HEART RATE, RESPIRATORY FREQUENCY AND WING BEAT FREQUENCY OF FREE FLYING BARNACLE GEESE

BRANTA LEUCOPSIS

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SUMMARY

1. Two barnacle geese (Branta leucopsis) were successfully imprinted on a human and encouraged to fly behind an open-topped truck containing the foster parent. A two channel radio-transmitter was implanted into these geese so that heart rate and respiratory frequency could be recorded before, during and after flights of relatively long duration. The resting value for heart rate was 72 ± 4 (10) beats min⁻¹ and for respiratory frequency, 8.5 ± 0.6 (10) breaths min⁻¹.

2. Five flights of a mean duration of 14.4 ± 1.3 (5) min and at a mean air velocity of 18.7 ± 0.3 (54) m s⁻¹ were performed. Both heart rate and respiratory frequency increased before the birds began to flap their wings for take off. Mean heart rate during flight was 512 ± 4 (54) beats min⁻¹ (7.24 x resting). At take off, wing beat frequency was 356 ± 7 (4) beats min⁻¹ and respiratory frequency was 121 ± 10 (5) breaths min⁻¹. Both of these variables then declined and reached average flight values of 287 ± 3 (37) beats min⁻¹ and 99 ± 2 (54) breaths min⁻¹ (11.7 x resting) respectively. There was no relationship between any of the measured variables and flight velocity. There was however, a 3:1 correspondence between wing beat frequency and respiratory frequency and a tight phase locking between the two. The wings were fully elevated at 6.0 ± 1.1 (20)% of the respiratory cycle. On two occasions the birds slope soared on the air rising over the top of the cab for a mean duration of 52 s and at a mean air velocity of 14.2 ± 0.5 (4) m s⁻¹. Heart rate was 261 ± 18 (4) beats min⁻¹ and respiratory frequency was 68 ± 5 (4) breaths min⁻¹.

3. Upon landing, heart rate returned to its preflight value within 3 min. Respiratory frequency, however, increased as the birds began to pant and reached a maximum value of 255 ± 11 (5) breaths min⁻¹ 4 min after landing.

INTRODUCTION

It has been shown that when in a wind tunnel, the flight pattern of a pigeon is different from that of the freely flying bird (Butler, West & Jones 1977), and this difference could be the result of physical restrictions imposed by the wind tunnel (e.g. size of the test section, constant flight velocity). In order to make physiological measurements, masks, trailing tubes and leads are attached to the birds (Tucker, 1968; Butler et al. 1977) and these attachments are bound to affect the power re-
quirements of flight. Although allowances can be made for these effects, there still remains some uncertainty with respect to the final results. In addition to these physical factors, there is also the strong possibility that psychological factors could adversely affect the birds' performance (Greenewalt, 1975).

The use of wind tunnels is, however, the only realistic method of studying the physiological changes in birds during flights of relatively long duration. Radio telemetry has been of limited value, largely because of the short range of the transmitters restricting the flights to short duration (< 20 s) and also because the transmitters have been mounted externally, thus having likely effects on the flying performance of the birds (Butler, 1979). Perhaps the best compromise to date is that used by Torre-Bueno (1976) when studying temperature regulation in starlings. He implanted a small (3% of body wt), temperature-sensitive transmitter into the birds and trained them to fly for more than 30 min in a wind tunnel. This technique eliminated the adverse effects of externally mounted equipment and trailing leads but probably retained the physical and psychological factors imposed by the tunnel itself.

In order to obtain simultaneously a large number of physiological variables, larger multichannel transmitters would be required and, to maintain the necessarily low ratio between the sizes of the transmitter and bird (Woakes, 1979), these could only be used with larger birds, which would probably require larger wind tunnels than those presently in use. This latter constraint may explain why no physiological data have been obtained from birds weighing more than 1 kg when flying in a wind tunnel.

Thus, although there is a need for data from larger birds and implanted transmitters could be used to obtain these data, there is the problem of maintaining the receiver close enough to the transmitter during flights of long duration. The present investigation was initiated to test the feasibility of imprinting large birds (geese or swans) on a human so that they would follow him, and then implanting a radio transmitter into the birds. This report gives details of the technique and of results obtained using relatively small geese and an existing 2 channel transmitter.

