*The Condor* 93:546–554
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# FLIGHT PERFORMANCE, ENERGETICS AND WATER TURNOVER OF TIPPLER PIGEONS WITH A HARNESS AND DORSAL LOAD[1]

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*Abstract.* We measured carbon dioxide production and water efflux of 12 tippler pigeons (*Columba* spp.) during seven experimental flights using the doubly labeled water (DLW) method. Prior to the experiment birds were randomly assigned to one of two groups. One group flew as controls (no load or harness) on all seven flights. The other group wore a harness on two flights, a dorsal load/harness package (weighing about 5% of a bird's mass) on two flights, and they were without a load in three flights.

Flight duration of pigeons with only a harness and with a dorsal load/harness package was 21 and 26% less, respectively, than the controls. Pigeons wearing a harness, or wearing a dorsal load/harness package lost water 50–90%, and 57–100% faster, respectively, than control pigeons.

The mean $CO_2$ production of pigeons wearing a harness or a load/harness package was not significantly different than pigeons without a harness or load. The small sample sizes and large variability in DLW measurements precluded a good test of the energetic cost of flying with a harness and dorsal load.

*Key words: $CO_2$ production; doubly-labeled water method; flight energy metabolism; radio transmitter; tippler pigeons; water flux; flight duration.*

## INTRODUCTION

Homing pigeons (*Columba livia*) fitted with a harness and dorsal load were slowed 27% and >31% on 90 and 320 km flights, respectively, and their hourly $CO_2$ production was 41–52% higher during 320 km flights (Gessaman and Nagy 1988). Those pigeons flew at 74 km/hr, which is faster than their most efficient speeds. Pennycuick (1968) used aerodynamic equations to compute a minimum-power air speed of 31 km/hr and maximum-range speed of 58 km/hr for pigeons, whereas a minimum-power air speed of 40 km/hr was measured by Rothe et al. (1987) on pigeons flying in a wind tunnel. Gessaman and Nagy (1988) concluded that high performance homing pigeons work longer and harder during a long distance flight when wearing a dorsal load (e.g., a radio transmitter), but that the effects of a dorsal load on flight performance and metabolism of avian species that normally fly at more efficient flight speeds would be less dramatic.

We designed the present study using tippler pigeons to overcome three limitations of the Gessaman and Nagy (1988) study: (1) the inefficient flight of homing pigeons (i.e., the high cost of transport), (2) the inability to track the flight of the pigeons, visually or by telemetry, so flight distances and durations of both controls and experimental birds could not accurately be measured, and (3) the lack of a measurement of the effect of the harness alone (not including a load) on flight metabolism. Tippler pigeons (*Columba livia*) typically fly in a flock of 3–12 birds at a slower air speed than homing pigeons (pers. observation), and remain in view throughout flights lasting several hours. Therefore, the flight duration of each bird can be measured accurately and flight distance flown per hour by control and experimental birds is nearly identical (although not measurable), because they remain in a flock throughout most of the flight.

[1] Received 9 August 1990. Final acceptance 6 March 1991.

## METHODS

### BIRDS

Juvenile tippler pigeons were purchased from suppliers in Arizona and Wisconsin in August 1987 and May 1988. Their sexes were unknown. Following the methods of Curley (1961), birds were trained to fly for several hours and then return to a loft in Smithfield, Utah. Training flights began in June 1988, using 26 birds. After five weeks, 14 birds that did not fly continuously for $\geq 2$ hr or did not fly in a flock were removed from the flock, leaving 12 pigeons for the experiment. Flocks of $\geq 12$ birds tended to separate into $\geq 2$ smaller flocks after several minutes of flight, making it difficult to visually track the groups, and the distances flown by the different groups could differ. Before the experiment we assigned each bird to either a control or an experimental group. The experimental birds flew without any load in flights 1, 2, and 7; wore a harness only in flights 3 and 4; and wore a harness and load in flights 5 and 6. The control group flew without a harness or load in all seven flights in which $\dot{V}CO_2$ and water flux were measured with doubly-labeled water (DLW), subsequently referred to in this paper as the DLW flights. We released all 12 pigeons together. We released all birds every other day for exercise flights between the seven DLW flights.

Each pigeon wore a numbered, colored leg band and was uniquely color marked on the underwings with Tester's fast drying paint. Individual birds could be identified during flight and their flight duration could be measured to the nearest minute.

