

THE ENERGETIC COST OF SHORT FLIGHTS IN BIRDS

ROBERT L. NUDDS* AND DAVID M. BRYANT

Department of Biological Sciences, University of Stirling, Stirling FK9 4LA, UK

*Present address: Department of Zoology, South Parks Road, University of Oxford, Oxford OX1 3PS, UK
(e-mail: robert.nudds@zoology.oxford.ac.uk)

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Summary

Many small birds perform short flights, for which take-offs, ascents and descents form a large component of the total flight time and which are characterised by low airspeeds. Using the doubly-labelled water technique, zebra finches *Taeniopygia guttata* engaging in repeated short flights were found to expend 13.65 kJ more than 'non-flying' controls, which equated to a flight expenditure of 27.8 times their basal metabolic rate. This is over three times the predicted flight expenditure derived from existing

aerodynamic models. These data were used to determine a coefficient (0.11) for converting the mechanical power derived from aerodynamic models into metabolic power. An equation is presented, based on body mass, which can be used to predict the costs of short flights in ecological and behavioural studies of birds.

Key words: flight, energy expenditure, doubly-labelled water, zebra finch, *Taeniopygia guttata*, bird.

Introduction

Flapping flight usually occupies only a small proportion of a bird's daily cycle. Nevertheless, its high energetic costs per unit time and central influence upon the biology of birds means that an understanding of the power requirements for flight is essential if the ecology, behaviour and life histories of birds are to be properly understood. The difficulties associated with measurements of flight energetic costs amongst free-living species have encouraged the development of models that can predict flight costs. Current models fall into three categories, based on aerodynamic theory (Greenewalt, 1975; Pennycuik, 1989; Rayner, 1979a,b; Tucker, 1973), on allometric equations using body mass (Berger and Hart, 1974; Kendeigh et al., 1977) and on equations using body mass and morphometrics (Masman and Klaassen, 1987; Rayner, 1995). All these models, however, provide estimates that are applicable only to horizontal steady-state flapping flight. Similarly, empirical measurements of flight energetic costs (see Table 1) have tended to concentrate on aerial foraging species (Hails, 1979), which are highly adapted to spending long periods on the wing, or on species performing sustained flights (i.e. Gessaman and Nagy, 1988; Masman and Klaassen, 1987).

Many birds, but particularly small passerines when foraging or feeding young, perform short flights, both in distance and time, for which take-offs, landings, ascents, descents and manoeuvring at speeds below minimum power speed (Pennycuik, 1989) make up a large part of each flight. One previous study using the doubly-labelled water (DLW) and time/energy budget (TEB) techniques has suggested that the energetic cost of these flights may be considerably higher than estimates derived from existing models (Tatner and Bryant,

1986). On the whole, however, this kind of flight, because of its untractability from a theoretical perspective, has been overlooked and its energetic costs remain uncertain. The present study uses the DLW technique with a novel controlled approach to quantify accurately the energetic cost of this type of flight in zebra finches *Taeniopygia guttata* (Clements, 1991), henceforth termed 'short flight' and defined as 'a flight beginning with a true take-off, at a positive angle to the horizontal and performed at speeds below the theoretical minimum power speed'. Here, the theoretical minimum power speed pertains to that predicted by aerodynamic theory (Pennycuik, 1989). The hypothesis tested was that the energetic cost of short flights would exceed predictions derived from existing models and surpass measurements from existing empirical studies involving sustained flight.

Materials and methods

Flight aviary and training procedure

Fourteen male zebra finches were trained inside a plastic-walled aviary (Fig. 1), which only allowed perching at single automated perches positioned at either end. The finches were trained to fly back and forth across the aviary by the sequential withdrawal (drawn tight against the wall – unavailable for perching) and presentation (0.18 m from the wall – available for perching) of the perches. On alternate days, finches were removed from their housing and placed in the aviary at 09:00 h. Initial training involved the finches being able to settle upon an extensive system of branches positioned around the mechanised perches within the aviary. The branches were

Table 1. *Metabolic cost P_{met} (including basal metabolic rate) of flight for various species*

Species	Body mass (kg)	P_{met} (W)	Method	Flight mode	Source
<i>Taeniopygia guttata</i>	0.013	6.60	DLW	S	This study
<i>Erithacus rubecula</i>	0.019	7.11	DLW	S	Tatner and Bryant (1986)
<i>Zonotrichia albicollis</i>	0.028	11.52	RPT	S	Teal (1969)
<i>Ramphocelus flammigerus</i>	0.045	22.09	RPT	S	Teal (1969)
<i>Icterus galbula</i>	0.038	16.70	RPT	S	Teal (1969)
<i>Scardafella squammata</i>	0.051	22.58	RPT	S	Teal (1969)
<i>Cyanocitta cristata</i>	0.084	33.98	RPT	S	Teal (1969)
<i>Turdus iliacus</i>	0.069	27.07	RPT	S	Teal (1969)
<i>Euplectes franciscanus</i>	0.019	7.0	RPT	S	Teal (1969)
<i>Spizella pusilla</i>	0.022	7.68	RPT	S	Teal (1969)
<i>Heterophasia capistrata</i>	0.038	11.96	RPT	S	Teal (1969)
<i>Lamprospree superbus</i>	0.054	15.18	RPT	S	Teal (1969)
<i>Passer domesticus</i>	0.029	10.30	RPT	S	Teal (1969)
<i>Cyanocitta cristata</i>	0.094	27.59	RPT	S	Teal (1969)
<i>Colaptes auratus</i>	0.147	41.89	RPT	S	Teal (1969)
<i>Parus montanus</i>	0.012	3.19	DLW	I	Carlson and Moreno (1992)
<i>Columba livia</i>	0.384	25.9	DLW	F	LeFebvre (1964)
<i>Falco tinnunculus</i>	0.213	14.6	DLW	F	Masman and Klaassen (1987)
<i>Columba livia</i>	0.412	43.7	DLW	F	Gessaman and Nagy (1988)
<i>Oenanthe oenanthe</i>	0.031	4.5	ML	F	Nisbet (1963)
<i>Melospiza melodia</i>	0.022	1.55	ML	F	Nisbet (1963)
<i>Erithacus rubecula</i>	0.016	1.57	ML	F	Nisbet (1963)
<i>Regulus regulus</i>	0.003	0.29	ML	F	Nisbet (1963)
<i>Dendroica striata</i>	0.019	1.18	ML	F	Nisbet et al. (1963)
<i>Columba livia</i>	0.254	33.1	ML	F	Pearson (1964)
<i>Fringilla montifringilla</i>	0.023	5.06	ML	F	Dolnik and Blyumenthal (1967)
<i>Fringilla coelebs</i>	0.022	5.33	ML	F	Dolnik and Blyumenthal (1967)
<i>Spinus spinus</i>	0.013	2.93	ML	F	Dolnik and Blyumenthal (1967)
<i>Pluvialis dominica</i>	0.14	8.96	ML	F	Johnstone and McFarlane (1967)
<i>Vermivora peregrina</i>	0.011	2.21	ML	F	Raveling and LeFebvre (1967)
<i>Catharus fuscescens</i>	0.032	4.53	ML	F	Hussell (1969)
<i>Fringilla montifringilla</i>	0.023	4.61	ML	F	Dolnik and Gavrilov (1973)
<i>Fringilla coelebs</i>	0.022	4.25	ML	F	Dolnik and Gavrilov (1973)
<i>Anas platyrhynchos</i>	1.0	44.2	ML	F	Dolnik and Gavrilov (1973)

