METABOLISM AND HEAT LOSS DURING FLIGHT IN PIGEONS

By Oliver P. Pearson

By weighing pigeons with sealed cloacas immediately before and after flight, it has been possible to measure directly the non-excretory weight loss and thereby to establish an upper limit to the metabolic cost of flight. I have used Tippler pigeons, a breed developed for its inclination and ability to fly many hours over the home loft. When released, they ascend for hundreds of feet and circle lazily without soaring and without aerobatics.

Food and water were removed from the experimental bird several hours before a flight; a few minutes before takeoff the cloaca was sealed with Testors Extra Fast Drying Model Cement, the bird was weighed on a triple-beam balance to one-tenth of a gram, and it was then released in company with other Tipplers. The bird was weighed again as soon as possible after it landed. In four of the flights recorded in figure 1 (triangles), between 9 and 54 minutes elapsed before the bird could be caught for weighing; a correction of 3 gm./hr./kg. of body weight, the rate at which resting, sealed pigeons at similar temperatures lose weight, was applied to these measurements. In five flights illustrated in figure 1 (solid circles), the bird was shot with .22 caliber dust shot within seconds of landing, and the probable weight of shot in the carcass (0.2 gm.) was subtracted from the body weight. The birds at takeoff weighed between 221 and 293 grams (average 254). I have included all flights lasting more than 3 hours; the longest was 6.23 hours and the average 4.33.

The average weight lost per pigeon was 3.0 grams per hour of flight, or 11.87 gm./hr./kg. of initial body weight. The least weight loss was 7.7 gm./hr./kg. and the greatest loss 15.4 (fig. 1). These rates vary from 2.6 to 5.1 times the rate of loss in resting pigeons and are much less than the rate calculated for flight on theoretical grounds by Salt and Zeuthen (1960:402).

In an attempt to determine the turnover of water during flight, I had, in addition to the procedures outlined above, introduced 1 cc. of tritiated water (HTO) into the crop of each experimental bird two hours before flight and had removed ½ cc. of blood from a vein in the foot a few minutes before takeoff. Birds so treated, possibly because of the blood removal, did not fly as long as they had flown on many of their training flights, but it is not likely that these procedures caused a significant change in the rate at which they lost weight during flight. Support for this belief is available from a flight of six untreated birds that flew 4.13 hours at an average weight loss of 17.6 gm./hr./kg., and of another flight of four untreated birds that flew 3.17 hours with an average weight loss of 13.6 gm./hr./kg. (open circles in fig. 1). The more rapid loss of weight of these unbled, unsealed birds suggests that the experimental procedures did not cause appreciably "labored" flight, although it must be recognized that some of the extra loss of weight of these control birds may have resulted from loss of feces either in flight or between the time of landing and weighing.

Metabolic cost of flight.—The only measurements of the metabolic cost of bird flight are those of Pearson (1950) and Lasiewski (1963) who induced hummingbirds to hover in small containers while oxygen consumption was being measured. They found that the average oxygen consumption during hovering was 5½ to 6 times (Pearson, p. 151) and 6½ times (calculated from table 4 and fig. 7 of Lasiewski) that of hummingbirds resting at the same environmental temperature. Since hovering flight differs aerodynamically, anatomically, and probably physiologically from linear flight, I have attempted to use the weight-loss data on pigeons given above to establish an
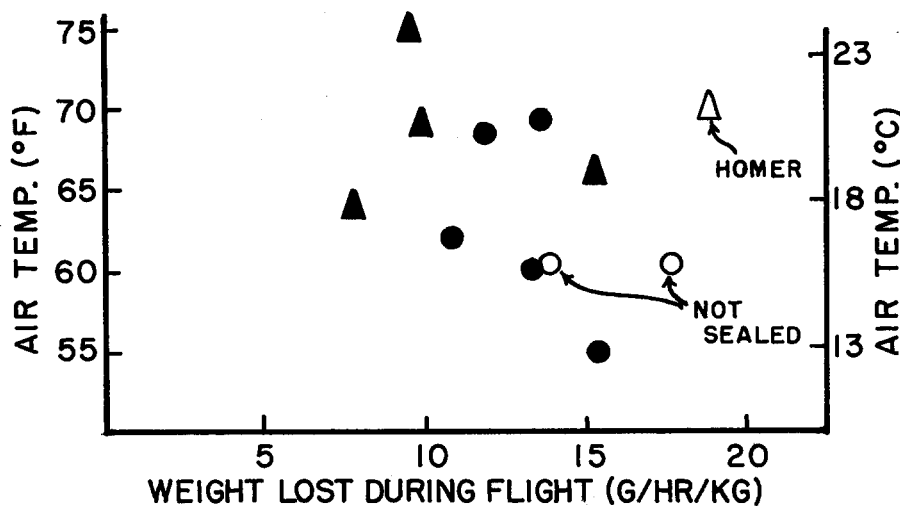
Fig. 1. Weight lost during flights at different air temperatures. Solid circles, birds weighed at the time of landing; solid triangles, birds weighed 9 to 54 minutes after landing; open circles, two groups of birds in which the cloaca was not sealed; open triangle, homing pigeon during 5-hour flight.

