

RICE UNIVERSITY

TEMPERATURE REGULATION AND METABOLIC RHYTHMS
IN POPULATIONS OF THE HOUSE SPARROW PASSER DOMESTICUS

by

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Thesis Director's signature:

A handwritten signature in cursive script, reading "Jack W. Hudson", written over a horizontal line.

Houston, Texas

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ABSTRACT

This study was an attempt to correlate the influences of the environmental stresses of high ambient temperatures and high humidities on selected physiological properties related to temperature regulation in the house sparrow, Passer domesticus. Measurements were made of metabolism, evaporative water loss, and body temperatures at various ambient temperatures. These physiological properties were compared among four populations of house sparrows from Boulder, Colorado; Syracuse, New York; Ann Arbor, Michigan; and Houston, Texas.

It was found that both the diurnal and nocturnal levels of metabolism of the Houston population were significantly lower than any of the other populations at all temperatures tested. Evaporative water loss did not differ significantly among the populations in the absolute amount lost at various ambient temperatures. However, by virtue of its reduced level of endogenous heat production, the Houston population was able to dissipate a greater percentage of its heat load. There was no significant difference in the body temperatures of the four populations within the range of ambient temperatures measured. The Houston population was able to tolerate a higher ambient temperature than any of the other populations, though the mechanism of this response is not clear.

This study suggests that there has been evolutionary alteration of some of the metabolic processes of house sparrows since their introduction into the United States about the middle of the nineteenth century. It is evident from this study that metabolism does not possess the adaptive "rigidity" ascribed to it by many earlier workers,

(abstract, cont'd.)

and that under certain conditions of environmental stress, metabolism may exhibit adaptive alteration. Because this change in metabolic rate persists for long periods of time in absence of environmental stresses, it is suggested that this is genotypic alteration. This would be indicative of evolutionary rates much faster than previously ascribed to for higher organisms.

Stephen Lee Kenney

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I. INTRODUCTION

Although there has been considerable study of the physiology of the avian fauna from desert habitats (reviewed by Bartholomew and Cade, 1963; Dawson and Schmidt-Nielsen, 1964) there is little information about birds from hot-humid climates. In a recent review devoted to an analysis of the adaptive features of birds living in tropical climates, King and Farner (1964) suggested that specific, genetically fixed adaptations are relatively uncommon and unimportant. They suggest there is some genetic adaptation for heat conductance, with a correlated shift in the critical temperature, but little or no genetic adaptation of basal metabolism. Such a conclusion is realistic in light of the abundant literature supporting the concept that basal metabolism shows little adaptive modification commensurate with different climatic environments (Scholander et al., 1950; Scholander, 1955). This conclusion should be tempered with cognizance of acclimation and acclimatization phenomena (Hart, 1957; 1962) in which metabolism shows some modification, but not at the thermal neutral level.

In a recent publication, Johnston and Selander (1964) have noted a significant evolution in morphological features of the house sparrow since its introduction into the United States in the middle of the nineteenth century. Their conclusions are based on the assumption that these changes are genotypic as well as phenotypic.

While the climate of the Coastal Prairie of Southeastern Texas is not identical to the tropical climate referred to by King and Farner (1964), it is basically a hot-humid climate throughout the summer months. During 111 out of the 153 days from May through

September, 1963, the daily maximum temperature exceeded 90° F with an average relative humidity in excess of 70% (U. S. Weather Bureau Climatological Data, 1963). Such conditions would seriously restrict dissipation of metabolic heat by evaporation when the gradient between body and ambient temperature is small. Many of the resident birds of the Southeastern Coastal Prairie are observed to retreat to shaded microhabitats during the daily peak of solar radiation. House sparrows, however, continued their activities apparently unhampered by the heat.

A detailed examination of the metabolic and temperature regulative performance of populations of house sparrows, including those of the Coastal Prairie of Southeastern Texas, was undertaken as a means of evaluating the extent to which this species might exhibit physiological (and evolutionary) adaptations to a hot and humid climate.

There are a large number of physiological features which could be used as a basis for comparing different populations of birds. The particular parameters selected (body temperature, metabolism and evaporative water loss) can be fitted within the general framework of existing information so that significant quantitative changes can be discerned. In addition, preliminary observations indicated the importance of the photoperiod for accurate measurement of diurnal and nocturnal metabolism. Therefore, the nature of daily cycles in body temperature and metabolism were explored.

II. MATERIALS AND METHODS

Birds were kept in Hendryx Electroplated Double Breeder cages in a windowless room with overhead fluorescent lights controlled by a time clock. The temperature of the room varied from 22-26° C. An artificial dawn was effected by a single 60 watt incandescent bulb, with a hemispherical metal shield, connected to a variable transformer adjusted so that the initial daily illumination was between 2.8 and 5.5 lux. The intensity of the overhead illumination was 175-900 lux. They were fed on wild bird seed, Purina chick starter, sand and water, ad libitum. Survival was excellent so long as the high protein diet of the chick starter was available during the period of molt.

The population of house sparrows from Houston was collected near the Rice University campus using Glenhaven, Standby--two cell size traps. The populations of house sparrows from Ann Arbor, Boulder and Syracuse were trapped near the campuses of the University of Michigan, University of Colorado, and Syracuse University, respectively.

For experiments involving maintenance of birds in total darkness, they were transferred to a darkened, windowless room in which the cage was placed behind a light shield. No light was detectable using a Gossen Lunasix light meter.

An open circuit system utilizing a Beckman G-2 Paramagnetic oxygen analyzer was used to measure oxygen consumption. The air was dried by passing it through silica gel before entering the metabolism chamber. Before entering the analyzer, the air was again dried by silica gel and the carbon dioxide absorbed by ascarite. Thus, variations in the respiratory quotient were corrected by utilizing the

equation of Depocas and Hart (1957) for calculation of oxygen consumption. For body temperature measurements, copper-constantan junctions were implanted in the pectoral muscles and connected to a Leeds and Northrup Speedomax G. Temperature - Millivolt Recorder. The metabolism chamber was constructed from a one-gallon paint can by adding a platform of hardware cloth over a layer of mineral oil in the bottom of the can. In this way evaporation from excreta was precluded. Three one-fourth inch copper tubes were placed through the lid of the chamber as ports for air and thermocouples.

