Body Temperature of the Lammergeier *Gypaetus barbatus* (Aves: Accipitridae)

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Dedicated to Dr. H. Kumerloeve at the occasion of his 70th birthday

Introduction

Much information has been accumulated on avian body temperatures and thermoregulation. However, most of this information relates to small birds (Dawson and Hudson, 1970). Benedict and Fox (1927) reported body temperatures and metabolic rates for a number of birds weighing more than 1 kg but their method of measuring body temperature, by inserting a mercury thermometer into the cloaca, gives unreliable results due to stress induced thermogenesis. This problem has been largely overcome with the modern development of indwelling thermocouples, thermistors and miniature temperature transmitters. Moreover it is now possible to undertake continuous long-term monitoring of body temperatures.

One of the species investigated by Benedict and Fox (l. c.) was the Lammergeier *Gypaetus barbatus*. This is a bird predominantly of high mountains where extremes of temperature prevail. Sub-zero temperatures frequently occur, especially at night. Sunbirds (Nectariniidae) living permanently under these conditions at high altitudes in Africa have been found to have a diel temperature rhythm with nocturnal despressions of 5—17° C (Cheke, 1971). The significance of this hypothermic response is that the birds lose heat at a reduced rate; and the energy saved enables them to withstand better long periods of extreme cold. A similar diel temperature rhythm was reported by Heath (1962) for the large (2,200 g) Turkey Vulture *Cathartes aura,* though the nocturnal body temperatures averaged only 4° C lower than those recorded during the day. According to Heath (l. c.), the ability of the Turkey Vulture to regularly lower its body temperature during the night must constitute a favourable device for the saving of energy, especially when considering the variable nature of this scavenging species' food supply.

The Lammergeier is a specialist scavenger depending on bones and offal, though live prey may also be taken (Glutz von Blotzheim, Bauer and Bezzel, 1971). In nature the Lammergeier's food sources are liable to unpredictable fluctuations, and presumably food may not always be readily available. In the Drakensberg massif of South Africa, carrion placed near an observation hide attracted Lammergeiers only during the winter months. Birds did not come to the carrion during summer, presumably because weather conditions then made food finding easier. The high incidence of cold nights, long periods of inclement weather and the supposition that the species may have to cope with a fluctuating, sometimes precarious food supply, suggests that the Lammergeier might show a marked diel rhythm with depressed nocturnal body temperatures. This paper reports on the diel temperature cycle of a Lammergeier for which adverse thermal conditions or experimental stress were not complicating factors.

Methods and Results

The Lammergeier had been obtained locally as a full grown nestling, and had been kept captive for 12 months in a outdoor enclosure, about 2000 m^2 in area, at Ladybrand, South Africa (29°9'S, 27°29'E; 1,600 m above sea level). The bird appeared to be in good condition when examined by us; it weighed 3,400 g, 36 hours after having been fed.

During the experiment the bird was kept in a soundproof room with a natural photoperiod. Mean ambient temperatures during the period local sunrise (05.15 hr) to local sunset (18.35 hr) was 18.5 ± 0.2° C (all measures of statistical variation are ± one standard deviation). During the period local sunset to local sunrise the mean ambient temperature was 18.6 ± 0.2° C.

A solid partition separated the investigator and the temperature-recording apparatus from the bird which was provided with a floor-space area of three square metres. Body temperature was detected with a vinyl covered thermistor probe (YSI # 402) inserted six centimetres into the cloaca. The probe was held in position with surgical adhesive tape. A flat banjo type probe (YSA # 409) was taped directly against the skin under the feathers of the bird's back. These probes were connected to fine flexible cables which were taped to the bird's central tail feathers and led from there to a tele-thermometer (YSI model 47TD). The bird appeared to be undisturbed by the probes and cables, and moved freely over the space allocated to it. Measurements of ambient, cloacal and skin temperatures were made to the nearest 0.1° C at 15 minute intervals over an unbroken period of 24 hours commencing at 1800 hr local time. In addition, temperatures were monitored during the four hours preceding, and the four hours following, the experimental period. During the experiment, the bird was denied food and water which were last given 12 hours before observations commenced.

The results are given in Figure 1. The temperature varied with a monophasic 24 hr cycle between 38.1° C and 39.0° C. Mean cloacal temperature during this perios was 38.4° C. This is slightly below the 39.1° C predicted by the empirical equation $Tb = 14.3\ W^{-0.09} + 32.2$ (where W is the body weight in grams), formulated on the basis of avian body weights by McNab (1966). Our value is also considerably lower than the mean figure of 39.7° C recorded for a 5,070 g Lammergeier by Benedict and Fox (1927). However, for reasons already stated, the latter value does not repesent a realistic measurement of normal body temperature.

