Flexible energetics of cheetah hunting strategies provide resistance against kleptoparasitism

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Population viability is driven by individual survival, which in turn depends on individuals balancing energy budgets. As carnivores may function close to maximum sustained power outputs, decreased food availability or increased activity may render some populations energetically vulnerable. Prey theft may compromise energetic budgets of mesopredators, such as cheetahs and wild dogs, which are susceptible to competition from larger carnivores. We show that daily energy expenditures (DEE) of cheetahs were similar to size-based predictions and positively related to distance travelled. Theft at 25% only requires cheetahs to hunt for an extra 1.1h/day, increasing DEE by just 12%. Therefore, not all mesopredators are energetically constrained by direct competition. Other factors that increase DEE, such as those that increase travel, may be more important for population viability.

The acquisition and expenditure of energy by animals unifies physiology with population ecology and viability, although interactions between energetics, ecology and survival can be complex (*1*,*2*). Indeed, of the studies that have investigated how energetic factors affect population dynamics, most are concerned with the effects of changes in abiotic conditions such as ambient temperature (*3*), with few examining the effects of changes in biotic conditions, such as the abundance and distribution of prey and competitors (*1*,*4*).

Although recent human activities have driven declines in large mammalian predators (*5*), intraguild interactions may also shape carnivore communities. One persistent hypothesis suggests that, because carnivores may be routinely working close to maximum sustained power outputs, decreases in food availability or increases in activity may push them over an energetic precipice (*6*). Kleptoparasitism, the theft of prey captured by another animal, is one critical element in this interaction, particularly for mesopredators such as wild dogs *Lycaon pictus* and cheetahs *Acinonyx jubatus*, which are prone to competition with and displacement by larger more dominant carnivores such as lions *Panthera leo*, and spotted hyaenas *Crocuta crocuta* (*7-11*). The details of such intraguild interactions with respect to energetic implications are, however, poorly understood.

Carnivores hunt using a combination of sit-and-wait, stalk, ambush and charge, or extended coursing strategies (*12-15*). While the short-term energetic consequences of hunting (i.e. the ways which predators chase and subdue prey) are profoundly different (*2*,*16*), the long-term costs such as the energy required to locate prey and avoid predators are rarely considered. These costs may be pivotal in determining the viability of different hunting strategies, particularly as it relates to prey abundance, accessibility and loss (*2*,*6*,*17*).

We combined behavioral observations of 14 cheetahs from the Kgalagadi Transfrontier Park (‘Kalahari’) with measurements of daily energy expenditure (DEE) to estimate the energetic cost of foraging. We also obtained DEE measurements of five free-ranging cheetahs from

Karongwe Game Reserve ('Karongwe'). The cheetah is an appropriate study species as it is regarded as vulnerable to kleptoparasitism (*8,9,18*), and has the highest power per given body mass (W/kg) of any mammal during short periods of pursuit (*19*). This leads to the perception that they experience overall high sustained energetic costs (*7*). Over two-week periods, we measured cheetah DEE using the doubly labeled water (DLW) technique *(20)* while following the animals most days. Various behaviors were recorded (e.g. lying, sitting, walking, chasing prey) and scat samples were collected periodically. We examine the relationship between DEE and the 'prey location' and 'prey pursuit' phases of hunts and how this affects their vulnerability to kleptoparasitism. We calculated DEE using isotope analysis of water extracted from multiple excreta samples to provide one measurement of DEE per individual over the two-week period ('MS-DEE') as well as on a per diem basis using pairs of samples collected consecutively, providing several measurements of DEE per animal within the period ('SS-DEE'). Means are presented ±1SD. For full methodological details, see Supplementary Information.

Mean MS-DEE (8883 ±3854kJ/d, N=19) was not significantly different from predictions for free-ranging mammals of similar size (Table 1). The values of sustained metabolic scope (SusMS) - a measure of work rate independent of body size (*21*) (1.55 ±0.69 x RMR) - were also not significantly different to allometric predictions (Table 1). There were no study-site or sex-related differences in MS-DEE (χ^2=0.234, p=0.629 and χ^2=0.209, p=0.647, respectively). Cheetahs were mobile for 2.86 ±0.95h (12%) per day moving at an average speed of 0.83 ±0.54m/s (excluding prey pursuits), and chased prey 1.2 ±0.49 times per day for an average of 37.9 ±11.6s per chase.

