

COORDINATION OF RESPIRATORY CYCLES WITH WINGBEAT CYCLES IN THE BLACK-BILLED MAGPIE (*PICA PICA*)

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Summary

Magpies fly with a variable pattern of wingstroke, including high-amplitude rapid flaps and low-amplitude slower flaps with interspersed brief glides. This allowed us to test the hypothesis that if phasic coordination between respiratory and wingbeat cycles is important mechanically and energetically, then, as a bird changes its wingbeat cycle, its respiratory cycle should change with it. We also tested the strength of the drive to coordinate respiratory to locomotor cycles by stimulating breathing with 5% CO₂ during flight. We found that magpies ($N=5$) do shorten their breath cycle time when they shorten their wingbeat cycle time and prolong their breath cycle time when they glide. When the coordination ratio of wingbeat cycles to breaths is 3:1, the pattern of phasic coordination ensures two upstrokes per inspiration and two downstrokes per expiration. Upstroke tends to coincide with the transition into inspiration or with early inspiration and late inspiration. Downstroke tends to coincide with the

transition into expiration or with early expiration and late expiration. When magpies switch from a 3:1 ratio to a 2:1 ratio of wingbeat cycles to breaths, they shorten inspiratory time to ensure that upstroke occurs through most of inspiration and downstroke corresponds to the transition into expiration. These phasic coordination patterns ensure that the compression of the airsacs during downstroke can provide a net assistance to expiration and that the expansion of the airsacs with upstroke can provide a net assistance to inspiration. The failure of an atmosphere containing 5% CO₂ to disrupt these phasic coordination patterns between respiratory and locomotor cycles suggests that there may be a potent mechanical and energetic benefit to such coordination.

Key words: flight, breathing pattern, black-billed magpie, CO₂, respiratory-locomotor coordination, *Pica pica*.

Introduction

A number of different ratios between wingbeat and respiratory cycles have been reported in birds (e.g. 1:1, 2:1, 3:1, 4:1, 5:1, 5:2 and 7:2) (Berger *et al.* 1970; Butler and Woakes, 1980; Funk *et al.* 1993), but a 3:1 ratio seems to be the most common. The existence of integer ratios has been used to argue that there may be a coordination between respiratory and locomotor cycles in birds (Funk *et al.* 1993), as has been described in numerous mammals (Bramble, 1989; for a review, see Boggs, 1992). However, because a 1:1 synchrony is uncommon and because the ratios used by a given bird may change, it has also been suggested that there may be no significant mechanical impact of locomotion on respiration in birds (Berger and Hart, 1974; Banzett *et al.* 1992).

We have demonstrated a substantial effect of flight kinematics on airsac pressures and tracheal airflows in black-billed magpies (*Pica pica*) (Boggs *et al.* 1997). In free flight as well as in a windtunnel, magpies have a variable flight style, characterized by longer-duration lower-amplitude wingbeats

interspersed with either brief glides or higher-amplitude shorter-duration wingbeats for acceleration (Olson and Dial, 1992). If there is a significant mechanical effect of the wingbeat cycle on the respiratory cycle that contributes to a coordination between the two in an energetically efficient manner, then it would be expected that, as the wingbeat pattern changes, the respiratory pattern would also change. The magpie, with its variable flight style, represents a useful species in which to test that hypothesis. We did this by recording airsac pressure and tracheal airflow in magpies flying at various speeds in our windtunnel. Furthermore, if there is a significant mechanical benefit to coordinating respiratory to wingbeat cycles phasically, then it should be difficult to change that coordination by stimulating breathing while flying. We tested this hypothesis by exposing magpies to an atmosphere containing 5% CO₂ while they flew at their preferred speed (6–8 m s⁻¹) in the windtunnel.

Some of the data presented here have been summarized in a review (Boggs, 1997).

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Materials and methods

Black-billed magpies (*Pica pica*) ($N=5$, mass 170 ± 13 g, mean \pm S.E.M.) were trapped locally in western Montana, housed in flight cages in our animal facility and trained to fly in a variable-speed windtunnel. The windtunnel in the University of Montana Flight Laboratory has an acrylic flight chamber that is $76\text{ cm}\times 76\text{ cm}\times 91\text{ cm}$, through which air is drawn by a Buffalo 36-d-vanaxial asymmetric fan powered by a 15 kW d.c. motor. After straightening by a 5 mm honeycomb baffling (10 cm thick) upwind, airflow is laminar in the flight chamber. Birds were trained for 30 min per day for several weeks before being instrumented for experimental flights. The windtunnel is normally an open type, but we closed it for the CO₂ studies so that the air would recirculate and CO₂ could be added to it. This was achieved by attaching a sheet-metal 'elbow' at the inlet end to which a plastic tube of the same diameter as the fan sections (102 cm) was attached and joined to the fan outlet end. A cuffed tube inlet to the recirculating tube, at the fan output end, allowed addition of CO₂ to the airstream. Samples of air within the test section were continuously monitored using an Electrochemistry carbon dioxide analyzer (model CD3A), and air temperature was monitored using a YSI thermistor in the test section.

