ENERGY RESPONSES OF BIRDS TO THEIR THERMAL ENVIRONMENTS[1]

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THE ability of a species to mobilize energy under different environmental conditions may greatly affect its responses and behavior, as shown by the limits it can extend its distribution, the size and fluctuations in its population in any area, whether or not it is a permanent resident, the time of year at which it initiates migration, nesting, and molt, the length of single migratory flights, the size of egg clutches, etc. Energy metabolism is well known to vary with ambient temperature, but these interrelations are complex. There is need of a generalized physiological model, applicable to all species, to show the interrelations between food intake, standard metabolism, existence metabolism, productive energy, limits of tolerance, evaporative cooling, body temperature, and the thermal environment.

Kleiber and Dougherty (1934) were among the first to make such a figure model based on their work with baby chicks (Fig. 1). This original figure was later greatly modified both by Kleiber (1961) and by King and Farner (1961) in ways with which I cannot agree. West's (1960) figure for the Tree Sparrow (*Spizella arborea*) is more nearly correct but omits consideration of several of the above mentioned parameters. The present study is my attempt at a generalized model (Fig. 2) based largely on information developed in this laboratory for the House Sparrow (*Passer domesticus*) but with additional data from other species where pertinent.

Standard metabolism, or the heat production of the fasting bird at complete rest, appears to have a zone of thermal neutrality with a lower critical temperature at 21°–22°C in three northern populations of House Sparrows, when measurements are made at night (Fig. 2). During the daytime, however, the zone disappears and the regression line of metabolism on temperature becomes curvilinear (Hudson and Kimzey, 1966) or linear with an upper critical temperature at 37°C (Kendeigh, 1944). Similarly in the Evening Grosbeak (*Hesperiphona vespertina*) the zone of thermoneutrality present at night disappears during the day (West and Hart, 1966). Above 37°C, metabolism increases, correlated with a rise in body temperature, to about 47°C ambient temperature, a short exposure to which is lethal to the bird. At the other extreme, standard metabolism increases to at least –40°C, although this temperature can be tolerated for only 5 or 6 hours.
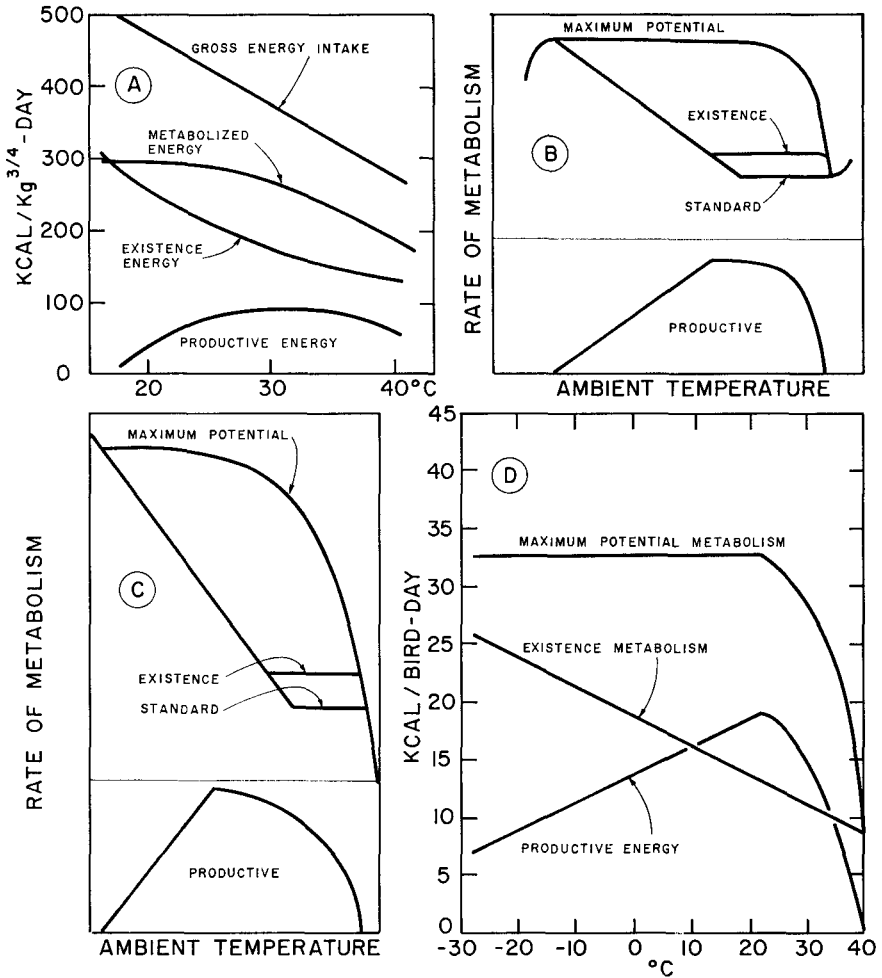
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FIG. 1.   Physiological models of previous workers: (A) Kleiber and Dougherty (1934) for baby chicks, (B) King and Farner (1961), (C) Kleiber (1961), and (D) West (1960) for the Tree Sparrow. These figures and terminology have been modified from the originals to make them comparative to Figure 2. It should be understood that A is for growing chicks while in the other models the birds are maintaining constant weight.