There were significant intra- and inter-individual differences in SS-DEE for each cheetah followed ($F_{18,62}$=1.83, p=0.041, Fig.1). For predators, with a tendency towards a feast or famine feeding regime, this variation in DEE is expected; individuals are likely to skip hunting on days following kills of large prey (*2*). Cheetahs were observed to capture prey on 52% of days, and for 65% of those 'successful' days, did not capture anything the following day. However, this was not significantly different from the expected capture rate (χ^2=1.47, p=0.225) and therefore does not provide direct evidence for less hunting following kills. This crude analysis though does not factor in how much the animals eat at each kill. There was a positive relationship between distance travelled and the mass of prey eaten on a particular day ($F_{1,46}$=5.98, p=0.018) and a negative relationship between the mass of prey eaten and the distance travelled the next day ($F_{1,19}$=7.21, p=0.015) indicating that cheetahs travel less after eating more, and when they travel less they have lower intake. A positive relationship also exists between the energy costs of foraging and the perceived risk of predation or interference by predators (*22*). Consequently, the large variation in MS-DEE observed indicates that cheetahs are capable of operating at high sustained energy expenditures when necessary, while the large daily variation in SS-DEE is likely to be driven by variation in activity as a result of differences in feeding success (*2*), and/or the avoidance of competitors (*8,9,18*).

Importantly, we observed a significant positive relationship between the travel distance on a particular day and SS-DEE (χ^2=6.36, p=0.012) but not between pursuit distance and SS-DEE (χ^2=0.024, p=0.878). SS-DEE was related to distance travelled by the relationship:

DEE (kJ/day) = 447 x distance (km) + 7103 (i)

(least-squares regression, $F_{1,52}$=5.978, p=0.018, r^2=0.103). There was also a significant positive relationship between the travel distance on a given day and the distance prey were chased on that day ($F_{1,49}$=5.920, p=0.019, r^2=0.108). In terms of daily variation in SS-DEE, we found no evidence that DEE was reduced following days with greater than average DEE (χ^2=1.60, p=0.206), although DEE was greater following days with less than average DEE (χ^2=5.33, p=0.021). Similarly, cheetahs did not travel further following days of less than average distance moved (χ^2=3.27, p=0.071), although they travelled less following days with greater than average distanced moved (χ^2=5.44, p=0.020). Since travel distance was the main driver of DEE, any increase, such as might be caused by the need for extra hunting to compensate for kleptoparasitism, will also increase DEE. Kalahari cheetahs were mobile for 12% of the day, which accounted for 42% of the 8.84MJ total DEE, as being mobile was 5.4 times more costly than resting. The positive relationship between travel distance and pursuit distance may be because increased movement provides additional opportunities for hunting, as observed here, and in Kalahari leopards *Panthera pardus* (*23*).

Using African wild dogs as an example, Gorman *et al.* (*6*) suggested that kleptoparasitism affects the population viability of mesopredators. They suggested that activity budgets could be separated into energetically expensive hunting, and resting. Escalating losses of prey through kleptoparasitism necessarily increased the time and energy required for hunting, rapidly creating an untenable situation. Kalahari cheetahs are also subject to kleptoparastism: of the 43 observed cheetah kills, four (9.3%) were kleptoparasitised (two by brown hyaenas *Hyaena brunnea* and two by lions). Although, losing kills increases the time required to hunt (Fig.2), our model suggests that, unlike wild dogs, cheetahs are able to cope with kleptoparasitism rates of 25%, as this would only require an additional 1.1h/d (a 38% increase) in time spent mobile and increase DEE to 10.0MJ/d (a 12% increase). Wild dogs may be exceptional in this regard because the high power costs (25 x RMR, 35W/kg) and long durations of prey pursuits (3.5h/day) make their hunting strategy extremely costly. This contrasts with the hunting strategy of cheetahs, even though power use during pursuit may reach 120W/kg (*19*), prey pursuit takes only a few seconds, and constitutes a small component of the daily energy budget (undetectable here using doubly labeled water).

Recorded rates of kleptoparasitism in cheetahs are lower than the untenable threshold of over 50% (Fig.2), 14% in Kruger National Park *(24)*; 11% in the Serengeti *(25)* and 9.3% in the Kgalagadi Transfrontier Park (current study). Relatively low kleptoparasitism rates in cheetahs that do not change greatly between ecosystems may be due to effective competitor avoidance strategies *(9)* and a diurnal hunting strategy *(26)*. The comparatively low cost of food acquisition and flexible energy budget of cheetahs compared to that of wild dogs *(6)* are likely to provide a buffer against varying ecological conditions.

This study lends support to suggestions that interspecific competition does not necessarily suppress cheetah populations (27-30). Instead, it shows that cheetahs are well adapted to the presence of competitors, and costs incurred by travelling drive their energy budgets, rather than those encountered securing prey. Human activities which force cheetahs to travel large distances to avoid disturbance and persecution, may push DEE to the limit and consequently compromise their population viability.