Electromyograms (EMGs) from the pectoralis muscle were used to assess phases of the wingbeat cycle and the type of wingbeat, which is reflected in the intensity and duration of the pectoralis EMG (Olson and Dial, 1992). Bipolar silver electrodes (0.1 mm, California Wire Co.) were inserted into the pectoralis muscle. These, and the cannulae described below, were implanted while the bird was anesthetized with ketamine (25 mg kg^{-1} , intramuscularly) and xylazine (2 mg kg^{-1} , intramuscularly). The EMG wires emerged from under the skin between the scapulae to a small connector (Microtech GM6, GF6) to which a cable (Cooner Wire Co. NMUF6) could be attached during experiments to carry the signal to a Grass P511 preamplifier. The respiratory cycle was monitored by recording airsac pressure. Interclavicular airsac pressures were recorded by inserting a cannula (PE 200 tubing with side holes) into the interclavicular airsac, securing it to the sac with cyanoacrylic adhesive (superglue), suturing it to the furcula, and connecting it *via* silastic tubing to a miniature piezoresistive pressure transducer (Endevco model 8507C-2) that the bird carried within a Velcro backpack during flights in the windtunnel the following day. The pressure transducer was insensitive to acceleration and had a response time of 1.4 ms. It was calibrated with a water manometer before and after each experiment. Tracheal airflow was measured with a dual thermistor bead anemometer (Hector Engineering model 132C). The flow signal was linearized and integrated to give volumes (see Boggs *et al.* 1997, for further details on this technique). Flows were calibrated with a 12 L Brooks Instrument Division volumeter. Data were stored either on a TEAC MR40 tape recorder or on disc using a Zenith Data Systems 486 computer and Keithley A/D converter. Differences between means were assessed using a Student's two tailed *t*-test, and significance was taken at the $P<0.05$ level.

Results

When the magpies changed their flapping pattern, their breathing pattern changed with it (Fig. 1). Low-amplitude wingbeat cycle times are longer than high-amplitude wingbeat cycles ($P<0.001$), and the breath cycle times are also longer when associated with low-amplitude, longer-duration wingbeats and shorter when associated with high-amplitude, shorter wingbeats ($P<0.05$) (Fig. 1). In the one magpie which would consistently glide for brief periods (only equivalent to a few wingbeat cycles), the breathing pattern again changed to one with a longer breath duration ($P<0.05$) during the non-flapping periods ($0.435\pm 0.01\text{ s}$ versus $0.34\pm 0.01\text{ s}$; values are means \pm S.E.M., $N=26, 30$). Tidal volume during glides ($5.1\pm 0.2\text{ ml}$) was not statistically significantly different from that during flapping flight ($4.6\pm 0.2\text{ ml}$; means \pm S.E.M., $N=25, 30$).

The ratio of wingbeats to breaths at the bird's preferred speed ($6\text{--}8\text{ m s}^{-1}$, as observed in the field, Olson, 1993) is generally close to 3:1. Under these conditions, the magpies coordinate the two cycles phasically to achieve the pattern represented in Fig. 2A. There are two upstrokes and one downstroke during inspiration, and two downstrokes and one upstroke during expiration. The upstrokes tend to occur either with the transition into inspiration (T) or during early inspiration (EI), during late inspiration (LI) and during mid-expiration (ME). Downstrokes are most likely to occur during mid-inspiration (MI), and either at the transition (T) into expiration or during early expiration (EE) and late expiration (LE).

When the magpies accelerate while flying at their preferred speed ($6\text{--}8\text{ m s}^{-1}$) or when they are made to fly at faster speeds (up to 11 m s^{-1}), they sometimes switch wingbeat-to-breath ratios from 3:1 to 2:1. When the ratio is 3:1, the phasic coordination pattern is as described above, and inspiratory (T_I) and expiratory times (T_E) are equal (Fig. 3). However, when the bird switches to a ratio of 2:1, the breathing pattern changes. The inspiratory time is shortened to ensure that upstroke overlaps most of inspiration and downstroke occurs with the transition into expiration (Fig. 3). This shortening of T_I with the change in wingbeat to respiratory cycle ratio from 3:1 to 2:1 occurred in five magpies for whom the mean values of T_I/T_{ROT} are presented in Fig. 4 and was statistically significant ($P<0.01$).

