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100 Years Ago in The Auk

From "Third Meeting of the American Ornithologists' Union" (1886, Auk 3: 117-118):

"It became apparent more than a year ago that the work of this Committee [on the Migration and Geographical Distribution of North American Birds—Ed.] was fast assuming such formidable proportions that the Union would soon be unable to sustain the financial burden thus entailed, and at the meeting of the Union last year the Council was instructed to prepare a memorial to Congress asking for Government aid. In considering this matter the Council decided to advise the establishment of a Division of Economic Ornithology under the Department of Agriculture, which should not only carry on the investigations necessary to a thorough understanding of the movements and distribution of our birds, but should also enter upon a systematic inquiry into their food-habits and practical relations to Agriculture. The Chairman of the Committee was accordingly requested to prepare and present a draft of a memorial, embodying this plan, to the Council, which was in due time received and approved by the Council. The Chairman, on presenting this memorial to Congress, was accorded a hearing before the House Committee on Agriculture, through the assistance of Prof. C. V. Riley, Chief of the Division of Entomology of the Department of Agriculture. Prof. Spencer F. Baird had the kindness to appear before the Agricultural Committee and personally urge the practical importance of the investigations thus proposed, while Senator Warner Miller, Chairman of the Committee on Ag-

riculture, not only brought the memorial favorably to the notice of the Committee on Agriculture, but afterward made an influential speech in its behalf on the floor of the Senate, and secured for the work contemplated an appropriation of $5000, after the item had been dropped in the House. It is thus to Senator Miller that ornithologists are indebted more than to any other person for the appropriation, as without his efficient aid the appeal to Congress would have been in vain. The House Committee on Agriculture, however, placed the work under the Division of Entomology, instead of creating for it an independent division, as contemplated in the memorial.

"The appropriation became available July 1, 1885, at which time the investigations in Economic Ornithology now in progress under the Department of Agriculture were begun. The Council of the Union was invited by the Commissioner of Agriculture and Professor Riley—in recognition of the interest in the work manifested by the Union, and of its efforts in securing the appropriation from Congress for these investigations—to nominate a person to take charge of, and conduct, the work. This the Council did at a meeting held in Washington on the 21st of last April, unanimously and very fittingly selecting for this position the Chairman of the A. O. U. Committee on the Migration and Geographical Distribution of North American Birds, Dr. C. Hart Merriam, to whom also had fallen the labor of presenting the memorial and

THERMAL INSULATION OF THE DOWN AND FEATHERS OF PYGOSCELID PENGUIN CHICKS AND THE UNIQUE PROPERTIES OF PENGUIN FEATHERS

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ABSTRACT.—The thermal insulation of the down and feathers of Chinstrap (*Pygoscelis antarctica*) and Gentoo (*P. papua*) penguin chicks was measured throughout development in still air and in wind parallel and perpendicular to the plumage. Insulation increased with age. Whole-body insulation of chicks measured in still air (body core to environment) was significantly correlated with the insulation of their pelts at a given age. The insulation of the downy pelts of 10- and 15-day-old chicks was significantly lower than that of all older chicks, and explains the dependence of chicks of that age on continuous brooding by parents, despite their high thermogenic capacities. The down of older chicks provided good insulation in wind speeds of 3–5 m/s. With no wind, the down of Gentoos immediately before molting was a better insulator than feathers of prefledged chicks. The insulation of the feathers of prefledged chicks in parallel air flow up to 5 m/s was 87–112% of its value in still air. However, the insulation increased at higher wind speeds; in Gentoo pelts at winds of 15 m/s, it averaged 136% (maximum 179%) of the insulation in still air. Increasing insulative values of feathers or fur under increasing wind speeds have not been demonstrated previously in any bird or mammal. The insulation of down at various wind speeds and micrometeorological data from the Gentoo Penguin rookery on King George Island, Antarctica were compared. It follows that heat loss of older downy Gentoo chicks is not affected significantly by wind. These chicks can remain within their thermoneutral zones on windy days. *Received 6 March 1985, accepted 16 September 1985.*

ONE of the basic adaptations of homeothermic animals to cold is a thick, dense coat of fur or feathers that effectively diminishes heat loss (Scholander et al. 1950). There are few data on the insulative value of penguin feathers, but plumage provides most of their insulation (Le Maho 1977) and antarctic penguin species tend to have longer feathers than penguins in warmer climates (Stonehouse 1967).

Penguin chicks spend their prefledging development on land. They are covered with down during this time, but just before they leave land, feathers replace down. At least until chicks achieve homeothermy, they are brooded by their parents, and thereafter are frequently exposed directly to the prevailing climatic conditions. The chicks of antarctic penguins, in particular, are exposed to low temperatures and strong winds typical of that

region (Sapin-Jaloustre 1960, Goldsmith and Sladen 1961, Prévost 1961, Boyd and Sladen 1971). It is thus of interest to determine the extent to which the down protects penguin chicks from heat loss in these circumstances. Except for studies by McNabb and McNabb (1977) and Chappell (1980), no research has been done on the insulative value of the down of chicks of wild birds, or the influence of wind on the insulation of down.

One object of my work was to define the insulative properties of the down and feathers of Chinstrap (*Pygoscelis antarctica*) and Gentoo (*P. papua*) penguin chicks. Measurements of insulation were carried out on pelts of chicks when they were partially (at 10–15 days of age) or fully (when they were no longer brooded) exposed to climatic conditions.

The second object of the study was to estimate the extent to which wind affected the insulation of down and feathers of penguin chicks. I measured pelt insulation with a simulated wind. These measurements make the metabolic data of pygoscelid penguin chicks

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more useful in extrapolations to natural conditions.

MATERIALS AND METHODS

All pelt samples were collected on King George Island, the South Shetlands, Antarctica in the vicinity of the Polish Academy of Sciences Henryk Arctowski Station, during the austral summer of 1979–1980. Pelts were obtained from 10-, 15-, and 25-day-old Chinstrap and Gentoo penguin chicks; from 40-day-old downy Gentoo young; and from fully feathered, prefledged chicks of both species (about 55-day-old Chinstraps and 70-day-old Gentoos). Because 40-day-old Chinstrap chicks were molting, I did not use their pelts.

Pelts were collected from two individuals in each age category. Two dorsal pelts were obtained from each 10-day-old chick, two dorsal and two ventral pelts from 15-day-old chicks, and three dorsal (one from the front, one from the middle, and one from the back region of the body) and three ventral pelts from each older chick. The positions of the pelts were thus fairly evenly distributed over the trunk of each chick. The whole collection comprised 84 pelts.

Fat and flesh were removed from skins, and 10 × 10-cm squares of skin were pinned flat and dried slowly at room temperature.

The thermal insulation of a sample of the coat (I_c, $m^2 \cdot °C \cdot W^{-1}$) of an animal was defined as

$$I_c = (T_s - T_a)/H,$$

where T_s is the temperature of the lower surface of the skin (°C), T_a is the air temperature, and H is the heat flow through the coat (W/m^2). I_c is the sum of the thermal insulation of the skin, the thermal insulation of down or feathers, and the thermal insulation of the boundary layer of air above the coat. The reciprocal of I is thermal conductance.

For measurements of thermal insulation, pelts were mounted on a conventional heat-flow apparatus that consisted of a heat source and heat-flow meter (Fig. 1). A constant controllable temperature was provided by one face of a 9 × 9 × 2.5-cm steel chamber. Water at a constant temperature of 40°C (±0.1°C), monitored with a thermistor probe within the chamber, was circulated continuously from a temperature-controlled reservoir. The edges and bottom surface of this steel box were covered with a 2-cm layer of Styrofoam to minimize heat loss. A heat-flow meter 3 mm thick and 5 cm in diameter (WS 32, Dutch Office of Technical Physics) was attached centrally to the face of the chamber and was mounted within a sheet of plastic that formed the upper surface of the apparatus (Fig. 1). The plastic sheet had a thermal conductivity similar to that of the heat-flow disc. The meter consisted of thermopile embedded in a flexible material. The heat flow through the disc generated
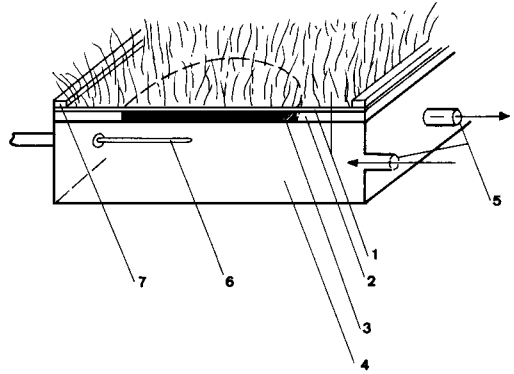

Fig. 1. Apparatus used in heat-flow measurements. 1 = skin with down or feathers, 2 = plastic sheet, 3 = heat-flow meter, 4 = steel box, 5 = inlet and outlet for temperature-controlled water, 6 = thermistor probe, 7 = clamp.

an electromotive force due to the temperature difference between the thermocouple junctions of the thermopile. The output was measured with a potentiometer. A sample of each pelt mounted on a wooden frame was placed over the upper surface of the apparatus. The bonding between the pelt and plate was achieved with a thin film of grease.

The entire complex (pelt, heat-flux transducer, hot plate) was placed in an open-ended wind tunnel, 40 cm in diameter. Air was drawn through the tunnel by a fan. Air turbulence was reduced by the presence of flutes at the inlet and outlet ends of the tunnel. For each pelt sample the insulation was determined in still air and at 1, 3, 5.5, 8, 10, and 15 m/s. Air speed was measured with a Prandtl tube. In these experiments air flow was parallel to the surface of the sample and, in the case of pelts from prefledged chicks, perpendicular to the shafts of the feathers. While the temperature of the air in the tunnel, measured with a mercury thermometer (±0.1°C) was constant during each experiment, it varied between 10 and 15°C in different experiments.

The same measurements were carried out with the heat-flow apparatus placed upright, with the wind flow perpendicular to the plumage. These measurements were performed without the wind tunnel, using a blower only, at wind velocities of 1, 3, 5.5, and 10 m/s.

The temperature gradient between the water in the metal chamber and the air above the pelt was divided by the measured value of heat flow (H) through the pelt, the meter, and the upper wall of the chamber. The resulting figures yielded the total insulation of the three layers. The insulation of the pelt was obtained by subtracting the known value of the insulation of the meter and the wall (1.2–12% of the total insulation of three layers).

JAN R. E. TAYLOR

TABLE 1.   The effect of wind on the thermal insulation ($m^2 \cdot °C \cdot W^{-1}$) of downy pelts of Chinstrap and Gentoo penguin chicks parallel to the direction of air movement.[a]

Species	Age (days)	n	Pelt thick-ness[b] (mm)	Wind speed (m/s)						
				0	1	3	5.5	8	10	15
Chinstrap	10	4	8	0.258	0.210	0.198	0.161	0.127	0.113	0.092
Penguin	15	8	11	0.298	0.246	0.232	0.212	0.194	0.178	0.148
				±0.028	±0.028	±0.027	±0.027	±0.024	±0.019	±0.009
	25	12	21	0.488	0.457	0.431	0.429	0.415	0.372	0.262
				±0.029	±0.027	±0.030	±0.029	±0.036	±0.040	±0.039
Gentoo	10	4	8	0.272	0.224	0.211	0.192	0.180	0.174	0.159
Penguin	15	8	10	0.279	0.238	0.221	0.203	0.184	0.168	0.136
				±0.017	±0.014	±0.014	±0.016	±0.018	±0.015	±0.011
	25	12	19	0.467	0.426	0.402	0.397	0.369	0.348	0.292
				±0.031	±0.024	±0.021	±0.024	±0.025	±0.027	±0.041
	40	12	27	0.610	0.592	0.588	0.581	0.508	0.441	0.312
				±0.030	±0.032	±0.052	±0.074	±0.088	±0.070	±0.060

[a] Values represent means ± SD.
[b] Including 0.5 mm of skin in the pelts of 10- and 15-day-old chicks and about 1 mm in other chicks.

RESULTS

The thermal insulation of the first down of 10- and 15-day-old chicks was low, even in still air, and never exceeded 0.3 $m^2 \cdot °C \cdot W^{-1}$ (Table 1). Insulation increased as the coat of down grew thicker and doubled in value from 10 to 25 days of age when measured in still air. In down-covered 40-day-old Gentoo Penguin chicks, the insulation with no wind was the highest among all such values.

The pelt insulation of prefledged chicks with fully grown feathers, measured in still air, was 0.541 ± 0.047 $m^2 \cdot °C \cdot W^{-1}$ ($n = 12$) for Chinstraps and 0.557 ± 0.029 $m^2 \cdot °C \cdot W^{-1}$ ($n = 12$) for Gentoos. There was no statistically significant difference between these values ($P > 0.4$, t-test). The insulation of the ventral pelts of prefledged birds of both species was significantly greater than that of their dorsal pelts ($P < 0.001$, Table 2). The down of Gentoo chicks immediately before molting was a better insulator in still air than feathers (by about 10%; $P < 0.001$).

Heat loss from the pelts of 10- and 15-day-old chicks was strongly affected by wind, even at low velocities (Tables 1 and 3). The insulative value of these pelts decreased by nearly 20% at wind speed (u) = 1 m/s and 40–50% at u = 10–15 m/s. In the pelts of 15-day-old chicks such deterioration of insulation occurred in wind flows both parallel and perpendicular to the pelts (Fig. 2).

As chicks grew older the thicker down became a better insulator in windy conditions. The insulation of downy pelts of 25- and 40-day-old chicks measured parallel to the direction of air movement remained, in general, fairly high for wind speeds up to 5.5 m/s but diminished rapidly when wind speeds exceeded this critical value (Table 1). For wind speeds less than 5.5 m/s and in parallel air flow, the reduction of insulation of the pelts of 25-day-old chicks did not exceed 15% of values in still air. The decrease in the insulation of the pelts of 40-day-old downy Gentoo chicks at u ≤ 5.5 m/s did not exceed 5% (Fig. 2A, B).

In winds perpendicular to the pelts, the insulation of the down of older chicks remained high up to about 3 m/s. Contrary to the measurements with parallel air flow, the insulation of longer down was more affected by wind than the insulation of shorter down. At u ≥ 3 m/s the insulation of the thickest downy pelts of 40-day-old Gentoo chicks was considerably lower than that of both 15- and 25-day-old chicks (Table 3, Fig. 2C).

The relationship of insulation to wind speed when the wind was parallel to the plumage was entirely different in the case of feathered pelts (Table 2, Fig. 2A, B). At lower wind speeds insulation diminished, but by less than 15% of the value measured in still air. At wind speeds greater than 5.5 m/s, however, the insulation value increased, and at u = 15 m/s achieved a mean of 125% of the value measured in still air

TABLE 2. Effect of wind on the thermal insulation ($m^2 \cdot {}^\circ C \cdot W^{-1}$) of dorsal and ventral feathered pelts of Chinstrap and Gentoo penguin chicks parallel to the direction of air movement.[a] The slopes of the regression lines of the insulation on the pelt thickness (an increment of the insulation per 1 mm of pelt thickness) also are given.

	Chinstrap Penguin			Gentoo Penguin		
	Dorsal	Ventral	Slope	Dorsal	Ventral	Slope
Pelt thickness[b]						
(mm)	18	25		23	28	
Range	16–20	22–27		22–24	26–31	
Wind speed						
0 m/s	0.499 ± 0.009	0.582 ± 0.026	0.0111	0.532 ± 0.013	0.583 ± 0.012	0.0092
1 m/s	$0.459^* \pm 0.014$ (92)	$0.551^* \pm 0.027$ (95)	0.0124	$0.498^* \pm 0.015$ (94)	$0.560^* \pm 0.012$ (96)	0.0109
3 m/s	$0.439^* \pm 0.016$ (88)	$0.552^* \pm 0.027$ (95)	0.0150	$0.493^* \pm 0.017$ (93)	0.585 ± 0.016 (100)	0.0159
5.5 m/s	$0.434^* \pm 0.019$ (87)	0.594 ± 0.049 (102)	0.0218	$0.508^* \pm 0.017$ (95)	$0.654^* \pm 0.033$ (112)	0.0246
8 m/s	$0.441^* \pm 0.026$ (88)	0.652 ± 0.068 (112)	0.0285	0.551 ± 0.033 (104)	$0.741^* \pm 0.077$ (127)	0.0333
10 m/s	$0.448^* \pm 0.034$ (90)	$0.709^* \pm 0.082$ (122)	0.0353	$0.605^* \pm 0.042$ (114)	$0.819^* \pm 0.092$ (140)	0.0367
15 m/s	0.477 ± 0.055 (96)	$0.769^* \pm 0.086$ (132)	0.0393	$0.678^* \pm 0.049$ (127)	$0.848^* \pm 0.155$ (145)	0.0277

[a] Values of the insulation represent means $\pm$ SD; $n = 6$ in each case. Numbers in parentheses are the percentages of the value in still air (0 m/s). * = insulation value significantly different from that at 0 m/s ($P < 0.01$, paired-sample t-test).

[b] Including 1 mm of skin. Average length of dorsal and ventral feathers measured by the method of Stonehouse (1967) was 37 mm in Gentoos and 36 mm in Chinstraps.

(Table 2). With the exclusion of dorsal pelts of Chinstrap chicks, the insulation value at u = 15 m/s was always greater than the one measured under zero wind conditions, and it reached a mean of 135% of the value measured in still air. The greatest increase of insulation (79%, from 0.575 $m^2 \cdot {}^\circ C \cdot W^{-1}$ at u = 0 m/s to 1.03 $m^2 \cdot {}^\circ C \cdot W^{-1}$ at u = 15 m/s) was observed for one of ventral pelts of a Gentoo prefledged chick (Fig. 3).

The thermal insulation of feathered pelts of both species measured at a given wind speed in air flow parallel to the plumage had a positive linear correlation with pelt thickness (Fig. 4; correlations were calculated for dorsal and ventral pelts together). All correlation coefficients were statistically significant (t-test, $P < 0.05$ for Gentoos at u = 15 m/s; $P < 0.001$ in all other cases). The increase in insulation value at high wind speeds was greater in the case of thicker pelts. The pelt must be at least 29 mm thick for insulation at increased wind speeds (e.g. 3 m/s) to be greater than in still air; for u = 8 m/s the pelt must be only 22 mm thick, and for u = 15 m/s only 19 mm thick (Fig. 4).

In air flow perpendicular to feathered pelts, insulation diminished over the entire range of wind speed (Table 4). However, the rate of this decrease was lower than in down (Fig. 2C).