To measure evaporative water loss, after birds had reached a stable level of metabolism and body temperature, weighed "U" tubes of Drierite (CaSO_4) were inserted into the effluent line and then reweighed after 30 to 60 minutes (depending on ambient temperature) to determine weight of water evaporated from the pulmocutaneous surfaces. The flow of air was monitored with a Roger Gilmont Instruments flowmeter at the rate of 350 cc air/min. With the data on evaporative water loss, ambient temperature, and flow rate, it is possible to calculate the maximum relative humidity to which the animal's evaporating surfaces were exposed (Table I.).

To determine lethal ambient temperatures, birds were placed in a walk-in incubator in which the temperature was controlled to $\pm 0.2^\circ \text{C}$ with an air current of less than 200 feet/minute. After the incubator had been at the experimental temperature for at least two hours, the birds were brought from the animal room to the incubator in their cages and exposed to the experimental temperature for two hours.

Table 1

Representative relative humidities in metabolism chambers at various ambient temperatures during determination of evaporative water loss in house sparrows (Lasiewski, 1964).

Ambient Temperature (°C.)	Relative Humidity (Per Cent)
20	39.4
30	23.6
35	27.0
38	35.9
40	37.4

This procedure was repeated once every 3 to 4 days until an ambient temperature was found which was differentially fatal to the different populations within 2 hours of exposure.

III. RESULTS

Rhythms

A daily cycle of high diurnal metabolism and low nocturnal metabolism was illustrated in two experiments, in which groups of birds were kept in complete darkness for 30 days and 9 days, respectively. In the group kept in continuous darkness for 30 days the time of the daily increase in metabolism varied by less than 10 minutes over three days. In the second experiment, the birds exhibited a periodicity (time from increase to the following increase with one intervening decline) of 23 hours. During the nine days of continuous darkness there was a progressive lengthening of the time between the bird's increase in metabolism and scheduled onset of illumination (hereafter described as the anticipatory period) (Figure 1).

Like the results from birds kept in continuous darkness, metabolism and body temperature measured in complete darkness following removal from a light regimen illustrates a daily cycle (Figure 2) with a relatively constant anticipatory period (Table II). The anticipatory period for all four populations is precise and precedes the scheduled onset of diurnal illumination by one hour and 28 minutes. The metabolism and body temperature is exceptionally high during the first 20 minutes after the initiation of diurnal metabolism, though typically it takes 45 minutes to one hour to peak.

The onset of the nocturnal level of metabolism typically precedes the scheduled onset of darkness by 1 hour 14 minutes \pm 28 minutes (for 14 birds). The decline in metabolism takes a longer period

Figure 1

Successive times for the onset of the "anticipatory period" for three house sparrows maintained in continuous darkness for nine days. The dotted line (D) represents the time of the last artificial dawn to which the birds were exposed. The dashed line (L) represents the time of the last scheduled onset of full illumination.

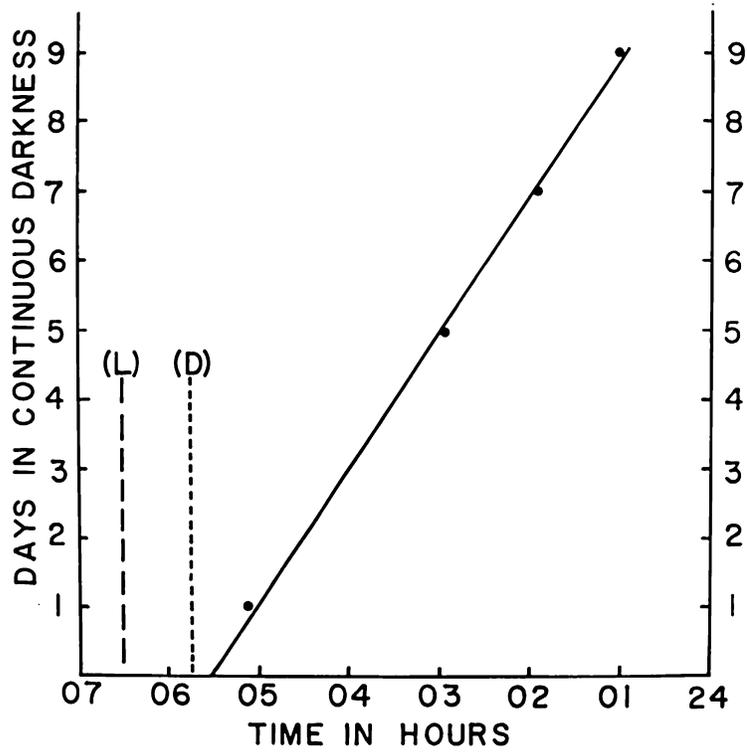


Figure 2

A typical daily cycle of metabolism (closed circles) and body temperature (closed squares) exhibited by house sparrows measured in continuous darkness. The previous experimental photoperiod is represented by the bar at the top of the graph.

