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## ENERGY REQUIREMENTS OF ADULT CAPE VULTURES (*Gyps coprotheres*)

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**ABSTRACT.**—Outdoor feeding trials were used to determine gross energy intake, energy assimilation efficiency and metabolizable energy intake of captive adult Cape Vultures (*Gyps coprotheres*). The mean ash-free dry energy density of daily pooled samples of feces and urine was  $14.0 \pm 0.2$  kJ/g. A consistently high mean energy assimilation efficiency of  $86.2 \pm 2.7\%$  caused daily energy content of excreta to fluctuate according to the quantity of energy assimilated. Mean gross energy intake was  $2926.8 \pm 349.1$  kJ/day and mean metabolizable energy intake was  $2552.9 \pm 300.9$  kJ/day for birds with changes in body mass of 2% or less between start and end of feeding trials. The daily energy expenditure of a free-living adult, weighing 8.3 kg, was estimated to be 3006 kJ/day ( $DEE = 826.7$  kJ/day  $\times$  kg<sup>0.61</sup>).

### Requerimientos de energía del buitres de la especie *Gyps coprotheres*

**EXTRACTO.**—Experimentos de alimentación al aire libre, con buitres de la especie *Gyps coprotheres* en cautividad, fueron realizados para determinar: la cantidad total de energía ingerida en el alimento; la eficiencia en la asimilación de esa energía; y la cantidad de energía ingerida y disponible para el metabolismo. La media de la energía, libre de carbón de todas las muestras diarias de la combinación de heces y orina, fue de  $14.0 \pm 0.2$  kJ/g. La media de la eficiencia de asimilación de energía, que fue consistentemente alta:  $86.2 \pm 2.7\%$ , causó que el contenido de energía excretada por día fluctuara de acuerdo con la cantidad de energía asimilada. La media de la energía total ingerida fue  $2926.8 \pm 349.1$  kJ/día; y la media de la energía ingerida y disponible para el metabolismo fue  $2552.9 \pm 300.9$  kJ/día, para aves con cambios en la masa corporal de 2% ó menos, entre el comienzo y el fin del experimento. El gasto diario de energía de un adulto que vive en libertad, y que pesa 8.3 kg, se estimó en 3006 kJ/día ( $GDE = 826.7$  kJ/día  $\times$  kg<sup>0.61</sup>).

[Traducción de Eudoxio Paredes-Ruiz]

Vultures include some of the heaviest raptorial birds, yet constitute a poorly studied group in bioenergetics research (Komen 1991). Intrinsically difficult to study in the field, bioenergetic research of vultures has only been done under captive conditions, and has mostly been limited to measurements of gross food intake for a few vulture species (Jarvis et al. 1974, Hiraldo 1976, 1983, Houston 1976, Mendelsohn and Leshem 1983, Komen 1991).

Like their congeners elsewhere, Cape Vultures (*Gyps coprotheres*) are scavengers of ungulate carcasses, and, in rural areas which no longer support wild ungulate herds, scavenge domestic livestock (Mundy 1982, Robertson and Boshoff 1986). Foraging success of adult Cape Vultures is dictated by unpredictable food resources and climatic conditions (Boshoff et al. 1984,

Robertson and Boshoff 1986), and, while rearing nestlings, vultures may only forage once every two days (Komen 1991). If we assume that the maximum food intake of Cape Vultures is dictated by stomach and crop capacity (Komen 1986), measurements of daily metabolizable energy intake for existence, and estimates of daily energy expenditure in this study, provide an indication of energetic constraints on these large raptorial birds while breeding.

### METHODS

Ten adult Cape Vultures were maintained in captivity at the De Wildt Raptor Research Centre (25°41'S 27°56'E), Transvaal, South Africa. For the purpose of this study an "adult" vulture is defined as a full-grown vulture which is one year old or older, and falls within the normal range of adult body mass and standard wing-length (Mundy 1982, Komen 1986).

Table 1. Water, lipid, protein, ash and carbohydrate content, and energy density in kJ/g (Ash-free dry (AFD) and wet) of different meat types consumed by adult Cape Vultures during three feeding trial periods.

