THE ENERGETIC CONSEQUENCES OF INCUBATION FOR TWO PASSERINE SPECIES

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ABSTRACT.—A previously developed model of heat transfer in incubating birds is applied to data describing the microclimate and nest/clutch/parent complex of the Red-winged Blackbird (*Agelaius phoeniceus*) and the Willow Flycatcher (*Empidonax traillii*) in southeastern Washington. Over an average 24-h cycle, the resting energy expenditure of an incubating female in both species averages 16–18% below that of a female perching on top of the vegetative canopy near the nest. This reduced energy requirement for incubating birds results from both the insulation of the nest and microclimatic amelioration associated with the nest's location. Accounting for the heat required to raise egg temperatures after parental inattentive periods lessens, but does not eliminate, this reduction in resting energy expenditure in incubating compared to nonincubating adults. *Received 27 December 1977, accepted 2 March 1978.*

In a previous account (Walsberg and King 1978) we presented a deterministic model of the thermal balance of the avian nest/egg/parent complex during incubation, and showed for one species that power consumption by the parent during this period is no greater than that of a nonincubating individual, and is probably less. A substantial range of comparative data will be needed to show whether this result is general or is peculiar to the species in question. In this report we present data on two additional species of songbirds (the Red-winged Blackbird, *Agelaius phoeniceus*, and the Willow Flycatcher, *Empidonax traillii*) and describe empirical and theoretical improvements in the mode of analysis. In particular, we subject our measurements, estimates, and equations to an error-propagation analysis of the type that is especially necessary in examining the reliability of deterministic models. In this, we hope to assist in extending the general and comparative powers of the model.

THEORY

Previously (Walsberg and King 1978), we developed a thermal model of an incubating songbird in an open nest. This is an extension of a general model of animal heat transfer that has been shown to predict heat exchange accurately in small birds (Monteith 1973, Robinson et al. 1976, Campbell 1977, Mahoney and King 1977). Our model incorporates characteristics of the physical environment (i.e. meteorological factors) as well as properties of the bird/clutch/nest complex (Fig. 1). Meteorological variables include radiation and convection; the latter is itself a product of a number of factors, including wind velocity, air temperature (T_a), and the characteristic dimension. Within the model, these environmental properties are subsumed in two variables, T_e and r_e. r_e is the parallel equivalent resistance to convective and radiative heat transfer between the bird's surface and the environment. T_e is the black-body equivalent temperature of the environment, which expresses the sum of air temperature plus a temperature increment incorporating radiative and convective factors. (See Walsberg and King [1978] for equations and assumptions used to calculate T_e and r_e.) The difference between T_e and body temperature (T_b) defines the thermal gradient between animal and environment. Net heat flux is

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proportional to this gradient divided by the total thermal resistance of the system (r_{total}).

$$M - \lambda E = \rho c_p (T_b - T_e)/r_{total}$$

Here, M is the metabolic rate, λE is latent heat loss, and ρc_p is a constant equal to 1,200 J/m^3 − °C when the units of M and r are W/m^2 and s/m, respectively. In the simplest case of a bird perching outside of the nest, r_{total} equals the sum of the whole-body thermal resistance (r_b) plus r_e. For an incubating bird, this model is applied by accounting for modifications of heat flow induced by the brood patch, eggs, and nest. Heat flux is calculated across three portions of the bird's surface: (1) the dorsal area exposed directly to the environment (circuit 1 in Fig. 1), (2) the area enclosed within the nest, but excluding the brood patch (circuit 2 in Fig. 1), and (3) the brood patch (circuit 3 in Fig. 1). The electrical circuit analogues illustrated in Fig. 1 incorporate only characteristics of the bird/clutch/nest complex; not shown are the additional functions T_e and r_e that account for environmental variables. r_e is added in series to each of the three circuits shown and, because of the differing radiative properties of the upper and lower hemispheres, separate values of T_e are calculated for the bird's dorsum, which is exposed to the upper hemisphere, and for the area of the bird enclosed within the nest, which is exposed to the lower hemisphere. Thus, to estimate an incubating bird's resting energy expenditure, information is required that describes: (1) the thermal resistances shown in Fig. 1, (2) the body surface areas over which each thermal resistance is operative, and (3) the environmental factors shown in Fig. 1 that are used to calculate T_e and r_e.

METHODS

Red-winged Blackbird nests and their microenvironments were studied in cattail (*Typha*) marshes near Pullman, Whitman County, Washington. In 1977, the main incubation period was approximately 20 May–5 June. Nests were typically suspended 0.5–1.5 m from the top of reeds. Willow Flycatcher nests and their microenvironments were studied in riparian vegetation along Rose Creek in the George E. Hudson Biological Reserve at Smoot Hill, Whitman County, Washington. The main incubation period for this species in 1977 was approximately 25 June–15 July. Of 10 nests located, 4 were placed in rose (*Rosa*), 2 in cow parsnip (*Heracleum*), 2 in nettles (*Urtica*), 1 in willow (*Salix*), and 1 in poison hemlock (*Conium*).