Body temperature is unaffected by fluctuations in medium ambient temperatures, and in several passerine species standard temperature, or core temperature at standard metabolism, averages about 40.5°C (Baldwin and Kendeigh, 1932). Winter acclimatized caged House Sparrows do not live indefinitely at temperatures below about –35°C, and there is a

BODY TEMP, °C

MAXIMUM NORMAL TEMPERATURE
STANDARD TEMPERATURE
UPPER LETHAL TEMP.

LOWER LETHAL TEMPERATURE
35.8 = MAXIMUM POTENTIAL METABOLISM

EXISTENCE METABOLISM
M = 25.2 - 0.296 T

M = 22.5 - 0.356 T (DAYTIME)
STANDARD METABOLISM:
M = 20.7 - 0.568 T (NIGHT)

WINTER
(January)

MAXIMUM TOLERANCE OF LOW AMBIENT TEMPERATURE

MAXIMUM TOLERANCE OF HIGH AMBIENT TEMPERATURE

LOWER CRITICAL TEMPERATURE
ZONE OF THERMAL NEUTRALITY
UPPER CRITICAL TEMP.

PRODUCTIVE ENERGY

EVAPORATIVE WATER LOSS AT STANDARD METABOLISM

KCAL / BIRD-DAY

25.9 MAXIMUM POTENTIAL METABOLISM

EXISTENCE METABOLISM

SUMMER
(July)