**METHODS**

Barnacle geese (Branta leucopsis) were raised from eggs and imprinted (Lorenz, 1970) upon one of the authors (A.J.W). They were kept close to the foster parent for approximately 16 h per day for the first 7 days after hatching. For the next 6 weeks they were kept indoors and in close proximity to the foster parent for 9 h per day and the 'following response' (see Brown, 1975) was re-inforced by the foster parent taking them for a walk for about 1 h each day. They were then left outside all day in an open-topped enclosure which contains two ponds and is located on the campus of the University of Birmingham. They were still taken for a 1 h walk each day, during which they flew around the campus for approximately 10 min. They were kept indoors at night. Initially there were six geese, but three were lost during their early exploratory flights before they became accustomed to the local geography. The remaining three were eventually taken to an airfield where their willingness was tested to fly behind a moving Marina 1300 pick-up truck (British Leyland) containing their foster parent.
One bird at a time was free, the others were caged in the back of the open-topped pick-up truck, and they, together with the foster parent, who was also in the back of the truck, were fully visible to the free bird. This goose was placed on the ground and as the truck accelerated away, the bird flew after its foster parent and companions. At the first attempt, two of the geese successfully followed the truck around the airfield and allowed themselves to be caught at the end of the flight. The other bird began to follow the truck but soon flew too far away and lost contact with the foster parent. It was never recovered. The two remaining geese were trained until they could fly for at least 15 min at ground speeds between 15–26 m s⁻¹. They were both female with masses of 1.7 and 1.5 kg. A two-channel transmitter (Woakes & Butler, 1975) was then implanted into these geese. The bird was anaesthetized with a mixture of halothane-saturated air, air and oxygen (8:4:1). The transmitter, bipolar e.c.g. electrode and the thermistor (for obtaining an indication of air flow along the trachea) were implanted as described by Butler & Woakes (1979). Briefly, the transmitter (mass 6.5 g) was placed in the abdominal cavity, the e.c.g. electrode was located close to the heart and the thermistor was inserted into the lumen of the trachea. The birds were kept indoors for 2–3 days and recordings from flights began 7 days after the operation.

The circuit at the airfield consisted of 2 slightly converging straight sections (one being the main runway) both of which were 1.25 km long. The bend at one end was relatively tight and limited the speed of the truck to 16 m s⁻¹. The other bend imposed no such restriction. One complete lap of the circuit was 3 km. The truck was driven at a range of speeds, the limits of which were determined by the bird, because it was necessary to keep the receiver (Sony CRF 5090) mounted on the truck, within range of the transmitter in the animal. The normal range of ground speeds was 16–22 m s⁻¹. Occasionally it was possible to encourage the birds to fly beyond these limits. At the lower end, they would not fly below 15 m s⁻¹. They either stopped flapping and slope-soared on the air rising over the cab, or they continued flapping and drew away in front of the truck. At the upper end of the range, ground speeds of up to 26 m s⁻¹ were recorded along the main runway, but neither bird would maintain these speeds for longer than 10 s.

The received data were stored on one track of a Store 4D tape recorder (Racal Thermionic Ltd) which was housed in the cab of the truck. At regular intervals, ciné film of the goose was taken by the foster parent either with a Bolex 233 Compact S super 8 camera or with a Bolex 16 mm camera. Wing-beat frequency was obtained from this film and during certain sequences, when the bird was opening and closing its mouth during ventilation, it was possible to synchronize this activity on the ciné film with the simultaneous recording of air flow in and out of the lung which was stored on the tape. Thus, the relationship between ventilation and wing beating could be investigated and accurate values for the frame frequency of each camera could be determined. A commentary on the behaviour of the bird and of when film was being shot was recorded on one track of the tape recorder. The driver of the truck gave a continuous spoken account of ground speed (read from the calibrated speedometer of the truck) which was also recorded on tape.

