cm X 78cm). The test chamber of the wind-tunnel was constructed of clear plexiglass for filming and observing flight behavior. Air was drawn through the test chamber by a 20 HP DC motor and Buffalo 36-b-
vanaxial-asymmetric fan. The overall dimensions of the wind tunnel were 4.57 m x 2 m x 1.27 m. Wind speed was measured with a Dwyer airspeed indicator and calibrated with a Davis TurboMeter electronic wind speed indicator (accurate to $\pm 3\%$).

Training consisted of flying the birds for approximately 30 minutes twice each day for two weeks and once a day thereafter. Magpies were trained to fly at speeds ranging from 0 to 15.7 m/s (0-35 mph). Prior to experimental recordings I fastened a light weight (30 g) cable to the birds backs with tape to prepare them for recording conditions.

Muscle Anatomy

I investigated six major flight muscles (pectoralis, supracoracoideus, scapulohumeralis caudalis, biceps brachii, humero- and scapulo-triceps) (Fig. 1) in the Black-billed magpie. The pectoralis originates along the sternum and clavicle of the magpie and inserts on the deltoid crest of the proximal humerus (Dial et al., 1988; Raikow, 1985; Chiasson, 1984; Baumel, 1988). The pectoralis was believed to be a simple depressor of the wing (Raikow, 1985; Chiasson, 1984; Baumel, 1988). However Dial et al. (1988) observed the pectoralis to be strongly active during the upstroke and therefore, in addition to accelerating the wing during downstroke, it is also responsible for decelerating the wing at the end of upstroke. Recently, it has been suggested that the pectoralis is capable of producing other complex wing actions due to the intricacy of the muscle fiber orientation and innervation patterns (Dial et al., 1988; Boggs and Dial, 1993).

The supracoracoideus lies deep to the pectoralis, originating on the base of the carina of the sternum and inserting via a long, thin tendon that passes through the triosseal canal to the dorsal surface of the proximal humerus (Raikow, 1985; Chiasson, 1984; Baumel, 1988). This muscle is the main elevator of the wing, but also shows activity during the end of downstroke (Dial et al., 1988).

The triceps are divided into two main heads, the humero- and scapulo-triceps. While the scapulotriceps originates on the scapula, the humerotriceps originates on the caudal shaft of the humerus. Both muscles insert on the olecranon process of the ulna (Raikow, 1985; Chiasson, 1984; Baumel, 1988).

These muscles are believed to extend the elbow in all tetrapods.

Antagonistic to the triceps is the biceps brachii. The biceps has a double origin, it originates from the superior aspect of the coracoid and proximal humerus and inserts into the proximal radius and proximal ulna (Raikow, 1985; Chiasson, 1984; Baumel, 1988). This muscle is thought to flex the elbow in all tetrapods.

Little was known about the action of the scapulohumeralis caudalis. This muscle originates along the scapula and inserts on the border of the crus ventrale fossae of the proximal humerus (Dial, 1992a; Raikow, 1985; Chiasson, 1984; Baumel, 1988). In the past the proposed action for this dorsally positioned muscle was to retract and elevate the humerus during upstroke (Raikow, 1985; Chiasson, 1984; Baumel, 1988). However, Dial (1992) recently proposed that the scapulohumeralis may be involved in ventrally rotating the wing during the second half of downstroke, thus providing forward thrust.

Electromyography

Electromyograms were obtained using direct-wire implantation as described by Dial et al., (1988). Each electrode consisted of two tightly wound, teflon coated silver wires (California Fine Wire Company, .04 mm). These bipolar electrodes were prepared for implantation by scraping (using a #15 scalpel blade) the insulation off the wires 0.5 mm from the end to be implanted and 2 mm from the end to be soldered to a connector plug. To measure differences in electrical potential within the muscle, the wires were off-set 0.5

mm at the implanted end. At the plug end, the wires were soldered to a 6-pin miniature connector (Microtech, FG-6).

Magpies were anesthetized for surgical implantation with three to six injections of ketamine (25 mg/kg) and xylazine (2 mg/kg) over a 1-2 hour period. Body temperature was monitored continuously during surgery using a YSI Telethermometer with a YSI series 400 probe in the cloaca. Body temperature was maintained at $40^{\circ}\text{C} \pm 0.5^{\circ}\text{C}$ using a heating pad and infra-red lamp. Feathers were removed from around the area of the incisions. An incision was made dorsally between the scapulae for positioning of the back plug. Another incision was made ventrally along the carina for implantation of electrodes. A third incision was made proximally on the ventral surface of the wing to access the wing muscles. Bipolar electrodes were threaded subcutaneously from the back plug to the area of implantation. A 25 gauge hypodermic needle was used to insert the electrode into the muscle. Each electrode was then sutured into place so it would not be displaced during recording. Finally, all skin incisions were closed with 4-0 silk suture.

A six-lead shielded cable (Cooner Wire, Chatsworth CA.) was connected to the back plug for recording EMG signals. The signals generated by muscle contractions were amplified (1000 - 2000 x), and filtered (100 Hz highband pass and 3000 Hz lowband pass) using Grass P511 preamplifiers. Signals were simultaneously sent through a 16-channel, Keithley analog-to-digital 12 bit converter and the data was then stored to disk using a Zenith 386SX personal computer. Electromyographic data were plotted on paper using a Graphtec

Thermal Arraycorder (WR 4000).

Analysis consisted of measuring the duration, onset, offset, and intensity of 20 EMG bursts per bird ($n=6$) and for each speed (5, 10, 15, 20, 25, and 30 mph) [Note 5 and 10 mph were not recorded for biceps brachii and triceps]. The data were plotted on a Zenith 386sx computer using specialized signal analysis software (DMAN, Datacrunch, San Clemente, California). The duration was measured directly from the plotted data on the computer. This was accomplished by measuring the onset and offset of the EMG. The area under the curve of the rectified EMG signal was then measured, giving the intensity of the burst ($V^2\text{sec}$). Two-way analysis of variance (SPSS inc. 1990) was employed to examine the variance in intensity and duration among birds and speeds.

Cinematography

A high-speed 16mm camera (Lo-Cam, Red Lakes) set at 100 frames per second was used to document the wing kinematics and body angle for each Black-billed magpie flight. Film was synchronized to the EMG signals by a shutter-pulse signal sent to the recording equipment. Kinematics of a given flight sequence were analyzed by digitizing anatomical landmarks (distal tips of the wings, eye and base of the tail) along with fixed reference points (Grid on far side of test chamber, with 10 cm squares) on the frame of the wind tunnel (software courtesy of Dr. Stephen Gatesy). Film was projected on a Summagraphics Bit Pad Plus for digitizing. Variables examined included

wingtip elevation (perpendicular distance of the wing above or below the midline of the body as in Fig.9) and body angle (angle relative to the horizontal axis of the tunnel), altitude (height in cm relative to a fixed reference point in the flight chamber) and body position (position fore and aft in the test section, relative to a fixed point).

Field Observations

Field observations of magpie flight were carried out in the Missoula and Bitterroot valleys of western Montana. Video footage (5 hours) of magpies flying in the wild was obtained using a VHS video camera (30 Hz, Panasonic AG170, High-speed shutter). Flight attitude (e.g. ascending, descending, level flight) was analyzed from video footage (62 different flights were analyzed). Flight speeds ($n = 39$ flights) were calculated by observing flight bouts and timing the bird with a stopwatch (Timex, Ironman Triathlon), then measuring the distance flown for each flight with a range finder (Ranging opti-meter 620). The average speed of the magpie (level flights on days with little or no wind) was used as a comparison to the speeds we found inside and to estimate the preferred speed of the bird. Wind speeds were recorded using a Davis TurboMeter electronic hand held wind speed indicator (accuracy $\pm 3\%$) and the direction of the wind was measured using a hand held compass (Silva). I recorded the direction the bird flew in relation to the wind as either, with, into, or across the wind. Flights were categorized into either long (50m or greater) or short flights (less than 50m); consistent with work done by Mugass and King (1981). This was done to

evaluate if birds flew differently (e.g. and therefore more efficiently) during long range flights. I investigated how birds varied flight style (wingbeat frequency, amplitude and flapping vs. non-flapping) with flight modes (ascending, descending and level flights).

Using the field data, I examined the relationship between flight style modulation and several independent variables: wind direction relative to flight direction, distance flown and flight attitude. Univariate chi-square analysis tests (Sokal and Rohlf 1981) were performed to test whether the occurrence of modulation was random relative to these independent variables.

RESULTS

Muscle activity

Magpies vary their wingbeat amplitude in a non-continuous manner consisting of two major categories; 1) large-amplitude, high-frequency wingbeats interrupted by 2) low-amplitude, slower wingbeats. The electromyographic activity patterns of flight muscles strongly correlated with these two wingbeat categories (Fig 2-5). During a typical high-amplitude wingbeat, the pectoralis was active during the last half of upstroke and continued through the first half of downstroke, the biceps began its EMG activity concurrent with the pectoralis and remained active throughout the first 3/4 of the downstroke (Fig. 6). The supracoracoideus was active during the last 1/4 of the downstroke and during the first third of upstroke. The scapulohumeralis caudalis was active during the second half of the downstroke and remained active through the beginning of upstroke. The scapulothoracalis exhibited approximately the same activity as that of the scapulohumeralis caudalis; that is, during the second half of downstroke.

Muscular activity during low-amplitude wingbeats differed from high-amplitude wingbeats (Fig. 6). In low-amplitude wingbeats, the pectoralis was inactive during the upstroke. It became active during the last quarter of the upstroke and remained active through a full 3/4 of the downstroke. During low-amplitude wingbeats, the supracoracoideus was active only during the first 3/4 of the upstroke. The biceps was active for the second half of upstroke through

the beginning of the next upstroke. The greatest difference between high- and low-amplitude wingbeats was the observed absence of activity in certain muscles. For example, the scapulohumeralis caudalis and scapulotriceps were not always active during the wingbeat cycle. During low-amplitude wingbeat cycles, the scapulohumeralis caudalis was not consistently active. When it was active, it showed approximately the same activity pattern as observed in high-amplitude. The scapulotriceps, on the other hand, was never observed to be active during low-amplitude wingbeat cycles.

Analyses of EMG's from individual birds (Fig. 2-5), as well as pooling data for all birds ($n = 4$) (Fig. 7 and Table 1), shows that muscle activity was minimal at 15 mph (6.7 m/s) and increased at both slower and faster speeds. These data confirm that magpies generate a "U-shaped" EMG intensity curve. Duration of muscle activity from one wingbeat to the next is not as variable as intensity, but much of the variation that does occur is correlated with speed and bird (Table 1). Overall mean durations for the six flight muscles are indicated in Table 2. For the variable speed, the variance components of duration ranged from 13.2 to 73.85 percent and for intensity the range was 9.01 to 54.64 percent. The variance components for the within bird category also showed a broad range. Duration ranged from 9.23 to 69.23 percent and intensity ranged from 14.98 to 85.29 percent. All muscles exhibited significant F-values ($F < 0.01$) with respect to intensity except the humerotriceps (speed = 0.024, bird = 0.274) and scapulotriceps (speed < 0.001, bird = 0.391). For duration the only muscle to show significant results for bird and speed are the scapulotriceps (speed <

0.001, bird = 0.002).

Wingbeat frequency, calculated by dividing one by the duration of a wingbeat cycle (in seconds, taken from the EMG onset of the pectoralis) and multiplying this number by 1000, averaged 6.33 Hz (S.E. = 0.0078, range 1.7 to 9.2 Hz) (Fig. 8). Two-way ANOVA's indicated that there was no significant difference in wingbeat frequency among birds or speeds (Table 1). The largest variance component was located in the error category (49.2 %) suggesting there were significant differences among runs. Wingbeat frequency changed between low and high-amplitude flight styles (range 1.7 to 9.2 Hz, respectively). Low-amplitude wingbeat cycles were much slower (fewer wingbeats per minute) than those of high-amplitude wingbeats.

