

Energetics-informed behavioral states reveal the drive to kill in African leopards

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Citation: Wilmers, C. C., L. A. Isbell, J. P. Suraci, and T. M. Williams. 2017. Energetics-informed behavioral states reveal the drive to kill in African leopards. *Ecosphere* 8(6):e01850. 10.1002/ecs2.1850

Abstract. The drive to kill prey is central to understanding the population viability and ecological effects of large carnivores. This drive is modulated by behaviorally determined energetic expenditures, yet current methods of estimating the energetics of terrestrial carnivores are too coarse to inform the fine time scale behavioral decisions that incur the energetic costs leading to predation. Here, we use combined GPS and accelerometer collars calibrated to measure energetic outputs at scales of seconds to months on African leopards in Kenya. Fine-scale data on energetic expenditures and movement allowed us to determine energetically informed behavioral states that accurately identified when animals killed or scavenged prey, and allowed us to visualize novel details concerning the cryptic natural history of these predators. Our results revealed large variation in daily field metabolic rate ranging from 11,000 to 32,000 kJ depending on the animal and the specific behaviors undertaken. Leopards expended 47,470 kJ between kill events on average, but this was increased if meal size from the previous kill was large. Our methods also allowed us to estimate the energetic costs of dispersal, territorial patrol, and parental care, considered important factors in overall energetic balance and thus the drive to kill. Based on this approach, we demonstrate how the cycle of behavior, energetic expenditure, and predatory drive underlies population trajectories of large carnivores as well as their direct and indirect effects on ecosystems.

Key words: energetics; environmental change; field metabolic rate (FMR); human-wildlife conflict; indirect effect; kill rate; *Panthera pardus*; predation rate; trophic cascade.

Received 28 April 2017; accepted 5 May 2017. Corresponding Editor: Debra P. C. Peters.

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INTRODUCTION

Predation is central to understanding the population viability and ecological effects of large carnivores (Estes et al. 2011, Ripple et al. 2014). Yet little is known about the drive to kill prey which underpins predation. This is due, in part, to the paucity of information regarding the interplay between the energetic costs and longitudinal changes in behavior that underlie predation, especially for highly cryptic carnivores. The need

to kill is ultimately determined by an animal's energy expenditure which is modulated by behavior. Individuals engaging in more energetically costly behaviors such as those linked to reproduction (e.g., parental care or territorial patrol) should have a higher field metabolic rate (FMR) than individuals engaging in less costly behaviors. Energy expenditure in turn influences the ecological effects of large carnivores, as changes in FMR are likely to influence selection of and/or kill rates on prey. Higher kill rates can

lead to changes in prey density or behavior, the effects of which can cascade to lower trophic levels (Soule et al. 2005). And to achieve higher kill rates, large carnivores often incur additional risk by preying on domestic livestock, which can lead to human–wildlife conflict (Woodroffe 2000). The critical link (i.e., the relationship between behavior and FMR) to understanding these phenomena has yet to be fully developed, however, given the substantial logistical challenges of linking energetics and behavior at appropriate time scales. Doing so will be critical to developing a mechanistic understanding of large carnivore viability and their cascading impacts on ecosystems.

Our ability to determine the energetics of terrestrial carnivores is mostly limited to daily averages of FMR measured over weekly time scales. The most common methods for evaluating FMR involve summing behavior-specific energetic costs according to daily activity budgets (e.g., Yeates 2006) or using doubly labeled water techniques (See Nagy et al. 1999 for a review). The latter involves injecting isotopically labeled water into subjects and then measuring the ratio of isotopes remaining upon recapture (Nagy et al. 1999). This provides an estimate of mean daily FMR over the inter-capture period (typically five to seven days depending on the size of the subject), but is too coarse to match energetics to the diversity of daily behaviors that drive the impulse to kill, and lacks the longitudinal breadth to capture changes in energy expenditure related to major life history transitions (e.g., between breeding and non-breeding periods). In the best case, field energetics should provide a unique window into the physiological demands of an animal, ranging from parental care to foraging behavior, and how these physiological demands drive disparate ecological phenomena through species interactions. This understanding is dependent on the ability to measure energetic costs at appropriate ecological and physiological time scales.