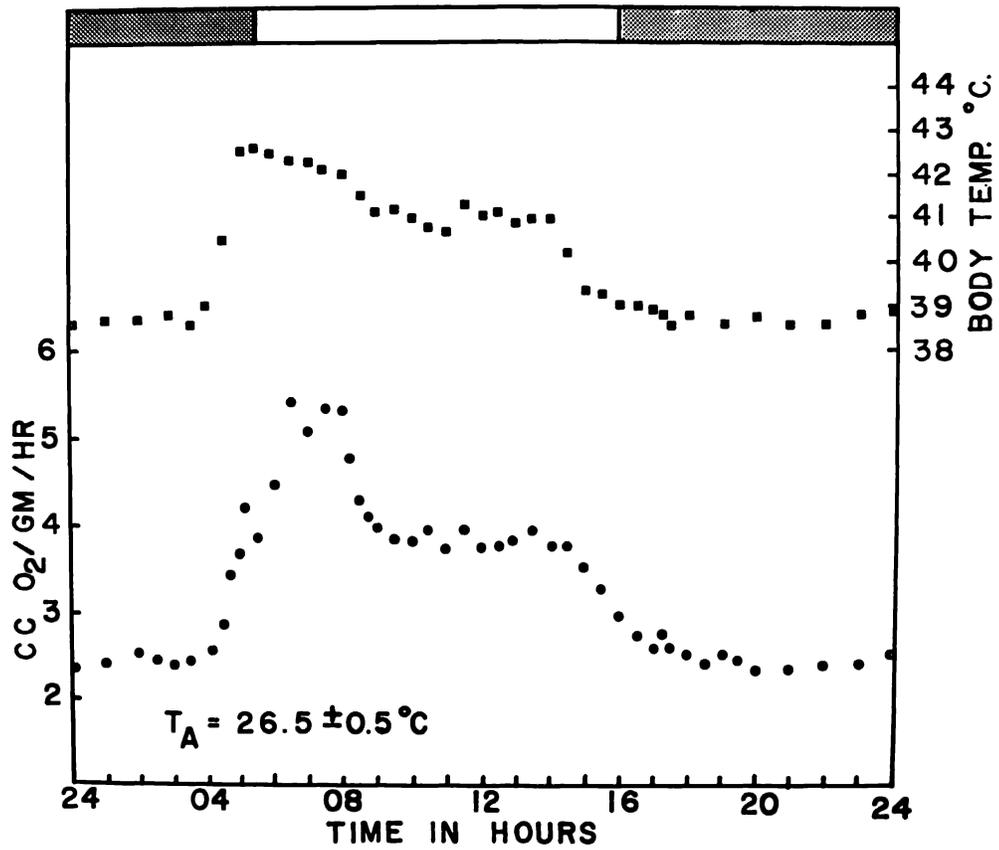


Table II

Magnitude of the "anticipatory period" for the various populations of house sparrows. These times were determined for birds in continuous darkness for less than 24 hours.

POPULATION	BOULDER	SYRACUSE	ANN ARBOR	HOUSTON	MEAN
Anticipatory Period + se	1 hr. 27.9 min. + 6.1 min.	1 hr. 27.8 min. + 17.7 min.	1 hr. 36.9 min. + 16.1 min.	1 hr. 21.0 min. + 6.4 min.	1 hr. 28.4 min. + 4.9 min.
Number of Individuals	20	9	13	26	68

of time, gradually declining over 1-1/2 to 2 hours. The body temperature closely parallels that of the metabolism during entry into nocturnal levels (Figure 2).

The period of alternate total darkness and full illumination was modified by the insertion of a daily period of dim illumination (artificial dawn) of 45 minutes. During the ensuing 10 days, birds were periodically removed from the animal room and their metabolism was measured in total darkness for 24 hours. Birds exhibited a 35-minute shift in the initiation of their diurnal metabolic level so that it commenced 45 minutes ahead of the scheduled full illumination (Figure 3). In a subsequent experiment, the anticipatory period was rescheduled by an artificial dawn 2 hours ahead of the main illumination. This group exhibited an anticipatory increase of 2 hours. Although each group was kept on their respective experimental protocol of dim illumination they both returned to anticipatory arousals (when measured in complete darkness) of one hour and 21 minutes. The exact time for the return is unknown, though it transpired within 3 to 4 weeks. An artificial twilight period of 45 minutes had no effect on the time of decline into the nocturnal level of metabolism.

Metabolism

If the standard metabolism is plotted against ambient temperature, birds have conspicuously different nocturnal and diurnal curves (Figure 4). Only nocturnal metabolism illustrates the typical relationship described by Scholander et al. (1950), in which the line relating metabolism to ambient temperature extrapolates to 36.7° C,

Figure 3

The transient shift in the onset of the anticipatory period in response to an artificial dawn (lightly shaded area). Time is designated as hours before (-) or after (+) full illumination (O) and total darkness (O). (A) represents the phasing of the normal anticipatory period. (B) and (D) demonstrate the initial shifts in the onset of the anticipatory period 5 to 10 days after the first exposure to an artificial dawn. (C) and (E) illustrate the return to the "normal" pattern in the presence of the artificial dawn 3 to 4 weeks after the initial exposure.

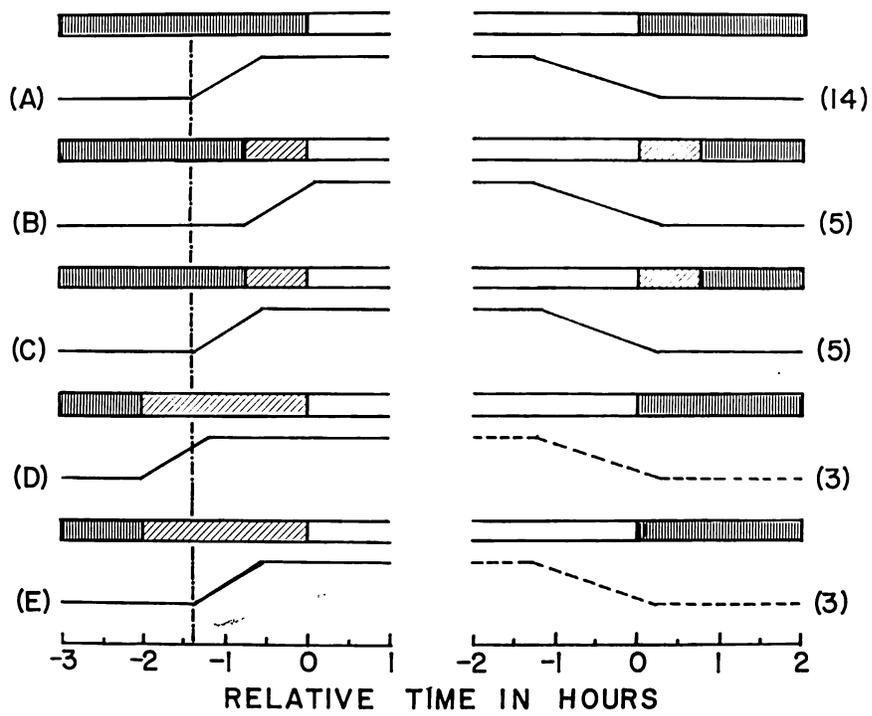
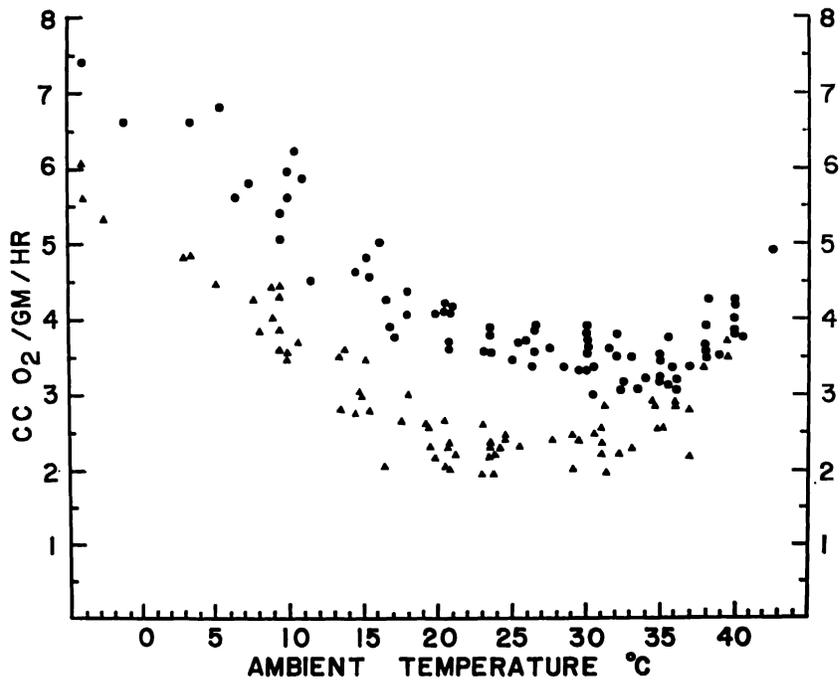