We exposed three magpies to an atmosphere containing 5% CO₂ during flight. The data presented in Fig. 5A indicate that peak airsac pressures were significantly elevated during the CO₂-exposed flights compared with flights in air, indicating that the bird's respiration was indeed stimulated by the CO₂. However, there was no change in the wingbeat-to-breath ratio (Fig. 5B). The phasic coordination pattern did not change when breathing was increased by inspiring 5% CO₂ during flight (Fig. 2B). The response to CO₂ while magpies sat on the perch in the windtunnel was due to a large increase in tidal volume (mean values $2.63\pm 0.7\text{ ml BTPS}$ while breathing air and $10.47\pm 2.3\text{ ml BTPS}$ while breathing 5% CO₂; means \pm S.E.M., $N=3$) with no significant increase in frequency (Fig. 6). While flying, the response was also due to an increase in tidal volume, from 7.76 ± 1.8 to $13.95\pm 4.8\text{ ml BTPS}$ (means \pm S.E.M., $N=3$),

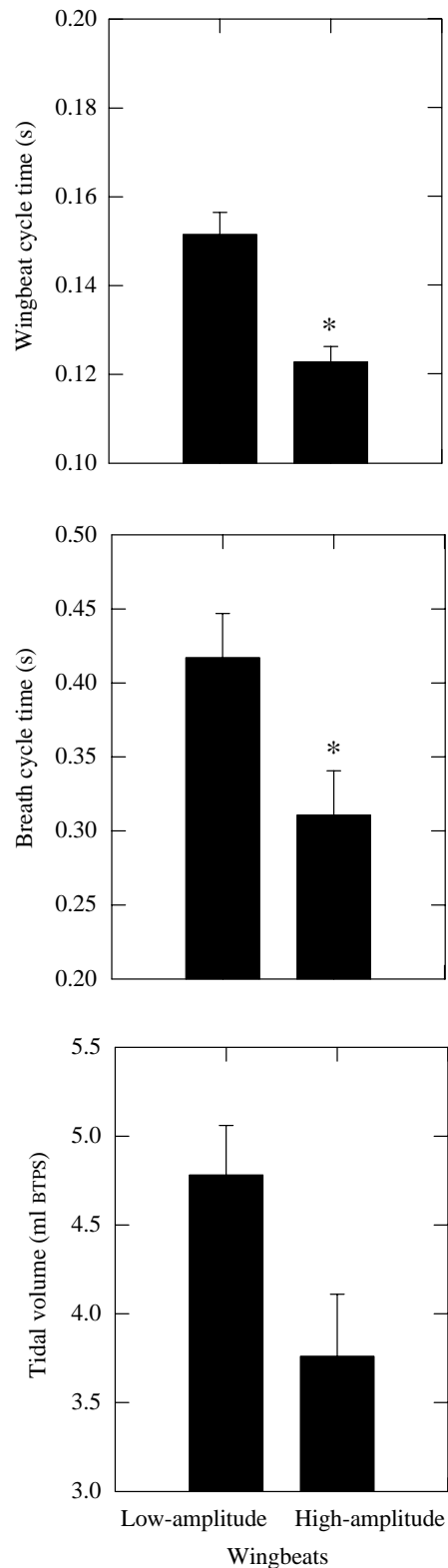


Fig. 1. Mean (+1 S.E.M.) values for wingbeat cycle time, breath cycle time and tidal volume during low-amplitude and high-amplitude wingbeats in five magpies. High-amplitude wingbeats are significantly ($P < 0.001$) shorter than low-amplitude wingbeats, and the associated breaths are also shorter ($P < 0.05$). The tidal volumes were not significantly different.

with no significant change in frequency. There was a large variance in the tidal volumes among the three birds during flight: in one, tidal volume increased by 3.6-fold compared with the resting value, whereas in the other two, tidal volume increased by only twofold and 2.3-fold, and the change in tidal volume during flight in response to CO_2 was greater for one bird than for the other two, i.e. 55.2%, 54.7% and 115%. The reason for this individual difference is not apparent.

Discussion

We found that our prediction that respiratory pattern would change as wingbeat pattern changed was true and that we could not disrupt the coordination between respiratory and locomotory cycles by stimulating breathing during flight with an atmosphere containing 5% CO_2 . These results support the hypotheses that a coordination between respiratory and locomotory cycles exists and that the neural mechanisms responsible for it are quite robust since chemical stimulation of breathing does not alter the coordination.