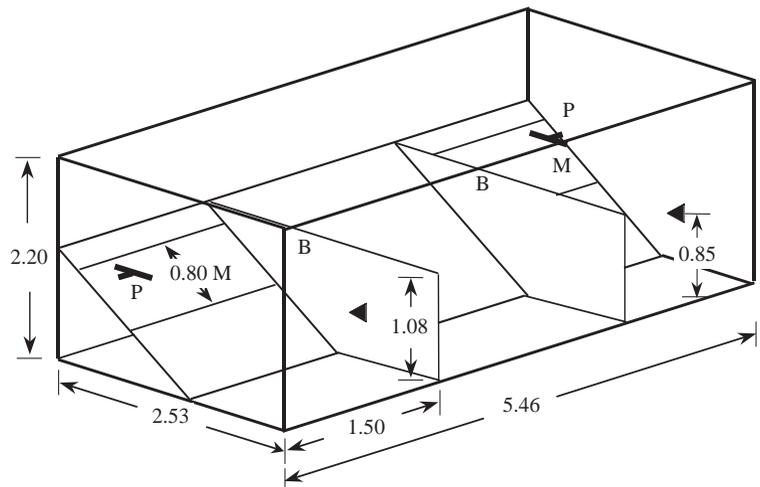


Fig. 1. Diagram of the flight aviary. All dimensions are in metres. The perches (P) were positioned 1.08 m above the ground and 0.7 m from the back wall. The mirrors (M) were angled at 45° and were 1.5 m x 0.8 m in size. The baffles (B) and aviary walls were constructed from black polythene. Cameras (black triangles) were positioned so as to cover the take-off phases of the short flights.

gradually reduced in size until the finches were using the perches alone (after 2 training days). Finches were then flushed from one end of the room to the other. Once the finches were

finding them easily, the perches were switched on. Somebody remained in the aviary during training days (approximately 3 weeks) until the finches had learned to fly from the withdrawn

Table 1. Continued

Species	Body mass (kg)	P_{met} (W)	Method	Flight mode	Source
<i>Larus marinus</i>	0.8	36.3	ML	F	Dolnik and Gavrillov (1973)
<i>Pyrrhula pyrrhula</i>	0.030	5.61	ML	F	Dolnik and Gavrillov (1973)
<i>Spinus spinus</i>	0.013	2.98	ML	F	Dolnik and Gavrillov (1973)
<i>Progne subis</i>	0.051	3.88	DLW	S-G	Utter and LeFebvre (1970)
<i>Delichon urbica</i>	0.018	1.01	DLW	S-G	Hails (1979)
<i>Hirundo rustica</i>	0.019	1.3	DLW	S-G	Hails (1979)
<i>Riparia riparia</i>	0.014	2.05	DLW	S-G	Turner (1982)
<i>Hirundo rustica</i>	0.019	1.62	DLW	S-G	Turner (1982)
<i>Sterna fuscata</i>	0.188	4.7	DLW	S-G	Flint and Nagy (1984)
<i>Delichon urbica</i>	0.018	1.26	DLW	S-G	Westerterp and Bryant (1984)
<i>Riparia riparia</i>	0.013	1.6	DLW	S-G	Westerterp and Bryant (1984)
<i>Sula sula</i>	1.014	19.0	DLW	S-G	Ballance (1995)
<i>Delichon urbica</i>	0.019	0.95	ML	S-G	Kespaik (1968)
<i>Delichon urbica</i>	0.020	1.08	ML	S-G	Lyuleeva (1970)
<i>Apus apus</i>	0.040	1.84	ML	S-G	Lyuleeva (1970)
<i>Hirundo rustica</i>	0.018	1.34	ML	S-G	Lyuleeva (1970)
<i>Melopsittacus undulatus</i>	0.037	4.12	RWT	W-T	Tucker (1966)
<i>Anas rubripes</i>	1.026	78	RWT	W-T	Berger et al. (1970)
<i>Larus delawarensis</i>	0.427	21.6	RWT	W-T	Berger et al. (1970)
<i>Hesperiphona vespertina</i>	0.059	11.1	RWT	W-T	Berger et al. (1970)
<i>Larus atricilla</i>	0.34	25.7	RWT	W-T	Tucker (1972)
<i>Corvus ossifragus</i>	0.275	22.5	RWT	W-T	Bernstein et al. (1973)
<i>Columba livia</i>	0.442	30.5	RWT	W-T	Butler et al. (1977)
<i>Sturnus vulgaris</i>	0.073	8.9	RWT	W-T	Torre-Bueno and LaRochelle (1978)
<i>Falco sparverius</i>	0.12	13.8	RWT	W-T	Gessaman (1980)
<i>Corvus cryptoleucus</i>	0.48	37.5	RWT	W-T	Hudson and Bernstein (1983)
<i>Columba livia</i>	0.33	34.3	RWT	W-T	Rothe et al. (1987)

Methods are the doubly-labelled water technique (DLW), mass loss (ML), respirometry in a wind-tunnel (RWT) and respirometry within a plastic tube (RPT).

Flight mode: short (S), see definition in introduction; free (F), free flapping flight carried out over greater distances. Steady-state flapping flight dominates, although the flights may contain a very small take-off (short) flight component. Semi-gliding (S-G), mode of flight employed by aerial foraging species (see Hails, 1979); wind-tunnel (W-T), steady-state flapping flight performed within a wind-tunnel, where flight is unidirectional and flight conditions remain constant; intermediate (I), short flight, but reducing metabolic costs by using a 'drop-off' to become airborne.

to the presented perch without the need for flushing. During this period, two baffles were introduced into the aviary (Fig. 1). Their function was to prevent the finches from avoiding training by performing 'drop-offs' (dropping from the perch and using gravity to gain airspeed before swooping and regaining altitude) when tired. In the absence of baffles and before tiring, the finches usually performed a take-off at an angle above the horizontal. Training continued until the finches were capable of performing the protocol outlined below, without human presence. The perches took 12 s to move from the presented to the withdrawn position and *vice versa*. The slowness of perch movements and their sliding action promoted a natural and 'un-startled' take-off. The flights performed therefore avoided the stress that might be associated with a startle-induced take-off, such as that used in studies of predator avoidance. On completion of a training day, the finches were returned to their housing (0.89 m × 0.435 m × 0.455 m) and randomly assigned to one of two cages (seven per cage), where they remained until the next training day.

During the training period, all finches spent time inside open-fronted boxes (0.155 m × 0.230 m × 0.210 m). Inside each box was a perch 0.08 m from the back of the box and 0.07 m from the floor (Fig. 2). The boxes were introduced into their housing cages and provided the only perches above the cage floor. Once the finches had become used to being inside the boxes, wire-mesh fronts were added. The finches spent time completely enclosed within the perching boxes, with no access to their housing cages. Post-training, the finches, when placed within the boxes, quickly settled upon the perches, where they appeared to be at ease. Throughout the training and experimental periods, the ambient temperature was maintained at 20–22 °C.

An initial effect of the training was a reduction in finch body mass. Body masses were monitored throughout the training period and used as a guide to determine whether the finches could sustain the energy demands of the training and final experimental protocol. During the latter stages of training, their body masses had stabilised, indicating that the finches were not suffering from energetic stress (Fig. 3).

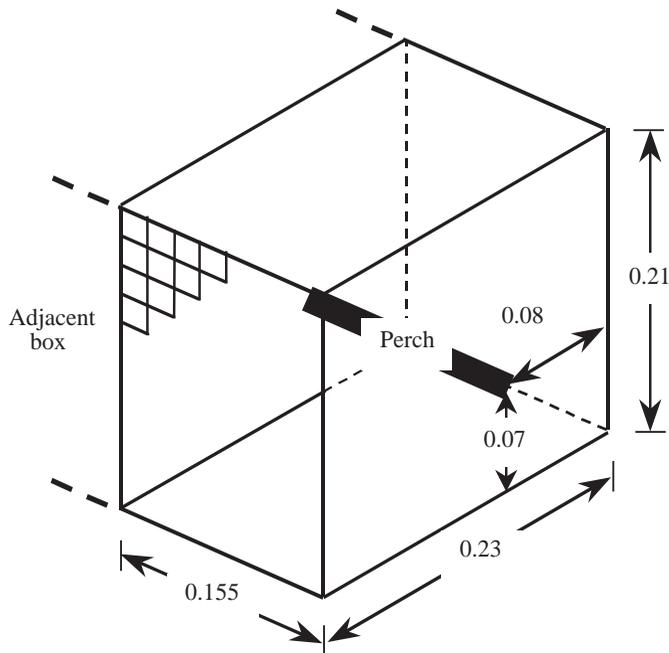


Fig. 2. Diagram of a perching box. Only one finch was placed in each box. The top, bottom and back of the box were constructed from cardboard. The front was constructed of wire mesh, and the sides were of transparent polythene. This allowed visual contact between finches in adjacent boxes, reducing isolation-induced stress, but prevented any energetically expensive physical interactions. All the dimensions are displayed in metres.