Here, we measured behaviorally linked energetic expenditures at the scale of seconds to months in a large terrestrial carnivore, the African leopard (*Panthera pardus*), to determine the suite of behaviorally specific caloric demands leading to predation. By linking energetics and behavior at appropriate time scales, our approach allows

deconstruction of how life history-specific behaviors influence energetic demand and consequent killing and feeding behavior.

METHODS

Study site

We conducted our study at the Mpala Research Centre in Laikipia County, Kenya (0.29° N, 33.90° E). The habitat consists of semi-arid bushland and riverine woodland receiving an average of 508 mm of rainfall in two to three rainy seasons per year (Augustine and McNaughton 2006). Leopards used a combination of conservancy, private ranch, and adjacent community lands. Livestock share the habitat with wildlife in both areas. This stock is tended by herders during the day and penned into either thornbush or metal fence bomas (i.e., corrals) at night. The study area also supports populations of other large carnivores (lion *Panthera leo*, cheetah *Acinonyx jubatus*, wild dog *Lycaon pictus*, spotted hyena *Crocuta crocuta*, as well as leopards) and a full suite of antelope and other herbivores ranging in size from rodents to elephants *Loxodonta africana*. Our work was conducted during the dry season from January to March 2015. Average daily low and high temperatures were 12° and 29°C, respectively, during this period.

Leopard capture and collaring

Five leopards (Table 1) were captured using foot snares (Frank et al. 2003) and anesthetized using ketamine and medetomidine which was reversed with atipamezole. Animals were sexed, weighed, aged, and instrumented with a species movement, acceleration, and radiotracking (SMART) collar (Fig. 1A). Collars were Vectronics GPS PLUS brand collars with a custom 3-axis accelerometer with a range of ± 8 g's. The Global Positioning System (GPS) was set to sample every five minutes and the accelerometer at 32 hz continuously. Collars were retrieved using a remote drop-off mechanism on the collar at which point we manually downloaded the accelerometer data. GPS data were downloaded daily via either Iridium satellite uplink or a handheld Ultra High Frequency (UHF) terminal. The GPS fix success rate ranged from 99.7% to 99.9% across collars. Collars were deployed for about 2 months in order to not run out of battery, but long enough to test our research questions.

Table 1. Description of leopards collared.

Leopards	Gender	Age (yr)	Weight (kg)	Days collared	Descriptor
Mzee	M	5–8	58	59	Adult male
Chumvi	F	5–8	27	66	Adult female with one cub
Ewaso	F	3–4	27	50	Adult female without cubs
Limofu	M	1–1.5	27	66	Yearling male cub
Morani	M	2–4	43	53	Dispersal-aged male

Feeding sites

Feeding sites were ground-truthed by visiting GPS locations clustered within 50 m of each other and lasting more than 2 h. We visited the centroid of each cluster (and subclusters) usually within one to two days of the animal leaving but sometimes as long as five days after the animal left, and searched for the remains of consumed prey. When we located prey remains, we identified them to species. Aging and sexing prey was not possible because of the lack of appropriate evidence. In this system, prey remains disappear quickly such that the only consistent remains are hair and stomach contents.

Energetics calibration

Energetic expenditure was related to tri-axial accelerometer data from the collars by placing pumas (*Puma concolor*) on Plexiglas-enclosed treadmills as has been reported previously (Williams et al. 2014). Because energetic expenditure is related to body size in carnivores (Nagy et al. 1999), and because pumas and leopards share similar locomotor gaits and kinematic patterns, we assume that energetic calibrations performed on similarly sized pumas are an appropriate felid model for the leopards in this study. Recordings from the tri-axial accelerometer were converted to overall dynamic body acceleration (ODBA) as described in Qasem et al. (2012). Overall dynamic body acceleration was then averaged over one-minute intervals and converted to oxygen consumption (VO_2) according to the empirically derived relationship developed by Williams et al. (2014)

$$VO_2 = 3.52 + 58.42 \times ODBA \quad (1)$$

where VO_2 is in $mL\ O_2 \cdot kg^{-1} \cdot min^{-1}$. This mass-specific value was then converted to mass-specific leopard metabolism (MVO_2 in $mL \cdot kg^{-1} \cdot min^{-1}$) by multiplying by the mean body mass (in kg) of the

pumas used in the collar calibration divided by the body mass of each leopard in the current study.

