AN EVALUATION OF THE USE OF TRITIUM FOR ESTIMATING DAILY ENERGY EXPENDITURE FOR WILD BLACKSHOULDERED KITES *ELANUS CAERULEUS* AND GREATER KESTRELS *FALCO RUPICOLOIDES*

by

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SUMMARY

A tritium dilution technique was used to investigate the relationship between water turnover and Existence Metabolism (EM) of captive and wild Blackshouldered Kites and water turnover of wild Greater Kestrels. In the laboratory, water turnover determined by this method and independently calculated from food and faeces analysis agreed to within 2,8%. EM for kites was 986,85 kJ/kg/day (28 C). For non-breeding wild kites DEE was 1,16EM and for breeding males, 1,44EM. The lowest DEE (0,99EM) was for a female kite prior to egglaying; the greatest (1,55EM) for a breeding male tending a single fledgling. Based on a 'minimum energy wastage factor' and an assimilation efficiency of 80%, it was estimated that to satisfy DEE, a non-breeding kite would need to capture 66 g of fresh rodent/day and a breeding male 81 g. There was no significant difference in mass specific water turnover between non-breeding kites and kestrels.

INTRODUCTION

Methods for directly estimating Daily Energy Expenditure (DEE) for freeliving animals are few and have been reviewed by Gessaman (1973). As a consequence, attempts to quantify DEE frequently rely on indirect methods of assessment. This is particularly true for raptors where time budget analyses are generally coupled with a variety of metabolic coefficients associated with various activity states (Tarboton 1978; Wakeley 1978; Koplin *et al*. 1980; Mendelsohn 1982). Energy budgets constructed in this way can be extremely useful but suffer two serious disadvantages. Firstly they presuppose a high degree of behavioural and physiological inflexibility which rarely exists and secondly they depend on metabolic rate coefficients derived largely from laboratory studies on passerines. It is therefore important to test the validity of these estimates by more direct and stringent means.

In this regard, doubly labelled water has been used for measuring oxygen consumption indirectly for a number of animal species and has provided valuable insights into the energy requirements of some freeliving birds (Weathers & Nagy 1980; Bryant & Westerterp 1980, 1982, 1983). Although the technique provides reliable data it is costly, particularly where large animals are to be investigated. It also requires that hydrogen and oxygen turnover rates be determined over a period of a few days. For these reasons, its application is limited to studies where (i) the chances of recapture within a short time period are high, and (ii) body weights of animals are relatively low.

Green *et al.* (1983) used the tritium dilution technique described by Lifson & McClintock (1966), to measure water turnover in the marsupial carnivore, *Dasyurus viverrinus*. Since this species and most other carnivores drink little free water, they related turnover to energy requirement. This conversion requires that body water and mass specific energy content of prey items is predictable, that free water intake is minimal and that the mass specific body water pool remains constant.

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Since many raptor species appear to be relatively independent of free water (Kabayashi & Takei 1982), we investigated the relationship between water turnover and energy requirement in Blackshouldered Kites *Elanus caeruleus*, a species that has never been observed to drink in the wild. In addition, water turnover was investigated in the Greater Kestrel *Falco rupicoloides*, another species not known to drink (A.C. Kemp pers. comm.).

This paper reports on the preliminary findings of an ongoing study and suggests that this relatively inexpensive method may provide a reliable means for determining DEE in raptor species which drink infrequently or not at all and whose diet is known. In addition, the technique is suited to monitoring DEE over relatively long periods of time, an important consideration where recapture of isotopically labelled animals shortly after release is unlikely.

MATERIAL AND METHODS

The study was carried out in the Settlers area (24 57S, 28 33E) of the central Transvaal during April/May, 1982 and February/March, 1983.

Total body water and water turnover rates were obtained for nine wild-caught kites and nine kestrels using tritium.

Birds were captured using Balchatri noose-traps baited with either laboratory white mice or laboratory-reared *Mastomys coucha*. On capture each bird was weighed and injected intraperitoneally with 10 mCi of sterile tritium solution and the isotope allowed to equilibrate with the body water space for a period of four hours. A 1,0 ml blood sample was then withdrawn from a brachial vein, and stored in a sealed polythene tube. The bird was then released at the site of capture. On recapture, three to four weeks later, the bird was weighed again and a second blood sample obtained and stored as before.

Water was extracted from blood samples by vacuum sublimation in liquid nitrogen, sealed in polythene vials and stored in the refrigerator at 4 C. Tritium activity was measured within two days of extraction.