MAXIMUM TOLERANCE OF LOW AMBIENT TEMPERATURE

MAXIMUM TOLERANCE OF HIGH AMBIENT TEMPERATURE

PRODUCTIVE ENERGY
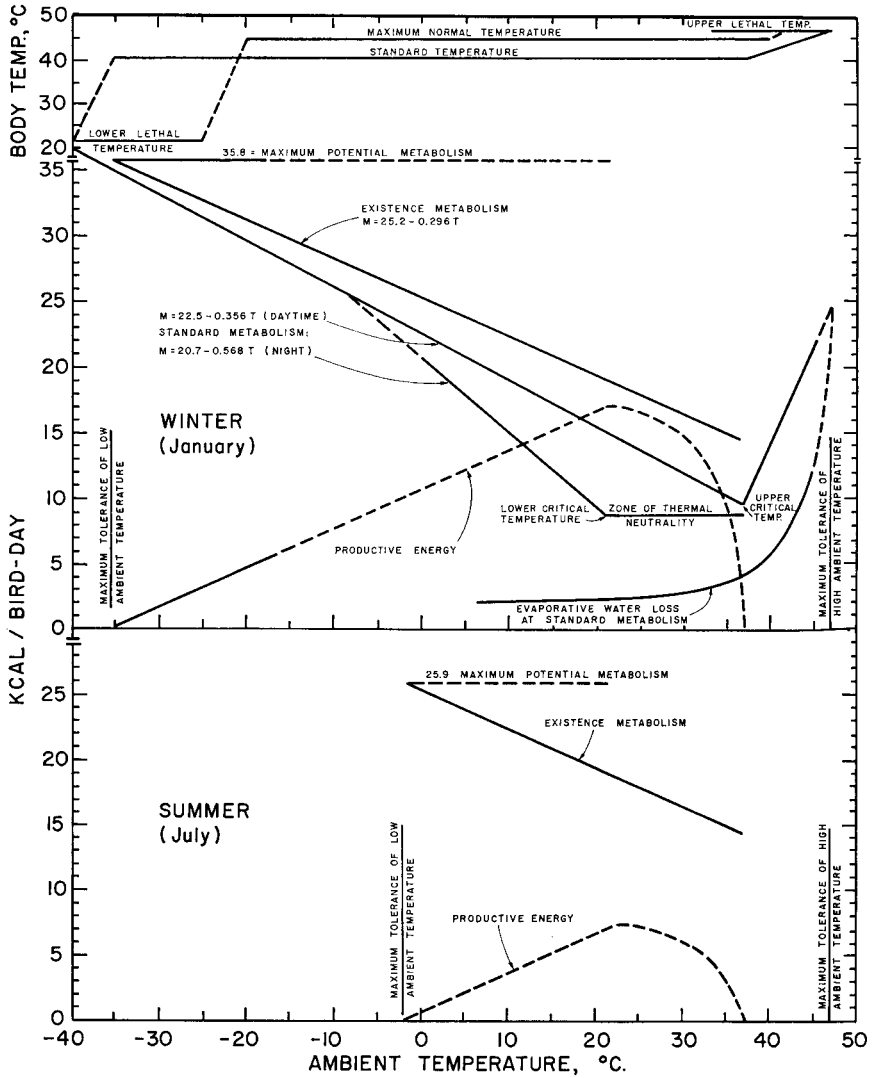
AMBIENT TEMPERATURE, °C.

Fig. 2. Energetics of the House Sparrow: full lines are based on experimental data, broken lines on extrapolations or calculations.

drop in body temperature until death (Giaja and Gelineo, 1933). The House Wren (*Troglodytes aedon*) may recover from a body temperature of 23.7°C but dies at 21.7°C. At the other extreme, a body temperature of 46.8°C is fatal (Baldwin and Kendeigh, 1932), this commonly occurring at ambient temperatures between 42° and 47°C.

When extremely excited or active, body temperatures in passerine species may rise to 45°C. The margin between 45° and the upper lethal temperature (1.8°C) is narrower than between the standard temperature and lower lethal temperature (18.8°C). Kontogiannis (1968) has shown for the White-throated Sparrow (*Zonotrichia albicollis*) that birds subjected to forced activity, compared with quiet birds, tolerated 5°C less extreme high ambient temperature and about 15°C less extreme low ambient temperature. The same relation in the House Sparrow would mean that deaths would occur at ambient temperatures of 42°C instead of possibly 47°C and hypothermy at −20° instead of −35°C (Fig. 2).

Existence metabolism is determined by measuring the amount of food consumed by caged birds over periods of three or four days while maintaining constant weight. The caloric equivalent of the excreta voided is subtracted from the caloric equivalent of the food consumed to give the actual energy metabolized (Kendeigh, 1949; Davis, 1955). Existence metabolism increases linearly from the upper critical temperature of 37°C to the lower limit of temperature tolerance. There is no zone of thermal neutrality as shown in the models of Kleiber (1961) and King and Farner (1961) (Fig. 1). Existence metabolism at ambient temperatures above 37°C has not been studied in this species. Probably the birds become nearly or entirely aphagic as King and Farner (1961) suggest.

