

## SHORT COMMUNICATION

### COORDINATION OF WING BEAT AND RESPIRATION IN CANADA GEESE DURING FREE FLIGHT

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*Accepted 10 November 1992*

It remains unclear whether coordination of wing and respiratory movements is universal among birds during flight (Tomlinson, 1963). However, it is certain that many species demonstrate some form of coordination between wing and respiratory movements (Marey, 1890; Groebbels, 1932; Zimmer, 1935; all cited in Hart and Roy, 1966; Tomlinson, 1957, 1963; Lord *et al.* 1962; Hart and Roy, 1966; Berger *et al.* 1970*b*; Butler *et al.* 1977; Butler and Woakes, 1980). Ratios of wing beat frequency to respiratory frequency ( $f_w/f_v$ ) ranging from 1:1 to 5:1 have been described, some species showing variation in  $f_w/f_v$  (Lord *et al.* 1962; Berger *et al.* 1970*b*; Butler and Woakes, 1980).

Recent experiments using decerebrate Canada geese (*Branta canadensis*), examining the mechanisms responsible for generating coordination between wing beat and respiration and controlling the number of wing beats per breath ( $f_w/f_v$ ), indicate that coordination of wing beat and respiration is produced *via* a collective interaction of feedforward locomotor inputs (Funk *et al.* 1992*b*) and mechanoreceptive feedback (Funk *et al.* 1992*a*) on some portion of the respiratory rhythm-generating networks.

Afferent feedback associated with active limb movement, either metabolic or kinesthetic, is important in determining  $f_w/f_v$  (Funk *et al.* 1992*a*). In decerebrate geese, wing beat and respiratory rhythms are always coordinated and, as seen for several species during free flight (Lord *et al.* 1962; Berger *et al.* 1970*b*; Butler and Woakes, 1980), the relationship between  $f_w$  and  $f_v$  varies considerably. Following removal of feedback by paralysis, the relationship between the neural outputs of the locomotor and respiratory systems does not vary (Funk *et al.* 1992*b*).

The relevance of these findings to free flight, however, remains unclear because the relationship between  $f_w$  and  $f_v$  has not been described for free-flying Canada geese. Measurements of  $f_w/f_v$  have been made for two barnacle geese during free flight (Butler

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and Woakes, 1980); however, barnacle geese (1.6kg) are much smaller than Canada geese (3.8kg) and weight, relative to wing area, may affect  $f_w/f_v$  (Berger *et al.* 1970b).

Thus, the first goal of this study was to describe the relationship between  $f_w$  and  $f_v$  in free-flying Canada geese. Furthermore, little information is available on the alterations in respiratory pattern required to provide the increased oxygen requirements of flight while maintaining coordination between wing beat and respiration. The second goal of this study was to describe, in detail, the changes in respiratory pattern (duty cycle) that occur during flight in Canada geese.

Experiments were performed on five Canada geese (mass  $3.8 \pm 0.2$ kg) during free flight using methods similar to those described by Butler and Woakes (1980). Birds were raised from hatching and imprinted on one of the authors (G.D.F.). The goslings spent at least 4 h per day with the foster parent for their first 4 months, 1h of which was spent wearing both a cylindrical facemask and a lightweight nylon harness. The harnesses, to which a radiotransmitter would later be attached, did not interfere with wing or leg movements in any way. At approximately 4 months of age, flight feathers were fully developed and flight training was initiated.

Daily training sessions involved four consecutive flights up and down a 1.0km road with the birds following the foster parent, who was riding a bicycle. The birds wore the harnesses and facemasks during all training flights. Experimental trials were begun following 3 weeks of flight training.

Recordings were made during experimental flights by having the birds fly behind a motorcycle. The birds' flight was recorded using a videocamera (JVC model GS-CD1U;  $33 \text{ frames s}^{-1}$ ) and recorder (JVC BR-1600U). An internal digital clock recorded time to 0.01s on the videotape. Measurements of wing beat frequency ( $f_w$ ) were obtained for all flights (instrumented and uninstrumented) *via* frame-by-frame analysis of the video tape. Each wing cycle occupied 8 video frames.

