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# NOCTURNAL VARIATION IN BODY TEMPERATURE OF GRIFFON VULTURES[1]

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*Abstract.* The variation in body temperature over 24 hr was measured by implanting temperature measuring radio transmitters in the abdominal cavity of six captive Griffon Vultures (*Gyps fulvus*). Body temperature was measured when the birds were under three different feeding regimes: within 24 hr of feeding (while digesting), 2–3 days after feeding (post-absorptive state), and 9.5–10.5 days after feeding (food deprived). For all birds, nocturnal body temperature was significantly lower than diurnal body temperature. The decline in body temperature at night was significantly greater in food deprived birds, which at 10.5 days post-feeding had dropped by 4–6°C. We suggest that this is an adaptation to reduce energy requirements of Griffon Vultures during periods of food shortage.

*Key words: ambient temperature, body core temperature, daily temperature variation, food deprivation, Griffon Vulture,* Gyps fulvus.

Birds usually show a daily variation in body core temperature ($T_b$), with maximum temperatures occurring during the period of activity and minimum temperatures occurring during the period of inactivity (Calder and King 1974, Aschoff 1982). In small diurnal birds, the nocturnal drop in $T_b$ is known to be greater in periods of food shortage (Stuebe and Ketterson 1982, Hohtola et al. 1991, Waite 1991) or exposure to cold stress conditions (Saarela et al. 1989, 1991). In these situations, nocturnal drop in $T_b$ is commonly used to conserve energy (Reinertsen 1983). Nocturnal drop in $T_b$ also has been demonstrated in several species of birds of prey, which are often exposed to extensive periods of food deprivation as a result of irregular feeding or food shortage (Hatch 1970, Larochelle et al. 1982, Chaplin et al. 1984).

Griffon Vultures (of the genus *Gyps*) are a group of large birds which might be particularly expected to have developed adaptations for conserving energy. Being obligatory scavengers, they are totally dependent on finding dead animals, which are an unpredictable and irregular food supply (Houston 1974). Radio telemetry tracking in Israel has shown that Eurasian Griffon Vultures (*Gyps fulvus*) regularly withstand periods of 7 to 10 days between successive feedings (Bahat et al. 1993). We examined the hypothesis that in order to decrease the metabolism needed for maintenance during a prolonged fast, the Eurasian Griffon Vulture reduces the gradient between ambient temperature ($T_a$) and $T_b$ by decreasing its $T_b$. We also investigated the daily $T_b$ variation of Griffon Vultures and considered whether the extent of nocturnal drop in $T_b$ is influenced by their plane of nutrition.

## METHODS

Four immature (between 2 and 4 years old) and two adult birds (over 6 years old) were used in this study. All were hatched in captivity or had been in captivity for over 3 years and were accustomed to handling. Birds were kept in individual outdoor cages (2 × 4 × 2 m) at the Zoological Garden, Tel-Aviv University. Experiments were done between 29 July and 13 September 1993 (summer), when ambient temperature ($T_a$) ranged from 18.7°C to 35.2°C. Average (± SD) $T_a$ during the experiments was 21.0 ± 3.3°C. The birds were not exposed to $T_a$ exceeding the limits of their thermoneutral zone (Bahat 1995), therefore exposure to heat or cold stress was avoided. All birds were exposed to natural light/dark cycles.

$T_b$ was measured by implanted transmitters (model TM-Disc, Mini-Mitter, Sunriver, Oregon). Each transmitter weighed 13.5 g, measured 34 mm in length and 18 mm in diameter, and had a 6 month battery life.

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The transmitters were implanted in the abdominal cavity through a 3-cm-long incision in the abdominal skin under general anesthesia, using a combination of Xylazine (average dose of 0.66 $mg \cdot kg^{-1}$) and Ketamine (average dose of 10 $mg \cdot kg^{-1}$). The incision was sutured and two weeks were allowed for recovery. Each transmitter was calibrated in a controlled temperature bath prior to the implantation and after the end of the experiment, at 1°C intervals from 33°C to 43°C. Measurement accuracy was ± 0.2°C. A regression equation was calculated from the calibration curve to transform the pulse repetition frequency into body temperature data. Calibration regression coefficients ($r^2$) varied between 0.992–0.999. Comparative calibrations of each transmitter before and after the experiments showed no significant drift in the transmitter data. $T_a$ (in the shade) was measured using a copper-constantan 2.4 mm gauge thermocouple with a Wescor TH-65 digital thermometer with measurement accuracy of ± 0.1°C. All average $T_b$ data in this paper are given ± SD.