The phasic coordination pattern observed in magpies during their common ratio of three wingbeats to one breath cycle is similar to the phasic coordination pattern reported for two other species with a ratio of 3:1, the barnacle goose (Butler and Woakes, 1980) and the Canada goose (Funk *et al.* 1993). Although the latter authors state that inspiration did not occur preferentially during upstroke, their data seem to indicate a similar distribution of upstrokes through a breath cycle to that observed here, wherein there are two upstrokes per inspiration and one at mid-expiration. The 'peak' or end of upstroke occurs very early in inspiration in the Canada goose, but this is consistent with upstroke overlapping the transition from expiration to inspiration in the magpie. There seems to be a small phase shift (fraction of a wing cycle with respect to breath cycle) in the study of Funk *et al.* (1993) compared with the present study because nasal airflow (or an open or closed mouth) was the indicator of breath cycle in the Canada goose study, combined with or taken from film of the wing cycle, whereas airsac pressure was the indicator of breath cycle in the present study and the pectoralis electromyogram was the indicator of wing position, and we found that the pressure changes always preceded the recorded tracheal airflow changes by a few milliseconds. In other words, had Funk *et al.* (1993) recorded airsac pressures rather than nasal airflow, they would probably have seen the transition from expiration to inspiration (and from inspiration to expiration) occurring slightly earlier with respect to upstroke in the former case and with respect to downstroke in the latter, resulting in phasic relationships that would be very similar to those reported here for magpies.

Coordination of respiratory and locomotory cycles in mammals and birds has been attributed to two types of input to the respiratory control centers: feedforward control, whereby neural connections between the hypothalamic/brainstem locomotory control centers and the medullary respiratory control centers ensure an increased and coordinated ventilation with exercise (Eldridge *et al.* 1985; Persegol *et al.*