Doubly-labelled water

The doubly-labelled water technique was used to measure energy expenditure (Lifson and McClintock, 1966; Tatner and Bryant, 1988). The finches received intraperitoneal injections of DLW ($10 \mu\text{l g}^{-1}$ body mass). The injectate was prepared by adding 0.374 g of 99.9 atom % excess (APE) deuterium (D) to 5 ml of 20.0 APE H_2^{18}O . After labelling, the finches were placed inside holding bags for a 1 h equilibration period (Williams, 1985; Williams and Nagy, 1984). Initial blood samples were then taken from femoral veins distal to the tarsal joint. After the experimental period, final samples were taken from either the femoral or brachial veins (over the humerus-ulna joint). Blood samples ($5 \mu\text{l}$) were immediately flame-sealed within Vitrex capillaries (Modulohm, Denmark), a maximum of seven being taken per finch. Injection and bleeding sites were cleaned with ethanol before and after injection and venipunctures. Background isotope levels were determined from blood samples taken from two finches (out of the 14) that did not take part in the experiments, but were nevertheless subject to the same training regime and water supply. Both background blood samples, one during each experiment, were taken after the initial samples of experimental finches (D, 142.85 p.p.m.; ^{18}O , 1993.85 p.p.m.). Isotope (label) concentrations were determined following the methods of Tatner and Bryant (1988). A respiratory quotient (RQ) of 0.75 was used in the calculations of energy expenditure (R. L. Nudds and D. M. Bryant, unpublished data).

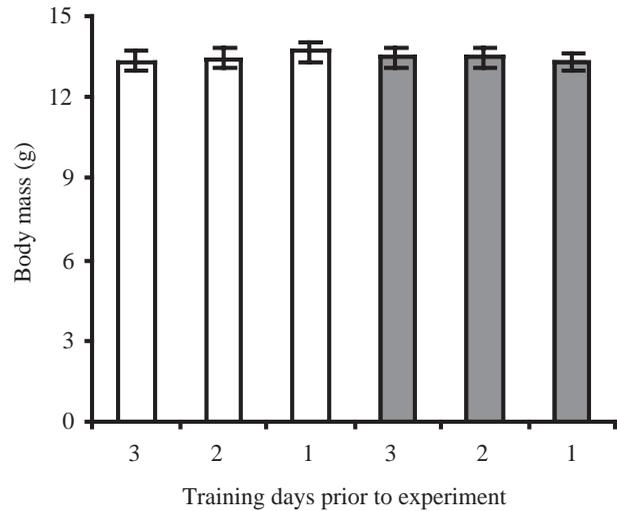


Fig. 3. The mean body mass (g) of finches on the three training days preceding each experiment part: part I (open columns) and part II (filled columns). Only the body masses of the nine finches used in the final analyses are included. There were no significant (test power for both factors <0.05) differences between training days or experimental parts (two-way ANOVA: part, $F_{1,50}=0.06$, $P=0.808$; day, $F_{2,50}=0.04$, $P=0.962$). Values are means \pm S.E.M.

The time between initial and final samples in this experiment was 28 h. The ^{18}O turnover (the difference between the specific activities of the initial and final samples) during this period was 58%, which is greater than the 50% minimum suggested by Nagy (1980) and remains sufficiently above background abundance to achieve accuracy (Tatner and Bryant, 1988). In addition, the chosen time interval provided the largest proportion of flight activity and the greatest control of non-flight activities.

Experimental protocol

On the morning of the experiment, six of the 14 trained finches were chosen at random by ballot, weighed and labelled with DLW (see above). Each finch was then assigned to one of two treatments: flying in the aviary or perching inside a perching box. Each successive finch was placed in the opposite treatment until there were three in each treatment (Table 2). Each of the three perching-treatment finches had a box to itself (Fig. 2). Transparent walls allowed the finches to see each other, but did not permit physical contact. The perching boxes were situated in the same room as the flight aviary and were shielded, preventing human disturbance. During the flying/perching periods, these finches remained upon the perches. Flying finches were placed in the flight aviary where the automated perches were set to alternate at 1 min intervals. The finches experienced three flying/perching periods interspersed with a 12 h night phase (lights out) and feeding periods (Table 2). All activities other than during the flying/perching periods were kept identical (Table 3). Hence, any difference in the total energy expenditure between the two groups, measured using the DLW technique, could be

Table 2. *Experimental protocol*

Period beginning (h)	Day 1	Day 2
07:00		Lights on and food and water introduced to finch cage for feeding
08:00	Six finches injected with DLW	
09:00	Initial samples taken and finches placed into either the flight aviary ($N=3$), where they performed flights at 1 min intervals, or the perching boxes ($N=3$), where they settled upon perches	Finches placed into the flight aviary ($N=3$), where they performed flights at 1 min intervals, or the perching boxes ($N=3$), where they settled upon perches*
13:00	All six finches captured and placed together in a finch cage for feeding	Finches removed from flight aviary/perching box and final samples taken in same sequence as initial sampling (First finch at 13:00h sixth finch at approximately 14:10h)
14:00	Finches placed into flight aviary ($N=3$), performing flights, or perching boxes ($N=3$)	
18:00	All six finches captured and placed together in a finch cage for feeding	
19:00	Lights out. All six finches spend a 12h night period together in a finch cage minus food and water	

*During this period the second group of six finches began the same protocol as the first six finches. Hence, at the beginning of the period, there were three finches in each treatment, but by the end there were six in each treatment. At the end of this period and while the first six finches were undergoing final sampling, the second group were feeding. After feeding, they continued the remainder of the protocol taken by the first group (three per treatment).

DLW, doubly-labelled water.

attributed to flight alone. Following the completion of the third flying/perching period, finches were captured (starting at 13:00h), weighed and had final blood samples taken in the same sequence as they had been initially sampled.

On the second morning, a further six finches, chosen at random from the remaining eight finches, began the same protocol. This meant that they overlapped with the first six finches during one flying/perching period (Table 2). This overlap was a necessary consequence of six finches being the maximum that could be handled under the experimental protocol. At the end of the experiment (part I), the finches were

given a 1 week rest period before re-entering the training regime. The experiment was repeated 1 month after the original experiment (part II), by which time body masses had again stabilised (Fig. 3). This time, however, the finches were placed into the opposite treatments: experimental finches were placed in the perching (control) regime and perching finches experienced the flying (experimental) regime. Therefore, each finch served as its own control.

Video recording

Two video cameras (Sony VHS running at 25 Hz) were positioned outside the aviary so that the take-off phases of the flights were covered (see Fig. 1). Video recordings were made twice during each of the three flight periods (at 10:00 and 12:00 h, at 15:00 and 17:00 h, and at 10:00 and 12:00 h). During each observation period, the finches were filmed flying once in each direction. The cameras were synchronised so that the duration of single flights could be calculated from the video clips. To permit accurate measurement of flight components, mirrors were placed along the opposite side of the aviary (opposite the video cameras) so that they were perpendicular to the camera lenses, but angled up at 45° to the horizontal. Each video frame therefore had a side-view image of the finch in flight plus a mirror image of the view from beneath the finch from the same flight. From this, three-dimensional analyses of the flight components, take-off angle, take-off duration (from take-off to the point at which altitude gain ceases) and take-off acceleration, were obtained. Video recordings were edited in Adobe Premier version 4.2.1 (Adobe Systems Incorporated),

Table 3. *Time budgets for the two treatments*

Activity	Flying (min)	Perching (min)
Inside perching box/ flight aviary (flight included in above)	716.5±2.9 (35.7±5.0)	719.9±2.7 (nil)
Night	720.0±0.0	720.0±0
Feeding	231.8±0.4	231.6±0.4
Handling	18.9±1.5	20.4±2.5
Total time budget	1687.2±3.1	1691.9±3.7

The activity times outside the perching/flying periods were almost identical for the two groups.