$$MVO_2 = \frac{65.7 \times VO_2}{\text{leopard mass}} \quad (2)$$

This was converted into whole-body energetic cost in kJ using a conversion factor of 20.1 J/mL O_2 (Schmidt-Nielsen 1997) where

$$\text{Energetic cost}_{LEOPARD} = \frac{MVO_2 \times \text{leopard mass} \times 20.1}{1000} \quad (3)$$

Animal speed (in m/s) on the landscape was calculated from the difference in subsequent GPS locations divided by the sampling interval.

RESULTS AND DISCUSSION

Mean daily FMR derived from the SMART collars and averaged over the five study leopards was 20,029 kJ/d (range 17,000–23,000 kJ/d). To evaluate the accuracy of these FMR predictions, we regressed this value, along with previously reported FMR values for terrestrial carnivores using doubly labeled water (Nagy et al. 1999), against body mass. Collar-derived mean daily FMR was well predicted by this relationship (Fig. 1B). Unlike previous studies of FMR in terrestrial carnivores, however, we were able to predict energetic expenditure from instantaneous to monthly time scales. Rather than summing the energetic cost of individual behaviors to determine FMR as typically done, we used high-resolution, animal-borne accelerometers and the ODBA– VO_2 relationship (Eq. 1) to parse FMR into a behavioral storyline detailing energetically costly events. This revealed the underlying factors for the substantial variation in daily energetic expenditures we observed, with energetic outlays doubling or tripling between low- and high-energy days depending on the leopard's

