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MAMMALIAN ENERGETICS

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 expenditure (DEE) of cheetahs was similar to size-based predictions and positively related to distance traveled. Theft at 25% only requires cheetahs to hunt for an extra 1.1 hour per 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 *Lycan 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). Although the short-term energetic consequences of hunting (i.e., the ways that 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 because 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 2-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, and 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 2-week period [multisample DEE (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 [sequential sample DEE (SS-DEE)]. Means are presented ± 1 SD. For full methodological details, see the supplementary materials.

Mean MS-DEE (8883 ± 3854 kJ/d, $N = 19$ cheetahs) 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) [$1.55 \pm 0.69 \times$ resting metabolic rate (RMR)]—were also not significantly different from allometric predictions (Table 1). There were no study-site or sex-related differences in MS-DEE ($\chi^2 = 0.234$, $P = 0.629$ and $\chi^2 = 0.209$, $P = 0.647$, respectively). Cheetahs were mobile for 2.86 ± 0.95 hours (12%) per day moving at an average speed of 0.83 ± 0.54 m/s (excluding prey pursuits) and chased prey 1.2 ± 0.49 times per day for an average of 37.9 ± 11.6 s per chase.

There were significant intra- and interindividual differences in SS-DEE for each cheetah

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Table 1. Means and SDs of body mass (kg), DEE (kJ/d), predicted DEE (kJ/d), SusMS, and predicted SusMS for cheetahs from Karongwe and the Kalahari (31–34). MS-DEE was calculated using the multisample approach of estimating CO₂ production (30). *Significant difference between predicted and measured values at $P < 0.05$.

	Karongwe ($n = 5$ cheetahs)		Kalahari ($n = 14$ cheetahs)	
	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)	12,563	755	11,212*	853
SusMS	1.37	0.55	1.61	0.74
Predicted SusMS (34)	1.44	0.02	1.47	0.02

followed ($F_{18,62} = 1.83, P = 0.041$) (Fig. 1). For predators, with a tendency toward a feast or famine feeding regime, this variation in DEE is expected; individuals are likely to skip hunting on days after 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 next day. However, this was not significantly different from the expected capture rate ($\chi^2 = 1.47, P = 0.225$) and therefore

does not provide direct evidence for less hunting after kills. This crude analysis, though, does not factor in how much the animals eat at each kill. There was a positive relationship between distance traveled 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 traveled 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, whereas 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 ($\chi^2 = 6.36, P = 0.012$) but not between pursuit distance and SS-DEE ($\chi^2 = 0.024, P = 0.878$). SS-DEE was related to distance traveled by the relationship $DEE \text{ (kJ/day)} = 447 \times \text{distance (km)} + 7103$ (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 after days with greater than average DEE ($\chi^2 = 1.60, P = 0.206$), although DEE was greater after days with less than average DEE ($\chi^2 = 5.33, P = 0.021$). Similarly, cheetahs did not travel further after days of less than average distance moved ($\chi^2 = 3.27, P = 0.071$), although they traveled less after days with greater than average distance moved ($\chi^2 = 5.44, P = 0.020$). Because 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 8.84 MJ total DEE, because being mobile was 5.4 times as costly as 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 kleptoparasitism: Of the 43 observed cheetah kills, four (9.3%) were kleptoparasitized (two by brown hyaenas *Hyaena brunnea* and two by lions). Although losing kills increases

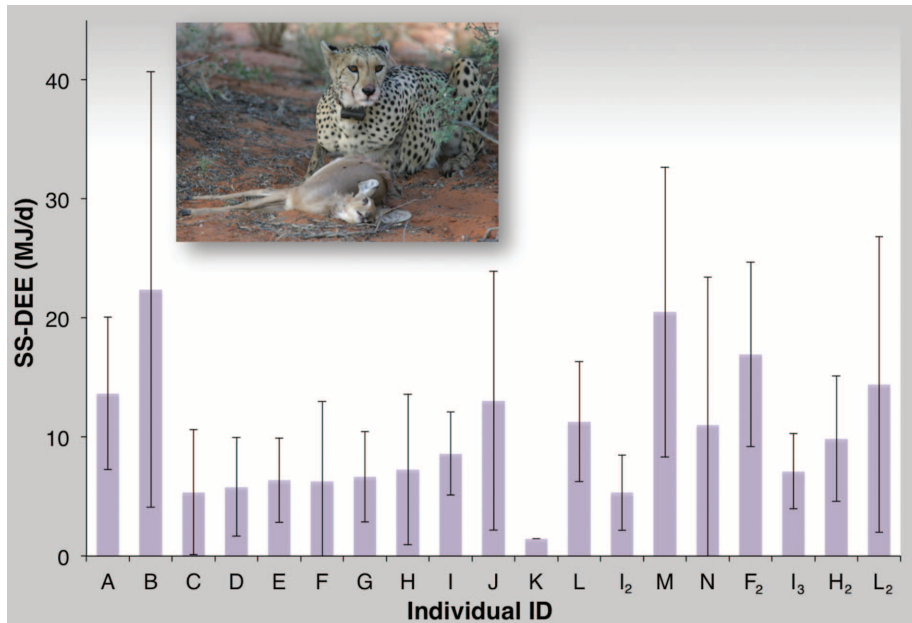


Fig. 1. DEE of cheetahs. Mean energy expenditures (SS-DEE, kJ/d) for 19 measurements, calculated using the two-point method to estimate CO₂ production. Animals A to E were from Karongwe; animals F to L were from the Kalahari. Subscripts indicate repeated measurements within individuals. The order left to right reflects the date of measurement. Error bars denote standard deviations of daily SS-DEE measurements over 2-week periods.

