THE INFLUENCE OF SIMULATED SOLAR RADIATION ON THE METABOLIC RATE OF WHITE-CROWNED SPARROWS

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Intuition and formal energy-budget equations (e.g., Birkebak 1966, Porter and Gates 1969) indicate that homeotherms can reduce the energy costs of thermoregulation by behaviorally exploiting sources and sinks of radiation of various wavelengths. For example, sunbathing while in cool surroundings is interpreted as an important mode of behavioral thermoregulation (Hamilton and Heppner 1967, Morton 1967, Ohmart and Lasiewski 1971) although additional functions for sunbathing are also plausible (Simmons 1964, Cowles et al. 1967, Goodwin 1967, Teager 1967, Kennedy 1968, Mueller 1972, Cade 1973). In spite of increasing attention to the role of insolation in the energy economy of homeotherms (Bakken 1959, Whittow 1970, Marder 1973), there have been no systematic empirical investigations of the interacting effects of air temperature and solar radiation in the energetics of thermoregulation in wild species of animals. Our quantitative appreciation of the ecological significance of such interactions depends at present on rather large-scale theoretical models of "climate space" (Porter and Gates 1969, Gates and Porter 1970) that serve only to delimit the temperature-radiation boundaries within which an animal can function in a steady state. This paper is an effort to quantify, on a more refined scale, the effects of simulated solar radiation on the energy costs of thermoregulation in the White-crowned Sparrow (*Zonotrichia leucophrys*). This small (24–30 g) finch has previously been the subject of studies of thermoregulation (King 1964), including the effects of natural and artificial radiation (Morton 1967).

METHODS

White-crowned Sparrows (*Z. l. gambelii*) were captured during their northward and southward migrations in mist nets near Pullman, Washington, and were housed in outdoor aviaries. Later the birds were transferred to an acclimation room (air temperature 19° to 20°C, daily photoperiod 8 hr). The transfer occurred at least 3 months before use in measurements of metabolism. Only adult birds were used. Except during metabolism measurements, chick-starter mash and water were freely available. For measurement of oxygen consumption a bird was placed in a thin-walled copper chamber (3.4 l, height = 23 cm, diameter = 13.7 cm; see fig. 1) whose interior surfaces were painted ultraflat black to minimize reflection of the radiation (Porter 1969). The removable top of the

chamber consisted of a disk of Plexiglas 12 mm thick. For control of temperature the chamber was submerged in a 190-l water bath. A disk of window glass (5 mm thick) mounted on 1-cm spacers was used to adjust the depth of the chamber beneath the water surface so that a layer of water exactly 1 cm thick always covered the Plexiglas lid. This arrangement was necessary to prevent thermal damage of the Plexiglas and to assure a constant thickness of the water layer during the experiment. The thickness of the water layer has a very important effect on amount of transmitted radiation (Curcio and Petty 1951). A small auxiliary pump maintained a continual flow of water through the 1-cm layer to prevent the accumulation of air bubbles beneath the glass disk.

Oxygen consumption was measured for 10 different birds at each of 4 chamber temperatures: 1°, 10°, 20°, and 30°C (i.e., 40 different birds). The temperature of the water bath was maintained at the designated level ± 0.7°C. Preliminary measurements showed that the irradiated chamber bottom or walls remained within 1°C of the water bath. Air temperature of the chamber, measured by means of a thermocouple placed in the exit vent as well as by a shielded probe near the chamber bottom, was about the same as the bath temperature.

Each bird was subjected to 5 intensity levels of simulated solar radiation: 0.0, 0.25, 0.5, 1.0, and 1.5 gcal/cm²-min, although not necessarily in that sequence. Radiant energy was supplied by a 250-watt Special Service Ken-Rad infrared lamp positioned over the chamber. Measurements of intensity were obtained by a Kahlsico star pyranometer placed in the chamber at bird level. The height of the lamp was adjusted to obtain desired incident radiation intensity, and then the lamp-to-water distance was measured. In view of (1) the specifications of the pyranometer (sensitive to radiant energy between 0.3 and 3 μ), (2) the specifications of the lamp (92.8% of the spectrum falls between 0.3 and 3 μ, Ken-Rad Lamp Department, pers. comm.), and (3) the absorption by water above 1.4 μ, it can be safely assumed that the pyranometer measured virtually all the lamp-supplied radiation at bird level.

