Shivering and digestion-related thermogenesis in pigeons during dark phase

MICHAEL E. RASHOTTE,¹ SEppo SAARELA,² ROSS P. HENDERSON,³ AND ESA HOHTOLA²

¹Program in Neuroscience, Department of Psychology, Florida State University, Tallahassee, Florida 32306-1270; and ²Department of Biology, University of Oulu, FIN-90401 Oulu, Finland

Rashotte, Michael E., Seppo Saarela, Ross P. Henderson, and Esa Hohtola. Shivering and digestion-related thermogenesis in pigeons during dark phase. Am. J. Physiol. 277 (Regulatory Integrative Comp. Physiol. 46): R1579–R1587, 1999.—The pigeon’s main source of regulated heat production, shivering, is especially likely to be used for thermoregulation during the dark phase of the day when there is little heat from locomotor activity. However, food stored in the pigeon’s crop is digested during the night, and digestion-related thermogenesis (DRT) will provide heat that should decrease the need for shivering to maintain body temperature (Tb). We investigated the conditions under which DRT alters the occurrence of nocturnal shivering thermogenesis in pigeons. In fasting experiments, in which DRT was minimal, variations in pectoral shivering were closely related to the kinetics of nocturnal Tb when the ambient temperature (Ta) was moderate (21°C). In that case, shivering was low while Tb fell at the beginning of the night, moderate during the nocturnal plateau in Tb, and strong during the prelight increase in Tb. Similar kinetics of nocturnal Tb occurred when Ta = 28°C, but shivering was negligible throughout the dark phase. In restricted feeding experiments, nocturnal DRT was varied by providing different amounts of food late in the light phase. When Ta = 21°C, 11°C, and 1°C, nocturnal Tb and O₂ consumption were directly related to the amount of food ingested. However, nocturnal shivering tended to decrease as the food load increased and was significantly reduced at the higher loads. Because nocturnal shivering did not become more efficient in producing heat as the size of the food load increased, we conclude that nocturnal DRT decreased the need for shivering thermogenesis.

fainting; restricted feeding; body temperature; energy reserves; birds; circadian

The pigeon’s nocturnal body temperature (Tb) falls to different levels, depending on its energy reserves. In fed pigeons, nocturnal Tb falls 1–2°C below diurnal values. In fasting pigeons, Tb falls to progressively lower levels on successive nights and can be as much as 7–8°C below light-phase values when 20% loss of body weight (BW) has occurred (19). Pectoral shivering is the pigeon’s primary source of regulated thermogenesis (10, 23, 26), and the nocturnal decrease in the pigeon’s Tb is related to a lowering of the cold threshold at which shivering is initiated (6–8).

When pigeons are exposed to cool (12°C) ambient temperatures (Ta), there is a close relationship between the kinetics of shivering and Tb across the hours of a typical 12-h dark phase (5). For 1–2 h near the beginning of the phase, shivering is greatly reduced and Tb decreases at a more or less steady rate. For several hours near the middle of the phase, shivering occurs at moderate levels and Tb remains close to its nocturnal plateau level. Finally, for 1–2 h near the end of the phase, shivering is relatively strong and Tb increases, even approximating light-phase levels shortly before lights on. When Ta is warmer (24°C), the kinetics of nocturnal Tb persist as in the cooler Ta, but the overall level of shivering is greatly attenuated, and within-night variation in shivering thermogenesis plays only a small role (5). Peripheral vasomotor action and changes in respiration are the primary influences on Tb in warmer Tas (5).

“Digestion-related thermogenesis” (DRT) is one of several terms used in the literature to describe the metabolic consequences of feeding and digestion (also, “heat increment of feeding” and “specific dynamic action”) (3, 6). DRT is traditionally inferred from increased oxygen consumption (1a) or changes in operant heat-seeking behavior (29) during a relatively short period of time after the ingestion of food. However, in animals that store food in their crop for digestion at later times, ingestion and digestion can be dissociated so that DRT might occur several hours after feeding. This kind of effect has been shown in the kestrel (Falco tinnunculus) in a restricted feeding procedure in which oxygen consumption during the dark phase was elevated in rough proportion to the amount of food consumed 2 h before dark (14).