### HARNESS AND LOAD DESIGN

The harness was a 2.5 × 6 cm piece of leather held flat on the back of the bird by a loop of flexible, vinyl-coated, multi-stranded wire in front of the wings and another behind the wings. The front loop fit around the crop and the rear loop fit around the chest and over the keel (Fig. 1, Kenward 1987). A 1 cm length of monofilament line connected the two loops ventrally along the midline. We adjusted the harness so that an index finger (about 1.75 cm diameter) could be easily inserted beneath the anterior half of the leather piece and a little finger (about 1.5 cm diameter) beneath the posterior half. We attached a harness weighing an average of 7.2 g (SD = 0.1) to each experiment bird 11 days before flight 3; the harness loops were completely covered by breast feathers within a few days. These birds were then flown on four different days before flight 3 to allow them to habituate to the harness.

We fastened loads to the harnesses of the experimental birds six days before flight 5. Birds were then flown on two separate days before flight 5 to allow habituation to the additional load. Each load was designed to simulate the size and mass of a radio transmitter. Each load (made from a plastic vial cap) weighed 6.5 g (SD = 0.4), had a diameter of 1.8 cm and a thickness of 0.3 cm. Each load had a whip antenna (guitar string) 18 cm in length. The load was weighted with steel shot so that the total weight of the harness and load was 5% of the body mass ($M_b$) of the pigeon (Fig. 1). A load was fastened to the leather patch with Velcro and oriented so that the whip antenna extended over the tail. We removed the load/harness from the experimental birds one day before the seventh flight.

### $CO_2$ PRODUCTION AND WATER FLUX

We measured rates of $CO_2$ production and water flux of each pigeon with doubly-labeled water (Lifson and McClintock 1966, Nagy 1980) during seven flights between 16 July and 2 September 1988. Before each DLW flight we weighed each bird and injected each with 0.4 ml of isotopic water (containing 95.9% $^{18}O$ and 0.3 mCi $^{3}H$) into the abdominal cavity along the midline, midway between the cloacal opening and the posterior edge of the keel. One to 1.5 hr later, we punctured the brachial wing vein of each bird with a 21-gauge hypodermic needle and collected the blood in 2–3 heparinized glass capillary tubes. We flame-sealed the tubes with a propane torch within 15 min. Prior to flights 1 and 2, birds were injected the previous evening, blood was sampled 1 hr later and they were held in carrying cages for 11 hr and 9.5 hr, respectively, before releasing them the next morning. For the other flights, we injected birds about 05:00 hr, sampled blood 1 hr later, and released them as a group near sunrise about 15 min after collecting the last blood sample.

Typically the birds flew in a flock for $> 1.5$ hr. During the next few hours birds landed in small groups or alone on one of four perches (the loft roof, a house TV antenna, power lines, or a barn roof). The birds usually sunned for $> 1$ hr before entering the loft. After entering the loft, we weighed the birds, collected a second blood sam-

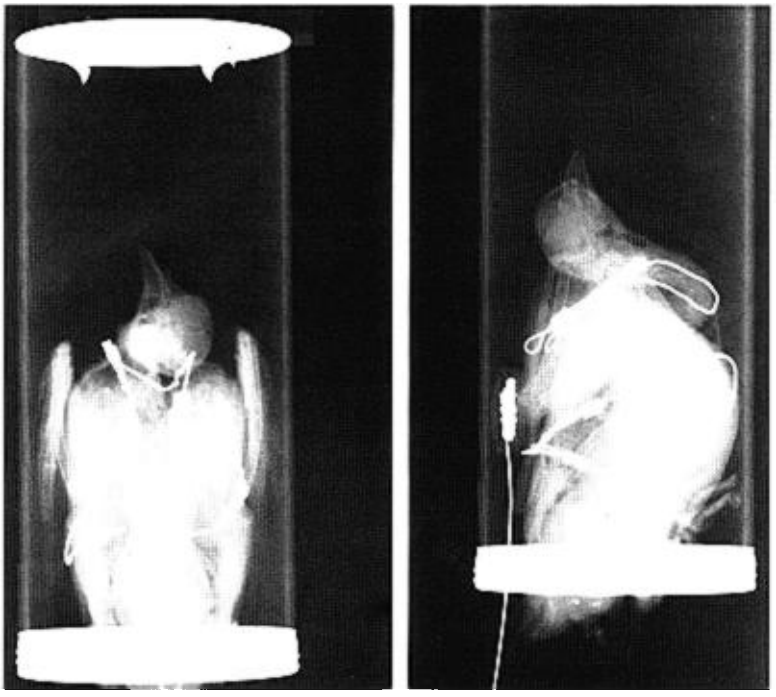

FIGURE 1. Radiographs of the dorsal and lateral surfaces of a tippler pigeon wearing a mock radiotransmitter attached to a harness. (See text for description of the harness). Two features of the mock transmitter show up in the radiograph: (1) steel shot used to adjust the total weight of the harness and transmitter to about 5% of the body mass of the pigeon, and (2) the whip antenna (a piece of guitar string) that extended beyond the tail of the pigeon.

