CIRCADIAN METABOLIC RESPONSES TO FOOD DEPRIVATION IN THE BLACK-SHOULDERED KITE[1]

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Abstract. Circadian metabolic responses to food deprivation were measured in Black-shouldered Kites (*Elanus caeruleus*) at thermoneutral and cold ambient temperatures. The basal metabolic rate (BMR) of the kites was 60–70% of that predicted by various allometric equations. They displayed marked circadian rhythms of BMR and body temperature (T_b), but did not show any indication of metabolic depression or adaptive hypothermia in response to food deprivation. Instead, moderate reductions in metabolic rate and T_b were observed, resulting in significant reductions in the daily energy expenditure. The conservative metabolic traits shown by the kites and their responses to food deprivation suggest tolerance of periodic, limited food supplies.

Key words: Black-shouldered kites, circadian rhythms, Elanus caeruleus, *food deprivation, metabolic depression.*

The amplitude of body temperature (T_b) cycles in endotherms scales allometrically with body mass (Aschoff 1982, Prinzinger et al. 1991). Endotherms respond to starvation or a reduction in food supply by decreasing their metabolic rate (MR) and T_b (Prinzinger et al. 1991, Withers 1992). In birds, this typically occurs by means of rest-phase (ρ) metabolic depression, resulting in an increase in the amplitudes of circadian cycles of MR and T_b (Reinertsen 1983, Prinzinger et al. 1991). Rashotte et al. (1995) showed that in pigeons an ad libitum food supply was associated with circadian cycles of relatively small amplitude (normothermia), whereas a restricted diet generated higher amplitudes mainly due to nocturnal hypothermia and hypometabolism. For raptors, similar data on metabolic responses to food deprivation are limited and are restricted to a few Holarctic species (Chaplin et al. 1984, Hohtola et al. 1994).

We investigated the metabolic responses to food deprivation of a common, small Afrotropical raptor, the Black-shouldered Kite (*Elanus caeruleus*), which occurs in southern Europe and throughout sub-Saharan Africa and tropical Asia (Maclean 1985). Black-shouldered Kites occur in a wide range of habitats, including grassland, farmland, savannah, and semi-arid scrub (Maclean 1985). In southern Africa, Black-shouldered Kites encounter large-scale temporal and spatial fluctuations in rodent populations, which constitute the majority of their diet (Mendelsohn 1982, Slotow 1987). Because of this unpredictable food supply, we

hypothesized that Black-shouldered Kites in southern Africa should show metabolic traits which are indicative of energy conservation. We tested the prediction that, to conserve energy in response to short-term food shortages, kites increase the amplitude of circadian cycles of MR and T_b primarily by lowering the rest-phase MR and T_b rather than the active-phase MR and T_b.

METHODS

Four kites were used in this study. Two adult kites were trapped near Pietersburg, South Africa, during April 1996 using Bal-chatri raptor traps baited with mice. The birds were initially kept on arched perches outdoors (Mendelsohn 1981) under shade cloth during the day and indoors at night, using falconry jesses and leashes. In early May, they were transferred to outdoor aviaries where they were housed for the remainder of their time in captivity. Each bird was maintained in a separate aviary (3 × 1 × 2.5 m). In mid-May, a further two captive-bred sub-adults were obtained from a breeder near Pietersburg and housed in the same aviaries. The birds were acclimatized to natural conditions of temperature and photoperiod, and were fed day-old chicks and mice. All the birds were weighed every second day prior to feeding. A control diet of 1–2 chicks or mice per day was continued until the commencement of food deprivation experiments. Water was available in the aviaries ad libitum, although the kites were not observed to drink. In August at the end of the study, the two wild-caught birds were released into the wild at their site of capture, whereas the captive-bred birds were transferred to the Centre for the Rehabilitation of Wildlife, Durban, for rehabilitation and possible release.

MEASUREMENT OF T_b

Body temperature was measured using temperature-sensitive telemeters (Model XM, Mini-mitter Co., Sunriver, Oregon), calibrated and implanted as described in Boix-Hinzen and Lovegrove (1998).