The routine for measurement of oxygen consumption was as follows: A bird was selected from the acclimation room about 3½ hr after the end of its 8-hr photoperiod (02:00–10:00). It was weighed, then placed in the metabolism chamber. Only birds weighing between 24.5 and 29.5 g were used. Oxygen analysis was begun at this point, but no values were taken until the records indicated stable conditions (minimum oxygen consumption for 12 min with no greater than 0.04% change). During this time the bird was illuminated by a microscope lamp mounted about 70 cm above the chamber. This aided in keeping the bird quiet, but supplied essentially no measurable radiant energy. Any locomotor activity of the bird was apparent from (1) the oxygen consumption record, (2) recorded values from the perch-micro-switch apparatus (fig. 1), or (3) direct observation. (In addition to providing information regarding movement of the bird, the perch assembly kept the bird in a
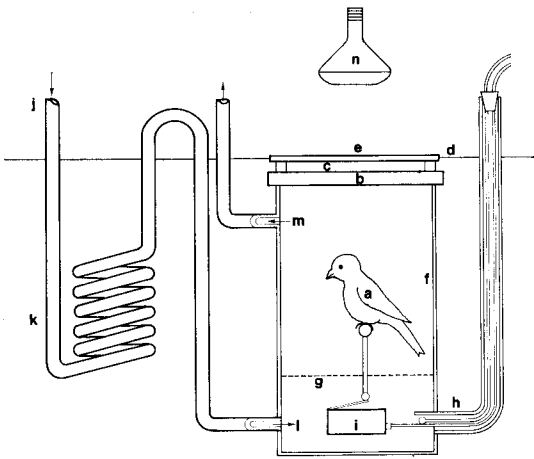
FIGURE 1. Plan of respiration chamber: a, bird being studied; b, Plexiglas chamber top; c, 1-cm layer of water; d, water level in temperature bath; e, glass plate; f, chamber wall (copper painted black); g, wire mesh elevated floor; h, portal for microswitch and thermometer probe leads; i, perch–microswitch assembly; j, dry air from air pump; k, submerged coil of copper tubing; l, air inlet; m, air exit (to analyzer); n, lamp.

TABLE 1. Metabolic rates of birds subjected to various intensities of simulated solar radiation at four different ambient temperatures.

Temperature °C	gcal/cm²-min Irradiation	Oxygen consumption ml O_2/gram-hr mean ± SEM (n)
1	0.0	6.92 ± 0.14 (10)
	0.25	5.96 ± 0.16 (9)
	0.5	5.57 ± 0.18 (10)
	1.0	4.32 ± 0.30 (8)
	1.5	3.86 ± 0.16 (9)
10	0.0	5.33 ± 0.25 (10)
	0.25	4.38 ± 0.19 (9)
	0.5	3.89 ± 0.27 (10)
	1.0	3.42 ± 0.22 (10)
	1.5	3.32 ± 0.18 (10)
20	0.0	4.61 ± 0.16 (10)
	0.25	3.81 ± 0.16 (9)
	0.5	3.80 ± 0.12 (10)
	1.0	3.65 ± 0.09 (10)
	1.5	3.82 ± 0.35 (10)
30	0.0	3.45 ± 0.09 (10)
	0.25	3.49 ± 0.16 (9)
	0.5	3.87 ± 0.12 (10)
	1.0*	5.58 ± 0.61 (10)
	1.5*	6.18 ± 0.37 (10)

* 10-min exposure.

constant position below the lamp.) Most birds remained relatively quiet, only turning their head or occasionally pecking at their feet or feathers. Records from noncooperative birds were not used. After this first equilibration period the infrared lamp was turned on, delivering 0.5 gcal/cm²-min at bird level. Time was allowed to establish equilibrium with new conditions of irradiation intensity. The procedure was then repeated with intensity levels of 1.5, 0.0 (lamp off), 0.25, and 1.0 gcal/cm²-min. After the sequence, which usually lasted 3 to 4 hr, the bird was again weighed, then returned to the acclimation room.