ple, and provided water and food. We microdistilled pure water (Wood et al. 1975) from each blood sample and assayed tritium activity of each distilled water sample using Beckman Ready Safe scintillation cocktail and a liquid scintillation counter (Beckman LS 5801). A separate portion of each distillate was assayed for $^{18}O$ by K. A. Nagy's laboratory at the University of California at Los Angeles by converting $^{18}O$ to $^{18}F$ (by cyclotron-generated proton activation of $^{18}O$ to $^{18}F$) and subsequently counting the $^{18}F$ in a Packard Autogamma system (Wood et al. 1975).

We calculated water flux and $CO_2$ production from the isotope measurements using the appropriate equations (Nagy and Costa 1980, Nagy 1980). For flight 1, we estimated total body water (TBW) volume from the dilution of tritium injected into the bird about 1 hr before the flight. In the remaining flights we did not measure the TBW of each bird; the mean value of TBW before flight 1 was used in calculating water flux and $CO_2$ production for these six flights. We assumed that fractional water content of a bird remained constant through time, and we calculated TBW at recapture as the product of body mass at recapture and fractional TBW of the animal at time of injection. Also, we assumed any change in absolute TBW volumes was linear through time.

The DLW method measured $CO_2$ production between the times of the initial and final blood sample, i.e., a sum of $CO_2$ production that occurred during rest and during flight. We computed $CO_2$ production during the flight by subtracting an estimate of the bird's $CO_2$ production while at rest from the total $CO_2$ production between the initial and final blood samples. We estimated an hourly rate of $CO_2$ production during rest, i.e., resting metabolic rate (RMR), by measuring the resting rate of $CO_2$ production of each pigeon in an open circuit respirometer at 20°C, and by measuring the average daily rate of $CO_2$ production, i.e., average daily metabolic rate (ADMR) by DLW of pigeons confined to the loft for 24 hr. ADMR was measured on a day between experimental flights. RMR was measured for 2 hr about two months following the exper-

imental flights. Mean ratio of ADMR to RMR was 2.17; we selected 2 times RMR as the best estimate of the $CO_2$ production of pigeons resting outdoors either in or out of the loft.

Several of the calculated values of $CO_2$ during flight were unexpectedly very high or very low and we questioned their validity. In the literature, ratios of flight metabolism (during continuous flapping flight) to RMR for pigeons range from 8.0 (LeFebrve 1964) to 32.4 (when the birds carried a harness and dorsal load that weighed 5% of the bird's body mass, Gessaman and Nagy 1988). We evaluated the probable validity of these high and low values by dividing them by RMR. If a value of flight metabolism in our study was less than 7.5 times RMR or more than 34.0 times RMR we regarded it as an error and it was eliminated from the data set. In a few instances, the sample size was reduced more when the quantity of water distilled from the blood was inadequate for isotopic analysis.

The DLW method also measures water influx (water gained from food, drink, oxidative water and air breathed in) and water efflux (water lost by evaporation and excretion) between the time of the two blood samples. We measured water flux of pigeons on seven flight days and during one 24-hr period when they were confined in the loft. During the 24-hr confinement in the loft the pigeons had access to food and water, but not between the time of initial and final blood samples on the seven flight days. We calculated water flux of a pigeon during a specific flight as the difference between water flux measured between initial and final blood samples taken on that flight day and an estimate of the water flux of that pigeon when resting during the same period. We estimated water efflux occurring between the initial and final blood samples when the birds were at rest by multiplying the total duration of rest (hr) by the hourly rate of water efflux measured on pigeons confined to the loft for 24 hr. We could not calculate water influx during a flight, however, because we did not have an estimate of water influx of resting pigeons without food and water (i.e., our only measure of the water influx of resting pigeons was from pigeons that ate and drank during confinement in the loft for 24 hr).

Flight time, $CO_2$ production and $H_2O$ efflux were each analyzed separately with one-way ANOVA of 14 treatments; the data from the experimental and control groups within a flight were each a data subset, resulting in 14 subsets (treatments) for the seven flights. Linear contrasts were computed to compare: (1) the two subsets of birds wearing only a harness with the 10 subsets of birds without a harness or load, (2) the two subsets of birds wearing a harness and a load with the 10 subsets of birds without a harness or load, and (3) the two subsets of birds wearing only the harness with the two subsets of birds wearing a harness and load.