Resting values of heart rate and respiratory frequency were obtained from the birds individually when they were close to the foster parent in the laboratory. All of the
other values were recorded before, during and after flights at the airfield. Hard copies of the e.c.g. and respiratory air flow were made by a two-channel pen recorder (Devices Ltd) and heart rate was determined by an instantaneous rate meter (Devices Ltd). Air velocity of the birds was computed from ground speed, wind speed and wind direction. The latter two variables were average values obtained from a weather station located < 1 km from the airfield. The instruments at the weather station are 3 m above the level of the airfield and the terrain between the instruments and airfield is flat. This method of computing air velocity of the birds may be slightly inaccurate, as continuous recordings of wind speed at the point where the bird was flying were unobtainable. The fully trained birds generally flew within a 'corridor' 1–6 m from either side of the truck, 0–10 m behind the foster parent and 2–5 m above ground level. During the first one or two training flights they frequently flew closer than 1 m to the side or behind the truck, but it was clear from the flight pattern of the birds that the air in this region was very turbulent. It was noticeable that the birds avoided this position during subsequent flights. Whether or not there were any vertical velocity components of the air that would have affected the power requirements of the birds was not determined. The birds did not appear to have a preferred flight position within the 'corridor'. Such a preferred position might be expected if the birds were obtaining any assistance (e.g. lift) from stable air currents in the vicinity of the truck. It is therefore doubtful if vertical velocity components had any significant effect on the power requirements of the birds. Mean air temperature during the experimental periods was 11.4 ± 1.5 °C.

Numerical data are given as means ± s.e. of mean with the number of observations in parentheses. The method of paired comparisons or Students t test were used to test the significance of any difference between two mean values and the word significant in the present report means significant at the 95% confidence level.

RESULTS

Five flights were performed and the mean values for heart rate and respiratory frequency are shown in Fig. 1. The resting values for these variables were 72 ± 4 (10) beats min⁻¹ and 8.5 ± 0.6 (10) breaths min⁻¹ respectively. Both variables were significantly higher than these values when the birds were at the airfield. Details of a typical take-off can be seen in Fig. 2(a). Both heart rate and respiratory frequency increased several seconds before the goose began to fly and even before the truck began to move. A steady heart rate was maintained until the truck began to accelerate away. The bird then started to run and flap its wings while chasing the truck. Over this 2 s period, heart rate increased by 15 beats min⁻¹. The bird then became airborne and over the next 16 s at least there was a steady increase in heart rate. During the 2 s period just before take off, air flow through the trachea appeared to be reduced and rather erratic. Just after take off there were two respiratory cycles which were at a higher frequency than the subsequent cycles.

On average, heart rate was 173 ± 7 (5) beats min⁻¹ and respiratory frequency was 23.3 ± 2.3 (5) breaths min⁻¹ 30 s before take off, whereas 2 s before take off these variables had increased to 377 ± 52 (5) beats min⁻¹ and 45.0 ± 4.5 (5) breaths min⁻¹ respectively. Within 2 s after take off, heart rate was 463 ± 3 (5) beats min⁻¹ and res
Fig. 1. Changes in heart rate (○) and respiratory frequency (●) in free flying barnacle geese. The time base is expanded at take off and at landing (which are represented by vertical dashed lines). The resting levels (R) are shown as isolated points at the beginning of the graph and are mean values from 10 observations. The remaining points are mean values from five flights. Vertical lines associated with each point are ±s.E. of mean. Where vertical lines are absent, the s.E. of mean is within the limits of the symbol. The mean duration of the flights, ±s.E. of mean is given at the top of the graph.

Fig. 2. Traces from a ♀ barnacle goose of mass 1.7 kg showing heart rate and respiratory frequency before, during and after a flight of 11 min 52 s duration. (a) Take off (note the clean e.c.g. signal during flight); (b) steady, flapping flight at 22 ms⁻¹, 5 min after take off; (c) 3 min after landing. The vertical dashed lines in (a) indicate when (i) the truck starts to move; (ii) the bird begins to run and flap its wings; (iii) the bird is airborne.
Respiratory frequency reached 121 ± 10 (5) breaths min⁻¹. Heart rate then increased slightly during the remainder of the flight and the highest mean value of 530 ± 6 (5) beats min⁻¹ was recorded 7 min after take off. Thirty seconds after take off respiratory frequency had declined to 79 ± 6 (5) breaths min⁻¹. It then increased steadily throughout the flight, reaching a maximum mean value of 116 ± 12 (5) breaths min⁻¹ 30 s before landing. At take off, wing beat frequency was 356 ± 7 (4) beats min⁻¹, but then rapidly declined and its mean value during the flights was 287 ± 3 (27) beats min⁻¹. The average duration of all flights was 14·4 ± 1·3 (5) min and the mean air velocity of the birds was 18·7 ± 0·3 (54) m s⁻¹.

