The energy cycle and thermal tolerance of the starlings (Aves, Sturnidae) in North America

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Gross energy intake, excretory energy, and metabolizable energy of both the common starling and the crested myna were obtained at outdoor temperatures through 12 consecutive months. Basal metabolic rates for the two species were determined to be 12.6 and 9.5 cal/g h for starlings and mynas respectively.

The thermal response of both species was determined over a range of controlled temperatures between −20°C and +30°C, with birds acclimated to the outdoor ambient temperatures of June and November. No seasonal differences were revealed. Starlings were found to have a higher temperature tolerance (above 40°C) than the crested myna (mean lethal dose (LD_{50}) = 40°C). The insulating quality of the plumage of the two species was determined by measurements of rate of cooling. Starlings had a relatively lighter total plumage (7% of body weight) than mynas (9.4% of body weight). Even so, the mean insulating value of myna plumage was found to be only $3.4 \pm 0.50 \times 10^{-2}$ cal/g h °C cm² compared to $6.2 \pm 0.50 \times 10^{-2}$ cal/g h °C cm² for starling plumage.

Mynas were shown to have less tolerance of cold and of heat than the ubiquitous starling.

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On a évalué l'ingestion brute d'énergie, l'énergie excrétée et l'énergie métabolisable chez l'étourneau sansonnet et le mynah (*Sturnus cristatellus*) aux températures extérieures ambiantes, durant 12 mois consécutifs. Les taux de métabolisme basal sont de 12.6 cal/g h chez l'étourneau et de 9.5 cal/g h chez le mynah.

On a mesuré aussi la réaction à des températures controlées variant de −20°C à +30°C, en utilisant des oiseaux des deux espèces acclimatées aux températures extérieures ambiantes de juin à novembre. On ne constate pas de changements saisonniers. Les étourneaux ont une tolérance thermique plus grande (au-dessus de 40°C) que les mynahs (LD_{50} = 40°C). Les propriétés isolatrices du plumage, chez les deux espèces, ont été évaluées en mesurant le taux de refroidissement. L'étourneau a un plumage total (7% du poids total) relativement plus léger que le mynah (9.4% du poids total). En dépit de cela, la valeur moyenne d'isolation du plumage, chez le mynah, est seulement de $3.4 \pm 0.50 \times 10^{-2}$ cal/g h °C cm² alors que cette valeur est de $6.2 \pm 0.50 \times 10^{-2}$ cal/g h °C cm² chez l'étourneau.

Chez les mynahs, la tolérance au froid et à la chaleur est inférieure à celle de l'étourneau dont la répartition est si étendue. [Traduit par le journal]

Introduction

In 1967 a study was initiated to investigate the reasons for the difference in colonizing success by European starlings (*Sturnus vulgaris vulgaris* L.) compared with crested mynas (*Sturnus cristatellus cristatellus* (Diegnan))[1] in North America. An earlier paper (see Johnson and Cowan 1974) described the various aspects of natural history affecting colonizing success by these two species of introduced North American Sturnidae, and the purpose of this paper is to describe that portion of the comparative study relating temperature and metabolic response in adults of both species.

[1]Taxonomy of the crested myna is unsettled.

Methods

Captive adult starlings and mynas were obtained from wild populations in the Vancouver area in winter, 1968–69. In winter the sex of starlings can be determined externally (Kessel 1951), and an even number of males and females were selected. Crested mynas, however, show no external sexual characteristics at this time of year; therefore birds could not be collected on this basis. No experimentation or data collection was initiated until the weight and behavior of the birds indicated that they had become adjusted to confinement (1–3 months).

Experimental birds were housed in 0.5 × 1 × 1 m cages outdoors at the Vivarium, University of British Columbia, where they were exposed to Vancouver temperature and light conditions (Fig. 1). A roof over the cage area and opaque polyethylene sheeting around it gave shelter from precipitation and wind (Table 1). Ten birds of each species were confined one per cage. Food and water were available on an ad libitum basis from

Protein (min.)	Fat (max.)	Fiber (max.)	NaCl	P	Vit. A (min./lb)	Amprolium
20%	3.5%	5.5%	0.45%	0.7%	1500 I.U.	0.0125%

specially constructed containers designed to reduce spillage. All experimental birds were fed Buckerfield's Chick Starter with Amprolium crumbles (coccidiostatic agent). Buckerfields guarantees the above analysis of their Chick Starter.

Energy utilization experiments were conducted for the period 1 January 1969 to 1 January 1970. Feed cans were weighed (before and after each trial) and filled with fresh feed every 2 days. Water was changed every 2 days except in winter when freezing temperatures necessitated changes every day.

Each 100-lb lot of feed purchased was subsampled twice. Four energy determinations were performed for each feed subsample on a Gallenkamp adiabatic oxygen bomb calorimeter. The mean energy content of the food was 4.53 ± 0.01 kcal/g for 8- to 100-lb lots.

Two perches were placed in each cage from which birds excreted onto non-absorbent paper unrolled beneath each row of cages. The paper was pulled from the ends of cage rows and the excrement was collected from each cage on sections cut from the roll. Excreta collections were made over 2-, 4-, 6-, and 8-day periods throughout the year. Twenty-three collections were made representing 102 days of sampling.

Excrement was dried at 32°C in a steam-heated room for at least 7 days, after which the dried samples were scraped from the paper and placed in plastic bags. After drying was complete, feathers and spilled food were separated from the excreta, which was then ground, mixed thoroughly, and deposited in polyethylene bags. Later, four 0.5- to 1.0-g subsamples were withdrawn from this mixture and dried in an oven at 50°C until their weights stabilized. Calorimetric determinations were conducted over two summers; no changes in performance by the Gallenkamp O_2 bomb calorimeter were noticed. All caloric values are expressed as kcal/g of ash-free dry material.