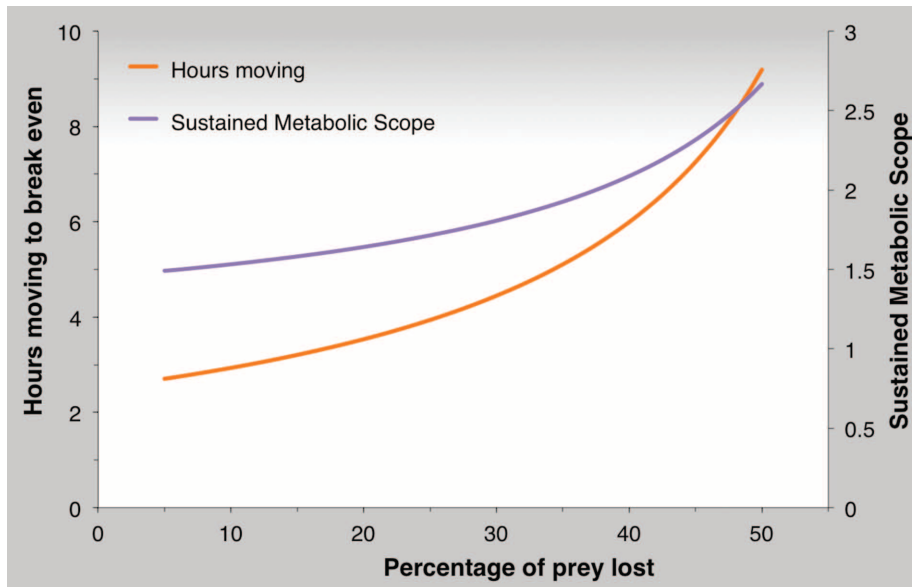


Fig. 2. Model of hours moving to break even and energy balance in cheetahs under different levels of kleptoparasitism. The black line denotes hours spent moving and the red line SusMS (DEE/RMR). The bioenergetic model (6) predicts that if cheetahs lost 25% of their prey to rival predators, they would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

the time required to hunt (Fig. 2), our model suggests that, unlike wild dogs, cheetahs are able to cope with kleptoparasitism rates of 25%, because this would only require an additional 1.1 hour per day (a 38% increase) in time spent mobile and increase DEE to 10.0 MJ per day (a 12% increase). Wild dogs may be exceptional in this regard because the high power costs ($25 \times$ RMR, 35 W/kg) and long durations of prey pursuits (3.5 hours per day) make their hunting strategy extremely costly. This contrasts with the hunting strategy of cheetahs; even though power use during pursuit may reach 120 W/kg (19), prey pursuit takes only a few seconds and constitutes a small component of the daily energy budget (undetected 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 with 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 that costs incurred by traveling drive their energy budgets, rather than those encountered securing prey. Human activities that 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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SUPPLEMENTARY MATERIALS

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Materials and Methods
Figs. S1 and S2
Table S1
References (35–53)

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MAMMALIAN ENERGETICS

Instantaneous energetics of puma kills reveal advantage of felid sneak attacks

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Pumas (*Puma concolor*) live in diverse, often rugged, complex habitats. The energy they expend for hunting must account for this complexity but is difficult to measure for this and other large, cryptic carnivores. We developed and deployed a physiological SMART (species movement, acceleration, and radio tracking) collar that used accelerometry to continuously monitor energetics, movements, and behavior of free-ranging pumas. This felid species displayed marked individuality in predatory activities, ranging from low-cost sit-and-wait behaviors to constant movements with energetic costs averaging 2.3 times those predicted for running mammals. Pumas reduce these costs by remaining cryptic and precisely matching maximum pouncing force (overall dynamic body acceleration = 5.3 to 16.1g) to prey size. Such instantaneous energetics help to explain why most felids stalk and pounce, and their analysis represents a powerful approach for accurately forecasting resource demands required for survival by large, mobile predators.

A central tenet of foraging theory is that animals manage energetic costs and benefits when feeding (1). Yet measuring these costs for large, highly active predators that hunt, chase, and kill mobile prey has been exceedingly difficult, resulting in a poor understanding of how physiological capacities and environmental factors affect foraging success (2).

This is especially apparent for species within the family *Felidae*. Among terrestrial carnivores, felids show a large range in body size, prey preferences, and predatory movements, each of which are linked to the landscape in which they live (3–6). The lankiest cat, the African cheetah (*Acinonyx jubatus*), engages in astonishing high-speed pursuits in open habitats to outmaneuver and overtake smaller, swift prey (7, 8). In contrast, heavy-bodied species including African lions [*Panthera leo* (9)], leopards (*Panthera pardus*), tigers (*Panthera tigris*), and pumas residing in forested or grassland habitats tend to stalk, ambush, and pounce to overpower prey up to several times their size (6).

Of the 36 extant wild felid species, the majority are considered cryptic ambush hunters

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