TRIAL PERIOD AND FOOD- TYPE	PERCENT					ENERGY DENSITY	
	WA- TER	LIP- ID	PRO- TEIN	ASH	CAR- BOHY- DRATE	kJ/g AFD	kJ/g Wet
1 (Horse)	71.2	1.7	22.0	3.4	1.8	25.1	6.4
2 (Cow 1)	72.5	2.4	21.7	2.8	0.6	27.0	6.7
3 (Cow 2)	69.7	1.9	19.2	8.7	0.5	26.0	5.6
Mean	71.1	2.0	21.0	5.0	1.0	26.0	6.2
±SE	1.4	0.4	1.5	3.3	0.7	1.0	0.6
CV <sup>1</sup>	2.0	20.0	7.1	66.0	70.0	3.9	9.7

<sup>1</sup> CV = Coefficient of variation.

Of the ten vultures, three, five, and seven vultures were used in three feeding trial sessions, for a total of 15 feeding trials, with some of the vultures used in more than one trial. Trial vultures were removed from their flight aviary, weighed and placed in trial-cages on the same day at the start of the acclimation period of a particular feeding trial session. During these outdoor feeding trials, the vultures were maintained separately in visually-isolated cages (2 × 1.5 × 1 m), large enough to allow the birds to turn around and extend their wings fully. Each cage had a wire-mesh floor under which a removeable plastic-lined tray was placed to facilitate the collection of excreta. During the feeding trials, monthly minimum temperatures ranged between 3–8°C during June through September (trial sessions 1 and 2) and 14–17°C during October and November (trial session 3). Maximum monthly temperatures were 21–25°C during July through September and 26–33°C during October and November. Ambient temperature did not appear to have an effect on food intake (see results).

Energy requirements for maintenance (gross energy intake and metabolizable energy) were determined by the food consumption method (Gessaman 1973). Each vulture was allowed to acclimatize for a few days preceding the trial. During this acclimation period the birds were fed to satiation and provided free drinking water. Depending on how quickly each individual settled down behaviorally (e.g., cessation of restlessness and acceptance of hand-fed meat), a vulture's pre-feeding starvation period would be initiated. This period lasted between 2–4 d to ensure a post-absorptive state. Food was first offered on the morning when the most recently voided excreta no longer had a visible black fecal fraction; this suggested that all meat last consumed (from two to four days previously) had been assimilated and excreted. At this stage of starvation the white urinary fraction had a green tinge in most individuals.

On the first day of feeding birds mostly ate to satiation (in excess of 1.0 kg meat). Thereafter food intake decreased to almost negligible amounts after 4–5 d of feeding (pers. observations). Accordingly, the number of days on which food

was offered was dictated by individual demand; a feeding trial was ended when a bird no longer demanded food.

To measure existence metabolism which requires the maintenance of "constant" body mass (i.e., 2% or less change in body mass between the start and end of a trial), feeding trials included post-feeding starvation periods lasting as long as 5 d, depending on the body mass of a bird on the morning after the day of last feeding. The 15 trials (including pre- and post-feeding starvation periods) therefore lasted between 12 and 18 d, with periods of actual feeding ranging from 6–11 d.

Each bird was weighed at least four times during a feeding trial: prior to the pre-feeding starvation period, prior to the feeding period, after the feeding period, and at the end of the post-feeding starvation period. Water was not offered at any stage of the feeding trial. The vultures were fed lean cow or horse meat obtained from livestock carcasses. Their diet was supplemented with a mineral-vitamin mixture (Beefee, Centaur Co., Johannesburg, South Africa). Three different types of meat were used in the trials. Meat was deep frozen in labeled plastic bags, and on the evening prior to the next morning's feeding bags were removed and defrosted. Care was taken to give all trial birds the same type of meat on a given day of feeding. The same three types of meat were available for all three feeding trial sessions. On feeding days, each bird was fed once by hand to satiation, and food intake was determined by weighing meat before feeding and leftovers immediately after feeding. Spilled food and regurgitations were collected whenever these occurred. Regurgitations were oven-dried at 60°C to constant mass. The dry mass of a regurgitation was subtracted from the calculated dry mass of food consumed on the same day the regurgitation occurred.