Weight of the experimental birds was measured biweekly and cage area ambient temperatures were measured every 2 days on maximum–minimum thermometers.

Bioenergetics data for captive sturnids were processed on an IBM 1130 computing system. Data were pooled into monthly means and an analysis of variance was run on an IBM 360 computing system. A value of $\alpha = 0.10$ was chosen for all statistical tests of significance.

Energy metabolism experiments were conducted on postabsorptive adult birds at night between 1 h after sunset and 1 h before sunrise in a Bellcraft controlled-environment cabinet (temperature fluctuations of ±1.0°C). Rate of passage was determined by the use of food marked with carmine dye and these data were applied to the determination of postabsorptive state. A closed-system technique was used in which the birds were placed on a perch in a 0.8-m^3 plexiglass box within the darkened environment cabinet. Relative humidity in the respiration chamber was kept at about 20% during experiments. Air temperatures were monitored using a YSI telethermometer with YSI No. 401 probes. Oxygen utilization was measured with a Beckman F-3 paramagnetic oxygen analyzer (circulation rate of 250 cm^3/min); ascarite tubes were used to analyze CO_2 from air samples withdrawn from the closed system. Birds were weighed and core (proventricular) temperatures were taken orally before and after experiments.

Trials of 3 h duration were performed on both species at ambient temperatures of −20°C through +40°C, except at +20°C, at which trials lasted from 6 to 9 h.

Experiments to determine insulative values for adult winter plumage of both species were conducted on fresh specimens in the environmental cabinet during late November 1969. Five starlings and four mynas were killed and immediately suspended by the beak in a cabinet and allowed to cool. The rate of natural body heat loss from freshly killed feathered specimens was recorded with a YSI model 524 needle probe inserted into the carcass core during cooling experiments at 0°C. Several birds were artificially reheated to normal core temperatures and cooled again to test for possible differences between the loss of artificially induced and natural heat. Finally, the feathered carcass was again artificially reheated, quickly stripped of feathers (feathers were dried and weighed), reheated the last few degrees to normal core temperature, and allowed to cool without feathers.

Surface areas of defeathered bird carcasses were determined by covering the carcass with a thin layer of Dow-Corning Silicone Sealant. The sealant was allowed to cure and was removed in a manner similar to skinning. The carcass mold was then cut into sections, pinned out flat, and traced. A polar planimeter was used to determine the surface area of the tracings. Surface area data obtained in this manner were compared with those calculated using the formula of Meeh (1897), S.A. = $kW^{2/3}$), and the constant (k) obtained by Rubner (1902), $k = 10.4$, for domestic fowl.

Results

The Energy Cycle

Starling gross energy (G.E.) intake, excretory energy (E.E.) output, and metabolizable energy (M.E.) and ambient temperature fluctuations throughout the 1-year experimental period are represented in Fig. 1.

Caloric value of excreta and the digestion efficiency (M.E./G.E. × 100 = digestion efficiency) both indicate the efficiency of food conversion (Fig. 2). The mean monthly energy content of starling excrement fluctuated between 4.03 kcal/g (February) and 4.19 kcal/g (October). Except for the November value (58.78%), starling digestive efficiency was relatively constant throughout the year.

TABLE 1

Meteorological data for lower mainland areas, British Columbia, 1969

	Exptl. cage area Vivarium, UBC			UBC weather station						Vancouver International Airport					
	Temp., °C			Temp.			Pptn., cm			Temp.			Pptn., cm		
Month	Mean	Max.	Min.	Mean	Max.	Min.	Rain	Snow	Total[a]	Mean	Max.	Min.	Rain	Snow	Total
Jan.	−2.1	1.3	−5.5	−2.4	0.3	−5.2	9.4	54.3	14.8	−3.0	0.0	−6.0	7.3	65.0	12.8
Feb.	4.7	8.3	1.0	3.5	6.4	0.5	5.6	2.6	5.8	3.5	6.5	−0.5	4.4	6.9	5.0
Mar.	6.4	10.3	2.5	6.3	9.6	3.0	9.8	—	9.8	6.0	10.1	1.8	9.0	—	9.0
Apr.	10.4	12.8	5.1	7.9	10.9	4.9	13.0	—	13.0	8.4	11.9	4.9	10.8	—	10.8
May	14.8	20.6	8.9	13.1	17.0	9.1	3.4	—	3.4	13.0	17.5	8.5	2.8	—	2.8
June	20.1	26.3	13.8	16.8	20.0	13.5	2.2	—	2.2	17.4	21.5	13.3	1.7	—	1.7
July	20.4	27.7	13.1	16.5	20.3	12.6	2.0	—	2.0	17.3	22.0	12.5	1.2	—	1.2
Aug.	17.4	22.3	12.5	15.5	18.3	11.8	6.2	—	6.2	15.8	20.0	11.6	5.2	—	5.2
Sept.	14.9	20.1	9.6	14.1	16.7	11.5	15.7	—	15.7	14.1	17.6	10.6	14.0	—	14.0
Oct.	11.4	16.8	5.9	10.1	13.1	7.0	10.1	—	10.1	9.6	13.4	5.8	10.4	—	10.4
Nov.	7.4	10.7	4.0	7.1	9.4	4.9	9.4	—	9.4	6.5	9.4	3.6	9.9	—	9.9
Dec.	5.4	8.6	2.2	5.6	7.4	3.8	17.7	—	17.7	5.2	8.0	2.4	15.4	—	15.4

[a]10 cm snow ≅ 1 cm rain.