Values are means ± S.E.M. ($N=9$).

The slight difference in the total time budget (time between initial and final blood samples) of the two treatments was due to small variations in the time taken to obtain blood samples.

and the resulting clips were transferred into NIH image version 1.60 (US National Institutes of Health, available on the Internet at <http://rsb.info.nih.gov/nih-image/>) for frame-by-frame positional analyses.

The flight velocity at the ninth frame after take-off was calculated from the distance travelled between the eighth and ninth frames. This value was then divided by 9/25 to give a time-averaged acceleration value. The simultaneous take-offs by the finches meant that individual birds were initially obscured. By the eighth frame, however, finches were further apart and, consequently, could be readily identified and their positions accurately determined. A comparative analysis indicated that, because of the relatively slow camera speed, the video data were not suitable for deriving instantaneous measurements of acceleration by the conventional application of a numerical differentiation algorithm (see Harper and Blake, 1989; Rayner and Aldridge, 1985; Walker, 1998).

Energy expenditure during feeding periods

All six finches were placed within one housing cage and filmed (Sony VHS) during three 5 min periods per hour of feeding (at 0–5 min, 25–30 min and 50–55 min). Food and water were given *ad libitum* in four large dishes to reduce exclusion *via* competitive ability. Feeding rate was then determined later by counting the number of pecks performed by the finches.

Impromptu flights

The design of the experiment was such that finches should have flown for similar amounts of time (i.e. once each time the perches alternated). In practice, however, some finches performed impromptu flights. These consisted of flying from a perch (before it retracted) to the other end of the aviary, turning, making the return journey and alighting back on the original perch. The number of impromptu flights made by each finch ($29.1 \pm 5.1\%$ of total flights performed, mean \pm S.E.M.) was recorded throughout the experiment and their duration determined by stopwatch.

Data analyses

All statistical tests were parametric and performed using Minitab version 11.2. Calculation of statistical powers was in accordance with Cohen (1988). In the time/energy budget (TEB) approach to flight energetic cost determination, wing disk loading (Q_d , see Table 6) is the variable used to correct for mechanical size differences between finches: Q_d is more applicable than wing loading when looking at slow flapping flight (Pennycuik, 1975). To control for the mean effect of body size and to assist interspecific comparisons, flight energy expenditure was expressed in multiples of basal metabolic rate (BMR). Gavrilov's (1997) empirically determined BMR for an 11.8 g zebra finch is 19.7 kJ day^{-1} . This 11.8 g, however, is below the body masses of the finches in the present study. Hence, individual finch BMR was calculated using the night-time resting phase equation for passerines of Aschoff and Pohl (1970), which adjusts for mass and yields a closely comparable

value of 19.1 kJ day^{-1} for an 11.8 g bird. Unless stated otherwise, means \pm S.E.M. are given.

The energy expenditure of perching finches was reduced according to the time spent in flight by flying-group finches (Table 3). Whilst 'flying' finches were in flight, 'perching' finches were expending energy *via* BMR + perching costs. To act as true controls, perching finches are required to have activities identical to those of flying finches throughout the experiment and, during the activity of interest, in this case flight, to be expending energy at a basal rate only. Consequently, a reduction of the perching-group finches energy expenditure equal to 35.72 min (the total time that flying finches were in flight) of perching costs was required. This was calculated as follows: day-time energy expenditure ($E_{\text{day-time}}$; kJ) was calculated from:

$$E_{\text{day-time}} = (E_{\text{total}} - \text{BMR}) - (E_{\text{night}} - \text{BMR}), \quad (1)$$

where E_{total} is the mean total energy expenditure of perching finches as measured by DLW (includes BMR), BMR is calculated using the passerine night-phase equation of Aschoff and Pohl (1970) and E_{night} (kJ) is the overnight energy expenditure, including BMR, derived from the equation:

$$E_{\text{night}} = 1.24M_b^{1.1} \quad (2)$$

(R. L. Nudds and D. M. Bryant unpublished data), where M_b is body mass (g). $E_{\text{day-time}}$, which is net of BMR, was then split between the daylight activities of perching and feeding. Feeding was estimated to be twice as energetically costly as perching (see Bryant et al., 1985). The overall effect of the adjustment was to reduce the mean energy expenditure of the control birds and, hence, to increase that attributable to flight by 0.49 kJ (3.7%). It should be noted that three finches were excluded from the analyses. One became (temporarily) ill between experiments and hence did not take part in the flying treatment. One finch did not provide an analysable initial blood sample and a third was excluded as its failure to settle in the perching box violated the conditions necessary to act as a control finch (see below for effect on Results).

Results

Energy expenditure, determined by DLW, was significantly different for flying and perching finches. Flying finches expended 13.65 kJ (27%) more energy than perching finches over the duration of the trial (means 64.72 ± 3.02 and 51.07 ± 1.69 kJ, respectively; one-tailed paired *t*-test, $t=5.35$, $N=9$, $P<0.001$). Attributing the extra energy expenditure to the 35.72 min that 'flying' finches spent in flight means that the energetic cost during short flights was 6.37 W (27.8 ± 5.3 BMR). The value in multiples of BMR is the average of the individual finch means and therefore differs from the result obtained if the BMR value appropriate to a 13.05 g finch was used. The gross cost of flight (6.60 W, 28.8 BMR) can be obtained by adding the BMR to the measured net cost (6.37 W). Inclusion of the finch that was excluded on the *a priori* rule of not settling when in the control treatment (both its flying and perching

measurements), increased the net flight energy expenditure to $30.1 \pm 5.24 \text{BMR}$.

The validity of the flight energetic cost determined by this study was dependent upon the perching finches representing true controls. Although the time budgets of both treatments were the same (Table 3), there remained the possibility that differential energy expenditure could occur during either the feeding periods or overnight period. There was, however, no apparent difference in feeding rate (pecks h^{-1} of the feeding period) between flying and perching finches [two-tailed paired t -test on \log_{10} -transformed data, $t = -0.73$, $N = 9$, $P = 0.48$, $\text{power} < 0.10$; back-transformed means $571.48 \text{ pecks h}^{-1}$ ($+197.47$, $-95.16 \text{ pecks h}^{-1}$) and $518.8 \text{ pecks h}^{-1}$ ($+118.28$, $-84.69 \text{ pecks h}^{-1}$), respectively]. Similarly, flying and perching treatments did not produce a detectable difference in overnight energy expenditure (means 23.12 ± 1.19 and $22.71 \pm 1.19 \text{ kJ}$, respectively; R. L. Nudds and D. M. Bryant, unpublished data).

Individual variation in time spent flying meant that energy expenditure could be plotted against the proportion of time spent in flight (T_p). Hence, a TEB approach was also used to calculate the metabolic cost of flight. This analysis used the flying-group data alone. T_p , Q_d and the three take-off variables (take-off angle, take-off duration and take-off acceleration) were included in the original statistical model (GLM). The data used were the individual finch means (averaged over all video recordings) for each variable. Neither take-off angle nor take-off duration significantly influenced flying-group energy expenditure (expressed in multiples of BMR), and they were consequently removed from the final model (Table 4). There were insufficient degrees of freedom to incorporate interaction terms. Consequently, relationships between individual flight variables, T_p and Q_d were investigated separately. The linear associations (Pearson product moment correlation) between the individual variables used in the model (Table 4) were all non-significant (Table 5). The body mass and wing dimensions of the finches used to calculate Q_d are given in Table 6.