Figure 4

The relationship between metabolism (oxygen consumption) and ambient temperature at the diurnal (closed circles) and nocturnal (closed triangles) level for the Houston population of house sparrows.



close to the body temperature (mean of 9 birds is $38.6^{\circ} \pm .32^{\circ}$) recorded at the lower limit of thermal neutrality. In contrast to the rectilinear relationship between metabolism and ambient temperature at night, metabolism recorded during the daytime illustrates a curvilinear relationship between ambient temperatures of 20 and 35° C. As a consequence of this curvilinear relationship, extrapolation of the line yields unreasonably high body temperatures. The regression equation for nocturnal metabolism below the zone of thermal neutrality is $\text{cc O}_2 / \text{gm-hr} = 5.29 - 0.144T$ with the slope of the line representing the minimal thermal conductance. Because of the curvilinear relationship between diurnal metabolism and temperature, the slope of the line varies continuously, suggesting varying conductance.

The nocturnal metabolism of populations of house sparrows from Boulder, Ann Arbor, Syracuse and Houston are represented in Figure 5. The slope of the line (Table III) relating temperature to metabolism is less for the Houston population than it is for the Syracuse and Boulder populations. The Michigan population lies between the Houston and Boulder populations. The metabolic level at thermal neutrality is lowest for the Houston population and highest for the Boulder population (Table III). These metabolic differences are statistically significant at the 95% level of confidence (using Student's "t" test).

The intersection of the horizontal and oblique lines (Figure 5) represents the lower critical temperature, i.e., the ambient temperature below which the birds must increase their metabolism in

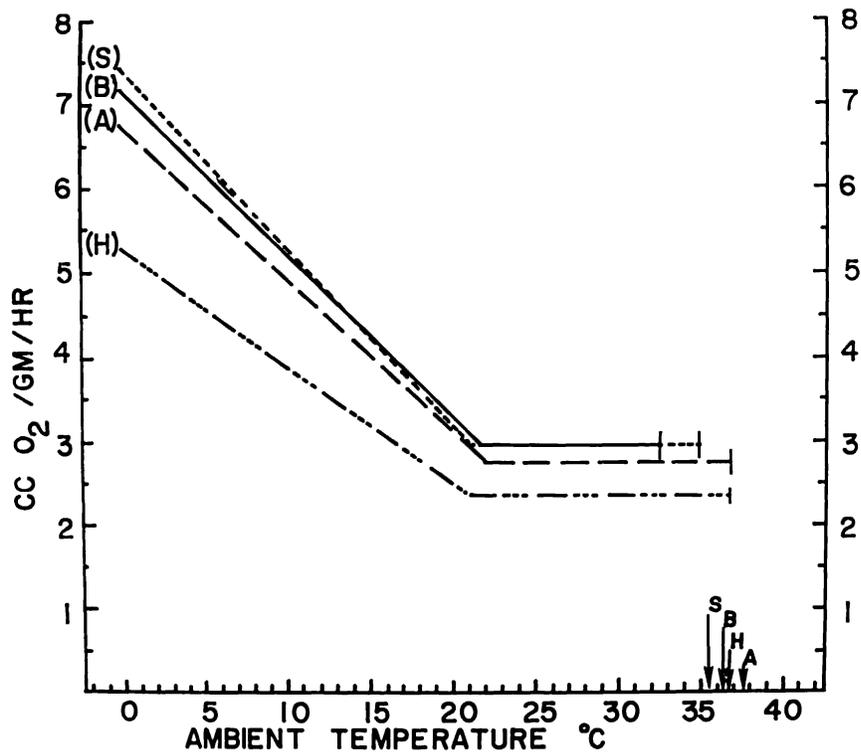
Table III

A comparison of the metabolism at various ambient temperatures for the four populations of house sparrows. The diurnal metabolism is given at the four test temperatures (30, 35, 38, 40° C.). The nocturnal metabolism is given in the zone of thermal neutrality (20-35° C.) and is represented at ambient temperatures below thermal neutrality by the regression line (also an indication of the thermal conductance of each population). The body weights of the various populations are also compared. The numbers in parentheses represent the number of measurements at that temperature. The values are given with ± 2 standard errors of the mean.