Oxygen consumption was measured by means of a Beckman Model G-2 paramagnetic analyzer in a routine open-circuit system (Depocas and Hart 1957, Dawson 1958, King 1964). Air flow through the chamber was 875 ml/min, adequate to maintain water vapor pressure in the system at low levels not impeding evaporative heat transfer (Lasiewski et al. 1966). Lowest steady state values were used in the appropriate equation (Depocas and Hart 1957) to estimate oxygen consumption (corrected to STP).

In order to estimate the simulated solar flux absorbed by the bird in the respiration chamber it was necessary to correct for the radiation reflected from the plumage and for the geometric differences between the pyranometer (a flat plate) and bird's body (a spheroid). The absorptance of the plumage was estimated by graphically subtracting the mean spectral reflectance of the dorsal plumage of White-crowned Sparrows (Lustick et al. 1970, Lustick 1971) from the spectral distribution of the incident radiation as determined from the output of the lamp and the spectral transmissivity of the glass-water-Plexiglas lid of the respiration chamber. An illustration of this method was provided by Heppner (1970). The source of radiant energy in this study (infrared lamps, which were relatively easy to use and readily available) was different than that used by Heppner ("Sun-Gun" lamp). Nevertheless it can probably be assumed that the water layer (used in both experimental setups) above the chambers made the resulting spectra somewhat comparable. The mean absorption coefficient estimated for White-crowned Sparrows in the present experimental system is 0.614.

The horizontal flat-plate area equivalent to the bird's dorsum was estimated by measuring the area of the shadow cast by the bird (less tail) at the median distance from the lamp when the bird's body was at its usual angle of inclination (ca. 30°) from the horizontal. The average shadow (A_h) measured 19 cm². Assuming that the bird's head and torso approximated a prolate sphere with a minor axis of 3.5 cm and a major axis of 7.0 cm, one can estimate surface area (A) to be 67.7 cm². The shape factor A_h/A describing the equivalent flat-plate area exposed to the simulated solar radiation from a zenith angel of 60° is therefore 19/67.7 = 0.28. As expected, this is less than the shape factor (0.37) for a cylinder of the same dimensions in the same attitude (Monteith 1973).

RESULTS

The data are summarized in table 1 and mean values are presented graphically in figure 2. Oxygen consumption rates for control birds (0.0 gcal/cm²-min) as a function of ambient temperature were essentially parallel to those found by King (1964) for White-crowned Sparrows over a similar temperature range, but averaged about 60% greater. This is to be expected considering that the birds in the
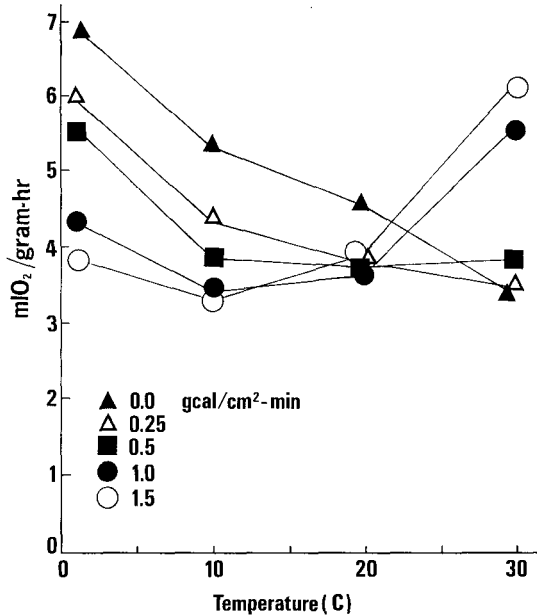
FIGURE 2. Rate of oxygen consumption of birds subjected to different intensities of simulated solar radiation at four different ambient temperatures (1, 10, 20, 30°C). Points shown are mean values ($n =$ 8 to 10).