Five samples (100 g each) of each meat type (Table 1) used for a feeding trial were taken for analyses. Each sample was oven-dried at 60°C to constant mass. Water loss was calculated by subtraction, and mean water content calculated for the five samples. The dried samples were pooled, ground to a powder and analysed for energy density (Gallenkamp ballistic bomb calorimeter) and inorganic content by ashing (see Komen 1986, 1991 for details). Metabolizable energy and assimilation efficiency of birds in any one trial period were calculated using the mean composition data for all meat types consumed during that trial. The mean "wet" energy density of all meat types consumed was 6.2 kJ/g (SE ± 0.6 kJ/g, range 5.6–6.7 kJ/g; Table 1).

All feces and urine (hereafter referred to as excreta) were collected from each bird twice daily, for each day after the initiation of feeding until the end of post-feeding starvation period (i.e., when a black fecal fraction was no longer present in excreta) and pooled. These daily quantities of excreta from each bird were oven-dried at 60°C to constant mass and weighed separately. They were then analysed for energy density and inorganic content (see Komen 1986 for details). To determine assimilation efficiency the daily excreta weights were pooled for each trial. Twenty-three day-samples were randomly selected from all individual day-samples (N = 186) collected during the three feeding trial sessions and analysed for energy density (kJ/g ash-free dry mass) and ash content.

The efficiency with which birds assimilate energy was determined following Gessaman (1973):

$$ME = GEI - (F + U)$$

Table 2. Changes in body mass during 15 feeding trials of 10 Cape Vultures (A–J), showing percentage change between the pre-feeding and post-trial body masses.

TRIAL PERIOD AND BIRD	DURATION OF TRIAL <sup>1</sup> IN DAYS	BODY MASS (g)						% CHANGE (B – A)/ A•100
		PRE-TRIAL	PRE- FEEDING (A)	POST- FEEDING	POST-TRIAL (B)	MEAN	±SE	
1 A	15 (12)	9150.0	8800.0	9220.0	8840.0	9002.5	184.7	0.5
B	17 (14)	9580.0	9200.0	10 080.0	9445.0	9576.3	321.2	2.7
C	14 (11)	9600.0	9250.0	9455.0	9200.0	9376.3	160.7	0.5
2 D	17 (14)	7100.0	6720.0	7165.0	6785.0	6942.5	192.8	1.0
E	17 (14)	7620.0	7220.0	7615.0	7225.0	7420.0	197.5	0.1
F	12 (9)	8050.0	7720.0	7715.0	7715.0	7800.0	144.4	–0.1
G	13 (10)	8150.0	7770.0	7465.0	7465.0	7712.5	281.6	–3.9
B	18 (15)	9070.0	8670.0	10 665.0	9630.0	9508.8	749.6	11.1
3 D	15 (12)	7550.0	7170.0	7675.0	7140.0	7383.8	233.2	–0.4
E	17 (13)	7740.0	7370.0	8275.0	7640.0	7756.3	328.7	3.7
F	17 (13)	7445.0	7070.0	7975.0	7350.0	7460.0	327.7	4.0
G	17 (13)	6650.0	6270.0	7225.0	6585.0	6682.5	344.6	5.0
H	17 (13)	7575.0	7170.0	7975.0	7300.0	7505.0	308.2	1.8
I	14 (11)	6860.0	6470.0	7175.0	6550.0	6763.8	278.6	1.2
J	15 (12)	6825.0	6470.0	7275.0	6600.0	6792.5	306.2	2.0
Mean		7931.0	7556.0	8197.0	7698.0	7845.5		1.9
±SE		955.4	960.1	1084.9	1026.7	985.8		3.2

<sup>1</sup> First numeral represents duration of each trial, numeral in brackets represents number of days between pre-feeding and post-trial weighings.

where ME = metabolizable energy, GEI = gross energy content of food consumed, F = energy content of feces and U = energy content of urine; and assimilation efficiency (AE):

$$AE = 100 \times \{GEI \pm (F + U)\} / GEI[\%]$$

## RESULTS

The mean change in individual adults' pre-feeding and post-trial body masses was 1.9% (SE ± 3.2%, range 0.1–11.1%,  $N = 15$  trials) and the majority of birds gained body mass during the trials (Table 2). During 10 of the 15 trials, the vultures had body mass changes of about 3% or less, and of the remaining trials, only one bird had a marked decrease (–3.9%) in body mass, the rest ( $N = 4$ ) had body mass increases ranging between 3.7% and 11.1%. Mean pre-feeding body mass of all birds was 7556.0 g (SE ± 960.1 g, range 6270–9250 g) and mean post-trial body mass was 7698.0 g (SE ± 1026.7 g, range 6550–9630 g).