Because the pigeon stores food in its crop during the day for digestion during the night (15, 22), DRT could be a potent influence on nocturnal Tb and the effector systems responsible for the kinetics of nocturnal Tb in this species. The present experiments investigated how the kinetics of nocturnal Tb and pectoral shivering are influenced by DRT in the pigeon. Continuous measurements of pectoral shivering (by chronically implanted electrodes) and of abdominal Tb (by telemetry) were made in freely moving pigeons that lived in large metabolic chambers. DRT was varied by altering food availability during the light phase. In one procedure, food was withdrawn for several days of fasting. In a second procedure, the amount of food provided on a restricted feeding procedure was changed on single days, and the effects in the subsequent dark phase were examined. In both procedures, Ta was varied to alter the background level of shivering against which the effects of DRT were assessed.

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METHOD

Animals. Thirteen adult pigeons (Columbia livia) were obtained locally. Before the experiment, the birds were housed for several weeks in a free-flying indoor aviary maintained on a 12:12-h light-dark regime, Ta = 19–22°C, and with food and water available ad libitum. The food was a commercial high-carbohydrate pelleted food (Purina Nutriblend Gold) with a caloric value of 18.4 kJ/g, as determined by bomb calorimetry. The composition of the food is described by the manufacturer as ~60% carbohydrate, 14% protein, 7% fat, 6.5% ash, and 3% added minerals. The preexperimental BWs of the pigeons averaged 393.4 g (SE = 8.2 g).

Apparatus. Details of the experimental chambers and the devices used to measure Tb and pectoral EMG are described elsewhere (11). Briefly, each pigeon lived individually in a metabolic chamber housed inside an environmental chamber that provided precisely controlled levels of Ta (±0.1°C) and a daily photoperiod when an overhead incandescent lamp was lighted (illuminance ~40 lx of 2,250-K light measured at the approximate height of the pigeon’s head). The chamber was completely darkened during the daily dark phase. The air-tight metabolic chambers were made of clear acrylic plastic and were sufficiently spacious (53 x 27 x 28 cm; total capacity 40 dm3) to permit normal walking and movement patterns in a horizontal plane. Fresh air was supplied to the chamber at a rate of 2 l/min. Food and water were available in separate reservoirs that minimized spillage. The food in the metabolic chamber was the same as in the aviary (above). A low perch running the width of the chamber and mounted on the floor, ~20 cm from the wall where the food and water reservoirs were located, was typically the pigeon’s roosting location for quiet periods in the light phase and for the entire dark phase.

Oxygen consumption (in ml/min) was measured by open circuit respirometry (paramagnetic O2 analyzer, Servomex 1155) such that O2 content (1 part/million resolution) of samples from the chamber and from the supply air was obtained every 2.5 min. The difference between the supply-air and the chamber-air concentrations was corrected to standard temperature and pressure (0°C; 760 mmHg) and stored in a computer. Instantaneous values of O2 (ml/min) were calculated by isolating each sample point using the dynamic equations of Bartholomew et al. (see Ref. 1). These values were converted to weight-specific values (in ml·min⁻¹·kg⁻¹).

Tb was measured by a thermosensitive radio transmitter (Barrows, Palo Alto, CA, model FT) implanted in the pigeon’s abdominal cavity under halothane anesthesia. The transmitter pulse rate (~500 Hz at 37°C) was processed by software to provide mean Tb measurements with high resolution (0.01°C) in every 2.5-min period or in every 30-s period of each 24-h cycle (measurement at 30-s periods became available part way through the project as a result of equipment upgrades and was used for the later birds studied).

Electromyograms (EMG) related to shivering thermogenesis were recorded from three gold-plated hook electrodes chronically implanted into the pectoral muscle of the pigeons under halothane anesthesia. The electrodes were positioned in a triangular configuration 10–14 mm away from the keel and ~30 mm caudally from the cranial tip of the sternum. The electrodes were inserted at a depth of ~10 mm and with 4 mm distance between them. Ultraflexible multistrand Teflon-coated steel wires attached to the electrodes were threaded subcutaneously to the back of the bird, where they were connected to a miniature plug in an acrylic saddle that the pigeon wore continuously. Electrical signals from the pectoral muscle were routed through a miniature swivel on the saddle and a flexible cable to a Grass P511 amplifier located outside the chamber. The amplifier had a gain of 5,000 and a high-pass frequency of 50 Hz and a low-pass frequency of 580 Hz (~3 dB points). Remote television observation showed that the cable did not affect general activity of the birds, including feeding and sleeping behavior. Root mean square (rms) EMG was collected in 2.5-min or 30-s periods (depending on equipment availability, see above) for the entire light and dark cycles of each day.