PHASIC COORDINATION PATTERNS

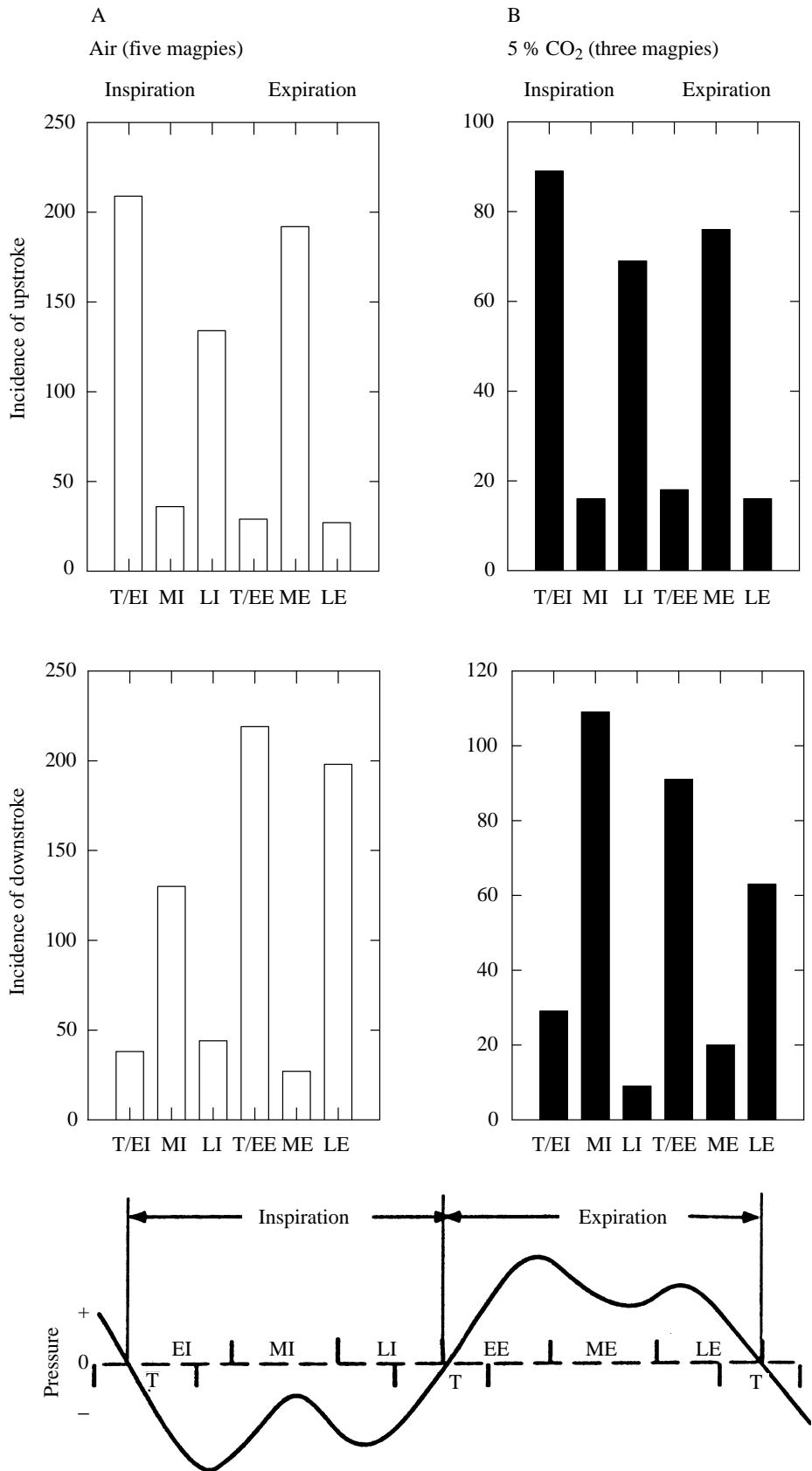


Fig. 2. (A) The distribution of upstrokes and downstrokes through a breath cycle (from 250 breath cycles from five birds) while breathing air during flight (open bars). As indicated in the diagram at the bottom of the figure, the breath cycle is broken up into periods of transition (T) from one phase to the other, early inspiration (EI), mid-inspiration (MI), late inspiration (LI), early expiration (EE), mid-expiration (ME) and late expiration (LE). (B) Distribution of upstrokes and downstrokes through the breath cycle while exposed to an atmosphere containing 5% CO₂ during flight (from 103 breath cycles). The phasic coordination patterns do not differ from those observed in air.

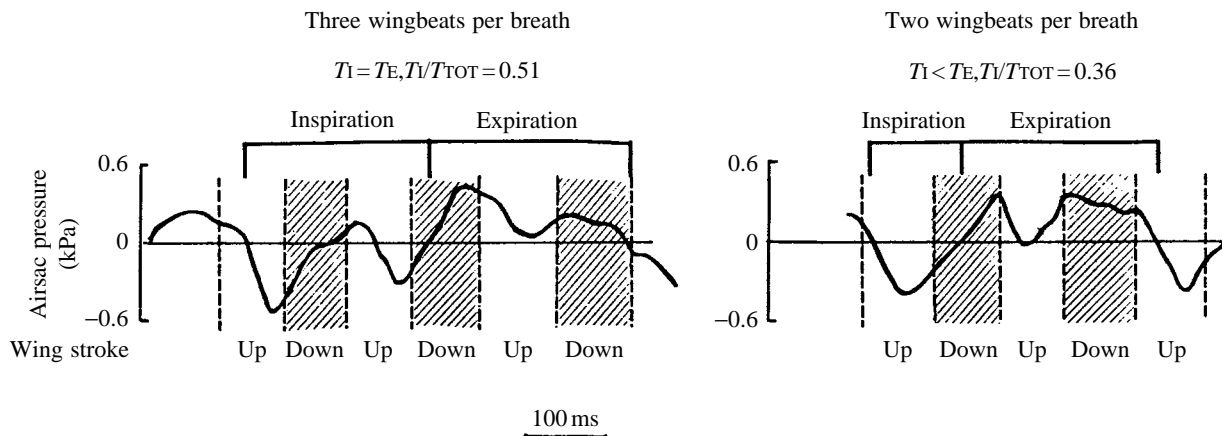
Magpie 15 (R4) (8.8 m s^{-1})


Fig. 3. Examples of the phasic relationship between wingbeat cycle phases and respiratory cycle phases during two breaths in which the ratio of wingbeats to breaths changes from 3:1 to 2:1. While the ratio was 3:1, the inspiratory time (T_i) and expiratory time (T_e) were nearly equal; hence, inspiratory time as a fraction of total breath time (T_i/T_{TOT}) was 0.51. When the ratio was 2:1, inspiratory time shortened to 0.36 of total breath time.

1988; Kawahara *et al.* 1989; Funk *et al.* 1989*a,b*, 1992*b*); and feedback control from a variety of peripheral mechanoreceptors during locomotion (Remmers and Martilla, 1975; Iscoe and Polosa, 1976; Petrillo *et al.* 1983; Funk *et al.* 1992*a,b*). The lift forces transmitted to the sternum during downstroke can cause sufficient compression of the airsacs in magpies to change their pressure by 0.37 kPa, while the expansive effects of upstroke can change airsac pressures during expiration by 0.26 kPa (Boggs *et al.* 1997). Such volume and pressure changes within the airsacs would seem to be ample stimulation for stretch receptors in their walls and may represent one of several potential peripheral feedback

signals (e.g. intrapulmonary chemoreceptors which may be sensitive to flow, and muscle spindles in the intercostal and abdominal muscles) contributing to the coordination patterns observed in magpies and other birds.