There was considerable variation in individual gross daily food intake (Table 3). Mean daily gross food intake was 479.2 g meat/day (SE ± 52.9 g meat/day, range 372.6–558.7 g meat/day), and represents 6.5% of body mass (SE ± 1.3%, range 4.0–8.4%; Table 3).

Gross energy content of the daily excreta of individual birds changed proportionally to the energy content of food consumed. The mean ash-free dry (AFD) energy density of daily excreta was 14.0 kJ/g AFD (SE ± 0.2 kJ/g AFD,  $N = 23$  individual daily samples analysed, range 13.9–14.1 kJ/g AFD). The mean inorganic content of these excreta samples was 7.1% (SE ± 0.2%,  $N = 23$ , range 6.9–7.2%).

There was no significant difference between mean gross energy intake of each trial session (ANOVA,  $F = 3.29$ ,  $df = 2, 12$ ,  $P > 0.05$ ), and the results for all three trial sessions were combined. Mean daily gross energy intake for all birds was 2926.8 kJ/day (SE ± 349.1 kJ/day,  $N = 15$  trials, range 2347.5–3743.3 kJ/day). Gross energy assimilation efficiency was consistently high at 86.2% (SE ± 2.7%, range 83.2–88.2%) and mean daily metabolizable energy was 2522.9 kJ/day (SE ± 300.9 kJ/day, range 2023.6–3226.7 kJ/day,  $N = 15$  trials).

Existence metabolism, which is equivalent to metabolisable energy providing the birds undergo body mass changes of about 2% or less between the start and end of a trial (*sensu* Gessaman 1973), was 2420.3 kJ/day (SE ± 93.2,  $N = 9$  trials).

Table 3. Gross food intake (g meat/day and % of pre-feeding body mass (BM)), and daily energy requirements (kJ/day, gross energy intake (GEI) and metabolizable energy (ME)) of ten captive adult Cape Vultures (A-J) calculated for the number of days between pre-feeding and post-trial weighings (see Table 2) during feeding trials.

TRIAL PERIOD AND BIRD	TOTAL MEAT	MEAT/ DAY	% OF BM	DAILY GEI kJ/day	DAILY ME <sup>1</sup> kJ/day
	CON- SUMED g				
1 A	5005.0	417.1	4.7	2669.4	2301.0
B	6735.0	481.1	5.2	3079.0	2654.1
C	4099.0	372.6	4.0	2384.6	2055.5
2 D	6965.0	497.5	7.4	3333.3	2873.3
E	5904.0	421.7	5.8	2825.4	2435.5
F	4145.0	460.6	6.0	3086.0	2660.1
G	4531.0	453.1	5.8	3035.8	2616.9
B	8380.0	558.7	6.4	3743.3	3226.7
3 D	5020.0	419.2	5.8	2347.5	2023.6
E	6615.0	508.8	6.9	2849.3	2456.1
F	7145.0	549.6	7.8	3077.8	2653.1
G	6610.0	508.5	8.1	2847.6	2454.6
H	6220.0	478.5	6.7	2679.6	2309.8
I	5960.0	541.8	8.4	3034.1	2615.4
J	6235.0	519.6	8.0	2909.8	2508.3
Mean	5971.3	479.2	6.5	2926.8	2522.9
±SE	1168.0	52.9	1.3	349.1	300.9

<sup>1</sup> ME calculated using mean energy assimilation efficiency of 86.2%.

## DISCUSSION

Cape Vultures are relatively inactive raptors; soaring flight presumably allows them to forage in an energetically inexpensive fashion (Pennycuik 1972), and they spend a major part of each day roosting (Mundy 1982, Boshoff et al. 1984, Robertson and Boshoff 1986). Taking advantage of prevailing climatic conditions, wind and thermals, Cape Vultures in summer rainfall areas of southern Africa generally leave their colonial roosts to forage from early to mid-morning and return in the afternoon, generally precluding more than one foraging trip per day (Brown 1988, J. Komen unpubl.). While rearing young, each parent may therefore only forage once every 2 d (Komen 1991). Cape Vultures have been reported to forage as little as once every 3 d (Robertson and Boshoff 1986) and during the post-fledging dependency, young birds may go without food for much longer periods (up to 16 d; Robertson 1985).