METABOLIC MEASUREMENTS

Metabolic rate was measured indirectly as oxygen consumption ($\dot{V}O_2$). All metabolic measurements were made in 17.5 dm³ respirometers (35 × 20 × 25 cm) constructed from clear Plexiglas. The respirometers were placed in a 1 m³ sound-proof constant environment cabinet. The experimental photoperiod was matched to that of the natural photoperiod prevailing at the time. Measurements of $\dot{V}O_2$ were made using an open flow-through system as described in Boix-Hinzen and Lovegrove (1998). Flow rates of approximately 1.2 L min^{-1} were used, so as to maintain <1% oxygen depletion between the incurrent and excurrent air.

EXPERIMENTAL PROTOCOL

For the determination of the lower critical limit of thermoneutrality (T_{lc}), the birds were placed in respirometers at approximately 16:15 and measurements commenced at 16:30, approximately 1.5 hr before the commencement of the experimental scotophase (dark phase). Data analysis was restricted to the ρ phase. At each ambient temperature (5, 15, 25, 32, 34, 36, and 38°C), resting metabolic rate was calculated as the mean of the three lowest consecutive data points during the last 30 min of a 2-hr period at each temperature. Linear regressions of RMR as a function of T_a at $T_a < 32°C$ were calculated for each bird using the method of least-squares-fit. Individual T_{lc}s were calculated as the intercept of regression line of $\dot{V}O_2$ as a function of T_a with the mean BMR calculated from the lowest RMR values at T_as $> 32°C$. During all subsequent trials, the T_a in the cabinet was maintained at the mean T_{lc} (31.0 ± 6.6°C), or at $T_a = 10°C$ during the trials involving the effects of lower ambient temperatures.

Oxygen consumption and T_b were measured at 5-min intervals for 24 hr in fed birds, and the BMR, daily energy expenditure (DEE), and the maximum amplitude of the circadian T_b rhythm (R_t) calculated. The latter was calculated as the difference between the maximum T_b during the active phase (αT_bmax) and the minimum during the rest phase (ρT_bmin), hence $R_t = \alpha T_b$max $- \rho T_b$min. The effects of food deprivation at $T_a = 31°C$ were investigated by feeding the birds one chick or mouse every second day, representing a reduction of 75% of their food intake. Oxygen consumption and T_b were measured every second day. For each trial the birds were weighed and placed in the respirometers at about 10:30. Measurements commenced at 12:00, allowing the birds at least 1 hr to acclimate. Measurements were made for 24 hr, after which the birds were removed, returned to their aviaries, and immediately fed.

On termination of the food deprivation trials at 31°C, the birds were fed ad libitum in the aviaries until their masses returned to the pre-food deprivation values. Thereafter they were fed the maintenance diet for four days. They were then placed in the respirometers at an T_a of 10°C for one circadian cycle, and measurements were made as described above to assess the effect of mild cold load. They were then returned to the aviaries and starved for three days before another circadian trial at 10°C was undertaken to investigate responses to the combined effects of food deprivation and cold load. This trial was undertaken to assess the kites' response to more severe energetic stress than that encountered during the food-deprivation trials at thermoneutrality at 31°C.

DATA ANALYSIS

For each physiological variable displaying circadian rhythms, four stages are apparent: plateau α and ρ phases, as well as two transitional phases between the α and ρ plateau phases involving either an increase or decrease in the parameter concerned. For statistical purposes, ρ was taken as the time period occurring between the lower points of inflexion (Yeager and Ultsch 1989) of the transition phases, whereas α was taken as the time period occurring between the upper points of inflexion of the transition phases. Values within the transitional phase were thus ignored, except when daily energy expenditure was calculated. Mean values were calculated between points of inflexion because transition periods did not correspond exactly with lights-on and lights-off periods. Maximum and minimum values within α and ρ were calculated as the mean of the three highest and lowest consecutive data points within the calculated transition inflexion points, respectively. The BMR of each individual was calculated as the mean of the three lowest consecutive ρ-phase values.