Environmental measurements.—Short- and long-wave radiation, air temperature, and wind velocity were measured continuously in the open over 10-day periods during the incubation period of each species (26 May–4 June for *Agelaius*, 30 June–9 July for *Empidonax*) and averaged by a Campbell Scientific Co. CR5 recorder over 1-h periods. Radiation was measured using standard and modified Moll-Gorczynski sensors, as described by Walsberg and King (1978). Hemispherical (scattered) short-wave radiation was measured midway through each hourly period with a disc held about 15 cm above the sensor surface to occlude direct solar radiation. Direct short-wave radiation was computed as the difference between total and scattered short-wave radiation. Direct short-wave radiation perpendicular to the solar beam was calculated using Lambert's cosine law. Upward short-wave flux reflected from the substrate was comparatively small and ignored when calculating energy budgets. Five sets of measurements at each of 10 *Agelaius* nest sites between 0600 and 1800 showed that upward short-wave flux averaged only 5.5% of downward short-wave flux in the open. Six sets of comparable measurements at each of seven *Empidonax* nest sites yielded a value of 4.2%. The absolute maximum upward short-wave flux measured at any nest site was 72 W/m^2 (*Agelaius* nest, 1200 PST, clear sky). At a typical vegetation surface temperature (T_r) of 20°C, this equals only 15% of the total upward flux. Long-wave radiation from the substrate and vegetation was calculated using the Stefan-Boltzmann relationship by assuming that substrate and vegetation surface temperatures equalled air temperature (T_a), which was measured using a shielded thermocouple 1 m above ground. This assumption should be maximally in error when vegetation is exposed to direct solar radiation. A total of 85 simultaneous measurements of T_r in full sun (using a Wahl HSA-120 infrared thermometer) and T_a at the nest sites of both species showed that T_r averaged 1.2°C above
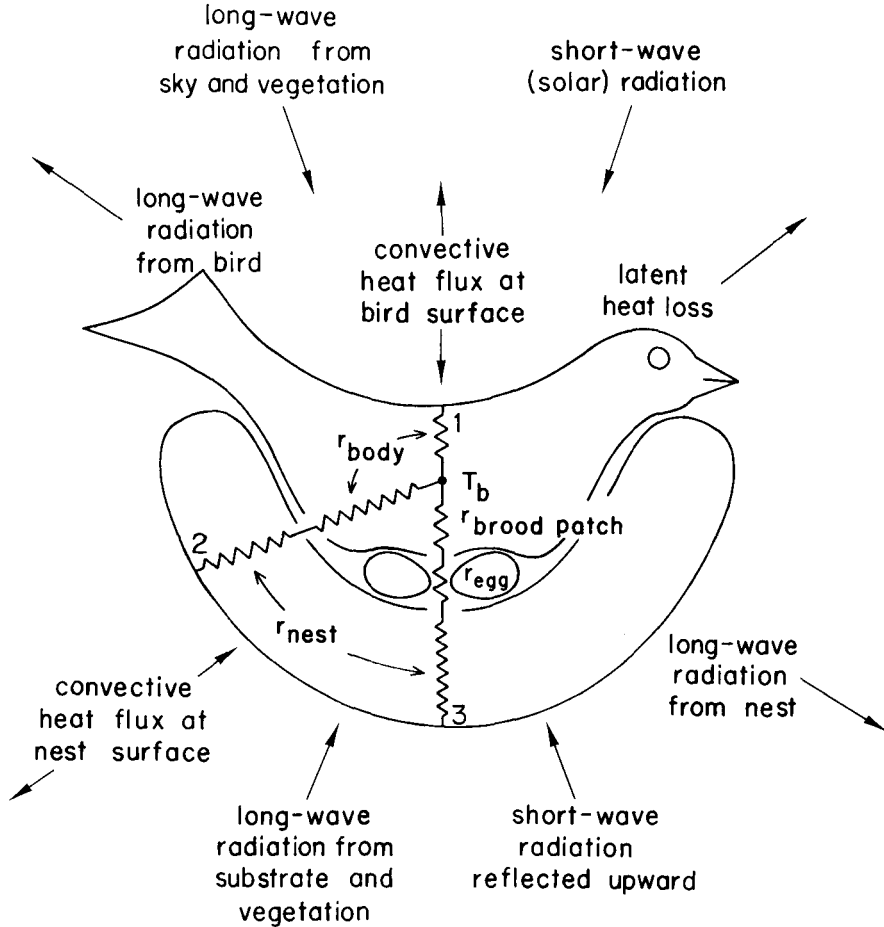
Fig. 1. Factors affecting the steady-state heat balance of a bird incubating in an open nest. Characteristics of the bird/clutch/nest complex are shown as components in an electrical circuit analogue. Environmental properties are shown with arrows indicating direction of energy flow.

T_a. At a typical T_a of 20°C and a vegetation emissivity of 0.98 (Idso et al. 1969), this difference produces an error of 1.6% in the estimate of long-wave flux. Differences observed between T_a and temperatures of shaded vegetation were smaller. The absolute maximum difference observed was at 1300 on 2 June, when T_a = 20°C and T_v (cattails in full sun) = 25°C. This would produce an error of only 6.4% in the estimate of long-wave flux.

The relative contributions of sky and vegetation to the radiative environment of the nest site were determined by analyzing hemispherical ("fisheye") photographs taken looking upward from 10 nest sites of each species. Photographs were analyzed by the method of Walsberg and King (1978), except that a more fine-structured analysis grid was used; each photograph was divided into 9 concentric annuli 10° wide, centered on the zenith, and azimuthal grid sectors 7½° wide (0–30° elevation), 15° wide (30–80° elevation), or 45° wide (80–90° elevation). Periods of the day during which the nest was exposed to the direct solar beam were computed by plotting sun paths onto the photographs.

Wind speed 1 m above ground was recorded continuously with a sensitive cup anemometer. Five sets of wind velocity measurements using a Hastings hot-wire anemometer equipped with an omnidirectional probe were made immediately above each of 10 *Agelaius* nests and 8 *Empidonax* nests. Wind speeds at the nest averaged 16% (*Agelaius*) or 38% (*Empidonax*) of the values for simultaneous measures made in the open 1 m above ground. These proportions were used by extrapolation of the cup anemometer data to estimate mean wind velocity at the nest.