It was possible to quantify locomotor activity in two (of the four) metabolic chambers used, and some of these data will be presented. Locomotor activity was measured by mounting the metabolic chamber on a frame attached to an electronic load beam in a way that measured changes in the center of gravity in the lengthwise dimension of the cage. As the pigeon moved in the chamber, the center of gravity moved, and the cumulated distance of that moving point was calculated every 30 s and reported in units of meters traveled.

Procedure. The pigeons lived in the metabolic chambers for at least 3 wk before data collection began. Throughout the experiment, a 12:12-h light-dark regime was in effect. Each day the birds were removed from the chamber for a few minutes to be weighed and to allow the chamber and all food and water reservoirs to be refilled. In most cases, the daily chamber maintenance was carried out 2 h before the dark phase began, but in some cases, it occurred at the time of the light-dark transition. Because the metabolic chamber required ~20 min to equilibrate after being closed, measurements of O2 were not used for approximately the first 30 min after the maintenance. Measurements of Tb and EMG were typically interrupted for only a brief time at maintenance. During adaptation to living in the metabolic chamber, food and water were available on an ad libitum basis.

Tb and pectoral EMG activity were compared during the daily cycle in nine pigeons when they were being fed ad libitum and after they had fasted to ~83% of their baseline BW. The pigeons fasted in either of two Ta: five birds fasted in 28°C, which was chosen to minimize shivering thermogenesis on the basis of ambient conditions alone; the other four pigeons fasted in 21°C, which was chosen to be closer to the reported lower critical temperature for shivering (23) and approximates the Ta in most laboratory studies of fasting. Four of the five birds that fasted in Ta of 28°C had 13-day adaptation to that Ta in the metabolic chamber before fasting began; the fifth bird had 30-day adaptation. There was no obvious effect of these different adaptation periods. In fasting, food was withdrawn until the birds had lost 17–20% of their baseline BW.

To test the effects of consuming different amounts of food before the dark phase began, four additional pigeons were trained on a restricted feeding procedure when Ta = 21°C. At hour nine of each day’s light phase, these pigeons normally received a limited amount of food, which resulted in reduced BW (~12% below the value when food was available) and highly repeatable nocturnal plateaus in Tb from day to day. For the four pigeons, these food amounts averaged 10.75 g (12, 11, 11, or 9 g for the individual pigeons) and will be referred to as the 1× amount. When the daily cycle in Tb was well established on 1×, the amount of food presented was changed on occasional days to the following values: no food (0 g), twice the usual amount (2×), and three times the usual amount (3×). Each of these changed amounts was presented only once, and the order in which they occurred was not the same in all pigeons. After a change, the pigeons returned to the 1× amount until the nocturnal Tb plateau characteristic of the 1× amount was reinstated. This typically required ~3
days, although recovery from the 0-g amount usually occurred in 1–2 days. When all food amounts had been tested in Ta = 21°C, three pigeons continued in the experiment, and the effects of the 0-g, 1×, 2×, and 3× amounts were evaluated when Ta was reduced to 11°C and to 1°C. The goal of this procedure was to investigate the effects of the different food amounts when the baseline level of shivering was elevated. In each case, the pigeons were exposed to the lower Tas for ~7 days while the testing was done. In between these cold exposures, Ta remained at 21°C. Transition to a lower Ta occurred in 1–2 days. When all food amounts had been tested in 1×, 2×, and 3×, each order was used for the third pigeon. Examination of the data indicated that neither the different orders of exposure to the Tas nor the different orders in which the food amounts were presented at each Ta had apparent effects on the outcome. Consequently, the data from all birds were combined for each Ta condition and for each of the 0-g, 1×, 2×, and 3× food amounts.

Data analysis. Data from the 12-h dark phase are the focus of the analyses but some data from the light phase are presented also. Statistical comparisons were made with unpaired and paired t-tests, as the data required, and by repeated-measures ANOVAs. Occasional equipment failures reduced the group number in some comparisons. The level of statistical significance at which hypotheses were rejected was P < 0.05.