Birds were supplied with drinking water ad libitum, and Turkey meat was provided as food during the period of experiments. $T_b$ of the birds was recorded every hour through a 24-hr period. Three different experiments were done: First, body temperature was measured in the 24-hr period following feeding. Birds were allowed to eat ad libitum. Griffon Vultures have large crops, which can hold up to 1.5 kg, and it takes approximately 34 hr for this quantity of food to pass through the alimentary tract (Houston and Cooper 1975). The 24 hr period following feeding therefore represents the period during which digestion occurred. Second, birds were monitored from 48 to 72 hr after having been fed. This period covers the post-absorptive state, when digestion is no longer taking place. Finally, birds were deprived of food for up to 10 days until their next feeding, and temperature readings were taken from birds at the end of this period—that is from birds that had not received any food for 9.5 to 10.5 days. We call this the food deprivation state. The average (± SD) body mass of the six birds in the post-absorptive state was 6,580 ± 890 g, and in food deprived birds it was 5,730 ± 790 g. Each bird was weighed daily without handling, using a wooden perch which covered a portable, battery powered weighing device (model B50-P, Shekel Inc., Israel, accuracy ± 5 g).

There are important ethical considerations involved in any experiment in which animals are deprived of food for long periods. We do not consider that depriving Griffon Vultures of food for 10 days presented an unnatural situation or resulted in any distress, as this species withstands long intervals between feeding in the wild; even in captivity, when provided with food every day, Griffon Vultures will voluntarily avoid food for several days (Bahat, unpubl. data). In the present experiment, all birds were in good condition and at their normal body mass before each feeding trial. They were continuously observed and we planned to terminate a trial immediately if any of them had shown signs of discomfort or distress. Therefore, we consider this period of food deprivation to be a perfectly normal experience for this species and one for which it is apparently adapted.

## RESULTS

The six experimental Griffon Vultures showed various degrees of variation in $T_b$ between day and night, depending upon the duration of food deprivation (Fig. 1). Figure 1A shows that while digesting food, birds had an average $T_b$ variation of 1.8 ± 0.4°C, and their maximum $T_b$ range was 36.6–40.6°C, with average maximum $T_b$ of 39.7 ± 0.8°C and average minimum $T_b$ of 37.9 ± 0.8°C. Figure 1B shows that when birds were in the post-absorptive state, their average $T_b$ variation increased to 2.5 ± 0.6°C, and maximum $T_b$ range was 35.5–40.4°C, (average maximum $T_b$ of 39.3 ± 0.8°C, average minimum $T_b$ of 36.8 ± 0.7°C). Figure 1C indicates that food deprived birds showed still greater average $T_b$ variation of 3.0 ± 0.7°C, with a maximum $T_b$ range of 35.3–39.9°C.

There was a significant increase in the maximum $T_b$ variation shown by birds as they were in more advanced stages of food deprivation (ANOVA, $F_{2,5} = 19.1$, $P < 0.001$). This was not the result of a change in the average maximum daily $T_b$, which did not differ significantly between birds in different feeding regimes ($F_{2,5} = 0.58$). However there was a significant decrease in $T_b$ at night, with the average minimum $T_b$ dropping to lower levels when birds were deprived of food for 10 days ($F_{2,5} = 29.8$, $P < 0.001$).

If we consider the effect of $T_a$ on the average $T_b$, there was a significant correlation ($r = 0.93$) only when birds were deprived of food ($F_{2,5} = 9.1$, $P < 0.01$) (Fig. 2). Birds, therefore, reacted to food deprivation by increased $T_b$ variation, which resulted from a greater nocturnal decrease in $T_b$.

## DISCUSSION

Body temperature variation in Griffon Vultures under outdoor ambient temperatures maintained a rhythmic circadian pattern and showed a diurnal cycle. $T_b$ fell at night in all conditions, but more so when birds were deprived of food.