Calculating flight energy expenditure from the slope of the multiple regression (Table 4) gave 26.9BMR (sum of T_p + acceleration + Q_d coefficients). This estimate is net of resting

Table 4. Results of a statistical model (GLM) using a time/energy budget approach to calculate the energetic cost of short flights

Predictor	Coefficient	S.D.	t -value	P
Constant	-2.4658	0.9197	-2.68	0.044
T_p	25.9660	4.6340	5.60	0.003
Acceleration	0.5836	0.1489	3.92	0.011
Q_d	0.3633	0.0978	3.71	0.014

The proportion of time spent in flight (T_p), wing disk loading (Q_d) and acceleration during take-off all affected flight energy expenditure in a predictable manner. The final model was produced by stepwise deletion of take-off duration ($t = -0.03$, $P = 0.977$) and take-off angle ($t = 1.09$, $P = 0.357$). The resulting regression equation was significant ($F_{3,5} = 24.81$, $P = 0.002$, $r^2 = 0.94$).

Table 5. Correlation coefficients between the individual variables used in the GLM model (see Table 4)

Variable 1	Variable 2	Correlation coefficient (Pearson product moment)
Q_d	Acceleration	-0.176
	T_p	0.185
	Take-off angle	0.145
	Take-off duration	0.002
Acceleration	T_p	0.143
	Take-off angle	-0.201
	Take-off duration	-0.457
T_p	Take-off angle	0.418
	Take-off duration	0.558
Take-off angle	Take-off duration	0.085

$P > 0.05$ in all cases.
 Q_d , wing disk loading; T_p , the proportion of time spent in flight.

metabolic rate (i.e. non-flight activities metabolism) and, therefore, would be expected to produce an estimate below the previously derived value, which was net of BMR only. Hence, it was closely comparable with the 27.8BMR calculated in the first analysis. The intercept value, however, which equates to the perching treatment (i.e. at zero T_p , acceleration and Q_d), does not agree with the 2.1BMR expended by these finches while perching, instead yielding an unrealistic value of -2.47BMR . This was probably due to the individual effects of acceleration and Q_d , which may be related to energy expenditure in a curvilinear way (probably exponentially). Because of the narrow range of values obtained in this study, however, a linear relationship was found to fit the data best. Extrapolating backwards beyond the data range could therefore be misleading; when included in a model with T_p , Q_d and acceleration may have the effect of reducing the intercept value, as seen here. Simplifying the analysis, by removing Q_d and acceleration, results in the regression equation

Table 6. Body size variables of flying finches

Variable	Mean
Body mass (g)	13.05 ± 0.348
Perching (g)	12.97 ± 0.315
Wing area (m^2)	0.0031 ± 0.00007
Wing loading (N m)	41.801 ± 0.583
Wingspan (m)	0.1602 ± 0.00306
Wing disk area, S_d (m^2)	0.0202 ± 0.00078
Disk loading, Q_d (N m)	6.358 ± 0.139

Wing area and wingspan were calculated after Pennycuik (1989). $Q_d = mg/S_d$ (i.e. the weight supported per unit of disk), where S_d is the area of a circle whose diameter is the same as the wingspan, m is mass and g is the acceleration due to gravity.

The body mass of the perching group of finches is also given. Values are means \pm S.E.M. ($N = 9$).

Table 7. Mean take-off variables measured during each of the six observation periods

Observation period	<i>N</i>	Acceleration (m s ⁻²)	Angle (degrees)	Duration (s)
1	5	10.69±0.44	10.84±0.88	0.172±0.031
2	5	11.29±0.52	23.37±7.96	0.208±0.042
3	4	10.32±0.53	9.96±1.50	0.330±0.191
4	4	10.50±0.41	10.30±1.60	0.345±0.033
5	4	10.85±0.14	16.24±6.65	0.225±0.095
6	3	11.28±0.75	15.15±3.94	0.287±0.037

Values are means ± S.E.M.

$E_e = 2.02 + 31.8T_p$ ($F_{1,7} = 12.09$, $P = 0.01$, $r^2 = 0.63$), where E_e is energy expenditure expressed as a multiple of BMR. The intercept value (2.02BMR) in this case is comparable with the control value of 2.1BMR ($t = -1.6089$, $N = 9$, $P > 0.05$).

The direction of flight did not affect take-off acceleration (mean left-to-right 11.11 ± 0.28 m s⁻², right-to-left 10.72 ± 0.39 m s⁻², $t = 0.88$, $N = 9$, $P = 0.40$), take-off angle (mean left-to-right $16.67 \pm 3.44^\circ$, right-to-left $14.3 \pm 3.43^\circ$, $t = 0.41$, $N = 9$, $P = 0.69$), take-off duration (mean left-to-right 0.23 ± 0.05 s, right-to-left 0.24 ± 0.03 s, $t = 0.15$, $N = 9$, $P = 0.89$) or flight duration (mean left-to-right 1.57 ± 0.03 s, right-to-left 1.47 ± 0.06 s, $t = 2.12$, $N = 9$, $P = 0.67$). In view of this, the mean of the two opposite-direction flights recorded for each finch was used to represent a single observation in the following analyses. A repeated-measures analysis of covariance (ANCOVA) showed that none of the three take-off variables (Table 7) differed between individual finches or related to observation period in a predictable manner: acceleration

(individual, $F_{8,15} = 2.46$, $P = 0.064$; period, $F_{1,15} = 2.46$, $P = 0.194$), duration (individual, $F_{8,15} = 1.50$, $P = 0.238$; period, $F_{1,15} = 2.01$, $P = 0.177$) and angle (individual, $F_{8,15} = 0.55$, $P = 0.802$; period, $F_{1,15} = 0.08$, $P = 0.786$). The repeatability of take-off variables for each finch was calculated after Lessells and Boag (1987) using the mean square values taken from ANOVAs created by removing the non-significant covariate (period) in the ANCOVAs described above. Acceleration ($F_{8,16} = 2.13$, $P = 0.095$, power < 0.6), duration ($F_{8,16} = 1.54$, $P = 0.22$, power < 0.47) and angle ($F_{8,16} = 0.57$, $P = 0.785$, power < 0.16) did not vary significantly between finches, and the repeatability of all three measures was low. Acceleration (0.589), however, showed relatively more repeatability than both duration (0.216) and angle, which had a negative value.

Discussion

Measured flight energetic costs compared with existing models and studies

This study has shown that the metabolic cost of short flights in zebra finches is at least three times the predicted values derived from current models (Table 8). The metabolic cost of different flight modes (see Table 1) can be described as a function of body mass (Fig. 4). The different types of flight provide significantly different estimates of flight metabolic costs, suggesting that separate models may be useful for different types of flight. The regression line for values derived from steady-state flapping flight (within wind tunnels and on free-living birds) is shown in Fig. 4; these are the studies upon which the existing models tend to be based and are those for which aerodynamic theory (e.g. Pennycuick, 1989) conventionally aims to provide accurate predictions.

Table 8. Predictions of zebra finch metabolic costs (including basal metabolic rate) during flight

Model	Type	Flight metabolic cost		Method
		(×BMR)	(W)	
Berger and Hart (1974)	Single-variable equation	9.1	2.1	Body mass
Pennycuick (1975) equation 25 ¹	Aerodynamic theory	5.6 (11.7)	1.3 (2.7)	Body measurements and flight speed
Masman and Klaassen (1987)	Multi-variable equation	6.5	1.5	Body mass and wing dimensions
Teal (1969)	Single-variable equation ²	23.5	5.4	Body mass
Tatner and Bryant (1986)	Empirical study (<i>Erithacus rubecula</i>)	23.0	7.1	DLW
Carlson and Moreno (1992)	Empirical study (<i>Parus montanus</i>)	14.7	3.2	DLW
Present study	Empirical study	28.8	6.6	DLW

Represented are examples of the three model types described in the Introduction. Also included are the empirically measured costs from the three previous studies that have recorded relatively high flight metabolic costs.

Measurements are for the mean zebra finch variables from the present study (see Table 6); mean flight speed 3.3 m s⁻¹.