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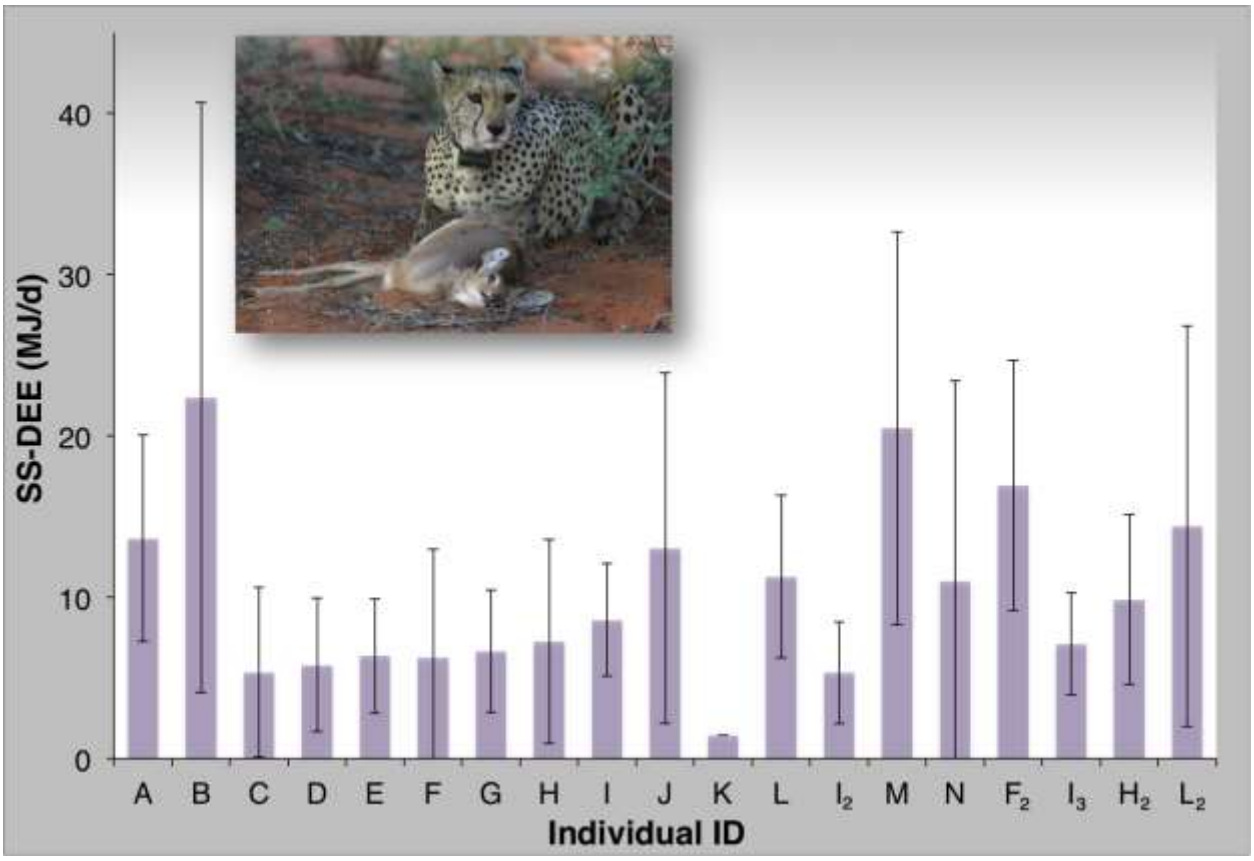

Fig. 1. Daily energy expenditure of cheetahs.
Mean energy expenditures (SS-DEE, kJ/d) for 19 measurements, calculated using the two-point method to estimate CO_2 production. Animals A-E were from Karongwe, animals F-L from the Kalahari. Subscripts indicate repeated measurements within individuals. The order left to right reflects the date of measurement. Error bars denote standard deviations of daily SS-DEE measurements over two-week periods.