POPULATION	N	Wt (gms) ± S	DIURNAL CC O ₂ /GM-HR				NOCTURNAL CC O ₂ /GM-HR	
			30° C	35° C	38° C	40° C	20-35° C	Regression Equation
Boulder	22	25.2 ± 2.0	4.16 ± 0.24 (11)	3.88 ± 0.24 (14)	4.48 ± 0.50 (7)	5.03 ± 0.36 (7)	2.93 ± 0.16 (12)	CC O ₂ /Gm-Hr = 7.17 - 0.198T (29)
Syracuse	10	24.9 ± 1.8	4.08 ± 0.17 (11)	3.88 ± 0.25 (13)	4.43 ± 0.27 (12)	5.04 ± 0.33 (7)	2.94 ± 0.16 (12)	CC O ₂ /Gm-Hr = 7.39 - 0.208T (16)
Ann Arbor	24	25.8 ± 1.7	4.03 ± 0.16 (8)	3.58 ± 0.18 (11)	4.04 ± 0.22 (7)	4.50 ± 0.26 (6)	2.80 ± 0.14 (9)	CC O ₂ /Gm-Hr = 6.74 - 0.180T (18)
Houston	40	25.5 ± 2.0	3.53 ± 0.19 (9)	3.22 ± 0.15 (12)	3.68 ± 0.24 (7)	3.96 ± 0.17 (6)	2.34 ± 0.10 (36)	CC O ₂ /Gm-Hr = 5.29 - 0.144T (36)

Figure 5

Nocturnal metabolism of populations of house sparrows from Boulder (B), Syracuse (S), Ann Arbor (A), and Houston (H) at various ambient temperatures. Regression lines (Table III) are fitted by least squares method. The arrows at the bottom of the graph represent the body temperature to which each regression line extrapolates (from Scholander's application of Newton's law of cooling).



order to maintain a constant body temperature. The lower critical temperature is approximately 20-22°C for all four populations. The similarities in the lower critical temperatures occurs in spite of differences in temperature-metabolism slopes and thermal neutral levels of metabolism because both vary in the same direction and to the same extent for all four populations. Thus, with a flatter line there is also a lower thermal neutral metabolism and vice versa. The definition of an upper critical temperature is complicated by the fact that metabolism throughout the zone of thermal neutrality increases slightly as the ambient temperature increases (Figure 4). However, there appears to be a marked change in slope at an ambient temperature of 37-38°C which can be designated as the upper critical temperature.

The curvilinear relationship between diurnal metabolism and ambient temperature makes comparisons between populations difficult. Therefore, the diurnal metabolic performance was measured at selected ambient temperatures for all four populations (Table III). The metabolism at 30, 35, 38 and 40°C shows a gradation between the lowest, exhibited by the Houston population, to the highest, exhibited by the Boulder and Syracuse populations. There is a statistically significant difference (95% confidence) between the Houston population and any of the other populations. There is no significant difference at this level of confidence among the other three populations when compared with each other.

Evaporative Water Loss

Evaporative water loss, evaluated on an absolute basis, increases as the ambient temperature increases between 30 and 40° C (Table IV). There is no significant difference in the absolute level of evaporative water loss among all four populations. However, when evaporative water loss is expressed as percent of heat load dissipated (Figure 6), there is a "marked" difference between the Houston population and the other three populations. This is obviously a reflection of the lower metabolism of the Houston population. There is a difference in absolute levels of evaporative water loss between the diurnal and nocturnal periods (Table IV).

Body Temperature

Because there was no detectable difference in the range of body temperatures of the various populations, data from all four populations has been pooled (Figure 7). There is a progressive increase in body temperature as the ambient temperature increases from 32 to 40° C, regardless of whether the body temperature is measured during the day or at night. At ambient temperatures between 0 and 30° C, there is about a two degree difference in the diurnal and nocturnal body temperature levels. However, as the ambient temperature increases above 30° this difference lessens and at 38° C the two levels are indistinguishable (Figure 7).

Lethal Ambient Temperatures

The highest ambient temperatures tolerated by birds varies with the conditions of measurement. Birds confined within the darkened

Table IV

Absolute water loss of the various populations of house sparrows (in mgm water/gm body weight/hour \pm 2 standard errors of the mean) at various ambient temperatures. The nocturnal evaporative water loss is given for the Houston population. The numbers in parentheses represent the number of measurements at each temperature.

POPULATION	DIURNAL at °C.						NOCTURNAL at °C.			
	20	30	35	38	40	43	30	35	38	40
Boulder		5.6 ± 0.3 (5)	9.3 ± 0.9 (5)	13.9 ± 0.8 (5)	16.0 ± 0.9 (6)					
Syracuse		6.0 ± 0.9 (6)	7.7 ± 1.1 (8)	15.0 ± 1.1 (8)	16.7 ± 0.8 (6)					
Ann Arbor		5.8 ± 0.7 (4)	7.2 ± 0.6 (4)	13.2 ± 0.7 (4)	16.2 ± 0.1 (3)					
Houston	6.0 ± 0.7 (3)	6.7 ± 0.5 (6)	9.1 ± 0.9 (6)	14.3 ± 1.0 (4)	17.2 ± 1.2 (3)	18.2 (1)	3.6 ± 0.2 (3)	9.0 ± 1.7 (3)	11.4 ± 1.2 (3)	15.2 ± 0.8 (3)

Figure 6

Evaporative cooling expressed as percent heat lost by evaporation at 30, 35, 38, and 40° C. for the four populations of house sparrows. The bars represent (from left to right in each temperature group) the Boulder, Syracuse, Ann Arbor, Houston (diurnal), and Houston (nocturnal) populations. The percent heat lost is plotted on a \log_{10} scale. The horizontal line within the clear area (representing 4 standard errors of the mean) represents the mean of each population at that temperature.