Radioactivity was measured by diluting 20 ul of the sample with 2,0 ml of Beckman EP scintillation fluid and the samples counted in a Beckman LS7500 scintillation counter. Total body water was determined by comparing the activity of the sample with that of a standard (10 mCi/100 ml distilled water), treated in the same way as the sample. Water turnover was then calculated according to the method of Lifson & McClintock (1966), which is based on the dilution of tritium in the body against time.

In order to compare water turnover rates using tritium with turnover rates determined from an analysis of food, excreta and pellets and to relate water turnover and Metabolised Energy (ME), a validation trial was run using three captive hand reared kites in the laboratory. The birds were housed separately in cylindrical wire-mesh metabolism cages fitted with removable plastic sheet floors. Each trial lasted eight days during which food consumption and pellet and excreta production were measured. Ambient temperature was maintained at 28 ± 1 C. Pellets and excreta samples were separated into a white urinary fraction and a dark, egesta fraction. These fractions were analysed separately in order to determine the metabolic water content of egesta. Since the urinary fraction comprised largely uric acid with a high non-protein nitrogen content, protein determinations were carried out on pooled egesta samples only. Total energy of food, pellets and excreta were determined using a ballistic bomb calorimeter (Gallenkamp).

Water turnover from food, pellet and excreta analyses was determined by summing metabolic water of assismilated carbohydrate, lipid and protein and free water of ingested prey. Total metabolisable energy assimilated was then determined by subtracting the energy content of pellets and excreta from total energy ingested.

During these energy balance trials, kites were fed laboratory-reared M. coucha after the gut contents had been removed (wild kites seldom eat rodent guts - Mendelsohn 1982). In order to determine free water and metabolic water content the following conversion constants were used: protein - 0,5 ml/Dg; lipid - 1,07 ml/Dg and carbohydrate - 0,56 ml/Dg (Schmidt-Nielsen 1979). Each bird was weighed after regurgitating a pellet in the morning before the start of the trial and again at the end.

During the energy balance trials on the three captive kites, water turnover was also measured using the tritium dilution technique. Each bird was injected intraperitoneally with 0,5 mCi of tritium and total body water and water turnover determined as before. Water turnover rates obtained in this way were compared with turnover rates obtained from food, faeces and pellet analyses.

In order to obtain realistic values for energy and water content of natural prey items fed on by kites in the field, a sample of five adult M. coucha and two adult Otomys angoniensis were trapped in the study area and analysed for free water, metabolic water and total energy (Table 1). Based on these analyses, the relationship between water and energy content of prey items was established and used to relate water turnover and metabolisable energy for wild birds. Kestrels were observed feeding largely on locusts and since no prey items were collected and analysed from the study area, no attempt was made to relate water turnover and energy requirements for this species.

The t-statistic for two means was applied to appropriate data sets and the 95% level considered to reflect a significant difference.

TABLE 1. Water and energy relations of field-caught and laboratory-reared rodents.

SPECIES	n	Lab (L) Field (F)	% Free Body Water	% Total Body	KJ /DG	kJ/g Fresh
Mastomys coucha	5	F	72,60	88,35	23,13	6,34
Otomys angoniensis	2	F	71,98	-	22,86	6,41
$\bar{x}$			72,29		23,00	6,38
Mastomys coucha	6	L	67,90	-	24,05	7,72
Lab. white mice	10	L	66,85	-	25,20	8,35
$\bar{x}$			67,38		24,64	8,03

TABLE 2. Relationship between water turnover and Existence Metabolism (EM) for captive Blackshouldered Kites fed laboratory <u>Mastomys coucha</u> (TA = 28C)

Kite No.	Mean Body Mass (kg)	Total Energy Assimilated (kJ/day)	Total Energy Assimilated kJ/kg/day	Water Turnover (ml/day) (food & faeces)	Water Turnover (ml/day) (tritium)	kJ/ml H_2O (food)	kJ/ml H_2O (tritium)
1.	0,243	236,13	971,73	29,02	25,03	8,14	9,43
2.	0,213	226,26	1062,25	28,79	29,25	7,86	7,74
3.	0,213	215,89	926,57	26,99	28,20	8,00	7,76
$\bar{x}$	0,230	226,09	986,85	28,27	27,49	8,00	8,31
S.D.	0,02	10,12	69,09	1,11	2,20	0,14	0,97

RESULTS

In the laboratory validation trials using captive kites, measurements of water turnover based on food consumption, pellet and egesta analysis were similar to those obtained by the tritium method (Table 2). Although no consistent trend was apparent, mean turnover rates based on tritium dilution were 2,8% lower than estimates based on food, pellet and egesta analysis.