TABLE 2. Reduction in energy utilization of irradiated birds with respect to control birds at the same temperature.

Temperature °C	Radiation intensity gcal/cm²-min	Reduction of metabolic rate	
		gcal/hr[a]	Per cent[b]
1	0.25	27.3	14.3
	0.5	37.1	19.5
	1.0	68.9	36.2
	1.5	84.8	44.5
10	0.25	23.4	16.3
	0.5	38.8	27.0
	1.0	51.5	35.8
	1.5	54.2	37.7
20	0.25	20.0	16.8
	0.5	20.9	17.6
	1.0	24.8	20.8
	1.5	20.4	17.1
30	0.25	– 1.2	– 1.3
	0.5	–11.6	–11.2
	1.0	–58.6	–61.7
	1.5	–75.1	–79.1

[a] Reduction in energy (gcal/hr) = difference in rates (ml O_2/g hr) × body weight (g) × energy equivalent (4.8 gcal/ml O_2).

[b] [(control-irradiated)/control] × 100.

present experiments were in an illuminated rather than darkened environment (cf. Pohl 1970).

Oxygen consumption rates of irradiated birds at 1°C were significantly lower ($P <$ 0.05) than rates for control birds (no irradiation). Rates at 10° and 20°C for irradiated birds were also lower than corresponding rates for control birds, but differences were not as great as at 1°C. At 30°C, values for oxygen consumption were higher in irradiated birds than in control birds, significantly higher in the case of intensities of 1.0 and 1.5 gcal/cm²-min. The latter values were obtained after only a 10-min exposure, since the birds were obviously being stressed and continuation of the experiment was undesirable.

The limits of the thermoneutral range in White-crowned Sparrows in a black-body environment and in a state of acclimation like that of birds in the present experiments (King 1964) are about 23°C (lower critical temperature) and about 37°C (upper critical temperature). The effect of the simulated solar radiation on these limits cannot be accurately ascertained by the present experiments, but it is nevertheless evident that the lower critical temperature was reduced to 10°C or less at the higher levels of irradiation, and that the upper critical temperature was reduced to 15–20°C.

DISCUSSION

The energy budgets of the birds in my experiments were affected not only by the intensity of the simulated solar radiation, but also by the temperature of the chamber walls (via net infrared exchange) and air temperature (via convective heat transfer), acting in part through their influences on the temperature of the boundary layer of air and of the plumage surfaces. Simulated or real solar radiation heats the surface layers of the feathers (Heppner 1969, 1970, Marder 1973) and in black-body conditions the temperature of the surface layers is a direct linear or near-linear function of ambient temperature (Veghte and Herreid 1965, Evans 1971). Lacking measurements of surface temperatures in the present experiments, one cannot accurately estimate convective or net radiative heat transfer or rigorously analyze the partitioning of heat transfer in birds exposed to the several temperature-radiation regimes. Comparisons within a temperature group are nevertheless valid and informative. I emphasize that my data apply only to the ambient temperatures specified (air temperature and radiant temperature of the chamber, which were the same in these experiments), and that quantitative extrapolations of the effects of simulated solar radiation to other temperature regimes are inappropriate.

TABLE 3. Effect of simulated solar radiation on metabolic rate (MR) or food consumption (FC) in different species of birds.

Species	Conditions °C; gcal/cm²-min	Per cent reduction	Variable	Source
Geococcyx californianus (Greater Roadrunner)	9–22; 0.8	41[a]	MR	Ohmart and Lasiewski 1971
Molothrus ater obscurus (Brown-headed Cowbird)	10; 0.9	26[a]	MR	Lustick 1969
Poephila castanotis (Zebra Finch)	10; 1.23; albino	6[b]	MR	Hamilton and Heppner 1967
	10; 1.23; black	23[a]	MR	
	10; 0.9; albino	5[b]	MR	Lustick 1969
	10; 0.9; gray	26[a]	MR	
Zonotrichia leucophrys gambelii (White-crowned Sparrow)	7; 1.0	22[b]	FC	Morton 1967
	10; 1.0	36	MR	This report

[a] Reported by investigators.
[b] Estimated from original data.