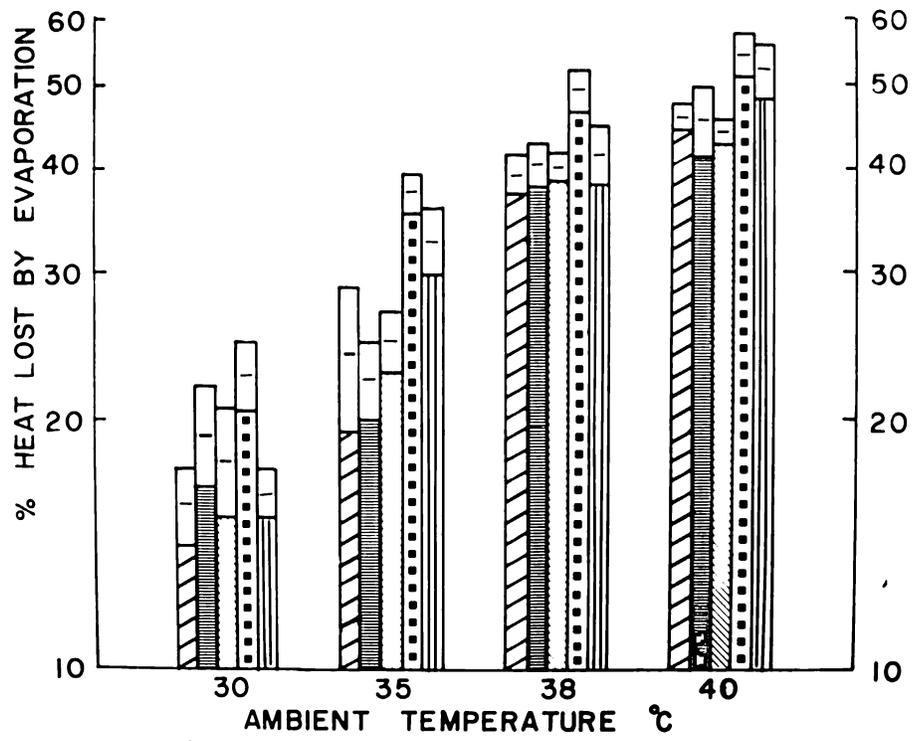
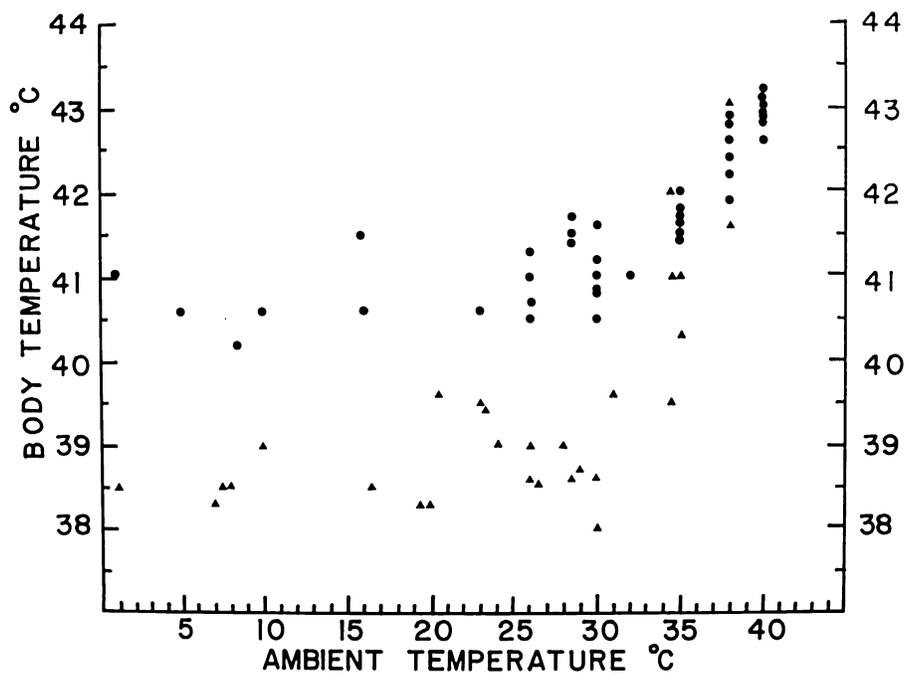


Figure 7

The relationship between diurnal (closed circles) and nocturnal (closed triangles) body temperatures and the ambient temperature. Data from all four populations has been pooled.



metabolism chambers, where air movement was slight and humidity high, could not tolerate temperatures much above 42° C. However, birds kept in their cages and placed in a walk-in incubator, where there was a slight air movement (though no wind velocity was detectable with a Biram Pattern Taylor anemometer and a relative humidity of 20 per cent (when the ambient temperature exceeded 44° C) tolerated much higher ambient temperatures.

The various populations exhibited clear-cut differences in lethal ambient temperatures. Among a group of 9 birds exposed once every 3 to 4 days for 2 hours to ambient temperatures progressively increased by 1° C increments each exposure from 42.5 to 48.6° C, only the Houston population remained unaffected by the highest temperatures. In contrast, the three Boulder house sparrows died at 48.6° C, and one of the three Michigan house sparrows died at 47.6° C.

There were obvious behavioral differences among the various populations. At ambient temperatures between 42.5 and 44.5° C, all populations remained relatively motionless and panted intensely throughout the two hours of exposure. Above 44.5° C, the Boulder house sparrows exhibited poor muscle coordination whereas the Michigan and Houston house sparrows increased their levels of activity. The postural and activity coordination of the Boulder house sparrows progressively worsened as the ambient temperature approached 48.6° C, though there was no apparent change in either amount or form of activity among the house sparrows from Houston. The body temperature of a Houston bird measured with an implanted thermocouple during the two hour exposure period at 48.6° C remained below 46.5° C.

IV. DISCUSSION

RHYTHMS

The relationship between photoperiod and metabolism in house sparrows is indicative of a circadian rhythm. The endogenous aspect of this cycle is demonstrated by: 1) its persistence in birds kept in continuous darkness and 2) a precise "time-sense" indicated by the appearance of the diurnal level of metabolism ("anticipatory increase") in continuous darkness 1 hour and 28 minutes \pm 12 minutes prior to the scheduled onset of daily illumination. Furthermore, with birds kept in continuous darkness the daily increase in metabolism appeared at progressively earlier times. This period of alternate high and low levels of metabolism is approximately 23 hours.

