ELSEVIER

Thermochimica Acta 250 (1995) 329–336

thermochimica
acta

Calorimetry in flying birds, using the wind tunnel technique ☆

Werner Nachtigall

Zooligisches Institut der Universität des Saarlandes, 66041 Saarbrücken, Germany

Received 30 May 1994; accepted 4 July 1994

Keywords: Bird; Evaporation; Pigeon; Respiratory quotient; Wind tunnel

1. Introduction: Respirometry and the wind tunnel technique

Flight is generally accepted as the mode of locomotion with the highest energy consumption in the animal kingdom. Measurements of metabolic power as well as registration of thermoregulation and water balance are not easily accomplished. In addition to free flight measurements using the double-labelled water technique and/or telemetry, the wind tunnel method is a good source for data. Basic results are used to describe and demonstrate how, in Saarbrücken, this method was applied along with respirometry to determine basic metabolic flight characteristics in flying pigeons. Data are taken from Refs. [1–5].

2. Animals and methods

2.1. Pigeons

In addition to homing pigeons we tested the wind tunnel flight performance of English Tippler pigeons, Russian Griwuni and Nikolajew pigeons, as well as Hannover, Vienna and Serbian pigeons. Hybrids were bred from an English Tippler and Russian Griwuni pigeon and were called 'Gripplers'. Griwuni or Grippler

---

☆ Presented at the Ninth Conference of the International Society for Biological Calorimetry, Berlin-Schmerwitz, 27–31 May 1994, and dedicated to Ingolf Lamprecht on the occasion of his 60th birthday.

SSDI 0040-6031(94)01962-2

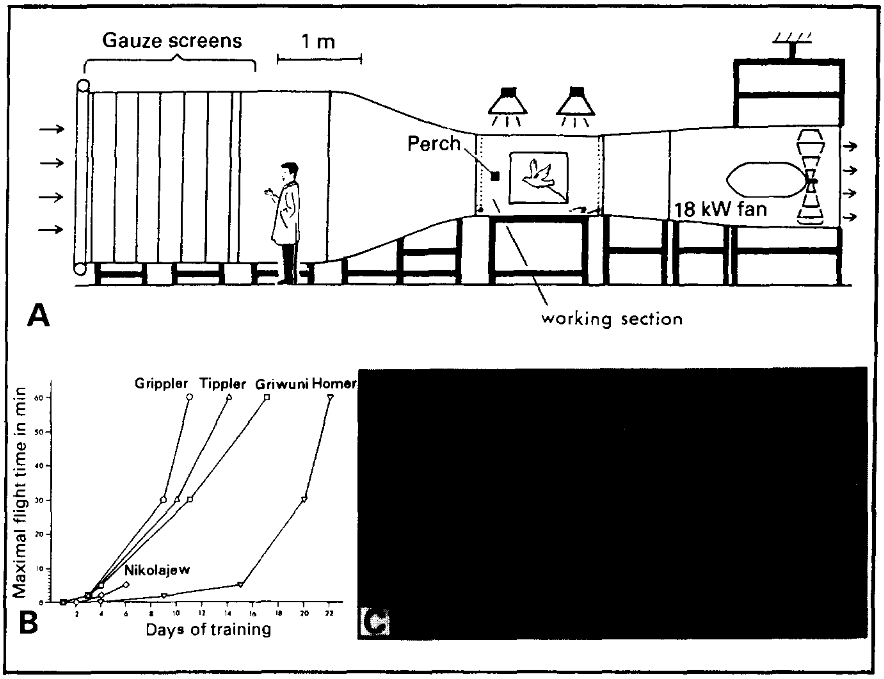

Fig. 1. Wind tunnel technique and bird flight. A, geometry of the wind tunnel used. B, flight time-training-relation of different pigeon races. C, flying pigeon, wearing a respiration mask.

pigeons which were able to fly non-stop for at least 60 min in the wind tunnel could be trained, for later respiratory measurements, to fly with a mask so that the bird was part of an open circuit respiratory system.

The maximum non-stop flight duration of the pigeons depends on the number of days they are trained. Grippler pigeons were the first to reach a maximum flight time of 60 min. They were followed by Tippler, Griwuni and homing pigeons (Fig. 1B). All experiments were permitted and run according to German laws of animal protection.