A conversion factor of 20.083 kJ L^{-1} O_2 was used to convert O_2 to energy expenditures (Withers 1992). Mass-specific energy expenditures were calculated by integrating at 5-min intervals mass-specific O_2 data. To partly overcome the statistical problems associated with a small sample size, we used nonparametric resampling statistics to compare means, following Simon (1995). This method yields a statistic, Z, which is equivalent to the significance level of the test.

RESULTS

BODY MASS

The body mass of control (nonstarved) birds during the trial at 31°C before the commencement of the food deprivation was 242.5 ± 7.6 g. During the final food deprivation trial after 8 days of restricted feeding, the M_b was 195.0 ± 12.3 g, representing a significant mean decrease of 19.6 ± 3.4% from the initial trial ($Z = 0.02$; Fig. 1). During the trial involving fed birds at 10°C, the M_b was 239.8 ± 8.5 g, which was not significantly different from that of the trial at the start of the food deprivation trials at thermoneutrality ($Z = 0.32$). During the trial involving both cold load and food deprivation, M_b decreased to 195.3 ± 9.3 g, which was significantly lower than that during the trial involving fed birds ($Z = 0.01$). This decrease represented a mean body mass loss of 18.6 ± 2.6%. The body masses of the starved birds during the 10°C and 31°C trials were not significantly different ($Z = 0.91$).

BODY TEMPERATURE

The birds showed clear circadian patterns of T_b (Fig. 2). The mean T_b during the initial circadian trial with fed birds at 31°C was 40.1 ± 0.2°C, whereas the mean αT_b and mean ρT_b were 41.1 ± 0.3°C and 39.1 ± 0.1°C, respectively (Table 1). The mean R_t was 3.4 ± 0.4°C. Differences between fed and food-deprived birds were significant in the case of mean T_b ($Z = 0.03$), mean αT_b ($Z = 0.04$), and ρT_bmin ($Z = 0.01$, Table 1). The rates of decrease of the various T_b variables were similar (Fig. 1), and as a result there was no change in R_t during the 8-day food-deprivation period.

There were significant decreases in mean T_b ($Z = 0.01$), mean αT_b ($Z = 0.01$), mean ρT_b ($Z = 0.01$), and ρT_bmin ($Z = 0.02$) between fed and starved birds at 10°C (Table 1).