Basal metabolic rate (BMR) was calculated using the night-phase equation for passerines of Aschoff and Pohl (1970) (0.23 W).

¹Calculated using a 23% (11% mechanical to chemical energy conversion figure).

²Equation created by a linear regression ($r^2 = 0.91$) through empirical data in Table II of Teal (1969): $y = 271.93M_b^{0.9034}$, where M_b is body mass in kg.

DLW, doubly-labelled water.

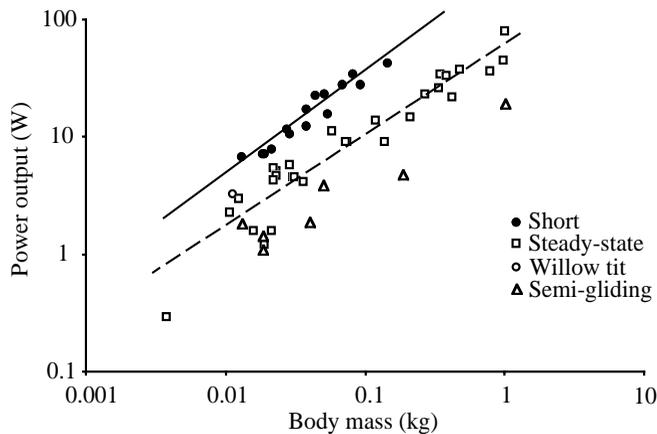


Fig. 4. Double logarithmic plot of the metabolic cost of flight (power output) of birds (see Table 1) as a function of body mass. Least-squares regressions for the three types of flight are as follows: steady-state (wind tunnel and free flight) $y=61.718x^{0.7902}$, $r^2=0.90$, $P=0.019$ (broken line); semi-gliding $y=16.384x^{0.6005}$, $r^2=0.90$, $P=0.007$ (not plotted) and short $y=250.05x^{0.8741}$, $r^2=0.92$, $P<0.001$ (solid line). When body mass was controlled for, the energy expenditures of the three flight types were significantly different (mass, $F_{1,62}=73.28$, $P<0.001$; type, $F_{2,62}=10.92$, $P<0.001$). Where a species appears more than once within the same flight mode (see Table 1), the mean of the values was plotted. Because of its intermediate nature, the data point for the willow tit *Parus montanus* (Carlson and Moreno, 1992) has not been included in the analyses.

Three studies, including the present one, have reported flight energetic costs of more than twice steady-state predictions (Tatner and Bryant, 1986; Teal, 1969). The present study, however, is the first to use a controlled experimental approach. Without information about flight variables, it is difficult to identify the specific reasons for the two earlier studies finding slightly lower flight costs, when expressed as multiples of BMR, than those measured here (Table 8). It is likely that, methodological and morphological differences aside, the flights made by the birds in both studies violated the criteria of our definition of short flight. For example, if during some of the flights the birds performed a drop-off then flight energetic costs would be reduced because a vertical component included in getting airborne requires work to be done against gravity (Norberg, 1990). The degree to which measured energetic costs in other studies fall below those measured in the present study is also likely to reflect the relative proportions of flights made that met the short flight criteria. This is illustrated by Carlson and Moreno (1992), who found that willow tits *Parus montanus* had a flight metabolic cost intermediate between steady-state estimates and the value recorded for the robin *Erithacus rubecula* (Table 8). The willow tit is an arboreal forager, and the aviary used was furnished with hanging pine branches and feeders, which suggests that arboreal foraging conditions were simulated. Therefore, although the flights performed were apparently short, there was more opportunity to reduce flight energetic costs by becoming airborne using a 'drop-off' launch.

Because of their extreme estimates of flight energetic costs, two other studies warrant consideration but were omitted from the above analysis (Fig. 4). Bautista et al. (1998) estimated flight costs in the starling *Sturnus vulgaris* to be at least $69\pm 33\text{BMR}$. This is well above the estimate of $39\pm 21\text{BMR}$ derived for the same species by Westerterp and Drent (1985). Nevertheless, these values are 1.4–2.5 times greater than the costs measured in the present study. Bautista et al. (1998) and Westerterp and Drent (1985) used the DLW technique to measure total energy expenditure and then used time/activity laboratory estimates and TEB techniques to arrive at flight costs. Because the energetic costs of flight are high in terms of cost per unit time (Alerstam, 1991), any error in the sampling of time spent in flight will have a large effect on flight cost estimates derived using a TEB approach (Masman and Klaassen, 1987; Tatner and Bryant, 1986). In the study of Bautista et al. (1998), the duration of flights was determined in a separate experiment and may have involved different starlings from those used in the main energy-expenditure experiment. In addition, the time spent in flight by the starlings in both studies was a small percentage of the total period of energy expenditure measurement (<3.6%). Hence, a small sampling error in total flight time would be magnified greatly when extrapolating to 100% flight to arrive at an energetic cost within the TEB framework. The fact that the confidence intervals associated with both estimates are large is perhaps indicative that sampling errors have occurred. Therefore, although the results cannot be dismissed, particularly without further details of the experiments, they should be treated with caution.

Any changes in the predictions of flight energetic costs will have implications for studies of avian foraging economics and foraging tactics (for examples, see Cowie, 1977; Norberg, 1981, 1996). Studies that have investigated the costs of short flight (present study) or flight containing a high proportion of short flights (Tatner and Bryant, 1986; Teal, 1969) have, in effect, determined the average energetic costs of time spent in the air. That is, as defined in the present study (see Introduction), the average energetic cost of flying from zero flight velocity to a speed near the minimum power speed and a return to zero velocity. By apportioning the flights of birds in the field into short flight (speeds below minimum power) and sustained flight (speeds including minimum power and above) and then assigning an energetic cost estimate to each portion, derived from two separate equations, a more accurate prediction could be achieved. The costs of the sustained portion can be derived from our equation for steady-state flight (Fig. 4) or from the equations of Masman and Klaassen (1987) and Rayner (1995), which incorporate morphometric measures. Although studies of short flight are limited, a predictive equation can be derived by combining the data of Teal (1969) with that measured for the robin (Tatner and Bryant, 1986) and the zebra finches of the present study. The equation can be used to predict the metabolic costs P (in W) of short flight (inclusive of BMR) for birds with body masses M_b (in kg) of up to 150 g: $P=250.05M_b^{0.8741}$ (Fig. 4). The

equation ($r^2=0.92$, $P<0.001$) gives a value for the 13 g zebra finches used in this study of 5.63 W, which is below the 6.60 W actually measured. Despite underestimating the flight costs in the zebra finches, it is a substantial improvement over estimates of 2.00 W derived from the free-flight equation (Fig. 4) and 1.49 W calculated from Masman and Klaassen (1987). In the absence of further empirical measurements, the predictive power of the equation cannot be improved.

Mechano-chemical conversion efficiency

The coefficient required to convert estimates of mechanical power produced by aerodynamic models into metabolic power remains uncertain. The present study has determined metabolic power and therefore provides an opportunity to address this question. The net power (i.e. not including BMR) required for short flight recorded here was 6.37 W. To enable an efficiency value to be determined, flight muscle mass and the mass-specific power output of avian flight muscle must be known. The mass of zebra finch flight muscle was not established here. Rayner (1988), however, estimates flight muscle mass in the Fringillidae to be 22.2% of total body mass (pectoralis 20.6% and supracoracoideus 1.6%). This gives a flight muscle mass of 2.9 g for the finches used in the present study. The upper limit of aerobically sustainable muscle-mass-specific mechanical power output is thought to be around 100 W kg⁻¹ (Marden, 1994). Values for short-burst flights (i.e. short flight) are less certain, but estimates of more than 300 W kg⁻¹ for ruby-throated hummingbirds *Archilochus colubris* (Chai and Dudley, 1996), 245 W kg⁻¹ for Harris' hawks *Parabuteo unicinctus* (Marden, 1990; Pennycuick, 1989) and 250 W kg⁻¹ from theory (Weis-Fogh and Alexander, 1977) have been suggested. Extrapolation from the results derived for hummingbirds is, because of their different flight muscle fibre composition, ill-advised (Ellington, 1991). Therefore, assuming a muscle-mass-specific power output value of 250 W kg⁻¹ yields a mechano-chemical efficiency coefficient of 11%. This is below estimates (13–40%) derived from other studies during sustained flights (Bernstein et al., 1973; Biewener et al., 1992; Masman and Klaassen, 1987; Tucker, 1968, 1972). Because of the assumptions made, however, the true value may differ from this. For example, no reduction in the power attributable to the flight muscles has been made for power produced by the leg muscles. Although studies have considered the force that can be produced by leg muscles (Bonser and Rayner, 1996; Heppner and Anderson, 1985), the power production of leg muscles during take-off has not been determined. Similarly, it is likely that the respiratory apparatus is required to work at an elevated rate which, in turn, increases energy demand and again serves to lower the amount of energy expenditure attributable to the flight musculature. The final limitation, of course, is the assumption about mechanical muscle power output. Any reduction in the amount of energy attributable to the flight musculature or a reduction in the mechanical muscle power output value used would serve to reduce the efficiency estimate. The situation is further complicated because 11%