2.2. Wind tunnel

Wind tunnel flight of birds is highly sensitive to the aerodynamic peculiarities of the tunnel construction used. We used a specially built suction wind tunnel (Eiffel type) with which maximum flight speeds of 24 m s^{-1} can be simulated (Fig. 1A). The working section of the tunnel was 1 m × 1 m in cross-section and 1.4 m long. In the velocity range in which the birds fly (8–18 m s^{-1}), the wind speed varied less than ± 3%. Static pressure was approximately constant along the longitudinal axis. The turbulence factor was 1.25 (15 m s^{-1}) and 1.4 (24 m s^{-1}). Thus the tunnel was of good aerodynamic quality.

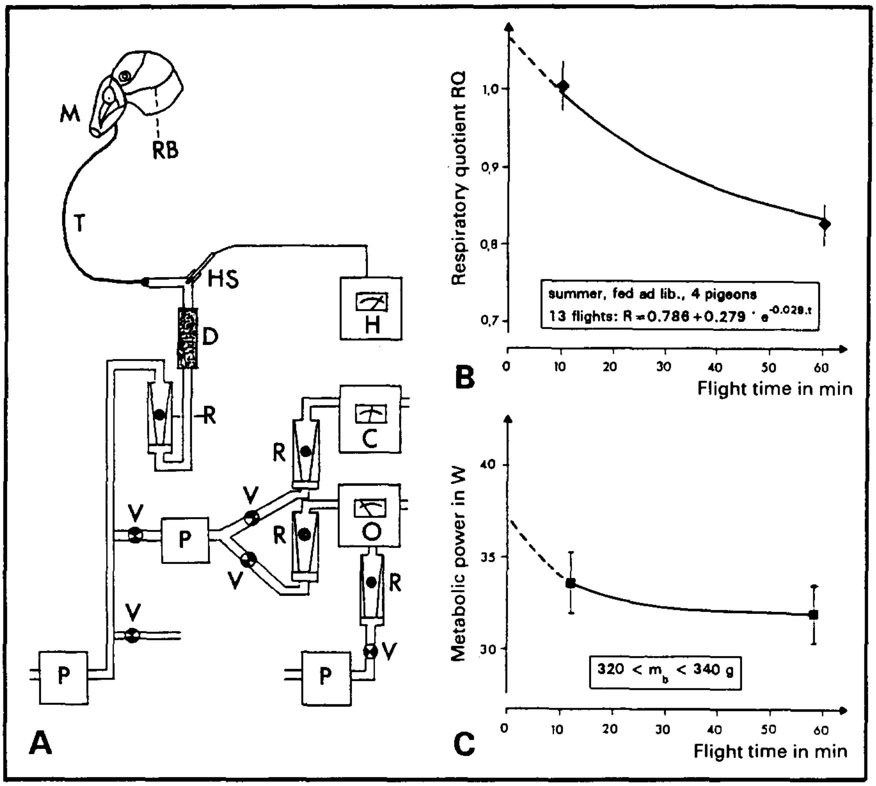

Fig. 2. Respirometric technique and results from respirometric measurements. A, flow-through respiratory system for gas exchange measurements in the pigeon during wind tunnel flight: C, CO_2 analyser; D, desiccator; H, humidity meter; HS, humidity sensor; M, mask; O, O_2 analyser; P, pumps; R, rotameters, RB, rubber band; T, tube; V, valves. B, change of respiratory quotient within the first hour of flight. C, change of metabolic power within the first hour of flight.

2.3. Respirometry via a respiration mask

Respiratory gas exchange was measured using a flow-through respirometry system similar to that used by Tucker [6]. The bird was connected to the analysing system via a mask and a sampling tube (Fig. 1C) through which room air mixed with the expired air was sucked and directed to the analysers (Fig. 2A). Excurrent air from the mask was sucked by pumps P (P_1, Multifix piston compressor MR 110; P_2, Multifix M 400; P_3, Multifix MV-268) through a system of flow regulators (rotameter R, valves V) and a desiccator D (containing phosphorus pentoxide) and led to a paramagnetic O_2-analyser, O (Servomex-OA-184), and an infrared CO_2-analyser, C (Hartmann and Braun, Uras MT). The analysers were connected to a chart recorder (Linseis Ls 64), calibrated to provide information on the fractional content of O_2 and CO_2.