This cycle can be entrained to light cues since 1) the time of the daily increase in metabolism is influenced by the past experimental photoperiod 2) there is a complete reversal of the cycle when the photoperiod is reversed and 3) there is a transient susceptibility of the daily anticipatory increase in metabolism to differing periods of an artificial dawn.

METABOLISM

The rectilinear relationship between ambient temperature and metabolism during the night illustrates clearly the relevance of Scholander et al's application of Newton's Law of Cooling to small birds. Newton's law of cooling states that a body will cool at a rate that is proportional to the difference between the temperature of the body and that of the surrounding environment (assuming, of course, that the environment is at a lower temperature than the body).

This relationship can be expressed by the equation:

$$Q_l \text{ (heat loss)} = k (T_b - T_e).$$

T_b and T_e represent the temperature of the body and the environment respectively. The proportionality constant is represented by k .

In a homeotherm, if the body temperature remains constant, heat production must equal heat loss. Therefore, the following relationship can be expressed between heat production (MR), body temperature (T_B), and ambient temperature (T_A):

$$MR = C (T_B - T_A)$$

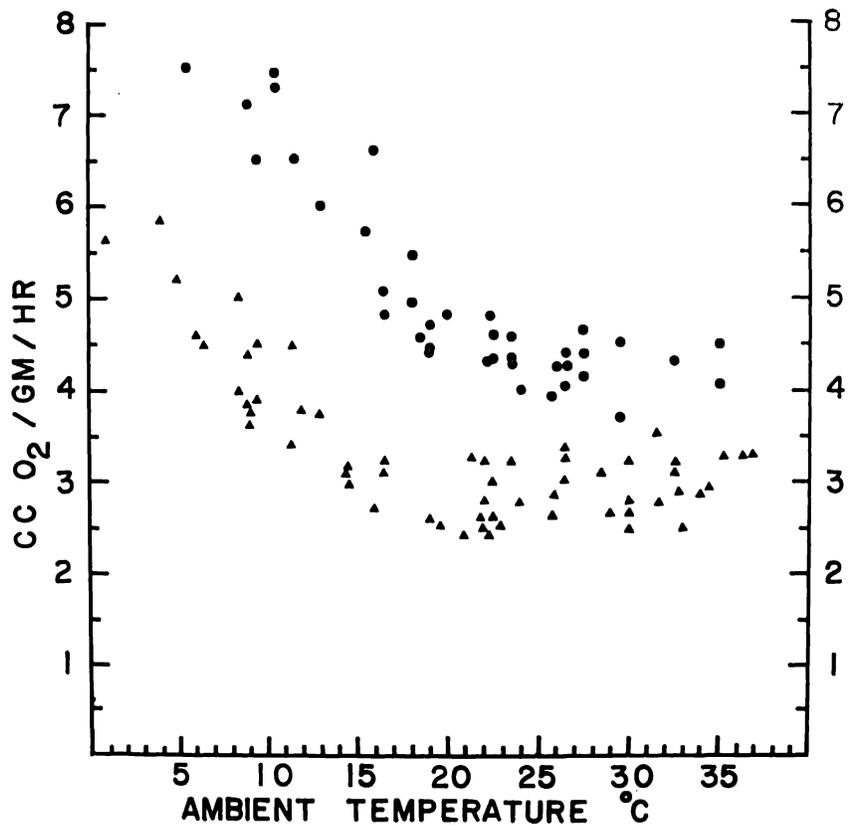
where C represents the thermal conductance of the animal (assumed to be a constant at temperatures below the thermal neutral zone). From this equation it can be seen that at a theoretical MR of zero, the body temperature would equal the ambient temperature. This relationship is surprisingly accurate for a large number of homeotherms.

In contrast to West's observations (1962) it was found that the metabolism of these small passerines exhibit a distinct zone of thermal neutrality when measurements are made during the "true" nocturnal period. A similar response occurs for the White-throated Sparrow. (Figure 8, unpublished observations).

The failure of the temperature-metabolism curve to extrapolate to the measured body temperature when metabolism is measured during the day is a consequence of the curvilinear relationship between ambient temperature and metabolism. It might be argued that the unusual flatness of the line is the result of a decline in body temperature, with a concomitant reduction in metabolism, at low ambient temperatures. Not only is there abundant evidence in the literature

Figure 8

The relationship between diurnal (closed circles) and nocturnal (closed triangles) metabolism and the ambient temperature for the white-throated sparrow, Zonotrichia albicollis.



demonstrating that body temperature remains relatively constant, but this is confirmed by our own measurements (Figure 7).

The curvilinear relationship between metabolism and ambient temperature, described as a characteristic feature of most small passerines (West, 1962), applies to these populations of house sparrows only with respect to the diurnal metabolism. Exposure of the birds to simulated nocturnal conditions is inadequate for induction of nocturnal levels of thermal regulation, unless this exposure occurs for a total of five days prior to the determination of the metabolism.

The unusually high level of heat production (and therefore high heat loss) over that range of ambient temperatures where there is a curvilinear relationship appears enigmatic. The metabolism during the night is lower than can be attributed solely to the maintenance of a lower body temperature..

The reason for the higher thermal conductance associated with the diurnal curvilinear relationship is unknown, both in terms of its mechanism and its adaptive features. These observations suggest that the range of postural adjustments utilized by nocturnal birds allows maximum heat conservation. Thus a bird with maximally erected feathers, resting so as to cover its bare tarso-metatarsus, more nearly portrays the morphology of the standard homeotherm, and this is conducive for maximum heat conservation. If this interpretation is correct, then the uneconomical level of diurnal metabolism can be interpreted as an inescapable correlate of activity.

Among the various populations of house sparrows, measurements of the nocturnal metabolism exhibit a distinct zone of thermal neutrality over which comparisons can be satisfactorily made without the complications of the diurnal curvilinear relationship. It is apparent that the Houston population is metabolising at a level significantly lower than the other populations of house sparrows. This is distinct evidence that metabolism exhibits adaptive modification as a means of coping with the environment with its high temperatures and high humidities. Efforts to increase the metabolism by prolonged exposure to low temperatures were unsuccessful. Although there is no unequivocal evidence that the low metabolism is genetic, its persistence throughout protracted periods of captivity when all populations were exposed to the same conditions is suggestive that this is an irreversible phenotypic feature, and probably is genetic. It has become increasingly clear that metabolism of homeotherms does not have the evolutionary rigidity previously ascribed by Scholander (1955). (See Johansen, 1962; McNab and Morrison, 1963; Bartholomew, Hudson, and Howell, 1962; Hudson, 1964.)