## RESULTS

### $CO_2$ PRODUCTION AT REST

The average RMR of 10 pigeons weighing 317.8 g (SD = 25.9) was 0.8017 ml $CO_2$ $g^{-1}$ $hr^{-1}$, and the mean ADMR ($n$ = 20) of 14 birds (six birds were measured twice), weighing an average of 265.9 g (SD = 23.1), was 1.7397 ml $CO_2$ $g^{-1}$ $hr^{-1}$. The ADMR/RMR ratio averaged 2.17 (SD = 0.88) and ranged from 1.08 to 4.6 for individual birds.

### $CO_2$ PRODUCTION DURING FLIGHT

Mean $CO_2$ production of control birds for the seven DLW flights ranged from 13.0 ± 2.7 to 15.5 ± 6.4 ml $g^{-1}$ $hr^{-1}$ (Table 1). Mean $CO_2$ production of experimental birds during flights 1, 2, and 7 was less than that of control birds, but the differences were not significant ($P > 0.05$).

The $CO_2$ production of pigeons wearing either a harness or a load attached to a harness did not differ significantly from the control pigeons ($F < 1.0$), even though the experimental birds produced, on the average, more $CO_2$ when wearing a harness or a load/harness package than control birds in flights 3 through 6.

Average flight metabolism/RMR ratios of control birds for flights 1, 2 and 7 combined and for all seven flights combined were 17.2 (SD = 3.0, $n$ = 9) and 17.8 (SD = 4.0, $n$ = 22), respectively. For experimental birds the ratio was 14.6 (SD = 2.8, $n$ = 9) for three control flights (flights 1, 2 and 7), 21.3 (SD = 5.8, $n$ = 8) when carrying a harness (flights 3 and 4) and 21.2 (SD = 4.7, $n$ = 7) when carrying a load/harness package (flights 5 and 6) (Table 1).

We believe that the present study is the first to measure flight metabolism with DLW several times on the same individuals. We expected that the rate of carbon dioxide production ($\dot{V}CO_2$ of a control bird would be similar from flight to flight. This was the case with Pigeon 1 and Pigeon 2, the SD of the mean $\dot{V}CO_2$ was 7.4% ($n$ = 4)

TABLE 1. Mean rate of metabolism (± SD) [ml $CO_2$ $hr^{-1}$ $g^{-1}$] of two groups of tippler pigeons that flew together in the same flock during seven flights. Metabolism was measured with doubly-labeled water. Experimental birds wore a harness during flights 3 and 4. During flights 5 and 6 they wore a mock transmitter attached to the harness (this load weighed about 2.5% of the bird's $M_B$). In flights 1, 2, and 7, experimental birds were not wearing a harness or transmitter. Control birds flew unencumbered in all seven flights.

| Flight ID | Type of treatment to experimental birds | Flight metabolism [ml$CO_2$ $hr^{-1}$ $g^{-1}$] | | Flight metabolism/RMR[b] | |
|---|---|---|---|---|---|
| | | Experimental birds (*n*) | Control birds (*n*) | Experimental birds (*n*) | Control birds (*n*) |
| 1 | none | 11.5 ± 1.0 (2) | 13.0 ± 2.7 (3) | 14.7 ± 2.0 | 15.9 ± 2.9 |
| 2 | none | 11.1 ± 3.1 (5) | 13.6 ± 2.0 (4) | 14.2 ± 3.7 | 16.8 ± 3.4 |
| 3 | harness | 17.4 ± 7.7 (3) | 14.3 ± 2.1 (4) | 21.0 ± 8.5 | 17.5 ± 3.7 |
| 4 | harness | 16.4 ± 3.0 (5) | 14.9 ± 0.1 (2) | 21.5 ± 4.8 | 18.6 ± 0.2 |
| 5 | T[a] + harness | 14.6 ± 4.3 (4) | 14.0 ± 2.5 (3) | 19.2 ± 5.4 | 18.0 ± 3.3 |
| 6 | T[a] + harness | 18.4 ± 3.9 (3) | 15.5 ± 6.4 (4) | 23.7 ± 2.2 | 19.0 ± 7.8 |
| 7 | none | 11.8 ± 1.2 (2) | 15.3 ± 0.2 (2) | 15.7 ± 1.4 | 20.1 ± 0.4 |

[a] T = a mock transmitter.
[b] RMR = resting metabolic rate, measured on these pigeons in the laboratory.

and 10.1% ($n$ = 5), respectively (Table 2). This was not the case with Pigeons 3, 4, and 5, where the SD was 36.5% ($n$ = 4), 23.4% ($n$ = 4) and 15.2% ($n$ = 3), respectively, of the mean $\dot{V}CO_2$. The large variance of $\dot{V}CO_2$ of Pigeons 3, 4, and 5 is undoubtedly a reflection of the low turnover of $^{18}O$ during the flights (discussed below).