The excellent study by Funk *et al.* (1992*b*) demonstrated the importance of peripheral feedback in creating a variety of coordination ratios typical of flying birds. By inducing 'fictive' flight in Canada geese and Pekin ducks by electrical stimulation of brainstem locomotor regions, they demonstrated a predominantly 1:1 coordination between wingbeat frequency and respiratory frequency in paralyzed birds, but other coordination ratios occurred in birds which were allowed to flap their wings (2:1, 3:1 and 4:1). Their data clearly demonstrated the importance of central coactivation of respiratory (and cardiovascular) control centers by central locomotor drive, but also indicate the importance of phasic peripheral feedback in creating the patterns of coordination seen in freely flying birds, although the source or sources of that afferent feedback could not be specifically identified. In another study (Funk *et al.* 1992*a*), they demonstrated that the removal of afferent signals from the wings did not alter the ability of passive wing movements to entrain respiratory movements, suggesting that the effect of wing movements on afferent feedback from the respiratory system may be more important to entrainment of the two cycles than feedback from the wings.

The mechanical impact of flight on the respiratory system would seem to make a coordination of inspiration with upstroke and expiration with downstroke energetically beneficial. Pigeons that use a 1:1 ratio of wingbeats to breaths do this (Berger *et al.* 1970; Butler *et al.* 1977; Boggs, 1997), as do the ducks and geese under 'fictive' flight conditions (Funk *et al.* 1992*b*). Preliminary data, using integrated respiratory muscle EMGs as an index of respiratory muscle effort in pigeons (Boggs, 1997), indicate that the same

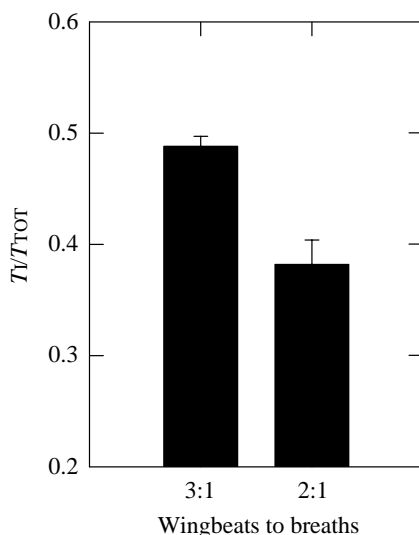


Fig. 4. Mean values (+1 S.E.M.) for the ratio of inspiratory time to total breath time (T_i/T_{TOT}) for five magpies when the ratio of wingbeats to breaths is close to either 3:1 or 2:1. T_i/T_{TOT} is significantly smaller ($P < 0.01$) when the ratio of wingbeats to breaths is 2:1.