During high-amplitude flapping phases all implanted muscles exhibited activity (Fig. 9). However, glides and low-amplitude wingbeat phases were accompanied by a significant decrease in muscle activity, with some muscles completely inactive. Although intensity and duration changed during these differing flight styles, the pectoralis and biceps were active during all styles of flight. The supracoracoideus also exhibited appreciable activity, but during glides it exhibited low EMG intensity with irregular durations. The scapulohumeralis caudalis and scapulothoriceps exhibited activity during high-amplitude wingbeats, however during low-amplitude wingbeats and gliding phases these muscles were either inactive or exhibited dramatically-reduced EMG signals (Fig. 9).

Kinematic data

Position (body angle, altitude, acceleration, and wing-tip position) of magpies changed predictably with the change in flight style. Glides were consistently initiated at mid-downstroke, at which time the pectoralis EMG activity was continuous (i.e. isometrically). The tip of the wing was held extended at approximately the midline of the body during the glide with slight vacillations in the wing as the wing stabilized. During the glide the body angle decreased, altitude decreased and the magpie moved back in the flight chamber, thus resulting in a negative acceleration (Fig. 9).

Wing and body kinematics were also measured as the magpie accelerated (from gliding to flapping flight) in the wind tunnel. During acceleration, the wing underwent a greater pitch (ventral rotation) and body angle (angle of attack) increased. During low to mid range flight speeds, gliding phases were always followed by high-amplitude wingbeats and correspondingly the flight muscles showed increased activity (becoming active or showing greater intensity) (Fig. 9). The wing changed its pitch at mid-downstroke (from visual observations of film), and was ventrally rotated and hyperextended possibly causing an increase in the surface area. These events correspond to the onset of activity of the scapulohumeralis caudalis and scapulotriceps. At this time there was an increase in the body angle of the bird. The bird regained altitude and moved forward or stopped falling backward (indicating an acceleration of the bird) (Fig. 9).

During low-amplitude wingbeats body angle decreased, altitude leveled off or slightly decreased and the magpie would either move forward or backward in the test chamber depending on body angle and altitude. The corresponding EMG activity indicated an overall decrease in muscle activity, with the scapulohumeralis caudalis and scapulotriceps completely inactive.

During these low-amplitude wingbeat cycles there is a decrease in wingbeat frequency (mean high-amplitude wingbeat frequency = 7.4, S.E. 0.098; mean low-amplitude wingbeat frequency = 4.5, S.E. = 0.25). This trend was also clearly observed in films from field observations. Brief periods of increased wingbeat frequencies and high-amplitude phases appear as rapid bursts, thus giving magpies their characteristic flight style which is referred to as "gait modulation". These brief high-amplitude phases were followed by prolonged periods of low-amplitude wing beats.

Factors affecting gait modulation

As with EMG intensity, the percent of time the magpies performed high-amplitude wingbeats in relation to velocity when flying in the wind tunnel followed a "U-shaped curve" (Fig. 11). Low-amplitude flight was observed most frequently at 15 and 20 mph (~70 percent) and decreased to near zero percent when birds flew very slow or very fast. Low-amplitude wingbeats were eliminated when the bird was weighted. Regular patterns of high- and low-amplitude wingbeats were observed at flight speeds of 15 to 20 mph. As flight speed increased or decreased from this range there was a significant increase

in the percentage of high-amplitude wingbeats (Fig. 10 and 11). Raw EMG's from different flight speeds also exhibit an increase in the percentage of high-amplitude wingbeats when the bird flew from 15 to 30 mph (Fig. 2-5).

Field observations indicate that the angle (level, ascending and descending) of flight also correlates with the modulation of gait in the magpie (Fig. 12). Level flapping flight occurred in 61.3 percent of the observations. Modulation of gait occurred 97 percent of the time the magpie was in level flight. Ascending flights were observed in 16.1 percent of the observations and of these only 10 percent included modulation of flight. Descending flight accounted for 22.6 percent of the observed flights and all of these descents included some form of modulation. Flight angle was the only significant observation with respect to modulation ($p < 0.01$, Chi-square value = 170.32 with 2 degrees of freedom) in the field. There was a significant difference in the amount of modulation that occurred between the different flight angles (Fig. 12).

Short flights (< 50m) occurred 39 percent of the time and, therefore, 61 percent of flights were considered long (Fig. 13). In long and short flights, modulation in gait was observed 87% and 79% of the total time respectively. There was no significant difference in these values, (chi-square value = 5.12 with 1 degree of freedom).

Wind did not seem to play any significant role in predicting gait modulation in magpies. During periods of negligible wind (less than 5 mph), the birds to exhibited modulated-gait flight 58.3 percent of that time (Fig. 14). In windy conditions, (greater than 5 mph), 35.5 percent of the time magpies flew

into the wind, 11.3 percent they flew with the wind and 33.9 percent of the time they flew in a cross wind. The mean percentage of flights where the birds modulated gait was 86.4 percent for head wind, 85.7 percent for tail wind and 95.2 percent for cross wind (Fig. 14). This also was not significant in the chi-square analysis (chi-square value = 3.88 with 2 degrees of freedom). Average flight speed of magpies in the wild was 18.82 mph (8.43 m/s) (S.E. = 0.49, range 12 to 25 mph).

DISCUSSION

Variability of gait modulated flight

Magpies performed gait modulation in a manner that was consistent with theoretical changes in power requirements associated with flying at different speeds (Pennycuick 1968, 1989; Tucker 1973; Rayner 1979, 1985) and during different modes of flight (ascending, descending and level flapping) (Tucker 1968; Goldspink 1981). This conclusion was drawn from several lines of direct and indirect evidence which strongly suggested that power output by the flight muscles of the magpie was lower during low-amplitude flapping than in high-amplitude flapping. Mechanical power (P) was defined as a force (F) applied over a distance (D) for a given duration of time (T):

$$P = (F \times D) / T$$

Herein, I substitute the relative intensity of EMG signal for force of contraction (F) based on the positive correlation between these two variables as shown by Dial and Biewener (1993). Wingbeat amplitude is substituted for the distance (D), which is correlated with the force applied by the primary flight muscles (pectoralis and supracoracoideus). Lastly, time of contraction (T) may be inversely correlated with wingbeat frequency, thus indicating an increase in power.

EMG signals from all six flight muscles investigated exhibited a positive increase from low to high relative intensity with an increase in flight speed from

15 to 30 mph (6.7-13.4 m/s). The pectoralis, supracoracoideus and scapulohumeralis caudalis all display a "U-shaped" curve in relation to speed (Fig. 7). Intensity increased at slow and fast speeds as the bird departed from its preferred speed of approximately 15 mph (6.7 m/s). Moreover, the percentage of the total flight time during which high-amplitude flapping was employed also exhibited the characteristic "U-shaped" curve (Fig. 11). These data agree with the classical "U-shaped" mechanical power curve derived from theoretical predictions of flying animals (Pennycuik 1968, 1989; Tucker 1973; Rayner 1985). This suggests that these birds are flying at speeds that require minimum power during flight in the wild (average flight speed in the wild = 18 mph, range 12-25 mph).

My field observations of Black-billed magpie flight reveal that gait modulation was assumed primarily during level and descending flight (Fig. 12). According to the metabolic measurements of Tucker (1968) studying budgerigars (Melopsittacus undulatus) and strain-gauge recordings of Dial and Biewener (1993) studying pigeons, power output for flying birds is greatest during ascending flight. Thus it appears that magpies adjust their power output by assuming lower amplitude flapping during non-strenuous (i.e., lower power) flight and possibly reducing energy expenditure. With a mean flight speed of 18 mph in the field, magpies appeared to spend the greatest amount of flight time using low-amplitude wingbeats. Data from the wind tunnel indicates they used a slightly greater percentage of high-amplitude wingbeats at this speed (Fig. 11). Low-amplitude wingbeats were most prevalent within the 15 mph flight

range during wind tunnel flight. This suggests a slight discrepancy between the flight conditions in the wind tunnel and in the field and points out the importance of augmenting laboratory investigations with field studies to compare results.

Muscle activity and function

Upon inspection of the recent information on avian flight muscle activity from various electromyographic studies (Dial et al., 1988; 1991; Dial, 1992 a, b; Tobalske and Dial in Press) the function of each muscle is reevaluated from that presented in the traditional literature. The following discussion is based primarily on work with pigeons (Columba livia) and the European starling (Sturnus vulgaris). Two major muscles perform the bulk of the work done in flapping flight, the pectoralis and supracoracoideus (Fig. 1). These antagonistic muscles have traditionally been regarded as simple depressors and elevators of the wing. However, recent studies suggest that the pectoralis is capable of producing complex wing actions (Dial et al., 1988; Boggs and Dial, 1993). The pectoralis is the single largest pair of muscles found in any tetrapod and constitutes up to 25 percent of the total body mass in a flying bird (Greenwalt, 1975). In addition to wing depression action, the pectoralis apparently has the potential to act as a retractor and a protractor of the wing thus providing a wide range of humeral excursions. The pectoralis in the starling and pigeon is active during the final third of the upstroke and the first half of the downstroke; it acts to both decelerate and reaccelerate the wing during each wingbeat cycle (Dial et al., 1988). Observations of high-amplitude wingbeats in the magpie concurred

with those found in starlings (Dial et al, 1988) (Fig. 6) with respect to these timing patterns. However, during low amplitude wingbeats the timing of the pectoralis activity suggested it may be less important in the deceleration of the wing and active mainly during the downstroke (Fig. 6).

Located deep to the pectoralis, the supracoracoideus is the primary elevator of the wing (George and Berger, 1966; Baumel, 1979). The supracoracoideus in pigeons and starlings shows electromyographic (EMG) activity during the terminal phase of the downstroke as well as during the initial phases of upstroke (Dial et al., 1988). The magpie supracoracoideus shows similar activity during high-amplitude wingbeat cycles. However, during low-amplitude wingbeats the supracoracoideus does not show significant activity during the terminal phases as did the pigeon (Dial et al., 1988), rather it exhibits greatest activity during the first part of the upstroke, as the wing decelerates (Fig. 6).

The dorsally positioned scapulohumeralis caudalis, also referred to as the scapulohumeralis posterior or dorsalis scapulae, is a well developed muscle in most birds. This large, flat, triangularly shaped muscle is positioned deep to the scapulohumeralis anterior and is present in all corvids (Hudson and Lanzillotti, 1955). Though rudimentary in nonflying birds, the scapulohumeralis caudalis is massive in penguins and represents the third largest flight muscle in flying birds (Dial, 1992a), yet little was known regarding its function. My interpretation of its function agrees with that presented by Dial et al (1991) in showing that the scapulohumeralis caudalis is active during most of the

downstroke and continues to be active through the beginning of upstroke. Traditionally this muscle has been considered to be primarily involved in the retraction of the humerus (Raikow, 1985), but recently it has also been proposed to ventrally rotate (i.e. pronate) the wing to aid in propulsion during the final third of the downstroke (Dial, 1992a). The differential activity of this muscle in the magpie during different speeds and modes of flight strongly confirms its role as a ventral rotator of the wing, thus it should also assist in accelerating the bird during flight. From film analysis of wing and body kinematics, together with recorded EMG activity, I have obtained the first measurements to confirm that the SHC is actually correlated with the ventral rotation of the wing, thus increasing thrust during downstroke. Recent experiments employing "back-stimulation" demonstrate that this action is similar in pigeons (Gatesy and Dial, unpublished). It also undoubtedly retracts the humerus, but the significance of this action for flight is not as easily appreciated.

A dorsally positioned shoulder muscle functioning during the downstroke activity does not follow intuitively. However, the interpretation of this muscles function can more easily be appreciated after inspecting its origin and insertion and then identifying its activity during flight. As stated earlier, the scapulohumeralis caudalis originates along the lateral length of the scapulae, passes ventrally (under the humerus) and inserts on the crus ventrale fossae on the proximal ventral surface of the humerus known as the bicipital crest. During high-amplitude wingbeats this muscle is active during the end of downstroke. As the muscle is activated at mid downstroke it pulls on the insertion on the

As the muscle is activated at mid downstroke it pulls on the insertion on the ventral surface causing the wing to rotate ventrally and at the same time retract the humerus for propulsion.