Egg temperatures.—Egg temperatures were measured in order to calculate the heat expenditure for rewarming the eggs after inattentive periods. Such temperatures were measured using a 0.1-mm diameter thermocouple inserted through a small hole in the egg shell into the center of the egg. The thermocouple lead was cemented to the outside of the shell and passed through the bottom of the nest. Measurements were made with a Keithly 155 microvoltmeter equipped with a cold-junction compensator. The output from the microvoltmeter was recorded on a Rustrak 88 galvanometer chart recorder. The chart speed of the Rustrak varied with ambient temperature, and therefore an independent timing mechanism was attached to delineate hourly intervals on the strip chart. All measurements were made prior to the last 4 days of incubation.

Physical characteristics of the bird, eggs, and nest.—Long-wave absorptivity (=emissivity) of the bird, nest, and vegetation was assumed to be 0.98 (Hammel 1956, Idso et al. 1969). A value for short-wave absorptivity of the nest is not required since short-wave radiation from the lower hemisphere was insignificant and is ignored. The short-wave absorptivity of the dorsal plumage of the two species was measured with a YSI Kettering model 65 radiometer fitted with a 0.1-cm-thick quartz window. A 1.1-cm-diameter, 11.5-cm-long tube placed over the radiometer sensor restricted the field of view to 5°. Measurements of *Agelaius* were made by placing a frozen specimen so that sunlight was normal to the bird's dorsal surface and was reflected from the mid-dorsal region at approximately a 20° angle to the radiometer sensor. A plate with a 0.3-cm-thick coat of Kodak total reflectance paint (reflectivity = 0.99, Grum and Luckey 1968) was used as a standard by placing it in the position and height of the feather surface. All measurements were made under clear skies between 1000 and 1400 PST. Absorptivity, calculated as the average of 10 measurements made of each of five *Agelaius* specimens, equalled 0.76. This procedure was modified slightly for measurements of *Empidonax*, due to the small dorsal surface area of this species. A composite specimen of adequate size was prepared by mounting next to each other flat skins taken from the mid-dorsal area of two individuals. The feathers were arranged to produce a single continuous surface. Short-wave absorptivity, calculated as the average of 10 measurements, was 0.74.

Total body surface areas were estimated by the methods of Robinson et al. (1976) and equalled 0.00901 m² for *Agelaius* and 0.00487 m² for *Empidonax*. The surface area of the brood patch was estimated for three individuals of each species using the method of Walsberg and King (1978) and averaged 0.00101 m² for *Agelaius* and 0.00054 m² for *Empidonax*. From field observations, we estimate that 40% of the bird's surface (excluding the tail) is exposed outside of the nest in both species. For a bird perching outside of the nest, the fractional area (A_p/A_t) of the animal projected on a plane perpendicular to the solar beam was estimated by assuming that the bird approximates a prolate spheroid with a ratio of major to minor axes (based on measurements of three specimens of each species) of 0.49 for *Agelaius* and 0.50 for *Empidonax*. These values predict that A_p/A_t will range from 0.14 to 0.29 (*Agelaius*) or 0.14 to 0.28 (*Empidonax*). Variation within this range depends upon the bird's orientation to the solar beam. Since both species appear to orient at random, the intermediate values of 0.22 for *Agelaius* and 0.21 for *Empidonax* are used in all calculations. Assuming that the exposed dorsal portion of an incubating bird represents a hemicylindrical surface, A_p/A_t ranges from 0.32 to 0.64, depending upon the bird's orientation to the direct solar beam. Again, the intermediate value is used (0.48 in both species). The characteristic dimension (d) used in estimates of convective heat flow for incubating birds was assumed to equal the average nest diameter (0.08 m for *Empidonax*, 0.12 m for *Agelaius*). For birds perching outside of the nest, d was taken as the average horizontal diameter of the torso of three specimens of each species when held with the long axis of the body at a typical angle. Thus estimated, d equalled 0.048 m for *Agelaius* and 0.022 m for *Empidonax*. Latent heat loss (λE) is estimated by equation 56 of Calder and King (1974). The basal metabolic rate of female Red-winged Blackbirds is estimated as 0.711 W during daylight hours and 0.578 W at night, based upon measurements by Lewies and Dyer (1969) and assuming an average body weight of 41.9 g for females in May and June (Brenner 1967). Based upon five female Willow Flycatchers collected during the breeding season, body weight is estimated as 13.2 g. Using this value, the equations of Aschoff and Pohl (1970) predict basal metabolic rates of 0.325 W during daylight hours and 0.241 W at night. Body temperature is assumed to be constant and to equal 41.8°C in *Agelaius* (Lustick et al. 1970). Body temperature has apparently not been measured in Willow Flycatchers, but was assumed to be constant and to equal the average value (40.5°C) measured by Yarbrough (1971) for resting Acadian Flycatchers (*Empidonax virescens*).