Evaporative Water Loss

As to be expected, there is a significant difference in the absolute amount of water evaporated during the day in comparison with that lost during the night. Presumably this difference is a reflection of the difference in 1) body temperature (Figure 8) with the difference in "saturation deficit" (vapor pressure tension) and 2) ventilation volume associated with the difference in the

levels of metabolism (Kendeigh, 1944). This nocturnal-diurnal difference in the amount of water lost is greatest at the lowest ambient temperature measured (30° C), and like the differences in body temperatures and metabolic rates, it is less marked at the higher ambient temperatures. However, there is a statistically significant reduction in the absolute quantity of water lost during the night even at the highest ambient temperature measured (40° C) although there is no difference in the body temperatures. In addition, there appears to be a lower level of metabolism among the nocturnal birds even at 39.5° C. Thus, it appears that correlated with darkness is an ability to keep metabolism and therefore evaporative water loss at a lower level than occurs during the day, even though the body temperatures may be the same. One interpretation is that light evokes a higher level of metabolism irrespective of behavioral differences, and this difference persists even at very high ambient temperatures. There was no indication during metabolic measurements that differing levels of activity occurred during diurnal and nocturnal determinations.

The significance of evaporative water loss as an adaptive feature characterizing various populations of house sparrows lies in its relationship to metabolism. Although evaporative water loss does not vary significantly with the populations, a relatively constant amount is able to dissipate a larger portion of the metabolic heat in the Houston population by virtue of their lower heat production. By this means, it is possible to increase heat dissipation by evaporative cooling from the 40 to

50 percent of heat production characteristic of most small birds (King and Farner, 1964; Dawson and Schmidt-Nielsen, 1964) to the 60 percent level of heat production.

These observations confirm the current concept that regulation of evaporative water loss is not important as an adaptive feature, except as body size might be adaptive (Bartholomew and Dawson, 1953; Dawson and Schmidt-Nielsen, 1964; King and Farner, 1964). It is significant that the percent heat lost by evaporative cooling remains the same in spite of marked differences in metabolism, body temperature, and absolute water loss of diurnal and nocturnal birds. This indicates that pulmonary water loss is not regulated, but is merely a reflection of the ventilation volume which is regulated commensurate with the level of metabolism and body temperature maintained by the bird.

Body Temperature

There are no indications that any of these populations have body temperatures adaptive to their environments. This observation extends the conclusions of Dawson and Schmidt-Nielsen (1964) concerning desert birds to include populations of house sparrows from various climates. These birds exhibit the ability to tolerate several degrees (C) elevation in their body temperatures without any apparent ill effects. This "voluntary" hyperthermia serves two functions: 1) the bird can store a certain amount of heat in this way (though in a small bird this is very little), and 2) by increasing the gradient between body temperature and the ambient temperature, heat loss by radiation and convection is facilitated.

Lethal Ambient Temperatures

Presumably the differences in abilities of the various populations to withstand high ambient temperatures is a reflection of their different levels of endogenous heat production. Thus, the Houston population was able to withstand an ambient temperature of 48.6° C. for two hours. This is particularly surprising if the rate at which endogenous heat would accumulate when the body temperature is less than the ambient temperature is considered. This enigma is emphasized by considering the magnitude of heat production and dissipation known for this species. If the most favorable circumstances are assumed: 1) lowest metabolism ($2.34 \text{ cc O}_2/\text{Gm-Hr}$), 2) lowest body temperature (38.6° C.), and 3) 50 percent evaporative heat dissipation, then 1.17 cc O_2 with a caloric equivalent of approximately 5.62 calories (Brody, 1945) must be stored in each gram of body tissue in one hour. If we assume a specific heat of $0.8 \text{ cal/gm-degree}$ (Dawson, 1954), then in one hour the body temperature would increase from 38.6 to 45.6° C. and two hours later would increase to 53.6° C. Obviously this is impossible. Furthermore, we have omitted consideration of additional heat loads created by 1) heat flow from the environment to the bird and 2) a Q^{10} effect on metabolism produced by a progressive increase in body temperature, both factors intensifying a potentially fatal accumulation of endogenous heat.

V. SUMMARY

Various physiological parameters important in the maintenance of a constant body temperature were compared among four populations of house sparrows from differing climates. House sparrows from Houston had a diurnal thermal neutral metabolism of 3.22 ± 0.15 cc O_2 /Gm-Hr as compared to the other populations' levels of 3.58 to 3.88 cc O_2 /Gm-Hr. This is a significant difference at the 95% confidence level. Nocturnal thermal neutral metabolism of the Houston population is also significantly lower (2.34 as compared to 2.80-2.93 cc O_2 /Gm-Hr.). The maximum insulation of the Houston population as indicated by the slope of the temperature-metabolism curve at ambient temperatures below thermal neutrality was significantly greater than any of the other populations.

The amount of pulmocutaneous water loss by evaporation (mgm/gm-hr) did not vary significantly among the four populations at the ambient temperatures tested. However, the Houston population was able to dissipate a larger portion of its heat load by virtue of its reduced level of heat production. Body temperatures did not exhibit any noticeable difference at the ambient temperatures at which it was measured (1 to 40° C.).

The population of birds from Houston has adapted to the hot, humid environmental conditions by a reduction in their level of endogenous heat production. In view of the high ambient temperatures (which reduce heat loss by radiation, conduction, and convection) and high relative humidities (which limit evaporative cooling) to which the birds are exposed for several

months during each year, this would appear to be a logical solution to the problem of overheating.

Thus it would appear that in addition to the rapid evolution of morphological features exhibited by this species, evolution of physiological characteristics concerned with metabolism and temperature regulation has occurred in the past 100 years since the introduction of house sparrows onto this continent. This study suggests that metabolism is an evolutionary labile feature and is subject to the various stresses imposed upon the organism by its environment.

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