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Circadian rhythms of body temperature and metabolic rate in the House Sparrow (*Passer domesticus*)

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**Circadian rhythms of body temperature and metabolic rate in the House Sparrow
(*Passer domesticus*)**

A SENIOR THESIS

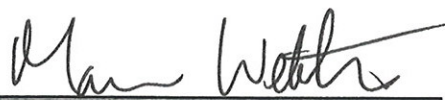
By Pericles Regas

St. John's University / College of St. Benedict

**In Partial Fulfillment of the Requirements for the Degree Bachelor of Arts In the
Department of Biology**

Circadian rhythms of body temperature and metabolic rate in the House Sparrow
(Passer domesticus)

Approved by:



Thesis Adviser, Professor of Biology



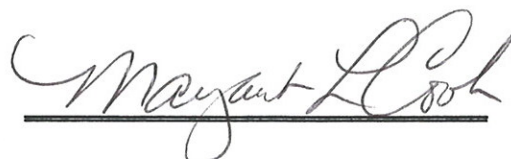
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Chair, Department of Biology



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Abstract:

Birds maintain a fairly high body temperature (T_b) compared to most mammals. In order to maintain a high T_b birds must have a high metabolic rate. High daytime energy expenditures are decreased during the night by lowering T_b . In this experiment daily T_b in house sparrows (*Passer domesticus*) were determined by telemetry methods. T_b ($n=6$) showed a decrease of 3.00 C from daytime to night time. The average daytime T_b was 42.7 C and night time was 39.7 C. Oxygen consumption (VO_2) was measured in an open flow metabolism system. Metabolic rate had a day time to night time difference of 2.40 ml O_2 / g*hr. Thermal conductance (K) decreased from a daytime K of .23 (ml O_2 / g*hr) / C to nighttime K of .14 (ml O_2 / g*hr) / C. At a T_b of 42.7 C the night time energy expenditure would be 38.8 KJ. At 39.7, the average night time T_b for house sparrows ($n=6$) the energy expenditure is 36.0 KJ. Therefore a house sparrow saves 7% energy in maintaining circadian rhythms. Deeper depressions of T_b , known as torpor, may be energetically efficient, but costly in predation.

Introduction:

Heat flows into or out of a system as a consequence of temperature differences. All objects on earth, living or non living are exchanging heat with their surroundings. Living organisms constantly produce heat in the body through metabolic processes. When the amount of heat is different between two systems, heat flows from one system to the other to reach an equilibrium (Calder and King 1974). Most organisms maintain a body temperature (T_b) with the functional range of enzymes, below 50 C and above 1 C. Vertebrate animals typically maintain an average T_b of about 35-45 C (Whittow, 1976).

There are two main classes of thermoregulating animals. Ectotherms depend on the surrounding physical environment to provide heat because their internal body heat production is low and their physiological thermoregulation capacity is low (Eckert, 1996). Endotherms, such as birds, produce sufficient heat internally, and therefore are less dependent on environmental temperatures (Aschoff 1982).

Ectotherms must live where they will have enough heat to sustain metabolic processes, and also shelter themselves from any environmental extremes. Most ectotherms have evolved a wide array of behavioral mechanisms that enable them to control their temperatures with remarkable precision (Bartholomew, 1982). They avoid high temperatures by burrowing and nocturnal timing of their surface activity (Licht et al. 1967).

Endotherms are capable of maintaining a fairly high and constant T_b through metabolic heat production and physiological and behavioral regulation (Bartholomew, 1982). Although they may be more independent of their environment, endotherms pay the price in metabolic cost.

To maintain T_b , An endotherm must produce heat through metabolism at a rate equal to the heat lost to the environment when the ambient temperature (T_a) is lower than the body temperature (T_b) (Calder and King 1974). Calder and King derived the relationship that heat loss, heat gain, heat production, and metabolic rate are equal in endotherms and can be expressed:

$$\text{Heat Loss} = \text{Heat Gain} = \text{Heat Production} = \text{Metabolic Rate}$$

Bartholomew (1982) identified seven characteristic features of physiological thermoregulation: 1) Control of heat production, 2) Control of heat loss 3), Two thermostats in the central nervous system to detect high and low temperatures, 4) Other peripherally located thermostats, 5) A system to coordinate signals from thermostats, 6) A system to allow the central thermostat to over-ride the peripheral ones, and 7) Channels of communication that allow the thermostats to activate the mechanisms of heat production and heat loss.