OXYGEN CONSUMPTION

Like T_b, $\dot{V}O_2$ showed marked circadian fluctuations (Fig. 2). The BMR of control birds at 31°C was 0.6 ± 0.1 ml O_2 g^{-1} hr^{-1} (Table 1). A significant decrease in BMR occurred in starved birds after eight days ($Z =$
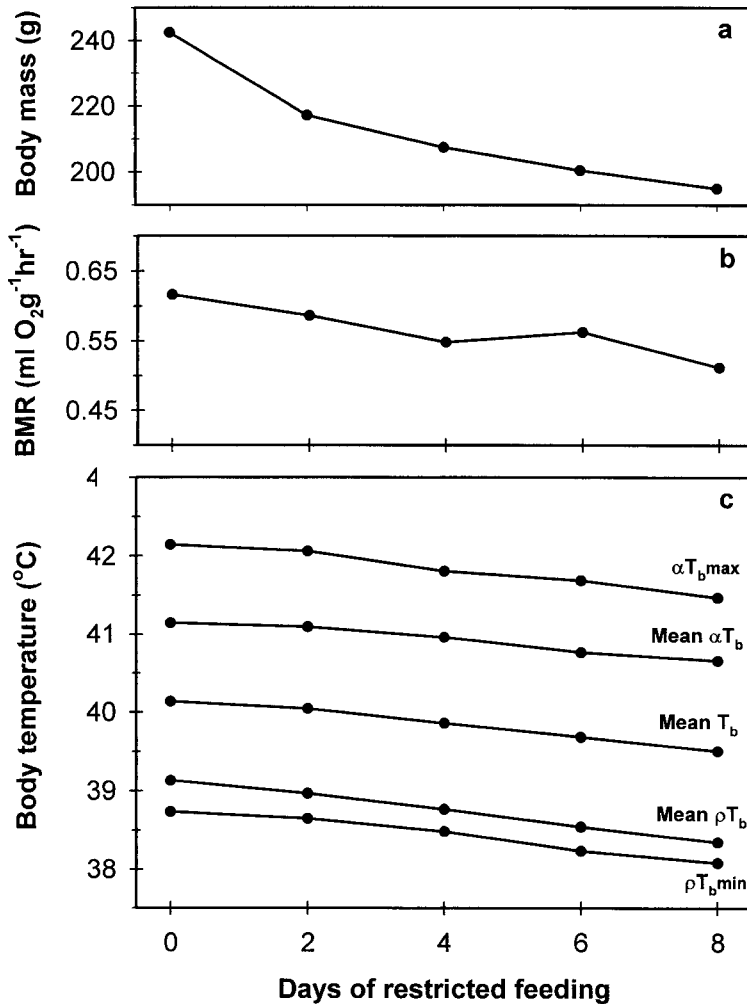
FIGURE 1. Loss of body mass (a), gradual decreases in body temperature (b) and basal metabolic rate (c) of four Black-shouldered Kites (*Elanus caeruleus*) fed 25% of maintenance diet. Data measured at thermoneutrality ($T_a = 31°C$).

0.02, Table 1). The RMR of control birds at 10°C was 1.1 ± 0.0 ml O_2 g^{-1} hr^{-1}, which represented 186.6 ± 45.3% of the BMR at 31°C and a significant increase ($Z = 0.01$, Table 1). No significant decrease in RMR occurred when the birds were deprived of food at 10°C ($Z = 0.10$, Table 1). The circadian amplitude of O_2 (R_{VO2}) at 31°C was 1.4 ± 0.5 ml O_2 g^{-1} hr^{-1} in fed birds and did not change significantly in starved birds ($Z = 0.17$, Table 1). The R_{VO2} of control birds at 10°C was similar to that of starved birds at the same temperature ($Z = 0.18$).

CIRCADIAN PATTERNS OF ENERGY EXPENDITURE

The daily energy expenditure (DEE) was calculated simply as the total energy consumption over a 24-hr period within the respirometers. The DEE of starved birds at 31°C decreased significantly ($Z = 0.05$) by

18.2 ± 16.1% below that of control birds. Rest-phase (ρ) energy expenditure also showed a significant decrease ($Z = 0.02$, Table 1).

At 10°C, the DEE of starved birds was significantly lower than that of control birds ($Z = 0.08$, Table 1). The energy expenditure of starved birds was significantly lower than that of control birds during ρ ($Z = 0.04$). The decreases in DEE in response to food deprivation at 31°C were not significantly different from the decreases that occurred when the birds were starved at 10°C ($Z = 0.91$). The same was true for ρ energy expenditure ($Z = 0.09$).