DISCUSSION

There is a constant increase in the thermal insulative value of downy pelts with the age of chicks (Table 1). This increase occurs because of the increased thickness of down and possibly because of changes of its quality. The skin contributes negligibly to the total pelt insulation value. If we assume that the thermal conductivity of skin equals 0.50 $W \cdot m^{-1} \cdot {}^\circ C^{-1}$ (Gates 1980), the skin contributes less than 1% of the insulation in both feathered and downy pelts. The insulation of chick pelts measured in still air was correlated significantly with the whole-body insulation of chicks at a given age ($r = 0.99$, $P < 0.001$, t-test; Fig. 5). The values of the whole-body thermal insulation, body core to environment, measured on live chicks (Taylor 1985) are the reciprocals of the whole-body conductances reported there.

TABLE 3. Thermal insulation ($m^2 \cdot °C \cdot W^{-1}$) of downy pelts of Gentoo Penguin chicks in winds perpendicular to the pelts.[a]

Age (days)	Wind speed (m/s)			
	1	3	5.5	10
15	0.225 ±0.023	0.208 ±0.028	0.174 ±0.017	0.170 ±0.012
25	0.428 ±0.026	0.401 ±0.029	0.305 ±0.021	0.263 ±0.017
40	0.522 ±0.040	0.446 ±0.030	0.324 ±0.032	0.281 ±0.038

[a] Values represent means ± SD. Sample sizes as in Table 1.

The ratio of pelt insulation value to the whole-body insulation of the chicks indicates the importance of insulative properties of down and chick feathers in reducing heat loss. This ratio was not lower than 0.80 for 25-day-old and older Chinstrap and Gentoo chicks. Thus, the role of down and feathers in the reduction of heat loss in these chicks is approximately the same as in adult penguins of other species. The ratio calculated from the differences between the body, skin, and ambient temperatures (at the lower critical temperature) is 0.86 for Emperor Penguins (*Aptenodytes forsteri*; Jarman 1973, Le Maho et al. 1976) and about 0.80 for Humboldt (*Spheniscus humboldti*) and Little Blue penguins (*Eudyptula minor*; Drent and Stonehouse 1971, Stahel and Nicol 1982). On the other hand, this ratio in pygoscelid chicks is higher than in summer and in winter-acclimatized King Penguin (*Aptenodytes patagonica*) chicks (0.74 and 0.56, respectively; Barré 1984).

The low insulative value of the short down of 15-day-old Chinstrap and Gentoo penguin chicks (Table 1) has a bearing on their low whole-body insulation (Fig. 5). The insulation value of down in 10- and 15-day-old chicks both in still air and wind was much lower than the down insulation of older chicks. For this reason 10- and 15-day-old chicks still depend on the heat provided by adult birds, in spite of their own high ability to produce heat and their homeothermy at about 15 days of age (Taylor 1985). Brooding of chicks by parents becomes less effective as they grow due to their large size (Taylor 1985). However, parents guarding 15–20-day-old chicks could serve as effective wind screens. The cessation of brooding and guarding and the beginning of full exposure of chicks to the physical conditions of the en-
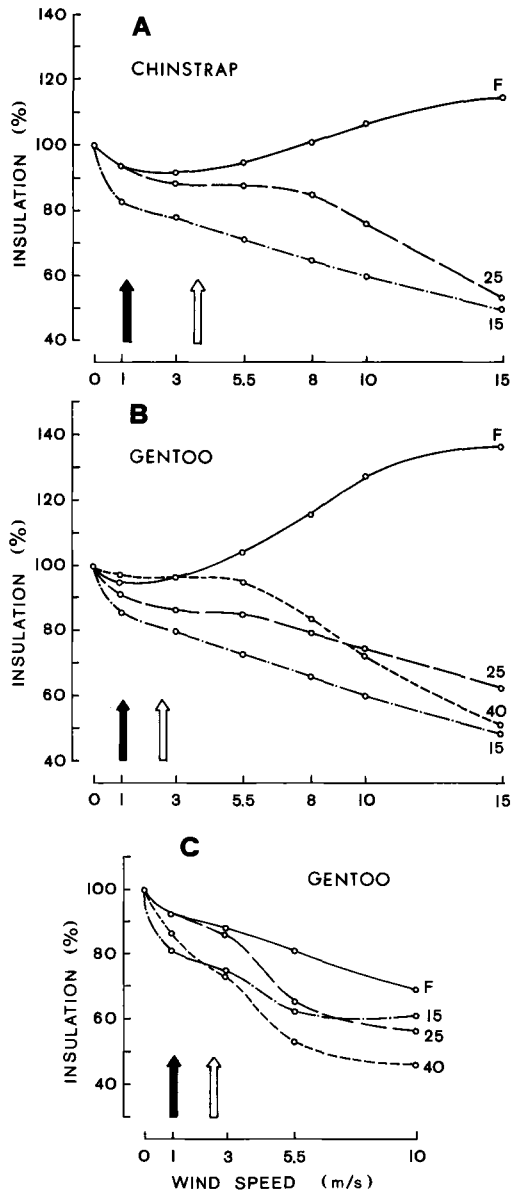

Fig. 2. Thermal insulation of the pelts of pygoscelid penguin chicks relative to wind speed. Insulation is expressed as a percentage of the value in still air. (A) Chinstrap Penguin, wind flow parallel to the pelt. (B) Gentoo Penguin, wind flow parallel to the pelt. (C) Gentoo Penguin, wind flow perpendicular to the pelt. The ages of the chicks are given next to the curves; F = feathered chicks. Black arrows indicate the average wind speed in the breeding colony of each species; white arrows indicate the average maximum wind speed.
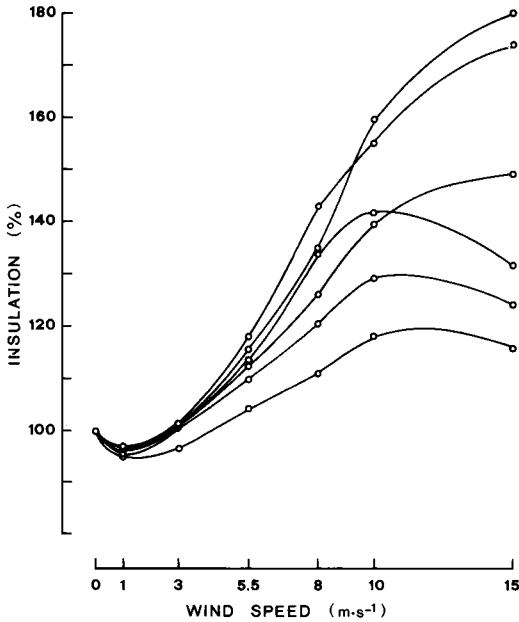
Fig. 3. The increase of thermal insulation of 6 feathered ventral pelts from prefledged Gentoo Penguin chicks as wind speed increased. Air movement was parallel to the pelts. Insulation is expressed as a percentage of the value in still air.

vironment coincides with the time that their down achieves high insulative value (i.e. between 15 and 25 days of age; Table 1). Barré (1978) found a similar correlation between the length of down in the chicks of King Penguins and the age of emancipation, which takes place after the chicks become homeothermic.

In still air or gentle wind the down of 25-day-old chicks was nearly equal, and shortly before their molt (40 days after hatching) was an even better insulator than feathers. This high insulation value of downy pelts of Gentoo chicks just before molting was due to the thickness of the coat of down at this age, which was even greater than the thickness of the feather layer in prefledged chicks (Tables 1 and 2). The highest insulation of 40-day-old Gentoos coincides with a very high whole-body insulation value ($0.735 \ m^2 \cdot °C \cdot W^{-1}$), which is greater than in Gentoo chicks shortly after molt (Fig. 5) and provides an exceptionally low lower critical temperature ($-15°C$; Taylor 1985). Fully grown but still downy King Penguin chicks are probably also better insulated than adult birds. This can be inferred from the fact that during
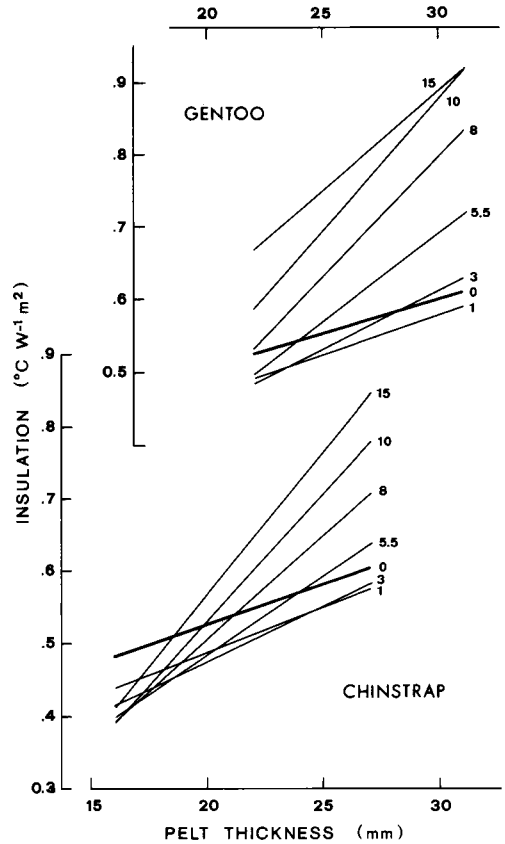

Fig. 4. Thermal insulation of the pelts of feathered Chinstrap and Gentoo penguin chicks as a function of pelt thickness at various wind speeds. Wind flow was parallel to the pelts. Wind speeds are given next to the regression lines. The linearity of the relationships was checked at $P < 0.05$ by the modified one-sample runs test, which is stronger than the ordinary test (Pawłowski 1976).

winter fast these chicks consume considerably less fat reserves than their parents (Mougin 1974, Barré 1976).

The insulation of feathered pelts in still air is similar to the values for pelts of adult Gentoo and Adélie (*Pygoscelis adeliae*) penguins given by Kooyman et al. (1976). There are no available data on the insulation properties of the integument of chicks or adult birds of other high-latitude species. The pelt insulation of young pygoscelid penguins, of 25 days of age and older, is very close to the insulation of summer pelts of arctic mammals and considerably lower than the insulation of winter coats of those animals (Hart 1956). The pelts of older

TABLE 4. Thermal insulation ($m^2 \cdot {}^\circ C \cdot W^{-1}$) of dorsal and ventral feathered pelts of Chinstrap and Gentoo penguin chicks in winds perpendicular to the pelts.[a]

Species	Wind speed (m/s)			
	1	3	5.5	10
Chinstrap Penguin				
Dorsal	0.409	0.392	0.379	0.353
	±0.021 ·	±0.027	±0.039	±0.035
	(82)	(79)	(76)	(71)
Ventral	0.549	0.524	0.481	0.362
	±0.027	±0.032	±0.028	±0.025
	(94)	(90)	(83)	(62)
Gentoo Penguin				
Dorsal	0.466	0.452	0.442	0.396
	±0.017	±0.022	±0.032	±0.041
	(88)	(85)	(83)	(74)
Ventral	0.557	0.530	0.460	0.373
	±0.043	±0.038	±0.020	±0.026
	(96)	(91)	(79)	(64)

[a] Values represent means ± SD; $n = 6$. Numbers in parentheses are the percentages of the value in still air (0 m/s).
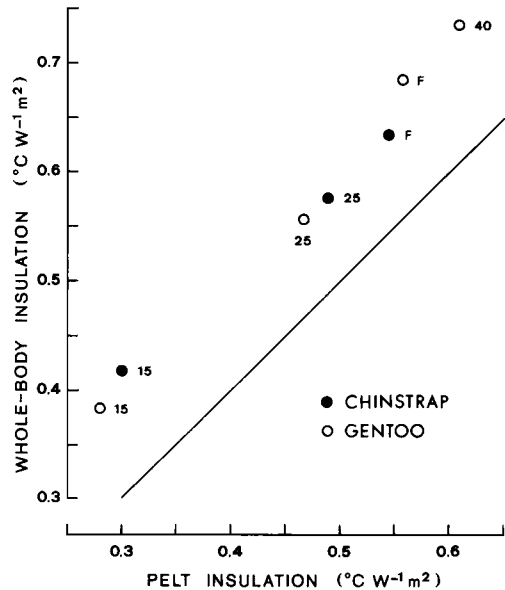

Fig. 5. Relationship between whole-body insulation and pelt insulation in Chinstrap and Gentoo penguin chicks at various ages. The diagonal line represents the equivalence of both types of insulation. Numbers next to circles indicate chick ages (days after hatching); F = feathered chicks.

pygoscelid chicks have insulation values similar to mammal pelts of the same thickness (Scholander et al. 1950, Hart 1956).

Increased thermal insulation of feathers under increased wind speeds (Table 2, Figs. 2A, B and 3) has not been reported previously. The insulation properties of feathers in wind have been described only in the Sharp-tailed Grouse (Tympanuchus phasianellus; Evans and Moen 1975) and the Rock Dove (Columba livia; Walsberg et al. 1978). In both cases, the insulation value decreased proportionally with the reciprocal of the square root of the wind speed. Similarly, the increase of total pelt insulation has not been noted in the more extensive studies on fur (Moote 1955, Lentz and Hart 1960, Tregear 1965, Hutchinson and Brown 1969, Ames and Insley 1975, Degabriele and Dawson 1979).

The mechanism of the phenomenon is unknown and requires an experimental explanation. Stonehouse (1967) stated: "The penguin feathers seem especially well adapted for resisting wind movement. The short, stiff rachis of adjunct feathers, overlapping like tiles on a roof, are pressed more closely together rather than parted by strong winds, and are likely to be more efficient than mammal fur in retaining an undisturbed stratification of air close to the skin." This may explain the increase of penguin feather insulation in high wind flow par-

allel to the plumage. The shafts of penguin contour feathers are flattened and elastic. The ends of the shafts are pointed toward the back of the body, and the top parts of vanes of neighboring feathers overlap flatly, forming a uniform surface. This structure and arrangement of feathers is primarily an adaptation to life in water. Under the influence of hydrostatic pressure the ends of the feathers lie more closely together, separating the insulating layer of air close to the skin from the water (Rutschke 1965). The pressure of the flowing air may produce an effect similar to hydrostatic pressure. This seems to be supported by the significant dependence between the rate of increase of insulation at a given wind speed and the thickness of the coat of feathers (Fig. 3). The longer the feathers are, the more elastic their shafts appear to be. On the other hand, it is difficult to explain in such a way the lack of increase in insulation when the pelts are placed perpendicular to the direction of air movement.

Nachtigall and Bilo (1980) stated that adult Gentoo Penguins have a surprisingly low coefficient of drag in water, lower than should re-

sult from their optimal shape. The authors suggested that this phenomenon is connected with the properties of their feathers, which damp the turbulence of water flowing around a penguin's body. It is thus possible that the increase in thermal insulation of feathers of Chinstraps and Gentoos in wind also is caused by the reduction of turbulence of air flowing over the pelt.

My results may be important for further investigation of the adaptations of penguins. If air flow reduces heat loss by the feathers, an analogous effect should be produced by water flowing around a penguin's body. If we accept Nachtigall and Bilo's (1980) hypothesis of damping turbulence, the laminar flow of water would enable the bird to move more quickly in water, and also would diminish heat loss. This is particularly important because heat loss in penguins is greater in water than in air (Kooyman et al. 1976, Stahel and Nicol 1982). However, this turbulence-suppression hypothesis requires supportive data.

The thermoneutral zones of Chinstrap and Gentoo penguin chicks 25 days old and older are 15–30°C wide, with a lower critical temperature as low as −15°C. These zones cover the range of air temperature variations common in the breeding colonies of both species at Point Thomas (King George Island, the South Shetlands) during the austral summer (Taylor 1985). The thermoneutral zones of these chicks were determined in a metabolic chamber in practically still air. On the other hand, heat loss in birds increases with the increase of wind speed (Goldstein 1983); air flow diminishes whole-body thermal insulation of birds and raises their lower critical temperature.

My results cannot give a quantitative estimate of rate of heat loss from the whole chick body despite the even distribution of collected pelts over the chick trunk. It is difficult to extrapolate from results obtained with a flat piece of pelt to heat transfer across the curved surface of a bird. However, these results provide an approximation of the extent to which heat loss from penguin chicks is affected by wind.

The slope of the regression line of energy metabolism on air temperature at low ambient temperatures can be considered in older downy Gentoo chicks as the whole-body conductance (Taylor 1985). The reciprocal of this conductance is whole-body insulation. I calculated a new slope of the regression line such that the lower critical temperature was equal to the mean air temperature in a Gentoo Penguin breeding colony (2.3°C, Point Thomas colony; E. Moczydłowski unpubl. data). It was found that in air at 2.3°C the whole-body insulation should decrease by at least 14% in 25-day-old Gentoo chicks and by at least 25% in 40-day-old Gentoos if these birds are outside their thermoneutral zones.

The average wind speed in the Gentoo Penguin colony at Point Thomas during the austral summer 1979–1980 was 1.1 m/s (measured 35 cm above the ground when adult birds ceased brooding chicks). The average maximum wind speed on subsequent days of this period was 2.5 m/s. In a Chinstrap rookery these wind speeds were 1.2 and 3.8 m/s, respectively (E. Moczydłowski unpubl. data). These wind speeds did not lower the insulation of downy pelts of 25-day-old Gentoos by more than 14% in experimental air flows or by more than 4% (parallel) and 27% (perpendicular) in 40-day-old Gentoo pelts (Fig. 2B, C). Because the insulation of down is a major part of the whole-body insulation (Fig. 5), I inferred that the wind does not affect significantly the heat loss of older downy Gentoo chicks and that they remain within their thermoneutral zones even on windy days.

It is more difficult to estimate, on the basis of the available data, the effect of wind on heat loss in feathered chicks. These chicks probably suffered considerable heat loss through their practically bare flippers. However, wind speeds to at least 5 m/s have no important effect on the metabolic rate of adult Emperor Penguins (Le Maho et al. 1976) and King Penguins (Barré 1980). The increase of feather insulation in pre-fledged Chinstraps and Gentoos recorded in stronger winds parallel to the pelts probably is not important in the reduction of their heat loss on land. Only at the highest recorded wind speeds of 5.6 m/s in the Gentoo rookery and 13.0 m/s in the Chinstrap rookery did the insulation value exceed the insulation in still air (by 5% and 12%, respectively).