The slopes of the regression lines for existence metabolism and daytime standard metabolism converge, in agreement with Rubner's (1910) law of compensation. The difference in elevation of the two lines is accounted for by the heat increments of feeding (specific dynamic action) and cage activity. According to Rubner's "law," the heat increment of feeding contributes toward temperature regulation at low ambient temperatures. This heat is not available in the fasting bird, hence standard metabolism must increase more rapidly at low temperatures to compensate for the absence of the specific dynamic action. That the two lines do not actually intersect within the range of tolerated ambient temperatures may be due to the heat production of the cage activity being additive rather than compensatory (Kontogiannis, 1968).

Maximum potential metabolism occurs at the lower limit of temperature tolerance. Hypothermy and eventual death develops at lower ambient temperatures because heat production cannot be increased sufficiently to balance heat loss. Recent experiments demonstrate that this same maximum energy can be mobilized at 18° higher temperature under stress of forced exercise (Kontogiannis, 1968) and presumably it could also be mobilized for other purposes. West's (1960) diagram is confusing because existence energy is drawn for birds on a 10-hour photoperiod and the maximum potential

metabolism is shown for birds on a 15-hour photoperiod involving nightly activity.

Existence metabolism subtracted from this maximum metabolism gives the potential *productive energy* available for other functions, such as locomotor activity, reproduction, molt, etc. The potential amount of productive energy available, as calculated for caged birds, increases linearly with rise in ambient temperature (Fig. 2), except that at very high temperatures the bird comes under heat stress and is not able to utilize all of this potential energy.

The maximum ability of birds to utilize their potential productive energy at high ambient temperatures may be indicated by the extent of their daily changes in weight. Birds decrease in weight between the time they stop feeding in the evening and begin feeding in the morning and gain in weight during the daytime. White-throated Sparrows, both those given a standard amount of forced exercise at night and those resting quietly on their roosts, varied least in weight between the late afternoon maximum and the early morning minimum at 22°C than at any other temperatures (Kontogiannis, 1968). Research now in progress indicates that this may also be true for the House Sparrow. Hence 22°C may represent the ambient temperature at which the species can carry on its activities most effectively. Although this temperature was not precisely determined, its apparent agreement with the lower critical temperature of thermal neutrality may be significant. Kleiber (1961) indicates maximum usable productive (net) energy as occurring at the lower critical temperature of well fed birds but below the lower critical temperature of birds at standard metabolism (Fig. 1). West (1960) estimated maximum productive energy as occurring within the range of 20° to 25°C. Calculations from King and Farner's (1961) figure indicate that productive energy would be maintained at a maximum level from the lower critical temperature of well fed birds well into the zone of thermal neutrality.

The daily fluctuation of weight is greater at low ambient temperatures because of the increased energy utilization for heat production and consequent greater depletion of body fat reserves. The greater daily fluctuation of weight above 22°C is because of increased vaporization of moisture from the respiratory tract for temperature regulation. Kontogiannis (1968) has shown that exercised birds utilize more water at these high temperatures because of the extra heat production of muscular activity and consequently cannot tolerate as extreme high ambient temperature. The decrease in work capacity between 22° and 37°C is probably inversely proportional to the increasing need for evaporative cooling and the energy expended to bring this about. West (1960), Kleiber (1961), and King and Farner (1961) all agree that there can be no sustained activity above the upper critical temperature, 37°C in the House Sparrow, without hyperthermy occurring.