Respiratory frequency ( $f_v$ ) was recorded using two methods: (1) frame-by-frame video analysis (uninstrumented flights) of mouth movements, and; (2) radiotelemetry (instrumented flights). A thermistor bead (Fenwall 112-202EAJ-B01) placed in the mask, overlying a nostril, was connected to a radiotransmitter (mass 19.5g; length 5.5cm; diameter 2.0cm) attached to the harness. Cyclical changes in thermistor resistance resulting from changes in the temperature of inspired *versus* expired air were transmitted *via* the radiotransmitter, received using an FM radio, and recorded on the audio channel of the video recorder. The signal was later demodulated and then synchronized, by means of the VHS internal clock, with the visual signal indicating  $f_w$ , to determine the relationship between  $f_w$  and  $f_v$ . The transmission range of the transmitter was less than 3.5m. Trained birds, however, generally flew within a corridor of 0.5–2m from either side of the cycle, 0–3m behind the cycle and 1–3m above the ground.

Experiments were carried out between 4:30 and 10:00h. Air temperature ranged from 11 to 16°C. Thus, periods of high ambient temperature, which could influence ventilatory patterns (Scheid and Piiper, 1986), were avoided. In addition, wind speeds at this time were less than  $5 \text{ km h}^{-1}$ . Thus, ground speed and air speed differed by less than 10%. Experimental trials consisted of approximately four consecutive 60 s flights (although

some were longer than 5min). The birds spent between 10 and 60s on the ground between consecutive flights. The use of relatively brief flight periods raises the possibility that some aspects of flight physiology may not have reached a steady state. However, values of  $\dot{V}_V$ ,  $\dot{V}_W$  and  $\dot{V}_W/\dot{V}_V$  were the same whether measured during a 5min or a 60s flight. Ground velocity, as read from the speedometer of the motorcycle, was held constant at  $50\text{km h}^{-1}$  for the instrumented flights and varied randomly between 50 and  $80\text{km h}^{-1}$  for the uninstrumented flights. The cruising speed of Canada geese recorded in the wild ( $13.9\text{ms}^{-1}=50\text{km h}^{-1}$ ; Tucker and Schmidt-Koenig, 1971) was chosen as the lower speed. The higher velocity of  $80\text{km h}^{-1}$  was established to increase work rate as much as possible without compromising the birds' ability to complete the flight trials (described above). Each bird was taken through this procedure only once per day. Owing to the difficulty in obtaining good transmissions from these animals, the frequency with which they flew away, the difficulty of recapturing them, and the associated risk of equipment loss, we were satisfied with one good recording sequence (minimum duration of 30s, permitting analysis of at least 20 respiratory cycles) from each animal during instrumented flight. Since there was no risk of equipment loss during the uninstrumented flights, a minimum of three flights (greater than 200 respiratory cycles per bird) was recorded from each animal.

During instrumented flight at  $50\text{km h}^{-1}$ , values of  $\dot{V}_V$ , the duty cycle for the respiratory rhythm ( $T_I/T_{TOT}$  and  $T_E/T_{TOT}$ , where  $T_I$  represents inspiratory duration,  $T_E$  represents expiratory duration and  $T_{TOT}$  represents the total respiratory period) and  $\dot{V}_W/\dot{V}_V$  were determined from the analysis of 20 respiratory cycles per bird.

During uninstrumented flight at 50 and  $80\text{km h}^{-1}$ , values of  $\dot{V}_V$ ,  $\dot{V}_W$  and  $\dot{V}_W/\dot{V}_V$  at 50 and  $80\text{km h}^{-1}$  were based on the analysis of 100 respiratory cycles per bird at each velocity. At the highest  $\dot{V}_V$  recorded, each respiratory cycle occupied 22 video frames, allowing easy identification of transitions from mouth open to mouth closed (inspiration to expiration) and mouth closed to mouth open (expiration to inspiration). These transitions never occupied more than two frames.  $T_I/T_{TOT}$  and the phase relationship between  $\dot{V}_W$  and  $\dot{V}_V$  were determined through analysis of 20 respiratory cycles per bird at each velocity. This was done by standardizing the respiratory period ( $T_{TOT}$ ) to equal one, and then determining the portion of  $T_{TOT}$  when either peak upstroke or peak downstroke occurred. Finally, the portion of inspiration during which the wings were moving up *versus* down was calculated to determine whether some locomotor assistance of respiration could be achieved if inspiration were to occur predominantly during upstroke.