The flow rate was adjucted to between 8 and 12 l min^{-1}, high enough to assure that all the expired air was collected (accuracy of flow-rate measurements: ± 1.7%). The gas analysers were calibrated using gas mixtures (O_2, CO_2, N_2) of known concentrations (Messer Griesheim). The O_2-analyser measured differences in the concentrations $\leqslant 0.1$ vol% O_2 with a response time of 15 s. The measuring range of the CO_2 analyser was set between O and 10 vol% CO_2, with an accuracy of $\leqslant \pm 2\%$ of the measured value; response time was $\leqslant 200$ ms (90%-time). The fractional concentration of CO_2 in the room air (0.03 vol%) was measured and found to be constant during the maximum measuring time. The fractional concentration of O_2 in room air could be measured simultaneously in a second measuring cell and was also found to be constant.

2.4. Mass loss measurements

The body mass of the bird m_b was determined by weighing it before and directly after flight or within 10 min intervals during short breaks of a flight (Sartorius 2116, accuracy ± 0.1 g).

2.5. Thermorecords

Body temperatures (core temperature T_c, breast temperature $T_{s\text{-br}}$, leg temperature $T_{s\text{-l}}$) were measured using Siemens M 85 thermistors. To determine T_c a thermistor was inserted approximately 10 cm into the colon and fixed by a 3-fold layer of adhesive tape over the cloaca. $T_{s\text{-l}}$ was measured with a thermistor fixed with tape onto the tarsometatarsus of the leg, and $T_{s\text{-br}}$ by attaching a thermistor directly onto the skin of the breast beside the sternum without disturbing the plumage. The additional mass of the measuring devices to be carried by the bird in flight was 4.0 g, or 1% of the body mass, which is assumed to have a negligible influence on the bird's behaviour.

3. Basic results

3.1. Transitory adaptations and metabolic power

The transitory adaptation procedures, especially of $\dot{V}_{CO_2}$ and of RQ (respiratory quotient) are very pronounced in the first hour of flight (Fig. 2B). This leads to RQ decreasing from mean values of 0.89 at flight minute no. 6 (irregularities in nos. 1–5), in some cases even of 1.0, to approximately 0.73 after one hour (Fig. 2B). Total transitory adaptation to $0.73 \leqslant RQ \leqslant 0.70$ was often achieved only after 1.5 h of flight. Metabolic power usually began with 35 W and decreased to 32 W at the end of the transitory adaptation period (Fig. 2C), i.e. to a more or less steady relative metabolic power of approximately 100 W kg^{-1}. Although a low-power fuel of mainly carbohydrate is burned at the beginning, relatively more of it is burned so that metabolic power is quite high, before deceasing to approximately 90% of the starting level. Thus, a bird has a minimum energy expenditure of 118.7 kJ within the first hour compared to 115.2 kJ during the second and following hours. This means that a minimum of 3% more energy is consumed in the first hour so that the switch from one fuel to the other is not very important for energetics.

3.2. Metabolic power, calculated from respirometry and from mass loss measurements, as limiting factors

Figs. 3A and 3B show graphs of metabolic power P_m and body mass loss $\dot{m}_b$ plotted over the speed range tested. Because the maximum range speed (below point of contact of the tangent to the $P_m(v)$ curve from source) could only be estimated (> 14 m s^{-1}), the minimum power speed (below minimum of the $P_m(v)$ graph) is taken as reference. It is approximately 12 m s^{-1}.

During 120 min flights the mean RQ was ≈ 0.72, signalling nearly pure fat combustion. From stoichiometric equations for combustion of fuel mixtures it follows that at this RQ, 1 g of fuel mixture (94% fat, 6% carbohydrates) has an energy content of 37.95 kJ and delivers 1.06 g oxidation water. A metabolic power of 37.95 kJ min^{-1} or 632.5 J s^{-1} and a water gain of 1.06 g_{H_2O} min^{-1} results from a combustion rate of 1 $g_{\text{fuel mixture}}$ min^{-1}.

From Fig. 3B a minimum body mass loss of 0.14 g min^{-1} (corresponding to 0.44 g min^{-1} kg^{-1} or 0.044%$_{mb}$ min^{-1}) may be derived at $T_a \approx 20$°C. Taking the fuel mixture burnt at $RQ = 0.72$, a metabolic power of $P_m = 0.14$ (g min^{-1}) $\times$ 7.95 (kJ g^{-1}) $\times$ 1000 (J kJ^{-1}) $\times$ (60 s min^{-1})$^{-1}$ = 88.6 W should have been delivered if the body mass loss measured was due to fuel mass loss. This is 2.77 times the metabolic power of 32 W measured by respirometry so there must be something wrong.