The rate of evaporative cooling has been measured in the House Sparrow with birds at the resting standard metabolic level (Kendeigh, 1944) and is shown in Figure 2. These measurements were made at a relative humidity of about 18 per cent, hence at a high vapor pressure gradient between the evaporative surfaces of the bird and the environment. At the higher relative humidities of the species' natural environment, the vapor pressure gradient would be decreased, evaporative cooling would be more difficult, and the curve would be shifted downward on the temperature scale. Likewise the increase in rate of water loss as the result of activity, noted above, would shift the curve downward.

The regression lines for evaporative cooling loss and standard metabolism above 37°C were fitted to the measured data by eye, and the great variation in the data do not give their precise slopes statistical significance. It is of interest, however, that their intersection comes at the extreme upper limit of temperature tolerance, 47°C, where ambient temperature equals body temperature and all heat production in the bird can be lost only by evaporative cooling. Perhaps this precise agreement of points is fortuitous, but it emphasizes the basic principles involved.

In order to obtain a first approximation of utilizable productive energy or work capacity at high ambient temperatures, the curve of evaporative water loss was shifted 10°C down the temperature scale so that the precipitous increase in water loss comes at 37° instead of 47°C. The reciprocal of this curve, or its mirror image, was then drawn between 22° and 37°C to indicate work capacity. The accuracy of these energy relations at high temperatures should of course be tested by experimentation.

Potential productive energy is reduced during the summer in this species as the maximum energy which it is capable of metabolizing for existence is approximately 25.9 kcal instead of 35.8 kcal/bird-day (Fig. 2). Perhaps such seasonal changes in energetics are typical of permanent resident species in temperate zones. House Sparrows do not tolerate ambient temperatures much below 0°C in the summer compared with −35°C in mid-winter (Kendeigh, 1949; Davis, 1955). Maximum productive energy at 22°C will therefore be 7.2 kcal instead of 17.1 kcal/bird-day. There is no evidence that the upper critical temperature changes appreciably from 37°C throughout the year. Actually the greater potential productive energy available at 22°C is seldom realized during the winter because this ambient temperature is seldom reached. Using mean monthly temperatures, Davis (1955) calculated that the productive energy available to the bird is approximately 7.5 kcal/bird-day throughout the year, but further study may show that this figure is not a constant.

Energy balance is the relation between energy intake and outgo, the

latter being the existence and productive levels already considered. If the total energy metabolized is less than the intake, the bird draws upon its reserves, loses weight, and dies. On the other hand, when intake is greater than outgo, there is deposition of energy, partly carbohydrates but mostly fats, and the bird gains weight. When a drop in ambient temperature persists over one or more days, the gain in weight with feeding during the daytime becomes greater than the loss at night, so that an increase in weight occurs until a new balance is attained (Kontogiannis, 1968). In permanent resident species, bird weights during the winter average higher than during the summer; in the House Sparrow this amounts to six per cent (Davis, 1955).

Gross energy intake may vary in total amount and rate dependent on photoperiod. In the House Sparrow, the average daily amount of food consumed at five different temperatures (0°–34°C) was nearly identical on a 10-hour and 15-hour photoperiod but on the 10-hour period the hourly rate was 31.5 per cent higher (Kendeigh, 1949; Davis, 1955). The amount of feeding during the daytime is determined largely by the amount of energy lost during the preceding night that needs to be replaced (Kontogiannis, 1968) and not by the number of daylight hours available for feeding. However, long photoperiods are usually correlated with greater amounts of activity and longer maintenance of high body temperature, so one would expect a greater total amount of food consumption. In other species where a significant difference between the two photoperiods can be demonstrated, the greater food consumption on the longer photoperiod is never, however, proportional to the increased number of daylight hours. One would also expect greater tolerance of extremely low ambient temperatures on a long photoperiod, both because it allows the bird a longer time for feeding and because the period of darkness when it cannot feed is shorter. However, the difference in tolerance is small or absent (West, 1960; Cox, 1961; Zimmerman, 1965).