Endotherms employ a variety of methods for thermoregulation. Shivering thermogenesis involves the contractile processes of skeletal muscles in the production of heat (Dawson and O'Connor, 1996). Non-shivering thermogenesis is an important mechanism of heat production in hibernating mammals but its occurrence in birds is controversial (Dawson and O'Connor, 1996). It is believed that heat production within the brown adipose tissue allows the hibernating animal to raise its T_b by non-shivering thermogenesis (Blaxter 1989).

in the cold, some species through vasoconstriction, postural adjustments or pilo- or pilomotor mechanisms, decrease thermal conductance by increasing the effectiveness of insulative mechanisms (Calder and King, 1974), Evaporative cooling, via panting or gular fluttering, is used to reduce T_b in high T_a conditions by evaporative heat loss (Whittow, 1976).

For a mammal with a large body surface area to volume ratio, more heat than larger animals is lost to the surrounding environment. Small endotherms, such as passerine birds, have a large surface area to volume ratio. They maintain a

body temperature of 38 - 41 C, 3 to 5 C higher than most mammals and other, larger, birds. (Whittow, 1976). Their high T_b along with a high surface to volume ratio means that passerine birds have a very high living metabolic rate (Kendeigh et. al., 1977)

When an endotherm is within a "comfortable" T_a , it is within the thermal neutral zone (Bartholomew, 1982). At the lower end of the thermal neutral zone is the lower critical temperature (T_{lc}) and the upper limit is the upper critical temperature (T_{uc}). Below the lower critical temperature, oxygen consumption increases linearly as T_a decreases. The point at which the line would intersect. If the x axis, represents the animals approximate T_b (Bartholomew 1982) .

Lowering thermal conductance can decrease the metabolic rate in a bird. Thermal conductance is the net rate of heat transfer of an organism per C difference between T_b and T_a . If an organism is exposed to lowering T_a , conductance should decrease and eventually reach a minimum value (Aschoff 1982). Methods employed by some birds in lowering thermal conductance is changing of blood supply to superficial areas, fluffing or compressing feathers or by simple postural adjustments (Aschoff 1982). Once the T_a is to lower than the lower critical temperature, postural and plumage adjustments alone are not adequate to control body temperatures. A bird must increase metabolic heat production.

Some mammals and birds undergo seasonal and/or daily relaxation of

thermal homeostasis so that they allow T_b to drop 5-35 C below normal (Reinertsen, 1996). Nocturnal hypothermia, depression of T_b 3 to 10 C, occurs when birds allow their T_b to fall during the night. In some extreme cases, birds have been observed to lower their body temperatures by 20 to 30 C. The common poorwill has been observed to lower T_b to about 3 C, a phenomenon known as torpor (Bartholomew et al. 1957). Poorwills can maintain this extreme temperature decrease for up to a month (Brigham 1992, Bartholomew et. al. 1957).

The benefit of lowering T_b by reducing metabolic rate is a decrease in energy requirements, because less heat is needed to maintain the lower T_b . Smaller animals, with higher mass-specific metabolic rates, save proportionately more energy by decreasing T_b (Aschoff 1982). Reinertsen (1989) observed a 5-10 C nocturnal decrease in T_b of hummingbirds.

Like torpor, circadian rhythms of T_b reduce heat loss and therefore conserve energy. In captivity, avian T_b varies about 1 to 2 C (Reinertsen 1996). These fluctuations in T_b , known as circadian rhythms, remain in an animal that has been removed from the natural environment and placed in a laboratory setting with constant environmental conditions (Randall 1997). A true circadian rhythm will persist most often as a continuation of that animal's normal daily cycles (Randall 1997). Circadian rhythms in diurnal T_b have been observed in the European kestrel (Falco sparverius), rock dove (Columba livia), ring dove (Streptopelia chinensis) and

wren (Troglodytes aedon) (Rashotte et. al. 1988).