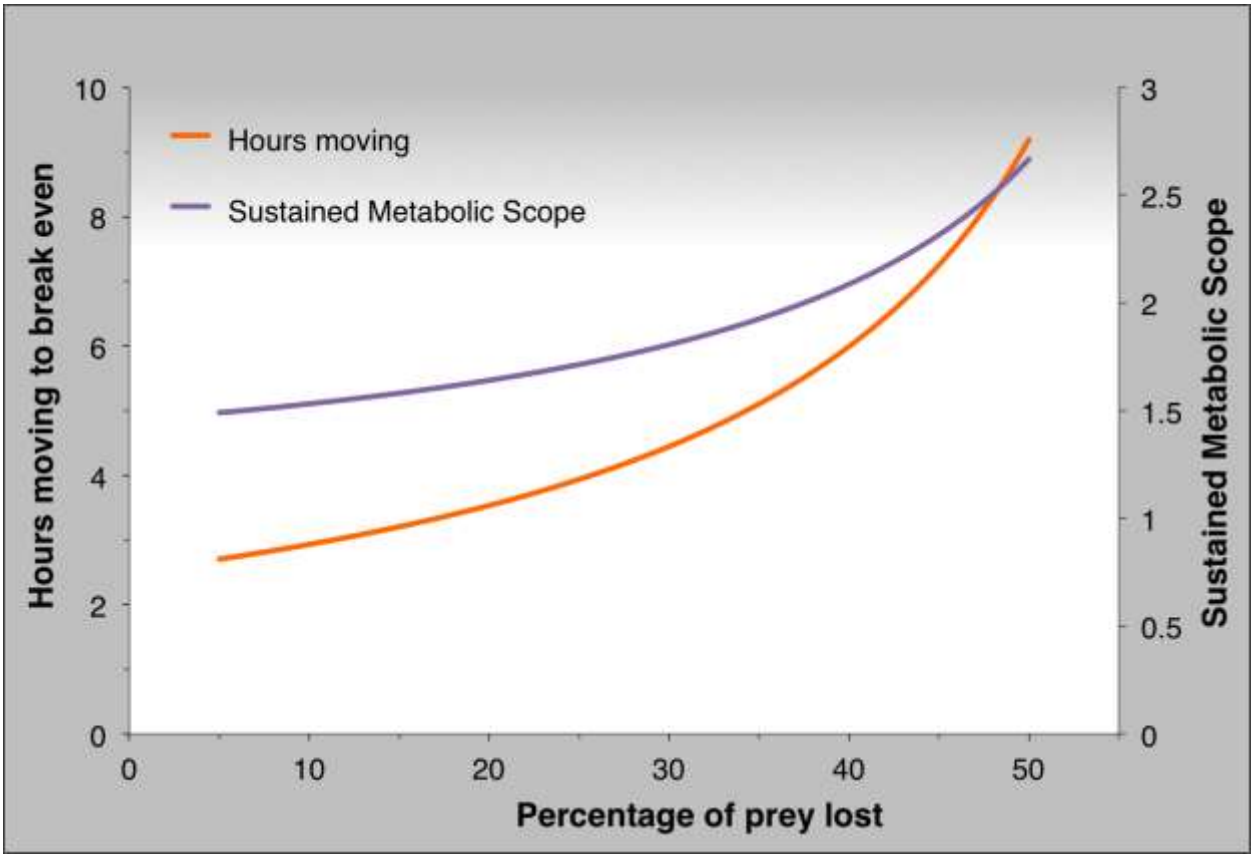

Fig. 2. Model of hours moving to break even and energy balance in cheetahs under different levels of kelptoparasitism.
The black line denotes hours spent moving and the red line sustained metabolic scope (SusMS, DEE/RMR). The bioenergetic model (6) predicts that if cheetahs lost 25% of their prey to rival predators, they would have to be mobile for 4.0h/d to balance energetic needs. Assuming the costs of moving remain the same, this would elevate daily energy expenditure during active periods to 5.1MJ/d or increase total daily energy expenditures to 10.0MJ/d (SusMS =1.7 x RMR). At higher kleptoparasitism rates of 35%, 5.1h would be required to be spent mobile (SusMS = 2.0 x RMR), and at 50%, 9.2h would be required (SusMS = 2.7 x RMR).

	Mean	SD	Mean	SD
Mass (kg)	41	5.6	34	4.1
MS-DEE (kJ/d)	9006	3879	8839	3991
Predicted DEE[31]	7942	499	7050	563
Predicted DEE[32]	8106	530	7162	596
Predicted DEE[33]	12563	755	11212*	853
SusMS	1.37	0.55	1.61	0.74
Predicted SusMS[34]	1.44	0.02	1.47	0.02

Table 1. Mean and standard deviations (SD) of body mass (kg), daily energy expenditure (MS-DEE, kJ/d), predicted DEE (kJ/d), sustained metabolic scope (SusMS) and predicted sustained metabolic scope for cheetahs from Karongwe game reserve (Karongwe) and the Kgalagadi Transfrontier Park (Kalahari) *(31-34)*. MS-DEE was calculated using the multi-sample approach of estimating CO_2 production *(30)*. * indicates significant differences between predicted and the measured values at $p<0.05$.

Supplementary Materials: Supplementary Methods

Study sites and animals

The study took place in two areas, Karongwe Game Reserve (24.1°S, 30.5°E) ('Karongwe') and southern Kgalagadi Transfrontier Park (26.3°S, 20.6°E) ('Kalahari'). Karongwe is an 85km^2 fenced conservancy characterized by a combination of undulating terrain with scattered rocky outcrops, and vegetation dominated by mixed *Combretum* bushveld (*35*). The Kgalagadi Transfrontier Park is a 36,500km² partially fenced region in southern Africa (*27*). In both areas cheetahs have been habituated to human observers making it possible to follow and observe them (*27*,*35*).

