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TRANSMITTER LOADS AFFECT THE FLIGHT SPEED AND METABOLISM OF HOMING PIGEONS[1]

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Abstract. Eight homing pigeons (*Columba livia*) were flown distances of 90 and 320 km with and without transmitters (weighing either 2.5% or 5.0% of the pigeon's body mass, M_B) mounted on a back harness. Flight times in April through June for the 90-km distance were 60 min without a transmitter or harness, 69 min with a harness alone and about 76 min with a harness and transmitter (weighing either 2.5% or 5.0% of M_B). Flight times for the 320-km distance were 4 hr 16 min for the controls and 5 hr 35 min for the two fastest pigeons wearing a harness and transmitter weighing 2.5% of M_B. The results show that on 90-km flights harnesses alone slow birds by 15% and harnesses and transmitters ($\leq 5\% M_B$) slow birds 25 to 28%; on 320-km flights harnesses and transmitters slow birds >31%. Moreover, on the 320-km flights, CO_2 production of the pigeons (measured with the doubly-labeled water method) was 41 to 52% higher per hour when encumbered with a transmitter and harness. Thus, encumbered pigeons produced 85 to 100% more total CO_2 covering the 320-km distance. Therefore, high performance homing pigeons work substantially harder and longer during a long distance flight when wearing harnesses and transmitters.

Key words: Flight metabolism; homing pigeons; radiotelemetry; flight speed; doubly-labeled water method; locomotion cost; activity metabolism.

INTRODUCTION

For many years wildlife biologists have been guided by an informal standard that limits the mass of a transmitter package attached to a bird to 5% of the bird's body mass (Cochran 1980, Caccamise and Hedin 1985). The rationale for selecting 5% as the upper limit is not in the literature. Biologists who follow this guideline implicitly assume that normal behavior and daily energy metabolism of the bird are not significantly changed by the transmitter package. The validity of this assumption, however, has not been rigorously evaluated for any avian species.

We reasoned that the effects of a transmitter on the behavior and energy metabolism of a bird would be most evident during flight and that measurements of flight speed (or flight duration) and energy metabolism of birds flying with and without transmitter packages would be a first step in evaluating the validity of the ≤5% guideline. The quantity of energy used by a bird during flight can be computed from any of the following measurements: (1) CO_2 production (measured with the doubly-labeled water method), (2) O_2 consumption of a hooded bird flying in a wind tunnel, and (3) the change in body energy content during a flight (see LeFebvre 1964). Each method has its limitations and errors (King 1974, Nagy 1980, Walsberg 1983, Gessaman 1987).

In this study we chose to use the doubly-labeled water (DLW) method on homing pigeons (*Columba livia*) because: (1) each pigeon could be flown outdoors over the same route more than once, so measurements could be made on each bird while flying with and without a transmitter; (2) the DLW method has been successfully used by LeFebvre (1964) to measure energy expended by homing pigeons on long distance flights (480 km); and (3) we were familiar with the DLW methodology.

METHODS

BIRDS

Eight male sibling homing pigeons were used in this study. These 2-year-old birds were in good health and had been flown several times during their first year for distances of more than 160 km.

The pigeons were trained to return to their

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home loft in Northridge, California (in the San Fernando Valley) from two release locations: a crossroads on Interstate 5 (I5) at Lebec, California and at Fresno, California.

All birds were released simultaneously on all flights. All flights began in the morning between 06:00 and 08:45. Sky conditions at release time varied from scattered clouds to completely clear. Within 1 min after release the pigeons were usually flying as a flock in the general direction of the home loft. Within another minute the flock was out of sight, and the birds were usually not seen again until they appeared in the air space above the loft.