Unless the data given are for individual birds, values represent means  $\pm$  S.D. Student's *t*-test was used to test the difference between means. Values of  $P<0.05$  were assumed to be significant.

Comparison of the respiratory data collected at  $50\text{km h}^{-1}$  *via* telemetry and through video analysis of mouth movements confirmed earlier observations in barnacle geese (Butler and Woakes, 1980) that inspiration occurs when the mouth is open and expiration when the mouth is closed. During telemetered flight at velocities of  $50\text{km h}^{-1}$ ,  $\dot{V}_V$  was  $79.8\pm 5.1\text{breathsmin}^{-1}$ ,  $T_I/T_{TOT}$  was  $0.54\pm 0.05$  and  $\dot{V}_W/\dot{V}_V$  was always 3:1. Virtually identical values were obtained during the uninstrumented flights at  $50\text{km h}^{-1}$ .  $\dot{V}_V$  was  $78.4\pm 4.4\text{breathsmin}^{-1}$ ,  $T_I/T_{TOT}$  was  $0.58\pm 0.02$  and  $\dot{V}_W/\dot{V}_V$  was 3:1. Because there is a

Table 1. *Effects of velocity on locomotor and respiratory patterns*

	<i>N</i>	<i>n</i>	Velocity (km h <sup>-1</sup> )		
			0.0	50.0	80.0
<i>f<sub>V</sub></i> (breathsmin <sup>-1</sup> )	5	200	14.8±2.8	78.4±4.4*	89.8±5.9†
<i>f<sub>W</sub></i> (breathsmin <sup>-1</sup> )	5	600	–	235±13*	270±18†
<i>f<sub>W</sub>/f<sub>V</sub></i>	4	200	–	3:1	3:1
<i>T<sub>I</sub>/T<sub>TOT</sub></i>	4	20	0.39±0.04	0.58±0.02*	0.56±0.02
Portion of inspiration occurring during upstroke	4	20	–	0.43±0.07 <sup>a</sup>	–

*N*, number of animals; *n*, number of events analyzed.

<sup>a</sup>Velocity unspecified for this value: since wing beat and respiratory duty cycles and the phase relationship between *f<sub>W</sub>* and *f<sub>V</sub>* did not change with velocity, the portion of inspiration occurring during the upstroke would also not change with velocity.

\* indicates a significant difference between values at rest and at 50kmh<sup>-1</sup>.

† indicates a significant difference between values at 50 and 80kmh<sup>-1</sup>.

When *N*=4, analysis was based on four birds that showed 3:1 coordination between wing beat and respiration 100% of the time.

larger data set available from the uninstrumented flights, the remainder of the data presented are taken from the uninstrumented flights.

Like barnacle geese (Butler and Woakes, 1980) and many other avian species (Hart and Roy, 1966; Butler *et al.* 1977; Berger *et al.* 1970a; Butler and Woakes, 1980), Canada geese showed dramatic increases in *f<sub>V</sub>* from preflight levels of 14.8±2.8breathsmin<sup>-1</sup> to 78.4±4.4breathsmin<sup>-1</sup> during flight at 50km h<sup>-1</sup> (13.8 ms<sup>-1</sup>) (Table 1). Increases in *f<sub>V</sub>* were produced more from decreases in *T<sub>E</sub>* than from decreases in *T<sub>I</sub>* as *T<sub>I</sub>/T<sub>TOT</sub>* (respiratory duty cycle) increased from 0.39±0.04 at rest to 0.58±0.02 during flight (Table 1). Therefore, average expiratory flow rates, which were normally less than mean inspiratory flow rates at rest, were greater than inspiratory flow rates during flight. Similar changes in duty cycle have been observed during thermal panting in chickens (Gleeson, 1985), flight in pigeons (Hart and Roy, 1966) and treadmill exercise in bar-headed geese (Fedde *et al.* 1989). It appears that an increase in duty cycle is associated with substantially elevated breathing frequencies, regardless of the stimulus responsible for producing the elevated *f<sub>V</sub>*.