Muscular investment of the brachium of the wing is dominated by three muscles; the biceps brachii, and the scapulo- and humero-triceps (Fig. 1). During ascending and descending flight in pigeons, the biceps brachii is most active (Dial, 1990, 1992a) and is thought to be responsible for flexing the elbow (Raikow, 1985). The triceps is divided into two heads; the scapular head (scapulotriceps) and the humeral head (humerotriceps). It has been shown recently that the two heads of the triceps muscles do not act concurrently during all modes of flight in starlings (Dial et al., 1991) and pigeon (Dial, 1990, 1992a). The humerotriceps was found to be active during the downstroke phase of takeoff, landing and vertical ascending flight, but during level flapping flight and descending flight it was active during the transition between upstroke and downstroke. The scapulotriceps was active during the downstroke phase among all modes of flight. The activity and function of these muscles during a glide phase, with wings outstretched, was previously unknown.

The scapulotriceps is a very interesting muscle as its activity accompanies the activity of the scapulohumeralis caudalis during the period the bird accelerates, from mid-downstroke to the end of downstroke. The scapulotriceps is an elbow extensor and it appears to hyper-extend the wing, thus increasing the wing surface area. The differential activity patterns exhibited by the flight muscles (especially the scapulohumeralis caudalis and

scapulotriceps) reveals their involvement in flight. These muscles are most active during high-amplitude wingbeats. The scapulotriceps always shuts off during low-amplitude wingbeats and the SHC turns off or decreases in its activity. From this we can infer that the SHC and scapulotriceps are primarily employed to accelerate the bird. If these birds are flying at slow enough speeds they may have to use this peculiar alteration of gaits to stay above stall speed.

While wing loading is the weight per unit wing area (Pennycuik, 1989), wing and tail loading provides information on the total surface area available for lift production. That is, the lower the wing and tail loading, the more surface area these structures provide. Large winged birds like the corvids and gulls, usually perform flap-gliding flight. Magpies have comparatively large wings and a very large tail that should increase the surface area for creating lift. Tucker (1992) has shown that the tail of the Harris' hawk (Parabuteo unicinctus) can generate about 10% of the birds lift during flight. This value may be greater for the magpie which possesses a relatively large tail, thus lowering tail loading. For example, a magpie's wing and tail loading (23 N/m²) is lower than that of many birds (e.g., the budgie = 45 N/m²), possibly permitting cost effective slow flight.

A major theme of avian wing design and the design of other vertebrates with fast moving appendages (e.g. ungulates) is the proximal distribution of the musculature (Hildebrand, 1988). Apparently the pigeon (Columba livia) does not require the distal muscles of its wing to perform symmetrical level flapping flight (Dial, 1992b; Gatesy and Dial unpublished data). Many papers, considered standards in the avian morphological literature, suggest the function

of muscles invested within the wing to be involved with active extension and flexion of the wing during each wingbeat (eg. Raikow, 1985). In contrast, Dial (1992b) suggests the function of distal wing muscles is more of fixation of the elbow and wrist during level flapping flight and to actively adjust shape of the wing during nonsteady flight. Dial (1992b) showed the automatic linkage system in a bird's wing provides control for proper extension and flexion during steady state flight without input from distal wing muscles.

The new information available on wing muscle activity patterns indicates that the automatic linkage system may be most important during low amplitude wingbeats. Electromyographic activity of all recorded muscles decreased or shut off (no electrical activity) during low-amplitude wingbeats. As the magpie switched to high-amplitude wingbeats, the EMG activity of the muscles was initiated or increased (showed distinct EMG bursts), suggesting the distal musculature control the wing's more complex actions as in maneuvering flight.

"An Alternative hypothesis"

If gait modulation is a means of adjusting to different power requirements and thereby reducing energy expenditure, why do not all birds perform this type of flight behavior? The flight behavior of a bird can be as characteristic of the species as are its vocalizations, plumage, size and mating rituals (Rowley and Chapman, 1985). These characteristics may be in part innate and in part learned. It is important to recognize which flight behaviors have been acquired genetically and which have been acquired through individual experiences in

life. Rowley and Chapman (1985) looked at two distinct species of Cockatoo, the galahs (*Cacatua roseicapilla*) and Major Mitchell's cockatoos (*Cacatua leadbeateri*). These cockatoos have differing flight styles. Galahs use a fast, strong flight with full wingbeats and little gliding while Major Mitchell's cockatoos use an alternating series of several fast, shallow wingbeats followed by a glide. They also make brief stops on their journey. Galahs raised by Major Mitchell's cockatoos mimicked the flight of the Major Mitchell's when in a flock of the latter, but lapsed into normal galah flight when alone.

Birds may be identified by characteristic flight styles. If this is true for the magpie, the modulation of gait may be a behavior that allows other individuals to recognize it from a distance. The routine flight styles that a bird exhibits through out each day may be an as yet unappreciated mechanism of communication among species. Future studies of magpie flight should focus on the variation in flight modulation of individuals and attempt to identify any correlation with age, sex, season and social status of individual birds. Additional laboratory studies of fiber type, metabolic costs and morphometrics may prove to be important in understanding flight.

Along with continued laboratory studies there is much work to be done in the field. The role of routine flight in communication is just one area that needs to be explored. The coloration of this bird may be important in signaling other birds of the same species during flight. The tail of the magpie is long and is not sexually dimorphic. This suggests that it is aerodynamically similar in both sexes and may be an important aspect in understanding the flight of the

magpie. There are many other studies in the field to be conducted; my study was just the beginning.

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Table 1. Variance components for 12 electromyographic variables from different muscles in the Black-billed magpie (*Pica pica*) and the wingbeat frequency. Each number within a row represents the percent variance for that variable.

Variable	Speed	Bird	Interaction	Error	Total(%)
Pects-D	20.69	34.48	3.45	41.38	100%
Pects-I	38.86*	54.5*	1.77*	4.85	100%
Supra-D	32.35*	44.12	5.88	17.65	100%
Supra-I	9.01*	85.29*	2.52*	3.18	100%
SHC-D	73.85*	9.23	3.07*	13.85	100%
SHC-I	52.85*	28.4*	5.2*	13.6	100%
Scap.Tri-D	23.08*	69.23*	7.69*	-	100%
Scap.Tri-I	41.97*	14.98	22.46*	20.59	100%
Hum.Tri-D	45.45*	54.54*	-	-	100%
Hum.Tri-I	19.3	21.7	40.86*	18.1	100%
Biceps-D	13.24	50.69*	2.94	33.09	100%
Biceps-I	54.62*	41.3*	1.73*	2.35	100%
WBF	14.33	34	2.5	49.2	100%

D = duration; I = Intensity

*Significant at 0.01

Table 2. The overall mean relative intensity (maximum = 1) and duration for six flight muscles in the black-billed magpie (*Pica pica*).

MUSCLE	MEAN RELATIVE INTENSITY	MEAN DURATION
PECTORALIS	0.417 (S.E. = 0.0325)	103 msec (S.E. = 3.9)
SUPRACORACOIDEUS	0.128 (S.E. = 0.0383)	70.2 msec (S.E. = 5.3)
SCAPULOHUMERALIS CAUDALIS	0.2299 (S.E. = 0.0245)	47.7 msec (S.E. = 3.9)
SCAPULOTRICEPS	0.163 (S.E. = 0.024)	22 msec (S.E. = 2.6)
HUMEROTRICEPS	0.153 (S.E. = 0.0311)	35 msec (S.E. = 3.7)
BICEPS BRACHII	0.371 (S.E. = 0.04)	128 msec (S.E. = 4.1)

Figure. 1. Superficial (left) and deep lateral (right) views of the musculature of the Black-billed magpie (Pica pica). Labelled muscles represent those studied herein.

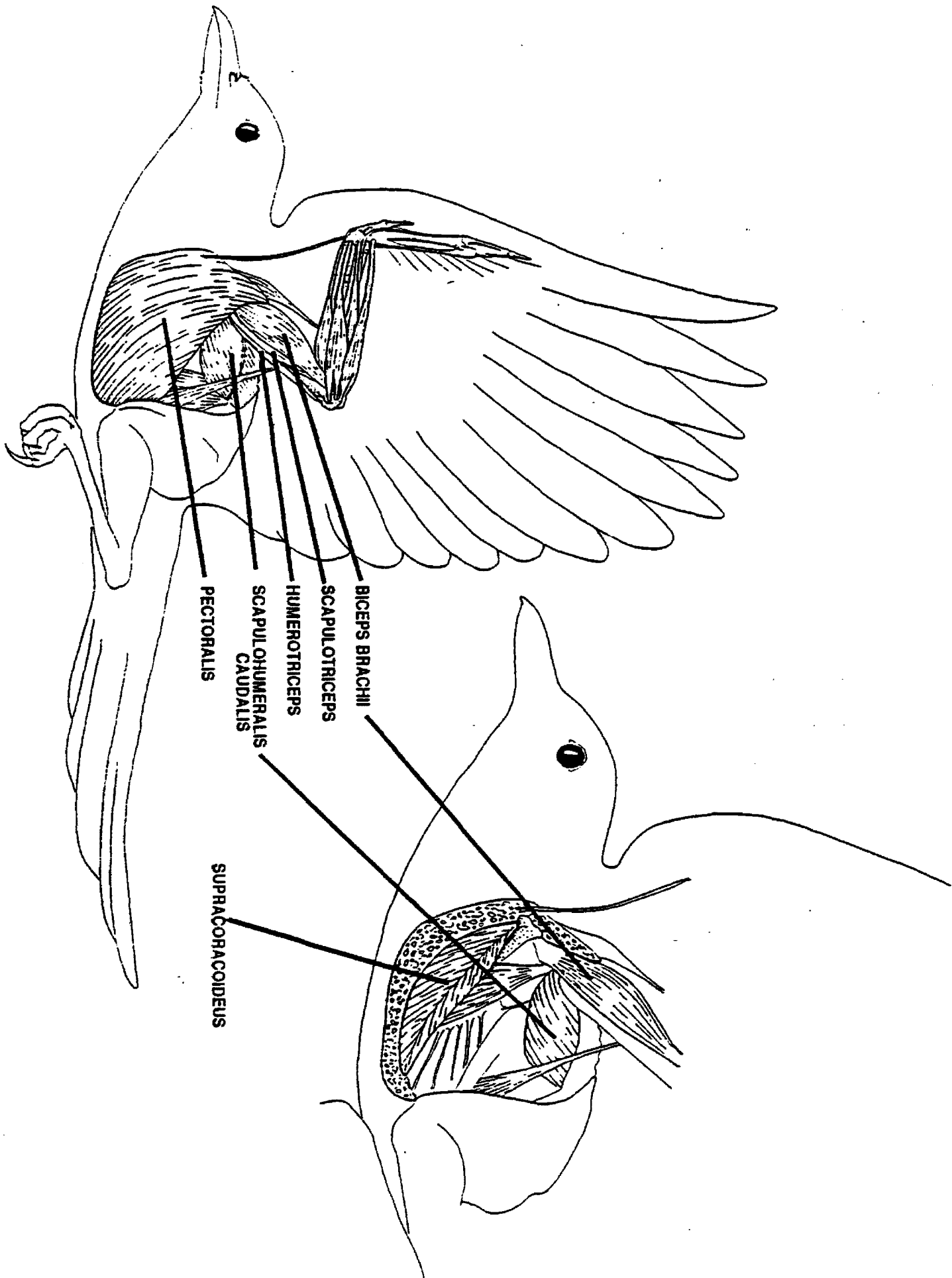


Figure. 2. Electromyographic data from the Black-billed magpie #6 flying at 15 mph (6.71 m/s) in the wind tunnel. Note the changes in the scapulothorax and supracoracoideus.