RESULTS

Fasting. The number of days in fasting before the birds lost ~17% BW was not statistically different in the two Tas (t = 1.13). In 21°C, BW fell 17% (±1.96%) below baseline values after 6.75 days fasting (±0.75 days); in 28°C, BW fell 16.22% (±0.69%) after 8.20 days fasting (±0.97 days).

Figure 1 summarizes the effects of Ta and fasting on the Tb, pectoral EMG, and O2 measures. In baseline, comparison of mean dark-phase values indicated that Ta did not significantly affect any measure. In fasting, however, mean dark-phase Tb was significantly lower than baseline in each Ta (t ≥ 7.61, P < 0.001), and the level reached when Ta = 21°C was significantly lower than in 28°C (t = 4.07, P < 0.01). Compared with baseline, mean dark-phase EMG increased significantly in fasting when Ta = 21°C (t = 4.96, P < 0.05), but not when Ta = 28°C. Pectoral shivering was negligible in baseline and fasting in the latter case. Fasting resulted in reduced nocturnal O2 consumption in both Tas (21°C: t = 4.43, P < 0.05; 28°C: t = 7.42, P < 0.01), and the level reached when Ta = 21°C was significantly higher than in 28°C (t = 2.81, P < 0.05). Figure 2 shows that when Ta = 21°C, nocturnal shivering progressively increased across the days of fasting, indicating an increasing role for shivering thermogenesis as the pigeon's energy reserves became depleted.

The averaged data for birds fasted when Ta = 21°C (shown in Fig. 1) indicate that the kinetics of nocturnal Tb and shivering in pigeons are closely related. For several hours near the beginning of the night, shivering was low when Tb was decreasing. During the midnight hours when Tb was near the nocturnal plateau, shivering occurred in a moderate range. In the final hours when Tb was increasing before lights on, shivering was relatively strong. Visual inspection of the data indicated that, for the four birds studied in this condition, Tb decreased during the first 2, 4, 4.5, or 7 h of the 12-h dark phase. During the period of decrease, Tb fell from
during the dark phase in individual birds fasted at Ta = 21°C. On the fasting day, pectoral EMG activity was very low while Tb decreased for 2 h at the beginning of the dark phase, at a rate 1.47°C/h. Moderate, episodic EMG activity occurred during the nocturnal plateau in Tb, which lasted for ~7 h. Finally, relatively strong shivering occurred during the final 3 h of the dark phase when Tb increased at a rate of 1.33°C/h. Allowing for individual differences noted in the duration of the decrease in Tb at the beginning of the dark phase, the kinetics of Tb and EMG activity shown here are representative of the other birds.

Figure 3 also shows that locomotor activity was negligible during the dark phase, in agreement with behavioral observations made by an infrared TV camera that indicated the pigeons remained in a roosting position on the perch. These locomotion data eliminate the possibility that our recordings of EMG activity during the night simply reflect gross bodily movements rather than pectoral shivering. Figure 3 also shows that the distance traveled in the light phase increased during fasting. The plotted data show distance in 30-s bins. The cumulated distance traveled between hours 12 and 22 of the light phase was 38 m on the baseline day and 226.7 m on the fasting day. The main features of these locomotion data and their relationship to the other measures were found in the other pigeons for which locomotion data were obtained.

Restricted Feeding. In the restricted feeding procedure, different amounts of food provided at hour nine of the light phase had large effects on the Tb, EMG, and Oz measures in the immediately following dark phase. In every case, the birds consumed all the food provided within a few minutes of its presentation. Figure 4 summarizes the average effects when Ta = 21°C. The nocturnal plateau to which Tb and Oz fell was directly related to the amount of food consumed in the preceding light phase. When no food was consumed (0 g), the

Fig. 2. Changes in pectoral shivering during dark phase on successive days of fasting for individual pigeons when Ta = 21°C. Each data point shows average EMG calculated across final 11 h of dark phase and expressed as a percentage of comparable average on final day of baseline. Last day plotted for each pigeon (P) is day on which its body weight reached criterion and fasting ended.