There was no relationship between any of the measured variables and flight velocity of the birds (Fig. 3). Mean heart rate during the flights was 512 ± 4 (54).
beats min\(^{-1}\), which is 7.24 × the resting value, and mean respiratory frequency was 99 ± 2 (54) breaths min\(^{-1}\), which is 11.7 × the resting value. It can be seen from Fig. 3 that there are low values of each variable at a flight velocity of approximately 19.5 ms\(^{-1}\). These are from one of the birds when it was flying in front of the truck, seemingly waiting for the vehicle to overtake it and indicate where it was supposed to be going. As well as this low value, there is an indication from Fig. 3 that there is a wider distribution of the values for respiratory frequency than for the other two variables. This distribution is illustrated more completely in Fig. 4. This histogram is based on larger amounts of data taken from the tape recordings. Above the histogram are points representing \(\frac{1}{4}\), \(\frac{1}{3}\) and \(\frac{1}{2}\) of the mean wing-beat frequency (287 beats min\(^{-1}\)) ± the standard deviation of the distribution of this variable. This indicates that respiratory frequency and wing beat frequency are interrelated with the possibility of coupling at ratios of 1:3 and 1:2.

The relationship between these two variables is given in Fig. 5. The solid line, represented by the formula, is not significantly different from the dotted line which represents the 1:3 ratio of the two frequencies. The one anomalous point is close to the line representing a ratio of 1:2. Fig. 6 shows a section of a recording of respiratory airflow which has been synchronized with a simultaneous film sequence (see Methods). The times when the mouth was open and when the wings were fully elevated (both obtained from the ciné film) are indicated on the trace. During the majority of the respiratory cycles, there were 3 wing beats per cycle with the wing always being fully elevated at the transition between expiration and inspiration. During longer respiratory cycles (when, incidentally, the mouth did not open) there were exactly 4 wing beats per cycle and the previous precise relationship was restored immediately the respiratory frequency returned to normal.
FIG. 5. Graph to show the relationship between respiratory frequency ($f_r$) and wing beat frequency ($f_w$) of barnacle geese. The line of best fit (solid line) is drawn through the points and the equation describing this line and the correlation coefficient ($r$) are given. The dashed lines indicate the theoretical coupling ratios of 1:2 and 1:3.

Mathematical equations:

$$f_r = a + bf_w$$

Where:

- $a = 5.14 \pm 5.90$
- $b = 0.317 \pm 0.021$
- $r = 0.938$

From the same flight sequence, 20 respiratory cycles were chosen which occupied 10 ciné frames per cycle and a histogram was constructed of the positions within the cycle when the wing was fully elevated (Fig. 7). It is evident that the wing beat was tightly locked to fixed phases of the respiratory cycle and, on average, the wing was fully elevated at $6.0 \pm 1.1$ (20)% $40.5 \pm 1.1$ (20)% and $74.0 \pm 1.1$ (20)% of the respiratory cycle (where 0% is taken to be the centre of the time slice represented by the first frame, i.e. that during which the mouth was seen to open). The mouth closed at $59 \pm 1.8$ (20)% of the cycle. Exactly the same phase coupling was seen when studying...
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One respiratory cycle

Fig. 7. Histogram showing the positions during the respiratory cycle at which the wings were fully elevated (called 'events') during the flight of a barnacle goose. The data were obtained from a particular flight sequence, part of which is shown in Fig. 6. Twenty respiratory cycles were chosen each of which occupied 10 ciné frames. Each interval therefore represents 1 ciné frame. Frame 0 is that in which the mouth was seen to open. Below the histogram is plotted the mean position of each group of events (○) and when the mouth closed (●). Horizontal lines associated with each point are ± s.e. of mean. Where horizontal lines are absent, s.e. of mean is within the limits of the symbol. The scale origin is taken to be at the centre of the time interval represented by the first ciné frame. Above the histogram is a trace of one of the chosen respiratory cycles (inspiration-up).

four other, shorter, film sequences taken during different flights. Fig. 7 illustrates that not only were the wings fully elevated at the transition from expiration to inspiration, but that they were at some part of their downstroke at the transition from inspiration to expiration.