Simulated solar radiation caused substantial reductions of thermoregulatory energy expenditure at all ambient temperatures (T_a) below the thermoneutral range (tables 1 and 2), resembling the extent of metabolic savings reported in other species in similar conditions (table 3). This reduction was a direct function of radiation intensity at $T_a = 1°$ and 10°C, but was unaffected by intensity at $T_a = 20°$C. At $T_a = 30°$C added radiation caused thermoregulatory stress in direct relation to intensity. The essentially identical reactions to all radiation intensities at $T_a = 20°$C may result from pilomotor and vasomotor adjustments within the range of the lower critical temperature (which varies between about 14° and 25°C in White-crowned Sparrows, depending on the state of acclimation [Southwick 1971]). These adjustments are presumably maximized at lower ambient temperatures, and the reduction of energy expenditure then becomes primarily a function of plumage heating by the added radiation.

These results illustrate the reduction of thermoregulatory energy expenditure in relation to realistic intensities of insolation. Their significance will increase if it can be shown that birds (1) voluntarily select radiation environments that minimize thermoregulatory costs, (2) reduce food intake in proportion to thermoregulatory savings, and (3) reduce foraging time and effort, thereby gaining time to engage in other essential functions (e.g., defense of resources, defense against predators, body maintenance, reproductive activities, and so on).

White-crowned Sparrows select progressively more intense radiation environments (up to the point of heat stress) as ambient temperature decreases (De Jong, unpubl. data), illustrating that they voluntarily exploit the thermoregulatory advantage of insolation as revealed by the restrained birds in these experiments. That White-crowned Sparrows reduce food intake when exposed to added thermal radiation was shown by Morton (1967), who found a reduction of 4.1 kcal in the food intake of birds exposed to 1 gcal/cm²-min of added radiation at $T_a = 7°$C for 6 hours of a 12-hr day, compared with controls without added radiation. The estimated amount of simulated solar radiation absorbed by the birds in the present experiments, computed on the basis of 0.614 absorptance and 19 cm² effective absorption area, is shown in table 4. The amount absorbed during 6 hours at 1.0 gcal/cm²-min is 4.2 kcal, or essentially identical with the reduction of food consumption observed by Morton (1967) in similar but not identical surroundings.

Morton (1967) also observed that the intensity of foraging in free-living White-crowned Sparrows during midwinter was markedly lower on days of bright sunshine (and higher air temperatures) than cloudy, colder days. The trail of evidence thus leads

TABLE 4. Estimated amount of incident radiant energy absorbed at different intensities of radiation.

Radiation intensity gcal/cm²-min	Energy absorbed[a] gcal/hr
0.25	175
0.5	350
1.0	700
1.5	1050

[a] Absorbed radiation (gcal/hr) = incident flux (gcal/cm²-min) × fraction absorbed × surface area (cm²) × 60 (min/hr).

to the view that the physiological and behavioral capacities to react to the thermoregulatory advantages of insolation have quantitatively important ecological ramifications with regard to energy and time budgets.

SUMMARY

Oxygen consumption rates of White-crowned Sparrows were measured at four temperatures (1–30°C) and five levels of simulated solar radiation (0.0–1.5gcal/cm²-min). At ambient temperatures, such as 1°, 10°, and 20°C, consumption rates of irradiated birds were lower than rates of the same nonirradiated birds. Control birds and irradiated birds differed substantially at low temperature-high radiation intensity conditions. For example, oxygen consumption at 1°C and 1.5 gcal/cm²-min was 44% lower than that for nonirradiated birds. At 30°C simulated solar radiation imposed a metabolic burden: irradiated birds had higher consumption rates. The results reveal a reduction of upper and lower critical temperatures in irradiated birds.

ACKNOWLEDGMENTS

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