Circadian cycles comparable to those observed in the Griffon Vulture have been described in other raptorial scavengers: among Old World vultures, $T_b$ in wild African White-backed Vultures (*Gyps africanus*) (average body mass 5.3 kg) between dawn and midday differed by approximately 2°C (Houston 1973). Among New World vultures, $T_b$ in a Black Vulture (*Coragyps atratus*) (body mass approximately 2,000 g) fasted for 36 hr and kept at $T_a$ range of 15–35°C showed a $T_b$ range of 5.3°C, between 37.7–43.0°C between day and night (Larochelle et al. 1982). A $T_b$ variation of 4°C (between 38.0–34.0°C) was reported for a single male (2,230 g) Turkey Vulture (*Cathartes aura*) fed ad libitum and kept in constant $T_a$ of 15°C (Heath 1962). $T_b$ in five Turkey Vultures (body mass 1,530–2,590g) fed daily and kept under winter conditions varied 0.4–2.6°C, from 39–40°C in the afternoon down to near 38°C in the early morning, regardless of the $T_a$ (Hatch 1970). An average $T_b$ of 39.7°C (range 38.0–41.7°C) was found in six Turkey Vultures at a $T_a$ range of 11–40°C (Arad and Bernstein 1988).

Considering the fact that the thermoneutral zones (TNZ) of Black and Turkey Vultures are between 25–40°C and 26–40°C, respectively (Larochelle et al. 1982, Arad and Bernstein 1988), the measurements

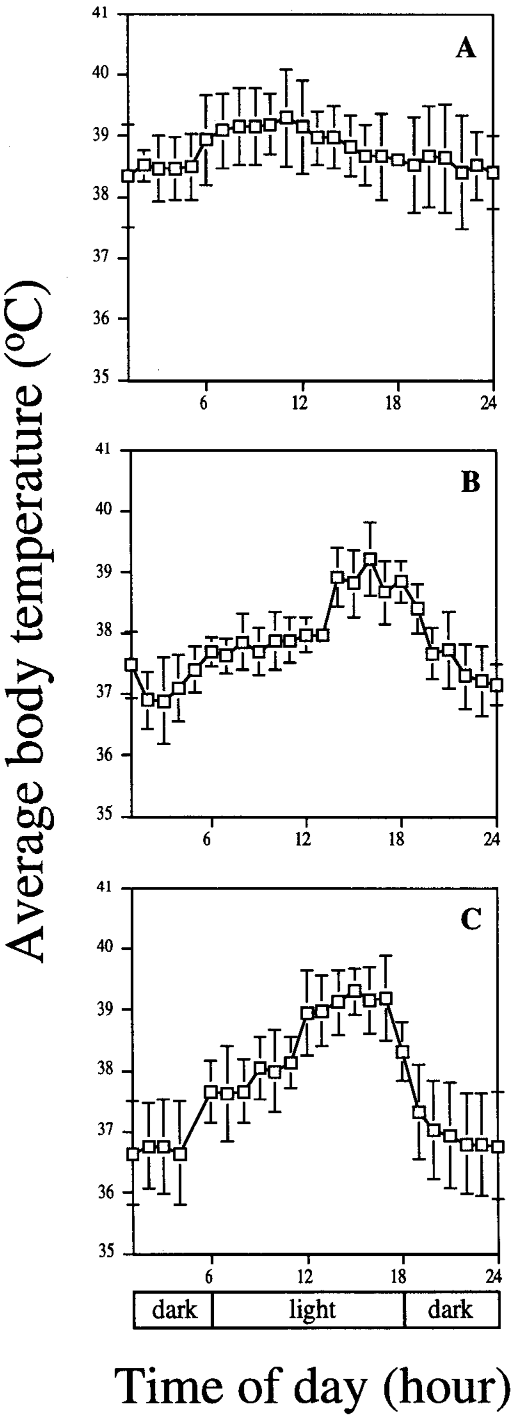


FIGURE 1. Average daily body temperature variations in Griffon Vultures under different feeding conditions. (A) values for birds while digesting food. (B) values for birds in the post-absorptive state. (C) values for birds following 10 days of food deprivation.

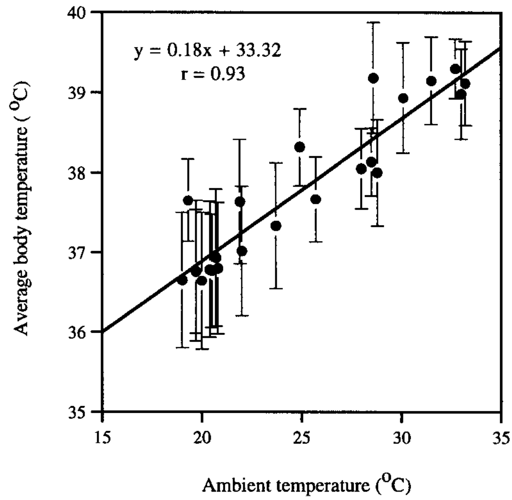


FIGURE 2. Effect of ambient temperature on average body temperature of six food deprived Griffon Vultures (9.5–10.5 days following last feeding).

mentioned above for the two species were made while the birds were exposed to $T_a$ values below their lower critical $T_b$ ($T_{lc}$). Some vultures at the lower ambient temperatures might have been cold stressed. One might expect that under these conditions, birds would drop their $T_b$ as much as possible in order to reduce the difference between $T_b$ and $T_a$ to a minimum. Consequently, one might anticipate that Black and Turkey Vultures which are kept only in their TNZ, would show a reduced degree of nocturnal drop in $T_b$.