When the birds slope soared on the airstream rising over the front of the truck, there were reductions in heart rate and respiratory frequency, both of which increased as soon as flapping flight was resumed (Fig. 8). The oscillations in heart rate during gliding, as shown in Fig. 8, are not related to respiratory movements. Only on two occasions were the periods of soaring of sufficiently long duration (> 20 s) for the variables to reach a relatively steady level, when heart rate was 261 ± 18 (4) beats min⁻¹ and respiratory frequency was 68 ± 5 (4) breaths min⁻¹. The average duration of the soaring period on these two occasions was 52 s and the mean air velocity of the bird was 14.2 ± 0.5 (4) m s⁻¹. When slope soaring, the birds lowered their feet and spread their toes, presumably to act as air brakes so as to steepen the
Fig. 8. Traces showing heart rate and respiratory frequency of a barnacle goose (1.7 kg) at the transition from slope soaring (for 51 s) to flapping flight. The vertical dashed line represents the beginning of sustained flapping flight.

angle of the glide (Pennycuick, 1975). For a short period (approximately 1 s), when the bird began to flap its wings, air flow through the trachea seemed to be reduced (cf. take-off Fig. 2a).

Upon landing, there was an immediate decrease in heart rate which was not significantly different from its 30 s preflight value 3 min after landing. Respiratory frequency, on the other hand, increased after the birds landed as they began to pant (Fig. 2c) and at 4 min after the flights, it had reached $255 \pm 11$ (5) breaths min$^{-1}$. This level was maintained for another 4 min when it began to decline. Ten minutes after the flight, it was not significantly different from its 30 s preflight value.

**DISCUSSION**

The values for resting heart rate and respiratory frequency measured in the present investigation are approximately 50% lower than the values for a 1.6 kg bird as calculated by the allometric formulae presented by Calder (1968) and Berger, Hart & Roy (1970). Calculated resting respiratory frequency is 14.9 breaths min$^{-1}$ whereas calculated resting heart rate is 140–158 beats min$^{-1}$. During flight, however, there is less of a discrepancy, with the value for heart rate calculated from the allometric formula presented by Berger & Hart (1974) being 492 beats min$^{-1}$, and the measured, average respiratory frequency during flight of the geese being at the lower assumed limit for a 1.6 kg bird (Berger & Hart, 1974). It is not surprising therefore, that the proportional increase in heart rate during flight above the resting level is much greater in the geese used in the present study, than the $2-4 \times$ increase that has been reported for other species (Berger & Hart, 1974). A previous study in which an internally placed radio-transmitter was used with ducks (Butler & Woakes, 1979) also reports resting heart rates which are considerably lower than those calculated from the
allometric formulae mentioned above. When a bird is flying, its heart rate is probably very close to its maximum. This would certainly be an explanation for the fact that heart rate is relatively constant over a range of flight velocities for both the barnacle goose and the kestrel (Johnson & Gessaman, 1973). However, the so called resting value of any variable is more difficult to obtain, and to make comparisons between different species on the basis of a proportional increase in a particular variable ‘above its resting level’ may be a rather fruitless exercise unless the method used to obtain the variable does not affect it to any great extent. It is suggested that more realistic values for ‘resting’ heart rate and respiratory frequency have been obtained for ducks (Butler & Woakes, 1979) and for barnacle goose by using implanted transmitters and allowing the conscious animals unrestricted movement.

The flight velocities recorded for the barnacle goose in the present experiments are higher than those reported for the Canada goose (Tucker & Schmidt-Koenig, 1971), and the lowest velocity (15 m s⁻¹) at which the barnacle goose would fly is towards the top end of the calculated speed range for a 1.6 kg bird (Pennycuick 1969). Also of interest as far as the migrating behaviour of these animals is concerned, is the fact that they will soar. It is a commonly held view that geese and swans migrate without soaring, although Pennycuick (1969) suggested that some of them might use lee wave systems to conserve energy during migration. The fact that heart rate during soaring was approximately 50% of its value during flapping flight is a clear indication that there was a dramatic reduction in oxygen uptake during soaring (Johnson & Gessaman 1973). This is in accord with the calculations of Pennycuick (1972) and the direct measurements of Baudinette & Schmidt-Nielsen (1974). Recordings from the flight muscles (Goldspink, Mills & Schmidt-Nielsen 1978) indicate that muscular energy is still expended during gliding which would account for the 2 × increase in oxygen uptake above the resting level during gliding flight (Baudinette & Schmidt-Nielsen, 1974).