The thermal resistance of 10 nests of each species were measured using the methods of Walsberg and King (1978). Body resistance was estimated using heat transfer coefficient values (h) derived from equation 13a of Calder and King (1974). The heat transfer coefficient (W/m² − °C) was used to calculate a total thermal resistance $(r_{total} = r_b + r_e = \rho c_p/h)$. This incorporates r_b plus the r_e operating on the bird under metabolic chamber conditions, in which free convection presumably dominates. Under these conditions,

TABLE 1. Mean meteorological data for Red-winged Blackbirds, 26 May–4 June

Time period (PST)	Air temperature (°C)	Wind velocity[a] (m/s)	Period of nest's exposure to direct solar beam (s)	Irradiance (W/m²)		
				Direct short-wave radiation[b]	Diffuse short-wave radiation	Downward long-wave radiation
0000–0100	6.4	1.38	0	0	0	299
0100–0200	5.9	1.28	0	0	0	303
0200–0300	5.6	1.08	0	0	0	304
0300–0400	5.6	1.04	0	0	22	300
0400–0500	6.1	1.03	0	69	36	300
0500–0600	9.4	1.33	108	294	186	311
0600–0700	11.4	1.68	702	421	131	313
0700–0800	11.4	1.97	922	596	82	307
0800–0900	13.4	2.19	875	669	146	309
0900–1000	14.3	2.36	893	383	336	313
1000–1100	15.4	2.48	1,350	303	440	306
1100–1200	16.4	2.44	1,566	430	404	324
1200–1300	16.5	2.31	1,494	395	324	323
1300–1400	16.4	2.10	1,134	313	300	321
1400–1500	16.1	1.99	1,296	243	296	319
1500–1600	15.7	2.00	1,278	207	232	321
1600–1700	14.4	1.99	954	467	69	320
1700–1800	13.1	1.69	738	332	82	315
1800–1900	12.0	0.88	162	195	58	310
1900–2000	9.6	0.89	0	0	28	304
2000–2100	8.4	1.06	0	0	19	279
2100–2200	8.2	1.18	0	0	0	303
2200–2300	7.9	1.45	0	0	0	307
2300–2400	7.2	1.30	0	0	0	301

[a] Wind velocity 1.0 m above ground in open
[b] Irradiance perpendicular to the solar beam

TABLE 2. Mean meteorological data for Willow Flycatchers, 30 June–9 July

Time period (PST)	Air temperature (°C)	Wind velocity[a] (m/s)	Period of nest's exposure to direct solar beam (s)	Irradiance (W/m²)		
				Direct short-wave radiation[b]	Diffuse short-wave radiation	Downward long-wave radiation
0000–0100	7.8	1.35	0	0	0	310
0100–0200	7.0	1.30	0	0	0	309
0200–0300	6.6	1.18	0	0	0	304
0300–0400	6.3	1.04	0	0	23	287
0400–0500	6.7	0.99	0	52	34	299
0500–0600	11.0	1.53	1,188	358	57	324
0600–0700	15.3	2.29	1,584	361	157	320
0700–0800	18.0	2.25	2,052	363	286	303
0800–0900	23.1	2.34	828	414	337	314
0900–1000	21.3	2.19	1,200	457	348	327
1000–1100	22.3	2.33	756	481	359	327
1100–1200	23.0	2.31	1,044	466	355	335
1200–1300	23.9	2.33	1,152	463	348	341
1300–1400	24.5	2.44	760	458	384	336
1400–1500	24.3	2.42	720	443	318	337
1500–1600	24.0	2.35	1,800	427	220	341
1600–1700	23.3	2.22	727	392	188	338
1700–1800	22.4	1.81	1,368	130	270	324
1800–1900	20.7	1.36	0	194	79	330
1900–2000	15.1	0.90	0	0	31	319
2000–2100	11.5	0.81	0	0	19	315
2100–2200	10.3	0.86	0	0	0	329
2200–2300	9.7	1.07	0	0	0	321
2300–2400	8.6	1.31	0	0	0	317

[a] Wind velocity 1.0 m above ground in the open
[b] Irradiance perpendicular to the solar beam

TABLE 3. Data on egg temperature and parental attentiveness

Time interval	Average number of inattentive periods		Average egg temperature increase at end of inattentive period (°C)		Heat required to increase egg temperature (J)	
	Agelaius[a]	*Empidonax*[b]	*Agelaius*[a]	*Empidonax*[b]	*Agelaius*[c]	*Empidonax*[d]
0300–0400	—	0.4	—	2.8	—	21
0400–0500	1.1	3.6	5.5	4.6	275	317
0500–0600	2.1	3.8	5.8	3.9	545	285
0600–0700	1.8	4.6	5.1	2.8	405	249
0700–0800	1.4	3.2	2.3	2.8	144	173
0800–0900	2.2	3.5	3.2	2.9	320	192
0900–1000	1.9	3.3	3.3	2.4	279	152
1000–1100	1.3	3.7	2.2	2.0	126	139
1100–1200	2.0	3.8	2.6	1.8	230	133
1200–1300	1.1	3.8	2.8	1.7	140	122
1300–1400	1.2	3.3	2.1	2.5	113	154
1400–1500	1.9	3.5	2.6	2.5	225	163
1500–1600	1.8	2.3	2.9	2.6	239	112
1600–1700	1.3	3.2	1.6	2.0	95	124
1700–1800	1.2	3.3	1.8	2.7	99	167
1800–1900	2.1	2.5	3.3	3.8	311	181
1900–2000	1.9	2.7	4.9	3.9	419	201
2000–2100	—	0.3	—	2.3	—	13
Mean	1.6	3.0	3.3	2.8	248	161

[a] Based on a total of 5 days of measurements at three different nests
[b] Based on a total of 12 days of measurements at three different nests
[c] Calculated assuming egg weight = 3.77 g (Hanna 1924), specific heat = 3.3 J/g–°C (Ricklefs 1974), and mean clutch size = 3.62 (based on a sample of 23 clutches)
[d] Calculated assuming egg weight = 1.68 g (Hanna 1924), specific heat = 3.3 J/g–°C (Ricklefs 1974), and mean clutch size = 3.42 (King 1955)

r_c may be estimated using the equation for r_r and equations 6 and 11 of Robinson et al. (1976). Since r_c makes up approximately 20–30% of r_{total}, even a 25% error in the estimate of r_c will produce an error of only 7–10% in the estimate of r_b. Estimated in this manner, r_b = 384 s/m for *Agelaius* and 283 s/m for *Empidonax*. These values are similar to those measured for White-crowned Sparrows (*Zonotrichia Leucophrys*) below thermal neutrality, which generally range from 330–400 s/m (Mahoney and King 1977). No other comparable data are available for small birds.