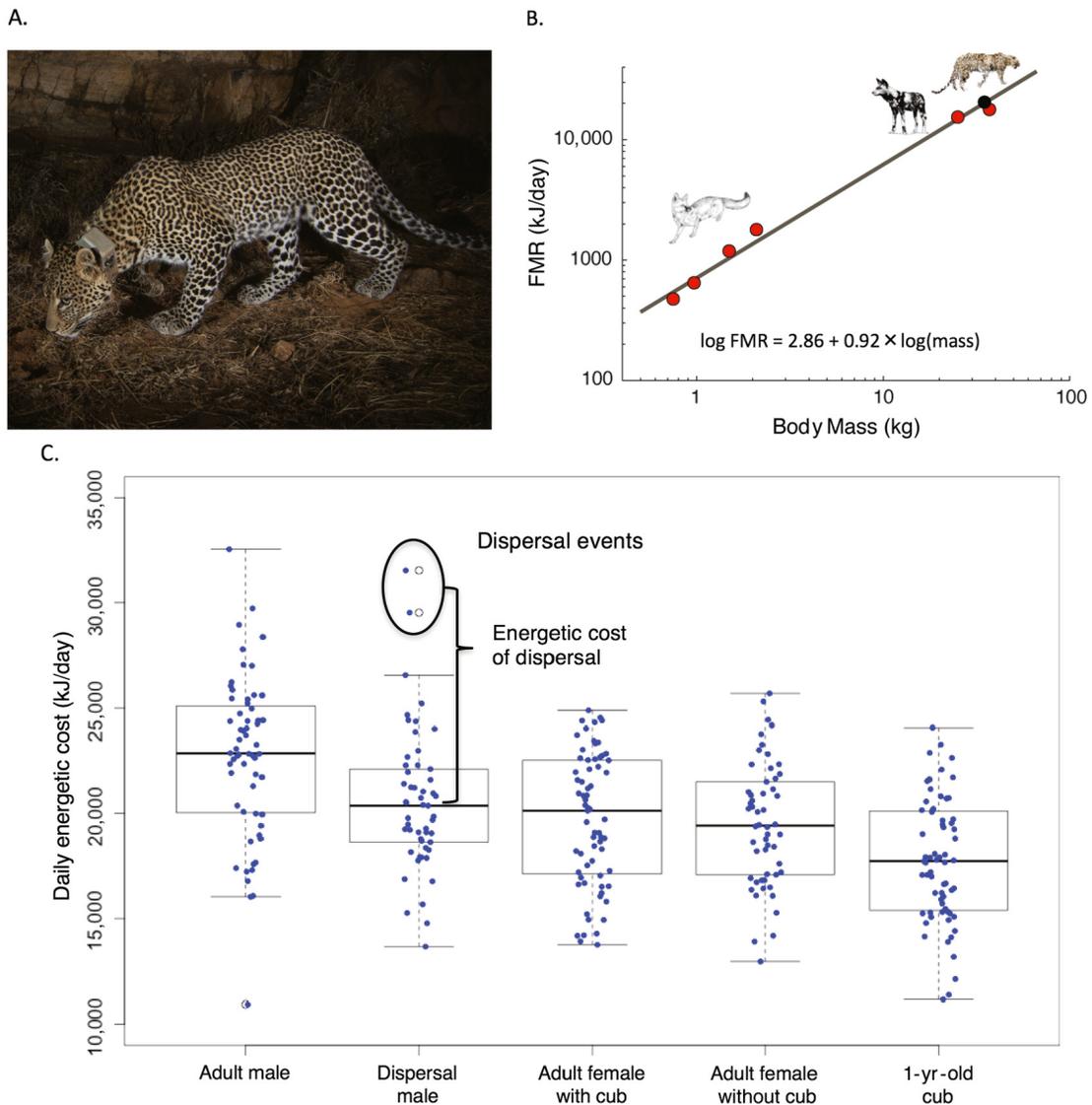


Fig. 1. Variability in daily energetic costs of wild leopards. Daily field metabolic rate (FMR) of leopards (A) estimated from animals wearing species movement, acceleration, and radiotracking collars is (B) well predicted from allometric regression including other terrestrial carnivores (black dot is the mean of leopards in this study; red dots are estimates of FMR using doubly labeled water from other studies; Nagy et al. 1999). (C) Boxplots of daily energy expenditure for each of the five leopards in our study, however, reveal substantial variation in daily energy expenditure. Points represent daily energy expenditures and are scattered horizontally for better visualization. One outlier for the adult male occurred on the first full day after being anesthetized. The two outliers for the dispersal male occurred on days that he dispersed.

behavior (Fig. 1C). For example, we documented one dispersal event during which a two- to three-year-old male spent two days exploring new habitat outside of his normal home range.

During that period, he expended 52% more energy than during his average energetic day.

On an even finer time scale, two-dimensional histograms of energy expenditure and speed over

five-minute intervals revealed four dominant behavioral states in leopards (Fig. 2A). Resting was the most common behavioral state for all five animals and was indicated by a combination of zero or near-zero speed and low energetic expenditure (Fig. 2A, I). Feeding was indicated by zero or near-zero speed with moderate energetic expenditure (Fig. 2A, II). We also identified two types of movement with different energetic profiles: “meandering movement,” which involved moderate speeds and energetic outlays and was characterized by an average step length of 80 m over five minutes and a wide variety of turning angles (Fig. 2B), and “directed movement,” which involved high speeds and energetic outlays and was characterized by an average step length of 200 m and small turning angles (Fig. 2B). The meandering movement state can be thought of as

interrupted locomotion, associated with multiple instances of stopping and starting and changing trajectory over a five-minute interval. Conversely, the directed movement state is generally characterized by continuous walking over the five-minute interval with only small changes in directionality as compared to the meandering state. The decision to use either mode of walking represents an important factor in setting the daily energetic costs of leopards due to the distance walked as well as the unique energetics of pausing (Kramer and McLaughlin 2001) and turning (Wilson et al. 2013). While all four non-dependent leopards (i.e., all but the yearling male cub) spent substantial time in both movement modes, the territorial adult male spent more time in directed travel than the others as indicated by the peak in his movement in this behavioral mode (Fig. 2A, IV).

