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ABSENCE OF LOCOMOTOR-RESPIRATORY COUPLING DURING SIMULATED DESCENDING FLIGHT IN THE CACKLING CANADA GOOSE¹

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Abstract. The locomotor and respiratory patterns of six cackling Canada Geese (*Branta canadensis minima*) were examined during simulated +10° descending flight to determine if locomotor-respiratory coupling occurred. In half the birds, there was no locomotor-respiratory coupling, the remainder exhibited minimal partial coupling. We hypothesize that the absence of locomotor-respiratory coupling is probably of little energetic significance as descending flights tend to be of short duration and reduced power output.

Key words: *wind tunnel, locomotor-respiratory coupling, descending flight, Branta canadensis minima.*

Locomotor-respiratory coupling occurs in birds during flight (Butler and Woakes 1980, Funk et al. 1993), and during quadrupedal and bipedal locomotion in mammals (Bramble and Carrier 1983, Young et al. 1992, van Alphen and Duffin 1994). Mammals usually complete one stride per respiratory cycle (1:1 frequency ratio), although humans exhibit a 2:1 frequency ratio (van Alphen and Duffin 1994). In birds, a variety of coupling ratios have been described, including 1:1 in pigeons (Butler et al. 1994), 3:1 in geese (Butler and Woakes 1980, Funk et al. 1993), and 5:1 in ducks (Berger and Hart 1970). In all cases where birds were engaged in sustained horizontal flapping flight, locomotor-respiratory coupling was exhibited almost continuously, with very few uncoupled cycles observed (Butler and Woakes 1980, Funk et al. 1993).

Locomotor-respiratory coupling may enable the mechanical assistance of ventilation by the locomotor muscles causing an overall decrease in the cost of locomotion (Berger et al. 1970). We hypothesized that if this is true, the reduced power output (Tucker 1968, Pennycuik 1989) and short duration of descending

flight may minimize the significance of coupling (in terms of energetic savings) and result in an absence of locomotor-respiratory coupling. Thus, the purpose of the present investigation was to determine whether locomotion and respiration are coupled in cackling Canada Geese (*Branta canadensis minima*) during simulated descending flight.

METHODS

Twenty-one cackling Canada Goose eggs were collected under Canadian Wildlife Service permit NWT-S26 from Baffin Island and transported to the wind simulator facility in Pickering, Ontario, Canada. The eggs were incubated and candled daily to determine development. When pipped, the eggs were transferred to a brooder until hatching. Three eggs did not hatch and two goslings died three days post-hatching.

The 16 surviving geese were hand raised and imprinted on the wind simulator operator. As in Rothe et al. (1987), we found it advantageous to house the birds in the same room as the wind simulator so that they could grow accustomed to the noise. Furthermore, the home cages (152 × 213 × 182 cm) were located downwind of the flight cage so that the geese could become acclimatized to the wind. Geese were placed in the home cage 7–10 days prior to the appearance of the first flight feathers and fed proprietary poultry diet (Shur-Gain) supplemented with fresh grass and given water daily.

Geese were allowed into the flight cage six days a week for approximately 1 hr a day. The wind simulator operator was always present in the flight cage during flights, because this was found to enhance the birds' willingness to fly. Geese were exposed to varying wind speeds and encouraged to leave the cage floor by a variety of stimuli (stick waving, clapping, shouting, and lifting by hand). Air flow was adjusted to +10° early in the training period. The entire wind simulator