Body resistance in the region of the brood patch is estimated as 45 s/m (Walsberg and King 1978). The thermal resistance of the eggs is assumed to equal that of chicken eggs (Henderson 1963). This equals 40 s/m across the mean maximum width of 1.76 cm for *Agelaius* eggs (Bent 1958) and 29 s/m across the mean maximum width of 1.30 cm for *Empidonax* eggs (Bent 1942). These values ignore the unknown thermal resistance of the air space between the eggs and are thus underestimates. However, such an error is probably of minor significance in estimates of power consumption (Table 5).

RESULTS

Meteorological variables and egg temperature data.—Tables 1 and 2 give average values for meteorological variables measured over 10-day periods. Analyses of hemispherical photographs from 10 nest sites of each species revealed that 50.3 ± 11.5% of the sky over *Agelaius* nests was occluded by vegetation. The comparable value for *Empidonax* nests is 65.6 ± 8.0% (here, as below, results are given as $\bar{x}$ ± SD). The average periods per hour during which the nests were exposed to the direct solar beam are given in Tables 1 and 2; these total 3.74 ± 1.37 h/day for *Agelaius* and 4.22 ± 1.73 h/day for *Empidonax*. Data on egg temperature and the energy requirements of reheating the eggs after inattentive periods are given in Table 3.

Nest conductance and thermal resistance.—The thermal conductance of 10 nests of each species equalled 3.02 ± 0.342 W/m²–°C for *Agelaius* and 4.77 ± 0.544 W/m²–°C for *Empidonax* (surface area is that of the nest cup). Converted to thermal resistances and subtracting the estimated r_c yields average nest resistances of 331 s/m for *Agelaius* and 205 s/m for *Empidonax*. Calculations using equation 6.8 of
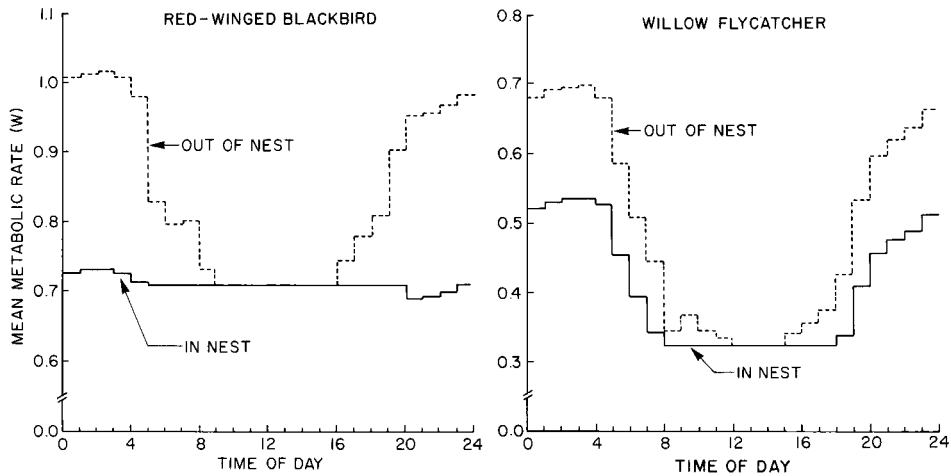
Fig. 2.　Mean energy expenditure for hourly intervals over an average 24-h cycle for an incubating bird and one perching on top of the vegetative canopy near the nest. Note that metabolic rate is scaled differently in the two graphs.

Campbell (1977) and average nest dimensions indicate that nest resistance equals about 33% (*Agelaius*) or 27% (*Empidonax*) of the resistance of an equal depth of still air.

Energy expenditure.—Figure 2 shows the estimated resting energy expenditure of the two species incubating over average 24-h cycles and compares these values with the estimated resting energy expenditure of a bird perching on top of the vegetative canopy near the nest. Resting metabolism averages 16% (*Agelaius*) or 18% (*Empidonax*) lower in incubating birds than in nonincubating birds (Table 4). Differences between incubating and nonincubating birds are similar on individual days with extreme high or low values for resting metabolism in incubating birds. Accounting

TABLE 4.　Average daily resting metabolic rates for an incubating adult and for an adult perching on top of the vegetative canopy near the nest[a]

	Species	
Status	*Agelaius*	*Empidonax*
"Average" day		
Perching	0.846	0.496
Incubating (without requirement for reheating eggs)	0.712 (−16%)[c]	0.407 (−18%)[c]
Incubating (including requirement for reheating eggs)	0.758 (−10%)	0.441 (−11%)
Lowest day[b]		
Perching	0.786	0.515
Incubating (without requirement for reheating eggs)	0.678 (−14%)	0.403 (−22%)
Incubating (including requirement for reheating eggs)	0.724 (−8%)	0.437 (−15%)
Highest day[b]		
Perching	0.903	0.546
Incubating (without requirement for reheating eggs)	0.755 (−16%)	0.439 (−20%)
Incubating (including requirements for reheating eggs)	0.801 (−11%)	0.473 (−13%)

[a] Watts
[b] Lowest and highest days refer to days on which the values for incubating birds reached minima and maxima, respectively
[c] Percentages indicate difference from value calculated for a bird perched near the nest

TABLE 5. Sensitivity of estimates of average resting energy expenditure to 25% errors in key variables