TABLE 2

Results of an analysis of variance on energy balance data

Gross energy: Calculated monthly constants presented in an ordered array (kcal/bird-day)

4[a] March	1 Jan.	6 April	8 May	10 Aug.	2 Feb.	12 July	9 Sept.	5 Nov.	11 June	7 Oct.	3 Dec.
18.62[b]	14.37	8.23	4.91	0.12	−0.57	−1.04	−1.68	−7.54	−9.97	−11.00	−14.44

Mean SE of difference between 2 months = 7.09
Mean SE of difference between two species = 2.74
F value for months = 4.41* with 11 and 372 df
F value for species = 6.74* with 1 and 372 df

Calculated species constants, kcal/bird-day: −4.37 (starlings), 4.37 (mynas)
Calculated estimate of mean, kcal/bird-day: 114.29

Excretory energy: Calculated monthly constants presented in an ordered array (kcal/bird-day)

4 March	6 April	7 Oct.	1 Jan.	8 May	10 Aug.	12 July	3 Dec.	11 June	2 Feb.	9 Sept.	5 Nov.
13.08	8.09	3.26	2.93	2.63	1.78	1.60	−2.28	−3.15	−3.25	−8.11	−16.53

Mean SE of difference between 2 months = 3.51
Mean SE of difference between two species = 1.36
F value for months = 12.45* with 11 and 372 df
F value for species = 0.12 with 1 and 372 df

Calculated species constants, kcal/bird-day: +0.24 (starlings), −0.24 (mynas)
Calculated estimate of mean, kcal/bird-day: 58.64

Metabolized energy: Calculated monthly constants presented in an ordered array (kcal/bird-day)

1 Jan.	5 Nov.	9 Sept.	4 March	2 Feb.	8 May	6 April	10 Aug.	12 July	11 June	3 Dec.	7 Oct.
11.45	8.99	6.43	5.57	2.63	2.27	0.14	−1.60	−2.66	−6.80	−12.16	−14.27

Mean SE of difference between 2 months = 5.30
Mean SE of difference between two species = 2.05
F value for months = 3.82* with 11 and 372 df
F value for species = 15.82* with 1 and 372 df

Calculated species constants, kcal/bird-day: −4.62 (starlings), +4.62 (mynas)
Calculated estimate of mean, kcal/bird-day: 55.64

[a]Denotes rank in the monthly array of ambient temperatures.
[b]Values joined by solid lines are not significantly different from each other.
*Designates significance ($\alpha = 0.10$).

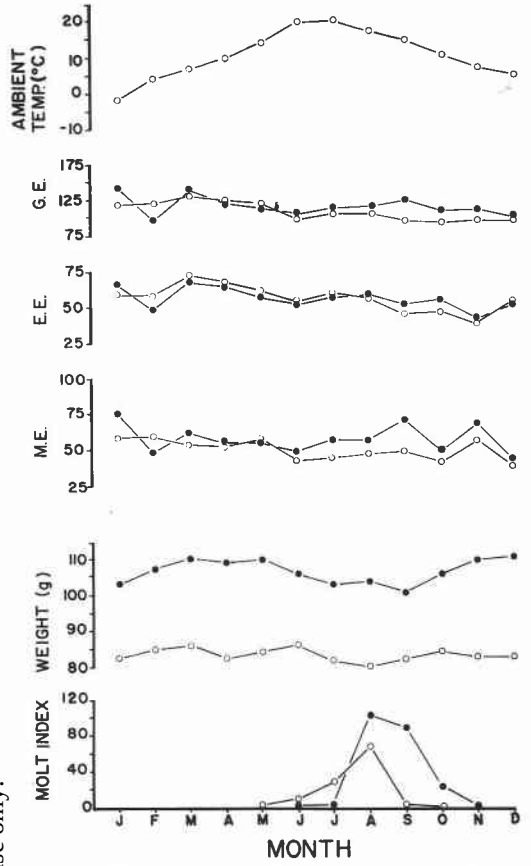

FIG. 1. Graphic presentation of annual pattern of sturnid gross energy intake (G.E.), excretory energy output (E.E.), and metabolizable energy (M.E.), all in kcal per bird-day, and patterns of molt (molt index = number of feathers per day found in excrement samples), and ambient temperature change (○ starling; ● crested myna).

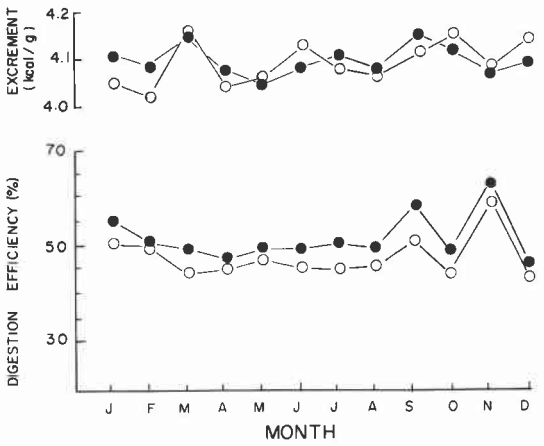

FIG. 2. Energy content of excreta and digestive efficiency during the 1-year experimental period (○ starling; ● crested myna).

North American sturnids molt once each year from late summer through early fall. Figure 1 illustrates this pattern of molt in birds held captive in Vancouver during the 1969 study period.

Starling weights were relatively stable throughout the year-long experimental period; however, during the molt, both sexes showed a statistically significant decrease in body weight.