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\text{an average of } 38.82 \pm 0.30°C \text{ to } 35.14 \pm 0.35°C (t = 10.76, P < 0.01), \text{ mean pectoral EMG activity was } 5.51 \pm 1.61 \mu \text{V rms, and mean Oz consumption was } 10.03 \pm 0.36 \text{ ml min}^{-1} \text{kg}^{-1}. \text{ In the remainder of the dark phase, pectoral EMG activity averaged } 43.47 \pm 6.75 \mu \text{V rms, and mean Oz consumption was } 13.39 \pm 0.37 \text{ ml min}^{-1} \text{kg}^{-1}. \text{ The EMG and Oz values in the remainder period were statistically higher than in the decrease period (EMG: } t = 7.11, P < 0.01; \text{ Oz: } t = 64.34, P < 0.001). \text{ At the end of the dark phase, Tb averaged } 39.44 \pm 0.25°C, \text{ which was not statistically different from that before the decrease began.}
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Figure 3 provides a detailed example of how the kinetics of pectoral shivering and Tb were related

Fig. 3. Tb, pectoral EMG activity, and locomotor activity for P69 from 21°C group on final day of baseline (A) and of fasting (B). Data are plotted every 30 s throughout each daily cycle. Locomotion data are expressed as meters traveled per 30-s period. Tb and EMG data in this figure have 5x greater resolution (30-s bins) than in Fig. 1 (2.5-min bins).
the kinetics of shivering and Tb during the dark phase were very similar to those when fasting occurred at the same Ta. Specifically, shivering was lowest during the decrease in Tb, moderate during the plateau, and strong when Tb was increasing. The 1x food amount was associated with low shivering activity throughout the night, except at the very end of the dark phase when Tb and EMG activity both increased. When the 2x and 3x amounts of food were given, however, shivering did not show systematic changes during the night. The impression from this figure is that pectoral shivering was recruited to support the nocturnal changes in Tb (particularly the late-night increase) when no food, or a small amount of food, was consumed. When larger amounts were consumed, the kinetics of nocturnal Tb occurred without systematic variation in shivering.

When the background levels of shivering were elevated by setting Ta at 11°C and 1°C, the differential effects of the full range of food amounts on shivering...
became evident. This result is illustrated in Fig. 5 with data from the 1°C condition, which resulted in the highest levels of shivering. As found when Ta = 21°C, there was a positive relationship between amount consumed and the nocturnal plateaus in the Tb and O₂ measures, and the highest level of shivering occurred when no food was consumed. In this case, however, there was also a tendency for the overall level of dark-phase shivering to be reduced as the amount consumed increased.

Figure 6 summarizes these features of the Tb and EMG data in all three levels of Ta. Nocturnal Tb increased in a generally linear fashion as the amount of food consumed in the previous light phase increased (Fig. 6A). As Ta decreased, the overall level of pectoral shivering increased, and there was a tendency for increased food amounts to be associated with less shivering at each Ta (Fig. 6B). When each pigeon's EMG data were normalized with respect to its 0-g level (Fig. 6C), it was possible to find statistical evidence concerning how the different amounts of food influenced shivering. In comparison with the 0-g level, shivering was significantly reduced when the 1× and higher amounts were consumed in Ta = 21°C, when the 2× and higher amounts were consumed in Ta = 11°C, and when the 3× amount was consumed in Ta = 1°C. In the cases in which shivering was significantly reduced by food consumption within a Ta condition, the level of shivering was not differentially related to amount of food.

We considered the possibility that instead of DRT providing heat that reduces the need for shivering, shivering might become more efficient in producing heat as the food amounts increase. In that case, the reduction in EMG activity when higher food amounts have been consumed (Fig. 6) would be associated with greater heat production per unit of EMG activity. To examine this possibility, scatterplots were made for each animal showing heat production (as reflected in O₂ consumption) versus EMG activity during the night after different food amounts were ingested. Regression lines were fitted to the plots in each case to determine if the slope increased as more food was consumed, which would indicate greater efficiency of shivering. A representative example is shown in Fig. 7. The slopes of the regression lines fitted to the data in each panel were quite similar and showed no trend towards greater slopes as the amount of food consumed became greater. For example, when Ta = 1°C, the slope of the regression line was 0.031 ml O₂/unit of EMG activity when 0 g food was consumed; when the 3× amount was consumed (27 g for this bird), the slope was 0.027 ml O₂/unit of EMG activity. More generally, Fig. 7 provides a different view of how the amount of food consumed alters the distribution of EMG activity during the night.