Observations

Cheetahs were followed for periods of two weeks from dawn to dusk and occasionally for a few hours after dark. Using the dosed animal as the focal animal, we recorded the time that it spent resting (lying down), sitting, standing, walking, socializing; e.g. allogrooming, playing, encountering prey (stalking, chasing, and subduing) and eating while under observation. Daily distances travelled were calculated as the sum of the distances between sequential GPS fixes, which were taken whenever cheetahs were observed to stop. The amount of meat eaten from each prey encounter was calculated after weighing the remains and subtracting it from the estimated initial mass of the prey (knowing the species and approximate age). These data were entered in real time onto a Fujitsu Siemens Pocket Loox, N520 palm computer onto which the program 'CyberTracker' ([*36*], www.cybertracker.org) with a customized data collection template had been loaded. For each entry, the GPS coordinates and time were automatically recorded. The data were later downloaded onto a computer for further analysis. The distances cheetahs moved between observation periods, usually overnight, were determined by measuring the straight-line distances between sequential GPS locations. For each observed chase, the tracks were examined and paced (by MGLM) to determine the pursuit distance. Cheetahs were located using VHF radio-telemetry (Telonics TR-4 in Karongwe and Advanced Telemetry Systems, model M2220B in the Kalahari) after each night's observation hiatus, and if they moved out of observers' visual range. Fecal and urine samples were collected for isotope analysis (see below).

Doubly labeled water fieldwork

The daily energy expenditures (DEEs) of free-ranging adult cheetahs were measured a total of 19 times on 14 individuals using the doubly labeled water (DLW) technique (*37*,*38*). Five individuals (four males and one female) were measured from Karongwe, and nine individuals were measured from the Kalahari. These data consisted of two females that were measured once, three males that were measured once, three females that were measured twice, and one female that was measured three times (Table S1). Individuals were measured at different stages of their life histories to provide information of the range of energy expenditures that are present in the population.

Animals were labeled with DLW in two ways. An initial two animals from Karongwe were dosed by feeding them fresh warthog (*Phacochoerus africanus*) meat that had been injected with a known mass (c. 1.5g per kg cheetah body mass) of DLW [2:3 parts 90% enriched ^{18}O water (Enritech Ltd., Rehovot, Israel) and one part 99.9% enriched ^{2}H water (MSD Isotopes Inc., Pointe-Claire, Quebec, Canada)]. Syringes were weighed before and after administration (±0.002g TANITA 1210N balance) to calculate the mass of DLW injected. Cheetahs were sufficiently habituated to humans to take bait that was left out for them. The remaining 17 DLW doses were administered IM to cheetahs under anesthesia. Cheetahs were anaesthetized with a 1.5cm^3 plastic DanInject dart at a dose of 80-110mg ketamine hydrochloride and 1.6-2.1mg medetomidine, depending on the sex of the animal. The medetomidine was reversed after 60min with 6.5-8.5mg atipamezole. Darted cheetahs were ataxic within 3-10min and recumbent within 5-15min. After injection of the antidote, cheetahs were awake within 5min. We remained with the cheetahs for up to several hours after anesthesia to ensure that they had recovered.

Anaesthetized animals were weighed (±0.5kg, Salter 100kg Spring Balance) and a 2.0ml blood sample was taken from a cephalic vein to estimate the background enrichments of ^{2}H and ^{18}O (*39*). The blood was initially collected into a heparinised Vacutainer® from which four 50µl glass capillaries were immediately filled and heat-sealed. Afterwards, a known mass of DLW was administered (IM, c. 1.5g per kg body mass). The dose was administered at several sites to minimize discomfort to the animal. Injections were carried out with care so that none of the dose leaked out from injection sites. As before, syringes were weighed before and after administration (±0.002g TANITA 1210N balance) to calculate the mass of DLW injected.

Urine and feces sample collection and storage

For the 19 different times cheetahs were dosed with DLW, we collected urine and fecal samples in two-week periods post dose. Cheetahs defecated approximately two times per day and males urinated approximately 10 times per day when they scent-marked and sprayed the vegetation (*40*). Feces were collected within five minutes after passing and placed in 50ml metal-topped glass containers that were frozen at -20^{o}C until analysis. Urine samples were obtained from droplets remaining on the vegetation where the cheetahs had sprayed and immediately heat-sealed in 50µl glass capillaries. Four capillaries were filled per urine sample. Urine was collected within three minutes of passing. For the two cheetahs that had been dosed orally, background isotope samples were obtained from fresh urine collected prior to dosing with DLW. Capillaries that contained urine were stored at room temperature.