HARNESSES AND TELEMETERS

Each harness was constructed of a rectangular piece of leather (2.5 × 6 cm) held flat on the dorsal surface of the bird by two chest loops of vinyl-coated fishing leader (Steelon leader, Berkley and Co., Iowa), one in front of the wings, the other behind the wings. Each loop was fastened to an end of a narrow strap of leather (0.7 × 4.0 cm) aligned along the keel. This keel-strap thwarted the anterior to posterior movement of the neck loop and stabilized the design and fit of the harness. Harnesses were attached to the birds several days before the flight. Adjustments were made in the length of the loops and the keel-strap if a harness appeared to hinder flying during the daily flights in the vicinity of the loft, or if it did not settle down within the breast feather layer. Within a few days of a harness being attached to a pigeon, the keel-strap and harness loops were covered by breast feathers and, therefore, not visible. The dorsal leather patch always remained on the surface of the contour feathers.

Each "transmitter" was actually a dummy transmitter made from a centrifuge tube (1.2 cm in diameter, 5 cm in length). The tube was filled with lead or steel shot and cotton or tissue paper and then sealed with tape to bring the weight of the transmitter to either 2.5 or 5.0% of body mass, M_B. The transmitter was fastened to the leather patch of the harness with Velcro and oriented so the rounded bottom of the tube faced forward. The opposite end of the transmitter was flat.

FLIGHT TIMES

We recorded flight times of pigeons traveling from Lebec to the home loft when the birds carried no harness or transmitter, when they carried a 4-g harness only, when they wore a transmitter and harness weighing 2.5% of M_B, and when they carried a transmitter and harness weighing 5.0% of M_B. On three control flights all birds flew without a harness or transmitter. On one experimental flight, all birds carried 5.0% of M_B. On three additional flights, four of the birds flew with a harness only, while the others in the flock flew without a load. On four more flights, four of the birds carried 5.0% M_B packages, with the other birds being unencumbered.

Flight times of pigeons traveling from Fresno to the loft were also recorded. On the first (control) flight, all eight pigeons flew without encumbrances. Four of the eight birds flew without a load on the second flight; on the third flight those four carried a load and the other four flew without a load. Conditions of the fourth flight are described below.

CO_2 PRODUCTION

During two of the four flights from Fresno, CO_2 production was measured with the DLW method. From 1.0 to 1.5 hr before a flight each bird was weighed and 0.6 ml of isotopic water (containing 95 atom-percent ^{18}O and 0.4 mCi ^{3}H) was injected into the abdominal cavity along the midline, midway between the cloacal opening and the posterior edge of the keel.

Ten to 25 min before the flight a blood sample was obtained from each bird by puncturing the bracheal wing vein with a 22 gauge hypodermic needle and collecting in one or more heparinized glass capillary tubes the drop(s) of blood that pooled on the skin of the undersurface of the wing. The tubes were temporarily capped (with Crito-caps®) within 10 min and then were flame-sealed within 24 hr. Following the flight the birds were recaptured a few minutes after they entered the home loft and were weighed; then a final blood sample was obtained as described above. Pure water was microdistilled (Wood et al. 1975) from each blood sample. Water samples were assayed for tritium activity (Beckman LS 230 liquid scintillation counter) using toluene-Triton X-100-PPO scintillation cocktail. A separate portion of each distillate was assayed for ^{18}O content 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 counting system (Wood et al. 1975). Rates of CO_2 production were calculated from the isotope measurements with the equations of

TABLE 1. Flight times of homing pigeons flying 90 km from Lebec to Northridge, California; n = number of determinations.

	Flight times (min)		
	Without harness/transmitter (control)	With harness only	With harness + transmitter
Early period (April to June)	60 (n = 8)	68	75
		70	78
		69	75
		$\bar{x}$ = 69 (n = 12)	$\bar{x}$ = 76 (n = 16)
Late periods (July, moulting)	72		85
	75		87
	$\bar{x}$ = 73.5 (n = 10)		$\bar{x}$ = 86 (n = 9)

Lifson and McClintock (1966) as modified by Nagy (1975).