**DISCUSSION**

Shivering thermogenesis is the pigeon's main source of regulated heat production (10, 23, 26), and it is especially likely to be used for thermoregulation during the dark phase of the day when pigeons are mostly inactive and heat from locomotor activity is minimal. We found that increased amounts of food ingested by pigeons during the day resulted in increased Tb and O₂ consumption during the night, as has been reported in previous restricted-feeding experiments (17, 19, 20, 22). However, we also found that these higher Tb and O₂ levels in the dark phase were not accompanied by increased shivering. In fact, at the higher food loads, nocturnal shivering decreased. Our explanation of this result appeals to the fact that pigeons store food in the crop for digestion during the night (15, 22), and, depending on their foraging success during the daytime, DRT can increase the heat content of the body and reduce the need for shivering thermogenesis in the
Because we showed that nocturnal shivering did not become more efficient in producing heat as the size of the food load increased, we conclude that the food loads decreased the need for nocturnal shivering because DRT was associated with nocturnal digestion also (14).

When our pigeons fasted for several days in Ta = 21°C, shivering became progressively stronger in successive dark phases, indicating greater shivering thermogenesis as tissue stores of energy reserves were depleted and nocturnal Tb fell to lower plateaus (9, 18, 20). When Ta was warm (28°C), nocturnal shivering thermogenesis was negligible during fasting. It is likely that changes in vasomotor tone and thermal conductance were the important influences on the pigeon's circadian temperature rhythm when Ta was warm (5). Flexibility in the use of effector systems for thermoregulation in various ambient and energetic conditions is well known (5, 16, 28).

The pigeon's energy status is indicated to central regulatory mechanisms by peripheral signals from tissues and dietary load. Although the nature of these signals and the pathways by which they operate remain to be elucidated in pigeons and other species (e.g., see Refs. 4, 25, 27, 30), it is clear that such signals influence the pigeon's nocturnal plateau in Tb by altering the threshold for shivering (7). One interesting possibility is that, in each daily cycle, a Tb value (or range) for the nocturnal plateau might be “set” about the time the dark phase begins (4, 24, 25). In that time window, peripheral signals indicating the pigeon's energy status would be “read” by central thermoregulatory mechanisms, and a nocturnal Tb plateau would be set that is directly proportional to the amount of energy reserves. In this case, the beginning of the night would be characterized by the suppression of heat production and, perhaps, an increase in heat loss until Tb nears the preset plateau value. Our data clearly show suppression of shivering thermogenesis at the beginning of the dark phase, and other experiments indicate that increased heat loss from vasomotor changes (5) and active suppression of metabolic heat production (12) can occur at this time in the daily cycle. These effects are not likely to be a consequence of the light-dark transition because the suppression of shivering also occurs at the appropriate time if lights are left on for an entire circadian cycle (5). It has recently been shown in fasted pigeons that the large decrease in Tb at the beginning of the night is accompanied by increased slow-wave sleep and paradoxical sleep (21), both of which are associated with reduced heat production (8).
One testable implication of the proposal that the nocturnal plateau in Tb is set at the beginning of the dark phase is that the plateau should not change when transient variations in energy status occur during the night. Data in support of this prediction have recently been obtained in our lab: large variation in Ta during the night had little effect on nocturnal plateaus resulting from different food loads (2). Further investigations to identify the location of the proposed time window in the daily cycle when the nocturnal Tb is set and to document the effects on nocturnal Tb of imposing various energy manipulations after that time window has passed would provide interesting data concerning this proposal.

The existence of various forms of DRT has been suggested in several avian species (see Ref. 3). Evidence for its contribution to thermoregulatory heat production has often been obtained by showing that the postfeeding rise in VO₂ is lower in cold-exposed animals. If we assume a constant and obligatory digestion-related component of VO₂, such results imply that other forms of thermogenesis have been replaced by DRT. Our work represents a novel approach in two ways. Firstly, because the pigeon stores ingested food in its crop, digestion is dissociated from ingestion, which allows adaptive timing of DRT. Secondly, we show the role of DRT directly at the effector level by measurements of shivering. Saving food in the crop for nocturnal digestion is dissociated from ingestion, which could represent extra heat that has to be dissipated, whereas in the dark phase, it can be used for the plateau and rising phase of Tb. Evidence for food retention in the crop, even after an early morning meal, has been obtained (22).

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Address for reprint requests and other correspondence: M. E. Rashotte, Dept. of Psychology, Florida State Univ., Tallahassee, FL 32306-1270 (E-mail: rashotte@sy.sy.fsu.edu).

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