Since individual body masses during these trials varied by less than 5%, and ambient temperature remained constant at 28 ± 1 C, Metabolisable Energy (ME) was equated with Existence Metabolism (EM). Mean mass specific EM for the three kites was 986,85 ± 69,09 kJ/kg/day.

For estimating Daily Energy Expenditure (DEE) from water turnover rates of wild kites, water and energy values for field-caught *M. coucha* were used (Table 1). This was necessary since the water content of wild rodents was found to be 4% greater than that of laboratory-reared mice, while mean energy content was 18,9% lower. These differences were due largely to the higher lipid content of laboratory mice. For wild *M. coucha*, total body water (free + metabolic) represented 88,35% of total wet mass after discarding gut content (Table 1).

Mean energy assimilation efficiency based on the results of the validation trial and other energy budget studies carried out on the three kites was 80%. Thus in transposing water turnover into ME, a conversion factor of 5,98 kJ/ml was used, which took into account non-metabolised energy of excreta and the metabolic water potential of egesta.

DEE estimates derived in this way are shown in Table 3. Mean mass specific DEE for breeding males (1429,67 ± 121,86 kJ/kg/day) was significantly greater than that for non-breeders (1141,09 ± 104,32 kJ/kg/day :$p < 0,02$). The highest value (1533,13 kJ/kg/day) was for a breeding male tending a single fledged young, while the lowest (825,34 kJ/kg/day) was for a female (# 091) just prior to egglaying. Comparing these data with mean EM(28 C) for the captive kites, mean DEE for non-breeders was 1,16 ± 0,01EM and for breeding males, 1,44 ± 0,10EM.

Using the allometric equation of Lasiewski & Dawson (1967) for SMR, mean DEE for breeding males was 2,35 ± 0,21SMR while for non-breeders it was 2,89 ± 0,23SMR. Since kites exhibit little sexual size dimorphism (Biggs *et al.* 1979), no attempt was made to differentiate between male and female non-breeders.

Although absolute water turnover rates for non-breeding kestrels were generally higher than for non-breeding kites (Table 4), no significant difference was observed at the mass specific level ($p > 0,1$).

DISCUSSION

The Blackshouldered Kite is a common inhabitant of open grassland savannah where it preys almost exclusively on small rodents (Mendelsohn 1982). In addition, kites appear to be independent of drinking water and have never been observed to drink in the field. This apparent independence of drinking water accords with observations on the three captive kites which thrived for a period of more than two years on a diet of day-old poults and laboratory mice but without access to drinking water. For these reasons, kites constitute ideal study animals for investigating the relationship between water turnover, metabolisable energy and food consumption using tritium.

TABLE 3. Water turnover and estimated Daily Energy Expenditure (DEE) for wild Blackshouldered Kites using tritium

Kite No.	Date	Min-Max Temp C	Mass (kg)	Water turnover		DEE kJ/day	DEE kJ/kg/day	DEE:EM	DEE:SMR*	STATUS
				ml/day	ml/kg/day					
315	Apr/May	3-33	0,231	52,12	225,63	311,68	1349,26	1,37	2,74	Male: Nest and Eggs
083	1982		0,228	52,23	229,08	312,33	1369,87	1,39	2,78	Male: Nest Building
086			0,243	62,30	256,38	372,55	1533,13	1,55	3,16	Male: With chick
$\bar{x}$ S.D.			0,234 0,01	55,55 5,85	237,03 16,85	332,19 34,96	1429,67 121,86	1,44 0,10	2,89 0,23	
091			0,328	45,27	138,02	270,71	825,34	0,84	1,84	Female: egg 'in situ'
251			0,218	37,57	172,34	224,67	1030,60	1,04	2,06	Unknown
258	Feb/Mar	15-36	0,238	46,33	194,66	277,05	1164,08	1,18	2,39	Non-breeder
268	1983		0,237	39,67	167,38	237,23	1000,97	1,01	2,05	Non-breeder
260			0,230	48,18	209,48	288,12	1252,69	1,27	2,55	Non-breeder
259			0,259	49,66	191,74	296,97	1146,60	1,16	2,41	Non-breeder
$\bar{x}$ S.D.			0,241 0,01	45,96 4,41	190,82 17,45	274,84 26,37	1141,09 104,32	1,16 0,11	2,35 0,21	

* kCal/day = 78,3 $W^{0,723}$ (Lasiewski & Dawson 1976)

TABLE 4. Water turnover estimated for wild non-breeding Greater Kestrels using tritium.