The DLW method measured the CO_2 produced between the times of the initial and final blood sample, which is greater than the amount produced during the flight alone. Ten to 25 min elapsed between the blood sampling and the release of a given bird, because birds were not released at Fresno until blood samples had been taken from all eight birds. Similarly, as much as 20 min elapsed between the end of the flight and the collection of all final blood samples, because the four control birds returned to the loft as a group. Carbon dioxide produced during the flight alone was computed, therefore, by subtracting from the DLW measure of CO_2 production, an estimate of the bird's CO_2 production between the initial blood sample and the bird's release, and between the bird's arrival at the loft and the final blood sample. The resting rate of CO_2 production of each pigeon was measured in an open circuit respirometer at 20°C in darkness and was multiplied by 1.7 to estimate the rate of CO_2 production before and after the flights from Fresno. This correction reduced CO_2 production totals by less than 2%.

The energy required for traveling from Fresno was calculated as a product of CO_2 production and the energy equivalent of CO_2 production. Biesel and Nachtigall (1987) reported that the RQ of homing pigeons flying in a wind tunnel decreased from about 1.0 to 0.7 during the first hour of flight and remained at 0.7 for the remainder of the flight. We assumed the same pattern of RQ change for our birds; therefore, we used 25.3 kJ/l CO_2 as the energy equivalent of CO_2 production for the first hour of flight and 28.2 kJ/l CO_2 for subsequent hours of flight or an average value of 27.5 kJ/l CO_2 over a flight of 4 hr 15 min.

RESULTS

FLIGHT TIMES

Seven flights from Lebec were made between 25 April and 27 June 1986 (the early period), and four more were made between 8 and 27 July (the late period). In the five of seven experimental flights from Lebec, where one-half of the birds flew with a load, all eight birds returned to the loft as a flock. Apparently pigeons in the flock which were not carrying a load remained with their siblings that were carrying a transmitter and/or a harness by flying at a slower than normal speed. In two Lebec flights, two birds carrying a load returned significantly later than the main flock. They had carried a load on a flight from Fresno a few days earlier and apparently had not yet recovered.

We believe that our pigeons followed I5 from Lebec until entering the San Fernando Valley and then turned westward on a direct route to the Northridge loft (a route distance of 90 km). On three occasions we saw our flock flying parallel to I5 during the return flight from Lebec. The distance by the most direct road from Lebec to the loft is 100 km.

During the early period one control flight took 60 min (Table 1). Three flights of birds carrying only a harness had an average duration of 69 min; two flights of birds carrying a transmitter weighing 2.5% of M_B took 75 and 78 min, and one flight, where all eight birds carried a transmitter weighing 5.0% of M_B, took 75 min.

In the late period two control flights averaged 73.5 min, and the average flight time in two flights of pigeons carrying a transmitter weighing 2.5% of M_B was 86 min. The slower flight times in the late period are a reflection of the loss of one to two flight feathers which occurred during molt in the late period; however, the difference between the control and experimental flight times is nearly the same in the early and late period.

The presence of a harness alone on four birds slowed the entire flock by 15%, and a harness plus a transmitter on four birds slowed the flock even more (25 to 28%). Flight times were affected to the same extent by transmitters weighing either 2.5 or 5.0% of the pigeon's body mass, which suggests that the birds flying with a load were slowed down primarily by the aerodynamic drag of the load rather than by the additional mass.

On the first flight from Fresno all eight control birds returned as a flock in 4 hr 16 min. In the second flight from Fresno the four pigeons without a load returned as a flock in 4 hr 17 min. Each of the other four birds, which carried a transmitter weighing 5% of their M_B, returned separately to the loft. The first and second pigeons arrived 9 hr 49 min and 10 hr 50 min after being released in Fresno. The last two birds returned the next day, about 26 hr after their release.

In the third flight from Fresno the birds that were controls in the first flight now carried a transmitter weighing 2.5% of their M_B; the other four were now controls. The controls returned to the loft as a flock in 4 hr 15 min. Two of the birds flying with a load returned together, 5 hr 35 min after release, and the other two returned separately, 10 hr 5 min and 10 hr 20 min after release.