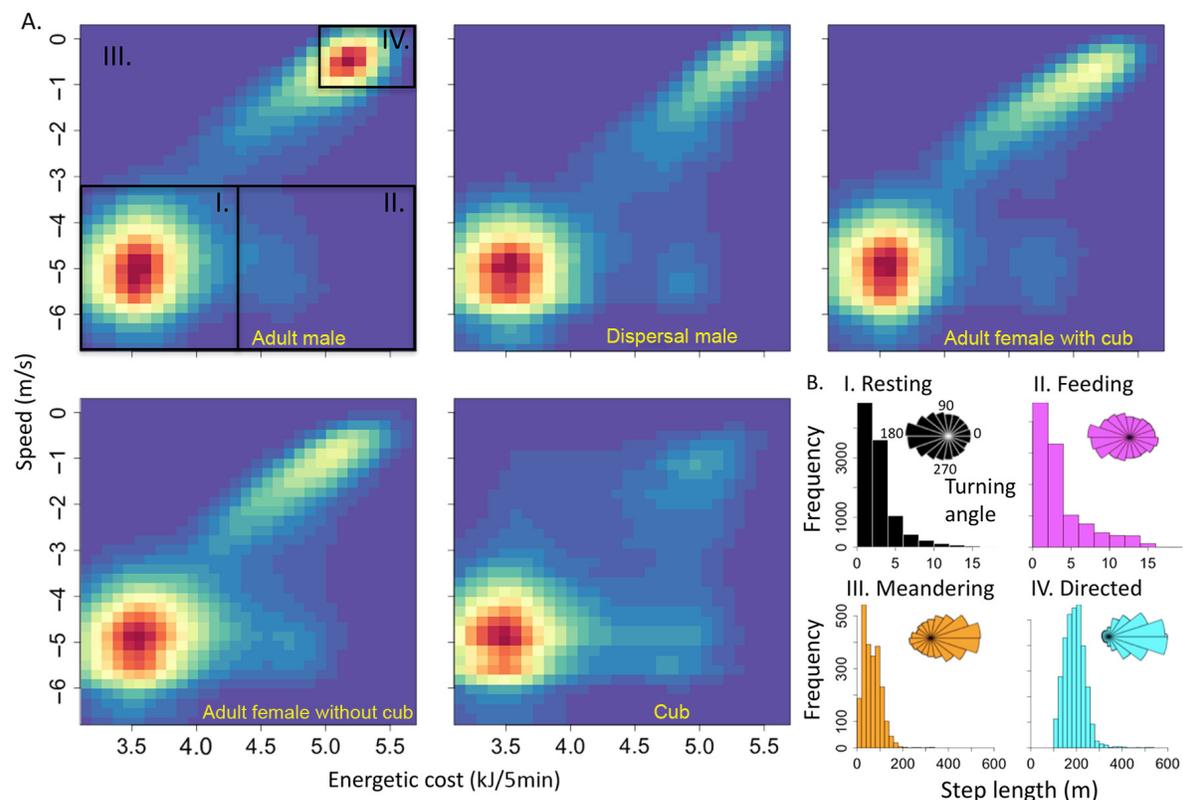


Fig. 2. Energy and speed shape the behavior of leopards. (A) Two-dimensional histograms of energetic cost and speed over five-minute increments for each of the five leopards. As the color transitions from purple to red, the time spent by the animal in that energetic by speed space increases. Areas of concentrated activity (red color) correspond to I. resting, II. feeding, III. meandering travel, and IV. directed travel. (B) Step length and turning angle distributions for each of these four behaviors.