Kestrel No.	Date	Min-Max Temp C	Mean body mass (kg)	Water turnover ml/day	Water turnover ml/kg/day
213	April/ May 1982	3-33	0,260	41,59	159,96
215			0,253	47,93	189,45
228	Feb/ March 1983	15-36	0,254	51,89	204,29
224			0,261	41,77	160,04
223			0,257	61,39	238,87
222			0,249	46,42	186,,43
221			0,232	37,29	160,73
154			0,246	48,72	198,05
213			0,258	54,64	211,78
		$\bar{x}$	0,252	47,96	189,96
		S.D.	0,01	7,38	26,93

The observed similarity between water turnover based on food, pellet and egesta analysis and independently by tritium dilution in captive kites supports this view and for the purposes of this study, it was assumed that wild kites derived water solely from prey items, The precision with which the relationship between water turnover and metabolisable energy can be established depends largely on the accuracy of water turnover measurements using tritium and on the predictability of the water and energy content of ingested prey. We considered that the various assumptions relating to water turnover assessment using tritium as outlined by Lifson & McClintock (1966), were met. However, mean body masses of kites varied by 8,02 ± 2,38% between initial capture and recapture and thus total body water estimates were based on the mean body mass for each individual. This served to reduce any body mass variation which may have been due to prey held in the stomach. This is an important consideration since captive kites may increase body mass by 10-12% after feeding (unpublished results).

Another source of potential error may occur when relating water turnover and metabolisable energy, since this relationship depends on the predictability of the water and energy content of prey items. It has been shown in a number of studies that the lipid content of rodents may undergo considerable seasonal variation (Jameson & Mead 1964; Perrin 1981) which in turn affects body wa content. For this reason, known prey items collected during the study per were analysed in order to minimise this potential source of error. In t regard, kites were observed to prey almost exclusively on M. coucha and Oto angoniensis during this study. It is also clear from the data (Table 1) t both species had similar water and energy contents and that some measure confidence can be expected when relating water turnover and ME.

Male kites are known to provide food for the female during courtship a incubation and for the female and nestlings during the nestling peri (Mendelsohn 1982). Thus the high DEE value for breeding males probab reflects increased energy demands associated with breeding. Although t sample size was small, DEE for all three males exceeded the maximum DEE f non-breeders and on average they expended approximately 28% more energy th non-breeders. Based on an assimilation efficiency of 80% and a minimum ener wastage factor of 15% during feeding (Sapsford, unpublished data), it estimated that non-breeders must capture at least 66 g of rodent per day whi breeding males require a minimum of 81 g per day in order to satisfy their o energy needs. These estimates are probably conservative, since duri feeding, captive kites discarded between 15-35% of the total energy of a giv prey item (Sapsford, unupublished data). Wild kites too discard so proportion of their prey. For very large prey items, Mendelsohn (198 estimated that on a wet mass basis the discarded fraction may be as high 50%. Therefore since tne above estimates of prey requirement are based minimum energy wastage, it seems likely that the actual mass of prey requir may in some instances considerably exceed these predictions.

Since minimum ambient temperatures were considerably lower during April/Ma than during February/March, the higher DEE values for breeding males may i part reflect an increase in thermoregulatory demand. This however seem unlikely since water turnover rates for the breeding female and kite # 25 during April/May were similar to or lower than those for non-breeders durin February/March when minimum ambient temperatures were considerably higher.

The observation that mass specific DEE for the breeding female (# 091 Table 3) was 27,7% lower than the mean value for non-breeders and 16,4% lowe than EM(28 C) is of interest since absolute water turnover rate was similar t the mean value for non-breeders (Table 3). This suggests that the mas specific DEE estimate may be misleading. It is therefore of interest tha body mass on recapture was 17,5% greater than on initial capture and that a least part of this difference can be ascribed to the presence on recapture o a shelled egg in the oviduct. If mass specific water turnover rate and DE however are based on the initial body mass (275 g), then values o 164,64 ml/kg/day and 984,40 kJ/kg/day are obtained. Since this body mass i probably more realistic, it is likely that DEE for this bird was closer t 0,99EM and approximately 14% lower than the mean for non-breeding kites.