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FLIGHT COST OF A SMALL PASSERINE MEASURED USING DOUBLY LABELED WATER: IMPLICATIONS FOR ENERGETICS STUDIES

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ABSTRACT.—The metabolic cost of rest and activity ($cm^3 CO_2 \cdot g^{-1} \cdot h^{-1}$) was measured for the European Robin (*Erithacus rubecula*, 18.6 g) at temperatures (T_a, °C) from −15 to +30°C. Regressions expressing these costs are: night resting (M_{rN}) = 4.23 − 0.0733T_a, day resting (M_{rD}) = 5.10 − 0.0807T_a, hopping (M_{hop}) = 8.60 − 0.1256T_a.

Daily energy expenditure (DEE) for robins held in an outdoor aviary was 64.8 kJ/day (SD = 9.2, n = 6), determined using the doubly labeled water technique. This was positively related to time spent in flight (t_{fly}, h) such that DEE = 50.9 + 23.4t_{fly}.

Flight cost for robins was estimated as 25.6 kJ/h (SD = 5.0, n = 6). This flight cost is about twice that predicted by various allometric equations. Robin flights in the aviary were short (3 m) and brief (0.78 s), indicating a mean flight speed (3.85 m/s) that was lower than the theoretical minimum power velocity (5.86 m/s). The European Robin has a relatively high wing loading (0.263 g/cm^2) and aspect ratio (7.33). In a small bird with flapping flight these characteristics imply a high cost, particularly at low flight speeds.

The high cost of flight was offset by its short duration. During 30-min observation periods, an average of 100.2 s was spent in flight, implying a sustained energy demand of only 3.04 kJ/h (2.7 × basal metabolic rate). The exceptionally high flight cost reported here (23 × basal metabolic rate) may be typical of short, brief aerial forays. Other doubly labeled water studies reveal a positive correlation between the time spent in flight and DEE, indicating its dominant impact on energy turnover in some free-living birds. *Received 17 April 1985, accepted 19 September 1985.*

THE accuracy of time-activity laboratory (Mugaas and King 1981) studies for determining the daily energy expenditure (DEE) of free-living birds depends upon representative time budgets and realistic values for the energy cost of activities (Weathers and Nagy 1980, Koplin et al. 1980, Williams and Nagy 1984, Bryant et al. 1985). This was well illustrated by Weathers et al. (1984) for low-cost activities that are pursued over long periods, but it is also important for high-cost activities that usually occupy only a small proportion of the day (Mugaas and King 1981).

This study is concerned with the determination of activity costs in a small, woodland passerine, the European Robin (*Erithacus rubecula*). It employs gas-analysis respirometry to measure resting and some locomotor costs. Time budgets and doubly labeled water measurements of DEE for aviary robins were used in combination with laboratory estimates of nonflight activity to establish the cost of flight for a species that exhibits a largely nonaerial existence. It contrasts with previous studies on this topic that have focused on mainly aerial

species (Utter and LeFebvre 1970, Hails 1979, Flint and Nagy 1984, Westerterp and Drent 1985).

METHODS

Energetic cost of activity.—Robins from a wooded area on Stirling University campus (56°08′N, 3°54′W) were caught at dusk between November and March during 1983–1985. Wing dimensions and body mass were noted, and the birds were placed in a respirometer overnight to determine metabolic rate for a range of temperatures (−15°C to +30°C). Three to five replicates were performed at 5°C intervals, each overnight trial maintaining one temperature (± 0.5°C). The birds were released approximately 1 h after dawn, having completed a bout of hopping activity in the spindle-mounted respirometer. Robins were caught direct from the wild so that the respirometry results would include the effects of acclimatization to seasonal and local conditions.

The respirometer train was an open-flow system, equipped with an MSA infrared gas analyzer for monitoring CO_2 production, and a Beckman OM2 polarographic oxygen analyzer. Carbon dioxide was removed from incurrent air using Carbasorb, and air leaving the respirometer chamber was passed over

Drierite prior to gas analysis. The respirometer was enclosed in a darkened incubator. Each overnight run was divided into a series of 2-h sample periods, interspersed with ambient air sampling. During the first 2 h the bird settled down in a darkened incubator at about the time it normally went to roost, and the mean for this period was taken to indicate the cost of resting during the day (M_{rD}). Metabolism usually reached its lowest levels at about 0300. At dawn the waking period was often characterized by intermittent activity, so this and the first period were excluded when calculating the average cost of resting overnight (M_{rN}). After waking, the bird was induced to hop by revolving the spindle-mounted respirometer until a steady trace was obtained from the gas analyzers. The speed of rotation was selected such that the individual's gait resembled that of a foraging bird (1.5–2.5 m/min). The energetic cost of ground activity (including foraging) is estimated in this work from the relationship established during hopping trials (M_{hop}). Individual response to a rotating chamber was unpredictable, and it sometimes was necessary to reject trials in which birds employed bouts of hovering or clung temporarily to the chamber wall. All gas volumes were corrected to STP.

Six robins were used to determine daily energy expenditure using the doubly labeled water ($D_2^{18}O$) technique (Lifson et al. 1955). They were held during July–August 1983 for 48 h in an outdoor aviary, as groups of 3 individuals. Different birds were placed in the respirometer on successive nights to establish summertime values for night resting, day resting, and hopping. Food [blowfly larvae (*Calliphora* spp.) and cheese] was supplied with water *ad libitum*. The aviary was partly exposed to the sky, but completely shielded from the wind by fencing and woodland.

Time budgets.—In the aviary, the activity of each bird was recorded for 3–5, 30-min periods ($n = 48$) per day. Individuals were recognized by colored ring combinations and by spots of white typist's correction fluid applied to the head or breast feathers.

Activities were timed using a microprocessor-based data logger, with event resolution limited only by the human response time (approximately 0.2 s). Three classes of activity were recognized: resting, flying, and ground activity. The latter category comprised principally hopping and pecking but also included occasional preening, bathing, and defecating as these activities entail broadly similar energy demands. We designated these minimal energy-demanding activities as ground activity to simplify the analysis, and because it is not yet possible to distinguish between the energy costs of these minor activities. Weathers et al. (1984) measured the energetic costs of alert perching, preening, eating, and hopping. The mean costs of each activity were ranked in the order mentioned, although there were no statistically significant differences.

The 24-h day was divided into three periods: (1) the dark period, during which robins were resting either in the aviary or in the respirometer; (2) the handling period, during which body mass was recorded, blood samples taken, and the birds then placed in a cloth bag; and (3) the light period, when the birds were active in the aviary.

Doubly labeled water technique.—The birds received intraperitoneal injections of 0.13 ml of 10 atom % D_2O and 0.22 ml of 20 atom % $H_2^{18}O$. Initial blood samples were taken 1 h later, after which one individual was placed in the respirometer and the others returned to the aviary. On the following morning a blood sample was obtained from the robin in the respirometer, after which it was returned to the aviary. Blood samples were obtained from all individuals 48 h after initial sampling. The samples were flame-sealed in Vitrex microcapillaries (5 µl) for later analysis. A different individual was monitored in the respirometer on the second night. Natural enrichment levels of deuterium and oxygen-18 were determined from other robins on the study site at the time of the experiment (D = 152.82 ppm, ^{18}O = 2,011.56 ppm).

Blood samples were processed according to the method given in Bryant et al. (1984) and Westerterp and Bryant (1984). The theory of measuring energy expenditure using doubly labeled water ($D_2^{18}O$) is described by Lifson et al. (1955), and assumptions associated with the method are outlined by Nagy (1980). Body water content was taken as 65% (after Newton 1968) of the mean body mass, itself derived from measurements taken at the beginning and end of a sampling period.

RESULTS

Respirometry measurements.—Figure 1 shows winter metabolism during night resting (M_{rN}), day resting (M_{rD}), and hopping (M_{hop}) as a function of ambient temperature (T_a). Predictive equations were produced using regression analysis (Table 1). McNab (1980) noted that regression coefficients derived in this manner are poor representations of minimal thermal conductance if the regression lines do not extrapolate to the animal's body temperature at zero metabolism. In this work the regressions extrapolate to 57.7°C (M_{rN}), 63.2°C (M_{rD}), and 68.5°C (M_{hop}), which are all much greater than the European Robin's proventricular temperature of 40.6°C (Udvardy 1953). For this reason the mean conductance method advocated by McNab (1980) was investigated, assuming a constant body temperature of 40.6°C. However, agreement between this method and measured metabolism was poor. This may have been due to an incorrect assumption of constant body temperature. Metabolic values reported here for
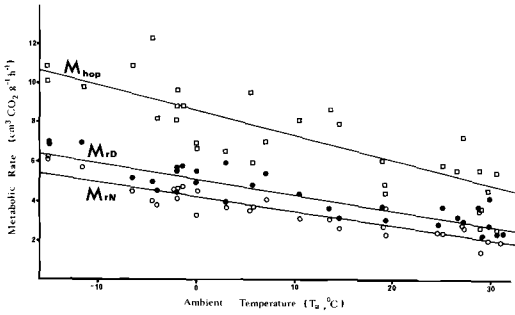
Fig. 1.   Robin winter metabolism as a function of ambient temperature. M_{rN} = night resting metabolism; M_{rD} = day resting metabolism, M_{hop} = hopping metabolism. Regressions are given in Table 1.

M_{rN} are nightly averages and therefore above the lowest resting level (40% greater, Tatner unpubl. data). Thus, the thermal conductance for M_{rN} does not represent the minimal value. These limitations, together with the extent of variability in measured metabolism (Fig. 1, S_{yx} in Table 1), render the use of regression analysis most appropriate in the context of this work.

Day resting was significantly more demanding than night resting ($t = 5.42$, $P < 0.05$), requiring 21% [$100 \times (4.23 - 5.10)/4.23$] more energy. A comparison of the respective regression coefficients (Table 1) indicates that this difference did not vary with ambient temperature ($t = 0.736$, $P > 0.05$; Zar 1974). An increase of this magnitude (20–25%) between the night and day phases is a general feature of avian resting metabolism (Aschoff and Pohl 1970b, Calder and King 1974).

The respirometry trials during summer, undertaken at a mean T_a of 25°C, indicated a higher CO_2 production (Table 2) than would be predicted from the winter metabolism relationships for both M_{rN} and M_{rD}. These increases were 32% for M_{rN} (2.41 to 3.17 cm³ $CO_2 \cdot g^{-1} \cdot h^{-1}$) and 24% for M_{rD} (3.10 to 3.85 cm³ $CO_2 \cdot g^{-1} \cdot h^{-1}$). Summer robins also exhibited higher respiratory quotients (RQs). The difference between

RQ in summer and winter was greater over the night-resting phase (0.95 compared with 0.75; $t = 5.24$, $P < 0.01$) than the day-resting phase (0.88 compared with 0.75; $t = 3.27$, $P < 0.05$). The apparent increase in metabolic rate indicated by the elevated CO_2 production of summer robins was reduced to 12% (M_{rN}) and 11% (M_{rD}) when corresponding changes in RQ were taken into account. However, differences between summer and winter resting metabolic rate at 25°C were still statistically significant (Table 2). Summer predictions using the winter regression equations therefore were incremented by 12% for M_{rN} and by 11% for M_{rD}. The energetic cost of hopping at 25°C for summer robins was not significantly different from that predicted by the winter regression equation (Table 2).

Time budgets.—Activity timed using the data logger was expressed in terms of the proportion of the 30-min sample devoted to resting, ground activity, or flying. These proportions were normalized using an arcsine transformation (Zar 1974) prior to statistical analysis. The values for each individual were determined on a daily basis and used to apportion the daylight period spent in the aviary (Table 3). Analyses of variance on pooled data showed that the three categories of activity occurred in similar proportions during each hour of daylight, indicating that diel activity rhythms were absent. The average proportion of time spent in flight was the only time-budget variable that differed significantly between individuals (one-way ANOVA, $F = 5.96$, $P < 0.05$). Flights were short, as the birds tended to fly from one side of the aviary to the other (3 m), landing on the sides only momentarily before making a return flight. Cumulative flight time as a function of the number of flights in a sampling period is shown in Fig. 2. Because the slope of the regression was significant ($t = 16.97$, $P < 0.001$), the duration of a single flight was taken as 0.78 s. During this time the bird flew approximately 3 m, so we necessarily considered the cost of

TABLE 1.   Robin winter metabolism as a function of ambient temperature (T_a, °C).

	CO_2 production (cm³·g⁻¹·h⁻¹)	S_{yx}	r^2 (×100)	n
Resting night metabolism (M_{rN})	$4.23 - 0.0733T_a$	0.52	81.2	32
Resting day metabolism (M_{rD})	$5.10 - 0.0807T_a$	0.65	77.4	32
Hopping metabolism (M_{hop})	$8.60 - 0.1256T_a$	1.40	79.7	30

TABLE 2. Robin metabolism in winter and summer at 25°C.[a]

	Night resting (M_{rN})			Day resting (M_{rD})			Hopping activity (M_{hop})		
	$\bar{x}$	(SD)	n	$\bar{x}$	(SD)	n	$\bar{x}$	(SD)	n
Summer									
$cm^3\ CO_2 \cdot g^{-1} \cdot h^{-1}$	3.17	(0.18)	6	3.85	(0.34)	6	4.81	(0.98)	4
RQ	0.95	(0.08)	6	0.88	(0.08)	6	0.94	(0.07)	4
$J \cdot g^{-1} \cdot h^{-1}$	69.55	(4.06)	6	89.63	(5.69)	6	106.45	(21.63)	4
Winter[b]									
$cm^3\ CO_2 \cdot g^{-1} \cdot h^{-1}$	2.41	(0.13)	31	3.10	(0.16)	31	5.46	(0.41)	29
RQ	0.75	(0.03)	19	0.75	(0.05)	19	0.82	(0.10)	17
$J \cdot g^{-1} \cdot h^{-1}$	63.46	(3.38)	31	81.70	(4.28)	31	134.38	(10.17)	30
Summer vs. winter									
Difference ($J \cdot g^{-1} \cdot h^{-1}$)	6.09			7.93			−27.93		
t (df)[c]	3.45**	(6.41)		3.24**	(6.14)		2.45[NS]	(3.19)	

[a] $J \cdot g^{-1} \cdot h^{-1}$ calculated using standard heat equivalents for CO_2 as follows (units $J/cm^3\ CO_2$): 21.95 at respiratory quotient (RQ) = 0.95, 23.30 at RQ = 0.88, 22.13 at RQ = 0.94, 26.44 at RQ = 0.75, 24.62 at RQ = 0.82 (Brody 1945).

[b] $cm^3\ CO_2 \cdot g^{-1} \cdot h^{-1}$ calculated from the regression equations in Table 1; standard deviations of predicted values were calculated using MINITAB regression (Ryan et al. 1976). RQ mean values are based on pooled data collected over the temperature range −15°C to +30°C.

[c] ** = $P < 0.01$, NS = not significant.

short, brief flights. This type of flight resembles that performed by the European Robin in its natural habitat when it moves short distances between a perch and the ground, or between bushes.

Nonflight daily energy expenditure (DEE) was calculated for aviary robins using the time-activity laboratory (TAL) method (after Mugaas and King 1981). For each individual, the costs of the five categories of activity (Table 3)

were calculated on a daily basis and then averaged ($n = 2$ days) to derive the figures given in Table 4. Energy costs were determined using the results of the winter respirometry, but taking into account the observed summer differences (Table 2). The appropriate equations are given in Table 4. It was not possible to measure flight cost directly, so for the present, the period spent in flight is assigned an energy expenditure equivalent to the day-resting level.

TABLE 3. Activity budgets for aviary robins.

		Average temperature (°C)		Night-time rest (h)	Daytime rest		Daytime ground activity		Daytime flying		Distur-bance[b] (h)
Individual	Day	Day	Night[a]		% of day	No. of hours	% of day	No. of hours	% of day	No. of hours	
RB35	1	18.7	23.0	8.67	87.3	11.19	6.9	0.88	5.8	0.74	2.51
	2	21.9	15.6	5.62	78.2	13.20	20.3	3.43	1.5	0.25	1.50
RB36	1	18.7	12.7	5.85	94.9	15.56	2.1	0.34	3.0	0.49	1.75
	2	21.9	25.0	10.23	88.0	11.24	7.6	0.97	4.4	0.56	1.00
RB37	1	18.7	12.7	6.1	89.0	14.15	4.2	0.67	6.8	1.08	2.00
	2	21.9	15.6	5.62	75.7	13.16	15.0	2.60	9.3	1.62	1.00
RB41	1	17.7	25.0	11.13	84.0	9.87	3.7	0.43	12.3	1.45	1.12
	2	20.1	11.2	8.75	86.9	12.18	6.2	0.87	6.8	0.95	1.23
RB42	1	17.7	14.4	8.45	99.1	14.88	0.8	0.12	0.1	0.02	0.53
	2	20.1	25.0	10.33	98.7	12.46	1.1	0.14	0.2	0.03	1.05
RB43	1	17.7	14.4	8.28	88.3	13.20	5.2	0.78	6.5	0.97	0.77
	2	20.1	11.2	8.04	87.0	13.01	8.5	1.27	4.5	0.67	1.01

[a] Night temperatures above 22°C indicate that the bird spent this period in the respirometer.
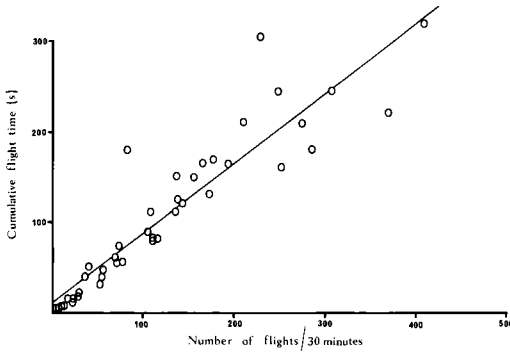
[b] Disturbance = when birds were handled.

Fig. 2. Robin flight activity in an aviary during time budgets of 30 min. Regression slope = 0.777 (SD = 0.046, t = 16.97, P < 0.01), regression constant = 8.35 (SD = 7.17, t = 1.16, NS); r^2 = 86.2, n = 47.

Doubly labeled water results. —The average daily metabolic rate for aviary robins was 5.46 cm^3 $CO_2 \cdot g^{-1} \cdot h^{-1}$ (SD = 0.67, n = 6), ranging from 4.21 to 6.07 cm^3 $CO_2 \cdot g^{-1} \cdot h^{-1}$ (Table 5). At an RQ of 0.75, this gives a daily energy expenditure of 64.8 kJ/day for an 18.6-g robin, which is 2.42 × BMR (where BMR = 2.26 cm^3 $CO_2 \cdot g^{-1} \cdot h^{-1}$ for an 18.6-g passerine; Aschoff and Pohl 1970a). Four overnight respirometry trials at 25°C with $D_2^{18}O$-loaded birds gave an average metabolic rate of 3.33 (SD = 0.50) cm^3 $CO_2 \cdot g^{-1} \cdot h^{-1}$, which was not significantly different from the 3.76 (SD = 0.27) cm^3 $CO_2 \cdot g^{-1} \cdot h^{-1}$ obtained simultaneously using infrared gas analysis.