During the first three flights from Fresno ground-level wind speeds, measured by the National Weather Service at Fresno and Bakersfield, averaged less than 15 kph. East and southeast winds averaged 13.3 (SD = 2.8) kph and 11.1 (3.3) kph at these two meteorological stations, respectively, during flight 1. During the second and third flights, winds were from the northwest, averaging 11.9 (4.3) kph and 6.8 (3.7) kph during flight 2 and 14.8 (2.8) kph and 10.7 (2.2) kph during flight 3. The mean flight path of our birds was toward the southeast.

On the fourth flight two of three control birds returned in 9 hr 20 min and 8 hr 40 min after release; the third appeared more than 24 hr after release. Two of four birds, which flew with only a harness, returned in 6 hr 15 min and 8 hr 15 min and the others returned the next day. The flight times of the controls on this flight were significantly different from those of the controls on the first three flights. The unsettled weather during the fourth flight is probably responsible for these inconsistent results. Skies were clear from Fresno to Bakersfield, then, a frontal system moving to the southeast over the mountains produced low clouds and strong winds along I5 up to Gorman, California. The clouds hid the mountain tops, but did not extend down to the highway. Skies were clear, again, from Gorman to the loft. The results of the fourth flight suggest that the control birds used a different flight path from Fresno to the loft. Homing pigeons will deviate from a direct route in order to avoid a storm front (E. Herren, pers. comm.).

The straight-line distance from Fresno to Northridge is 290 km. The distance by the most direct road (95% of it on I5) is 320 km. We do not know the actual route taken by our birds; we assume it was 320 km long.

TABLE 2. CO_2 production and energy metabolism of homing pigeons flying 320 km from Fresno to Northridge, California.

Pigeon body mass (g)	Without a harness and transmitter (control) Flying (4 hr 15 min) (l CO_2)	kJ/hr[1]	With a harness and transmitter Flying plus resting[2] (l CO_2)	Flying only (5 hr 35 min)[3] (l CO_2)
424	21.1	136.5	47.2	45.0
419	28.6	185.1	42.8	41.0
413	21.2	137.2	72.4	61.9
398	22.8	147.5	42.6	40.6
382	22.0	142.4	46.7	43.4
414	22.8	147.5	55.0	44.8
419	27.4	177.3	42.9	42.9
431	28.9	187.0	40.9	40.9
$\bar{x}$	24.4	157.6	48.8	45.1
SD	3.4	21.7	10.5	7.0
n	8	8	8	8

[1] Assuming 27.5 kJ/l CO_2.
[2] Corrected for rest periods in loft and in cage only.
[3] Corrected for nonflight CO_2 production during total period abroad.

CO_2 PRODUCTION

The control birds on flights 1, 2, and 3 from Fresno undoubtedly flew the 320 km nonstop (average ground speed was 74 kph); therefore, the energy expended while flying is accurately reflected by our estimate of CO_2 production between the time of release and return of pigeons to the loft in flights 2 and 3 (Table 2). Birds carrying a load returned to the loft significantly later than the controls; their flight behavior and path, however, was unknown. The 15-min difference in flight times between birds with and without a load on the 90-km flights suggested that control birds flying continuously from Fresno to the loft would arrive more than 50 min ahead of the birds with a load. Actually, the controls arrived 80 min ahead of the two fastest birds, which probably made the flight nonstop. The six birds that took from 5.5 to 23 hr longer than the controls to return home from Fresno probably stopped one or more times and rested; thus, part of the CO_2 produced between release and return occurred during rest. To obtain an estimate of CO_2 produced only while the birds were flying, we assumed that these birds flew for only 5 hr 35 min (the flight time of the two fastest birds), and subtracted 1.7 times resting CO_2 production for the remaining time. The average of total CO_2 production during flight alone was only 7.6% less than the average of values for total CO_2 production (Table 2).