Table 2 presents an analysis of variance for energy balance data. The data for starlings and mynas show identical trends from month to month (except for the low value for mynas in February). Therefore one set of monthly constants, when presented in an ordered array and summed with the appropriate species constant (in this case, starling) and the calculated estimate of the mean, yields a statistic which approximates the monthly parameter sought. The F values, with appropriate degrees of freedom, designate the significance of difference for energy values between species (myna and starling) and within months (any 2 months). Monthly values not connected with the same underscoring are those different from each other. In the case of starling G.E., the mean standard error (SE) of the difference between 2 months was 7.09 kcal/bird per day; therefore, values different by more than 7.09 (1 mean standard error), were considered different.

The E.E. and M.E. values for starlings were treated in the same manner and are also presented in Table 2.

Figure 1 also illustrates myna G.E. and temperature fluctuations on a monthly basis during the 1-year experimental period. For this species, G.E. showed a decrease from January through June, after which it stabilized.

Myna E.E. was more erratic throughout the year than the G.E., and this caused M.E. to fluctuate greatly also, especially during the second half of 1969. The mean monthly caloric values of myna excrement are presented in Fig. 2. In the aviary, the trend in digestion efficiency for mynas was similar to that for starlings (Fig. 2) despite a seasonal difference in food between the species in the wild (Johnson and Cowan 1974).

The pattern of molt in crested mynas closely overlapped that of starlings. It began in mid-July with loss of the crest and facial feathers, and

TABLE 3

Results of a regression analysis of temperature against G.E., E.E., and M.E. for starlings

	Correlation coefficients (product moment r)	Regression coefficients (b in $Y = bX+a$)	N
Temp. vs. G.E.			
Total year	0.28	−0.49	228
Jan.–June	0.56	−0.68	108
July–Dec.	0.79	+0.88	120
Temp. vs. E.E.			
Total year	0.00*	−0.03*	228
Jan.–June	0.10*	−0.09*	108
July–Dec.	0.53	+0.75	120
Temp. vs. M.E.			
Total year	0.45	−0.46	228
Jan.–June	0.78	−0.59	108
July–Dec.	0.12*	+0.13*	120

*Correlation or slope not significantly different from 0 ($\alpha = 0.10$).

TABLE 4

Results of a regression analysis of temperature against G.E., E.E., and M.E. for mynas

	Correlation coefficients (product moment r)	Regression coefficients (b in $Y = bX+a$)	N
Temp. vs. G.E.			
Total year	0.25	−0.48	228
Jan.–June	0.50	−0.12	108
July–Dec.	0.66	+0.89	120
Temp. vs. E.E.			
Total year	0.10	−0.11	228
Jan.–June	0.29	−0.31	108
July–Dec.	0.56	+0.56	120
Temp. vs. M.E.			
Total year	0.27	−0.37	228
Jan.–June	0.63	−0.83	108
July–Dec.	0.18	+0.31	120

TABLE 5

Change in body temperature (t_b) and body weight (W_b) during metabolism experiments

Exptl. temp. (°C)	Δt_b°C		ΔW_b, g/h	
	Starling	Myna	Starling	Myna
−20	0.42±0.085[a]	−0.11±0.182	1.18±0.033	1.73±0.099
−10	0.48±0.167	−0.04±0.225	0.91±0.106	1.44±0.078
0	0.53±0.257	−0.04±0.340	0.83±0.090	1.25±0.173
10	0.80±0.284	0.51±0.158	1.09±0.051	1.29±0.058
20	1.12±0.157	1.94±0.411	0.43±0.28	0.59±0.37
30	1.51±0.120	1.40±0.193	1.63±0.119	1.69±0.086
40	2.58±0.187	3.57±0.120[b]	2.02±0.076	3.77±0.714[b]
		4.70±0.286[c]		2.08±0.194[c]
		4.20±0.279[d]		3.04±0.517[d]

[a]Mean ± SE of the mean.
[b]Birds that survived ($n = 4$).
[c]Birds that died ($n = 4$).
[d]Total birds that lived and died ($n = 8$).

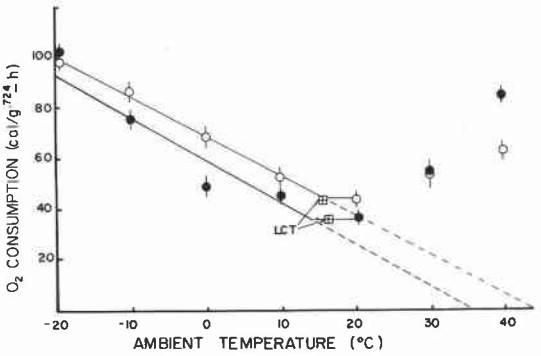

FIG. 3. Sturnid thermal-response curves illustrating theoretical LCT and experimentally observed LCT, and least squares regression lines extrapolated to theoretical body temperatures. Actual body temperatures at +20°C are 40.66°C for starlings (n = 38) and 39.93°C for mynas (n = 32). (○ starling; ● crested myna; vertical bar through symbol = ±1 SE.)

continued to mid-October with a peak in feather loss during late August and early September. The last rectrices and remiges did not completely harden until early November.

Weight dynamics of captive mynas are expressed in Fig. 1 also. The only statistically significant weight variations occurred during the molt. No analysis of sex-related weight variations was possible because of the lack of a reliable technique to determine sex of nonbreeding live adults. However, peaks in a bimodal distribution of weights of wild-shot birds were significantly different and were probably correlated with sex. Among birds of unknown age (but known to be adults) collected in winter and early spring, eight female mynas weighed 107.2 ± 1.56 g (mean ± standard error of the mean) and nine males weighed 111.53 ± 1.28 g. This established a significant (α = 0.10) weight difference between sexes in wild crested mynas.