can only be regarded as an average efficiency since there is no reason to expect conversion efficiency to be independent of flight speed (Rayner, 1995; Thomas and Hedenstrom, 1998). Efficiency estimates measured in a precise and controlled manner across a range of species are clearly needed.

What makes short-flight energetic costs high?

There are several reasons for short flights being more costly than steady-state flights. The flight velocities of the finches in this study were low. The U-shaped curve obtained from flight aerodynamic theory predicts that flight at low speeds should be more costly than at intermediate speeds as a result of the large induced power requirement needed to generate lift (Pennycuick, 1989). A second reason for the high cost is the take-off (and climbing) component. During ascending flight, work is done against gravity, and birds that take off vertically must therefore generate even more lift than required during hovering flight (Norberg, 1990, 1996). Short flight also has an acceleration component. Almost all the variation in energy expenditure ($r^2=0.94$) of flying finches could be explained by time spent flying, Q_d and acceleration during take-off, all variables being positively correlated with energy expenditure. The repeatability of take-off variables, in particular take-off angle measured for individual finches, was low. Previous studies have also found within-individual variation in take-off angle (Bonser and Rayner, 1996; Lee et al., 1996). It is possible that such variation in take-off angles could serve to confuse predators (Bonser and Rayner, 1996). The finding that energy expenditure during flight increased with wing disk loading is in agreement with aerodynamic theory (Pennycuick, 1989).

To extrapolate predictions made by existing flight energetic cost models to wild situations is to assume implicitly that the type of flight adopted by a study species is analogous to steady-state horizontal flapping flight at speeds at or around minimum power or maximum range speed. In practice, the type of flight adopted by a species and subsequently its metabolic cost will reflect flight gait which, in turn, will be influenced by other factors such as foraging and perhaps predation risk. Ultimately, when allocating flight costs, special attention should be given to factors such as flight duration and the proportion of flight contributed by a true take-off phase and, although at present limited in choice, an appropriate model should be used.

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References

- Alerstam, T.** (1991). Bird flight and optimal migration. *Trends Ecol. Evol.* **6**, 210–215.
- Aschoff, L. and Pohl, M.** (1970). Der Ruheumsatz von Vögeln als Funktion der Tageszeit und der Körpergröße. *J. Orn.* **III**, 38–47.
- Ballance, L. T.** (1995). Flight energetics of free-ranging red-footed boobies (*Sula sula*). *Physiol. Zool.* **68**, 887–914.
- Bautista, L. M., Tinbergen, J., Wiersma, P. and Kacelnik, A.** (1998). Optimal foraging and beyond: how starlings cope with changes in food availability. *Am. Nat.* **152**, 545–563.
- Berger, M. and Hart, J. S.** (1974). Physiology and energetics of flight. In *Avian Biology*, vol. IV (ed. D. S. Farner and J. R. King), pp. 416–477. London: Academic Press.
- Berger, M., Hart, J. S. and Roy, O. Z.** (1970). Respiration, oxygen consumption and heart rate in some birds during rest and flight. *Z. Vergl. Physiol.* **66**, 201–214.
- Bernstein, M. H., Thomas, S. P. and Schmidt-Nielsen, K.** (1973). Power input during flight of the fish crow, *Corvus ossifragus*. *J. Exp. Biol.* **58**, 401–410.
- Biewener, A. A., Dial, K. P. and Goslow, G. E.** (1992). Pectoralis muscle force and power output during flight in the starling. *J. Exp. Biol.* **164**, 1–18.
- Bonsler, R. H. C. and Rayner, J. M. V.** (1996). Measuring leg thrust forces in the common starling. *J. Exp. Biol.* **199**, 435–439.
- Bryant, D. M., Hails, C. J. and Prys-Jones, R.** (1985). Energy expenditure by free-living dippers (*Cinclus cinclus*) in winter. *Condor* **87**, 177–186.
- Butler, P. J., West, N. H. and Jones, D. R.** (1977). Respiratory and cardiovascular responses of the pigeon to sustained level flight in a windtunnel. *J. Exp. Biol.* **71**, 7–26.
- Carlson, A. and Moreno, J.** (1992). Cost of short flights in the willow tit measured with doubly-labeled water. *Auk* **109**, 389–393.
- Chai, P. and Dudley, R.** (1996). Limits to flight energetics of hummingbirds hovering in hypodense and hypoxic gas mixtures. *J. Exp. Biol.* **199**, 2285–2295.
- Clements, J. F.** (1991). *Birds of the World: A Checklist*. Vista, USA: Ibis Publishing Company.
- Cohen, J.** (1988). *Statistical Power Analysis for the Behavioural Sciences*. Hove, London: Lawrence Erlbaum Associates.
- Cowie, R. J.** (1977). Optimal foraging in great tits (*Parus major*). *Nature* **268**, 137–139.
- Dolnik, V. R. and Blyumenthal, T. I.** (1967). Autumnal pre-migratory and migratory periods in the chaffinch, *Fringilla coelebs* and some other temperate zone passerine birds. *Condor* **69**, 435–468.
- Dolnik, V. R. and Gavrillov, V. M.** (1973). Energy metabolism during flight of some passerines. In *Bird Migrations: Ecological and Physiological Factors* (ed. B. E. Byikhovskii), pp. 288–296. New York: John Wiley & Sons.
- Ellington, C. P.** (1991). Limitations on animal flight performance. *J. Exp. Biol.* **160**, 71–91.
- Flint, E. N. and Nagy, K. A.** (1984). Flight energetics of free-living sooty terns. *Auk* **101**, 288–294.
- Gavrillov, V. M.** (1997). *Energetics and Avian Behaviour*. Netherlands: Harwood Academic.
- Gessaman, J. A.** (1980). An evaluation of heart rate as an indirect measure of daily energy metabolism of the american kestrel. *Comp. Biochem. Physiol.* **65A**, 273–289.
- Gessaman, J. A. and Nagy, K. A.** (1988). Transmitter loads affect the flight speed and metabolism of homing pigeons. *Condor* **90**, 662–668.
- Greenewalt, C. H.** (1975). The flight of birds. *Trans. Am. Phil. Soc.* **65**, 1–67.
- Hails, C. J.** (1979). A comparison of flight energetics in hirundines and other birds. *Comp. Biochem. Physiol.* **63A**, 581–585.
- Harper, D. G. and Blake, R. W.** (1989). A critical analysis of the use of high-speed film to determine maximum accelerations of fish. *J. Exp. Biol.* **142**, 465–471.
- Heppner, F. H. and Anderson, J. G. T.** (1985). Leg thrust is important in flight take-off in the pigeon. *J. Exp. Biol.* **114**, 285–288.
- Hudson, D. M. and Bernstein, M. H.** (1983). Gas exchange and energy cost of flight in the white-necked raven, *Corvus cryptoleucus*. *J. Exp. Biol.* **103**, 121–130.
- Hussell, D. J. T.** (1969). Weight loss of birds during nocturnal migration. *Auk* **86**, 75–83.
- Johnstone, D. W. and McFarlane, R. W.** (1967). Migration and bioenergetics of flight in the Pacific golden plover. *Condor* **69**, 156–158.
- Kendeigh, S. C., Dolnik, V. R. and Gavrillov, V. M.** (1977). *Avian Energetics: Granivorous Birds in Ecosystems*. Cambridge: Cambridge University Press.
- Kespaik, J.** (1968). Heat production and heat loss of swallows and martins during flight. *Eesti. Nsv. Teaduste. Akadeemia Toimetised XVII Kooide Biol.* **2**, 179–190.
- Lee, S. J., Witter, M. S., Cuthill, I. C. and Goldsmith, A. R.** (1996). Reduction in escape performance as a cost of reproduction in gravid starlings, *Sturnus vulgaris*. *Proc. R. Soc. Lond. B* **263**, 619–624.
- LeFebvre, E. A.** (1964). The use of D₂¹⁸O for measuring energy metabolism in *Columba livia* at rest and in flight. *Auk* **81**, 403–416.
- Lessells, C. A. and Boag, P. T.** (1987). Unrepeatable repeatabilities: a common mistake. *Auk* **104**, 116–121.
- Lifson, N. and McClintock, R.** (1966). Theory of use of the turnover rates of body water for measuring energy and material balance. *J. Theor. Biol.* **12**, 46–74.
- Lyuleeva, D. S.** (1970). Energy of flight in swallows and swifts. *Dokl. Akad. Nauk SSSR* **190**, 1467–1469.
- Marden, J. H.** (1990). Maximum load-lifting and induced power output of Harris' hawks are general functions of flight muscle mass. *J. Exp. Biol.* **149**, 511–514.
- Marden, J. H.** (1994). From damselflies to pterosaurs: how burst and sustainable flight performance scale with size. *Am. J. Physiol.* **266**, R1077–R1084.
- Masman, D. and Klaassen, M.** (1987). Energy expenditure during free-flight in trained and free-living eurasian kestrels (*Falco tinnunculus*). *Auk* **104**, 603–616.
- Nagy, K. A.** (1980). CO₂ production in animals: analysis of potential errors in the doubly labeled water method. *Am. J. Physiol.* **238**, R466–R473.
- Nisbet, I. C. T.** (1963). Weight loss during migration. II. A review of other estimates. *Bird-Banding* **34**, 139–159.
- Nisbet, I. C. T., Drury, W. H. and Baird, J.** (1963). Weight loss during migration. I. Deposition and composition of fat by the blackpoll warbler, *Dendroica striata*. *Bird-Banding* **34**, 107–138.
- Norberg, R. A.** (1981). Temporary weight decrease in breeding birds may result in more fledged young. *Am. Nat.* **118**, 838–850.
- Norberg, U. M.** (1990). *Vertebrate Flight: Mechanics, Physiology, Morphology, Ecology and Evolution*. Berlin: Springer Verlag.
- Norberg, U. M.** (1996). Energetics of flight. In *Avian Energetics and Nutritional Ecology* (ed. C. Carey), pp. 199–249. London: Chapman & Hall.