Either method of computing CO_2 production indicates that the birds with a load were using 85 to 100% more energy to travel from Fresno to the loft. The hourly rate of metabolism of these birds was about 41 to 52% higher than controls. Thus birds were working harder and longer while carrying transmitters.

DISCUSSION

The results clearly show that the loads of 2.5 to 5.0% of M_B worn by our pigeons significantly decreased their speed and increased the intensity of their metabolism while flying. Why hasn't such a marked effect been observed in the many avian studies that have used transmitters weighing $\leq 5\%$ of M_B? Our pigeons were bred and trained to be high performance fliers; the average ground speed of our controls flying from Fresno was 74 kph (46 mph). The actual air speed may have been higher in flight 1 due to a small headwind, and lower in flights 2 and 3 due to a small tailwind. The minimum-power air speed for a pigeon, computed by Pennycuick (1968) from aerodynamic equations, is 31 kph (19 mph) and that measured in wind tunnel flights (Rothe et al. 1987) is 40 kph (24 mph). The minimum-power air speed occurs at the bottom of the presumed U-shaped relationship between energy expenditure (flight metabolism) and air speed; metabolism increases as air speeds rise above or drop below the minimum-power air speed. It is, therefore, not surprising that a transmitter weighing $\leq 5\%$ of the M_B of a high performance pigeon significantly increases the bird's flight metabolism because our birds were already operating on the steep part of the U-shaped metabolism-flight speed curve. Rothe et al. (1987) measured metabolism of pigeons at air speeds from 29.5 to 52.2 kph. An extrapolation of their data to 74 kph predicts a metabolic rate of 247.4 kJ/hr, 57% higher than that of our control birds and 22% less than that of our pigeons carrying a load. This disparity can be interpreted in different ways, e.g., (1) the actual air speed of our pigeons could have been less than 74 kph (either due to a small tailwind or a flight path of less than 320 km); or (2) the energy cost of flying in a wind tunnel may be greater than flying outdoors; and (3) the relationship of metabolism to air speed between 29.5 and 52.2 kph may be significantly different at 74 kph. The maximum-range speed computed by Pennycuick (1968) is 58 kph (35 mph). The effect of the high flight speed of our pigeons on their energy metabolism is clear when our results are compared to those of LeFebvre (1964). The average flight speed of his pigeons on a 480-km flight was 58 kph (16 kph slower than our pigeons) and their rate of energy metabolism was 92 kJ/hr (41.6% lower than that of our pigeons, 157.6 kJ/hr). He reported a ratio of 8.0 for rate of flight metabolism to rate of resting metabolism (he measured a resting metabolism that was 18.1% higher than our value). This ratio for our control birds was 17.5 ($n = 8$); it was 26.7 ± 3.0 ($n = 4$) and 32.4 ± 8.8 ($n = 4$) for pigeons carrying 2.5% and 5% of M_B, respectively. Another study reported a rate of metabolism of free flying pigeons (113 kJ/hr) 28.3% lower than our controls (Polus 1985 cited in Rothe et al. 1987).

It is likely that the majority of the flights of avian species in the wild are near or at the most efficient flight speeds (minimum-power and maximum-range speed); therefore, the effects of a transmitter on their flight speed, metabolism, and rates of food intake should be relatively smaller than in racing pigeons.

Probable differences in flight paths between the two studies may account for a small part of the difference in flight metabolism between our pigeons and those of LeFebvre. The 480-km flight path taken by LeFebvre's pigeons from Allerton, Iowa to St. Paul, Minnesota was probably at a significantly lower elevation (and had less ascent and descent) than the flight path of our control pigeons. The flight from the San Joaquin Valley (Fresno; 330 m elevation) to the San Fernando Valley (loft; 795 m elevation) probably followed I5 through the mountain range separating the valleys; the highest elevation on I5 in this range at Tejon Pass is 1,263 m (4,144 ft). The 90-km release location in this study was on I5 within a few kilometers of Tejon Pass; therefore, our birds were very familiar with the I5 "flyway."