Experiments on circadian rhythms in T_b of humans have shown that changes in metabolic rate account for about one-fourth of the 0.6 C daily swing in T_b , while three-fourths of the change result from changes in heat conductance between the body and environment (Randall, 1997).

House sparrows, Passer domesticus, are found abundantly worldwide throughout farms, cities and suburbs along with natural habitats (Lowther et. al., 1992). They over-winter in northern temperate climates, but are also found in hot deserts (Lowther et. al., 1992). To better understand the thermoregulatory processes of house sparrows I studied their T_b by telemetry. I looked for daytime and nighttime circadian rhythms in T_b . I also looked at the metabolic rate and thermal conductance to see what the energy changes were from daytime to nighttime.

Material and Methods:

Husbandry:

Four male and two female house sparrows were caught by a mist net in urban St. Cloud, Minnesota. They were housed in individual cages in an environmental chamber at 20 C and with a 12:12 photoperiod. The photoperiod was altered so that 06:00 standard time was 12:00 noon in the chamber ("time" as used hereafter refers to the birds' subjective time). The lights in the environmental chamber came on and turned off at 06:00 and 18:00 respectively. The birds were

fed ad libitum sunflower seed and meats along with commercial chicken starter mash.

Body temperature Measurements:

I recorded Tb by telemetry using Minimitters CX250 (MiniMitter Company Inc., Sunriver, OR). These sensors produce an audible tick that varies in frequency with temperature. To record Tb, MM were implanted surgically into the body cavity of the sparrows. Prior to implantation the MMs were coated with paraffin and calibrated to within ± 0.1 C using a water bath and thermocouple thermometer. Variation in measured temperature, according to the calibration tick versus time curve, was ± 0.2 C.

The MM transmitters used in this experiment worked through an AM frequency radio. An AM radio picked up the frequency as a constant rhythm of ticks. I wired two separate cages with a an am/fm radio and an antenna circling the outside of the cage. As figure 1 shows, I extended a battery pack, as well as a pair of head-phones, outside of the environmental chamber so that I could turn the radio on and count the ticks without entering the chamber and disturbing the birds. I entered the outside room quietly, and recorded tick rate six time within ± 10 minutes of the stated time. As temperature increased so did the frequency of ticks.

To test the efectifveness of my experimental set-up, I examined the effects of disturbance on Tb. At 02:00 I walked into the environmental chamber. I

then walked back out and measured the Tb.

After calibration of the MMs they were surgically implanted in the sparrows through a 10 mm abdominal incision (Southwick, 1971; Reinertsen 1982). Prior to the surgery the bird was weighed and anesthetized using a ketamine/ xylazine mixture administered intramuscularly (.005ml of the anesthetic was injected for every 1 gram of bird mass; Harrison, 1986). Two days were allowed for recuperation after surgery.

Tb was recorded at 04:00, 08:00, 12:00, 16:00, 20:00 and 24:00. I recorded the Tb for each bird three times at each designated hour. Tick rates were converted to Tb using calibration data specific to each minimitter. For the data of figures 2 and 5, average Tb were computed for each bird separately, then the individual bird data were pooled to estimate average sparrow Tb.