DISCUSSION

BODY TEMPERATURE

The mean $ρT_b$ of nonstarved *E. caeruleus* was similar to Prinzinger et al.'s (1991) mean for Falconiformes
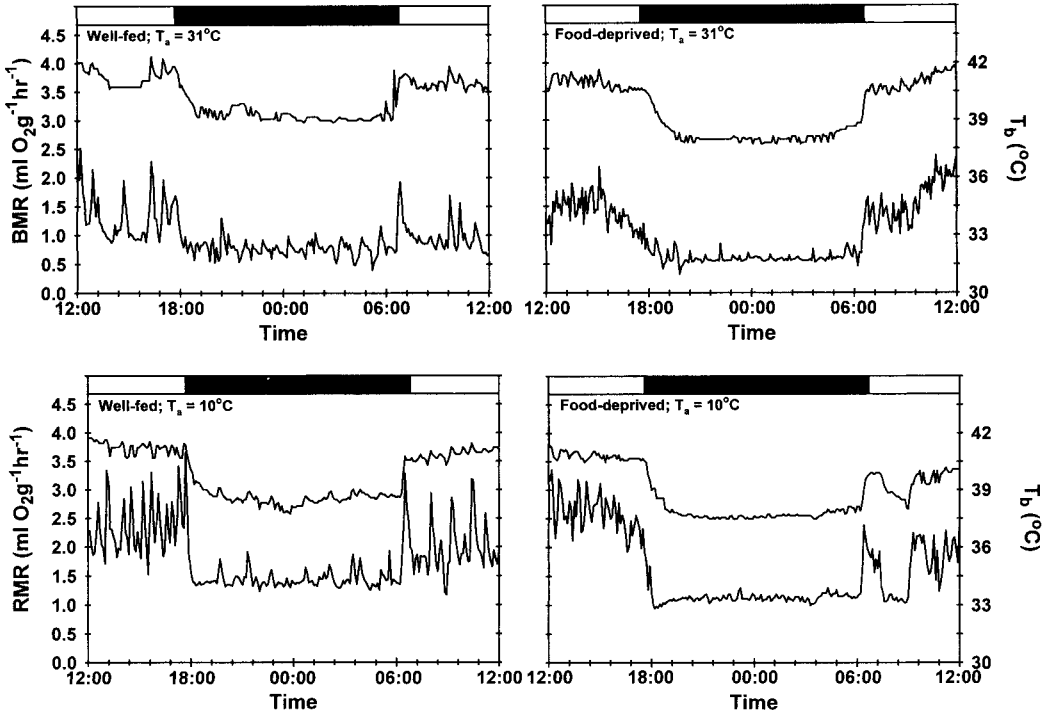
FIGURE 2.   24-hr plots of body temperature (upper lines) and oxygen consumption (lower lines) of a fed (left graphs) and starved (right graphs) Black-shouldered Kite (*Elanus caeruleus*) at T_a = 31°C (top graphs) and T_a = 10°C (bottom graphs).

TABLE 1.   Changes in body temperature (°C), oxygen consumption (ml O_2 g^{-1} hr^{-1}), and energy expenditure (kJ kg^{-1} day^{-1}) associated with food deprivation and weight loss in Black-shouldered Kites.

	31°C		10°C	
	Fed	Starved	Fed	Starved
Mass loss (%)		19.6 ± 3.4*		18.6 ± 2.9*
Mean T_b	40.1 ± 0.2	39.5 ± 0.1*	40.0 ± 0.2	39.1 ± 0.2**
Mean αT_b	41.1 ± 0.3	40.7 ± 0.4*	41.1 ± 0.3	40.3 ± 0.2**
Mean ρT_b	39.1 ± 0.1	38.4 ± 0.3*	38.8 ± 0.3	37.9 ± 0.2**
αT_bmax	42.2 ± 0.2	41.5 ± 0.7	41.8 ± 0.3	41.7 ± 0.6
ρT_bmin	38.7 ± 0.2	38.1 ± 0.3**	38.2 ± 0.3	37.6 ± 0.1*
R_t^a	3.4 ± 0.4	3.4 ± 1.0	3.7 ± 0.4	4.1 ± 0.6
BMR	0.62 ± 0.08	0.51 ± 0.02*		
RMR			1.13 ± 0.02	1.00 ± 0.02
$\alpha \dot{V}O_2$max	1.99 ± 0.52	1.57 ± 0.52	2.98 ± 0.29	3.07 ± 0.09
Mean $\alpha \dot{V}O_2$	1.17 ± 0.08	1.06 ± 0.32	2.002 ± 0.17	1.93 ± 0.22*
$\alpha \dot{V}_2$min	0.70 ± 0.05	0.62 ± 0.14	1.35 ± 0.19	1.19 ± 0.12
$\rho \dot{V}O_2$max	0.97 ± 0.11	0.75 ± 0.06*	1.88 ± 0.11	1.42 ± 0.25*
Mean $\rho \dot{V}O_2$	0.76 ± 0.02	0.60 ± 0.01	1.34 ± 0.11	1.13 ± 0.02*
$R_{VO_2}^b$	1.38 ± 0.54	1.06 ± 0.53*	1.86 ± 0.27	2.08 ± 0.10
DEE^c	460.7 ± 24.4	376.9 ± 60.7*	806.1 ± 68.7	728.9 ± 53.0*
αEE	261.4 ± 19.3	237.6 ± 72.0	461.4 ± 44.9	436.1 ± 54.4
ρEE	199.3 ± 6.1	156.3 ± 2.4*	344.7 ± 26.6	292.9 ± 4.2*