Not all energy taken in as food is digested nor is all the energy that is absorbed from the alimentary tract actually metabolized. As yet, no attempt has been made to determine the loss of energy in the digestive tract to bacteria but the percentages due to these losses are probably very small. There appears to be no significant loss of energy in gases voided (Blem, 1968). The *metabolic coefficient* (metabolized energy/gross energy intake) in the House Sparrow at low temperatures, 0°–10°C, averaged 77.4 per cent on the 10-hour photoperiod and 83.8 on the 15-hour photoperiod, while at 18°–34°C the coefficients were almost identical averaging 80.8, not significantly different from 83.8 (Kendeigh, 1949; Davis, 1955). The higher coefficient on the longer photoperiod and at higher temperatures may result from a slower movement of food through the digestive tract.

Several physiological variables shown in Figure 2 are of ecological im-

portance. The species extends northward to central British Columbia and
Saskatchewan, northern Manitoba and Ontario, and southern Quebec. The
mean monthly temperature in January at Churchill in northern Manitoba
is $-28°C$ with a photoperiod of only 7 hours and 18 minutes, and the species
is probably able to survive the frequently lower daily temperatures that occur
because it utilizes the local grain elevators for shelter and food. In June
the photoperiod reaches 18 hours and mean monthly temperatures in July
climb to $+12°C$. If the species loses as much of its tolerance to cold during
the summer at Churchill as it does farther south it would have only about
4 kcal/bird-day available for reproduction, although 7.5 kcal is required
(see above). Very probably the seasonal loss of temperature tolerance is
not so great as at southern latitudes. Hudson and Kimzey (1966) have
demonstrated a geographic difference in the standard metabolism of House
Sparrows, and a recent study in my laboratory shows geographic differences
in existence metabolism, seasonal variations in the limits of temperature
tolerance, and other parameters. (Charles R. Blem, Ph.D. thesis.)

In the other direction, the species' range extends to the shores of the Gulf
of Mexico and the West Indies. Mean July temperatures are about $28°C$
with maxima to $38°C$ (Reichelderfer, 1941).

In Illinois, near the center of its range, the species begins nesting in April
when the normal mean monthly temperature is about $11°C$ and continues
at an accelerated rate into the summer while mean temperatures go to $24°C$.
This range of temperatures on either side of $22°C$ would seem optimum for
reproduction. Toward the periphery of the species' distribution, abundance
decreases, correlated with temperatures falling either too far below $22°C$ or
going too far above.

The determination of these variables in other species may go far towards
giving an understanding as to what limits distribution and controls time of
nesting and migration, extent of reproduction, etc. Thus, there is no seasonal
change in the lower limit of temperature tolerance $(-28°C)$ in the migrant
Tree Sparrow, a species that nests abundantly at tree line in northern Canada
(for instance, Churchill, Manitoba) and winters in the northern States.
Compared with the 7.5 kcal/bird-day of productive energy available to the
House Sparrow (27–29 grams) throughout the year, the Tree Sparrow, a
smaller bird (18–20 grams), has from 8 kcal in the winter to as much as
12 kcal/bird-day in the summer (West, 1960). It appears a more efficient
metabolic machine in harmony with its more northern nesting distribution
and its common occurrence in open country throughout the winter.

SUMMARY

Critical features of ecological significance in the energy balance of the House Sparrow
include 1) the lower limit of ambient temperature tolerance $(-35°C$ in winter, $-2°C$ in

summer) where existence metabolism is maximum (35.8 kcal in winter, 25.9 kcal/bird-day in summer), 2) the temperature at which there is the greatest work capacity ($22\pm°$C, the lower critical temperature), 3) the potential productive energy available throughout the year (7.5 $\pm$ kcal/bird-day), 4) the upper critical ambient temperature ($37°$C) beyond which activity leads to hyperthermy, and 5) the extreme upper limit of ambient temperature tolerance ($47°$C). This information correlates well with the apparent environmental control over distribution, time of nesting, and extent of reproduction.

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