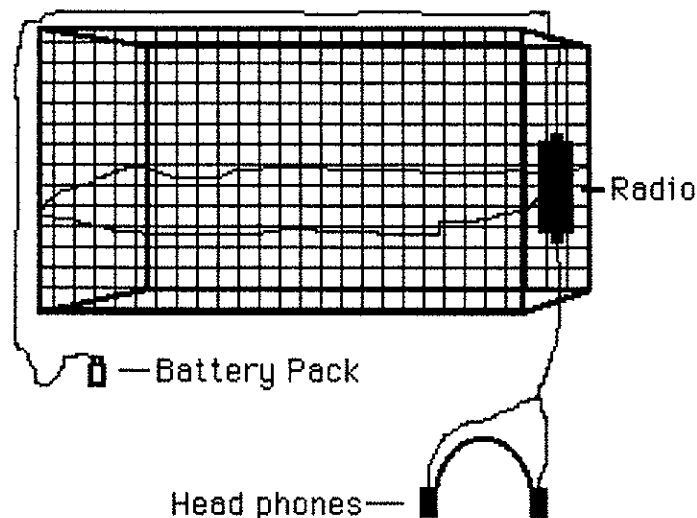


Figure 1: Environmental chamber with bird cage used for telemetry readings in the center.

Metabolism Measurement:

Oxygen consumption (VO_2) was measured in an open flow metabolism system. Air flow into the chamber was measured using calibrated flowmeters (Gilson 410). Water and CO_2 were removed by drierite and soda lime both before and after passing through the chambers. Percent O_2 of inlet and outlet air was measured using an Ametek S3A O_2 analyzer. Data were recorded on a microcomputer and converted to oxygen consumption ($\text{mL O}_2 / \text{g} \cdot \text{h}$) by the program Datacan (Sable Systems) using equation (2) of Hill (1972).

I calculated the surface area of the birds using the equation:

$$\text{Surface Area (m}^2\text{)} = 8.11 \cdot 10^{-4} (\text{bird mass})^{.67} \text{ (Walsberg and King 1978)}$$

I calculated the thermal conductance of the sparrows using the equation:

$$C = \text{Metabolic Rate} / (\text{T}_b - \text{T}_a) = (\text{ml O}_2 / \text{g} \cdot \text{h} \cdot \text{C}) \text{ (Aschoff, 1982)}$$

Protocol:

The birds were removed from the environmental chamber at 14:00 and weighed to the nearest 0.1 grams. They were then placed in the metabolic chamber. For the duration of the 8 hour trial, the birds were fasted. Experiments began at 16:00 and ended at 24:00: the lights were turned off at 06:00, the normal end of the birds active phase. All trials were done at T_a of 20 C.

Analysis:

I tested for differences between means using a two-tailed students t-test, and considered two values significantly different when $p < 0.05$. The data are expressed as means \pm standard error.

Results:

The average daytime T_b was $42.7\text{ C} \pm .36$ ($n=6$). During the night, the T_b decreased significantly to $39.7\text{ C} \pm .6$, a change of 3.05 C .

Metabolic rate in the house sparrows ($n=4$) declined in the late afternoon and after the bird's subjective night began (figure 4). The average daytime metabolic rate was $5.63 \pm .49\text{ mL O}_2 / \text{g*hr}$. Basal metabolic rate, during the night time, was $3.23 \pm .32\text{ mL O}_2 / \text{g*hr}$.

Thermal conductance also decreased from the the late afternoon and after the bird's subjective night began. Thermal conductance at 16:00 was 0.23 ± 0.01 ($\text{mL O}_2 / \text{g*hr}) / \text{C}$. It declined to 0.14 ± 0.008 ($\text{mL O}_2 / \text{g*hr}) / \text{C}$ at 24:00, a change of $.09$ ($\text{mL O}_2 / \text{g*hr}) / \text{C}$.

Disturbance increased the T_b to $40.8 \pm .04\text{ C}$ at 02:00, 1.61 C higher than normal T_b at this time (figure 5).