Laboratory methods and calculations

Urine and fecal samples were vacuum distilled (*41*). Water from the resulting distillates was then analyzed for ^{18}O and ^{2}H enrichment by gas-source isotope-ratio mass spectrometry (Optima, Micromass) (see methods in [*42*] for oxygen and [*43*] for hydrogen). The multiple-point intercept

method was used to derive elimination rates of oxygen (k_o) and hydrogen (k_d) (*30*). For each animal, CO_2 production was estimated using two different calculations:
(i) We used a two-pool model (*44*) which incorporates the mean dilution space ratio of both isotopes in the calculation of CO_2 production and is appropriate for use in animals greater than about 5kg (*30*). DEE values were calculated using specialist software (*45*). We term the overall measurement of DEE resulting from the multiple-point intercept method which incorporates information from all the samples collected over a two-week period for each cheetah "MS-DEE".
(ii) We used the two-point method to estimate CO_2 production between sequential samples that were collected on subsequent days, or, if no samples were collected on one day then an estimate of CO_2 production was determined between sequential samples (the "repeated 2-sample approach", [*30*]). This provided multiple values of DEE for the same individual to the maximum resolution of one day. We used a two-pool two-sample equation ([*44*], equation A6 as modified by [*46*]; equation 17.15 in [*30*]) to estimate CO_2 production. For this, we incorporated the measured values of k_o and k_d between subsequent samples collected on sequential days and the values of N_o and N_d from the multi-sample calculation (above). We term the daily measurement of DEE resulting from the sequential sample measurement of CO_2 production "SS-DEE". For all calculations, CO_2 production was converted to DEE using a respiratory quotient value of 0.9 (22.8kJ per liter of CO_2), which is appropriate for an obligate carnivore such as the cheetah.

Determination of isotope equilibrium and elimination rates

To determine the isotope equilibrium rate post dose and the isotope elimination rate for cheetahs, we performed a pilot study on a captive individual (30kg adult female) housed at Kapama Wildlife Sanctuary, Hoedspruit, South Africa (24.4^{o}S, 31.0^{o}E). Prior to dosing, the cheetah was encouraged to salivate by showing it a bowl containing 0.5kg of fresh minced beef. Four 50µl glass capillaries were then filled with saliva and immediately heat-sealed. To achieve this, an experimenter placed their gloved hand around the mouth and inside cheek of the cheetah, which, upon removal was covered with saliva. This sample was then used to determine background levels of deuterium. Afterwards, a known mass of deuterated water (c. 13.0g of 99% APE $^2H_2{}^{16}O$) was offered to the cheetah which was mixed with the 0.5kg of minced beef in a stainless steel dish. A further 0.5kg of minced beef was offered to the cheetah after it had eaten the labeled meat in order to "wash" the dose down. Thereafter, saliva samples were collected after three, six, and seven and then eight hours post dose and subsequently at 1, 2, 4, 7, 11, and 17 days post dose, at approximately 07:00 (Fig. S1). Isotope equilibration time was between three and seven hours post dose and isotope half life was approximately seven days.

Comparison between isotope enrichment of feces and urine in wild cheetahs

Urine, blood and saliva are common body fluids to collect for determination of DEE by the DLW technique (*47*). Fecal sampling has rarely been used in DLW studies of because of the likelihood of differences in enrichment between blood/urine and feces as a result of *in vivo* fractionation (*48*), because fecal samples, once voided, may become contaminated by the

environment, and because feces need to be collected immediately after passing. Therefore, there is often more variability in the measured isotope enrichment of feces compared with that of blood or urine (*49*). However, on some occasions it may be useful to collect fecal samples. In larger animals with longer isotope turnover rates (e.g. animals >30kg with isotope half lives of seven days or more), fecal sampling may be more appropriate because of the smaller difference between feces than of simultaneously collected urine as or blood (*49*). This technique has been used previously to measure DEE in free-living reindeer *Rangifer tarandus* (*50*). The advantages of fecal sampling for determination of DEE using the DLW technique in wild animals are that the study animals do not need to be immobilized and that multiple samples can be collected. Indeed, fecal sampling may be the only method of collecting a body 'fluid' sample from an undisturbed wild animal. Multiple sampling also allows the possibility of determining multiple measurements of DEE in the same animal over the course of an experiment (the "repeated 2-sample approach" [*30*]).