## WATER EFFLUX

The average rates of water efflux from control birds in flights 1, 2 and 7 (546.7 ml $H_2O$ $kg^{-1}$ $d^{-1}$, SD = 218.9, $n$ = 9) and in flights 3 through 6 (577.6 ml $H_2O$ $kg^{-1}$ $d^{-1}$, SD = 212.6, $n$ = 12) were similar ($P > 0.05$) (Table 3). For experimental birds the average rate of water efflux was 404.9 ml $H_2O$ $kg^{-1}$ $d^{-1}$ (SD = 86.5, $n$ = 9) in control flights 1, 2, and 7, 780.2 ml $H_2O$ $kg^{-1}$ $d^{-1}$ (SD = 246.5, $n$ = 8) in flights 3 and 4, and 821.6 ml $H_2O$ $kg^{-1}$ $d^{-1}$ (SD = 231.5, $n$ = 7) in flights 5 and 6. Therefore the rate of water efflux of experimental birds increased about 90% ($P$ = 0.014) with a harness and about 100% ($P$ = 0.011) with a harness and a load. The average water efflux of all birds flying without a load (516.4 ml $H_2O$ $kg^{-1}$ $d^{-1}$, SD = 102.3), also was 50% less than that of birds wearing a harness (776.8 ml $H_2O$ $kg^{-1}$ $d^{-1}$, SD = 19.1, $F$ = 37.6) and 57% less than those wearing a load and harness (811.6 ml $H_2O$ $kg^{-1}$ $d^{-1}$, SD = 101.6, $F$ = 4.6).

## FLIGHT PERFORMANCE

The flock flew in broad circles, ranging in width from 50 to 200 m. Typically the flock flew 75 to 125 m above the loft area for several minutes after release, and then moved to higher altitudes (altitudes were not measured) for 15 to 30 min. On some flights the flock moved alternately between low and higher altitudes, remaining at each for >15 min. The birds were usually in view throughout the entire flight, although at the high-

TABLE 2. $CO_2$ production ($\dot{V}CO_2$) [ml $CO_2$ $hr^{-1}$ $g^{-1}$] during flight of five control pigeons.[d] The ratio of flight $CO_2$ production to $CO_2$ production during rest is in parentheses.

| Flight ID | $\dot{V}CO_2$ during flight (flight $\dot{V}CO_2$/resting $\dot{V}CO_2$) | | | | |
|---|---|---|---|---|---|
| | Pigeon 1 | Pigeon 2 | Pigeon 3 | Pigeon 4 | Pigeon 5 |
| 1 | HV[a] | NM[b] | 10.1 (12.6) | 13.7 (18.2) | NM |
| 2 | 12.5 (15.6) | 16.7 (21.7) | LV[c] | LV[c] | 12.9 (14.0) |
| 3 | 13.3 (16.6) | 17.1 (22.2) | 14.5 (18.0) | NM[b] | 12.2 (13.2) |
| 4 | 14.8 (18.4) | NM[b] | 14.9 (18.7) | LV[c] | LV[c] |
| 5 | 13.2 (16.5) | 16.8 (21.8) | NM[b] | 11.9 (15.7) | NM |
| 6 | NM[b] | 13.3 (17.2) | 23.9 (29.8) | 8.6 (11.3) | 16.2 (17.6) |
| 7 | NM[b] | 15.2 (19.8) | NM[b] | 15.4 (20.4) | NM |
| $\bar{x}$ (±SD) = | 13.5 ± 1.0 | 15.8 ± 1.6 | 15.9 ± 5.8 | 12.4 ± 2.9 | 13.8 ± 2.1 |

[a] HV = high value. The value divided by RMR was greater than 34.0 and was removed from the data set.
[b] NM = no measurement, i.e., either the bird did not fly or the quantity of isotopic distilled $H_2O$ was too small to analyze.
[c] LV = low value. The value divided by RMR was less than 7.5 and was removed from the data set.
[d] $CO_2$ production of individuals on some flights was either not measured or was unreasonably high or low and, therefore, was removed from the data set (see footnotes and text for explanation). The two measurements of $CO_2$ production obtained on the sixth control pigeon are not shown.