Change[a] in energy expenditure produced by 25% change in:	*Agelaius*		*Empidonax*	
	Incubating	Perching	Incubating	Perching
Body surface area exposed above nest (brood patch area constant)	1.5–1.8%	—	2.4–2.5%	—
Surface area of brood patch (area enclosed within nest constant)	0.6–0.7%	—	1.0–1.1%	—
Body resistance (brood patch resistance constant)	4.1–7.0%	12–24%	7–13%	15–29%
Brood patch resistance	0.3–0.4%	—	0.2–0.4%	—
Egg resistance	0.3–0.4%	—	0.2–0.3%	—
Equivalent resistance (r_e)	1.0–1.1%	2.1–2.4%	1.0–2.4%	2.9–3.2%
Latent heat loss (λE)	0.7–0.8%	1.5–1.7%	1.6–1.7%	3.0–3.1%

[a] In each category, the larger of the two values given for percent change is produced by a change in the variable that increases heat flux (decrease in thermal resistance, increase in area exposed outside of nest, increase in λE)

for the heat required to raise the temperature of the clutch after periods during which the female is off the nest lessens the reduction in energy expenditure for incubating compared to nonincubating birds to 10–11% (Table 4).

The reduced energy requirements of incubating birds result from both the insulation of the nest and microclimatic amelioration associated with the nest's location. The relative importance of these factors can be illustrated by calculating the nocturnal energy requirements of a Willow Flycatcher under three conditions: (1) roosting exposed on top of a shrub; (2) roosting and exposed to the microclimate of the nest site (i.e. inside a bush), but outside of the nest; and (3) incubating. From data in Table 2 for the period 1000–0400, we estimate that the resting metabolism of a flycatcher roosting exposed on top of a shrub averages 0.663 W. This value would be reduced 5% to 0.628 W if the bird were roosting inside of a bush at the nest site. If the bird were incubating, there would be further reduction of 19% to 0.508 W. Thus, at night when climatic amelioration should be greatest at the nest site, its effect is small compared with the reduction in heat loss associated with the thermal resistance of the nest.

Sensitivity of energy estimates to error.—Table 5 lists a number of the more sensitive variables of the model and illustrates the effect that a 25% error in their evaluation would have on estimated average resting metabolism. The model is notably sensitive only to the estimate of r_b. However, even doubling or halving our estimates of r_b for the two species would not produce estimates of average resting metabolism that are higher for incubating than nonincubating birds. Tissue resistance in the region of the brood patch has never been measured; our estimate of 45 s/m is based on values for vasodilated peripheral tissues in other species (Walsberg and King 1978). However, even if the resistance of the brood patch is zero (i.e. brood patch temperature = core body temperature), our estimates of average resting metabolism are increased by only 1–2% in both species. We have assumed in our calculations that forced convection is dominant and have consequently ignored free convection. This assumption is probably violated at low wind speeds at the nest site. However, the error produced by this assumption should be minor. The lowest wind velocity used in our calculations was 0.14 m/s for *Agelaius* nest sites, based upon an average wind velocity of 0.88 m/s measured in the open at 1800–1900 (Table 1) and assuming that wind velocity at the nest is 16% of that in the open (see Methods). Assuming that forced convection is dominant, this wind speed predicts $r_e = 106$ s/m. From the equations of Robinson et al. (1976), $r_e = 124$ s/m if free convection domi-

nates and the bird's surface temperature (T_s) is 10°C above T_a. If $T_s - T_a = 2$°C, then $r_c = 147$ s/m. Thus, in this extreme case, our assumption that forced convection is dominant will probably produce an error in the estimate of r_c of approximately 15–40%. Since r_c makes up a relatively small proportion of the resistance operating on an incubating bird, such errors are minor in energy budget calculations. Assuming $r_c = 147$ s/m instead of 106 s/m would decrease the incubating bird's estimated energy expenditure only 5%. Note in Table 5 that a 25% error in r_c over the entire day would produce an error of only 1–2% in the estimated energy expenditure of incubating birds.

Our estimates of resting energy expenditure for nonincubating birds assume that perching during the entire 24-h period is done in the open. Though a reasonable assumption for Red-winged Blackbirds, this is not true at night for the Willow Flycatcher. However, as previously noted, nocturnal energy expenditure would probably be reduced only about 5% if the bird is assumed to roost inside of a bush exposed to a microclimate similar to that of the nest site. This produces only a 2% error in our estimate of average daily resting metabolism.

DISCUSSION

The results of this study plus our previous analysis of White-crowned Sparrows (*Zonotrichia leucophrys*, Walsberg and King 1978) indicate that in the three species considered the resting metabolism of incubating birds averages about 15–18% below that of nonincubating birds. This disagrees with opinions expressed by others (e.g. Kendeigh 1963, 1973) that incubation entails a substantial net energy cost to the incubating parent. One source of this disagreement is differences in the operational definition of incubation. In a restricted sense, incubation may be considered as only the transfer of heat from the adult to the egg; this definition would ignore the energetic consequences of other behavioral and physiological characteristics of incubating birds (e.g. occupation of a nest). Such a definition is implicit in the equations proposed by Kendeigh (1963) and Ricklefs (1974) to estimate indirectly the energy requirements of incubation. We believe that it is ecologically more appropriate to consider also the effects of incubation behavior on heat exchange across the adult's body surface in general. Thus, in our analyses we have compared the energy requirements of incubating birds to those of nonincubating birds outside of the nest, since nonbreeding adults typically do not occupy nests. In the species that we have studied, the effects of the nest's microclimate and insulation more than compensate for heat loss through the brood patch. Thus, considering only heat input to the eggs from the adult might stimulate misleading ecological inferences. A recent investigation in which effects of the nest might alter ecological interpretations is Biebach's (1977) study in which the nocturnal energy metabolism of starlings (*Sturnus vulgaris*) incubating in nest boxes was compared to that of nonbreeding starlings, also in nest boxes. Since the metabolic rate of nonbreeding birds was lower than that of incubating birds, Biebach concluded that incubation at night entailed a net energy cost to the adult. However, it is worth noting that the energy expenditure of these incubating starlings generally was lower than the nocturnal energy expenditure measured by Johnson (1972) at the same air temperatures for nonbreeding starlings not occupying nest boxes.