Canada geese, like budgerigars (Tucker, 1968) but not barnacle geese (Butler and Woakes, 1980), showed increases in *f<sub>V</sub>* with flight velocity. As flight velocity increased from 50 to 80km h<sup>-1</sup> (22.2 ms<sup>-1</sup>), *f<sub>V</sub>* increased by a small, but significant, 15% (*P*<0.05) to 89.8±5.9breathsmin<sup>-1</sup> (Table 1). *T<sub>I</sub>/T<sub>TOT</sub>*, although increasing significantly from rest to flight, did not change with flight velocity (Table 1). Inspiration occupied 0.58±0.02 of the respiratory cycle at 50km h<sup>-1</sup> and 0.56±0.02 at 80km h<sup>-1</sup>. Thus, the distribution of inspiratory *versus* expiratory effort during flight appeared to be tightly regulated. Without measurements of tidal volume to establish the degree to which a 30km h<sup>-1</sup> increase in velocity stimulates respiration, however, it is impossible to determine the significance of this apparent regulation. The Canada goose may be like the fish crow (Bernstein *et al.*

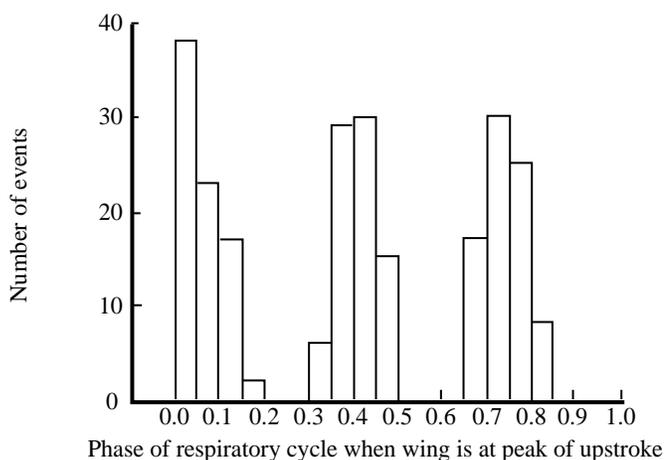


Fig. 1. Phase of the respiratory cycle when the wing is at the peak of upstroke. Pooled data were derived from the analysis of 20 breaths (60 wing beats) from each of the four birds that showed exclusive 3:1 coordination. Analyzed breaths were selected randomly and therefore encompass the 50–80 km h<sup>-1</sup> flight velocity range. Inspiration starts at 0.0. The end of expiration and the start of the next inspiration were normalized to occur at 1.0.

1973) and the starling (Torre-Bueno and LaRochelle, 1978), but not the budgerigar (Tucker, 1968), in which oxygen consumption is relatively constant over a large range of flight velocities.

Wing beat frequency also increased by 15% ( $P < 0.05$ ) from  $235 \pm 13$  to  $270 \pm 18$  beats min<sup>-1</sup> as velocity increased from 50 to 80 km h<sup>-1</sup> (Table 1). Increases in  $f_w$  matched increases in  $f_v$  such that the tight coordination between  $f_w$  and  $f_v$  observed at 50 km h<sup>-1</sup> was maintained at 80 km h<sup>-1</sup>. For 4 of 5 birds, every breath of the 200 analyzed was coordinated with wing beat at 3 wing beats per breath, regardless of velocity. The last bird also showed a predominant coupling ratio of three wing beats per breath. However, approximately 20% of the 200 breaths analyzed from this bird were coordinated with wing beat at 2 wing beats per breath. This bird sporadically switched between periods of 3:1 and 2:1 coordination. These shifts in  $f_w/f_v$  were not related to flight velocity. Transitions between 3:1 and 2:1 coupling were not observed during the telemetered flights. However, only 20 breaths were analyzed per bird during telemetered flight compared to 200 during uninstrumented flight. Therefore, failure to identify 2:1 coordination during telemetered flight may have been due to the small sample size.

The phase relationship between  $f_w$  and  $f_v$  was calculated for the four birds showing 3:1 coordination, based on the analysis of 20 breaths per bird (Fig. 1). Since  $f_w/f_v$  did not change with flight speed, the breaths were randomly selected from a 60 s flight. No distinction was made based on velocity. From the pooled data (Fig. 1), it is clear that the phase relationship between  $f_w$  and  $f_v$  was very tightly coordinated and that it showed little variation either within or between birds. Peak upstroke occurred at approximately 0.05, 0.40 and 0.70 of the respiratory cycle (0.00 represents the start of inspiration). In addition, inspiration did not occur preferentially during upstroke. The portion of inspiration

occurring during upstroke was less than 50% in all four birds examined (Table 1). Thus, locomotor assistance of respiration does not occur by having inspiration occur predominantly during upstroke (see Berger *et al.* 1970b).