TABLE 3. Mean water efflux rates (± SD) of two groups of tippler pigeons that flew together in the same flock during seven flights. Experimental birds wore a harness during flights 3 and 4. During flights 5 and 6 they wore a mock transmitter attached to the harness (this load weighed about 2.5% of the bird's $M_B$). In flights 1, 2, and 7, experimental birds were not wearing a harness or a mock transmitter. Control birds flew unencumbered in all seven flights.

| Flight ID | Type of treatment to experimental birds | ml $H_2O$ $kg^{-1}$ $d^{-1}$ | |
|---|---|---|---|
| | | Experimental birds | Control birds |
| 1 | none | 352.8 ± 59.8 (2) | 601.6 ± 394.5 (3) |
| 2 | none | 378.9 ± 69.8 (5) | 474.5 ± 49.3 (4) |
| 3 | harness | 885.0 ± 377.8 (4) | 561.3 ± 276.5 (4) |
| 4 | harness | 790.3 ± 208.1 (5) | 514.3 ± 171.6 (2) |
| 5 | T[a] + harness | 883.2 ± 216.4 (4) | 469.5 ± 339.5 (2) |
| 6 | T[a] + harness | 682.2 ± 248.2 (4) | 679.9 ± 128.0 (4) |
| 7 | none | 522.0 ± 26.0 (2) | 608.9 ± 164.3 (2) |

[a] T = mock transmitter.

est altitudes they were barely visible. On some flights birds moved to a lower altitude after flying for >2 hr, and remained there until some began to land. A "tired" bird that began to slow and hover in preparation for a landing would usually lure a few other tipplers in the flock to land with it; however, the lure was not effective before 1.5 hr into the flight. This behavior, which is well known among breeders and flyers of tippler pigeons, undoubtedly lured some birds to land even though they could have flown much longer. In addition, the availability of several potential perches near the loft (e.g., TV antenna, barn roof, silo, etc.) might have induced some birds to land prematurely, i.e., before they were fatigued. Flight duration, therefore, was probably not a true measure of flight duration capabilities of many of the pigeons; their capabilities undoubtedly exceeded the measured duration. In spite of these confounding circumstances, the flight time of the control birds (3.00 ± 0.58 hr; range = 1.92 to 4.88 hr) was significantly longer than that of the birds wearing only a harness ($\bar{x}$ = 2.36 ± 0.10 hr; range = 1.62 to 4.12 hr; $F = 33.0$, $P < 0.01$) and of birds wearing a load attached to a harness ($\bar{x}$ = 2.22 ± 0.002; $F = 19.87$, $P < 0.01$). Flight times of birds with a harness only and with a harness plus a load were not different ($F < 1.0$). This demonstrates that tippler pigeons, wearing a harness alone or a load attached to a harness, fatigue or tire of flying before control birds.

## DISCUSSION

### $CO_2$ PRODUCTION AND POWER OF FLIGHT

Mean rate of $CO_2$ production of control tippler pigeons in this study was very similar to that of homing pigeons flying without a harness or load (control birds) in the study of Gessaman and Nagy (1988) (Table 4). We anticipated that the rate of flight metabolism of tippler pigeons would be less than that of homing pigeons, because tipplers fly slower than homers and, therefore, their cost of transport should be less, i.e., less energy should be used per km flown. However, we were unable to determine the precise speed of flight of the tipplers, because the birds did not fly a straight path between two points.

The difference in mean $\dot{V}CO_2$ among control birds that were flying together throughout all or most of a flight was larger than expected. For example, mean $\dot{V}CO_2$ of Pigeon 2 was 9.6% higher than that of Pigeon 1 (Table 2). The sex of these birds was unknown. It appears that even within a flock of birds the energy expended by individuals can be quite different.

The somewhat similar increase in water efflux of birds wearing only a harness, and of birds wearing a harness/transmitter package, supports the idea that the effect of the transmitter is much less than that of the harness alone. Goslow et al. (1990), studying the flight of starlings (*Sturnus vulgaris*) in a wind tunnel with cineradiography, proposed that as the wing is depressed during the downstroke of flight the furcula spreads to inflate the clavicular air sac and the sternum elevates to compress the posterior air sacs. It is possible that the harness straps we used on our tipplers impeded the movement of their furcula or sternum and reduced their depth of breathing (tidal volume). They could have maintained adequate lung ventilation (minute volume) by increasing breathing frequency, a speculation that is consistent with our observations of increased water efflux.