Our estimates apply only to basal plus thermoregulatory requirements; they ignore embryonic heat production and the energy requirements of adult activity. Both of these factors probably reduce further the energy requirements of incubating birds

compared to nonincubating birds. The embryo's contribution of heat to the parent/
clutch complex may be estimated using the allometric equation of Rahn et al. (1974)
for oxygen consumption as a function of egg mass. Assuming a respiratory quotient
of 0.72 (Rahn et al. 1974), this equation predicts that heat production just prior to
pipping is 0.0142 W/egg in *Agelaius* and 0.00762 W/egg in *Empidonax*. The average
clutch size would produce 0.0514 W in *Agelaius* and 0.0261 W in *Empidonax*. These
maxima equal about 6–7% of the resting heat production of the adult in both species.
Embryonic heat production averaged over the entire incubation period should be
much lower, associated with low egg temperatures during parental inattentive pe-
riods, smaller embroynic body mass, and latent heat loss.

Differences in activity patterns may have much more important effects on the total
daily energy expenditure of incubating birds than does embryonic heat production.
Energy expenditure during flight, estimated using the equation of Hart and Berger
(1972), equals 5.23 W for *Agelaius* and 2.25 W for *Empidonax*. Thus, the afore-
mentioned estimates of the clutch's maximum heat production represent the energy
equivalent of only 0.6–0.7 min of flight per h. Likewise, calculated differences in
resting metabolism between incubating and nonincubating birds represent the energy
equivalent of only 1.0–1.5 min of flight per h. Obviously, changes in activity may
be of overriding significance in a species' daily energy budget. In studies of time and
energy use during the annual cycle of Black-billed Magpies (*Pica pica*, Mugaas 1976)
and Phainopeplas (*Phainopepla nitens*, Walsberg 1977), it was found that time spent
in flight per day was substantially reduced during incubation. Consequently, estimates
of daily energy expenditure based upon time-activity budgets indicated that daily
energy expenditure in both species reached its lowest annual level during incubation.
In magpies, the incubating female's energy expenditure averaged 25–39% below that
of nonbreeding females. The decrease is about 7% in the Phainopepla, a species in
which incubation is divided between the sexes. Black (1975) and Withers (1977)
studied the use of time and energy during the breeding period of Black-throated Blue
Warblers (*Dendroica caerulescens*) and Cliff Swallows (*Petrochelidon pyrrhonota*),
respectively. In these species also, time spent in flight is reduced substantially during
incubation. For Black-throated Blue Warblers, this results in the daily energy ex-
penditure of incubating females being 4% below that of females during nest con-
struction, 13% below that of females feeding nestlings, and 2% above that of pre-
nesting birds (Black 1975). Withers (1977) found that daily energy expenditure of
incubating Cliff Swallows was 21% below that of adults during nest construction
and 4% below that of adults feeding nestlings. Differing methods and assumptions
were used to estimate energy expenditure in these three species, but it is likely that
errors in estimates of resting energy expenditure while incubating or not incubating
are small compared to the effects of differing amounts of flight. It is thus notable
that no substantial increase in daily energy expenditure has been detected in any
free-living bird species during the incubation period, and in some species incubation
entails a large reduction in energy expenditure.

However, low levels of energy expenditure during incubation do not necessarily
mean that energetic considerations are not important. For example, the large amounts
of time devoted to incubation may significantly restrict time available for foraging.
From the data of Black (1975), Mugaas (1976), and Walsberg (1977), we have cal-
culated the average amount of energy that must be acquired during the bird's daily
active period, excluding time spent attending the eggs and assuming the adults
maintain energy balance. These calculations indicate for all three species that sub-

stantially more energy must be acquired per hour of available foraging time by incubating birds than by nonbreeding birds. Average values show approximately a 4–8-fold increase in incubating magpies in required energy intake per hour of available foraging time, a 4-fold increase in Black-throated Blue Warblers, and a 1.5–1.7-fold increase in Phainopeplas. Similarly, Withers (1977) found that in Cliff Swallows required energy intake per hour of available foraging time during incubation is 1.12 times that during nest construction. The above calculations are confirmed by Black's (1975) data on Black-throated Blue Warblers, which indicated that this species' foraging rate (foraging maneuvers per unit time spent foraging) peaks during incubation, exceeding even that observed when nestlings are being fed. Morse (1968) obtained similar results for four other parulid species. Thus, allocation of large amounts of time to incubation may reduce total energy expenditure, yet simultaneously increase required rates of energy acquisition because of reduced available foraging time. Mechanisms such as biparental incubation and the feeding of the incubating female by the male may attenuate this conflict between selective pressures favoring increased time spent in incubation and those favoring increased time spent foraging.

LITERATURE CITED

ASCHOFF, J., & H. POHL. 1970. Der Ruheumsatz von Vögeln als Funktion der Tageszeit und der Körpergrösse. J. Ornithol. 111:38–47.

BENT, A. C. 1942. Life histories of North American flycatchers, larks, swallows, and their allies. U.S. Natl. Mus. Bull. 179.

———. 1958. Life histories of North American blackbirds, orioles, tanagers, and allies. U.S. Natl. Mus. Bull. 211.