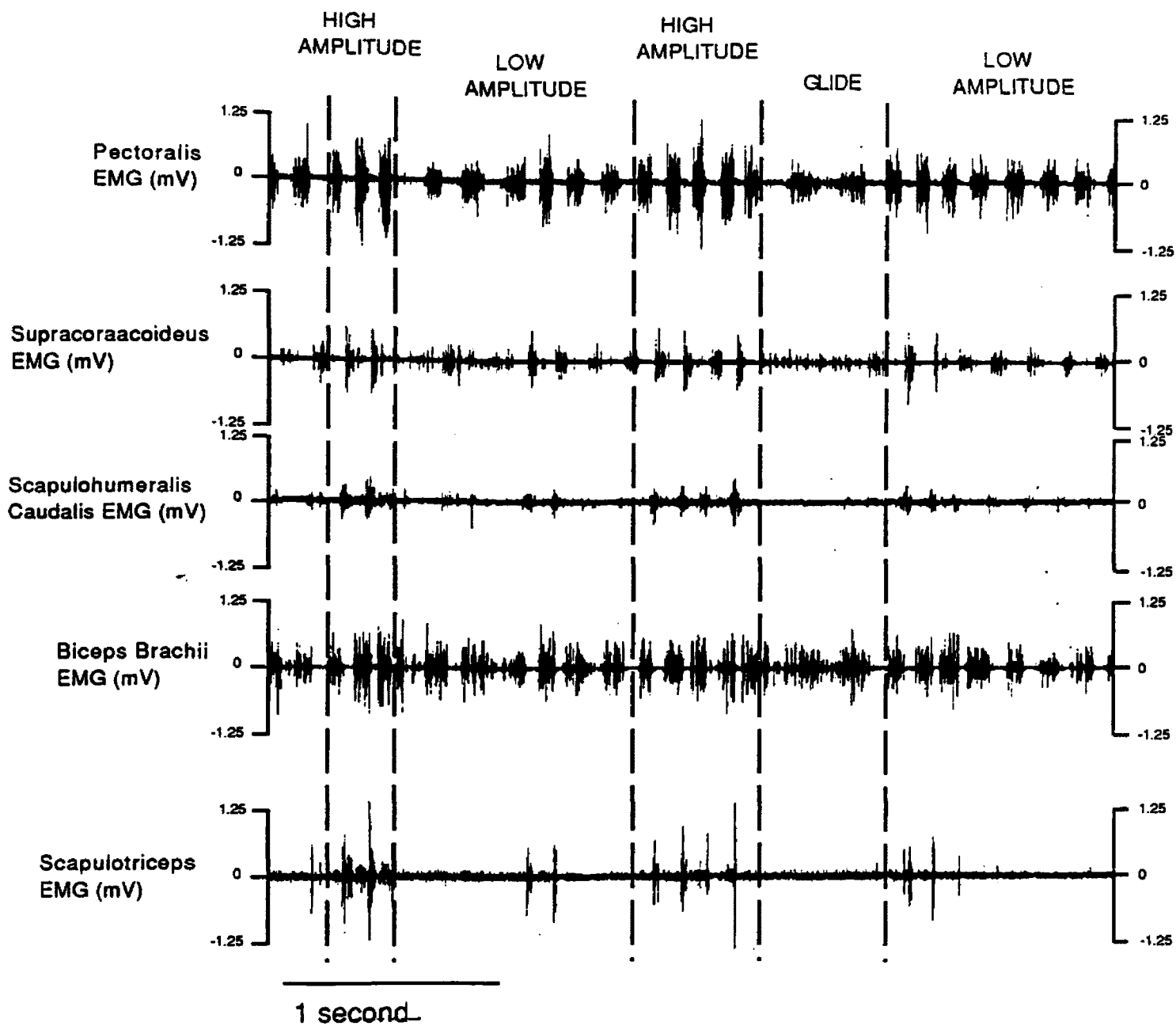


Figure. 2

Figure. 3. Electromyographic data from the Black-billed magpie #6 flying at 20 mph (8.94 m/s) in the wind tunnel. Note the changes in the scapulothorax and supracoracoideus.

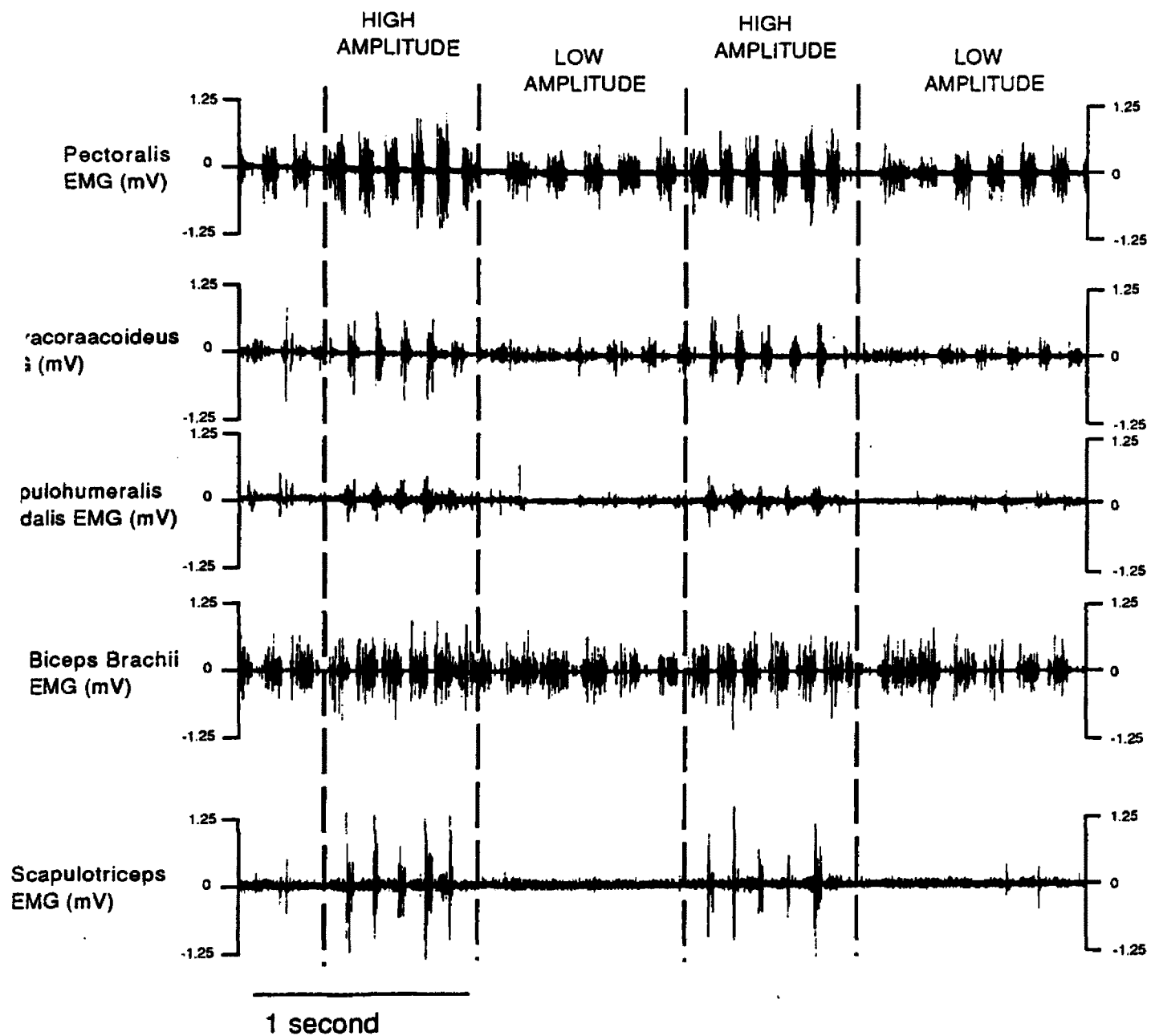


Figure. 3

Figure. 4. Electromyographic data from the Black-billed magpie #6 flying at 25 mph (11.18 m/s) in the wind tunnel. Note the changes in the scapulothorax and supracoracoideus.

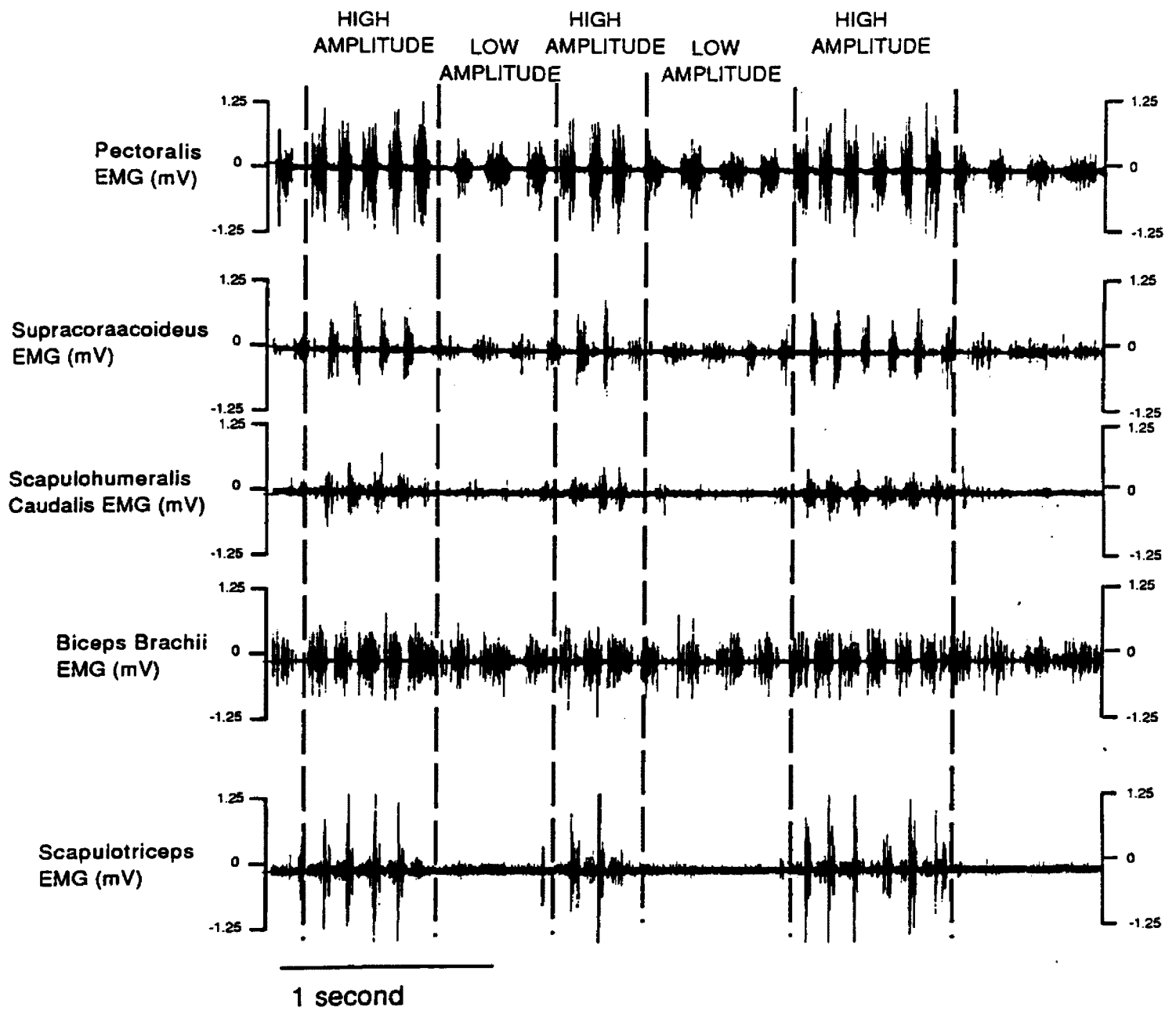


Figure. 4

Figure. 5. Electromyographic data from the Black-billed magpie #6 flying at 30 mph (13.41 m/s) in the wind tunnel. Note the changes in the scapulothorax and supracoracoideus.