Cost of flight. —Daily energy expenditure determined using the doubly labeled water (DLW) technique was significantly related to time spent in flight (Fig. 3A). This is described by the relationship DEE = 50.9 + 23.4t_{fly}, where DEE is daily energy expenditure (kJ/day) and

t_{fly} is time spent in flight per day (h). When no time was spent in flight the regression predicted DEE to be 50.9 kJ (SD = 4.3). This is 16% greater than the mean nonflight DEE of 44.0 kJ (SD = 2.3) estimated using the TAL method (Table 4). The regression equation also predicted that for every hour of the day that robins spent in flight there was an increment in DEE of 23.4 kJ (SD = 4.98, n = 6). At the same time, there was a corresponding reduction in the daytime nonflight DEE of 2.2 kJ [1/16 × (70 × 50.9/100)]. This is based on an average of 30% nonflight DEE devoted to nighttime rest (Table 4), occurring over an average of 8 h (Table 3), during which time robins do not fly. Thus, the flight cost of aviary robins was 25.6 kJ/h.

Flight cost can also be calculated using the TAL estimates of nonflight DEE (Table 4). These estimates do not include an estimate of flight cost, the period spent in flight having been allocated a cost equivalent to day resting. Thus, the difference between the DLW estimate of DEE and the TAL estimate may be regarded as the net energy devoted to flight (i.e. the energetic demand above the day-resting level). Figure 3B shows this difference as a function of the time spent in flight. Although the regression coefficient was significantly different from 0 (t = 4.05, P < 0.05), the constant was not (t = 2.06, P > 0.05). Hence, this regression predicted a net energy requirement of only 20.50 kJ when 1 h/day was spent in flight. The extra amount required to convert this figure to gross flight energy is the cost of day resting for 1 h at the mean daytime temperature during the experiment (19.6°C), which is 3.52 kJ/h. Hence, a second estimate of flight cost is 24.02 kJ/h. It

TABLE 4. Energetic costs for aviary robins based on two 1-day TAL predictions (kJ/day).[a]

Bird	Night resting	Disturbance cost	Day resting	Ground activity	Flight period at M_{rD} level	Nonflight DEE
RB35	10.46	3.26	22.10	5.59	0.92	42.33
RB36	12.71	2.47	27.06	1.86	1.05	45.15
RB37	10.84	2.67	27.13	4.60	2.65	47.89
RB41	15.37	1.95	21.18	1.80	2.35	42.65
RB42	13.92	1.29	26.26	0.36	0.05	41.88
RB43	14.11	1.43	24.43	2.76	1.54	44.27
Mean	12.90	2.18	24.69	2.83	1.43	44.03
(SD)	(1.94)	(0.76)	(2.57)	(1.94)	(0.96)	(2.26)

[a] Energy cost (J·g^{-1}·h^{-1}): night resting (M_{rN}) = 111.84 − 1.938T_a, plus 12% for summer metabolism; day resting (M_{rD}) = 134.84 − 2.134T_a, plus 11% for summer metabolism; ground activity (M_{hop}) = 211.73 − 3.102T_a. Disturbance cost (blood sampling, weighing, transit, etc.) taken as M_{rD} at 25°C, plus 12%.

TABLE 5. Metabolic rate of aviary robins during summer determined using doubly labeled water ($D_2^{18}O$).

Bird	Body mass (g)	Metabolism (cm³ CO₂· g⁻¹·h⁻¹)	DEE[a] (kJ/day)	DEE (×BMR[b])
RB35	17.9	6.07	70.32	2.67
RB36	19.7	5.50	68.83	2.48
RB37	19.5	6.02	74.68	2.70
RB41	18.4	5.55	65.07	2.46
RB42	18.2	4.21	48.61	1.85
RB43	17.8	5.39	61.07	2.36
Mean	18.6	5.46	64.76	2.42
(SD)	(0.8)	(0.67)	(9.17)	(0.31)

[a] Using RQ = 0.75, 1 cm³ CO₂ = 26.44 J (Brody 1945).
[b] Predicted from body mass, BMR = 1.11 kJ/h (night phase; Aschoff and Pohl 1970a).

may be argued that resting during the day includes a high proportion of alert behavior that may have a higher cost than indicated by M_{rD}. An estimate of the alert cost was made using the upper confidence limit of the M_{rD} regression ($M_{rD} + tS_{yx}$, t at 95%), which is equivalent to an addition of 0.4 BMR (0.85 cm³ $CO_2 \cdot g^{-1} \cdot h^{-1}$). Recalculating the nonflight TAL prediction of DEE gave a mean value of 53.98 kJ/day (SD = 3.21), which is close to that predicted above (50.9 kJ/day). Using these higher values of nonflight DEE produced only a slight change in the predicted flight cost, which was 23.47 kJ/h (19.95 + 3.52).

DISCUSSION

Winter/summer metabolism.—The winter metabolism results may be compared with those obtained by Gavrilov (*in* Kendeigh et al. 1977) for Russian robins of slightly lower average body mass (17.6 g). His equation for winter robins (night resting metabolism, cm³ $CO_2 \cdot g^{-1} \cdot h^{-1}$ = 5.84 − 0.1460T_a) indicates a much greater increase in energy requirement as T_a declines than we found (Table 1). Possibly, this was due to an adjustment of the relationship undertaken to ensure that metabolic rate was zero when the ambient and bird's body temperatures were equal (see Kendeigh et al. 1977: appendix 5.1). A similar procedure was investigated here (see Methods), and it produced the following equation for night resting metabolism: cm³ $CO_2 \cdot g^{-1} \cdot h^{-1}$ = 5.34 − 0.1315T_a. Although this is similar to Gavrilov's result, it was not acceptable because it overestimated
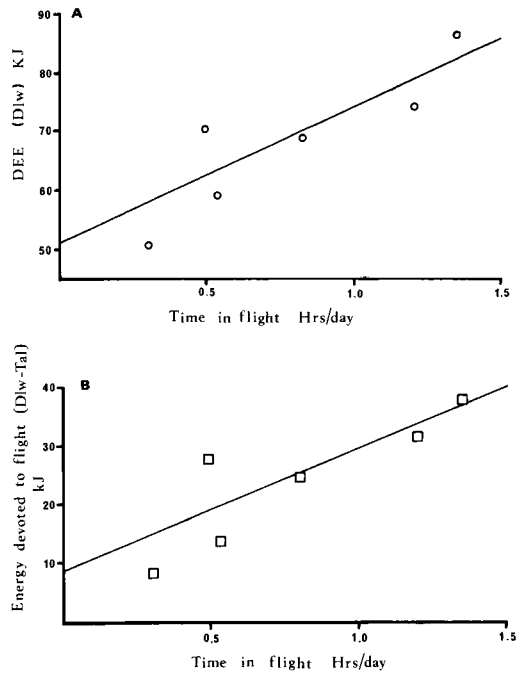

Fig. 3. Robin energy expenditure as a function of time spent in flight. (A) Regression slope = 23.4 (SD = 4.98, t = 4.69, P < 0.01), regression constant = 50.9 (SD = 4.29, t = 11.85, P < 0.01); r^2 = 80.8, S = 5.46. (B) Regression slope = 20.5 (SD = 5.07, t = 4.05, P < 0.05), regression constant = 8.98 (SD = 4.37, t = 2.06, P > 0.05); r^2 = 75.5, S = 5.55. Dlw = Doubly labeled water.

metabolism at low temperatures. Differences in the slope of metabolic equations for summer and winter given by Gavrilov indicate a reduction in conductance of 7%, probably due to thicker winter plumage. In Moscow, robin plumage increased from 7% of the body mass (14.0 g) to 9.1% of the body mass (17.2 g) between summer and winter (Shilov 1968). Seasonal shifts in thermoregulatory metabolism are well documented (Calder and King 1974) and have been related to body mass (Kendeigh et al. 1977). Regression coefficients for SMR (Kendeigh et al. 1977: 135) of an 18.6-g passerine, calculated for summer and winter, indicate a 12% increase in summer energy requirements [i.e. winter temperature coefficient (b) = 1.490 kJ·bird⁻¹·day⁻¹·°C⁻¹, compared with summer temperature coefficient (b) = 1.676 kJ·bird⁻¹·day⁻¹·°C⁻¹]. Elevated resting metabolic rates therefore are expected for summer robins, in accordance with the 11–12% increase we observed.

The reason for the higher RQ values for summer robins in this study is rather obscure. Work on substrate concentrations and turnover in birds has demonstrated that in some winter-acclimatized species there is a reduced reliance on carbohydrate as a metabolic fuel, although this was observed only for elevated rates of thermogenesis (Marsh and Dawson 1982, Marsh et al. 1984).

The absence of a significant metabolic difference between summer and winter hopping trials may be due to the small sample size and high degree of inherent variability. Pohl and West (1973) reported a greater heat production during forced exercise for Common Redpolls (*Carduelis flammea*) in winter compared with summer.

Daily energy expenditure.—Robins in the aviary spent a high proportion of the daylight period resting, with relatively little time devoted to activities akin to foraging (Table 3). These aspects of their daily behavior may be different from robins in their natural habitat at this time of year, as East (1982) has shown that robins forage for approximately 20% of the time at temperatures greater than 10°C. The proportion of time spent in flight also may be lower than the free-living level. Walsberg's equation relating percentage of active day spent in flight to body mass (Walsberg 1983: Eq. 11) predicts a figure of 7.6% ($\pm$1 SD, 3.1–18.7%) for an 18.6-g bird, compared with a mean of 4.3% ($\pm$1 SD, 1.1–9.2%) found here. So, it is likely that the mean DEE estimate (DLW; 64.76 kJ/day) reported in this study will be low compared with free-living individuals. This suggestion is in accordance with a DEE prediction of 76.40 kJ/day for an 18.6-g nonbreeding passerine (Bryant et al. 1985), which is 18% above the value we observed.

Flight costs.—Bird flight is recognized as a costly but highly efficient form of locomotion (Tucker 1970). Determination of flight costs has been approached using a variety of techniques, including material balance (Kespaik 1968, Lyuleeva 1970), flight mechanics (Pennycuick 1968, 1975; Tucker 1968; Greenewalt 1975; Rayner 1979a), and doubly labeled water (LeFebvre 1964, Utter and LeFebvre 1970, Hails 1979, Flint and Nagy 1984). The theoretical approach predicts a U-shaped curve relating power requirements to flight speed (Pennycuick 1975), but in studies of DEE the cost of flight usually is taken as a multiple of BMR (see Williams and Nagy

TABLE 6. Wing characteristics of small birds.

	Body mass (g)	Wing area (cm^2)	Wing loading (g/cm^2)	Aspect ratio (wingspan^2/ wing area)
Erithacus rubecula[a]	18.6	70.8	0.263	7.33
Lanius excubitor[b]	31	144	0.215	—
Parus major[b]	14.5	62	0.234	—
Emberiza gubernatrix[b]	25.5	100	0.255	—
Passer domesticus[b]	28.3	76	0.372	—
Spizella a. arborea[b]	18	90	0.200	—
Anthus spinoletta[b]	19	109	0.174	—
Parus ater[c]	9.1	53.8	0.169	6.02
Parus montanus[c]	10.9	61.9	0.176	5.53
Parus cristatus[c]	12.2	60.2	0.203	5.75
Regulus regulus[c]	5.9	35.4	0.167	5.94
Certhia familiaris[c]	9.1	62.4	0.146	5.72

[a] Measured, $n = 21$.
[b] Greenewalt 1962.
[c] Norberg 1979.

1984). There is an implicit assumption that the flight speed adopted coincides with the minimum power speed (base of the U power curve). However, the energetic cost of flight is likely to reflect a compromise between flight speed and flight gait, both being influenced by the current demands on a bird's time and activity budget (Norberg 1981, Pyke 1981). There is also likely to be an inverse relationship between the cost associated with the flight gait and the time spent in the air. Hails (1979) showed that avian aerial insectivores, which spend most of their life in the air, exhibit flight costs that are 49–73% lower than predicted on the basis of body mass for nonaerial species. More recently, a similar result was reported for a larger, nonpasserine seabird (Flint and Nagy 1984). Our study considers the opposite end of the spectrum in terms of adaptation to an aerial existence. For most of the year robins spend only a small proportion of their time in flight. Thus, during 172 h of time budgeting this species, East (1982) obtained such small sample sizes for birds in flight that it was necessary to pool the information with other activities of short duration or infrequent occurrence. The European Robin's mode of foraging involves hopping, although there are often short flights between perches and the ground (East 1980). The wing loading and aspect ratio of a robin are high compared with most other birds with a similar body mass or wing area (Table 6). A high aspect

TABLE 7. Predictions of European Robin flight cost.[a]

Source	Flight cost (kJ/h)	Method
Pennycuick 1975 (Eq. 25)	5.69	Body measurements and flight speed
Tucker 1973 (Eq. 49)	6.43	Body measurements and flight speed
Greenewalt 1975[b]	5.61	Body measurements and flight speed
Hart and Berger 1972	10.23	Body mass
Kendeigh et al. 1977	14.66	Body mass
Hails 1979	11.90	Body mass

[a] Robin measurements ($n = 21$): body mass = 18.6 g (0.182 N), wingspan = 228 mm, wing area = 70.78 cm^2, flight speed = 3.85 m/s, air density = 1.18 kg/m^3 (Hodgman 1959).
[b] Eq. 23 (1.09 kJ/h) × 4 (muscular efficiency 25%) + SMR (=1.24 kJ/h; Lasiewski and Dawson 1967).

ratio indicates relatively long wings, which may improve maneuverability, but this could be a disadvantage in a small bird that exhibits flapping flight because of the increased wing inertia. These characteristics suggest that the flight cost of foraging robins may be high.

Predictions of flight cost in the robin vary from 5.61 to 14.66 kJ/h (Table 7). The lowest estimates, derived using aerodynamic theory (Pennycuick 1975), indicated a flight cost of only 5.1 × BMR. This calculation is likely to have underestimated induced power for robins in this study, as the very short flight duration meant that a proportion of the time was probably very similar to hovering. Rayner (1979b: 751) noted that induced power is better predicted at low flight speeds using a model for hovering. The observed flight speed (3.85 m/s) was lower than the theoretical minimum power speed (5.86 m/s, Pennycuick 1975). This would also increase observed flight cost relative to the theoretical prediction. Limitations associated with the models of flight mechanics employed here are discussed by Rayner (1982).

The flight cost predictions based on body mass (Table 7) are much greater than those derived using theoretical flight mechanics, probably because the latter underestimate the physiological requirements of flight (Rayner 1982) and the increase in power required for low-speed flight in small birds (Tucker 1973: fig. 1, Westerterp and Drent 1985: fig. 4). Mechanical predictions of energy requirements for flight do not make provision for the cost of take-off, which is presumably greater than that of sustained flight and which assumes a high significance in the present work. Allometric equations relating body mass to physiological measures of flight metabolism tend to utilize data based on protracted flight duration, and therefore may reflect minimum power require-

ments. Teal (1969) provided data on the cost of brief flights ($\bar{x} = 68$ s, SD = 42, $n = 56$) in small birds based on direct measurement of CO_2 production. His passerine results are shown in Fig. 4, from which it can be determined that flight cost (cm^3 CO_2/h) = $53.70M^{1.03}$, where M is body mass (g). This relationship predicts that flight cost for an 18.6-g robin will be 30.14 kJ/h (assuming RQ = 0.71; Torre-Bueno 1977), rather higher than we observed.

The cost of flight for robins in this study was extremely high at 25.6 kJ/h [23 × BMR (night) = 1.11 kJ/h; Aschoff and Pohl 1970b]. This demand operates for only very short periods, however, as the average flight duration was 0.78 s. During the 30-min time-budgeting periods cumulative flight time for robins averaged 100.2 s. In this instance, 712.5 J would be required for flight, plus 866.3 J for the remaining period, assuming it was at the average nonflight level (Table 4; 44.03 kJ/day or 0.51 W). Hence, the overall average sustained energy demand may have been only 3.16 kJ/h (2.8 × BMR). The maximum cumulative time spent flying in a 30-min bout was 320 s; even when flying for three times as long, the sustained energy demand would not be exceptional (6.06 kJ/h, 5.46 × BMR; see Westerterp and Bryant 1984).

Energy demand for a single flight (0.75 s) is 5.3 W, of which 0.51 W may be accounted for by resting metabolism, leaving 4.79 W associated with flight activity. Maximum sustained output of striated muscle is estimated to be 250 W/kg of muscle tissue (Weis-Fogh and Alexander 1977). In the European Robin the pectoralis muscles weigh 3.0 g, implying a mechanical power output of up to 0.75 W. Assuming 23% muscle efficiency (Pennycuick 1975), the maximum power consumption of the flight muscles will be 3.26 W. This leaves a

shortfall of 1.53 W, which could be accounted for by the muscular activity of the legs during take-off and landing. If this is correct, the energy requirements during short forays can be partitioned as 61% flight, 29% take-off and landing, and 10% resting metabolism.

For sustained flight, most allometric predictions are based on body mass$^{0.75}$, which indicates that sustained power requirements in flight are a multiple of basal metabolic rate (Hart and Berger 1972). Hence, larger birds use proportionally less power in continuous flight. Theoretical aerodynamic predictions indicate a more direct proportionality with body mass ($M^{1.17}$ in Hart and Berger 1972, $M^{1.10}$ in Rayner 1979a). These calculations are based on structural and mechanical features and therefore are more likely to reflect the ability for maximal power output, the duration of which probably is limited in the longer term by physiological constraints, including substrate availability and oxygen debt. Maximal power output in flight is therefore likely to be greater than sustained output, and might be expected to occur during short, brief flights such as those documented by Teal (1969), Westerterp and Drent (1985: fig. 3), and the present study. This is in accordance with the reanalysis of Teal's data, which indicate power requirements that are proportional to body mass ($M^{1.03}$; see Fig. 4.).