To examine the relationship between the isotope enrichment of urine with that of feces collected during the same measurement period, we determined the elimination curves for both feces and urine in two male free-ranging cheetahs in Karongwe. Feces and urine were collected and analyzed as described above for a two-week measurement period. There were no significant differences in the elimination rates of either ^{2}H (cheetah 1: $F_{1,7}=2.33$, p=0.171; cheetah 2: $F_{1,5}=1.91$, p=0.225) or ^{18}O (cheetah 1: $F_{1,9}=4.55$, p=0.063; cheetah 2: $F_{1,9}=1.84$, p=0.208) between feces and urine. Nor were feces or urine significantly different from each other for ^{2}H (cheetah 1: $F_{1,8}=3.06$, p=0.118; cheetah 2: $F_{1,6}=0.05$, p=0.837) or ^{18}O (cheetah 1: $F_{1,10}=0.52$, p=0.487; cheetah 2: $F_{1,10}=0.08$, p=0.778). We therefore concluded that collection of feces was appropriate to determine isotope elimination rates for the determination of CO_2 production in this system.

Calculation of the potential energy costs of kleptoparasitism

In our observations, the maximum amount of meat cheetahs ate from a carcass in one sitting was 7.5kg. We therefore define kleptoparasitism having occurred if cheetahs lose more than 10% of their kill up to 7.5kg of prey. If they have already eaten 7.5kg of prey and a lion then chases them off a kill it will make no difference to the amount they are able to eat. The effects of kleptoparasitism were investigated using the same methods and model as Gorman et al. (*6*). In this model, $H_d = 24.E_r / (I + E_r - E_h)$ where H_d is the foraging effort (hours/day) needed to achieve energy balance, I the rate of prey capture (kJ/h), and E_r and E_h energy expenditure (kJ/h) when resting and hunting, respectively. We calculated mean E_r values of 242kJ/h, using the body masses of 14 Kalahari cheetah measurements for which we had foraging data, from allometric predictions of RMR in cheetahs (*51*). We calculated periods of time that cheetahs were mobile in a 24h period by the sum of (i) the observed time when they were mobile during the day, and (ii) the distance travelled during the night divided by the observed mean walking speed of cheetahs (Fig. S2). Night distances were calculated using two GPS fixes from where we left the cheetahs

in the evening (e.g. at 18:00) to where we found them the next morning (e.g. at 06:00). To check whether this provided an accurate measure of actual distance travelled during the night, we compared straight-line distances measured during the day (measured as the distance between initial and final GPS fixes for the day, obtained for example at 06:00 and 18:00) with actual distances travelled during the day (measured as the sum of the distances between sequential GPS fixes which were taken whenever cheetahs were observed to stop). We found that straight line distances were 70% of the actual distances measured during the day. Therefore, we applied the same correction factor to straight line night distances to calculate actual distances travelled at night. We assume that cheetahs metabolize at E_r for the 21.14h/day that they are inactive. Given a mean DEE for these 14 animals of 8839MJ/d, this means that 34.0kg cheetahs must be metabolizing an average of 1.30MJ/h (E_h) during the 2.86h per day that they are mobile each day. This equates to a metabolic scope of about 5.35 x RMR while mobile. Therefore, we can assume that cheetahs need to be mobile for 2.86h per day to obtain their daily energy requirement of 8839MJ equating to an average food intake whilst mobile of 3.10MJ per hour. We used these parameters to predict the numbers of hours that cheetahs would need to be mobile to hunt for food if they were losing various percentages of their prey to rival predators (Fig.2).

Statistical analyses

Analyses were performed in R version 3.0.2 (*52*). The relationship between MS-DEE, habitat and sex and between SS-DEE, the travel distance and the pursuit distance on a particular day were determined using general linear models (*53*). Body mass was entered as a covariate and cheetah ID as a random factor to account for repeated measurements within animals. Function "lmer" was used in the package lme4. Wald χ^2 statistics and p values were obtained using the function "Anova" in the package "car". Data were tested for normality and homoscedasticity of variance using Shapiro-Wilk and Levene's tests. Differences in SS-DEE between measurements of individual cheetahs were determined using one-way ANOVA. A general linear model was used to compare the enrichment of feces with urine in the validation study. We examined whether either excreta component was significantly elevated above the other and also whether the elimination rate over time differed between the two types of excreta.

Allometric equations of DEE and SusMS

- Log_e DEE (kJ/day) = 1.871 + 0.670 Log_e (body mass, g) for single species averages of terrestrial mammals (*31*)
- Log_{10} DEE (kJ/d) = 0.697 + 0.697 Log_{10} (body mass, g) for generic mammals (*32*)
- Log_{10} DEE (kJ/d) = 1.150 + 0.640 Log_{10} (body mass, g) for non-aquatic mammals (*33*)
- Log_{10} SusMS = 0.680 – 0.112 Log_{10} (body mass, g) for generic mammals (*34*)