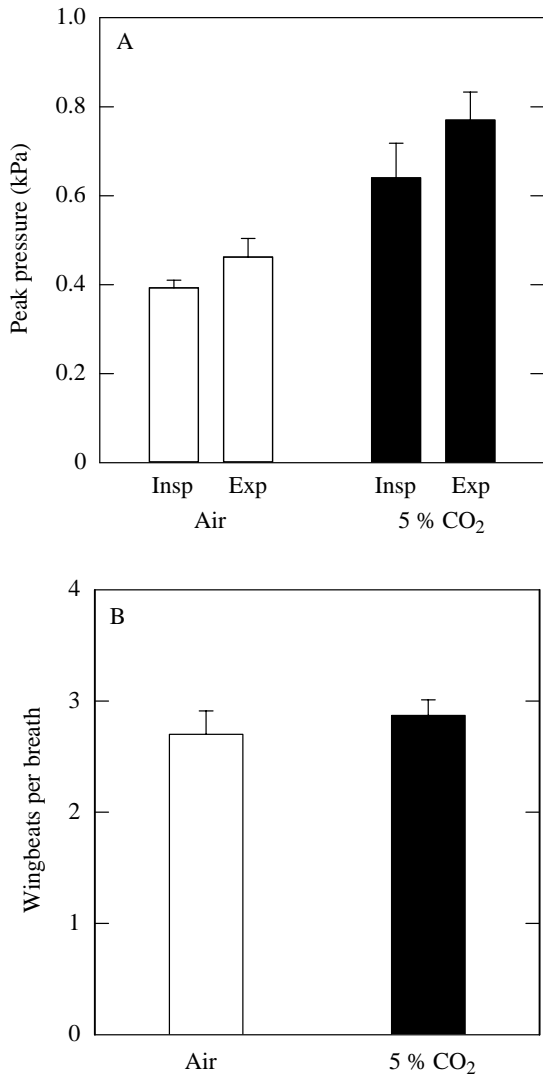


Fig. 5. (A) Mean values for three magpies (± 1 S.E.M.) of peak inspiratory and expiratory airsac pressures while flying and breathing either air (open bars) or an atmosphere containing 5% CO₂ (filled bars). Inspiratory peak pressures (Insp) ($P < 0.05$) and expiratory peak pressures (Exp) ($P < 0.01$) were significantly greater while breathing 5% CO₂ than while breathing air, suggesting that breathing efforts were increased. (B) The wingbeat-to-breath ratio is not significantly different when breathing 5% CO₂ and when breathing air.

respiratory pressures are generated with reduced respiratory muscle force during flapping than during non-flapping flight, supporting the concept that the flight muscles bear some of the cost of breathing when inspiration occurs with upstroke and expiration with downstroke. Ratios between wingbeats and breaths other than 1:1 are more common (perhaps to allow for a larger tidal volume and/or to avoid excessive hyperventilation), but can still be phasically coordinated to ensure more assistance than interference to inspiration from upstrokes and to expiration from downstrokes. For example, three different ratios can all contain phasic coordination patterns that achieve a net assistance to respiration from flight-induced forces (Fig. 7): in the 3:1 phasic coordination

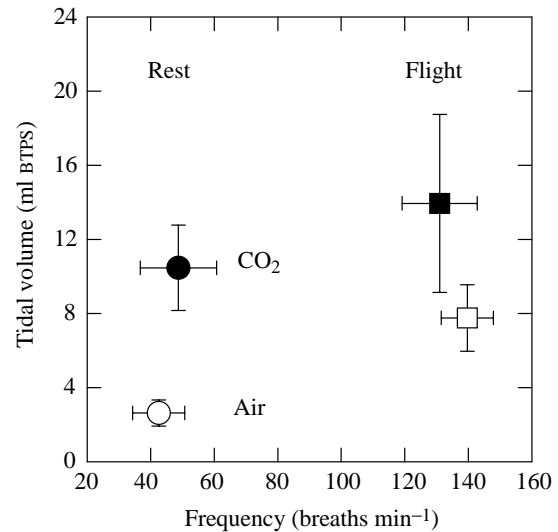


Fig. 6. Tidal volume plotted against respiratory frequency at rest (circles) and during flight (squares) while breathing either air (open symbols) or an atmosphere containing 5% CO₂ (filled symbols). In each case, there is little effect of CO₂ on frequency, but a considerable increase in tidal volume. Values are means \pm S.E.M., $N=3$.

pattern seen in magpies and geese, there are two 'assists' and one 'interference' from the wingstrokes to each breath phase, which amounts to a net assistance; in the 2:1 pattern, a net assistance (three assists and one interference) can be retained by shortening inspiratory time to correspond to upstroke and allowing downstroke to assist the transition to expiration. A 1:1 ratio allows for assistance in both breath phases without any interference from the wingbeat cycle. Resting birds generally breathe with equal inspiratory and expiratory times. During flight, the periods occupied by upstroke and downstroke are generally nearly equal. In pigeons and magpies when flying with either a 1:1 or a 3:1 coordination ratio, inspiratory and expiratory times remain equal, but the shortening of inspiratory time as a fraction of total breath time (or 'duty cycle') when magpies shift to a 2:1 ratio provides further evidence of the mechanical/energetic importance of phasic coordination and of peripheral mechanical feedback in achieving it through modulation of the breathing pattern. It would be interesting to determine whether T_I/T_{TOT} is consistently reduced in other even-numbered coordination ratios. However, it is also important to note that free-flying Canada geese (Funk *et al.* 1993) and barnacle geese (Butler and Woakes, 1980) are reported to have longer 'duty cycles' (T_I/T_{TOT}) during flight than the magpie, at 58% and 59% respectively, compared with 49% for the magpie.

The change in breath cycle time with changing wingbeat cycle time observed in the varying flapping pattern typical of magpies also supports the concept of an important central feedforward and peripheral feedback locomotory control of respiratory pattern.