Based on the DEE value for the female (275 g), and DEE estimates for breeding males, it is suggested that a breeding male kite would need to capture at least 146 g of rodent per day in order to satisfy the combined needs of the breeding pair. In addition, this requirement would probably increase during the nestling period when the male provides food for both the female and nestlings.

Since no locusts from the study area were analysed it is unwise to attempt to assess the energy and food requirements of kestrels now. However, since no significant difference was observed between mass specific water turnover rates for non-breeding kites and kestrels, it may be tentatively suggested that their energy requirements were similar. This however presupposes that the relationship between body water and energy content of locusts and mice are similar and that assimilation efficiency for both species is similar too.

From the analysis presented in Table 5, where for comparative purposes DEE is expressed for a 244 g bird (the average mass of a Blackshouldered Kite), a considerable degree of interspecific variation is apparent. Whether these differences are real or a consequence of using different methods of assessment, remains an open question. However, since DEE estimates, based on three separate studies, are available for Blackshouldered Kites, it may be valuable to compare these results directly. DEE estimates based on water turnover for non-breeders, breeding males and the breeding female presented in this study agree well with estimates based on time-energy budget analysis (Mendelsohn 1982). However these independent estimates for non-breeders are 33% lower than the value estimated in a third study using time-energy budget data (Tarboton 1978). His value is 1,71EM, while DEE based on tritium dilution suggests that for breeding males, DEE exceeds EM by a factor of only 1,47 and 1,15 for non-breeders.

TABLE 5. A comparison of Daily Energy Expenditure (DEE) for raptors from time-energy budgets (B) and tritium dilution (T): (DEE scaled to a body mass of 244 g).

kJ/day non-breeders	kJ/day breeders			
Both sexes	Male	Female	Class	Species and Reference
368,03			B	AK - Koplin <u>et al</u>. (1980)
348,21			B	WTK - Koplin <u>et al</u>. (1980)
281,58	341,16	249,07	B	BSK - Mendelsohn (1982)
411,44			B	BSK - Tarboton (1978)
255,06	424,51		B	EK - Vulink (1982)
	309,85	151,74	B	FH - Wakeley (1978)
278,43	348,84	240,19	T	BSK - this study
240,79			T	BSK - EM - this study

AK - American Kestrel; WTK - Whitetailed Kite; BSK - Blackshouldered Kite;
EK - European Kestrel; FH - Ferruginous Hawk.

It is of interest at this point to compare DEE and EM estimates from the present study with values predicted using existing allometric equations which predict EM and DEE on a basis of body mass. Since no distinction is drawn between breeders and non-breeders in these equations, the mean DEE value for non-breeding kites is used in this comparison. Observed EM is 21,2% less than that predicted using the equation of Koplin et al. (1980) and 89% greater than the value derived from Kendeigh's (1970) equation. In addition, our mean DEE estimate is similar to that predicted for a 244 g non-wing forager according to the equation proposed by Walsberg (1978), while the equation of King (1974), predicts a value 44% greater than our estimate.

From this brief comparison it is clear that the use of allometric equations to predict ME must be approached with caution since there is little agreement on either the numerical constants or exponents of the various equations. For EM(30 C), Kendeigh (1970) proposed an exponent of 0,7545 for non-passerines while an exponent of 0,6256 is used by Koplin et al (1980). Similarly, in predicting DEE, exponents of 0,7052 (King 1974) and 0,653 (Walsberg 1978) are proposed. It therefore becomes a matter of importance to establish realistic exponents and numerical constants if equations of this nature are to have any predictive value. In a study of water turnover on nine species of raptors covering a body mass range of 4,5 kg, the exponent for the regression of turnover rate on body mass was shown to be 0,60 (unpublished results). Thus for non-drinking raptors, if it is assumed that water turnover is directly proportional to ME as suggested by the present study, then the exponent of the equation relating DEE and body mass should be similar. It seems therefore that this exponent is probably close to 0,60 and not 0,70 or 0,75. Thus the EM equation of Kendeigh (1970) and the DEE equation of King (1974) probably overestimate EM and DEE respectively, particularly for larger birds, while the equation of Walsberg appears to provide more realistic estimates of DEE for diurnal raptors.

In conclusion and based on the results of the present study, we beleive that the tritium dilution technique can provide a useful means of estimating energy and food requirements for wild raptors which drink little or no water and whose diet is known. However, it is important to base ME estimates on a realistic assessment of the water and energy content of food preyed upon at the time of the study, since variable lipid content of prey may seriously influence both total body water and energy content of prey. This in turn would influence estimates of ME based on water turnover alone.

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