These energetics-informed behavioral states, coupled with geographic information, provide a simple and highly reliable tool for remotely identifying when and where a leopard attacks and kills prey, as well as when they scavenge. We visited 157 GPS clusters from the three adult leopards and found the remains of prey items at 39 of these sites ranging in size from African hare (*Lepus microtis*) to impala (*Aepyceros melampus*). Our energetics-based approach (i.e., Fig. 2) identified feeding at 37 (95%) out of 39 of these clusters. Raw accelerometer data for the remaining two clusters revealed them to be rest sites even though we found evidence of a kill (e.g., impala horns in a tree) at these locations. These prey remains were likely from a kill prior to our study. In total, our histogram approach identified 19, 26, and 36 kill or scavenging sites for the adult male, adult female without cubs, and adult female with cub, respectively, over the entire collar deployment period. Kill events were preceded by characteristic surges in accelerometer activity lasting 4–20 s, indicating the likely timing of the kill event (Appendix S1: Fig. S1); energetic expenditures ranged from 63 to 304 kJ in the two-minute period surrounding the kill surge. In a few cases, feeding commenced without any surge in acceleration, indicating scavenging activity. We documented scavenging at 21%, 19%, and 3% of the feeding sites for the adult male, adult female without cubs, and adult female with cub, respectively. These scavenging rates should be thought of as minimum scavenging rates, because while it is hard to imagine how a leopard could kill prey without causing a surge in accelerometer data, it is certainly possible that scavenging could follow a surge in accelerometer data that did correspond with an actual kill.

The energy expended between kill events varied substantially within and among leopards. The adult male leopard expended an average of 52,015 kJ between kill events, which was significantly (t test, $P = 0.01$) more than the average of each adult female (30,050 kJ and 30,355 kJ). Leopards also expended significantly more energy between kills as prey size increased (based on the number of minutes spent feeding at the first kill of each pair of kills as a proxy for prey size, Fig. 3; $P < 0.01$, $r^2 = 17\%$). Significant variation in energy expenditure between kills indicated that the ability to find and kill prey varies substantially from one kill to the next.

Visualizing these energetically informed behaviors in a spatial context can reveal cryptic natural history and generate hypotheses about the underlying drivers of leopard killing behavior. To illustrate this, we color-coded GPS locations according to the behaviors described above and plotted them on satellite imagery of the study area. Comparing the behavior of the adult male to the adult female without cubs reveals the preponderance of directed travel by the male and meandering by the female (as revealed by the histograms in Fig. 2) but, by placing these in a spatial context, the data suggest that he is using directed travel to patrol his territory while she is searching the landscape for prey (Fig. 4A). Successful hunts can be visualized by first finding clusters of magenta points indicating continuous feeding behavior and then scanning the raw accelerometer data for a few minutes prior to this feeding to locate the surge in accelerometer activity corresponding to the kill event (Fig. 4B). In this example, the adult male leopard approaches a small village in a meandering fashion. At 03:10 hours, he attacks and kills a goat inside a thorn boma (a type of corral in which pastoralists keep livestock at night). He then spends the next five minutes carrying the goat across the river where he commences feeding under the protection of vegetative cover. Parental care is also revealed by visualizing these energetics-informed behaviors. In Fig. 4C, the adult female kills an aardwolf (*Proteles cristata*; kill 1) on which she feeds. She then meanders and alternately rests for a few hours until she kills an impala (kill 2). After feeding briefly on the impala, she walks in a directed fashion back to her yearling cub who she then brings in a directed fashion to feed on the aardwolf and subsequently the impala. Comparison of the energetics of the adult female and her yearling son when they are moving together also shows the relative energetic efficiency of the female. Her cub expends 12% more energy to move an equivalent geographic distance. The track of the dispersing young male reveals that directed travel is driving his increased energy expenditure (Fig. 4D).