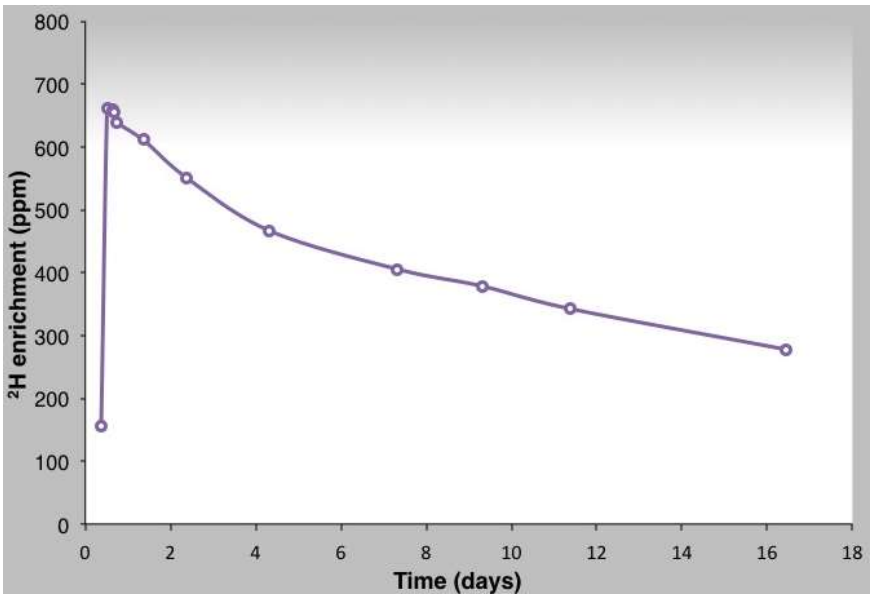

Fig. S1 Elimination of ^{2}H (deuterium) against time after oral dosing in a cheetah

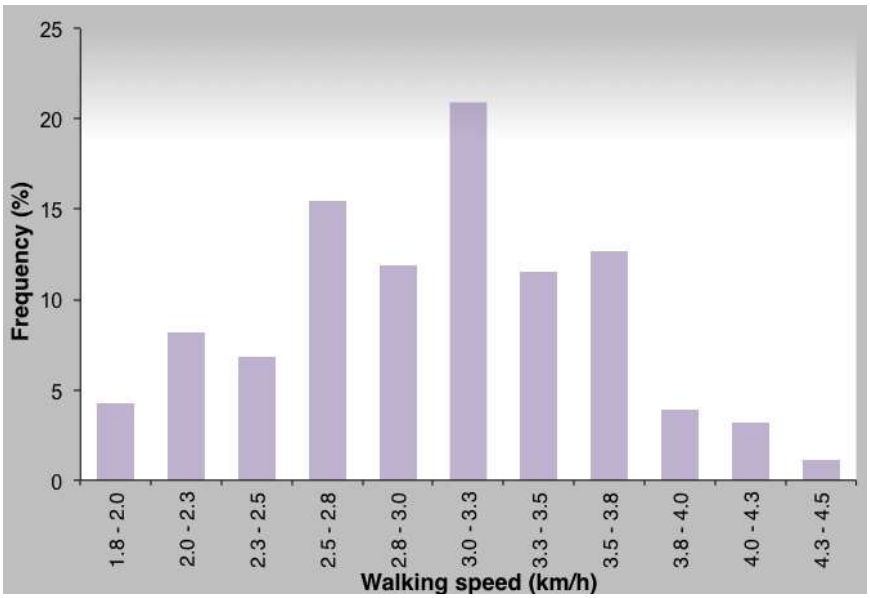

Fig. S2 Frequency distribution of walking speeds (km/h) of Kalahari cheetahs

Location	Measurement number	Date	DEE kJ/d	Sex	Reproductive status (F) or coalition size (M)
Karongwe	1	Oct-06	13792	M	Two
	2	Oct-06	12429	M	Two
	3	Oct-08	4965	F	Single, no cubs
	4	Jun-11	6403	M	Two
	5	Jun-11	7441	M	Two
Kalahari	6	Apr-10	7620	F	Pregnant, gave birth during measurement
	7	Jul-10	7147	M	Three
	8	Aug-10	7643	F	With two x 16 month old cubs
	9	Sep-10	7212	F	Single, no cubs
	10	Nov-10	7906	M	Three
	11	Dec-10	1455	F	With four x 20 month old cubs. Died from probable viral disease at end of measurement
	12	Mar-11	10104	F	Lactating had five cubs in den
	13	May-11	4653	F	With three x 2 month old cubs, lactating
	14	Jun-11	13849	M	One
	15	Nov-11	7559	F	Single, in estrous
	16	Jan-12	17855	F	With three x 9 month old cubs
	17	Feb-12	7946	F	With three x 10 month old cubs
	18	Mar-12	10356	F	With three x 12 month old cubs
	19	Mar-12	12438	F	Single. Came into estrous during the measurement

Table S1 Life histories of different cheetahs measured for DEE

List of supplementary content

Supplementary methods, including:

Supplementary references: (*31-53*)