The results of adult Cape Vulture feeding trials in

captivity provide data on gross energy intake and metabolizable energy which probably represent minimum requirements for existence, taking into account the relative inactivity of both free-living vultures and captive birds. Starved Cape Vultures can consume 1.5 kg meat in one feeding (Komen 1991). This equivalent to a gross energy intake of 9300 kJ, which, with a high assimilation efficiency (86.2%), represents a maximum metabolizable energy intake of 8017 kJ. Kirkwood (1980) predicted that the mean maximum daily metabolizable energy intake by any animal is  $1713 \text{ kJ/day} \times \text{kg}^{0.72}$  (SE of slope  $\pm 0.008$ ). Using Kirkwood's (1980) equation, the predicted maximum daily metabolizable energy intake for Cape Vultures ranges between 6409 and 8499 kJ/day (using the lowest and highest post-starvation body masses in this study; Table 2). Starved, low weight, adult Cape Vultures therefore appear to exceed the theoretical maximum for daily metabolizable energy intake, by being able to consume a single large quantity of food which provides metabolizable energy for more than one day of existence. This suggests a strategy to counter unpredictable food resource and extended periods of inclement weather.

Daily energy expenditure is estimated to be about 1.2 times existence metabolism in small, non-breeding (and thus relatively inactive), diurnal raptors (Sapsford and Mendelsohn 1984). Since metabolism does not scale in direct proportion to body mass, birds with large bodies would have relatively lower metabolic rates than birds with small bodies (Lasiewski and Dawson 1967, Walsberg 1980). Accordingly, daily energy expenditure of free-living Cape Vultures is probably not greatly elevated above existence metabolism, especially since they are inactive for a major part of each day, with little seasonal variability in this behavior.

The captive adults in this study were generally less massive than free-living adults, and assuming that energy requirements for existence are scaled to body mass regardless of differences in body constituent proportions, the energy requirements of free-living adults will be proportionally higher than that of captive adults. If existence metabolism and daily energy expenditure are scaled on body mass according to an exponent of 0.61 (Walsberg 1980), I estimate that daily existence metabolism of free-living adults is 2505 kJ/day ( $688.9 \text{ kJ/day} \times \text{kg}^{0.61}$ ) for body mass equal to 8300 g (mean body mass 8298.3, SE  $\pm 477.8$  g, 11 wild adults weighed; Komen 1986), and daily energy expenditure (1.2 times existence metabolism) is 3006 kJ/day or  $826.7 \text{ kJ/day} \times \text{kg}^{0.61}$ . This relatively low predicted value for daily energy expenditure is supported by

evidence from field and captive studies on diurnal and nocturnal raptorial birds (Koplin et al. 1980, Sapsford and Mendelsohn 1984, Wijnandt 1984, see also Walsberg 1980).

A single maximal feeding (9300 kJ) should theoretically provide enough energy to maintain an adult Cape Vulture for about 3 d, without expending body fat reserves. Fat content of free ranging adult Cape Vultures ranges between 9.5–15.7% of body mass, accounting for a fat depot of as much as 1346 g (Komen 1991). Assuming that stored fat has an energy density of 38 kJ/g AFD (Johnston 1970), and that 98% may be re-absorbed for metabolism, to the point where body condition is still "reversible" in the sense that an individual may be re-fed and thus survive the fast (Robin et al. 1988), then this fat reserve could theoretically maintain an adult bird during periods of food deprivation (assuming daily extence metabolism of 2505 kJ/day) for as long as 20 d, and probably longer if metabolic rate diminishes during fasting.

While rearing young, each parent should optimally be able to provide enough food on 1 d of every 2-d foraging cycle to satisfy the gross energy requirements of the nestling, for the duration of the nestling period of 136 d (Komen 1986, 1991). Daily gross energy intake of the growing nestling increases with age, and, during the period of maximum growth (about 40 d, or 20 parent foraging cycles), may be twice as much as the daily adult energy requirement for existence (Komen 1991, in preparation). However, at no stage does daily nestling gross energy intake exceed the maximum quantity set by adult crop and stomach capacity. Except during unusual periods of food deprivation, resulting from inclement weather conditions (Komen 1986, in preparation), both adult and nestling energy requirements should be satisfied, without undue demands on body fat reserves.

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