^{a} R_t = αT_bmax − ρT_bmin.
^{b} R_{VO2} = $\alpha \dot{V}O_2$max − $\rho \dot{V}O_2$min, where $\rho \dot{V}O_2$min = BMR and RMR at T_a = 31°C and 10°C, respectively.
^{c} DEE = total energy expenditure during a 24-hr cycle.
Significance levels: *P ≤ 0.05, **P ≤ 0.01 for comparisons of fed versus starved birds.

($39.0 \pm 0.9°C$), whereas the mean αT_b was $1.14°C$ higher than the mean α value for Falconiformes.

The amplitude of circadian cycles of T_b was considerably higher than predicted, being on average 276% of the values calculated from Aschoff's (1982) equation for nonpasserines. This high R_t value was generated by low rest-phase body temperatures, and alludes to a low BMR and the decreased energy expenditure discussed below.

Lovegrove and Heldmaier (1994) have argued that a large R_t may be indicative of energy conservation during the rest phase, for example by a depressed BMR, and is likely to be highly adaptive in regions in which resource availability is temporally and spatially unpredictable.

METABOLIC RATE

The BMRs of the kites under conditions of ad libitum food supply were $61.2 \pm 7.6\%$ of the BMRs predicted by Lasiewski and Dawson's (1967) allometric equation relating BMR to M_b in nonpasserine species, and $77.3 \pm 9.6\%$ of the RMRs predicted by Bennett and Harvey's (1987) equation. Perhaps more significantly, however, the BMRs of the kites were on average $71.7 \pm 8.9\%$ of the values predicted by Wasser's (1986) equation for 11 species of Northern Hemisphere Falconiformes. The low BMR and high R_t values shown by the birds in our study translate into the rest-phase energy savings discussed previously and suggest strong selection for energy conservation. It seems reasonable to suggest, therefore, that some aspect of the kites' habitat has selected for low BMRs and consequent reduced energy requirements. Because the birds used in this study showed metabolic traits which are likely to be adaptive in areas where resource availability is temporally and spatially unpredictable, a possible candidate for such a selective force is climatic variability. A major cause of climatic variability at Pietersburg, where the birds were trapped, and indeed over much of sub-Saharan Africa, is the El Niño Southern Oscillation (ENSO) phenomenon (Tyson 1986, Philander 1990, Stone et al. 1996). ENSO events are associated with huge population fluctuations in marine, aquatic, and terrestrial environments (Glynn 1990, Meserve et al. 1995). In sub-Saharan Africa, as well as in Australasia and Indomalaya, ENSO events generally increase rainfall variability in mesic areas (Stone et al. 1996), and hence may select for metabolic traits typical of species permanently resident in xeric areas where food supplies show a high degree of spatial and temporal unpredictability (Noy-Meir 1973).

RESPONSES TO FOOD DEPRIVATION

The results of the food deprivation trials show that whereas a slight decrease in mean T_b did occur, this involved decreases in both αT_b and ρT_b, rather than an increase in R_t generated by our predicted depression of rest phase T_b. There was no indication of controlled hypothermia as previously defined and discussed by Prinzinger et al. (1991). A slight decrease in T_b as observed in our birds under conditions of food scarcity is typical of most mammals and birds (Prinzinger et al. 1991).