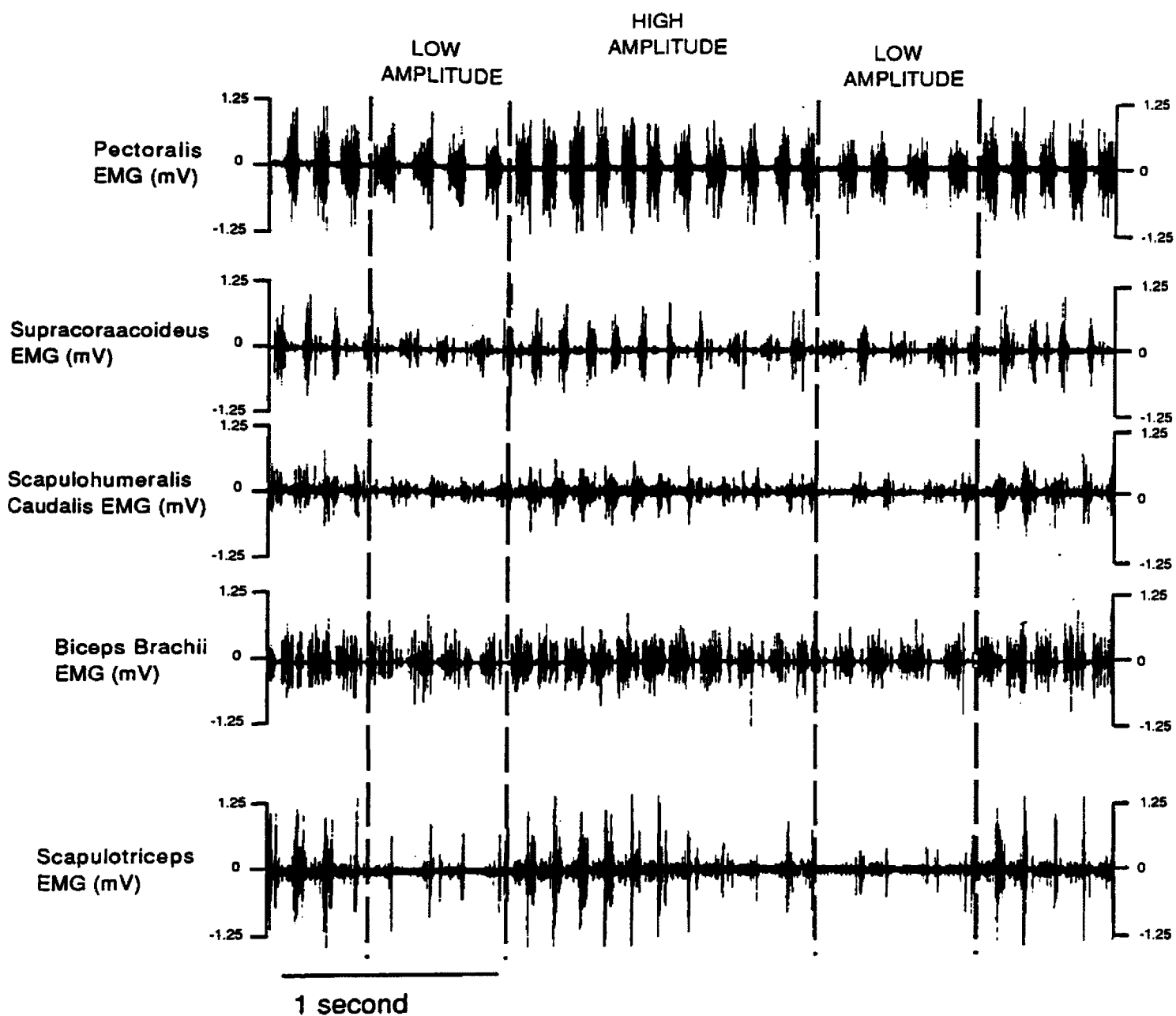
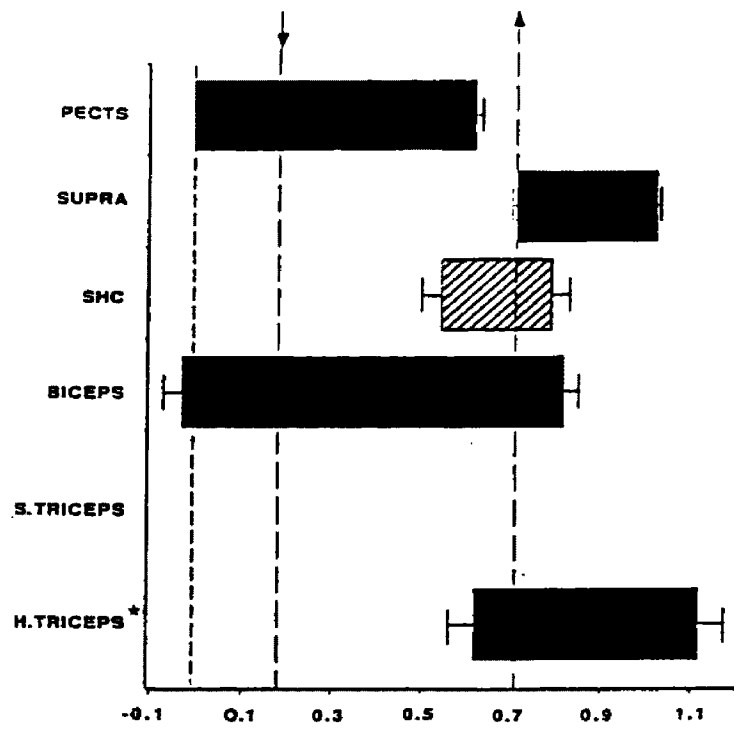


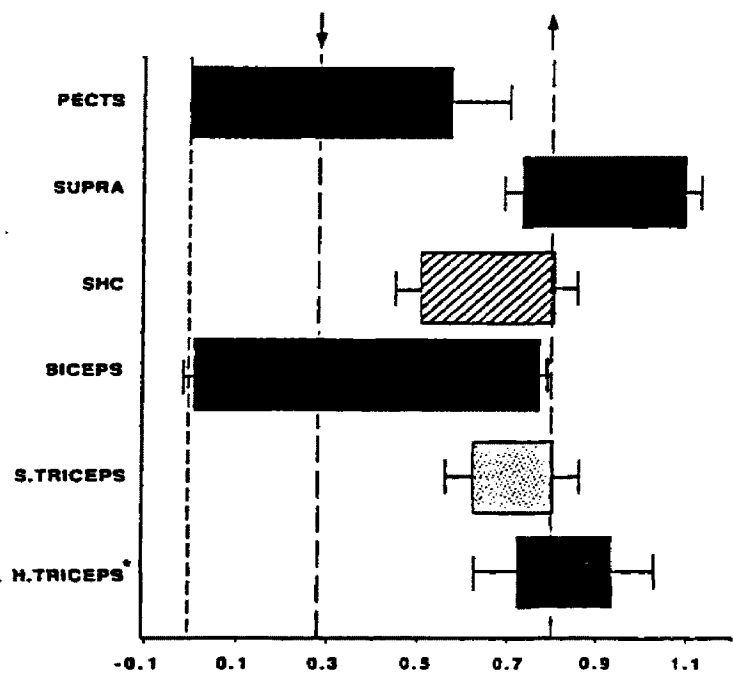
Figure. 5

Figure. 6. Summary statistics of muscle activity of a normalized wingbeat cycle. The dashed line represents the onset of pectoralis activity. Arrows represent beginning of downstroke (▼) and upstroke (▲).

MUSCLE TIMING DURING LOW AMPLITUDE WING BEAT



MUSCLE TIMING DURING HIGH AMPLITUDE WING BEAT



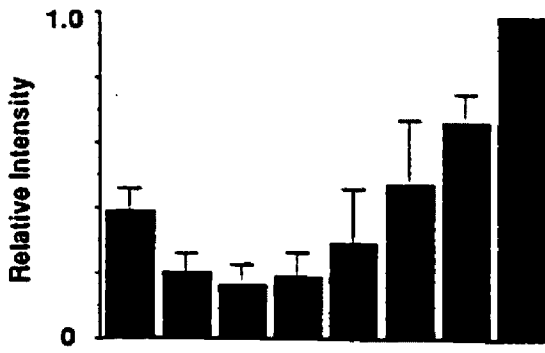
* Note: Humeral triceps not recorded simultaneously with other muscles.

- Always observed
- Not observed to be active in all low amplitude phases
- Never observed in low amplitude phases

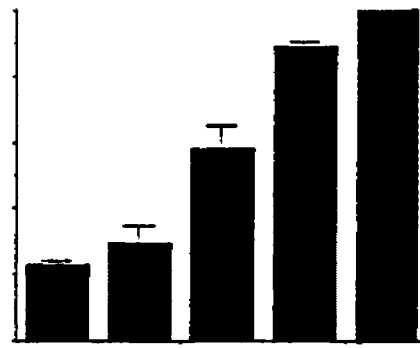
Figure. 6

Figure. 7. Intensity (square area) of EMG bursts (Y axis) varied positively with speed (X-axis) and also when the bird was weighted with a backpack, thus eliminating low amplitude wingbeats. High-amplitude flapping also increased positively with speed.