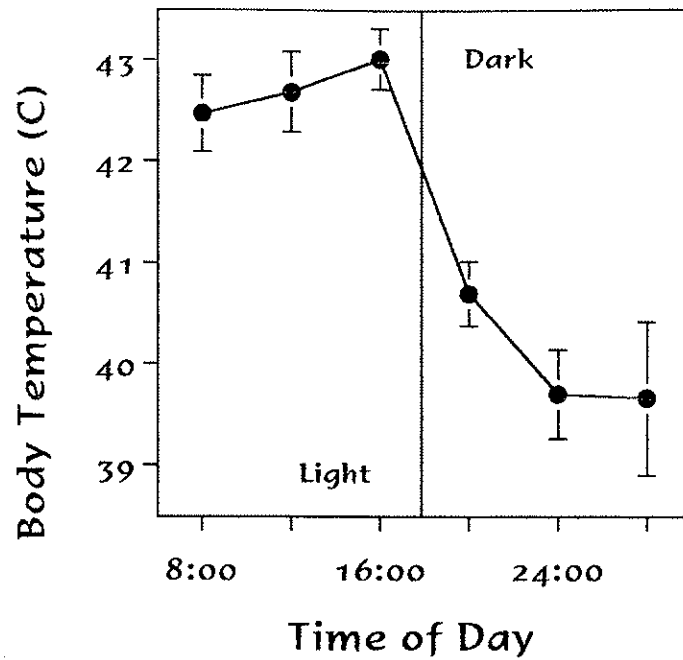


Figure 2. Tb in C of house sparrows (n =6) during the course of a day. Lights were turned off at 18:00. The error bars represent 95% confidence intervals.

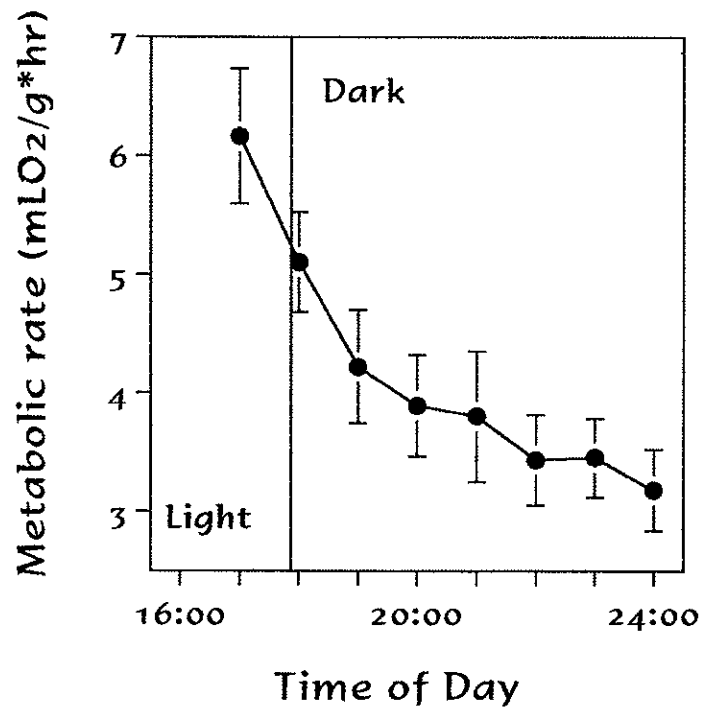


Figure 3. Metabolic rate of house sparrows (n=4) measured in mLO₂/g*hr. Lights went off in the environmental chamber at 18:00. The error bars represent standard error for each mean number.