upper limit to estimates of how strenuous it is for a bird to fly in the usual horizontal manner. The loss of weight during flight stems from evaporation of body water and from utilization of energy stores such as fat and carbohydrate which are lost in the form of water vapor and carbon dioxide. If *all* of the weight lost during flight was the result of the utilization of fat (1 gm. fat = 9.45 kcal.) and concomitant expiration of all of the water and carbon dioxide formed, then loss of 11.87 gm./hr./kg. would represent a metabolic rate of 112 kcal./hr./kg., which is 23 times the rate of metabolism of resting Tippler pigeons at comparable air temperatures (Riddle, Smith, and Benedict, 1934). This is probably an upper limit of the rate of metabolism during these flights because more water than that produced by the in-flight metabolism of fat is probably lost during flight. The tritium experiments were designed to establish the rate at which water of metabolism was being formed, but the measurements so far have defied reasonable analysis.

   Of various estimates that have been made of the probable energy cost of flight, that of Zeuthen (1942) is especially interesting because it combines the efforts of a talented physiologist and an aircraft engineer. Zeuthen calculated that a pigeon flying at 31 miles per hour would be expending energy 10 times as fast as at rest, and at 43 mph about 27 times as fast. Tipplers fly in a leisurely manner at an average air speed probably not over 30 mph. Zeuthen's estimate of energy expenditure at 31 mph lies well below the upper limit calculated for my Tipplers.

   On May 14, 1955, with the kind cooperation of Andy Chak of Martinez, California, a 419-gram homing pigeon was flown from Redding to Martinez in 5.0 hours at an average ground speed of not less than 35 mph. During the flight it lost 39.1 gm. (18.6 gm./hr./kg. in fig. 1). The cloaca was not sealed. If all of this weight loss was due to the utilization of fat (an assumption yielding, as above, an upper limit), the metabolic rate would have been 176 kcal./hr./kg., which is about 36 times the resting rate. Zeuthen's estimates again fall within the measured limit. Deuterium and oxygen–18

had been administered to this bird before the flight, but there is no reason to expect this treatment to have altered the rate of metabolism.

Temperature regulation.—If *all* of the weight lost during flight of the Tipplers with sealed cloacas stemmed from evaporation of water, then body heat would have been lost by evaporative cooling at a rate of 7.0 kcal./hr./kg. (0.59 kcal. of heat lost per gram of water evaporated). This is 1.4 times the rate of heat production at rest. Since, however, a considerable fraction of the weight is lost not as water but as carbon dioxide, 7.0 kcal./hr./kg. represents the upper limit of the amount of heat lost through evaporation. Any additional heat formed by metabolism must have been lost through radiation and convection, or it was stored in the body and recorded as increased body temperature at the end of the flight.

Zeuthen (1942) and Salt and Zeuthen (1960) estimated that pigeons flying at 43 mph must eliminate by evaporation heat equivalent to 16 times their rate of heat production at rest, or at 31 mph four times their resting rate. These estimates seem to be too high. Either the metabolic cost of flight is less than they estimated, or a greater fraction of the heat produced is dissipated by radiation or convection. The fact that Tipplers did not lose weight (and presumably water) faster while flying on warm days than on cool days (fig. 1) suggests that heat can be lost sufficiently rapidly at the temperatures of these flights without resorting to high rates of evaporation.

Temperatures of four of the birds shot immediately upon landing were taken by inserting a quick-registering thermometer deeply into the esophagus. Their temperatures, listed in increasing order of air temperature taken at the same time (in parentheses) were: 41.5°C. (13°), 42.5 (18), 42.5 (21), and 43.8 (26). These body temperatures are approximately 2°C. higher than would be expected for resting pigeons and reflect, for 250-gram birds, temporary storage of about 0.5 kcal. of heat during the flight. This is the amount of heat produced during not more than a few minutes of flight.

DISCUSSION

Zeuthen's estimates of the amount of heat produced by pigeons flying slowly fall well below the upper limit established by my experiments, and so may be considered to have been confirmed, at least within broad limits. My measurements of the maximum amount of water that might have been evaporated from the respiratory tract during the flights are, however, much less than those estimated by Zeuthen. When dealing with the dissipation of heat generated during flight, Zeuthen assumed that the feathers were such good insulators that a considerable fraction of the heat produced would have to be dissipated by evaporative cooling from the respiratory tract. This led to his stimulating and logical idea that the air sac system of birds may have evolved as a mechanism to evaporate large amounts of water without overventilating the alveoli of the lungs. It now appears that most of the heat must be lost from the body and wings by convection and radiation (see also Eliassen, 1963) and that the air sacs either serve some other purpose or become important evaporators only when birds are flying at much higher air temperatures than those prevailing during the flights reported here.

SUMMARY

Pigeons with sealed cloacas lost weight during flight at a rate of 3.0 gm. per hour or 11.87 gm./hr./kg. of initial body weight. This indicates a metabolic rate during flight of less than 23 times that of resting pigeons. Most of the heat generated during flight was dissipated through convection and radiation; not more than 7.0 kcal./hr./kg. were

dissipated through evaporative cooling. Body temperatures rose about 2°C. during flight. This rise represents storage of an amount of heat produced during only a few minutes of flight.

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