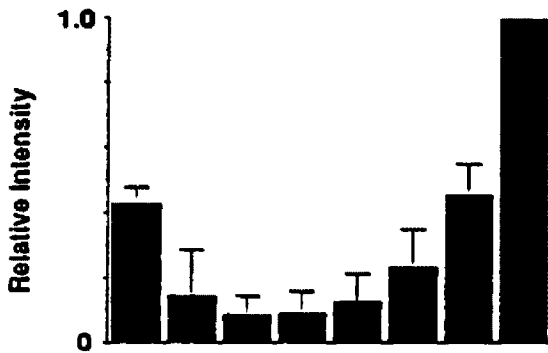
PECTORALIS



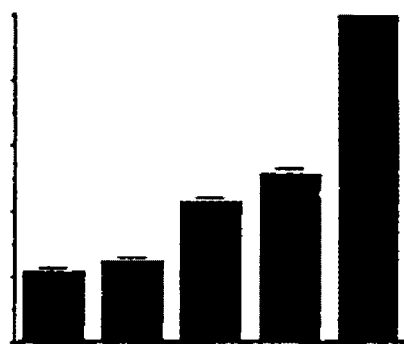
SCAPULOTRICEPS



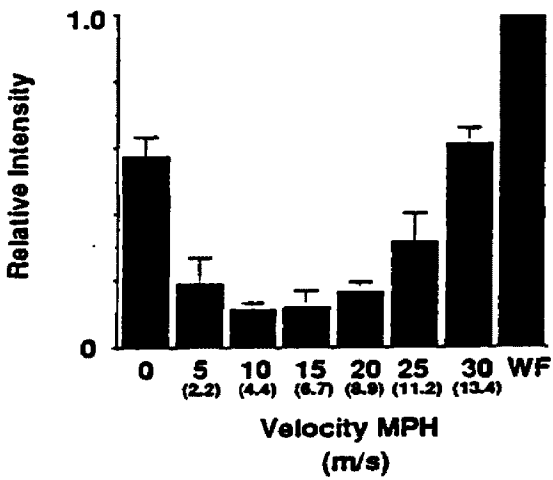
SUPRACORACOIDEUS



HUMEROTRICEPS



SCAPULOHUMERALIS CAUDALIS



BICEPS BRACHII

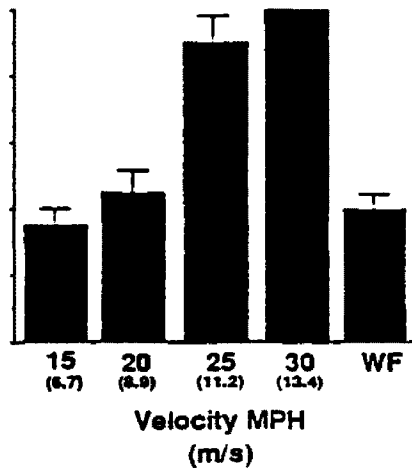
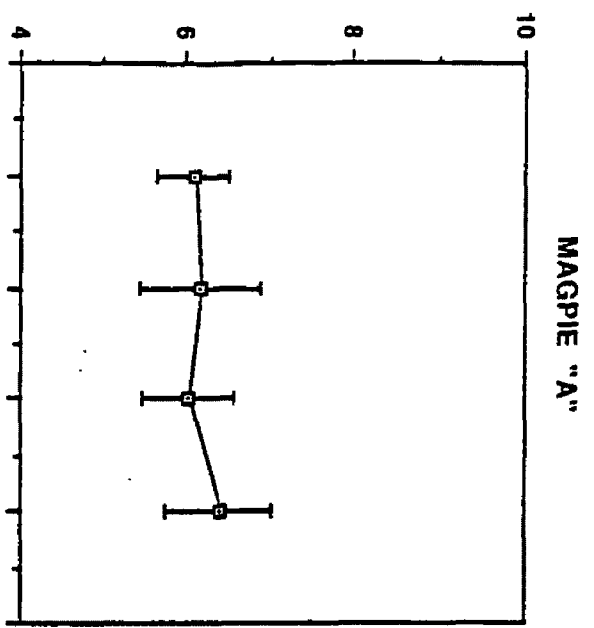
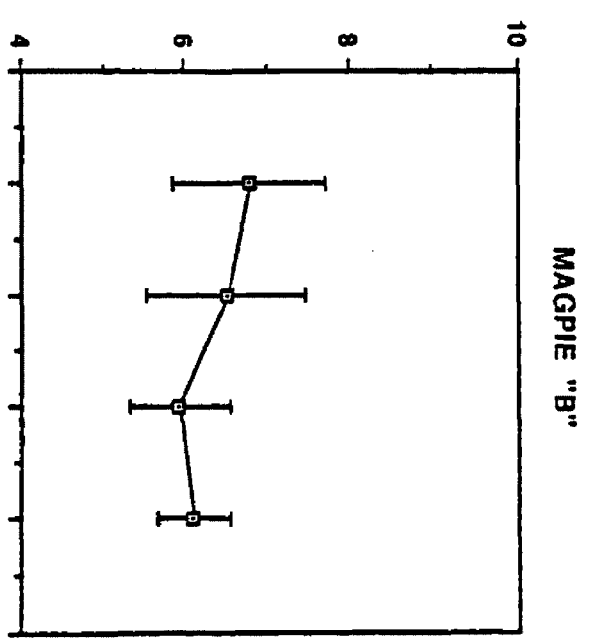
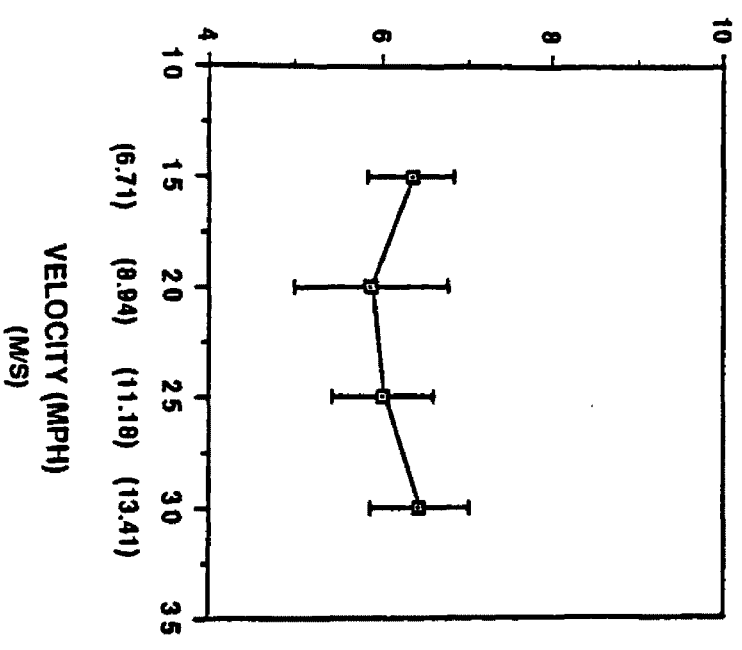


Figure. 7

Figure. 8. Mean wingbeat frequency of 4 birds at different flight speeds in the wind-tunnel. There is a fairly consistent wingbeat frequency at all speeds, for all birds.



MAGPIE "C"



MAGPIE "D"

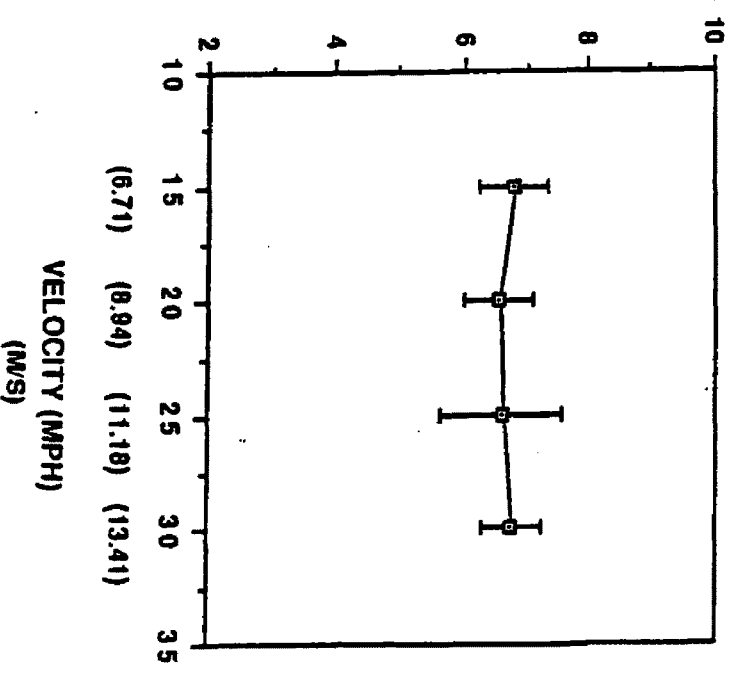


Figure 2

Figure. 9. Emg activity changes during glides, high- and low-amplitudes along with changes in body position in the flight chamber. A high-burst amplitude corresponds to an increase in amplitude and frequency of wingbeats, allowing for an acceleration of the bird.

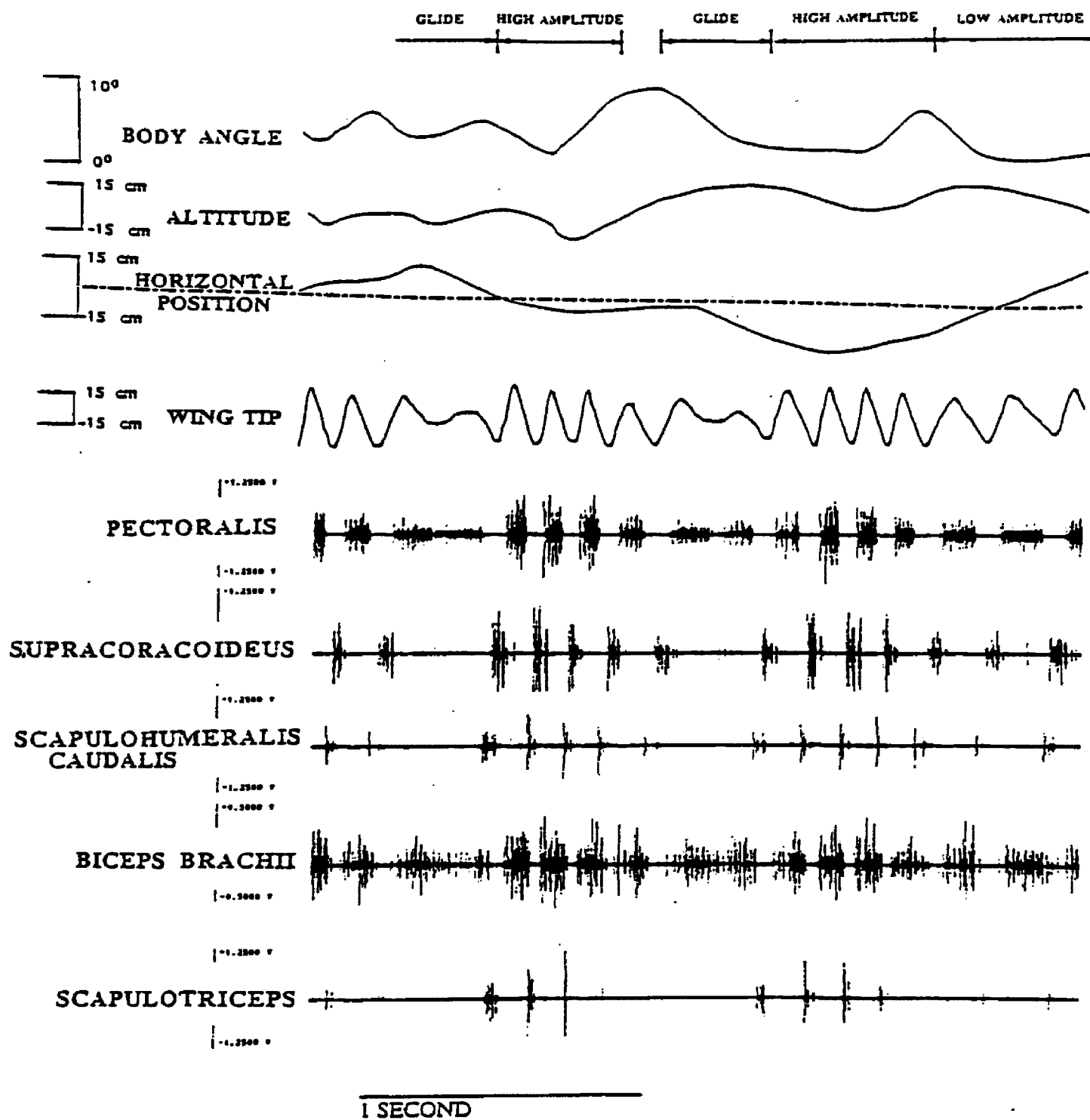


Figure. 9

Figure. 10. Patterns of high- and low-amplitude wingbeats during; A) slow flight (15 mph), B) higher flight speeds (30 mph) and C) weighted flight (84 grams added).