Breeders know that in well-flying homing pigeons, 10%, in extreme cases 30%, of body mass is fat. In extreme cases, pigeons weighing 325 g and flying at 12 m s^{-1} can fly theoretically for 0.3×325 (g) $\times$ 39 (kJ g^{-1}) $\times$ 1000 (J kJ^{-1}) $\times$ (32 J s^{-1})$^{-1}$ $\times$ (3600 s h^{-1})$^{-1}$ = 33 h over 33 (h) $\times$ 3600 (s h^{-1}) $\times$ 12 (m s^{-1}) $\times$ (1000 m km^{-1})$^{-1}$ = 1426 km if $P_m = 32$ W holds, and only 11.9 h and 515 km if $P_m = 88.6$ W holds. This leads to the conclusion that the body mass loss measured does not reflect true fuel loss only, but must also reflect a certain body water loss.

3.3. Heat loss and body loss as limiting factors

To formulate the energetic boundaries of longtime flight, heat transfer effects must be taken into account. One gram of evaporated water may absorb a heat (energy) of $H = 2.4$ kJ at the temperature of a bird's respiratory tract. Accepting a degree of efficiency of $\eta_{mu} = 0.25$ for the muscular flight motor and a metabolic power of 32 W, one can calculate what fraction of the heat produced will be drawn off by evaporation of the total amount of metabolic water gained. Water loss by metabolic water evaporation is $\dot{m}_{lwm} = 60$ (s min^{-1}) $\times$ 32 (J s^{-1}) $\times$ (1000 J kJ^{-1})$^{-1}$ $\times$ (37.95 kJ $g_{fuel}$$^{-1}$)$^{-1}$ $\times$ 1.06 (g_{H_2O} $g_{fuel}$$^{-1}$) = 0.05363 g_{H_2O} min^{-1}. This holds for a heat loss power of $\dot{H}_{lwm} = 0.05363$ (g_{H_2O} min^{-1}) (60 s min^{-1})$^{-1}$ $\times$ 2.4 (kJ g_{H_2O})$^{-1}$ $\times$ (1000 J kJ^{-1}) = 2.15 W. This is 8.9% of $\dot{H}_p = (1 - \eta_{mu})P_m = 0.75 \times 32$ W = 24 W. So 91.1% are left to be dispersed by other means of heat exchange. Which possibilities are left?