During flapping flight, the beating wings of the barnacle goose, like those of many other birds (Tucker, 1968, 1972; Torre-Bueno & Larochelle, 1978), maintain a more or less constant beat frequency over a wide range of flight velocities thus following the principles of a damped, driven oscillatory system (Greenewalt, 1960). On one occasion it was demonstrated however, that wing beat frequency could be reduced with little reduction in flight velocity.

Unlike the situation in the budgerigar (Tucker, 1968), respiratory frequency of the barnacle goose was also independent of flight velocity. This does not necessarily mean that respiratory tidal volume varied with flight velocity, for the barnacle goose may be similar to the fish crow (Bernstein, Thomas & Schmidt-Nielsen, 1973) and the starling (Torre-Bueno & Larochelle, 1978) (but again, unlike the budgerigar) and have a relatively constant oxygen uptake over a wide range of flight velocities. Although there was a wider distribution of respiratory frequency than of wing beat frequency during flight, one of the most notable features of the present observations was the strong coupling between these two activities.

Co-ordination between wing beating and ventilation has been demonstrated for a number of species of birds. In crows and pigeons there is a 1:1 correspondence between the two (Hart & Roy, 1966; Butler et al. 1977) whereas ratios as high as 5:1 have been reported for the black duck, quail and pheasant (Berger, Roy & Hart,
The latter authors also found that, in general, the wings were fully elevated at the beginning of inspiration and that the beginning of expiration occurred at the end of the downstroke. This is similar to the findings of the present study which also demonstrates that these phase relationships are present during flights of relatively long duration and that they can be maintained even during transient changes in frequency of one of the activities. The co-ordination of lung ventilation and limb movement during exercise is not restricted to birds. It has been demonstrated in galloping horses (Hörnicke et al. 1974) but there are conflicting accounts as to its occurrence in humans (Åstrand & Rodahl, 1977; Paulev, 1971; Kelman & Watson, 1973; Kay, Petersen & Vejby-Christensen, 1974; Bechbache & Duffin, 1977). It has been reported that repetitive electrical stimulation of afferent nerves from muscles of cats causes an increase in respiratory frequency and, at certain stimulus frequencies, can entrain it so that there is a whole number ratio between the two events (Iscoe & Polosa, 1976). Such a reflex mechanism capable of locking respiratory frequency to that of a periodic somatic afferent input (e.g. from the wings) could explain the tight phase locking that exists in birds. However, whether or not such phase locking confers any mechanical advantage to the process of lung ventilation, particularly at the beginning of inspiration and expiration (see Berger et al. 1970), remains to be seen.

The large increase in respiratory frequency (panting) at the end of flight is similar to that seen in pigeons (Butler et al. 1977) except that in the latter case peak panting frequency was reached within 1 min of landing and then it declined steadily back to its pre-flight value within 5 min of landing. This panting was assumed to be thermoregulatory in function in the pigeon as its decline was closely related to a reduction in deep body temperature which was elevated during flight. The difference in the duration of panting between the pigeons and the barnacle goose is probably related to the fact that the pigeons were in a wind tunnel that was still generating an air current after they had landed. Convective cooling was therefore greatly augmented. The webbed feet are an important route for heat loss in the herring gull (Baudinette et al. 1976) and a similar situation may be assumed to exist in the barnacle goose. If panting at the end of the present flights was an indication of an elevated body temperature, then it could mean that, unlike the situation that has been suggested to exist in the herring gull (Baudinette et al. 1976), the barnacle goose stored some heat because it was not able to remove (mostly via the feet) all of the excess heat generated. On the other hand, the barnacle goose may have actively adjusted its heat loss in order that body temperature did rise during flight (see Torre-Bueno (1976) working on starlings).

Clearly, there are many aspects of avian flight yet to be investigated, particularly in larger birds. The present study has demonstrated that it is possible to obtain physiological data from large, free flying birds during flights of relatively long duration using implanted radio transmitters. It is planned to develop a multi-channel transmitter for use with larger birds (Canada geese or swans) in order to obtain a greater number of variables, such as EMGs and body temperature. Ultimately it is hoped to incorporate an implantable air flow transducer (Woakes & Butler, 1979) into the system so that respiratory tidal volume can be measured during and after long flights.

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