TABLE 4. A comparison of measured $CO_2$ production ($\dot{V}CO_2$) of homing pigeons and tippler pigeons during flight and values predicted from allometric equations.

| Pigeon ID | Mean body mass (g) | Mean $CO_2$ production [ml $CO_2$ $hr^{-1}$ $g^{-1}$] Measured | (n) | Allometric prediction[a] | Allometric prediction[b] | Measured flight $\dot{V}CO_2$/ resting $\dot{V}CO_2$ |
|---|---|---|---|---|---|---|
| California homing pigeons[1] | 412.5 | 13.9 | (8) | 10.1 | 8.2 | 17.5 |
| Utah homing pigeons[2] | 412.8 | 16.5 | (4) | 10.1 | 8.2 | 21.5 |
| Tippler pigeon (this study) | 281.2 | 13.5 ± 3.1 | (31) | 11.1 | 9.1 | 16.9 ± 3.9 |

[1] Gessaman, J. A. and K. A. Nagy. 1988. Transmitter loads affect the flight speed and metabolism of homing pigeons. Condor 90:662–666.
[2] Gessaman, J. A. and M. R. Fuller. 1989 (unpublished data).
[a] Predicted from Eq. 8 in Bernstein (1987).
[b] Predicted from the equation for minimum power output in Figure 2.8 of Phillips et al. (1985).

## WATER EFFLUX

Bernstein (1987) reports that the rate of respiratory evaporation ($M_{re}$) from flying birds is related to body mass ($M_B$) by the allometric equation, $M_{re} = 259\ M_B^{0.80}$ where $M_{re}$ is in mg/min and $M_B$ is in kg. This equation predicts a respiratory evaporation rate of 480.7 ml $H_2O$ $kg^{-1}$ $d^{-1}$ for a tippler pigeon with a $M_B$ of 281.2 g, 18.5% higher than the average water efflux rate that we measured on experimental birds flying without a load (404.9 ml $H_2O.kg^{-1}$ $d^{-1}$) and 22.2% less than that measured on the control pigeons (577.6 ml $H_2O$ $kg^{-1}$ $d^{-1}$). Water efflux is a sum of water lost by respiratory evaporation, cutaneous evaporation and excretion. The results suggest that 20% or less of the water lost by our control birds was by cutaneous evaporation and excretion. We anticipated that excretory water loss would be small, because the birds were without food for about 18 hr prior to the flight. Hudson and Bernstein (1981) reported that about 20% of the total evaporative water loss (respiratory plus cutaneous) from Chihuahuan Ravens (*Corvus cryptoleucus*) flying in a wind tunnel was from cutaneous evaporation.

Our data indicate that birds flying with a load attached to a harness lose water at a much faster rate than controls (50 to 100% faster). Dehydration could limit flight duration of a bird carrying a harness/load well before the depletion of fat (energy) reserves. This needs further study.

## SOURCES OF ERROR

The mean error in DLW measurements of $CO_2$ production are in the range of ±7% when 50% of the $^{18}O$ injected into the animal is lost from the body during the measurement period (i.e., one-half life) (Nagy 1989). The error increases exponentially as the turnover drops below 50%. For example, when $^{18}O$ declines by only 20% of its initial value (regardless of the absolute level of $^{18}O$), a 1% error in any one of the 4 isotope measurements yields an error in calculated $CO_2$ production of about ±37% (Nagy 1980). The $^{18}O$ turnover was about 24% in flights 1, 2 and 3 which lasted about 2.5 to 3.8 hr, about 19% in flights 4 and 5 which lasted 2.2 to 2.5 hr, and about 22% in flights 6 and 7 which lasted 2.2 to 3.2 hr (Table 5). These low values of $^{18}O$ turnover can result in a very large error in $CO_2$ production and are undoubtedly the reason for the aberrant values of $CO_2$ production which we eliminated from the data set (see Methods section). Flight durations of 6–7 hr would be required to turnover about 50% of the isotopic oxygen.

A ±1% error in any one isotope measurement will yield a very large error in calculated $CO_2$ production when tritiated water (HTO) turnover is a large fraction (e.g., >90%) of $^{18}O$ turnover. In all flights HTO turnover was 40 to 60% of $^{18}O$ turnover, or about half of the $^{18}O$ loss was due to the loss of $CO_2$ from the body. Turnover rates of HTO, therefore, should not have been a source of error in this study.

The study has not shown that a dorsal load affects the flight metabolism of tippler pigeons. The sample size is too small, and its variability too large, to statistically elucidate any real effect. In DLW studies that compare two subgroups within a species a sample size of nine (per subgroup) is recommended for statistical tests (Nagy 1989). However, it is highly unlikely that a flock of 18 tippler pigeons (9 experimental and 9 control birds) could be trained to fly non-stop for 6–7 hours, because flocks >12 birds tend to separate, and pigeons carrying a harness or load seem to land before flying 6–7 hours.