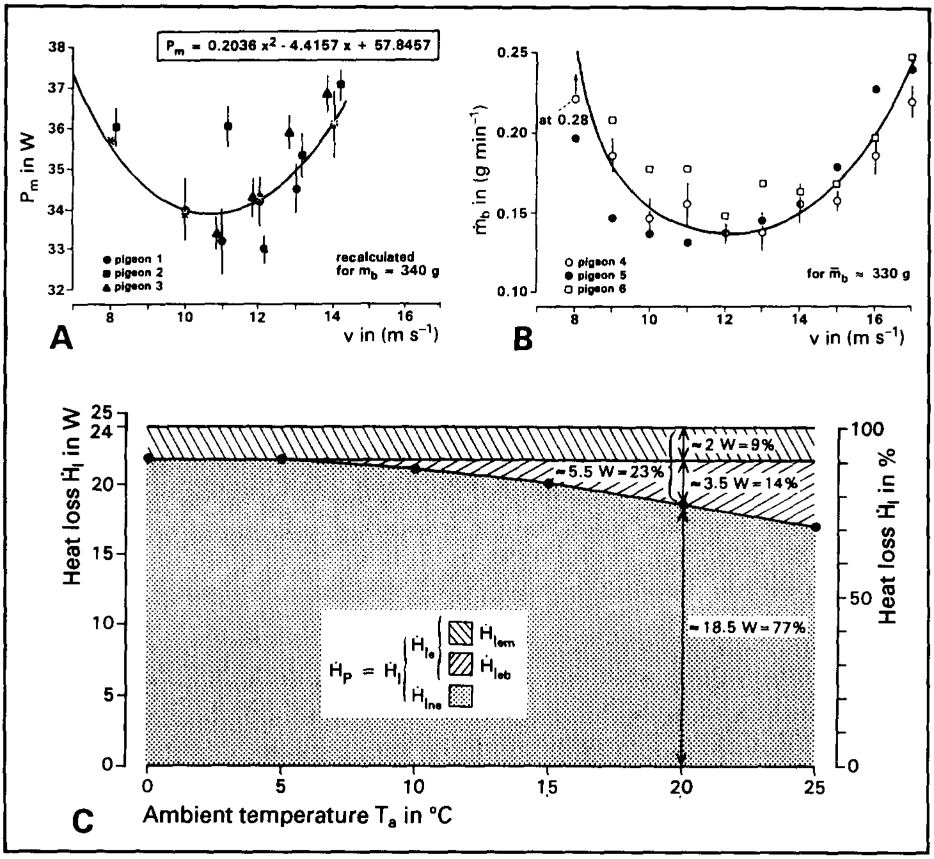

Fig. 3. Metabolic power, mass loss and heat loss plots. A, metabolic power as a function of flight speed. B, body mass loss as a function of flight speed. C, heat loss (in W and in % of the heat produced) for 24 W heat production as a function of ambient temperature: $\dot{H}_p$, heat production; $\dot{H}_l$, heat loss ; $\dot{H}_{le}$, evaporative heat loss ($\dot{H}_{lem}$ by metabolic water, $\dot{H}_{leb}$ by water from body stores); $\dot{H}_{lne}$, non-evaporative heat loss, mostly by convection.

Assuming that by raising body temperature to its utmost limit, heat from a few minutes of flight only can be stored, and that heat exchange by radiation is balanced, only non-evaporative heat loss ($\dot{H}_{lne}$) by conduction and convection, and evaporative heat loss by evaporating water from body stores ($\dot{H}_{leb}$) remain. If the pigeons are able to get rid of 91.1% by means of non-evaporative heat exchange they may fly as long as their fuel stores hold. If not, the birds would have to resort to their water stores to prevent overheating and thus risk dehydration. In this case their flight time would be limited by physiologically tolerated dehydration and they would have to stop even though their fuel stores were still replete.

The minimum body mass loss of 0.14 g min^{-1} measured (Fig. 3B) is 2.6 times higher than evaporative water loss and a difference of 0.0864 g min^{-1} remains to be explained. This must be due to water loss from body stores ($\dot{m}_{lmb}$) and correspondingly holds for a heat loss power of $\dot{H}_{\text{lwb}} = 3.46$ W. These two evaporative heat loss mechanisms together account for 5.61 W, thus leaving $\dot{H}_{\text{ne}} = 24 - 5.61 = 18.39$ W for non-evaporative pathways. These values almost coincide with the data plotted in Fig. 3C at $T_a = 20°\text{C}$. (Fig. 3C was constructed with slightly different boundary conditions, i.e. pure fat fuel, $RQ = 0.70$; 1.09 g_{H_2O} min^{-1} and 650 W for 1 g_{fuel} min^{-1}). It can be seen that heat losses $\dot{H}_{\text{lne}} + \dot{H}_{\text{lem}}$ only amount to 100% at very low ambient temperatures of $T_a \leqslant 7.5°\text{C}$ so that the required equilibrium is fulfilled at these low temperatures. At higher temperatures more and more body water must be used to replace the loss through heat disposal (heat loss $\dot{H}_{\text{leb}}$). At $T_a = 20°\text{C}$ this amounts to 14% of 24 W. Assuming that a maximum water loss of 10% of body mass is tolerated, it follows that the birds can fly only for 6.2 h over 268 km (at 43.2 km h^{-1}) at $T_a = 20°\text{C}$.

3.4. Overheating effects

Longtime flight boundaries do not even start to play a role if the metabolic power output necessary for flight is so high that it can hardly be provided, and/or the correlated heat production exceeds the abilities of heat loss mechanisms, so that overheating may occur. First signs of this are an increasing reluctance to fly,