The high cost of flight (23.4 kJ/h) reported here for the European Robin is a consequence of the short flight duration. It is thought to provide a realistic estimate for the cost of non-migratory flights because the gait exhibited was similar to that observed in the natural situation. As mentioned, structural aspects of the robin's wing and the slow flight speed indicate that short flights are likely to involve high cost.

Implications for energetics studies. — The discussion of flight cost indicates that attention should be paid to the foraging mode employed by the species when constructing a TAL budget. Thus, aerial-foraging species are adapted for low-cost flights of 2.9–5.7 × BMR (Hails 1979) or 4.8 × BMR (Flint and Nagy 1984), whereas foraging that involves many short flights may involve costs as high as 21 × BMR (this study), or even higher because the cost is not proportional to basal metabolism (Fig. 4). Current allometric flight equations (Hart and Berger 1972, Kendeigh et al. 1977, Hails 1979) employed to predict flight costs in TAL studies give estimates that are intermediate between these extremes.
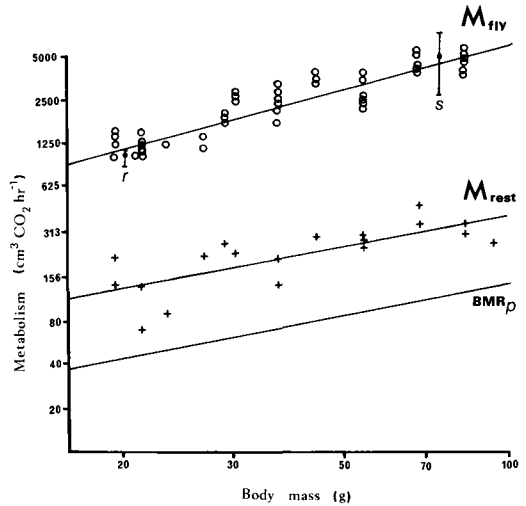

Fig. 4. Metabolic rate (cm^3 CO$_2$/h) as a function of body mass (g). Flight (circles) and resting (crosses) values are passerine data from Teal (1969). Robin flight cost (± 1 SD) = r. Starling flight cost (± 1 SD) = s (after Westerterp and Drent 1985). Regression equations are: Flight metabolism (M_{fly}) = 53.70$M^{1.03}$ (slope = 1.03, SD = 0.05, t = 19.12, $P < 0.001$; log$_{10}$ constant = 1.74, SD = 0.09, t = 20.01, $P < 0.001$; r^2 = 86.9, log$_{10}$ S = 0.09). Resting metabolism (M_{rest}) = 16.98$M^{0.69}$ (slope = 0.69, SD = 0.14, t = 4.93, $P < 0.001$; log$_{10}$ constant = 1.23, SD = 0.22, t = 5.45, $P < 0.001$; r^2 = 55.1, log$_{10}$ S = 0.14). Night basal metabolism (BMR) = 5.03$M^{0.726}$ (after Aschoff and Pohl 1970a). Body mass (g) = M.

Although accurate predictions of flight and other costs are important when constructing TAL estimates of DEE, they must be considered in conjunction with limitations of the time-budget technique. It is noteworthy that in most doubly labeled water studies where it was relatively easy to obtain an accurate estimate for time spent in flight as a result of its conspicuousness or duration, this has correlated well with the DEE (Table 8). There will be no variation in DEE due to the flight component, however, unless there is a significant difference between individuals in the amount of time they spend in flight. A priority in future studies of this type should be to ensure that the flight component is accurately sampled, even though it may form only a small proportion of the daily activity.

Interest in the field of free-living energetics studies has centered on obtaining a TAL model that will accurately predict DEE as revealed by

Table 8.   Correlation between DEE and flight parameters.

Source	Species	Corre-lation (r)	Flight parameter
Flint and Nagy 1984	Sooty Tern (*Sterna fuscata*)	0.92	Time in flight
Bryant and Westerterp 1980	House Martin (*Delichon urbica*)	0.49	Percentage of period in flight
Westerterp and Bryant 1984	Barn Swallow (*Hirundo rustica*)	0.85	Percentage of period in flight
	Bank Swallow (*Riparia riparia*)	0.82	Percentage of period in flight
Westerterp and Drent 1985	European Starling (*Sturnus vulgaris*)	0.94	Time in flight
Weathers and Nagy 1980	Phainopepla (*Phainopepla nitens*)	None	Time in flight
Williams and Nagy 1984	Savannah Sparrow (*Passerculus sandwichensis*)	None	Time in flight
Weathers et al. 1984	Loggerhead Shrike (*Lanius ludovicianus*)	None	Time in flight
Nagy et al. 1984	Jackass Penguin (*Spheniscus demersus*)	0.88	Distance swum
This study	European Robin (*Erithacus rubecula*)	0.90	Time in flight

the doubly labeled water method (Weathers and Nagy 1980, Williams and Nagy 1984, Weathers et al. 1984, Bryant et al. 1985). Weathers et al. (1984) emphasized the importance of obtaining an accurate estimate of the operative temperature (T_e; Bakken 1976) and using measured energy equivalents for various behaviors. The latter aspect was endorsed here by the comparison of resting metabolism results for Scottish and Russian robins. Operative temperature was not determined in the present study because the birds were sheltered from the effects of sun and wind. This may have affected the nonflight estimates of DEE (Table 4), but the similarity in predictions of flight cost indicate that this was of minor significance. Williams and Nagy (1984) published an analysis of DEE for the Savannah Sparrow (*Passerculus sandwichensis*) in which

TABLE 9.   Correlation between DLW and TAL measures of daily expenditure for the Savannah Sparrow (after Williams and Nagy 1984).

Model	Coefficient of determination (r^2) %	
	All data	Excluding bird No. 144
Schwartz and Zimmerman 1971	0	0
Utter and LeFebvre 1973	24	53
Walsberg 1977	0	12
Kendeigh et al. 1977	0	0
Holmes et al. 1979	11	89[a]
Walsberg 1980	19	60
Mugaas and King 1981	5	73

[a] Significant at 1%.

they concluded that three of the TAL models examined yielded mean estimates comparable to those given by the DLW method, but that there was no correspondence in the variability. When their DLW results are plotted as a function of TAL predictions, there are no significant correlations (Table 9). This lack of correlation appears to be due to a single individual (No. 144), which was the least intensively observed. Exclusion of this bird reveals an improved level of correlation between DLW and TAL results (Table 9), to the extent that the model of Holmes et al. (1979) provides a significant correlation. Although it is of questionable validity to have excluded individual 144, this reinterpretation does offer some encouragement for accurate prediction of intraspecific DEE variability using TAL methods. It also indicates the importance of both increasing the number of individuals sampled in each study and obtaining an accurate measure of time spent in brief but costly activities if the conclusions in this type of study are to withstand critical appraisal.

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ERRATA

In the memorial to Edmund W. Mudge (1985, Auk 102: 869), "Edmund W. Mudge" should read "Edmund W. Mudge, Jr."

There is an error in the article by Spencer G. Sealy (1985, Auk 102: 889–892). At the end of paragraph 2 on page 889, the sentence beginning "In 1979 a single 9-day-old cuckoo gradually assumed an erect posture ..." should read "In 1985 ...."

CHANGES IN BODY WEIGHT AND BODY COMPOSITION OF BREEDING RING-NECKED DUCKS (*AYTHYA COLLARIS*)

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ABSTRACT.—Body composition of male and female Ring-necked Ducks (*Aythya collaris*) changed substantially over the course of reproduction, with the largest nutrient reserves occurring before the onset of laying. Ring-necked Ducks used lipid reserves acquired before occupancy of nesting areas to meet subsequent reproductive requirements. Paired males reduced feeding and expended lipid reserves while attending prelaying and laying mates. Females depleted lipid reserves during ovarian follicle growth; after ovulation they were highly dependent on ambient food resources. Female Ring-necked Ducks obtain protein required for egg production from the diet during ovarian follicle growth. This conclusion was supported by (1) the limited extent of body protein fluctuation; (2) the absence of a relationship between body protein and protein contained in recrudesced reproductive tissues and expended in eggs; and (3) similarities in the rate of change in body protein by date between males and females, and among females before and after laying. Female energy expenditures during ovarian follicle growth are influenced by costs associated with obtaining nutrients needed for egg production. The level of lipid reserve needed for reproduction, therefore, changes with food availability. Deficiencies in female lipid reserve at the initiation of ovarian follicle growth further increase exogenous requirements for reproduction and may result in adjusted breeding patterns or deferred breeding. The contribution of body reserves to reproduction was partially a function of nutrient levels attained during the arrival period. Variations in Ring-necked Duck body-weight change, by year and by female age, suggest that nutrient acquisition and allocation for waterfowl nesting in temperate regions may be more indeterminant than has been implied previously. *Received 18 March 1985, accepted 20 September 1985.*

ENERGETIC costs of reproduction for ducks and geese are large relative to those of other major bird groups (King 1973, Ricklefs 1974). In general, birds have a substantial capability for storage and utilization of energy reserves, primarily in the form of lipids (Blem 1976). Such reserves play a prominent role in waterfowl reproduction (Barry 1962; Ryder 1967, 1970; Harvey 1971; Korschgen 1977; Ankney and MacInnes 1978; Raveling 1979; Krapu 1981; Drobney 1982; Reinecke et al. 1982; Ankney 1984; Tome 1984).

Ring-necked Ducks (*Aythya collaris*) are small-bodied (500–900 g), inland diving ducks (Tribe Aythyini), which have been studied principally in the northeast (Mendall 1958). They commonly nest in northern bog marshes, permanent wetlands characterized by low primary production (Reader 1978). I examined changes in body weight and body composition of breeding Ring-necked Ducks by sex and age. Attention was focused on body condition of returning birds, with the prediction that endogenous reserves accumulated before occupancy of wetlands used for nesting were critical to successful reproduction by this species.

METHODS

Breeding Ring-necked Ducks were studied from April to August 1978–1980 on Roseau River Wildlife Management Area (WMA) in northwestern Minnesota. Birds were collected by shooting, decoy trapping (Anderson et al. 1979), nest trapping (Weller 1957), or night-lighting (Lindmeier and Jessen 1961). Body weights (±5 g) were taken immediately after collection. Feathers (5th primary, 5th secondary, 12th and 13th greater upper secondary coverts) were removed in 1979 and 1980, and age (yearling = first-year bird, before prebasic II molt; adult = after-first-year bird, after prebasic II molt) was assigned on the basis of discriminant function analysis of feather measurements (Hohman 1984). Live-trapped birds were marked individually with a plastic nasal-saddle

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(Doty and Greenwood 1974). Birds collected by shotgun were frozen in sealed plastic bags for later dissection.

Females and their mates were assigned to the following reproductive categories, based in part on Krapu (1974):

Arrival.—Females returning to the breeding grounds with ovary weight <3 g.
Prelaying.—Preovulating females with ovary weight ≥3 g.
Laying.—Ovulating females.
Early incubation.—Postovulating hens captured on nest, estimated days of incubation ≤9 days as determined by field candling (Weller 1956) or embryonic inspection (Caldwell and Snart 1974).
Middle incubation.—Eggs incubated 10–18 days.
Late incubation.—Eggs incubated >18 days.
Early brood.—Hens attending age class I ducklings (Gollop and Marshall 1954).
Late brood.—Hens attending age class II ducklings.
Postbreeding.—Birds collected in July and August on molting areas before remigial feather molt.

Females initiated ovarian follicle growth after 6 May, as verified by back-dating on hens of known reproductive status. Consequently, all birds handled before 6 May were placed in the arrival category. Pairing status was assigned to marked males on the basis of behavioral observations made following capture. Paired individuals were birds showing active association, i.e. copulation, mutual display, female tolerance of male, or nonrandom spacing. Unmarked males were considered unpaired if observed on collection before 6 May without a mate.

Predictive indices were used to estimate ash-free, lean dry weight ("protein"), and lipid composition of whole carcasses less reproductive tissues (Hohman and Taylor 1986). Body lipid was regressed on wet weights of abdominal fat and skin tissues. Protein was estimated from eviscerated carcass, right breast muscle and right leg muscle weights, and bill length measurement. Lipid and protein content of ovary and oviduct tissues were derived using wet weights of these organs and estimates of composition of the ovary (35.2% lipid, 17.7% protein; Romanoff and Romanoff 1949) and of the oviduct (22.4% protein; Drobney 1980). To monitor change in mineral composition, ashed (550°C, 48 h) weights were taken on female femurs and tibiotarsi.

Statistical comparisons of body weight, body lipid and protein composition, and weight of ashed leg bones by reproductive status and 10-day Julian date interval were made using one-way analysis of variance. Multivariate (factors = age, year, date, and reproductive status) analysis of variance was performed on body-weight data using BMDP-4V statistical software (Dixon and Brown 1981). The maximum extent of seasonal body-weight change was

expressed as a percentage of maximum mean body weight (Reinecke 1977). Mean body weights by reproductive status and 10-day interval were compared between 1979 and 1980 using sign tests (Conover 1980). Regression procedures followed Weisberg (1981). Significance level was set at $P < 0.05$.

RESULTS

BREEDING PHENOLOGY

Paired Ring-necked Ducks began to arrive in the vicinity of Roseau River WMA in early April, soon after snowmelt. Sheet water on agricultural fields adjacent to the management area was used by birds initially. Birds remained on seasonal wetlands until about late April, when the study area became ice-free. Laying was initiated from mid-May to early June, and broods usually were evident by the fourth week of June. Males left Roseau River WMA by early July; females departed 4–6 weeks later, after their broods had attained class II stage of plumage development.

Breeding phenology for Ring-necked Ducks in northwestern Minnesota was similar to that observed by Sarvis (1972) in Michigan, but somewhat later than that recorded in Maine (Mendall 1958). Breeding phenology in northwestern Minnesota did not vary appreciably among years.

BODY WEIGHTS

Female.—Body weights were obtained from 263 breeding female Ring-necked Ducks. Female body weight changed substantially through reproduction (Table 1). Weight increased significantly from arrival to maximum seasonal levels at the initiation of ovarian follicle growth. Body weight declined after the onset of laying. Body weight recovered significantly in hens with class II ducklings after late July from seasonal minima observed in early brood rearing. The maximum body-weight change amounted to 29% (229 g) for breeding females.

The pattern of body-weight change differed for yearling and adult females, and varied among years. Adult females collected early in the arrival period were significantly heavier than yearlings in both 1979 and 1980 (Table 2). Mean body weights for adult and yearling birds, however, did not differ by reproductive status

TABLE 1. Body weight and body composition of breeding female Ring-necked Ducks collected in northwestern Minnesota, 1978–1980.

Stage of reproduction	Body weight	Lipid	Protein
Arrival	703 ± 8[a]	88.0 ± 7.0	119.7 ± 1.1
n	69	35	35
P[b]	***	NS	NS
Prelaying	803 ± 35	118.2 ± 24.1	123.8 ± 3.2
n	8	4	4
P	NS	**	***
Laying	782 ± 12	51.0 ± 4.0	116.1 ± 1.2
n	16	14	14
P	***	NS	NS
Early incubation	666 ± 14	35.5 ± 4.1	111.9 ± 0.9
n	5	4	4
P	NS	NS	NS
Midincubation	653 ± 15	37.8 ± 5.7	111.9 ± 2.5
n	9	2	2
P	**	NS	NS
Late incubation	594 ± 8	27.9 ± 3.2	106.9 ± 7.9
n	23	2	2
P	NS	NS	NS
Early brood rearing	574 ± 7	28.1 ± 3.5	103.3 ± 2.9
n	54	3	3
P	NS	NS	NS
Late brood rearing	588 ± 7	40.1 ± 4.2	101.3 ± 1.4
n	42	5	5

[a] Mean ± SE (g).
[b] P = probability (from one-way ANOVA) that adjacent means within a column are significantly different.
** = $P < 0.01$; *** = $P < 0.001$; NS = $P > 0.05$, not significant.

within years, suggesting that adult females returned heavier or gained weight more rapidly, or both, compared with yearlings.

Mean body weight by 10-day interval fluctuated more widely in 1979 than in 1978 and 1980 (Fig. 1). Differences among years were greatest early in the reproductive cycle. Before 6 May, adults and yearlings were significantly lighter in 1980 than early-arrival birds collect-

ed in the previous years (Table 2). Females by reproductive status (sign test, $T = 5$, df = 5, $P < 0.05$) and by 10-day interval (sign test, $T = 9$, df = 10, $P < 0.01$) were generally heavier in 1979 than in 1980. Outside of the arrival period, however, mean female body weight by 10-day interval or by reproductive status did not differ significantly between years.

Male.—Body weights were taken on 334

TABLE 2. Body weights of breeding Ring-necked Ducks collected in northwestern Minnesota early in the arrival period (before 6 May).

	Female				Male			
Year	Yearling	P[a]	Adult	All	Yearling	P	Adult	All
1978[b]				700 ± 13[c]				731 ± 8
n				15				44
1979	715 ± 20	*	777 ± 18	742 ± 16	772 ± 21	NS	793 ± 15	787 ± 12
n	9		7	16	6		16	22
P	**		**	NT	NT		NT	***
1980	632 ± 12	***	705 ± 9	670 ± 11	700 ± 12	NS	726 ± 7	718 ± 6
n	12		13	25	20		50	70

[a] P = probability that adjacent means within a column or row are significantly different. * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; NS = $P > 0.05$, not significant; NT = no test.
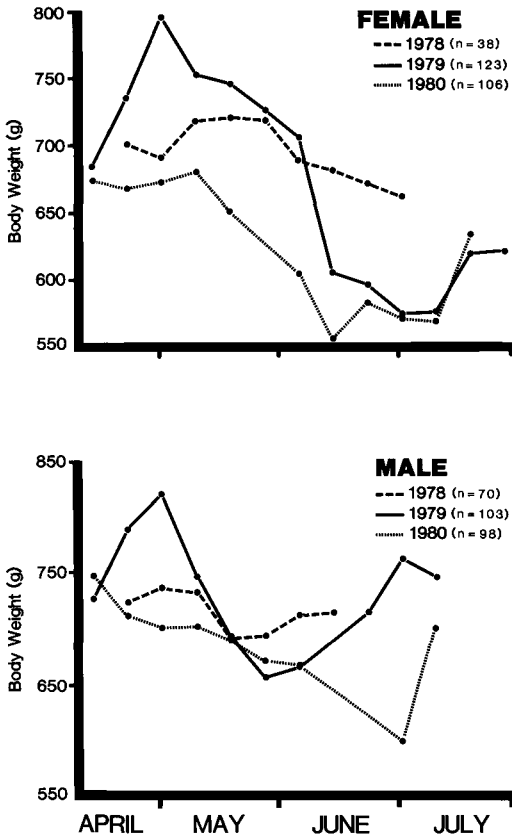[b] Age was not determined.
[c] Mean ± SE (g).