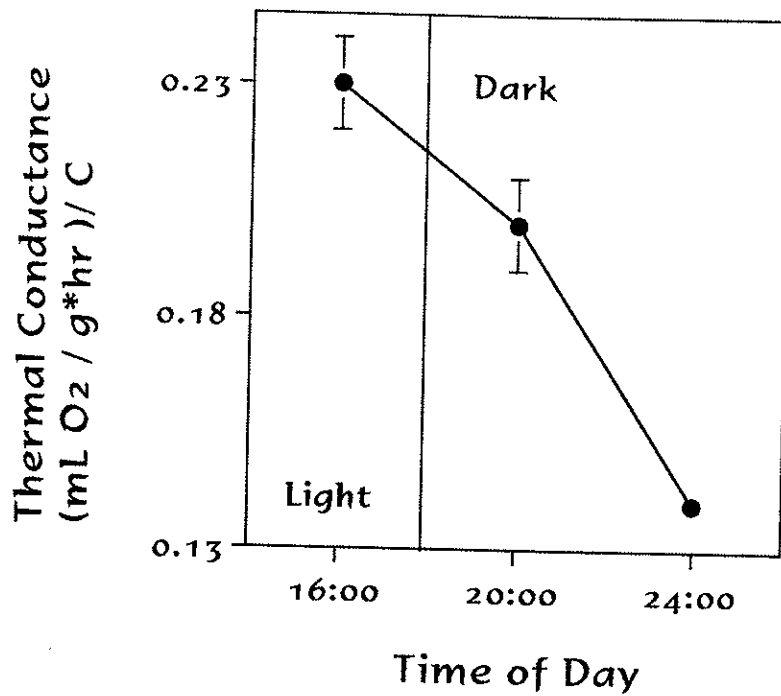


Figure 4. Daily variations in thermal conductance ($X \pm SE$) in house sparrows at 20 C. At 24:00, the SE is masked by the closed circle.

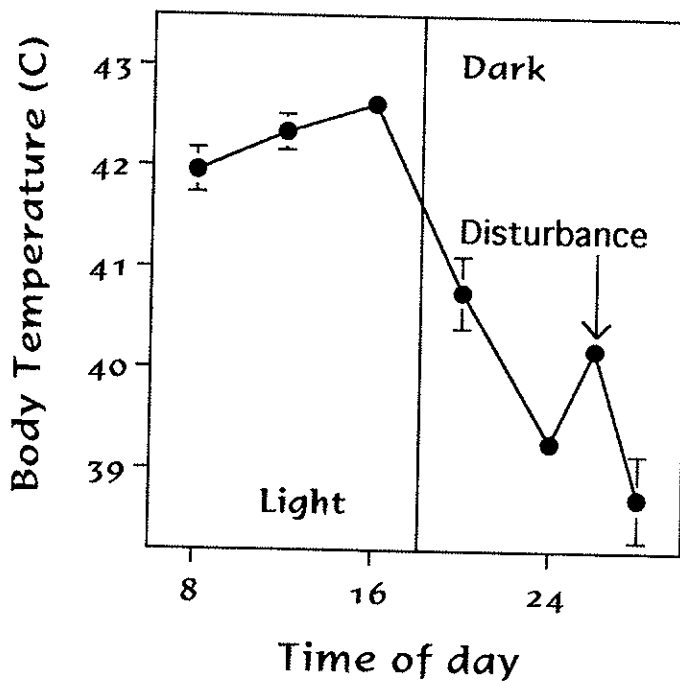


Figure 5. The effects of disturbance during the night ($X \pm SE$) (at 26:00) on Tb in house sparrows. Error bars represent standard error. At 16:00, 24:00, and 26:00, the SE is masked by the symbol

Discussion:

Circadian rhythms:

In 1970, Jürgen Aschoff explored the implications of circadian rhythms on the survival of a homeotherm (Aschoff, Daan and Aschoff, 1982). He investigated the idea that animals have a period throughout the day where they are most likely to be killed. For example an experiment done in 1963 by Pizzarello et al. exposed a group of rats to 900 roentgens of x - radiation at 09:00 and another group of rats at 21:00. The group of rats exposed to radiation at 21:00 only lasted 13 days while the 09:00 group lasted 130 days (Pizzarello et. al. 1963).

Since there are no anatomical differences in the rats at these two times of day, there must be something different physiologically or behaviorally (Aschoff). One example of behavioral circadian rhythms based on survival has been discovered in the foraging activity of hen harriers (Circus cyaneus), which feed on common voles. Voles emerge approximately every two hours to feed. It has been observed that the hunting patterns in hen harriers strongly correlates with that of the voles. Since hunting yield for the harrier hen is highest during vole emergence, they hunt every two hours (Aschoff).

More discrete physiological rhythms, such as in Pizzarello's rats, occur daily and/or seasonally and can increase or decrease survivorship in a species.