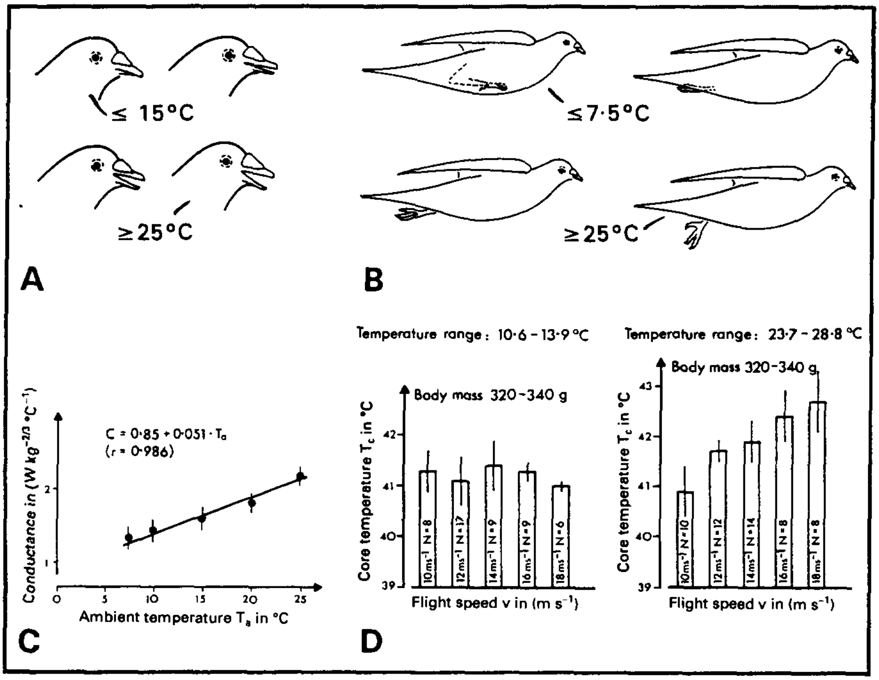

Fig. 4. Thermoregulatory effects. A, opening the bill. B, exposure of the legs. C, increase of thermal conductance with ambient temperature. D, mean core temperature at different ambient temperatures and flight speeds: left, no overheating; right, overheating.

followed by opening the bill (Fig. 4A) to improve respiration (thus increasing $\dot{H}_e$), stretching out the feet (Fig. 4B) (thus increasing thermal conduction and $\dot{H}_{ne}$) and trying to land. In any case, especially by stretching out the feet, the thermal conductance is increased (Fig. 4C) when necessary, i.e. at higher ambient temperatures. After landing, panting and wing stretching for cooling, as well as increased drinking were sometimes observed. The mean resting core temperature T_c (measured via the cloaca) was 39.8 ± 0.7°C. It was not correlated to T_a when the bird was resting, but when exposed to wind. However, it increased linearly with T_a between 41 and 42°C ($v = 12\ \mathrm{m\ s^{-1}}$) at T_a from 10 to 30°C during flight. The resulting temperatures were kept constant for several hours without the birds showing signs of overheating (Fig. 4D, left). Overheating tendencies were found to be correlated to core temperatures of 43°C and higher (maximum value 43.5°C) only when high speeds v were combined with high body masses m_b and/or high ambient temperatures T_a (Fig. 4D, right).

4. Conclusions from the calorimetric measurements as to longtime flight in migrant birds

After a transitory adaptation period of at least 1 h the birds fly with pure or almost pure fat fuel at or very near to the respiratory quotient (0.732), at which they neither lose nor gain weight by respiratory processes so that fuel consumption and metabolic water gain are nearly equal (condition A). Heat loss due to the evaporation of metabolic water, in addition to non-evaporative heat loss, is sufficient only at very low temperatures of $\leqslant 5$°C (condition B; high altitude flight, night flight). At higher temperatures the birds cannot make use of their complete fuel capacity because, although using non-evaporative heat loss mechanisms as far as possible, they suffer from dehydration. This limits flight times and distances. Because conditions A and B are more or less fulfilled in migrant birds during real long distance flights over seas and deserts, metabolic power estimates from body mass loss may come close to reality in those cases [7] but fail otherwise.

References

[1] H.J. Rothe and W. Nachtigall, Pigeon flight in a wind tunnel. I. Aspects of wind tunnel design, training methods and flight behaviour of different pigeon races, J. Comp. Physiol. B, 157 (1987) 91–98.

[2] H.J. Rothe, W. Biesel and W. Nachtigall, Pigeon flight in a wind tunnel. II. Gas exchange and power requirement, J. Comp. Physiol. B, 157 (1987) 99–109.

[3] K.D. Hirth, W. Biesel and W. Nachtigall, Pigeon flight in a wind tunnel. III. Regulation of the body temperature, J. Comp. Physiol. B, 157 (1987) 111–116.

[4] W. Biesel and W. Nachtigall, Pigeon flight in a wind tunnel. IV. Thermoregulation and water homeostasis, J. Comp. Physiol. B, 157 (1987) 117–128.

[5] W. Nachtigall, Long-time flight: Impositions on energy balance. Wind tunnel measurements with "model birds", (1994) (in press).

[6] V.A. Tucker, Respiratory exchange and evaporative water loss in the flying Budgerigar, J. Exp. Biol., 75 (1968) 231–236.

[7] J.C.T. Nisbet, W.H.J. Drury and J. Baird, Weight loss during migration. 1. Deposition and consumption of fat by the black poll warbler *Dendroica striata*, Bird Banding, 34 (1963) 107–138.