Fig. 1. Mean body weights of breeding female and male Ring-necked Ducks by 10-day interval and year, 1978-1980.

breeding males. Male body weight changed significantly with their mates' reproductive status and by 10-day interval (Table 3). Birds were heaviest during their mates' arrival and prelaying reproductive periods. A significant decrease in body weight corresponding to the period of ovarian follicular growth occurred in mid- and late May. Seasonal minima in male body weight were recorded after their females began incubation. The maximum extent of change in male body weight amounted to 10% (73 g).

No significant age-related differences in male body-weight change were detected, but male body weight by 10-day interval changed differently in 1979 and 1980 (Fig. 1). Seasonal fluctuation in mean body weight by 10-day interval was greater in 1979 than in either 1978 or 1980. Males collected early in the arrival period were significantly heavier in 1979 than in 1978 and 1980 (Table 2). Weight was gained

between mid-April and early May 1979, and similar gains were shown by recaptured individuals. Similar increases were not observed before the onset of ovarian follicle growth in other years. Outside of the arrival period the patterns of seasonal weight change for all years were alike.

BODY COMPOSITION

Female.—Lipid and protein composition was estimated for 72 breeding females. Lipid stores were largest in arrival and prelaying birds before mid-May (Table 1). Body lipid declined significantly when females began laying. Seasonal minima occurred during late incubation and early brood rearing, mid-June to late July. No significant differences between adult and yearling females, or among years, were apparent in body lipid by reproductive status or by 10-day interval, although small sample sizes in some categories may have prevented the detection of differences.

Body protein declined 19% (23 g) from prelaying to late brood rearing (Table 1). Seasonal decline in body protein was approximately constant (Fig. 2) and unrelated to changes in reproductive protein, i.e. protein contained in recrudesced reproductive tissues and expended in eggs ($r = -0.3467$, df = 15, $P > 0.05$).

Minerals required for eggshell formation apparently were deposited in the skeleton during the period of ovarian follicle growth. Femoral and tibiotarsal mineral content increased significantly from arrival to prelaying and laying. Ashed leg-bone weights before and after the period of ovarian follicle growth did not differ, and were equivalent in adult and yearling females.

Male.—Lipid and protein composition was estimated for 78 breeding males. Body lipid in males decreased significantly between their mates' arrival and laying reproductive stages (Table 3). Lipid level in males was greatest before mid-May, when some females initiated laying. Seasonal minima were recorded in mid-June at the termination of the laying period. Body lipid remained at low levels while birds were on the study area. Changes in male lipid and protein composition were not significantly influenced by age, year, or pairing status.

Body protein declined in males from May to July (11%, 14 g) at the same rate observed in females (Fig. 2).

TABLE 3. Body weight and body composition of breeding male Ring-necked Ducks collected in northwestern Minnesota, 1978–1980.

Stage of mate's reproduction	Body weight	Lipid	Protein
Arrival	735 ± 5[a]	102.5 ± 6.8	125.6 ± 1.0
n	144	38	38
P[b]	NS	NS	NS
Prelaying	752 ± 22	93.0 ± 44.3	126.6 ± 2.1
n	6	3	3
P	NS	NS	**
Laying	707 ± 11	54.6 ± 4.5	117.8 ± 1.8
n	13	12	12
P	NS	NS	NS
Incubation	679 ± 19	49.6 ± 4.6	117.2 ± 2.2
n	12	5	5
P	**	NS	NS
Postbreeding	735 ± 22	65.4 ± 11.1	121.2 ± 2.0
n	9	9	9

[a] Mean ± SE (g).
[b] P = probability (from one-way ANOVA) that adjacent means within a column are significantly different.
** = $P < 0.01$; NS = $P > 0.05$, not significant.

DISCUSSION

Body composition of male and female Ring-necked Ducks changed substantially over the course of reproduction, with the largest nutrient reserves occurring before the onset of laying. Ring-necked Ducks use lipid reserves acquired before occupancy of nesting areas to meet subsequent reproductive requirements. Females incur substantial costs from egg production. Lipid reserves are depleted during ovarian follicle growth; after laying, females are highly dependent on ambient food resources. Paired males reduce feeding (Hohman unpubl. data) and expend lipid reserves while attending prelaying and laying mates. Close attendance of the female minimizes the chances of a male being displaced by another male, or having his mate inseminated by other males. Moreover, male defense of the female against intrusions by other birds and vigilance against potential predators probably facilitate female feeding (Ashcroft 1976). This may be especially important during ovarian follicle growth, when female nutrient demands are greatest.

Protein stored in muscle sarcoplasm (Kendall et al. 1973) is used by Common Eiders (*Somateria mollissima*; Korschgen 1977) and some arctic-nesting geese (Ankney and MacInnes 1978, Raveling 1979) to produce eggs. Over 80 g of protein are required for production of an average clutch and biosynthesis of oviduct tissue by Ring-necked Ducks (Hohman 1984). This is equivalent to about 67% of the protein content of female carcasses before ovarian follicle growth. Female Ring-necked Ducks obtain protein required for production of eggs almost exclusively from the diet during ovarian follicle growth. This conclusion is supported by (1) the limited extent of body protein fluctuation; (2) the absence of a relationship between body protein and protein contained in recrudesced reproductive tissues and expended in eggs; and (3) similarities in the rate of change in body protein by date between males and females, and among females before and after laying. Other small-bodied waterfowl, such as Wood Ducks (*Aix sponsa*; Drobney 1982), American Black Ducks (*Anas rubripes*; Reinecke et al. 1982), Mallards (*Anas platyrhynchos*; Krapu 1981), and Ruddy Ducks (*Oxyura jamaicensis*; Tome 1984), also obtain protein required for egg production from the diet during prelaying and laying.

Female energy expenditures during ovarian follicle growth are influenced by costs associated with obtaining nutrients for egg production. Depletion of body lipid by prelaying/laying Mallard and Wood Duck hens may exceed the amount contained in a completed clutch of eggs (Krapu 1981, Drobney 1982). This difference was attributed to additional foraging costs incurred by females specializing on invertebrate foods. Hohman (1985) suggested that selecting food on a noncaloric basis (e.g. protein, balanced amino acid composition, minerals) may reduce net foraging gains and result in
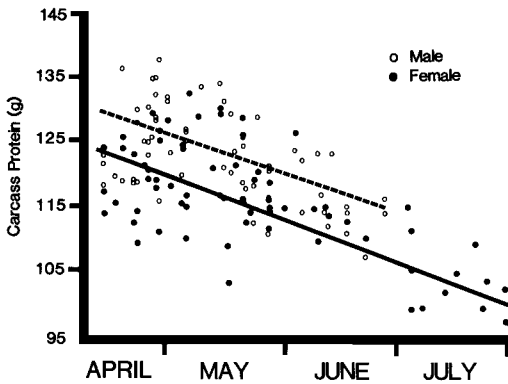
Fig. 2. Body protein composition by date for breeding male and female Ring-necked Ducks. Regressions significant at $P < 0.0001$.

expenditure of stored lipids, as noted in Mallard (Krapu 1981) and Wood Duck (Drobney 1982) hens. Birds may minimize the costs of obtaining reproductive protein requirements by timing laying to coincide with peak invertebrate abundance. This was suggested by a significant positive correlation between nonmollusc invertebrate biomass and the weight of female reproductive tissues (Hohman 1984).

Body weights are a useful index for examining nutrient changes in waterfowl (Bailey 1979, Raveling 1979, Wishart 1979, Ankney 1982, Drobney 1982). Body-weight data suggest that nutrient levels in Ring-necked Ducks entering reproduction may vary by year and by female age. Reduced reserves in females at the initiation of ovarian follicle growth increases reliance on exogenous sources for reproductive nutritional requirements. Deficiencies in female lipid reserve (i.e. lipid needed for egg production and energy costs associated with obtaining protein requirements) increase further the exogenous requirements for reproduction and may result in breeding adjustments such as altered time-activity patterns, delayed laying, or clutch-size reduction. Inadequate reserves coupled with reduced food availability could cause deferred breeding. Yearling females are lighter than adults early in the arrival period, and probably are more dependent than adults on food resources in wetlands used for nesting. Biomass and density of foods in these wetlands change seasonally and vary among years (Hohman 1984). Adult and yearling females entered reproduction in 1980 at reduced body weights, but available nutrients

(reserve + ambient food resources) apparently were inadequate for yearlings, most of which did not nest in 1980 (Hohman 1984).

The contribution of body reserves to reproduction was partially a function of nutrient levels attained during the arrival period. Whereas body weight during the arrival period was constant in 1980, weight gained before early May constituted over 50% (50% female, 62% male) of the total body-weight fluctuation observed in 1979. Before occupancy of the wetlands used for nesting, male and female diets consisted mostly of plant material, including seeds of native grasses and sedges, annual plants, and waste grain that birds gathered on temporally flooded wetlands (Hohman 1985). The rate of caloric intake by feeding Ring-necked Ducks was greater in temporary wetlands than in the semipermanent and permanent wetlands used for nesting. Deposition of lipids undoubtedly was facilitated by the use of high-carbohydrate plant foods, which were readily available in temporary wetlands. The lower body weights observed in 1980 were probably a consequence of drought, which reduced the area of temporary wetlands and, thereby, prevented access to seeds of wetmeadow vegetation.

Events occurring over winter and during migration also may influence the reserve status of returning birds. Ring-necked Ducks in southern Florida put on body fat and showed a constant weight gain through the wintering period (Hohman et al. 1986). The rate of increase was significantly greater in yearlings than adults, but varied annually. Yearlings in fall were initially lighter than adults, but body weights were equivalent by late winter. Ring-necked Ducks defer pairing until spring migration (Weller 1965) and, thus, simultaneously incur energetic costs of migration and courtship in March/April. Reductions in the body weight of returning birds from winter maxima presumably reflect these costs.

Similarities in the arrival body weights of males by age, and differences in adult and yearling female body weight (adult > yearling) early in the arrival period, suggest sex- and age-related differences in prearrival and arrival costs. Familiarity with food resources on staging and breeding areas may enable adult females to feed more efficiently than inexperienced yearling hens. Adult and yearling males following mates to their mates' natal areas were

presumably also naive regarding food resource availability in nesting wetlands and showed similar body weight changes. Krapu (1981) suggested that age-related differences in lipid reserve carried by Mallard females during the nesting season may result because inexperienced yearlings are less efficient at capturing invertebrates than adult females (i.e. incur greater energy costs). Differences in body weights of yearling and adult female Ring-necked Ducks, however, appeared before birds shifted to invertebrate foods.

Variation in the chronology of pairing also might account for initial differences in adult and yearling female body weight. Pair-bond formation entails costs and benefits that differ between the sexes. Males incur considerable energy costs during courtship and while attending mates. The advantages of early pair formation to the male, therefore, must be weighed against the risks of subsequent displacement by a bird in superior condition. Females benefit from mate attendance and may be ready to pair before males (Afton and Sayler 1982). Male investment probably is influenced by female quality. Thus, experienced females may obtain mates, and begin to accrue pairing benefits, before yearlings. Indeed, intensive courtship activity on nesting areas appears to involve primarily yearling individuals (Hohman unpubl. data). Extended courtship costs, or intrusions by unpaired males testing weak pair bonds and disrupting feeding, probably impair yearling female ability to accumulate nutrient reserves after their return to breeding areas.

Patterns of nutrient acquisition and allocation for ducks nesting in temperate regions, as evident in this study, may be more indeterminant than previously implied (Owen and Reinecke 1979). Waterfowl are long-lived occupants of variable environments and exhibit temporally dynamic reproductive strategies (Nichols et al. 1976). While ultimate control of factors such as clutch size and time of laying probably are genetically based (Batt and Prince 1979), expressed breeding patterns are the result of interplay between local environmental conditions (e.g. food availability) and the nutrient-reserve status of the parent. Changes in local environmental conditions or reserve status of the parent may result in altered, suboptimal breeding patterns. Studies that link the reproductive performance of individuals with their environment are a necessary first step toward the interpretation of the broad pattern exhibited by the species (Drent and Daan 1980). Future research examining the bioenergetics of temperate-breeding waterfowl must consider the individual variation, as well as behavioral plasticity, in birds that enables individuals to adjust breeding patterns to changing environmental conditions.

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MALE COURTSHIP VOCALIZATIONS AS CUES FOR MATE CHOICE IN THE SATIN BOWERBIRD (*PTILONORHYNCHUS VIOLACEUS*)

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ABSTRACT.—Male Satin Bowerbirds (*Ptilonorhynchus violaceus*) court females at specialized structures called bowers. Courtship includes a complex pattern of vocalizations in which a broad-band, mechanical-sounding song is followed by interspecific mimicry. We studied the effect of male courtship displays on male mating success in Satin Bowerbirds. Data from 2 years of field research showed low between-male differences in mechanical components of courtship song and high variability between males in mimetic singing. Older males sang longer and higher-quality bouts of mimicry than did younger males. In one year, courtship song features were correlated with male mating success. The results suggest that female Satin Bowerbirds use male courtship vocalizations in their mate-choice decisions. We discuss hypotheses about assessment of male age and dominance from courtship vocalizations and suggest that these songs have evolved as a result of selection for male display characteristics that provide females with information about the relative quality of prospective mates. *Received 27 June 1985, accepted 20 September 1985.*

MALE Satin Bowerbirds (*Ptilonorhynchus violaceus*) build specialized structures called bowers that are used as sites for courting females and for mating (Vellenga 1970, Donaghey 1981, Borgia 1985). Females raise their young unassisted by males, and males do not associate with females after mating. Males decorate their bowers with a variety of natural objects and attempt to steal decorations and destroy the bowers of other males.

Much effort has been focused on understanding the role of the bower and its decorations in female mating decisions. Borgia (1985) demonstrated a skewed distribution of matings among male Satin Bowerbirds, differences among males in bower decoration and construction, and a consistent pattern of female preference for males with well-constructed and well-decorated bowers. In addition, male mating success is influenced negatively by bower destruction and decoration-stealing (Borgia 1986a, Borgia and Gore 1986).

Male courtship vocalizations are another component of male sexual display that may have important effects on female mating decisions. Male courtship is intense, involving dance movements and postures that are coordinated with the simultaneous production of complex vocalizations. The female crouches within the bower, closely observing the male during the display, and controls the outcome of the courtship either by signaling her willingness to copulate or by flying away. Given the complexity of male display and the attention females pay to displaying males, it is likely that male displays have an important effect on female mating decisions, yet there have been no detailed studies of display in any bowerbird species.

The relationship between male display and female choice in polygynous species, such as bowerbirds, in which males do not provide material benefits to females or their offspring, has been the subject of considerable speculation (Fisher 1930, Zahavi 1975, Davis and O'Donald 1976, Emlen and Oring 1977, Halliday 1978, Borgia 1979, West-Eberhard 1979, Bradbury 1981, Hamilton and Zuk 1982, Bradbury and Gibson 1983, Kodric-Brown and Brown 1984, Borgia et al. 1985). One view of the sexual selection process is that females choose mates based on characters that indicate the relative ability of males to sire fit (e.g. viable) offspring (Zahavi 1975, Halliday 1978, Borgia 1979, Hamilton and Zuk 1982, Thornhill 1980, Borgia et al. 1985). An alternative model suggests that male sexual displays are arbitrary results of the runaway process of sexual selection (Fisher 1930). This implies that female preferences have evolved that have no effect on enhancing the viability of the offspring (Lande 1981, Kirkpatrick 1982, Arnold 1983).

Developing hypotheses that separate these models has proven very difficult. One method

is to consider the evolution of male display (Borgia 1986a). Models that predict gains in off-spring viability require that male displays provide cues that allow females to assess characters important to demonstrating the quality of males as sires. For example, female preference for older males may produce offspring with high survivorship because these males have demonstrated high viability through their own survival (Trivers 1972, Howard 1974, Halliday 1978, Wilbur et al. 1978). If such a model is operating, then we expect that cues exist in males that indicate male age and that these are correlated with male mating success. Alternatively, females may prefer dominant (Borgia 1979) or disease-resistant males (Hamilton and Zuk 1982). By contrast, runaway models make no predictions about the nature of male displays and are untestable on that basis.

Our objectives here are to describe intrapopulational variation in the courtship-display vocalizations of Satin Bowerbirds, to look for correlates between male vocal patterns and other male characteristics such as age and bower quality, and to use these results to determine if the minimum conditions for male assessment models have been met.

METHODS

Field research was carried out at Wallaby Creek, Beaury State Forest, New South Wales, Australia, from August through December in 1982 and 1983. The study site is characterized by open-canopy, subtropical eucalyptus scrub forest and patches of rain forest.

Recordings of male Satin Bowerbird courtship songs were obtained with Uher 4000L and Marantz PMD 220 tape recorders, using small condenser microphones suspended in the foliage 1 m from the bower platform. Only sexual display songs at or near the bower were recorded, although male Satin Bowerbirds use a variety of calls in other behavioral settings and at places away from the bower. Observations of focal displaying males were made by field observers from blinds stationed within 10 m of the bower. In addition, a camera system was used to monitor activities continuously at bowers and to obtain records of male mating success (see Borgia 1985).

We recorded vocalizations in 1983 for 22 individual males (20 adults and 2 juveniles). Recordings from 1982 for 2 additional juveniles and 11 of the same adults were included in the analysis, for a total of 24 individuals. A mean of 12.0 vocal samples were analyzed for each male, with a total of 288 samples. Spectrographic sound analysis was performed using a Princeton Applied Research FFT Real Time Spectrum

Analyzer (Model 4512). A Kay Elemetrics Digital Sono-Graph was used to prepare spectrograms.

Analysis-of-variance tests (one-way ANOVA), Spearman rank correlations (r_s), and the Student-Newman-Keuls (SNK) procedure for multiple comparisons of means were used for statistical comparisons (Helwig and Council 1982). Means are expressed as $\bar{x} \pm 1$ SD.

Because of the low amplitude of mimetic sounds (see below), it was not possible to accurately measure frequencies. However, it was apparent that quality of mimetic songs differed between males, and so a subjective method was used to produce an index of qualitative differences among mimetic songs of different males. All mimetic songs were given a score (1, 2, or 3) for "structural integrity": high-scored mimetic songs were of relatively pure tonal structure, free from broad-band and other atonal sounds produced by the singer, and were free from acoustical distortions resulting from production by the singer of other sounds during mimetic singing. Figures 2 and 3 represent several high- and low-scored mimetic songs.