The statistical analysis of myna energetics data was handled exactly as described for starlings (Table 2). Calculated monthly constants presented in an ordered array, when summed with the appropriate species constant and the calculated estimate of the mean, yield the estimate of either G.E., E.E., or M.E. The values not connected by the same underscoring are considered significantly different from others.

Myna G.E. consumption and M.E. utilization were significantly higher than observed for starlings. No significant difference between the two species was noted for E.E. (see F values for species in Table 2).

Effects of Ambient Temperature on Energy Utilization

Results of a regression analysis of temperature against starling G.E., E.E., and M.E. are presented to isolate the effects of ambient temperature on the energy cycle of captive sturnids. Energy values graphically presented in Fig. 1 were plotted against the mean monthly ambient temperatures in the aviary for the total, and first and second half-year periods (Table 3). For the first half year (January through June 1969), starling G.E. and M.E. were both significantly and negatively correlated with temperature; that is, as temperature decreased, energy utilization increased. All starling energy values for the second half year of 1969 (July through December) were positively correlated with temperature; both G.E. and E.E. showed statistically significant correlations with temperature. For the starling, G.E. and M.E. were significantly and negatively correlated with year-long temperature.

A regression analysis of crested myna G.E., E.E., and M.E. against ambient temperature showed correlations very similar to those for starlings during the same period (Table 4); both gross and metabolizable energy for the first half year showed the most significant negative correlations with temperature.

Oxygen Consumption

Laboratory investigations of sturnid thermal response were conducted to supplement energetics data collected in the aviary. Figure 3 illustrates the starling thermal response curve. Lower critical temperatures were calculated using the formula LCT = (t_b − BMR)/q (Kleiber 1961, p. 165), where q (feathered) is the value for conductance obtained from cooling experiments (see Table 6). We have interpreted BMR = MR (minimum resting metabolic rate) in cal/g h. For starlings, the calculated LCT was 14.70°C using a body temperature of 40.66°C (n = 38) and the MR (minimum resting metabolic rate) of 12.6 cal/g h (Fig. 3; LCT). Our comparisons of sturnid thermal response (Fig. 3) when calculated on the basis of cal/g$^{0.724}$ h do account for differences in heat production associated with body size, but these differences were minor.

The LD_{50} for upper temperature tolerance by starlings was not obtained. Starlings withstood +40°C for 3 h; their body temperatures increased an average of 2.5°C over their temperatures measured just before they were subjected

to experimental temperatures (Table 5). No facilities were available for testing birds below −20°C; therefore no lower tolerance limits could be determined. Weight loss during metabolic trials was attributed to water loss, tissue oxidation, and excretion. No attempt was made to measure respiratory water loss.

To examine the existence of seasonal differences in thermal response, starling metabolic trials were conducted at −20°C and +30°C in both late spring (June) and late fall (November). No significant differences were found.

Respiratory quotients (RQ) determined at −20°C and +20°C for starlings (0.74 ± 0.07 and 0.73 ± 0.06, respectively) were not significantly different from each other.

Observations of starlings during metabolism experiments revealed shivering only below 0°C.

The crested myna thermal response curve is also shown in Fig. 3. The calculated LCT was 15.34°C for mynas, using a body temperature of 39.93°C (n = 32) and a MR of 9.5 cal/g h (see Table 6 for q (feathered)).

The LD_{50} for upper temperature tolerance in crested mynas was 40°C (n = 8 birds); four died after considerable loss of weight and during hyperthermy when tested for 3 h at +40°C (see Table 5).

The effect of season on myna oxygen consumption was tested by measuring myna metabolism in late spring and late fall; as with starlings, no change was observed.

Myna RQ at +20°C (0.74 ± 0.08) was not significantly higher than at −20°C (0.71 ± 0.09). Shivering during metabolic trials was noticed for crested mynas at 0°C and below 0°C.

Cooling Experiments

Because metabolic trials suggested that mynas were producing more heat than starlings at both extreme low and high temperatures (Fig. 3), an attempt was made to determine the effectiveness of plumage as an insulative layer for both species. The results of cooling experiments were plotted, and regression lines relating cooling rate to external temperature were constructed for feathered and unfeathered starlings and mynas. Thermal conductance values were obtained using methods described by Morrison and Tietz (1957) and are expressed (Table 6) in cal/cm² h 0°C. The specific heat of bird tissue was assumed to be near 8.83 cal/°C g, which is the value given by Morrison and Tietz (1957) for small mammal tissue. Table 6 presents the pertinent data from which thermal conductance values were calculated; all were based on unfeathered weights.

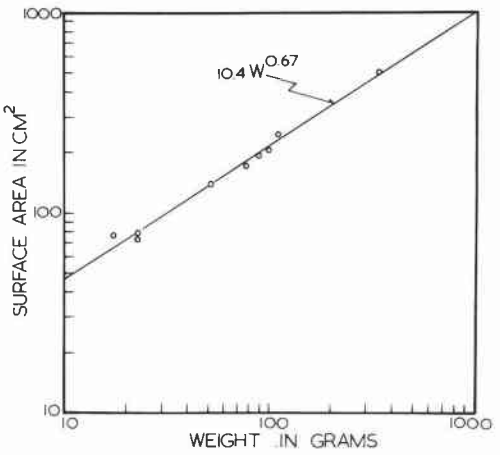

FIG. 4. Comparison of experimentally obtained (○) and theoretical (Meeh 1897: 10.4 $W^{2/3}$) surface area values for nine birds ranging in size from an immature barn swallow (*Hirundo rustica*) to an adult rock dove (*Columba livia*).