Our data are consistent with those of Shapiro and Weathers (1981) who investigated metabolic responses of American Kestrels (*Falco sparverius*) to short-term (79 hr) food deprivation at $27°C$. Individual kestrels decreased ρT_b by $0.2–0.4°C$ per day of fasting from $39.3°C$ to $38.3°C$. In our study, *E. caeruleus* decreased ρT_b by ca. $0.1°C$ day^{-1} on a restricted diet.

Although a decreased BMR associated with food deprivation at $T_a = 31°C$ was consistent with our initial prediction, the decreased amplitude of circadian $\dot{V}O_2$ cycles was unexpected. The reduced amplitude was generated by a greater decrease in $\alpha \dot{V}O_2$max (22.3%, Table 1) than that of the BMR (16.9%, Table 1). Although RMR did not decrease when the birds were food-deprived at $T_a = 10°C$, significant reductions in circadian energy expenditure occurred at both ambient temperatures. Thus, under the experimental conditions of this study, food deprivation tended to cause general reductions in metabolism, manifested as significant decreases in DEE. The decrease in BMR at $T_a = 31°C$ was similar to that observed in American Kestrels by Shapiro and Weathers (1981). Although this decrease in BMR was an acute, proximate response under laboratory conditions, such a response is likely to be adaptive for kites under natural conditions because it decreases the energy requirements of food-stressed birds.

A switch from carbohydrate or mixed-fuel metabolism to fat metabolism during food deprivation should slightly overestimate BMR in starved birds, because fat supplies 19.7 kJ L^{-1} O_2 compared, for example, with 20.9 kJ L^{-1} O_2 for carbohydrate (Withers 1992). Although mass loss does not necessarily reflect fat loss alone, this is apparently the case in Tengmalm's Owl *Aegolius funereus* (Hohtola et al. 1994). If we assume that the weight loss displayed by the kites during food deprivation is indicative of fat metabolism, then the maximum possible increase in BMR (ca. 6%) would have occurred if metabolism shifted from that of pure carbohydrate to pure fat metabolism. In other words, to meet the same basal energy demands, oxygen consumption would have increased if fat was the sole metabolic fuel, suggesting that observed BMR values of starved birds could be maximally overestimated by ca. 6% in food-deprived birds. Although this strengthens the conclusion that a significant reduction occurs in BMR at $31°C$, the subtraction of 6% from the RMR values of starved birds at $10°C$ does not change the conclusion that there was no significant reduction in RMR between fed and food-deprived birds.

One major observation of this study was that Black-shouldered Kites do not appear to employ controlled hypothermia in response to energetic stresses. This is interesting in light of the hypothermia which many diurnal raptors exhibit (Heath 1962, Chaplin et al. 1984). The metabolic patterns of *E. caeruleus* were, however, similar to those of Tengmalm's Owl (Hohtola et al. 1994). These latter authors suggested two factors accounting for the lack of hypothermia in this species. Firstly, the efficient conversion of digested food into fat deposits may increase tolerance to food deprivation, as discussed by Cherel and Le Maho (1985). No assessment of fat deposits in *E. caeruleus* was attempted, but it was observed that the birds were capable of large increases in M_b if fed ad libitum (M_bs of up to 306 g were recorded). If we reasonably assume that these

changes in body mass involved changes in fat mass rather than lean body mass, then Black-shouldered Kites seem to be adapted to food deprivation (sensu Cherel and Le Maho 1985).

Secondly, dependence on metabolic water may preclude the use of hypothermia and concomitant hypothermia. Like *A. funereus*, kites do not drink in the wild, and although water was available to the birds in our study, they were not observed to drink. Consequently, starved kites are dependent on metabolic water, and the lack of hypothermia may arise from the need to avoid dehydration.