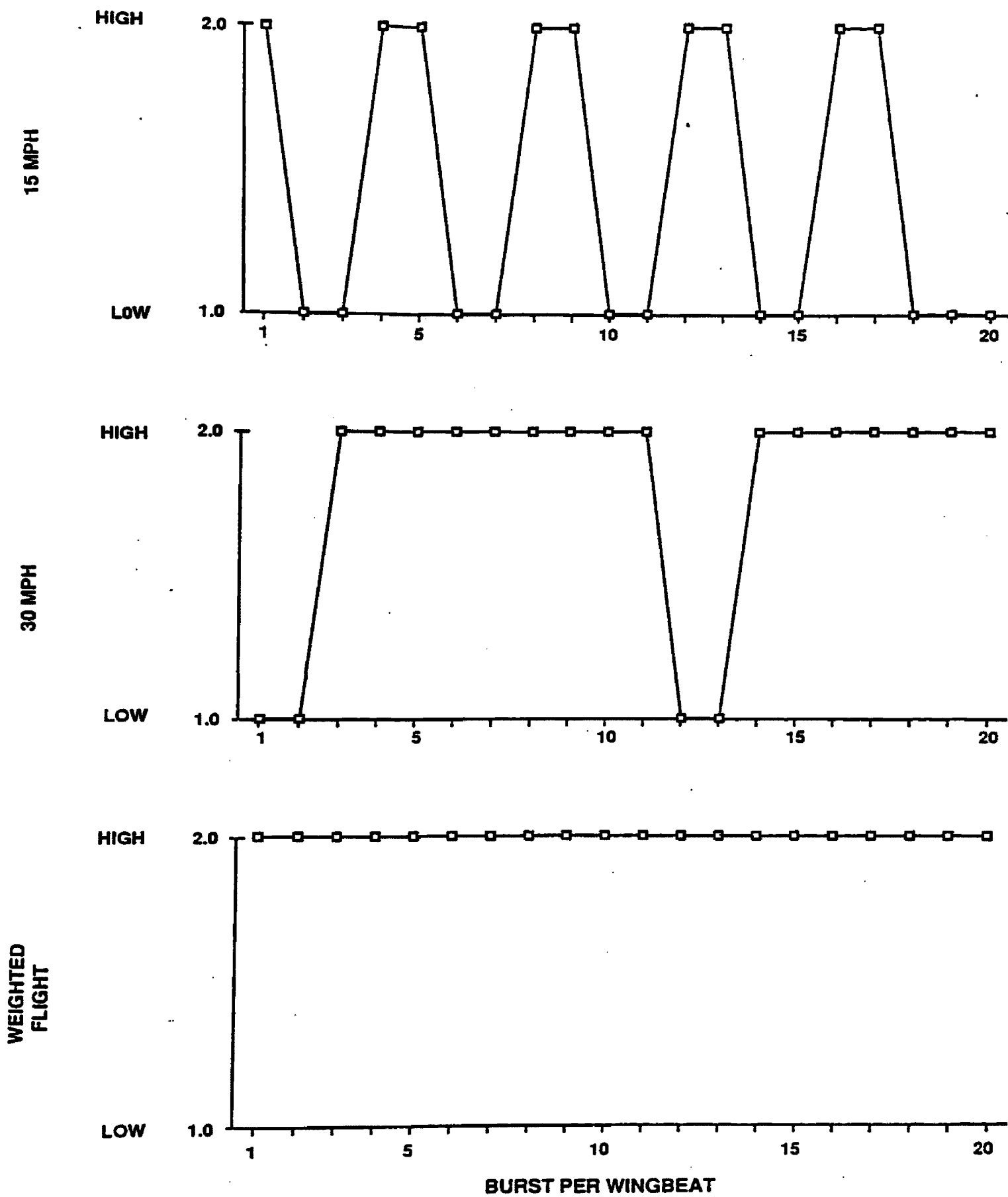
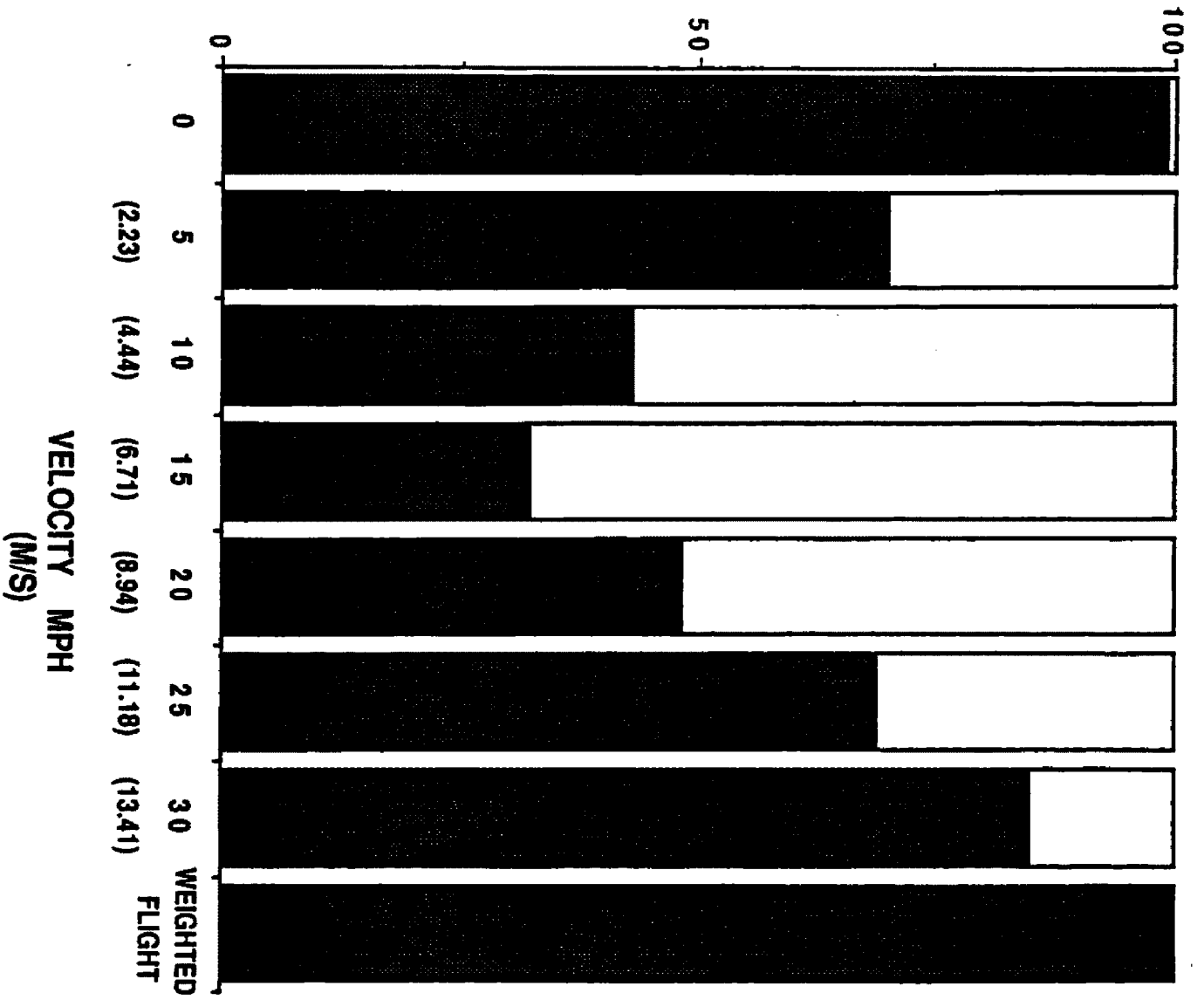


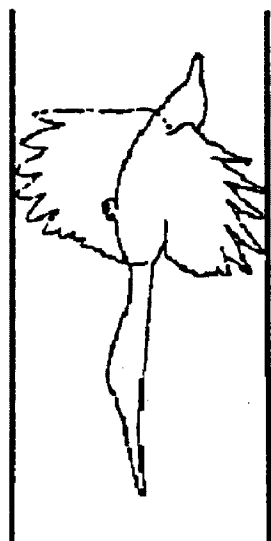
Figure. 10

Figure. 11. The percentage of time the magpie spends in high-amplitude wingbeats increases as you increase or decrease flight speed from preferred speeds of approximately 15 mph.

PERCENT OF TOTAL WINGBEATS



□ LOW AMPLITUDE



■ HIGH AMPLITUDE

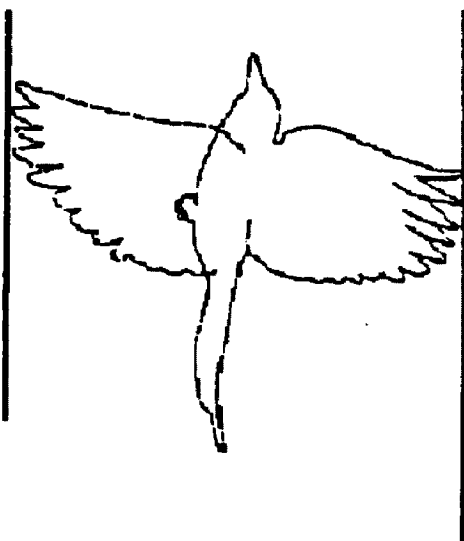
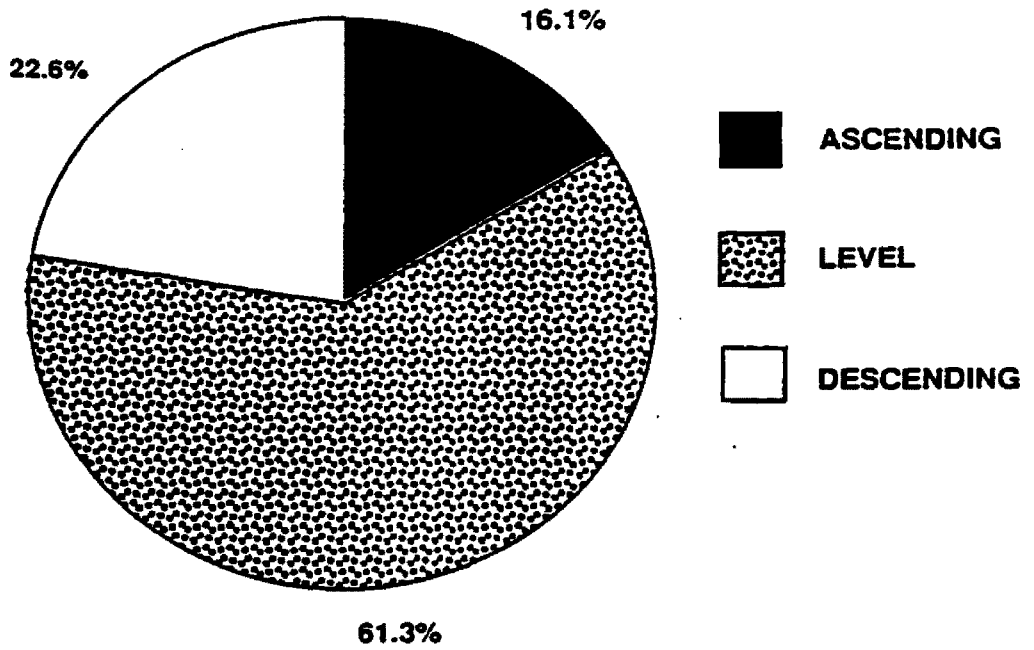


Figure. 11

Figure. 12. Three flight angles were observed in the field; ascending, level and descending. Gait modulation was observed more frequently during descents and level flights. A) Indicates the percentage of observations in each flight angle. B) Indicates the percent modulation at each flight angle.

A.

FLIGHT ANGLE



B.

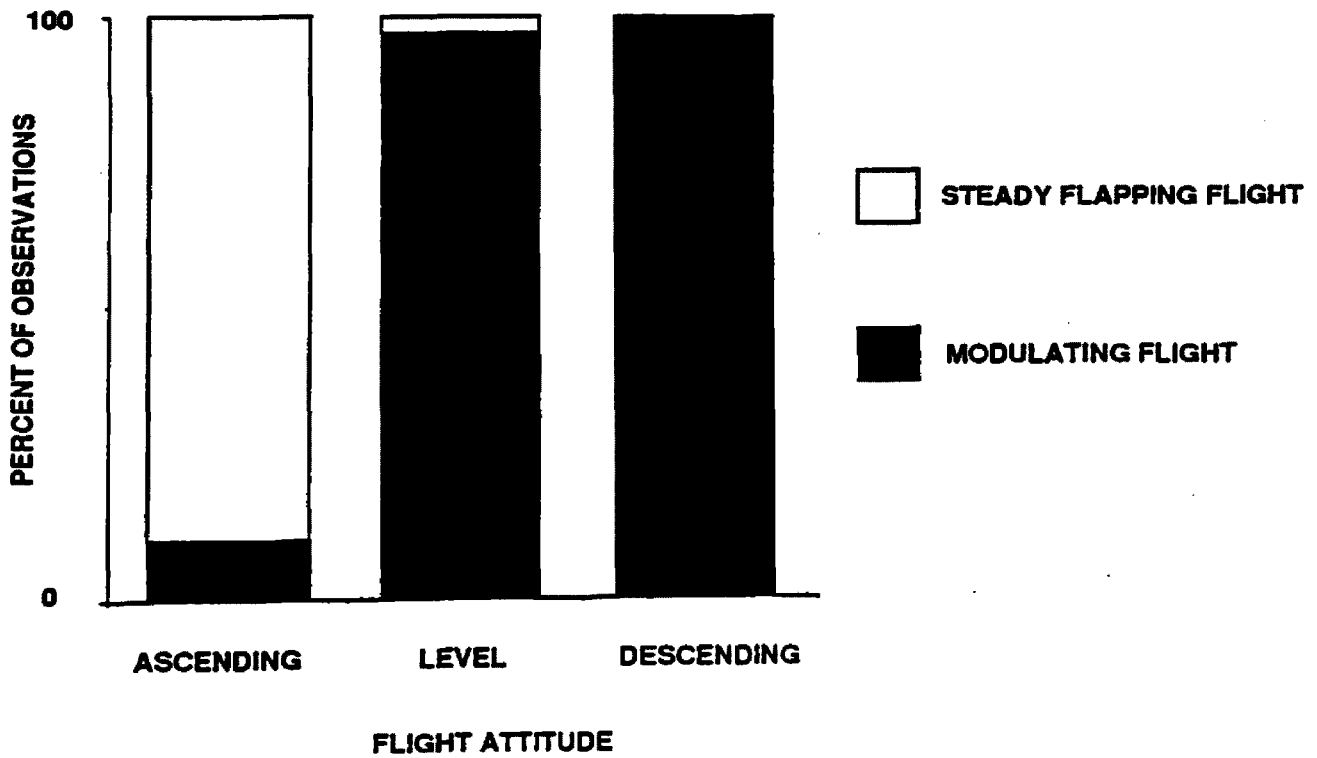
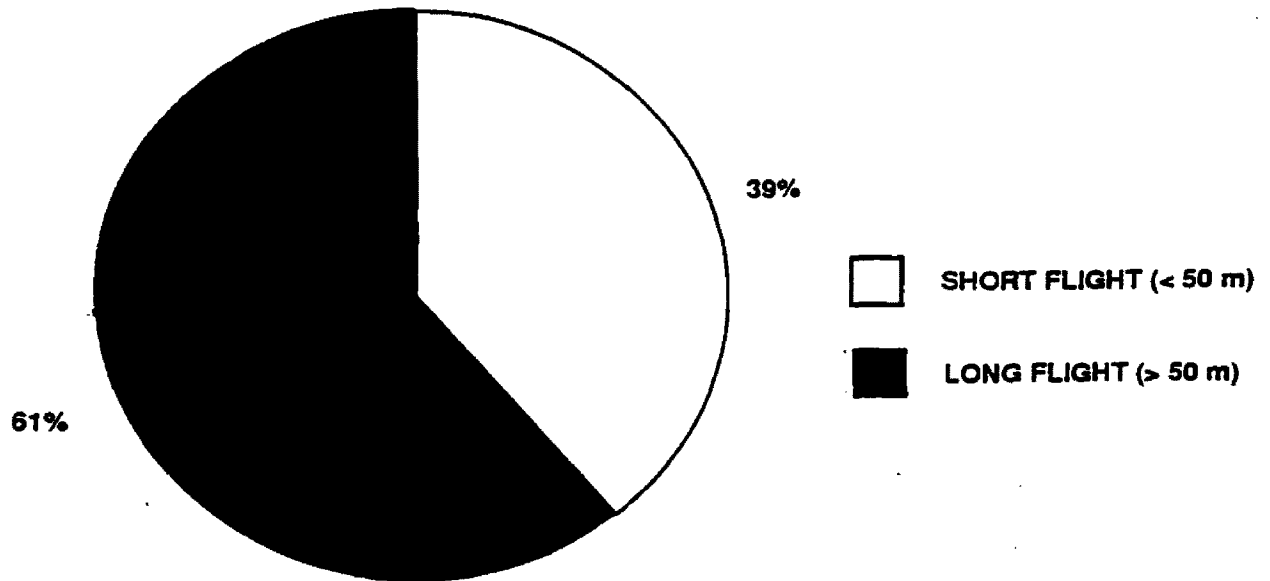