Surface Area

Surface area values were calculated from unfeathered weights after a series of experiments were conducted to test the accuracy of the formula given by Meeh (1897): surface area (cm²) = $kW^{2/3}$. A value of k = 10.4 was given by Rubner (1902) for domestic fowl; therefore the formula used was S.A. = 10.4 (unfeathered $W)^{2/3}$, where W (body weight) is expressed in $g^{1.0}$ (see Fig. 4).

To evaluate plumage quality, the value L was derived as follows:

$$L = \frac{(q_2 - q_1)\ (\text{specific heat})\ (\text{unfeathered weight})}{(\text{surface area})\ (\text{feather weight})}$$

where q_2 and q_1 are cooling constants for unfeathered and feathered carcasses, respectively (Table 6).

Starling $L = 6.2 \pm 0.05 \times 10^{-2}$ cal/g h °C cm², and the mean dry plumage weight of starlings (n = 5) was 6.3 ± 0.32 g (7% of total body weight).

Myna $L = 3.4 \pm 0.40 \times 10^{-2}$ cal/g h °C cm², and mean dry plumage weight (n = 4) was 10.5 ± 0.35 g (9.4% of the total body weight).

TABLE 6

Conductance values obtained from cooling curves of sturnids

	Weight (g)		Feather weight	Calculated surface area from unfeathered weight, cm^2	Cooling constants, h^{-1}		Thermal conductance, cal/cm^2 °C
	Feathered	Unfeathered			Feathered	Unfeathered	
Starling ($n = 5$)	88.2±0.77[a]	79.8±0.95	6.3±0.95	195.7±1.55	0.62±0.035	1.74±0.114	0.21±0.012
Myna ($n = 4$)	112.4±5.62	100.6±1.53	10.5±0.35	228.1±2.43	0.50±0.030	1.56±0.141	0.18±0.012

[a]All values are expressed as means ± standard error of means.

Discussion

The Energy Cycle in the Aviary

Mynas consumed and metabolized significantly more energy in the aviary (kcal per bird-day) than did starlings during the year-long utilization experiments (Table 2). However, if interspecific energy consumption is compared on the basis of mean monthly weight ($g^{0.724}$), no significant difference is observed between the two species. Thus, starlings had no apparent advantages over mynas with respect to energy conservation during the year-long energy utilization experiment.

Environmental temperatures were lower than normal in the first half of 1969; therefore regression analyses were conducted for one-half-year periods as well as for the total year period to isolate the effect of temperature on the energy cycle of these two sturnids.

Analysis-of-variance techniques (Table 2) indicated that monthly variations in gross and metabolizable energy consumption were significantly different ($\alpha = 0.10$), and the regression analyses (Tables 3 and 4) indicated that these differences were in part associated with temperature (product movement r values were significant).

There was a stronger negative correlation (although all were significant at $\alpha = 0.10$) between temperature and M.E. utilization for the first half of 1969 than for either the total or the last half of 1969 (Tables 3 and 4). This suggests that in a normal year, warmer winter ambient temperature would play an even more minor role in regulating energy expenditure of these birds. In fact, both starling and myna G.E. and E.E. were positively correlated with temperature during the last half of 1969. That is, as it became colder from July through December 1969, food consumption and excretory output were significantly reduced.

The above positive correlations are difficult to reconcile since they appear to be contrary to basic energetics theory. It is important, however, that metabolizable energy (that portion of the energy actually used by the birds) was, in general, not positively correlated with temperature. Except for the myna value encountered for the July through December period, all M.E. values were significantly negatively correlated with ambient temperature; this is consistent with basic theory. We should point out, however, that even though product-movement r values, with accompanying high degrees of freedom indicate significant correlations between energy values and temperatures (at $\alpha = 0.10$), the actual amount of variance observed in these energy values which would be accounted for by ambient temperature fluctuations (r^2), was negligible.

In starlings and mynas, total year G.E. and E.E. were both negatively correlated with ambient temperature, indicating that at least in part, the birds compensated for cold by increasing the volume of energy processed rather than by increasing the efficiency of utilization. No significant correlation was detected between temperature and either caloric value of excrement or digestive efficiency for either species. This agrees with the results of Kendeigh (1949) and Davis (1955) for house sparrows (*Passer domesticus*), West (1960) for tree sparrows (*Spizella arborea*), Zimmerman (1965) for dickcissels (*Spiza americana*), and others. However, this disagrees with results presented by Owen (1970) for the blue-winged teal (*Anas discors*), Williams (1965) for Canada geese (*Branta canadensis*), Brooks (1968) for redpolls (*Acanthis spp.*), West (1968) for Alaskan willow ptarmigan (*Lagopus lagopus*), and others.

The caloric values for excrement of our captive starlings and mynas were 10 to 15% higher than recorded for some other avian species (see Fisher 1972; Owen 1970; Zimmerman 1965; West 1960). These high excretory energy values are further reflected in the lower than expected digestion coefficients for both species. Avian excretory energy values and digestion efficiency coefficients reported in the literature were obtained from experiments conducted primarily on granivorous or herbivorous birds fed a chick-starter ration similar to that used in this study. We suggest that those species might be more efficient at digesting chick starter than are wild Vancouver sturnids that feed on insects and soil invertebrates most of the year (Johnson and Cowan 1974; Johnson, unpublished data).