Cloacal and skin temperatures recorded between the times of local sunrise and sunset averaged 38.6 ± 0.2° C and 21.4 ± 0.9° C respectiveley. Between the hours of local sunset and sunrise the corresponding temperatures aver-

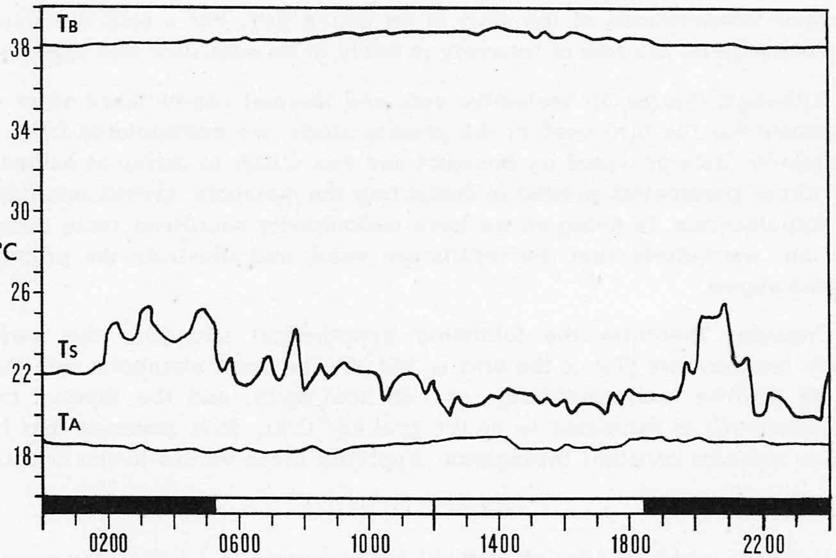

Figure 1. Cloacal (T_B) and skin (T_S) temperatures of the Lammergeier in relation to time of day and ambient (T_A) temperature.

aged 38.2 ± 0.1° C and 22.6 ± 1.8° C. Thus, cloacal temperatures averaged 0.4° C higher and skin temperatures 1.2° C lower during the day than at night. The difference between the means for day and night-time cloacal temperatures is statistically significant, ($t^2 = 16.59$, $n = 96$, $p < 0.001$). The difference between the means for day and night-time skin temperatures is less significant ($t^2 = 4.16$, $n = 96$, $p < 0.05$). Although the day/night differences in both sets of temperatures are statistically significant, it is clear that the amplitude of the daily cycle was small.

Discussion

Our findings indicate that under „normal" conditions the Lammergeier does not automatically undergo hypothermia at night. The possibility remains, however, that the Lammergeier may be capable of regulating its temperature below the level reported here when exposed to conditions of stress, resulting from sub-zero ambient temperatures and food shortage. Such a dual body temperature response has been shown by Lasiewski (1963) for hummingbirds (Trochilidae), where lowered body temperatures and concomitant entry into torpor was not a nightly occurrence but was dependent on the birds' available energy resources. However any advantage gained in the conservation of energy through lowered body temperature must be weighed against energy expended in rewarming the body to normal temperatures at the start of an active day. For a bird the size of a Lammergeier the rate of recovery is likely to be both slow and expensive.

Although figures for metabolic rate and thermal conductance were not obtained for the bird used in the present study, we extrapolated from the metabolic data provided by Benedict and Fox (1927) to arrive at estimates for those parameters needed in computing the metabolic credits and debits of hypothermia. In doing so we have undoubtedly sacrificed some accuracy, but we believe that the results are valid, and illustrate the principle stated above.

Consider therefore the following hypothetical situation: the normal body temperature (T_b) of the bird is 38.4° C; the basal metabolic rate (MR) is 45 kcal/kg bodyweight/day, or 1.88 kcal/kg/hr; and the thermal conductance (C) is estimated to be 0.1 kcal/kg/°C/hr. It is assumed that this value remains constant throughout. Applying these values to the equation

$$MR = C\,(T_b - T_a)$$

it becomes apparent that at ambient temperatures (T_a) below the zone of thermal neutrality (where the thermal conductance of the bird remains nearly constant) the saving in energy as a result of the 3° C drop in body temperature amounts to 0.3 kcal/kg/hr or for a 3.4 kg bird, 1.0 kcal/hr. If we are correct in our assumption that there will be no marked change in the thermal conductance below the zone of thermal neutrality, then, this energy saving remains constant irrespective of the ambient temperature. Taking the specific heat of the bird to be 0.83 kcal/kg/°C, the amount of energy required to raise the body temperature 3° C would be 8.5 kcal over and above the energy required for normal metabolic processes. To balance the debit incurred through having to rewarm the body, the bird would have to maintain reduced body temperatures for some 8.5 hours. To this must be added the time taken to enter into, and emerge from, hypothermia.

The apparently expensive rewarming process could be partly overcome through the use of an external source of heat. The significance of sunbathing as a supplement to metabolic heat has been appreciated only recently (see Ohmart and Lasiewski, 1971). The Lammergeier is a frequent sunbather. Lammergeiers, in nature and in captivity, have been observed to sit with wings spread and either back or front facing the early morning sun. In this connection the majority of Lammergeier roosting sites known to us face eastwards and receive sun first thing in the morning. Moreover Lammergeiers are early risers, and birds in captivity have been observed to move to a favoured perch and sit anticipating the sunrise. However, in the mornings the mountains are frequently shrouded in mist and cloud, and these conditions often persist for much of the day. Hence, conditions for sunbathing are unlikely to occur regularly enough for the bird to be able to depend on the behaviour as a supplement to metabolic heat for rewarming the body. Instead, sunbathing probably serves to supplement normal metabolic processes as and when conditions permit.