When human subjects are kept in isolation and without a time piece, circadian oscillations usually have periods longer than 24 h. The rhythm of temperature has a circadian period of about 24.4 h. During the 24.4 h cycle, T_b varied in humans

from 37.1 to 36.7 C (Aschoff and Pohl 1970). Most probably the circadian rhythm of oxygen consumption will be synchronous and in phase with the rhythm of activity (Aschoff 1982). Although in humans this has been shown, data from chaffinches (*Fringilla coelebs*) show variations between activity and oxygen consumption, as well as between activity and T_b (Aschoff and Pohl, 1970). There may exist a nonvariable phase relationship between T_b and O_2 consumption for this species. The decrease in metabolic rate and T_b in the house sparrows during the same time of day seems to support this idea. (Aschoff and Pohl 1970)

Pohl (1976) studied the circadian rhythms of oxygen consumption in the common redpolls (*Acanthis flamme*) and in pine siskins (*Spinus pinus*) under various levels of light intensity. He observed significant differences in the rhythm of metabolic rate due to the increase of light intensity. With increasing light intensity there was a marked increase also in metabolic rate. Pohl stated that the observed changes in metabolic rate suggest seasonal differences in the sensitivity of the circadian system to light. One description of circadian rhythms describes the dependency of the period on light intensity.

It was once believed (Hardy 1961) that most if not all of the diurnal temperature variation was due to ingestion of food and exercise because of basic diurnal metabolic rate patterns in man during the day due to the specific dynamic action (SDA) of food (Kreider et al. 1958). If these assumptions were true rhythms of oxygen uptake and T_b would not persist when the organism has food withheld and is at rest for 24 hours (Daan and Aschoff, 1982). Diurnal periodicity of

subcutaneous temperature and oxygen uptake for three mountain finches perched quietly in the dark without food were described by Aschoff and Pohl (1970) supporting the consistency of circadian rhythms independent of food availability.

Tb and metabolic rate:

The results of my Tb and metabolic rate measurements in house sparrows indicate circadian rhythms (figure 3 and 4). Many experiments with various passerine and non passerine birds have shown similar rhythms in Tb and metabolic rate (Daan and Aschoff 1982, Aschoff 1982; Brigham 1991; Aschoff and Pohl 1970, Pohl 1976; Reinertsen and Haftorn 1983 and 1986).

The circadian rhythms of thermoregulation in three small - sized northern species of birds, the willow tit (Parus montanus), the great tit (Parus major), and the common redpoll (Acanthis flammea), was studied by Reinertsen and Haftorn (1986). The mean daytime Tb of the great tit and common red-poll was 41.8 ± 0.49 C (n=6) and 41.7 ± 0.39 C (n=4) respectively and the willow tit was less at $41.35 \pm .32$ at Ta of 20 C (Reinertsen and Haftorn 1983). During night-time, the willow tit, great tit and the common redpoll dropped down to 38.3 ± 0.29 C , 39.4 ± 0.75 C and $39.7 \pm .6$ C respectively.

Telemetry experiments on white crowned sparrows showed a change of about 2 C from day to night Tb (43 - 41 C) (Southwick, 1973). The change in Tb for house sparrows in this study was .6 C greater than the average change in Tb of the common red-poll, willow and greater tit.

The mean T_b for red-tailed hawks and great horned owls is 41.1 C and 39.5 C respectively (Chaplin and Diesel, 1984). Red-tailed hawks showed a 2 C decrease from light to dark phase (Chaplin and Diesel, 1984).

The oxygen consumption of the common redpoll and the willow tit was $5.43 \pm .61$ and that of the great tit was 5.92 ± 0.62 . Their night-time oxygen consumption was 4.23 ± 0.21 , $4.25 \pm .36$, and $3.81 \pm .23$ mL O₂ /g*hr respectively (Rienertsen and Haftorn, 1986). The house sparrows (n=4) metabolic rate was fairly similar at $5.63 \pm .49$ for light phase and $3.23 \pm .32$ mL O₂ / g*hr, a 42% decrease.

Metabolic oxygen consumption values at 20 C of bramblings (*Fringilla montifringilla*) show a similar decline in activity from 16:00 to 24:00 hours (Aschoff and Pohl, 1970). There was an approximate change 1.71 ml O₂ / g*hr compared to 2.80 ml O₂ / g*hr in the house sparrows. Similar circadian rhythms of oxygen consumption have been determined in pocket mice and white footed mice (Aschoff and Pohl, 1970).