BIEBACH, H. 1977. Der Energieaufwand für das Brüten beim Star. Naturwissenschaften 64: 343.

BLACK, C. P. 1975. The ecology and bioenergetics of the Northern Black-throated Blue Warbler (Dendroica caerulescens caerulescens). Unpublished Ph.D. dissertation, Hanover, N.H., Dartmouth College.

BRENNER, F. J. 1967. Seasonal correlations of reserve energy of the Red-winged Blackbird. Bird-Banding 38: 195–211.

CALDER, W. A., & J. R. KING. 1974. Thermal and caloric relations of birds. Pp. 259–413 in Avian biology, vol. 5 (D. S. Farner and J. R. King, Eds.). New York, Academic Press.

CAMPBELL, G. S. 1977. An introduction to environmental biophysics. New York, Springer-Verlag.

GRUM, F., & G. W. LUCKEY. 1968. Optical sphere paint and a working standard of reflectance. Applied Optics 7: 2289–2294.

HAMMEL, H. T. 1956. Infrared emissivities of some arctic fauna. J. Mammal. 37: 375–378.

HANNA, W. C. 1924. Weights of about three thousand eggs. Condor 26: 146–153.

HART, J. S., & M. BERGER. 1972. Energetics, water economy, and temperature regulation during flight. Proc. 15th Intern. Ornithol. Congr.: 189–199.

HENDERSON, S. M. 1963. On-the-farm egg processing. III. Thermal conductivity, generalized cooling procedure, and cooling in water. Trans. Amer. Soc. Agr. Eng. 6: 95–97.

IDSO, S. B., R. D. JACKSON, W. L. EHRLER, & S. T. MITCHELL. 1969. A method for determination of infrared emittance of leaves. Ecology 50: 899.

JOHNSON, S. R. 1972. Thermal adaptation in North American Sturnidae. Unpublished Ph.D. dissertation, Vancouver, Univ. British Columbia.

KENDEIGH, S. C. 1963. Thermodynamics of incubation in the House Wren, Troglodytes aedon. Proc. 13th Intern. Ornithol. Congr.: 884–904.

———. 1973. Discussion. Pp. 311–320 *in* Breeding biology of birds (D. S. Farner, Ed.). Washington, D. C., Nat. Acad. Sci.

KING, J. R. 1955. Notes on the life history of Traill's Flycatcher (*Empidonax traillii*) in southeastern Washington. Auk 72: 148–173.

LEWIES, R. W., & M. I. DYER. 1969. Respiratory metabolism of the Red-winged Blackbird in relation to ambient temperature. Condor 71: 291–298.

LUSTICK, S., S. TALBOT, & E. L. FOX. 1970. Absorption of radiant energy in Red-winged Blackbirds (*Agelaius phoeniceus*). Condor 72: 471–473.

MAHONEY, S. A., & J. R. KING. 1977. The use of the equivalent black-body temperature in the thermal energetics of small birds. J. Therm. Biol. 2: 115–120.

MONTEITH, J. L. 1973. Principles of environmental biophysics. New York, American Elsevier.

MORSE, D. H. 1968. A quantitiative study of the foraging of spruce-woods warblers. Ecology 49: 779–784.

MUGAAS, J. N. 1976. Thermal energy exchange, microclimate analysis, and behavioral energetics of Black-billed Magpies, *Pica pica hudsonia*. Unpublished Ph.D. dissertation, Pullman, Washington State Univ.

RAHN, H., C. V. PAGANELLI, & A. AR. 1974. The avian egg: air-cell tension, metabolism and incubation time. Respir. Physiol. 22: 297–309.

RICKLEFS, R. E. 1974. Energetics of reproduction in birds. Pp. 152–297 *in* Avian energetics (R. A. Paynter, Jr., Ed.). Cambridge, Nuttall Ornithol. Club.

ROBINSON, D. E., G. S. CAMPBELL, & J. R. KING. 1976. An evaluation of heat exchange in small birds. J. Comp. Physiol. 105: 153–166.

WALSBERG, G. E. 1977. Ecology and energetics of contrasting social systems in *Phainopepla nitens* (Aves: Ptilogonatidae). Univ. California Publ. Zool. No. 108.

———, & J. R. KING. 1978. The heat budget of incubating Mountain White-crowned Sparrows (*Zonotrichia leucophrys oriantha*) in Oregon. Physiol. Zool. 51: 92–103.

WITHERS, P. C. 1977. Energetic aspects of reproduction by the Cliff Swallow. Auk 94: 718–725.

YARBROUGH, C. G. 1971. The influence of distribution and ecology on the thermoregulation of small birds. Comp. Biochem. Physiol. 39: 235–266.

The Ornithological Society of Turkey has expanded its geographical area of interest to include all countries of the Middle East, and its name has been changed to the **Ornithological Society of the Middle East.** Publication of a new journal, *The Sandgrouse,* will begin shortly. Additional information is available from **Don Parr, O.S.M.E., % R.S.B.P., The Lodge, Sandy, Bedfordshire, SG19 2DL, Great Britain.**

The **First Ibero-American Meeting on Ornithology and World Meeting on Ecology and Bird Behavior** will be held in Buenos Aires, Argentina during the last week of November 1979, under the sponsorship of the Asociación Ornitólogica del Plata. Abstracts of papers and communications, to be delivered in Spanish, Portuguese, or Enghish, should be received before 31 March 1979, and should contain less than 300 words. Registration fees vary from US $50–200, according to the kind of membership. Additional information is available from **Prof. Juan Daciuk, President, Organizing Commission, ler. Encuentro Iberamericano de Ornitología, Casilla de Correo 3368, 1000 Buenos Aires, Argentina.**