To validate subjective scoring of mimetic songs, two volunteers were each given the same random sample of spectrograms taken from the analyzed data and were asked to sort the spectrograms on the basis of this three-level subjective scoring system. There was complete agreement between the results of the two independent trials and the results obtained by the author for the same sample ($r_s = 1.00, P < 0.001$).

RESULTS

Description of the male courtship song.—The song used by male Satin Bowerbirds during courtship (and in other specific behavioral settings; see below) consists of a long series of harsh-sounding buzzes and pulses followed immediately by a bout of interspecific mimicry. The two major portions of the courtship song henceforth will be termed the "mechanical" and "mimetic" portions.

The courtship song lasts 24.0 ± 8.2 s. Within the mechanical portion there are 2–6 ($\bar{x} = 4.2$) wide-band "long buzzes" (Fig. 1), each of which is 0.35–1.50 s long with a frequency range of 0.06 ± 0.01 to 7.39 ± 0.02 kHz. Each long buzz is separated from the next by one or more "short buzzes" (harsh sounds with a frequency range of 4.00 ± 0.03 to 7.20 ± 0.05 kHz, each of which lasts for less than 0.20 s) and several short (<0.10 s) pulselike sounds (Fig. 1). The mechanical portion of the song lasts 17.0 ± 3.2 s. For each mechanical song analyzed, the following variables were measured: the duration of
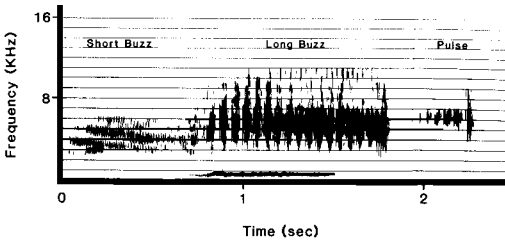
Fig. 1.   Components of the mechanical portion of male Satin Bowerbird courtship song.

Fig. 3.   Lewin's Honeyeater mimetic song: (A) high and (B) low scores for structural integrity. The sounds between 4.0 and 6.0 kHz are cicada calls.

the mechanical song; the numbers of long buzzes, short buzzes, and pulses; and the peak frequency (kHz), low frequency (kHz), and duration of each long buzz.

The mimetic portion of the courtship song consists of mimetic songs of either or both of two avian species: the Laughing Kookaburra (*Dacelo novaeguineae*) and the Lewin's Honeyeater (*Meliphaga lewinii*). No other bird species are regularly imitated by Satin Bowerbirds at Wallaby Creek, although individuals in other populations are known to mimic other bird species (Chaffer 1984). For the individuals in this study, when both kookaburra and honeyeater mimet-
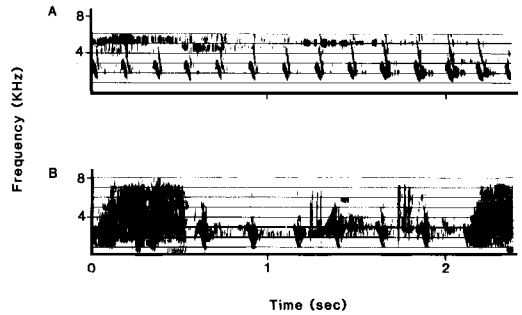
ic calls are given, the kookaburra call always precedes the honeyeater.

The kookaburra mimetic song is a structurally complex series of notes of gradually rising frequency and intensity (see Fig. 2A) and is given for 2.9 ± 1.6 s. The honeyeater call consists of a long train of simple, highly discrete notes of constant frequency (2.80–3.36 kHz). The notes are repeated rapidly for 4.0 ± 2.7 s (see Fig. 3A). For each mimetic song analyzed, the total mimetic, kookaburra, and honeyeater durations were measured.

Male courtship songs, age, and mating success.— For all 12 song variables measured, ANOVA tests indicated that a significant proportion of variability in these measurements was a result of between-male differences. For these variables, the average F-value was 4.24 (range: 2.26–6.51; each F significant at $P < 0.05$), and the average proportion of variability explained by differences among individuals (r^2) was 0.312 (range: 0.224–0.459).

We tested to determine if differences in the time of year at which the songs were recorded or if differences in behavioral settings affected song characteristics. Means for one- and two-week intervals were calculated for song variables in both years. Multiple comparisons of means (SNK) revealed no significant differences. Behavioral contexts in which recordings were obtained included male courtship songs given to females at the bower site, to juvenile and adult males at the bower, at empty bowers (i.e. no other conspecifics present), and from tree perches. Multiple comparison tests (SNK) of mean song characteristics by behavioral setting indicated that only songs given from tree perches differed significantly from other songs.
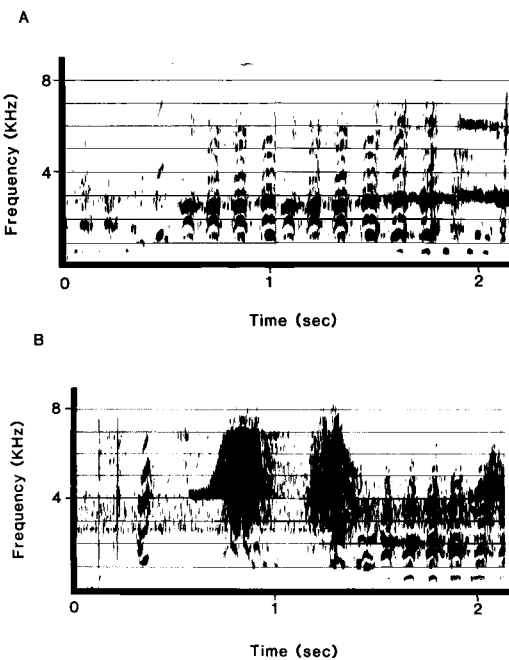

Fig. 2.   Laughing Kookaburra mimetic song: (A) high and (B) low score for structural integrity. Note band of cicada calls between 3.5 and 4.0 kHz.

LOFFREDO AND BORGIA

TABLE 1. Comparisons of male age with mechanical and with mimetic song variables. SI = structural integrity.

	1982		1983	
	r_s	P	r_s	P
Mechanical song	($n = 13$)		($n = 22$)	
Mechanical duration	0.022	NS	−0.062	NS
Peak frequency	0.167	NS	0.046	NS
Low frequency	0.124	NS	0.065	NS
Frequency range	0.072	NS	−0.166	NS
No. of long buzzes	−0.073	NS	−0.073	NS
No. of short buzzes	0.071	NS	0.011	NS
Mimetic song	($n = 13$)		($n = 22$)	
Mimetic duration	0.217	0.001	0.621	0.001
Kookaburra duration	0.813	0.002	0.459	0.023
Kookaburra SI	−0.457	0.001	−0.743	0.001
Honeyeater duration	0.225	0.034	0.381	NS
Honeyeater SI	−0.334	0.001	−0.621	0.002

Data on tree songs constituted a very small part of the sample, and these data were excluded from further analysis.

Having demonstrated intermale variability in male courtship singing, we then divided the individuals into seven age categories based on known histories of uniquely color-banded individuals (see Borgia 1985). Male age was correlated significantly with mimetic but not with mechanical song features (Table 1). Older males tended to give songs with significantly longer mimetic portions than did younger males. The mimetic songs also varied qualitatively with age: in both 1982 and 1983, older males gave kookaburra and honeyeater calls of higher structural integrity than did younger males.

Even when juvenile males were excluded from analysis, adult males showed significant age-correlated differences in mimetic singing.

In 1982, there was a significant correlation of male mating success and the number of short buzzes in the mechanical song (Table 2), but this correlation was not significant in 1983. None of the other mechanical song variables measured was significantly correlated with mating success in either year. Mimetic songs showed a similar pattern (Table 2): in 1982, male mating success was significantly correlated with total mimetic duration and with kookaburra structural integrity, while in 1983 there were no significant correlations of any mimetic song variables and male mating success.

TABLE 2. Comparisons of male mating success with mechanical and with mimetic song variables. SI = structural integrity.

	1982		1983	
	r_s	P	r_s	P
Mechanical song	($n = 11$)		($n = 22$)	
Mechanical duration	−0.484	NS	−0.357	NS
Peak frequency	0.355	NS	0.067	NS
Low frequency	0.429	NS	0.232	NS
Frequency range	0.050	NS	0.126	NS
No. of long buzzes	0.104	NS	−0.069	NS
No. of short buzzes	−0.706	0.003	−0.363	NS
Mimetic song	($n = 11$)		($n = 22$)	
Mimetic duration	0.774	0.040	0.007	NS
Kookaburra duration	0.270	NS	0.073	NS
Kookaburra SI	−0.635	0.024	0.080	NS
Honeyeater duration	0.522	NS	0.226	NS
Honeyeater SI	−0.079	NS	−0.234	NS

TABLE 3. Comparisons of mimetic song types with male age and mating success.

| Percentage of songs with: | Age | | Mating success | | | |
| | | | 1982 | | 1983 | |
	r_s	P	r_s	P	r_s	P
Both mimetic types	0.220	NS	−0.086	NS	−0.239	NS
Only kookaburra	0.282	NS	−0.272	NS	0.050	NS
Only honeyeater	−0.237	NS	0.387	NS	0.025	NS
No mimicry	−0.349	NS	0.275	NS	0.033	NS
	($n = 24$)		($n = 11$)		($n = 22$)	

Male Satin Bowerbirds do not invariably mimic both kookaburra and honeyeater calls each time they sing a courtship song. To test whether this variability is related to either age or mating success, we compared male age and mating success with the proportion of songs containing only kookaburra calls, those with only honeyeater calls, those with both types, and those with no mimicry at all. No significant correlations were found for either year (Table 3). There were no birds in the study that "specialized" exclusively in either one of the mimetic types, and all birds sang mimetic songs.

Spearman rank correlations were used to test for relationships between song features and bower quality and between song features and bower decorations (Table 4). Of the song variables measured, only the mechanical song duration was significantly correlated with bower quality (but only in 1983). Mechanical song duration was also correlated significantly with the total number of bower decorations (both years), but no other song variables (except honeyeater structural integrity and the low frequency of

long buzzes in 1982) were correlated with decorations.

DISCUSSION

We have described the relationship between intrapopulational patterns of male Satin Bowerbird courtship songs and characteristics such as male age and bower quality. Male age and mating success were positively correlated in both years (Borgia 1986b), so it appears that female Satin Bowerbirds prefer older males as mates. The significant correlation of male mating success with age-correlated features of songs in 1982, but not in 1983, suggests that females may use songs to assess male age. Male age is also positively correlated with bower quality (Borgia 1986b), which could provide another mechanism by which females can assess male age. However, the low correlation of courtship song variables with measures of bower quality indicates an independent effect of each of these factors on male mating success. These results are consistent with the hypothesis that male

TABLE 4. Comparisons of song variables with decorations and bower quality. SI = structural integrity.

| Song feature | Bower quality | | Total no. decorations | |
| | 1982 | 1983 | 1982 | 1983 |
	P	P	P	P
Mechanical duration	NS	0.033	0.030	0.038
Peak frequency	NS	NS	NS	NS
Low frequency	NS	NS	0.033	NS
Frequency range	NS	NS	NS	NS
Number long buzzes	NS	NS	NS	NS
Number short buzzes	NS	NS	NS	NS
Mimetic duration	NS	NS	NS	NS
Kookaburra duration	NS	NS	NS	NS
Kookaburra SI	NS	NS	NS	NS
Honeyeater duration	NS	NS	NS	NS
Honeyeater SI	NS	NS	0.001	NS
	($n = 11$)	($n = 22$)	($n = 11$)	($n = 22$)

courtship vocalizations function as age markers, independent from other aspects of male display, and as indicators of male genetic quality.

Several observations suggest that Satin Bowerbirds learn and practice mimetic singing. In other populations of Satin Bowerbirds mimetic songs exhibit much variation both within and between populations, while other song features are rather invariable (Loffredo and Borgia in prep.). Further, male bowerbirds, especially young males, spend a great deal of time both within and outside of the breeding season performing their displays (Vellenga 1970, Chaffer 1984, Borgia in prep.). Together with our observations of age-related increases in the quality of songs, these results suggest that learning and practice may be important in the use of mimetic songs, as appears to be the case in other avian species that use interspecific mimetic singing (Nottebohm 1972, Payne 1973, Howard 1974, Catchpole 1980). The use of mimetic songs by Satin Bowerbirds may have resulted from selection for reliable age cues (Zahavi 1977, Borgia 1979, Kodric-Brown and Brown 1984). These songs are reliable because they require learning and practice, and thus young males cannot easily "cheat" (if females prefer older males) by sounding like older individuals.

Another model concerning the role of male courtship songs in influencing female choice is the male dominance model. Dominant males may be preferred as mates because they are able to demonstrate their vigor relative to other males through aggressive interactions (Alexander 1975, Cox and LeBoeuf 1977, Borgia 1979, Borgia et al. 1985). This prediction is supported by observations that female Satin Bowerbird mating decisions are affected by indicators of male dominance such as bower destruction (Borgia 1986a) and feather stealing (Borgia and Gore 1986). Loud vocal displays may attract more attention from competing males than do low-amplitude displays; thus, a male's ability to give a loud courtship song without interruption from neighboring males could provide evidence to a female of a male's dominance status (Borgia 1979; but see Foster 1983, Bradbury and Gibson 1983). We could not quantify the vocal data adequately to test this hypothesis. However, after listening to many calls we heard no apparent amplitude differences among males.

Courtship songs are coordinated with male dancing at bowers. Intermale differences have not yet been quantified for these dances. It is likely that female choice of male characteristics depends on the assessment of interacting characters. The failure to explain a large proportion of variation in male mating success with vocal display data may be due to the absence of data on dancing. In addition, the lack of significant correlations of mating success with vocal display data in 1983 may be due to the early commencement of breeding that year, which resulted in a highly atypical breeding season.

The present study suggests that male courtship songs contribute to the process of female mate choice by allowing females to estimate male age. Differences among males in courtship vocalizations explain some of the variation between males in their mating success. These results are consistent, at least for one year of this study, with models that suggest that females assess male age and use this as an indicator of male quality as a sire. We cannot exclude the possibility that the songs have evolved through runaway sexual selection in which females have evolved preferences for certain features of male display vocalizations independent of male quality. This is an interesting possibility because it differs from the tightly genetically programmed features commonly discussed in runaway sexual-selection models. It suggests that female preference for exaggerated male display has led to selection in males for the ability to learn complicated songs.

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MULTIPLE BROODING AS A REPRODUCTIVE STRATEGY: TIME-CONSERVING ADAPTATIONS IN MOURNING DOVES

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ABSTRACT.—The Mourning Dove (*Zenaida macroura*) has a suite of adaptations that promotes multiple brooding, a common characteristic among columbids. Mourning Doves are well adapted for multiple brooding because they produce food (crop milk) for young nestlings *in vivo* and feed older nestlings a diverse granivorous diet. This facilitates extended breeding seasons and, thus, multiple brooding. Other traits such as constant incubation, fast nestling growth, and fledging at low weight serve to shorten the nesting cycle and enhance the number of broods that can be produced. Constant incubation also allows columbids to have no incubation patch. The effect of small clutch size on the length of the nesting cycle is ambiguous. Predation as a selective force augments the advantage of short nesting cycles.

Mourning Doves also are adapted to renest quickly. By constructing small nests and reusing old nests, they can initiate nesting cycles quickly despite their ritualized building behavior. Small clutch size and a lesser role in crop-milk production allow females to initiate new clutches quickly, and sometimes to overlap nesting cycles. *Received 7 January 1985, accepted 25 September 1985.*

THE importance of multiple brooding (i.e. producing two or more clutches per breeding season) as a reproductive tactic has been noted (e.g. Spencer and Steinhoff 1968, Burley 1980), but the relation between multiple brooding and other life-history traits has received little attention (but see Tinkle 1969, Parmelee and Payne 1973). Among North American birds, the Mourning Dove (*Zenaida macroura*) is the champion of multiple brooding. Unlike most temperate bird species that attempt one or two clutches per breeding season (Lack 1968), Mourning Doves often attempt from three to six (Swank 1955, Hanson and Kossack 1963). The species is impressively successful—although the Mourning Dove is the most frequently harvested game bird in North America (Keeler 1977), both the wintering (Alison 1976) and breeding ranges (Morse 1975) have extended northward in the last few decades. Mourning Doves are common breeders in all the contiguous states and parts of Canada, Mexico, and the Caribbean (Goodwin 1983).

Many behavioral and physiological traits of Mourning Doves can be explained by strong selection for multiple brooding. After briefly reviewing the breeding behavior of Mourning Doves, we identify a suite of traits that apparently are adaptations for multiple brooding. We focus on a single species for which there is extensive ecological and behavioral information, but the proposed "adaptive suite" (Bartholomew 1972) probably is applicable to pigeons and doves (family Columbidae) in general because members of the group are remarkably alike in breeding behavior (Kendeigh 1952).

BREEDING BEHAVIOR

Mourning Doves are monogamous, and pair bonds sometimes persist between nesting seasons (Mackey 1965). Pairs begin courtship in early spring, typically after the male has established a territory containing potential nest sites. During nest building, the male selects twigs and delivers them individually to the female, who arranges them into a small platform (Nice 1922). Pairs often reuse nests, including old nests of other pairs and other species (McClure 1950, Scanlon et al. 1981).

Egg-laying begins 2–3 days after nest initiation. Clutch size is constant at two eggs, and incubation begins after the first is laid (Cowan 1952). Larger clutches of three and four eggs occur about 1% of the time, but probably result from intraspecific nest parasitism (Weeks 1980). Mourning Doves incubate constantly, with males sitting from about 1000 to 1800 and fe-

males for the remaining hours (Harris et al. 1963, Blockstein 1982). Neither sex develops the vascularized incubation patch typical of other birds (Maridon and Holcomb 1971). The eggs hatch after 13–14 days.

Young Mourning Doves are fed crop milk, a cheesy conglomeration of epithelial cells sloughed from the crop mucosa of both parents (Levi 1963). Beginning about the third day after hatching, seeds are mixed with crop milk in gradually increasing proportions; at 6–8 days of age, the young are essentially granivorous (Taylor 1941, Mackey 1954, Laub 1956). The young fledge at about 14 days, but the male continues to feed them for about a week (Hitchcock and Mirarchi 1984).