- Pearson, O. P.** (1964). Metabolism and heat loss during flight in pigeons. *Condor* **66**, 182–185.
- Pennycuik, C. J.** (1975). Mechanics of flight. In *Avian Biology* (ed. D. S. Farner and J. R. King), pp. 1–75. New York: Academic Press.
- Pennycuik, C. J.** (1989). *Bird Flight Performance: A Practical Calculation Manual*. Oxford: Oxford University Press.
- Raveling, D. G. and LeFebvre, E. A.** (1967). Energy metabolism and theoretical flight range in birds. *Bird-Banding* **38**, 97–113.
- Rayner, J. M. V.** (1979a). A vortex theory of animal flight. Part 1. The vortex wake of a hovering animal. *J. Fluid Mech.* **91**, 697–730.
- Rayner, J. M. V.** (1979b). A vortex theory of animal flight. Part 2. The forward flight of birds. *J. Fluid Mech.* **91**, 731–763.
- Rayner, J. M. V.** (1988). Form and function in avian flight. In *Current Ornithology*, vol. 5 (ed. R. F. Johnston), pp. 1–66. New York, London: Plenum Press.
- Rayner, J. M. V.** (1995). Flight mechanics and constraints on flight performance. *Isr. J. Zool.* **41**, 321–342.
- Rayner, J. M. V. and Aldridge, H. D. J. N.** (1985). Three-dimensional reconstruction of animal flight paths and the turning flight of microchiropteran bats. *J. Exp. Biol.* **118**, 247–265.
- Rothe, H., Biesel, W. and Nachtigall, W.** (1987). Pigeon flight in a wind tunnel. *J. Comp. Physiol. B* **157**, 99–109.
- Tatner, P. and Bryant, D. M.** (1986). Flight cost of a small passerine measured using doubly labeled water: Implications for energetics studies. *Auk* **103**, 169–180.
- Tatner, P. and Bryant, D. M.** (1988). Doubly-labelled water technique for measuring energy expenditure. In *Techniques in Comparative Respiratory Physiology: An Experimental Approach* (ed. C. R. Bridges and P. J. Butler), pp. 77–112. Cambridge: Cambridge University Press.
- Teal, J. M.** (1969). Direct measurement of CO₂ production during flight in small birds. *Zoologica* **54**, 17–23.
- Thomas, A. L. R. and Hedenstrom, A.** (1998). The optimum flight speeds of flying animals. *J. Avian Biol.* **29**, 469–477.
- Torre-Bueno, J. R. and LaRochelle, J.** (1978). The metabolic cost of flight in unrestrained birds. *J. Exp. Biol.* **75**, 223–229.
- Tucker, V. A.** (1966). Oxygen consumption of a flying bird. *Science* **154**, 150–151.
- Tucker, V. A.** (1968). Respiratory exchange and evaporative water loss in the flying budgerigar. *J. Exp. Biol.* **48**, 67–87.
- Tucker, V. A.** (1972). Metabolism during flight in the laughing gull, *Larus atricilla*. *Am. J. Physiol.* **222**, 237–245.
- Tucker, V. A.** (1973). Bird metabolism during flight: evaluation of a theory. *J. Exp. Biol.* **58**, 689–709.
- Turner, A. K.** (1982). Optimal foraging by the swallow (*Hirundo rustica*): prey size selection. *Anim. Behav.* **30**, 862–872.
- Utter, J. M. and LeFebvre, E. A.** (1970). Energy expenditure for free flight by the purple martin, *Progne subis*. *Comp. Biochem. Physiol.* **35**, 713–719.
- Walker, J. A.** (1998). Estimating velocities and accelerations of animal locomotion: a simulation experiment comparing numerical differentiation algorithms. *J. Exp. Biol.* **201**, 981–995.
- Weis-Fogh, T. and Alexander, R. McN.** (1977). The sustained power output obtainable from striated muscle. In *Scale Effects in Animal Locomotion* (ed. T. J. Pedley), pp. 511–525. London: Academic Press.
- Westerterp, K. R. and Bryant, D. M.** (1984). Energetics of free existence in swallows and martins (Hirundinidae) during breeding: a comparative study using doubly-labeled water. *Oecologia* **62**, 376–381.
- Westerterp, K. R. and Drent, R. H.** (1985). Energetic costs and energy-saving mechanisms in parental care of free-living passerine birds as determined by the D₂¹⁸O method. *Proc. Int. Orn. Congr. Moscow XVIII*, 392–398.
- Williams, J. B.** (1985). Validation of the doubly-labeled water technique for measuring energy metabolism in starlings and sparrows. *Comp. Biochem. Physiol.* **80A**, 349–353.
- Williams, J. B. and Nagy, K. A.** (1984). Validation of the doubly-labeled water technique for measuring energy in savannah sparrows. *Physiol. Zool.* **57**, 325–328.