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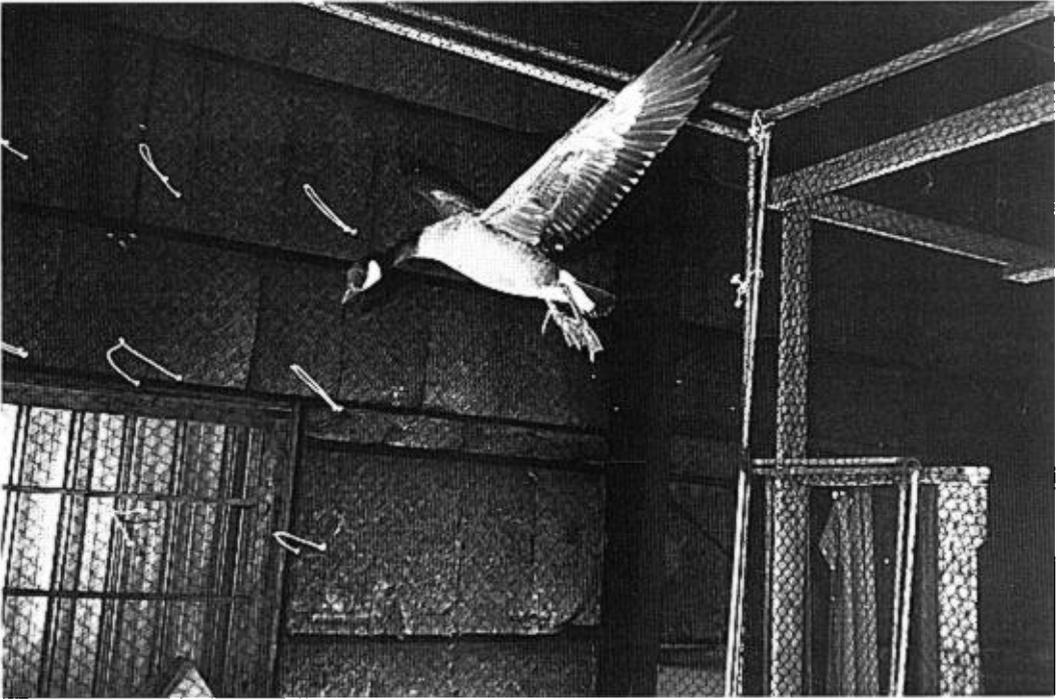


FIGURE 1. *Branta canadensis minima* during simulated descending flight. Air flow was at 10° from horizontal. Note the lowered feet, and head and neck angle, both characteristics of descending flight in the field.

(flight cage, fans, and motors) was mounted on a hinged frame and could be tilted between $+10^\circ$ and -5° from horizontal. Wind speed, measured by a hand-held vane anemometer (Davis Instruments, Turbo meter), ranged from 5 m sec^{-1} to 20 m sec^{-1} . All 16 birds were present together in the flight cage for the first two weeks, and then in groups of 8 for the next three weeks.

After five weeks of training, the process of rejecting poor flyers began. This was achieved by exposing birds in pairs to the wind simulator over three days. We spread the selection period out, as flight performance of each bird was still variable from day to day. We found that nonflying birds usually caused a flying bird to land. Only rarely did a flying bird stimulate a standing bird to take flight. Thus, the identification and rejection of nonflyers was done as early as possible.

Six birds of undetermined sex were chosen for experiments. Of these, two were fully accustomed to wind simulator flight and would take off when the wind simulator operator entered the flight cage, and then stayed aloft indefinitely. The remaining four required assisted take-off (lifted from beneath with a stick) and encouragement to stay aloft for extended periods. Geese were discouraged from landing by holding a stick underneath them when attempting to land.

Geese had two more weeks of individual daily flights. By this time, all birds flew sufficiently well and demonstrated a willingness to fly by taking-off in the home cage and by vocalizing when the wind simulator

was turned on. No additional training was required for the birds to become accustomed to the thermocouple taped to their bill. Training flight times ranged from 5–15 min. Geese flew more readily in cooler conditions.

During experiments, the six geese were approximately 2.5 months old and weighed $1.86 \pm 0.18 \text{ kg}$. Air speed during experimental flights was $13.8 \pm 0.1 \text{ m sec}^{-1}$. Recordings were made using a video camera (Sony, model 8NTSC, CCD-F77) and video tape recorder (Vetter, model 820H). Respiratory frequency was recorded by means of a thermocouple placed over the external nares. The thermocouple was connected with a 3 m fine wire extension to a BAT 10 thermometer (Physitemp Inc.). The extension was supported by a hand-held rod at 0.5 m from the goose to reduce drag. The visual image and respiratory air temperature were recorded simultaneously on the same video tape to facilitate the synchronization of measurements. Measurements of wing beat frequency were obtained for all flights by determining the time taken to complete approximately 70 wing cycles.