Thermal Conductance:

Thermal conductance (K), is a measure of the tendency for heat loss in an organism (Aschoff, 1982). Animals with high K (eg. small endothermic animals with high T_b) display a steeper slope of the metabolic rate versus T_a curve.

Bartholomew et al (1957) proposed that birds maintain their thermal conductance close to their minimal level while at the same time reducing their rate of energy

metabolism and allowing T_b to fall to a level determined by the reduced level of heat production .

In the house sparrows, the energy cost over a 12h night time period at the daytime average T_b of 42.7 C would be 38.8 KJ. The energy cost for the house sparrows at nighttime metabolic rate with an average T_b of 39.7 C were 36.0 KJ. Therefore circadian temperature difference of 3 C allows the sparrows a savings of 7% energy expenditure.

Nocturnal Hypothermia and Torpor:

Nocturnal hypothermia is important for balancing the intense metabolic demands and relatively low capacity for energy storage of small endotherms (Reinertsen 1996). The energy savings of 7% in the house sparrows may make the difference between survival and starvation. On the other hand, during states of decreased T_b , many birds are more susceptible to predation (Aschoff).

Torpor has been observed in hummingbirds in nature during stressful times, such as food deprivation (Hainsworth et al. 1977). Torpor was not used to reduce nocturnal energy expenditures when net energy gains during the day were sufficient for overnight expenditures (Hainsworth et al. 1977). The observation that hummingbirds undergo torpor only in energy emergencies, except for the andean humming bird (Powers, 1993), suggests that torpor has a cost, whether in energetic efficiency or predation (Hainsworth et al. 1977). Hummingbirds that were slowly starved over 15 days showed a decrease in body mass as the use of

torpor increased (Heibert 1990 and 1991; Reinertsen 1989).

When deprived of food and water, inca doves (Scardafella inca) undergo greater nocturnal hypothermia allowing them to conserve energy and water (MacMillen and Torst 1967). The difference in day time to night time Tb was 7.6 C (MacMillin and Trost 1967), a considerable difference from the house sparrow at 3.00 C.

Starvation induced torpor in adult colies showed a drop of 15 C in Tb below normothermic levels (Bartholomew and Trost, 1970). The adult colies are able to arouse from the profound hypothermia by means of their own metabolic heat production without the addition of heat from any external source (Bartholomew and Trost, 1970) which allows them to avoid predation better during states of torpor.

Geiser (1987) studied the reduction of metabolism during hibernation and daily torpor in a variety of mammals and birds, a temperature effect or physiological inhibition. He observed an increase of mass - specific metabolic rate with decreasing body mass. The increase of mass-specific metabolic rate with decreasing body mass, observed during basal metabolic rate, was not observed during torpor, and the slope relating metabolic rate with body mass was almost zero. In daily variations in body temperature, no inverse relationship between temperature and body mass was observed, and consequently the metabolic rate during torpor at the same Tb was greater than that during torpor. Geiser (1987) showed that the reduction in metabolism during torpor of large animals can be

explained largely by temperature effects, whereas a metabolic inhibition in addition to temperature effects may be used by small animals, such as some birds, to reduce energy expenditure during torpor and nocturnal hypothermia.

Conclusion:

In my house sparrow data I observed daily variations in the body temperature. The decrease in T_b was slightly lower than other passerine birds of similar body mass. Metabolic rate was lower at night than during the day, as shown for many passerine birds.

Circadian variations in T_b and metabolic rate serve as a form of reducing energy expenditure by decreasing the metabolic heat production used for thermal regulation. We observed a decrease in K from day to night. When looking at the energy expenditure at day time compared to night time T_b , there is a savings of 7% by decreasing the body temperature 3 C.

A 7% savings in energy expenditure may be adequate enough for the survival of the bird. Reducing T_b and metabolic rate may be costly, though, to some birds in that predation may increase. For some species, the risk of predation is masked by the necessity of the energy savings.

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