Nocturnal drop in $T_b$ also has been found among nonscavenging raptors: in Red-tailed Hawks (*Buteo jamaicensis*), a nocturnal decrease in $T_b$ of up to 1.8°C has been measured in the summer in birds deprived of food (Chaplin et al. 1984). When fed ad libitum, their $T_b$ variation was only 0.8°C. In winter, these birds had a maximum $T_b$ variation of 3.2°C during fast and a $T_b$ variation of 2.0°C when fed ad libitum. In all seasons, the range of $T_b$ variation in Red-tailed Hawks primarily was affected by food deprivation; changes in $T_a$ had a smaller effect (Chaplin et al. 1984).

The Griffon Vulture, although 20% heavier than the African White-backed Vulture, more than three times heavier than the Black and the Turkey Vultures, and nearly six times heavier than the Red-tailed Hawk, has a greater $T_b$ variation than any of these other species. In order to assess the magnitude of energy conserved by nocturnal drop in $T_b$ of Griffon Vultures, we used the data on $T_b$ changes which were obtained in this study, together with a specific heat capacity of the body of 3.35 $J \cdot g^{-1}$ $°C^{-1}$ (Hart 1951, Schmidt-Nielsen 1990). For a 6,580 g Griffon Vulture (average body mass in the present experiment), the amount of heat needed to increase $T_b$ by 1°C is 22.0 $J \cdot g^{-1}$ $°C^{-1}$. The amount of heat needed to increase $T_b$ by 1.8°C (average nocturnal drop in $T_b$ in digesting vultures) is 39.6 $J \cdot g^{-1}$ $°C^{-1}$. An increase in $T_b$ of 2.5°C (average nocturnal drop in $T_b$ in post-absorptive state) requires 55.1 $J \cdot g^{-1}$ $°C^{-1}$, and an increase in $T_b$ of

3.0°C (nocturnal drop in $T_b$ in food deprived vultures) requires 66.1 $J \cdot g^{-1}$ °$C^{-1}$. Thus, by lowering its body temperature 3.0°C in response to food deprivation, a Griffon Vulture may save a considerable amount of energy. However, there is a cost, in that energy will need to be expended to raise $T_b$ in the early morning, although Griffon Vultures can reduce this cost under natural conditions by using solar radiation (Bahat 1995).

As Griffon Vultures range from extreme arid deserts to high and cold mountainous areas, and as this species is mostly nonmigratory, it is exposed to a very wide range of $T_a$. Furthermore, as it nests and roosts on open cliff ledges and only rarely in caves (cave nesting is typical in the Turkey Vulture, Hatch 1970), it is fully exposed to $T_a$ effects. In view of the unpredictable nature of its food supply as an obligatory carrion feeder, the ability of the Griffon Vulture to lower its $T_b$ regularly and minimize the temperature difference between $T_b$ and $T_a$, and consequently its heat loss, is an important energy-saving adaptation to endure long periods of starvation. Although Griffon Vultures show a nocturnal drop in body temperature even when recently fed, this cycle of temperature variation is subjected to environmental influence: $T_a$ further influences the deviation of $T_b$ from $T_a$ but only under conditions of food deprivation. We suggest that body temperature variation in the Griffon Vulture is always present but is further shaped by changes of $T_a$ when a bird is deprived of food. By regularly reducing the difference between $T_b$ and $T_a$, and by reducing heat production, Griffon Vultures save energy otherwise used for thermoregulation. Accordingly, this substantial energy saving enables the Griffon Vulture to cope with regular periods of food shortage without decreasing its activity level. The maintenance of foraging activity is very important for this species because it is totally dependent upon finding carcasses which are searched for over extensive areas and regularly over periods of several days. Therefore, keeping a continual daily foraging activity, while minimizing nocturnal energy expenditure, is a major adaptation to the scavenging way of life of this species.

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