Figure.12

Figure. 13. Distance flown was broken into short (< 50m) and long (> 50m) flights. There was no significant difference between the amount of modulation occurring in the two distances. A) Percent of observations in short and long flights. B) Percent modulation at each flight distance.

A.

DISTANCE FLOWN

B.

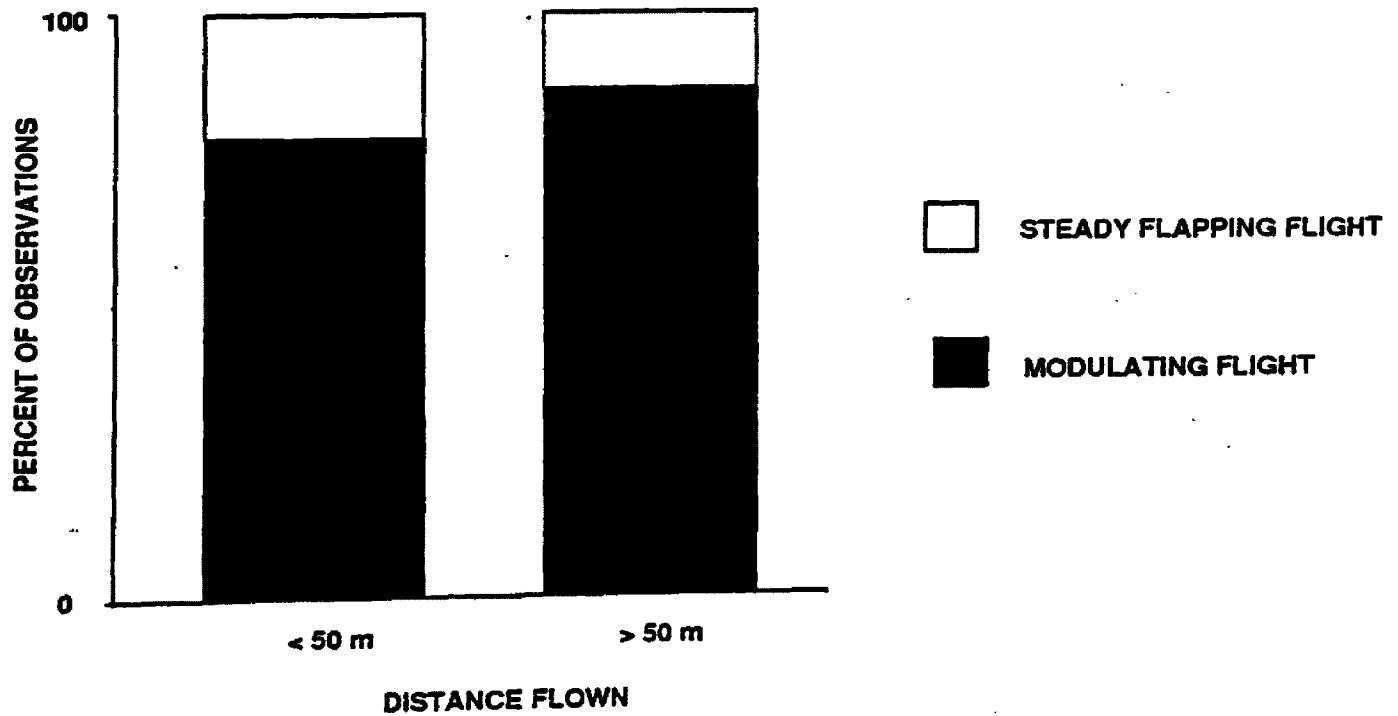
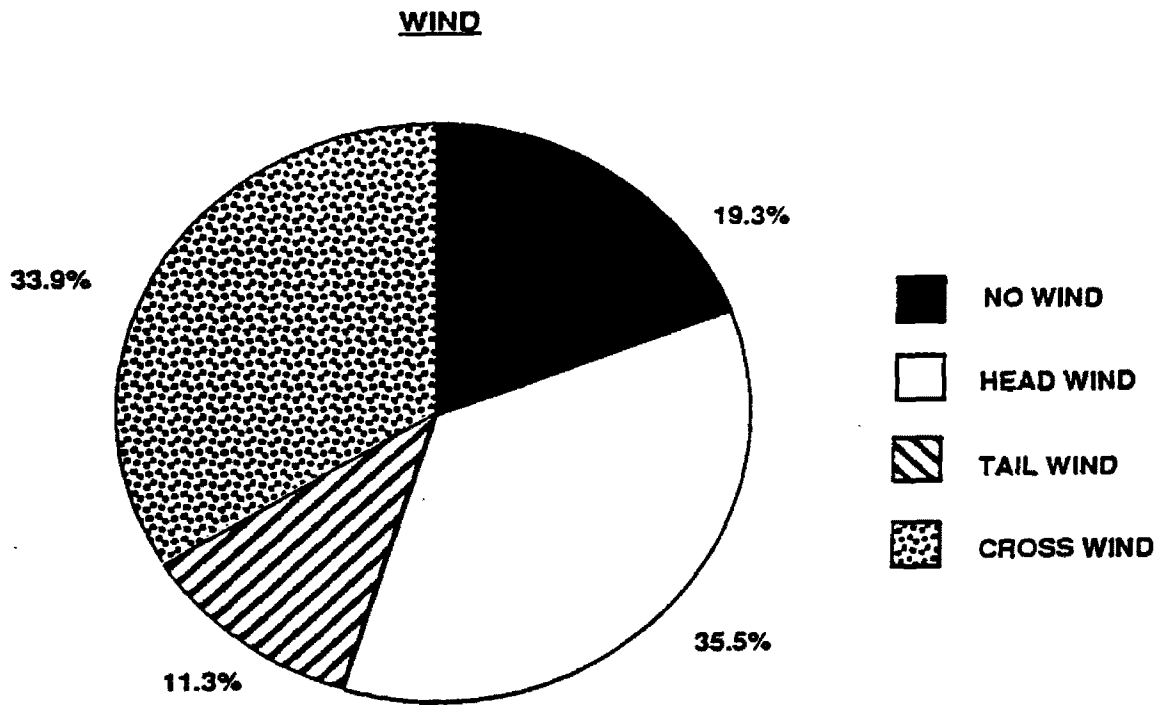


Figure. 13

Figure. 14. Four categories were chosen for affects of wind. Of these Head, Tail and cross wind were analyzed to see there affects on modulation. Wind does not have any significant affects on the modulation of the Black-billed magpie (Pica pica). A) percent of all observations at each wind condition. B) Percent modulation during head wind, tail wind and cross wind.

A.



B.

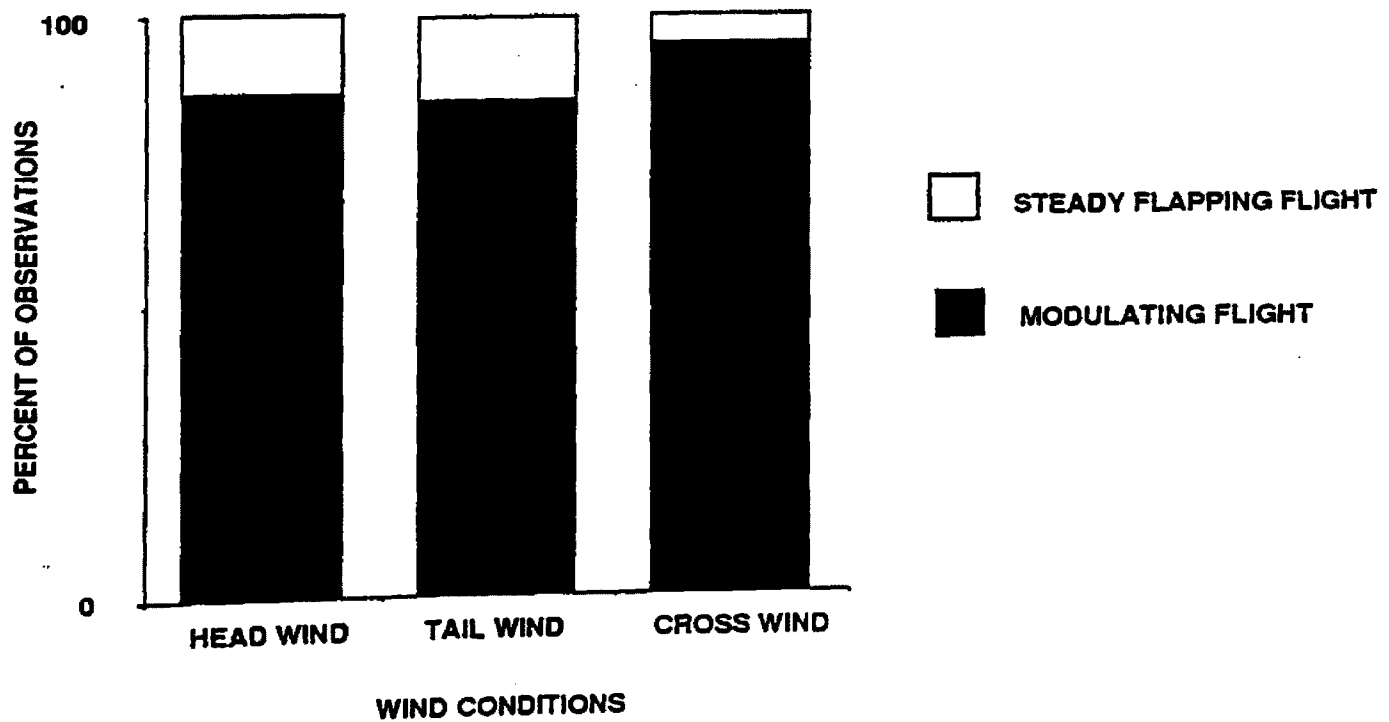


Figure. 14