Another possible explanation for the lack of hypothermia and hypometabolism may concern the low BMR of *E. caeruleus*. Whereas the high BMRs of raptors such as *A. funereus* are antagonistic to fasting endurance (Hohtola et al. 1994), the low BMR of *E. caeruleus* offers opportunities for significant savings in energy expenditure. It would appear that periods of limited food availability have selected for low BMRs together with high R_t values in this species. Such tolerance to food deprivation seems to have been selected for to the extent that the birds involved in this study did not need to utilize hypometabolism in response to the levels of energetic stress to which they were exposed.

Finally, the energetic costs and time required for arousal from hypothermia increase exponentially with M_b (Withers 1992). In *E. caeruleus*, hypothermia and hypometabolism would incur energy costs associated with arousal far greater than in smaller species, limiting possible energy savings and hence the adaptive value of these physiological mechanisms.

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HEAT PRODUCTION AND EVAPORATIVE WATER LOSS OF DUNE LARKS FROM THE NAMIB DESERT[1]

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Abstract. Dune Larks *Miafra erythrocephalus* are the only permanent residents living in the Namib Sand Sea, one of the driest regions on earth. For Dune Larks with an average body mass of 27.3 ± 1.8 g ($n = 12$), basal metabolic rate (BMR) equaled 36.0 kJ day^{-1}, a value near allometric predictions. Hence, I found no evidence that these birds have a reduced BMR. I suggest that because they live in a relatively cool environment in winter, which mandates significant metabolic machinery for thermogenesis, larks have an elevated BMR at this time. Below 30°C, total evaporative water loss (TEWL) varied little with ambient temperature (T_a), and averaged 66.0 mg H_2O hr^{-1}, or 1.58 g day^{-1}. The latter value was 21–44% lower than allometric predictions, supporting the idea that larks have a reduced TEWL, attributable, perhaps, to reduced cutaneous water loss. Metabolic water production may play a significant role in the water economy of larks in view of the fact that evaporative water losses are replaced at T_as below 17.0°C.

Key words: avian energetics, basal metabolic rate, Dune Lark, desert, evaporative water loss, heat transfer coefficient, Miafra erythrocephalus, Namib.

The Namib sand sea, a 34,000 km^2 expanse of sand dunes situated along the southwestern coast of Africa, is among the driest regions in the world (Logan 1960, Teller and Lancaster 1985). Because of its proximity to the ocean and the cool Bengula current, ambient air temperatures (T_a) can be relatively cool across this region, especially in winter when T_as often drop to <10°C at night (Lancaster et al. 1984). In contrast to

many other deserts, maximum T_as rarely exceed 40°C. Among desert ecosystems where annual net primary production typically varies from 15–200 g dry mass m^{-2} (Hadley 1979), the Namib sand sea has the lowest net primary production so far recorded, 5.7 g dry mass m^{-2} (Seely and Louw 1980). Because this desert is geologically older than many others (Axelrod 1950, Schwarzback 1961), one might expect inhabitants to possess finely tuned behavioral and physiological adaptations that permit a desert existence. Several bird species frequent the Namib, but only one species has evolved the capacity to reside year-round in the Namib sand sea, the Dune Lark (*Miafra erythrocephalus*) (Willoughby 1971, Boyer 1988, Williams 1992).

Although the physiological prowess of small mammals that have evolved in deserts to minimize energy expenditure and rates of water loss is well known (Schmidt-Nielsen and Schmidt-Nielsen 1950, Schmidt-Nielsen 1964, MacMillen 1983), attempts to elucidate similar physiological attributes among species of arid-adapted birds have proven less fruitful. Reviewing nearly a decade of work, Bartholomew and Cade (1963) concluded that many avian species found in deserts do not possess unique physiological adaptations compared with their nondesert counterparts. These authors lamented the paucity of data on Old World desert species and suggested that these populations might be expected to show more conspicuous physiological adaptations to arid conditions than their ecological equivalents in the New World. The perception that birds inhabiting deserts are able to do so because of a suite of avian design characteristics possessed by all birds, rather than as a consequence of specific adaptation(s) to the desert environment, persists in the literature (Maclean 1996).

Several reports have appeared since the work of