Although no significant correlations could be found between molt index or energy content of the excreta and digestive efficiency, a significantly higher M.E. was shown during the molt, and a subsequent decline in M.E. was observed after termination of the molt, indicating that the experimental birds did increase their M.E. during this period. At this time also, weight, corrected for feather loss, reached its lowest point

in both species. The diet contained 20% protein, which is sufficient to accommodate molt in captive birds (Martin 1967), thus some other explanation for this weight reduction must be sought.

During June when the mean cage area ambient temperature was 20.1°C, starling and myna M.E. in the aviary was about equal: 21.95 cal/g h and 20.99 cal/g h respectively. At about the same temperature in the environmental cabinet (20°C), postabsorptive and resting starlings and mynas metabolized 12.61 and 9.53 cal/g h, respectively, at night. Assuming the latter values are minimum rates at these temperatures, a remainder of 9.34 and 11.46 cal/g h exists for the starlings and mynas respectively, to carry out activities in their cages.

In April, when the mean cage area ambient temperature was very close to 10°C (10.4°C), starling and myna M.E. were 28.44 and 22.13 cal/g h, respectively, in the aviary. During respirometric trials at 10°C, starlings metabolized 15.02 cal/g h compared with a value of 12.97 cal/g h of energy available for daily activities for the respective species.

During January the mean cage area ambient temperature of −2.1°C was close enough to 0°C to make further similar comparisons possible. The values at −2.1°C for M.E. in the aviary were very similar for both species, with starlings consuming 31.26 cal/g h and mynas 31.12 cal/g h. During respirometric trials at 0°C, starlings metabolized 20.26 cal/g h compared with 13.59 cal/g h for crested mynas, leaving a remainder of 11.00 and 17.53 cal/g h, respectively, for activity in the cages.

Thus activity energy is more similar for starlings and mynas at 20.1° and 10.4°C than at −2.1°C, at which activity energy for mynas was about 60% greater than that for starlings and almost 100% greater than that for mynas at +10.4°C. These calculations would indicate that crested mynas are either more active than starlings in cages during cold (not measured) or they have trouble conserving energy at the lower temperatures (the former possibly a reflection of the latter).

Kendeigh (1970) presents a formula describing existence energy (M.E. when weight balance is maintained) requirements for 15 passerine species at 30°C ($M = 1.5720\ W^{0.621}$, where M = existence energy, and W = weight in grams), for nine non-passerine species at 30°C ($M = 0.5404\ W^{0.7545}$), and for both groups at 0°C ($M = 4.3372\ W^{0.5300}$). We had no mean monthly value near 30°C but comparisons were made between our sturnid data collected in the aviary at −2.1°C (January 1969), and Kendeigh's predicted values (calculated from $M = 4.3372\ W^{0.5300}$) for all species at 0°C. The predicted values for starlings and mynas, respectively, are 45.09 and 50.60 kcal/bird per day. Kendeigh includes standard metabolism, specific dynamic action, and locomotor activity within the cages as part of his existence energy. Kendeigh stated that cages used for housing birds "varied in size to permit approximately the same amount of free movement; e.g. hopping but not flight (Martin (1967)." Cages used in this study were large enough to permit flight for several feet, and birds did so readily. Aside from use of the more general formula, the discrepancy between values obtained in this study (62.5 and 71.7 kcal/bird per day respectively, for starlings and mynas; see Table 2 for metabolized energy), and those predicted by Kendeigh's equation could be attributed to more activity by our birds.

Oxygen Consumption

Oxygen consumption curves (Fig. 3) indicate that crested myna metabolism was lower than that of starlings except at the extreme ends of the experimental temperature spectrum. Mynas had difficulty keeping warm at −20°C and keeping cool at +40°C. The upper temperature tolerance level (LD_{50}) for a 3-h period was 40°C for crested mynas ($n = 8$ birds), which is lower than reported (46–47°C) by Kendeigh (1969) for several other species of passerine birds. Myna lethal temperature was also lower than reported for blue-winged teal (Owen 1970), but similar to that of Canada geese (Williams 1965).

Starlings survived temperatures slightly above 40°C for 3 h, showing no noticeable adverse effects; however, above 30°C both species panted vigorously. Relative humidity in the respiration chamber was close to 20% throughout all tests. Both species exhibited visible shivering at temperatures colder than 0°C, but mynas elevated metabolic rates at colder temperatures faster than starlings.

West (1962) suggested that most heat production in birds is a result of muscular activity. His experiments with evening grosbeaks (*Hesperiphona verspertina*) have shown that in both summer and winter these birds shiver all night out of

doors at all temperatures below thermal neutrality, and the intensity of shivering increases as the ambient temperature falls (West 1962, p. 299). Although starlings shivered at temperatures below 0°C, they maintained heat balance and even overcompensated to give a net increase in body temperature, which contrasted with the net temperature decrease exhibited by crested mynas at the same temperature (Table 5). Hart (1962) conducted metabolic tests (1-h trials) on starlings at temperatures near −70°C, which did not prove fatal. His cold resistance tests, however, are not comparable to ours because he used time as a variable (at −48°C) rather than temperature.

Only two other sources of sturnid metabolic data were found. Hart (1962) measured starling metabolism between −65° and +38°C, but all his measurements were made during daylight hours (in a darkened chamber). His values at 38°C and 30°C (1962, p. 22) compare favorably with ours at 40° and 30°C; further comparisons were less favorable. Brenner (1965) also measured metabolic rates of single roosting starlings at 2–4°C and 24–30°C. His values again are very close to ours at his 24–30°C range, but different at the 2–4°C range. Brenner (personal communication) performed metabolism trials in late afternoon and early evening.