From this we postulate that in the Lammergeier selection has favoured the maintenance of a nocturnal body temperature at a level close to that which normally prevails during the day, because this strategy is likely to be metabolically less expensive than one involving recovery of body temperature from a nocturnal low point. the problem of coping with conditions of cold stress and unpredictable food supplies is more likely overcome through behavioural adaptations.

Lammergeiers typically roost and nest in potholes, clefts and small caves in cliff faces; the nest is lined with hair. In these situations the harsh environmental conditions of low ambient temperatures and high wind are to some extent ameliorated, probably providing a relatively equable microclimate. In captivity, Lammergeiers will creep into any corner or container big enough to contain them during the night. The birds actively seek out these nocturnal shelters. As far as is known, no other large African vulture or eagle indulges in similar behaviour.

The experimental Lammergeier went to sleep as soon as its room became dark, within an hour after local sunset. The bird typically adopted a prone position with its neck retracted and the ventral surfaces of the body resting flat on the ground. The legs and feet were drawn up into the ventral feathers, the head drooped sideways and the eyes were closed. The bird remained in the same position all night. The nocturnal rise in the skin temperature of its back was undoubtedly a consequence of the bird's quiescence and plumage arrangement. In effect, a shell of relatively still warm air surrounded the Lammergeier.

The plumage of the Lammergeier is apparently well adapted to the environment. The plumage consists of relatively large, broad and stiff, overlapping contour feathers which would serve admirably in protecting the bird from the wind. Indeed, when the bird indulges in body shaking the sound of ruffled feathers is clearly audible over 30 metres. Beneath the layer of contour feathers lies a dense layer of down. The total effect of this plumage is to prevent the outflow of heat and to protect the resulting shell of warm air from the disturbing effects of strong cold winds.

In conclusion, the Lammergeier apparently does not normally undergo moderate hypothermia at night. Instead it normally employs behavioural mechanisms for thermoregulation, resulting in conservation of energy. Its habit of sleeping in caves represents an adaptation for exploiting the most favourable microclimate available at night. The bird's sleeping posture, and its plumage arrangement involving covering of the naked appendages, enhances the effectiveness of body insulation and reduces the thermal gradient. Quantitative information is lacking to indicate the extent of the thermal amelioration afforded by the situations and conditions in which Lammergeiers spend the night.

Summary

This paper reports the diurnal body temperature cycle of a Lammergeier *Gypaetus barbatus* for which adverse thermal conditions or experimental stress were not complicating factors. Cloacal temperature varied with a monophasic 24 hr cycle between 38.1°C and 39.0°C. Cloacal temperatures averaged 0.4°C higher during the day than at night. The findings are examined in relation to certain aspects of the physiology, ecology and behaviour of the species. The Lammergeier does not normally undergo moderate hypothermia to conserve energy at night. The maintenance of a nocturnal body temperature at a level close to that which normally prevails during the daytime is likely to be less expensive energetically than the process of rewarming the body from a moderate nocturnal low point. The Lammergeier normally employs behavioural mechanisms for thermoregulation, resulting in conservation of energy. Its habit of roosting in caves or in its well-lined nest represent adaptations for exploiting the most favourable microclimate available. The bird's sleeping posture, and its plumage arrangement involving covering of the naked appendages, enhances the effectiveness of body insulation and reduces the thermal gradient.

Zusammenfassung

In der vorstehenden Arbeit wird der Rhythmus der täglichen Schwankungen der Körpertemperatur bei einem Bartgeier, *Gypaetus barbatus*, beschrieben. Bei den zugrunde liegenden Versuchen war Beeinflussung des Temperaturganges durch ungünstige Außentemperaturen oder versuchsbedingten Stress ausgeschaltet. Im 24stündigen Zyklus variierte die in der Kloake gemessene Temperatur zwischen 38,1 und 39,0° C; während des Tages war sie durchschnittlich um 0,4° C höher als in der Nacht. Die Ergebnisse der Untersuchung wurden zu gewissen Aspekten der Physiologie, der Ökologie und des Verhaltens des Bartgeiers in Beziehung gesetzt. Im Gegensatz zu verschiedenen anderen Vögeln zeigt der Bartgeier nachts keine Hypothermie; die Aufrechterhaltung einer nächtlichen Körpertemperatur, die in etwa mit der am Tage übereinstimmt, verursacht beim Bartgeier möglicherweise weniger Energieverlust als das Erwärmen des Körpers von einem nächtlichen Tiefpunkt auf die normale Tagestemperatur. Das Übernachten in Höhlen oder im gut ausgelegten Horst ist eine adaptive Eigenart, die es dem Bartgeier erlaubt, das günstigste zur Verfügung stehende Mikroklima auszunutzen. Während der Nacht tragen die Schlafhaltung und die Anordnung der Federn, die dann unbefiederte Körperteile bedecken, ebenfalls zu einer energiesparenden Wärmeregulierung bei.

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