The failure of chemical stimulation of breathing to disrupt

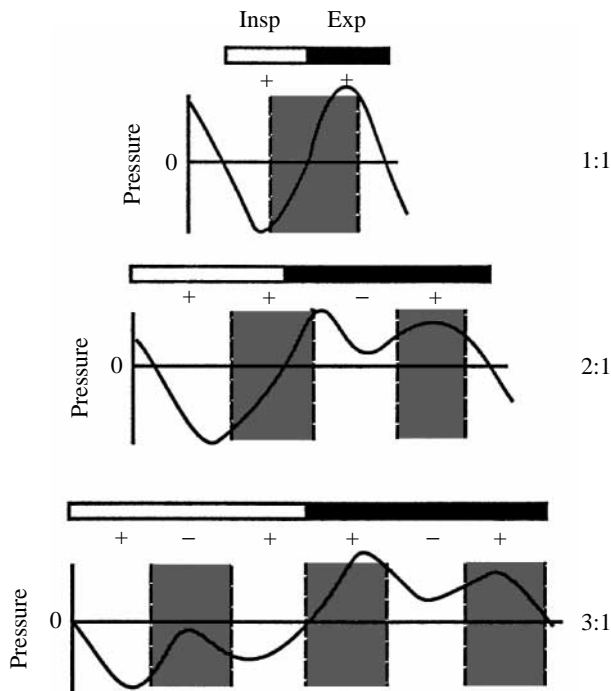


Fig. 7. General scheme of phasic coordination patterns between air sac pressure changes and upstroke (open) and downstroke (shaded) periods of the wingbeat cycle when the number of wingbeat cycles per breath cycle varies from 1:1 to 2:1 to 3:1. In each case, there are periods when the wingbeat cycle 'assists' (denoted by '+') the respiratory cycle (i.e. when downstroke occurs with the transition into expiration or during expiration, or when upstroke occurs during the transition into inspiration or during inspiration) and periods when the wingbeat cycle 'interferes' (denoted by '-') with the respiratory cycle. In each case, there are more 'assists' than 'interferences'. Exp, expiration; Insp, inspiration.

the coordination of respiratory and locomotory cycles is further testimony to the potency of the mechanical effects of flight on respiration. Other studies of the effects of increased respiratory drive on respiratory-locomotor entrainment have had variable results that seem likely to reflect the relative magnitudes of the mechanical effects of locomotion on respiration in the various species. In walking or running geese (Funk *et al.* 1989b) and humans (Paterson *et al.* 1987), the increased respiratory drive associated with hypoxia caused a loss of entrainment. The effects of 5% CO₂ on entrainment in running geese were too variable to identify a clear trend, but entrainment seemed to be reduced in two out of three individuals (Funk *et al.* 1989a,b). However, in bipedal runners, the mechanical effect of locomotion on respiration is far smaller than in quadrupedal runners or in fliers (Funk *et al.* 1989a,b; Paterson *et al.* 1987; Banzett *et al.* 1992). In horses, which are entrained 1:1 while galloping, attempts to uncouple respiratory and locomotory cycles with an atmosphere of 6% CO₂ were unsuccessful in five out of six individuals (Gillespie *et al.* 1991).

The ventilatory response to 5% CO₂ in the resting birds was due largely to an increase in tidal volume, with only a small contribution from an increase in frequency. During flight, the

increased ventilation in response to inspired CO₂ had almost no frequency component and was due almost entirely to an increase in tidal volume, allowing the coordination of respiratory to locomotory cycles to remain intact. In fact, one magpie had a somewhat 'sloppier' phasic coordination pattern before CO₂ exposure that became much more tightly coordinated in the patterns represented for the group in Fig. 7, as though it became even more important to coordinate respiratory and locomotory cycles with this increased ventilation state. Ventilation increased as much or more in response to a 5% CO₂ stimulus during flight as it did during resting. This suggests there is not a reduced sensitivity to CO₂ with exercise, as was suggested may exist in running geese (Funk *et al.* 1989b) but was not observed in running chickens (Brackenbury *et al.* 1982). The increases in tidal volume of similar magnitude in response to 5% CO₂ whether at rest or during exercise are comparable to the responses to 3% CO₂ in resting and running chickens (Brackenbury *et al.* 1982; Brackenbury, 1991). Hypoxia would be a better respiratory stimulus to use during flight because it is more natural and because it is more likely to affect respiratory frequency, as it does in resting and running chickens (Brackenbury, 1986), in resting pigeons (Bouverot *et al.* 1976), in resting bar-headed geese (Fedde *et al.* 1989) and in resting Pekin ducks (Kiley *et al.* 1985). It may therefore be more likely either to disrupt entrainment or to alter the coordination pattern in a bird with a ratio other than 1:1. It is interesting to note, however, that in Pekin ducks there is a reduction in tidal volume with the increase in breathing frequency associated with running during normoxia, but that there is an increase in tidal volume associated with a similar increase in frequency during hypoxic running compared with normoxic running (Kiley *et al.* 1985). Hypoxia (without a mask) has been more difficult to achieve in the windtunnel, but ongoing and future studies will measure the responses to hypoxia during flight.

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