Aschoff and Pohl (1970) have compared metabolic data obtained in darkened chambers during day (activity period) and night (resting period) and found a mean difference of 23% with day values higher. Data presented by Lewies and Dyer (1969, pp. 293–294) illustrate this phenomenon clearly. It is also interesting to note that at warmer temperatures the differences between day and night resting metabolism are possibly less than at colder temperatures (for example, see data presented by Lewies and Dyer 1969).

In view of these differences presented by Aschoff and Pohl (1970) and illustrated by Lewies and Dyer (1969), comparisons drawn between uncorrected day and night metabolic data are inappropriate and possibly explain variations between our data and those of Brenner (1965) and Hart (1962).

Starling and myna standard metabolisms compare favorably with the formula $M = 0.867\ W^{0.724}$, where M is resting metabolism in kilocalories per bird-day for passerine birds and W is weight in grams (Kendeigh 1970). Weights of 82.9 and 109.7 g, respectively, for starlings and mynas before 20°C metabolism trials were used to obtain these calculated values. Also basal metabolic rates calculated from

$$\text{BMR (cal/g h)} = \frac{\text{(specific heat) (weight) } (q_1)\ (t_b - \text{LCT}) \text{ (h/day)}}{\text{(weight) (h/day)}}$$

yield values of 12.8 and 10.4 cal/g h for starlings and mynas. These values are also close to 12.6 and 9.5 cal/g h obtained in our respiration trials for starlings and mynas, respectively.

Because metabolic trials were conducted at 10°C intervals, and because within-species oxygen consumption values were not significantly different in the region surrounding MR (minimum resting metabolic rate), we were not able to define clearly the upper and lower critical temperatures (which in turn define the thermal neutral zone). But calculated (Kleiber 1961) lower critical temperatures (LCT) of 14.07° and 15.34°C fall close to the intersection of the line describing the metabolism slope and the MR (Fig. 3). Extrapolation of metabolism slopes through calculated LCT's was attempted to obtain estimates of body temperatures for starlings and mynas. This technique, although based upon theory inappropriate for insulated homeotherms (see Kleiber 1961), was fairly accurate for starlings, but less satisfactory for mynas (Fig. 3).

Mynas did not immediately increase their metabolism as rapidly when temperatures became colder, which is reflected by the differences in metabolic slopes below the LCT. Also, myna body temperature decreased below the mean normal at low temperatures during metabolism trials (see Table 5), suggesting that mynas probably could not withstand long-term exposure to cold temperatures. This is substantiated by the fact that two mynas in good condition (normal weights) were found frozen to death in their cages in late December, 1968, when ambient temperatures were nearly −20°C for several days.

Thermal Conductance and Plumage Quality

Meeh's (1897) formula was found to be accurate for estimating surface area from bird weights (Fig. 4), and values obtained by this formula were used in our calculations of plumage quality and thermal conductance.

The advantages of using live birds for determining thermal conductance are obvious and

give support to the technique used by Lasiewski *et al.* (1967), but since Wallgren (1954) has shown the importance of intraspecific plumage differences as a factor which regulates cold tolerance, we elected to remove the feathers in an effort to evaluate plumage quality. Therefore it was useful to explore the technique using fresh bird carcasses. Our experimentally determined thermal conductance values were not significantly different from those calculated from the predictive equations presented by Herried and Kessel (1967) and Lasiewski *et al.* (1967) for passerines (see Drent and Stonehouse 1971).

The mean value ($n = 4$) for myna plumage quality, L, is $3.4 \pm 0.40 \times 10^{-2}$ cal/g h °C cm^2 compared to $6.2 \pm 0.50 \times 10^{-2}$ cal/g h °C cm^2 ($n = 5$) for starling plumage. These values represent the amount of heat (calories) conserved by 1 g of feathers over 1 cm^2 of surface area in 1 h for every 1°C of temperature gradient ($t_b - t_a$). They are significantly different and suggest gross differences in basic plumage quality of starlings and crested mynas. It is interesting to note that both mynas and starlings have more feathers, by weight, than predicted by Kendeigh's (1970) equation: $W_f = 0.068\ W^{0.95}$, where W_f is weight of the feathers in grams and W is body weight of the bird in grams. This equation is based on Wetmore's (1936) data, which did not include values for sturnids. Also interesting is that mynas in this geographic region appear to have heavier plumage as a percentage of body weight (9.4%) than do starlings (7.0%). Mynas also have heavier plumage than starlings if calculations are based on total surface area: 4.6 and 3.2%, respectively. Even so, the insulative quality of myna plumage seems to be inferior to that of starlings, and since this cannot be explained on the basis of plumage weight, other more subtle factors are probably involved.

In general, except for the apparent poor insulative quality of myna plumage, and the mynas' poor tolerance for extremes in ambient temperature, the two species seem remarkably similar in their responses to the thermal constraints of this new environment. Except for encounters with extreme cold, as during the winter of 1969–70, adult temperature tolerance seems to play a minor role in accounting for the colonizing successes of the species. Therefore, considering all the above-mentioned factors we suggest that introduced crested mynas have not evolved special morphological or physiological adaptations for their new environment. Further, they seem less well adapted, especially during the breeding season, to the climatic and phenological characteristics of the area of southwestern British Columbia, in which it was introduced, than is the European starling, which introduced itself (see Johnson and Cowan 1974). The summary effect on all the differences already exposed, probably supplemented by others not yet studied, has led to the greater effectiveness of the starling in its new environment. At the same time, the myna is successful in that it has survived here for some 80 years, the last 12 of which have been in competition with an expanding starling population.

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