Trials were carried out between 10:00 and 16:00. Air temperature ranged from 5° to 10°C . Average flight time was $5.4 \pm 1.6 \text{ min}$. Data were analyzed from three 15-sec periods for each bird during steady state flight in the wind simulator with the air flow ascending at an angle of 10° from the horizontal (Fig. 1). Steady state was determined by visual inspection of the respiratory waveform and flight performance.

TABLE 1. Respiratory and wing beat cycle for six cackling Canada Geese during simulated descending flight in a wind simulator.

Bird number	Mean preflight respiratory cycle time (sec)	Mean flying respiratory cycle time (sec)	Mean wing cycle time (sec)	Mean frequency ratio (respiratory cycle time divided by wing cycle time)	Integer frequency ratios as a % of total respiratory cycles	Consecutive integer frequency ratio as a % of total respiratory cycles	% Coordination of top of wing cycle with transition from expiration to inspiration
1	2.35 ± 0.01	1.01 ± 0.18	0.23 ± 0.01	4.29 ± 0.86	43	7	43
2	1.59 ± 0.02	0.88 ± 0.01	0.23 ± 0.01	3.87 ± 0.16	72	44	83*
3	2.11 ± 0.04	0.82 ± 0.05	0.22 ± 0.01	3.72 ± 0.13	38	13	27
4	1.27 ± 0.01	0.63 ± 0.01	0.22 ± 0.01	2.92 ± 0.02	36	14	58*
5	1.24 ± 0.01	0.74 ± 0.03	0.22 ± 0.00	3.32 ± 0.17	34	17	39
6	2.13 ± 0.01	0.86 ± 0.05	0.22 ± 0.01	3.91 ± 0.19	37	13	57*

* Indicates significant synchrony between the top of the wing cycle and the transition from expiration to inspiration.

RESULTS

Cackling Canada geese mean pre-flight respiratory frequency was 35.9 ± 4.1 breaths min^{-1} . Mean simulated descending flight respiratory rate was 74.6 ± 5 breaths min^{-1} . Mean wing beat frequency was 268 ± 8.0 beats min^{-1} . For individual bird data see Table 1.

DISCUSSION

Mean pre-flight respiratory frequency was similar to or greater than that observed previously in geese (Butler and Woakes 1980, Funk et al. 1993). However, the respiratory rate of cackling Canada Geese during simulated descending flight was significantly lower than that of Barnacle Geese (*Branta leucopsis*) during horizontal flight. The latter result was expected because

an ascending air flow angle of $+10^\circ$ would, according to aerodynamic theory, significantly reduce the power requirements of flight muscles (Pennycuik 1989). Furthermore, oxygen consumption of a Budgerigar (*Melopsittacus undulatus*) was approximately 40% lower during simulated descending flight than during horizontal flight at the same air speed (Tucker 1968).

Wing beat frequencies of cackling Canada Geese during simulated descending flight were similar to those observed in free-flying Barnacle Geese (Butler and Woakes 1980). A similar wing beat frequency (261 ± 3 beats min^{-1}) was observed in Barnacle Geese flying horizontally at 13 m sec^{-1} in the wind simulator (Stephenson et al., unpubl. data). Barnacle Geese and cackling Canada Geese are of similar size, so similar wing