The effect of the aerodynamic drag and weight of an object attached to a bird that is flying in a wind tunnel has been estimated in a few studies. Tucker (1972) estimated that flight metabolism of gulls was increased by 10% as a result of the drag of the hood (mask) and tube worn by the bird, and an additional increase of 2–3% was necessary to overcome the added weight. Rothe et al. (1987) reported that the metabolism of their pigeons flying in a wind tunnel (and wearing a hood and tube) may be 15 to 30% higher than it would be in comparable free-ranging flights (LeFebvre 1964, Polus 1985). A transmitter of 2.5% or 5.0% of M_B had the same slowing effect on our pigeons on the 90-km flights, which suggests that the pigeons were slowed down more by the drag than by the additional mass. The effect of the additional mass is clearer for the 320-km flights; mean flight metabolism was 53% and 85% higher when carrying transmitters weighing 2.5 and 5.0% of M_B, respectively.

WATER LOSS AND FLIGHT TIME

Biesel and Nachtigall (1987) measured the rate of evaporative water loss of pigeons flying in a wind tunnel at different air temperatures (T_a) and flight speeds. They argue that pigeons flying at T_as > 10°C will eventually reach a critical level of dehydration (they suggest 5% of body water) that forces them to land and seek water. The results from our control birds support their finding that water loss increases with T_a, but do not support their suggestion that a 5% loss of M_B by dehydration would force a pigeon to interrupt the flight.

The almost identical flight times for controls in flights 1 through 3 and the rate of travel (74 kph) clearly indicate that they flew nonstop from Fresno and, therefore, were not forced to stop for water.

For flights 2 and 3, air temperatures were measured at 5 m above ground level along I5 at Selma, Tulare and Bakersfield, California during the return trip to the loft (following the release at Fresno). The average T_as for these three locations during flights 2 and 3 were 24.6°C and 18.6°C respectively. The average percent decrease (±SE) in M_B (measured just before the flight) of controls during flights 2 and 3 was 7.9% (±2.3) and 3.3% (±1.0), respectively. All four birds carrying a load on flight 2 probably stopped at least once during the flight; their water loss was 10.1% (±0.9) of M_B. This reflects water loss since catabolism of 1 g of fat produces 1.06 g of metabolic water.

LeFebvre (1964) reported a water loss of 2.7% (±0.8) of M_B (10.5 ± 3.0 g per 384 g of M_B; n = 8) for a 8.6-hr pigeon flight. Air temperature was not reported for this flight on 31 July 1961. Thunderstorms occurred late in the day of the flight and only eight of 22 returned by evening of that day (four of which apparently flew nonstop).

In the final analysis our well-trained control pigeons, therefore, did not interrupt their flight after losing 5% of their body water; approximately 8% had been lost at the end of the flight. The experimental pigeons were capable of returning to the loft even though water loss was more than 10% of M_B. The critical level of water loss (dehydration) that would force a well-trained pigeon to stop flying and seek a drink is, clearly, more than 8% of M_B.

CONCLUSIONS

Flight performance of homing pigeons is negatively affected by an encumbering harness or transmitter (≤5% of M_B). On 90-km flights a harness alone increased flight duration by 15%; a harness/transmitter package makes the problem worse (25 to 28% longer flight times). A transmitter of 2.5% or 5.0% of M_B had the same effect, which suggests that the pigeons were slowed down more by the drag than by the additional mass.

Flight metabolism of homing pigeons increases significantly when wearing a harness/transmitter package. On 320-km flights CO_2 production was 41 to 52% higher per hour, and pigeons produced 85 to 100% more CO_2 covering the 320-km distance.

High performance homing pigeons, therefore, work longer and harder during a long distance flight when encumbered by a transmitter (≤5% M_B). The effects of a transmitter (≤5% M_B) on flight performance and metabolism of avian species that normally fly at an efficient flight speed (e.g., the maximum-range speed) will undoubtedly be much less dramatic.

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