An inaccurate estimate of TBW at the start of a DLW measurement period can result in a small

error in the estimate of $CO_2$ production. For example, a 5% error in TBW causes a 5% error in the estimate of $CO_2$ production (Nagy 1980). We measured TBW by $^{18}O$ dilution before the first flight, but not before the subsequent flights, since in flights 2–7 two blood samples would have been needed before each flight to measure TBW by $^{18}O$ dilution, one to measure background level of $^{18}O$ (before $^{18}O$ injection) and the other to measure $^{18}O$ dilution (1 hr after injection). (The background level of isotope preceding flights 2–7 probably contained residual isotope from the previous flight, since some DLW flights were only 5–7 days apart.) We were concerned that the handling associated with taking two blood samples from a bird before the flight would decrease the bird's willingness or ability to fly for several hours, so we took only one pre-flight blood sample (1 hr after injection) in flights 2–7. Since the background of $^{18}O$ was unknown before flights 2–7, the mean TBW measured before flight 1 was used in computing $CO_2$ production for all seven flights.

## LIMITATIONS OF TIPPLERS IN FLIGHT STUDIES

We learned in this study that a flock of tippler pigeons which flies in circles for hours is easy prey for raptors that move into northern Utah in November for five months of residency. We lost three tipplers in one November day to raptors. This restricts metabolic studies of tippler pigeons in northern Utah to April through October.

Properly trained tipplers can regularly fly nonstop for 8–10 hours. This is usually accomplished with a flock of 2–3 good flyers. Record tippler flights of more than 17 hr have been observed (Curley 1961, Smith 1983). On 18 October 1988, the mean flight duration of our control birds was 8 hr, 5 min, the longest flight observed in this study. Our tipplers did not fly as long in the summer months as in the cooler days of October. The longest mean flight duration of control birds in July and August was 3 hr, 54 min. The negative effect of heat on flight time was evident in another way; birds released at 07:00 hr (in the cool of the day, just before sunrise) flew longer than birds released at 10:00 hr.

## ACKNOWLEDGMENTS

We thank W. S. Seegar for providing support for this study, and D. G. McAuley and E. Klaas for useful comments on a draft.

TABLE 5. Mean (± SD) flight duration (hr), body mass and percent turnover of $^{18}O$ (injected before the flight) for seven flights of tippler pigeons that flew together in a flock. The experimental birds wore a harness during flights 3 and 4. During flights 5 and 6 they wore a mock transmitter attached to the harness (weight = 2.5% of the bird's $M_B$). In flights 1, 2, and 7, the experimental birds did not wear a harness or transmitter. The control birds flew unencumbered in all seven flights. $^{18}O$ in the blood samples preceding and following the flight were used to compute percent turnover, therefore, the value is a sum of turnover during the flight and during rest.

| Flight ID | Type of treatment to experimental birds | Date of flight | Flight duration (hr) | | Mean body mass (g) | | Percent of $^{18}O$ turnover during flight | Temperature on day of flight (C) | |
|---|---|---|---|---|---|---|---|---|---|
| | | | Experimental birds | Control birds | Experimental birds | Control birds | | Max. | Min. |
| 1 | none | July 16 | 2.5 ± 0.0 | 2.5 ± 0.1 | 286.3 ± 13.8 | 285.1 ± 16.3 | 23.8 ± 2.8 | 32.8 | 10.0 |
| 2 | none | July 21 | 3.9 ± 0.4 | 3.7 ± 0.7 | 280.0 ± 24.8 | 265.5 ± 15.7 | 24.1 ± 3.2 | 33.9 | 8.3 |
| 3 | harness | Aug 2 | 2.9 ± 0.9 | 3.7 ± 1.2 | 261.4 ± 16.0 | 267.0 ± 4.6 | 24.6 ± 3.8 | 31.7 | 15.0 |
| 4 | harness | Aug 11 | 2.2 ± 0.4 | 2.5 ± 0.2 | 273.6 ± 30.1 | 282.6 ± 18.9 | 19.7 ± 4.8 | 31.7 | 12.8 |
| 5 | T[a] + harness | Aug 18 | 2.2 ± 0.6 | 2.5 ± 1.0 | 284.1 ± 21.8 | 295.4 ± 15.7 | 18.9 ± 5.3 | 32.2 | 10.6 |
| 6 | T[a] + harness | Aug 26 | 2.2 ± 0.6 | 2.7 ± 0.1 | 268.2 ± 30.3 | 279.5 ± 20.2 | 22.0 ± 4.9 | 29.4 | 6.7 |
| 7 | none | Sept 2 | 3.2 ± 0.0 | 2.6 ± 0.9 | 272.0 ± 27.1 | 298.3 ± 17.0 | 21.6 ± 5.5 | 31.7 | 10.0 |

[a] T = mock transmitter.

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