The results of this study indicate that the relationship between  $f_w$  and  $f_v$  in geese is not dependent on body mass. Canada geese coordinate  $f_w$  and  $f_v$  in virtually the same way as do the much smaller barnacle geese (Butler and Woakes, 1980). 3:1 coordination predominates in both species. Canada geese express ratios of 2 and 3 wing beats per breath, while ratios of 2, 3 and 4 wing beats per breath occur in barnacle geese (Butler and Woakes, 1980). The phase relationship between  $f_w$  and  $f_v$  is also the same in both species (Fig. 1; see Fig. 7 of Butler and Woakes, 1980, for comparison).

The results also indicate that, although Canada geese, like barnacle geese (Butler and Woakes, 1980) and many other species (Lord *et al.* 1962; Berger *et al.* 1970b), have a preferred relationship between  $f_w$  and  $f_v$ , this relationship is not fixed. The number of wing beats per breath varies in many species during flight (Lord *et al.* 1962; Berger *et al.* 1970b; Butler and Woakes, 1980) and in decerebrate Canada geese during electrically induced wing flapping (Funk *et al.* 1992b).

The factors responsible for producing shifts in the type of coordination observed between locomotor and respiratory rhythms within a species remain unclear. Experiments on decerebrate Canada geese indicate that metabolic and/or kinesthetic afferent feedback associated with wing movement is somehow responsible for this variability (Funk *et al.* 1992b). Following paralysis and the removal of all wing-beat-related feedback, the relationship between the neural outputs of the locomotor and respiratory systems was 1:1. Ratios ranged from 1:1 to 4:1 when afferent feedback was present.

In intact Canada geese during free flight, however, changes in cyclic afferent feedback associated with increases in flight velocity and  $f_w$  did not produce changes in  $f_w/f_v$ . In the one bird that did show transitions in  $f_w/f_v$  from 3:1 to 2:1, the shifts occurred without changes in velocity. It remains possible that the increase in velocity from 50 to 80 km h<sup>-1</sup>, producing only a 15% increase in  $f_w$ , did not provide a metabolic or kinesthetic afferent stimulus of sufficient magnitude to produce shifts in  $f_w/f_v$ . Attempts to increase flight velocity further were unsuccessful. If oxygen consumption is independent of velocity in the Canada goose, as it is in the fish crow (Bernstein *et al.* 1973) and starling (Torre-Bueno and LaRochelle, 1978), shifts in  $f_w$  will only alter limb-related afferent feedback. In turn, if metabolic stress is more important in generating shifts in  $f_w/f_v$ , altering inspired oxygen levels by changing flight altitude may prove more effective in shifting  $f_w/f_v$ .

Alternatively, changes in body temperature accompanying flight (Bernstein, 1976; Butler *et al.* 1977; Butler and Woakes, 1980) may be involved in shifting  $f_w/f_v$ . Increased body temperature is a powerful respiratory stimulus in birds (Scheid and Piiper, 1986). Increases in  $f_v$ , serving to increase evaporative heat loss, could lead to decreases in  $f_w/f_v$ .

The physiological significance of changes in  $f_w/f_v$  remains unclear. However, this flexibility presumably enables the system to respond to environmental perturbations without compromising gas exchange. If the coordination were fixed, situations could inevitably arise where the advantages of entrainment (discussed in Berger *et al.* 1970b) might be outweighed by the constraints of obligatory coordination. If  $f_v$  were rigidly fixed by locomotor rhythm, then ventilation could increase only through increases in tidal

volume. This, in turn, would severely limit the ventilatory reserve upon which the animal could draw. It would also preclude increases in  $\dot{V}_E$  for the sake of thermoregulation. Although the exact nature of the factors leading to a shift in the coupling ratio remain unclear, this adaptability would seem essential if the coordination itself is not to become limiting to performance.

This work was supported by grants from the NSERC of Canada to W.K.M. and J.D.S. and an NSERC Postgraduate Scholarship and Killam Fellowship to G.D.F. Dr F. N. Smith kindly built the radiotransmitters used in this study and Sarah Bradley assisted in training the birds.

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