Mourning Doves have one of the longest breeding seasons of all North American birds (Peters 1961); nesting pairs sometimes breed from April through September (McClure 1950, Hanson and Kossack 1963). A single nesting cycle (defined as the period from laying the first egg to fledging the last young) is 28–30 days; pairs usually attempt to raise multiple broods.

The breeding behavior of Mourning Doves is typical of columbids. Columbids are monogamous (Delacour 1980), and they build small platform nests (Goodwin 1983). Nest building takes 1–3 days; the interaction between sexes is as described above (Kendeigh 1952, Goodwin 1983). Clutch size usually is constant for a species, at either one or two small eggs. Rahn et al. (1975) found that columbids produce eggs that are on average less than half the size of those laid by birds of equal weight. Incubation is continuous, with the exchange between sexes occurring in the morning and late afternoon. Columbids have a bare ventral apterium year-round that does not become vascularized during the breeding season. The length of time that nestlings are fed crop milk varies among species, but young columbids usually assume the diet of their parents midway through the nestling period. The long breeding season typical of Mourning Doves has been documented for many columbid species (Frith 1982), and multiple brooding has been reported for many of the species that have been closely studied [e.g. Band-tailed Pigeons (*Columba fasciata*), MacGregor and Smith 1955, Gutierrez et al. 1975; Rock Doves (*C. livia*), Burley 1980; Wood Pigeons (*C. palumbus*), Saari 1979; *Columbina talpacoti*, Haverschmidt 1953; *Ducula*

spilorrhoa, Crome 1975b; *Columbina inca*, Johnson 1960; White-winged Doves (*Zenaida asiatica*), Cottam and Trefethen 1968; *Z. galapagoensis*, Grant and Grant 1979]. Most columbids that have been bred in captivitiy produce multiple broods (Delacour 1980, Goodwin 1983).

The family Columbidae has colonized successfully an array of habitats that ranges from jungles to deserts. Of the 284 known columbid species, there are representatives on every continent except Antarctica and every major island in the world (Goodwin 1983). The Passenger Pigeon (*Ectopistes migratorius*) was perhaps the most numerous single avian land species of recent times (Schorger 1955).

REPRODUCTIVE STRATEGY

Most birds synchronize reproduction with a brief period of abundant, high-quality food for nestlings (Lack 1950, Skutch 1950, Thompson 1950). Columbids, however, produce food (crop milk) for young nestlings *in vivo* and feed older nestlings a diverse diet of seeds (Browning 1959). Thus, breeding need not be synchronized with availability of particular foods. The resultant protracted breeding season has led to a propensity for multiple brooding.

When multiple brooding strongly affects fitness, the time required to complete nestings is critical. The less time a single nesting takes, the more nestings are possible in a breeding season (see also Ricklefs 1984). Columbids could adapt for rapid production of multiple broods by (1) reducing the time interval between successive nesting attempts and (2) reducing the length of the nesting cycle. A complex of time-conserving traits allows Mourning Doves to accomplish both (Fig. 1).

The nesting interval.—Many studies have documented the short nesting interval of Mourning Doves. After a nesting failure, the period until a new clutch is begun ranges from 2 to 25 days, with the most frequent time interval being 6 days in one study (Hanson and Kossack 1963) and 3–5 days in another (Swank 1955). After a successful nesting, Mourning Doves usually begin a new clutch in 3–6 days (Harris et al. 1963, Caldwell 1964).

Accumulation of nesting material is a slow process for columbids because collecting and exchanging twigs is ritualized, at least partly to enhance gonadogenesis in females (Cheng and Balthazart 1982). Still, Mourning Doves
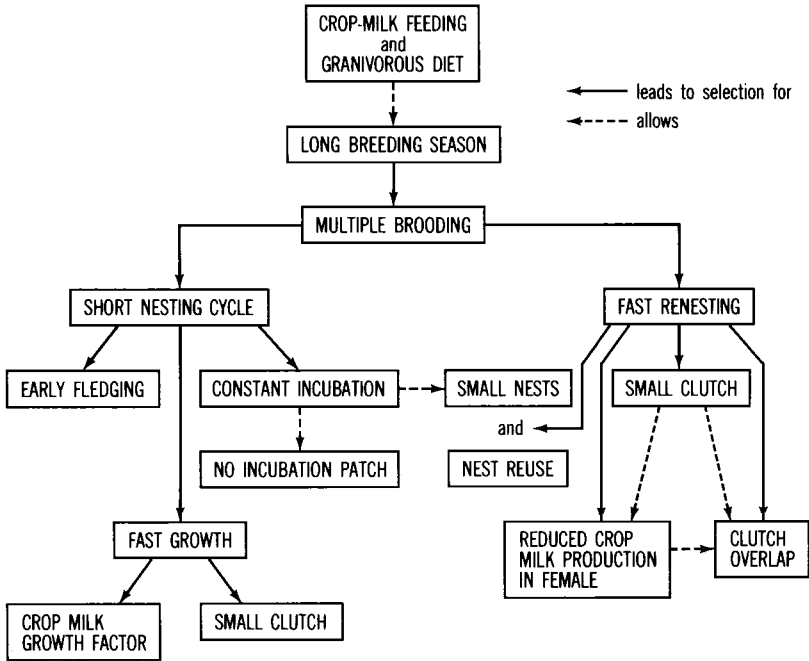
Fig. 1. Flow diagram outlining the proposed evolution of multiple brooding and associated traits in Mourning Doves.

shorten the process by building small, crudely structured nests. Mourning Doves also collect nesting material near the nest site (Cowan 1952, Sayre et al. 1980), which probably serves to ensure males of paternity (see Lumpkin et al. 1982) in addition to saving time and energy. Nests are completed in 2–3 days (Cowan 1952, Goforth and Baskett 1971). Under the constraint of ritualized building, collecting enough twigs to construct a nest comparable to those of other open-nesting birds probably would take Mourning Doves an additional 4–5 days. Poor nest construction evidently reduces nesting success for Mourning Doves (Coon et al. 1981), but this negative effect undoubtedly is ameliorated by constant incubation. Koepcke (1972) suggested that small nests are an adaptation for concealment, but this seems unlikely because parents much larger than the nest itself are always present.

By reusing old nests, columbids eliminate the time required for building. For Mourning Doves, nest reuse occurs in as many as 35–40% of nesting attempts (McClure 1950, Harris et al. 1963, Scanlon et al. 1981), but does not ensure better nesting success (Woolfenden and Roh-

wer 1969, Westmoreland and Best 1985). Thus, it seems plausible that it evolved to reduce time between nesting cycles.

Crop-milk production is stimulated by secretion of prolactin, which simultaneously suppresses gonadal activity (Bates et al. 1935, 1937). Female Mourning Doves play a lesser role than males in crop-milk feeding (Blockstein 1982) and reduce crop-milk production 4–6 days before males (Mirarchi and Scanlon 1980). This may allow the antigonadal effect of prolactin to wane, so egg production for the next clutch can begin (Hanson and Kossack 1963). By requiring less crop milk, small broods also may ameliorate the effect of prolactin in females, thus allowing quick "recycling" of the ovary after the crop-milk phase.

Individual columbids may eliminate nesting intervals altogether by overlapping nesting cycles, i.e. simultaneously caring for two sets of offspring at different stages of development. Small clutch size may facilitate nest overlap due to the comparatively low energetic cost of producing and feeding only two offspring (Burley 1980). Burley found that experienced captive pigeons care for two sets of offspring (one in
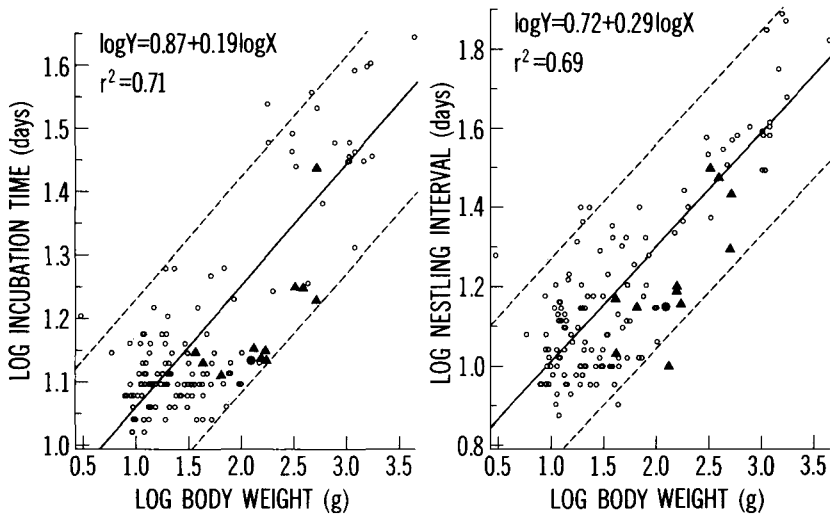
Fig. 2. Relationship between body weight and incubation or nestling interval for 140 species of altricial, open-nesting land birds. The regression line was calculated for noncolumbids (open circles). Triangles represent columbids, and the enlarged closed circle represents Mourning Doves. Incubation and nestling times from Harrison (1978); body weights from various sources (references available from senior author).

the egg stage and the other as nestlings) 70% of the time. Captive (Hanson and Kossack 1963) and wild (Mark Sayre pers. comm.) Mourning Doves sometimes overlap clutches by 14% or more by laying eggs when the young of the previous nest are 10 or 11 days old. There is also circumstantial evidence for overlap in wild Wood Pigeons and Stock Doves (*Columba oenas*) (Murton and Isaacson 1962).

The nesting cycle.—If columbids are strongly selected to have short nesting cycles (Fig. 1), the trend should be apparent when they are compared with other birds. To examine this, we compared the time required for incubation and nestling growth with body weight for 140 altricial species of open-nesting land birds (Fig. 2). The columbids save time in both the incubation and nestling stages. Overall, columbid nesting cycles are 22% shorter than those predicted by the regression line. Only one value for columbids lies outside the 95% confidence interval, but 11 of 12 of the incubation and 10 of 11 of the nestling intervals fall below the regression lines. The probability of this occurring by chance alone in either case is <0.01 (sign test, Gibbons 1976).

Several traits of Mourning Doves may serve to shorten incubation time. Small egg size undoubtedly has a large influence, as a positive correlation exists between incubation time and egg weight (Rahn and Ar 1974). However, constant incubation probably also plays a role. Mourning Dove eggs and nestlings less than 6 days old essentially are ectothermic (Breitenbach and Baskett 1967). Bird eggs cool rapidly when parents are absent and rewarm slowly after their return (Drent 1972). Most birds take respites from incubation, usually to forage (Skutch 1962, Ricklefs 1974, Drent 1975). Columbids store large quantities of food in their crops, so incubation is not interrupted by a need for food. The constant source of heat supplied from laying until late nestling growth ensures continuous development. Through constant nest attentiveness, Mourning Doves, Ringed Turtle-Doves (*Streptopelia risoria*), and White-winged Doves can maintain their eggs at viable temperatures even during extreme heat (Russell 1969, Walsberg and Voss-Roberts 1983).

Constant incubation probably also eliminated the need for vascularized incubation patches in columbids. According to Ackerman and Seagrave (1984), incubation patches in birds exchange little heat with eggs during the steady-state conditions that occur when eggs are covered continuously. Thus, for columbids, development of incubation patches would be unnecessary. Constant incubation also may have led to the evolution of white (noncryptic) egg coloration in columbids. However, cryptic col-

TABLE 1. Fledgling weight : adult weight ratios for columbids.

Species	Weight (g)		Ratio
	Fledgling	Adult	
Columba livia	352 (8)[a]	313 (8)	1.13
C. palumbus	277 (3)	500 (9)	0.55
Columbina talpacoti	28 (2)	45 (2)	0.62
Ducula spilorrhoa	260 (5)	500 (5)	0.52
Ptilinopus superbus	30 (6)	120 (5)	0.25
Streptopelia decaocto	<70 (7)	145 (7)	<0.48
Zenaida asiatica	113 (4)[b]	170 (4)	0.66
Z. macroura	72 (1)	115 (1)	0.63

[a] Sources: (1) McClure 1941, (2) Haverschmidt 1953, (3) Murton et al. 1963, (4) Cottam and Trefethen 1968, (5) Crome 1975a, (6) Crome 1975b, (7) Rana 1975, (8) Burley 1980, (9) R. A. Ackerman pers. comm.

[b] Estimated from linear extrapolation of growth-rate curve.

oration may result in higher hatching success even when eggs are incubated continuously (Westmoreland and Best 1986).

Columbids are an exception to the general rule that nestlings of species with small clutches have slow growth rates (Ricklefs 1968). Growth rates of columbids are comparable to, if not faster than, those of raptors and passerines. Their method of feeding young may be the reason. Crop milk is high-quality food for nestlings, being composed of 65–81% water, 13–19% protein, 7–13% fat, and 1.5% ash (Needham 1942). It also contains an unidentified factor that promotes fast growth. Pace et al. (1952) compared growth rates of White-rock (*Gallus gallus*) chicks fed chick ration *ad libitum* with those of chicks whose diet was supplemented with small amounts (5 g/day) of Rock Dove crop milk. Although crop milk was fed for only 6 days after hatching, treatment chicks grew significantly (*t*-test for slopes, $P < 0.001$; analysis ours) faster than controls until the experiment ended when chicks were 42 days old. Evidently, crop milk stimulated chicks to eat more ration.

Some young columbids feather quickly and leave the nest at relatively low weight. Ricklefs (1968) found that the ratio of fledgling weight to adult weight for 94 noncolumbid species ranged from 0.62 to 1.42. For seven of eight columbid species the ratio ranges from 0.25 to 0.66 (Table 1). In concert with fast growth, early fledging must significantly shorten the nestling period. After leaving the nest, young Mourning Doves usually become independent in 4–7 days (Hitchcock and Mirarchi 1984). Ad-

mittedly, our comparison of nesting cycle lengths would be more reliable if we included this period, but there are few published data on the postfledging period of columbids or noncolumbids.

Small clutches also may be an adaptation for a short nesting cycle. Mourning Dove eggs usually are laid on alternate days (Hanson and Kossack 1963), so increasing clutch size to three would have a direct, although minor, effect on the duration of the nesting cycle. A larger clutch also may prolong the incubation period, as Zimmerman (1983) found with Dickcissels (*Spiza americana*). During the early nestling stage, parents with a given amount of crop milk may opt to raise a small brood quickly or a large brood slowly (Lack 1968). Some evidence suggests, however, that some individual columbids may simply increase crop-milk production for a larger brood. Murton et al. (1963) found that adding a third nestling to some Wood Pigeon nests had no effect on growth during the crop-milk stage. This is not true, however, for other Wood Pigeons (Murton et al. 1974), feral pigeons (Burley 1980), or Mourning Doves (Blockstein unpubl. data). After the crop-milk phase, nestling growth may be limited by the rate at which the parents gather seeds. Haas (1980) found that Mourning Dove nestlings attended by a single parent after the crop-milk phase take up to 3.8 days longer than normal to fledge. He did not, however, report fledging weights. Murton et al. (1974) studied the effects of brood size on growth rates of nestling Wood Pigeons, a species that normally lays two eggs. They found that nestlings in broods of three grew more slowly than those in broods of two, but parents of three-young broods nevertheless were often successful in fledging the young. Band recoveries within one month of fledging indicated that young from broods of three had lower survival, but the difference was not statistically significant. Further study is necessary to resolve whether or not small clutch size is an adaptation for short nesting cycles.

The importance of predation.—Adaptations that shorten the nesting cycle also are advantageous in reducing the probability of predation. When the nesting cycle is short (i.e. there are fewer days of nest exposure), there is less chance of a nest being discovered by a predator (see Mayfield 1975). Also, the loss of a small clutch represents less wasted parental investment. Predation-related advantages undoubtedly

contribute to the success of the columbid reproductive strategy, but clutch overlap and reuse of nests built by other individuals or other species cannot be explained as adaptations for predator avoidance. Also, this proposed suite of adaptations is relatively ineffective at reducing losses to predation. From Ricklef's (1969: 12) data on daily nest failure, the mean rate for Mourning Doves is about the same as that for the 15 other open-nesting, altricial species listed (2.1% vs. 2.4%, respectively, Student's t-test, $P = 0.38$). Thus, we believe that predation probably is of secondary importance in the evolution of the columbid reproductive strategy.

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100 Years Ago in The Auk

From "Third Meeting of the American Ornithologists' Union" (1886, Auk 3: 117–118):

"It became apparent more than a year ago that the work of this Committee [on the Migration and Geographical Distribution of North American Birds—Ed.] was fast assuming such formidable proportions that the Union would soon be unable to sustain the financial burden thus entailed, and at the meeting of the Union last year the Council was instructed to prepare a memorial to Congress asking for Government aid. In considering this matter the Council decided to advise the establishment of a Division of Economic Ornithology under the Department of Agriculture, which should not only carry on the investigations necessary to a thorough understanding of the movements and distribution of our birds, but should also enter upon a systematic inquiry into their food-habits and practical relations to Agriculture. The Chairman of the Committee was accordingly requested to prepare and present a draft of a memorial, embodying this plan, to the Council, which was in due time received and approved by the Council. The Chairman, on presenting this memorial to Congress, was accorded a hearing before the House Committee on Agriculture, through the assistance of Prof. C. V. Riley, Chief of the Division of Entomology of the Department of Agriculture. Prof. Spencer F. Baird had the kindness to appear before the Agricultural Committee and personally urge the practical importance of the investigations thus proposed, while Senator Warner Miller, Chairman of the Committee on Ag-

riculture, not only brought the memorial favorably to the notice of the Committee on Agriculture, but afterward made an influential speech in its behalf on the floor of the Senate, and secured for the work contemplated an appropriation of $5000, after the item had been dropped in the House. It is thus to Senator Miller that ornithologists are indebted more than to any other person for the appropriation, as without his efficient aid the appeal to Congress would have been in vain. The House Committee on Agriculture, however, placed the work under the Division of Entomology, instead of creating for it an independent division, as contemplated in the memorial.

"The appropriation became available July 1, 1885, at which time the investigations in Economic Ornithology now in progress under the Department of Agriculture were begun. The Council of the Union was invited by the Commissioner of Agriculture and Professor Riley—in recognition of the interest in the work manifested by the Union, and of its efforts in securing the appropriation from Congress for these investigations—to nominate a person to take charge of, and conduct, the work. This the Council did at a meeting held in Washington on the 21st of last April, unanimously and very fittingly selecting for this position the Chairman of the A. O. U. Committee on the Migration and Geographical Distribution of North American Birds, Dr. C. Hart Merriam, to whom also had fallen the labor of presenting the memorial and

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