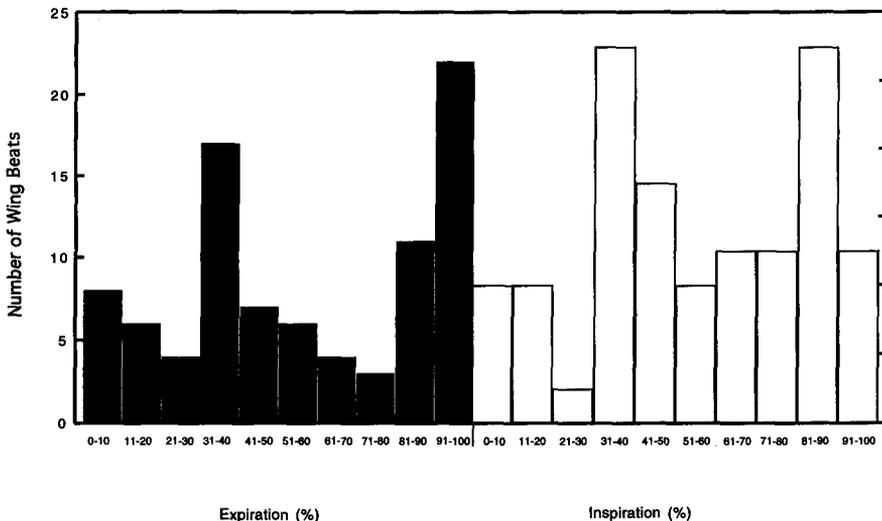


FIGURE 2. Distribution of the top of the wing cycle ($n = 161$) over normalized expiratory and inspiratory phases of the respiratory cycle in a simulated descending flight of a cackling Canada Goose. The data in this figure were taken from Goose #2, the most coupled individual (see Table 1).

beat frequencies would be expected on that basis (Pennycuik et al. 1996). However, the differences in lift afforded by an inclined air flow in the present study would be expected to cause reductions in wing beat frequency (Pennycuik et al. 1996). The present data do not permit an explanation for the absence of such an effect, although it is interesting to note that Pennycuik et al. (1996) observed that a flying Green-Winged Teal (*Anas crecca*) continued to flap its wings during simulated descending flight in a wind tunnel when theoretical considerations predicted that it should glide.

The combination of fixed wing beat frequency and reduced respiratory frequency resulted in an average locomotor-respiratory frequency ratio greater than 3:1 in all birds studied. We found that cackling Canada Geese exhibited a non-integer average frequency ratio during simulated 10° descending flights (Table 1). However, this in itself does not exclude the possibility that the two rhythms were coupled. This can only be established by an examination of the phase relationship between the two rhythms. The wing is always fully elevated at the transition between expiration and inspiration during horizontal flight in both Barnacle Geese and Canada Geese (Butler and Woakes 1980, Funk et al. 1993). We found that this tendency also was apparent in some of the Cackling Canada Geese during simulated descending flight (Fig. 2).

Two rhythms with different periods and non-integer frequency ratios would be expected to exhibit any given phase relation on a periodic basis. The regularity of this "random" synchrony will depend upon the exact value of the non-integer frequency ratio. Using the average frequency ratios for each bird (Table 1), and treating the wing beat and respiratory cycles as sine waves, we conservatively estimated that the transition from expiration to inspiration should be synchronized with the transition from upstroke to downstroke of a wing beat in up to 33% of the respiratory cycles. The actual occurrence of synchrony was statistically significantly greater than this "random" value in only three of the geese (Table 1). None of the birds exhibited the tight coupling that was reported for Barnacle and Canada Geese during level flight (Butler and Woakes 1980, Funk et al. 1993). We therefore conclude that half of the birds exhibited no locomotor-respiratory coupling and the remainder exhibited partial coupling.

Partial coupling could be achieved, even when the overall average frequency ratio is non-integer, by the use of an appropriate sequence of different integer frequency ratios (2:1, 3:1, 4:1, and 5:1). However, only one bird (#2; Table 1) exhibited a greater than random number of integer ratios and a significant number of consecutive breaths with integer wing beat ratio where the latter mechanism for partial coupling is implicated. In the other two "partially coupled" geese, the specified phase relation occurred in nonsequential breaths and often in breaths with a non whole number of wing cycles. Thus, we conclude that there is minimal locomotor-respiratory coupling during descending flight in geese.

Funk et al. (1992a, 1992b) have suggested that both central neural feedforward and mechanical and neural feedback mechanisms may be involved in the generation and maintenance of respiratory-locomotor cou-

pling during flight. The present study raises the possibility that these mechanisms may be conditional upon sensory input to the respiratory system, i.e., chemoreceptor drive. The ability to turn respiratory locomotor coordination on and off would be advantageous in situations where obligatory entrainment could represent a cost rather than a benefit (Funk et al. 1993). For example, changes in frequency ratio may allow for adjustment to environmental stresses without compromising gas exchange or thermoregulation. The absence of locomotor-respiratory coupling during descent is probably of little energetic significance as descending flights tend to be of short duration and lower energetic cost than horizontal flights.

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