Actograms, which allow us to visualize the behavior and energy expenditure of leopards over the entire collar deployment (Fig. 5A–E), reveal substantial variation in behavior among animals. For instance, actograms reveal that the

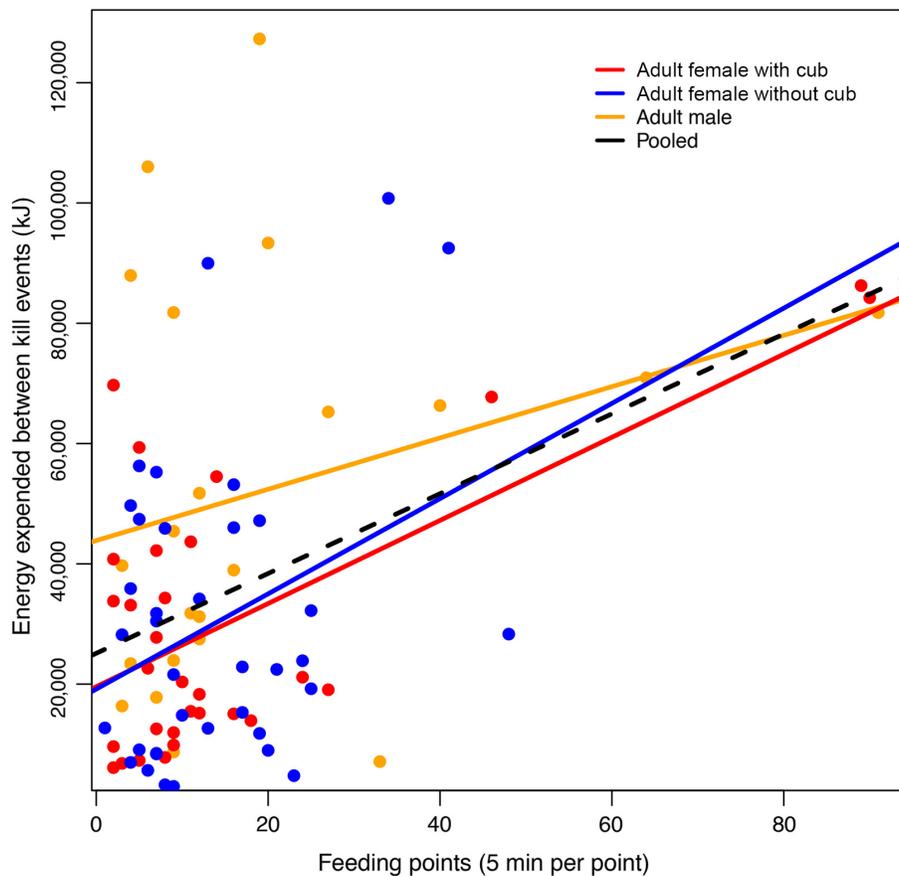


Fig. 3. Energy expended between kill events for the three adult leopards. The feeding time at the first kill of each pair is used as a proxy for prey size. Lines represent the best-fit linear model for each leopard independently (solid lines) and all three pooled together (black dashed line).

adult male is highly nocturnal (Fig. 5A), while the adult female with cubs is active at all times of day (Fig. 5B), and that her yearling cub is more diurnal or crepuscular (Fig. 5E). The adult male was also highly regular in his use of directed travel at night, indicating that he was using directed travel to patrol his territory. In contrast, the adult females were more sparing in their use of directed travel, preferring to meander, most likely in search of prey. The timing and duration of feeding (shown as magenta bands in the figure) also varied substantially within and among animals. For instance, the adult male fed for longer bouts but fewer times than the adult female with cubs, who fed more frequently but for shorter durations.

The role of behavior and life history in driving leopards to kill prey can be quantified by

summing the total contribution of each behavior to the average daily energy expenditure of each animal (Fig. 5F). We estimated the energetic cost of the adult male's territorial behavior by assuming that the extra directed travel he engaged in relative to the adult female without cubs (who neither dispersed, patrolled a territory, nor cared for cubs during the study period) was a result of needing to patrol a large territory. Using this approach, we estimate that the energetic cost of his territorial behavior constituted 25.8% (bracketed area in Fig. 5F) of his daily caloric expenditure or 5851 kJ/d on average. Such marked energetic demands due to movements associated with territorial behaviors might also explain the increased energetic expenditures associated with male movement documented in sea otters (Yeates 2006) and many canids (Girard 2001, Williams

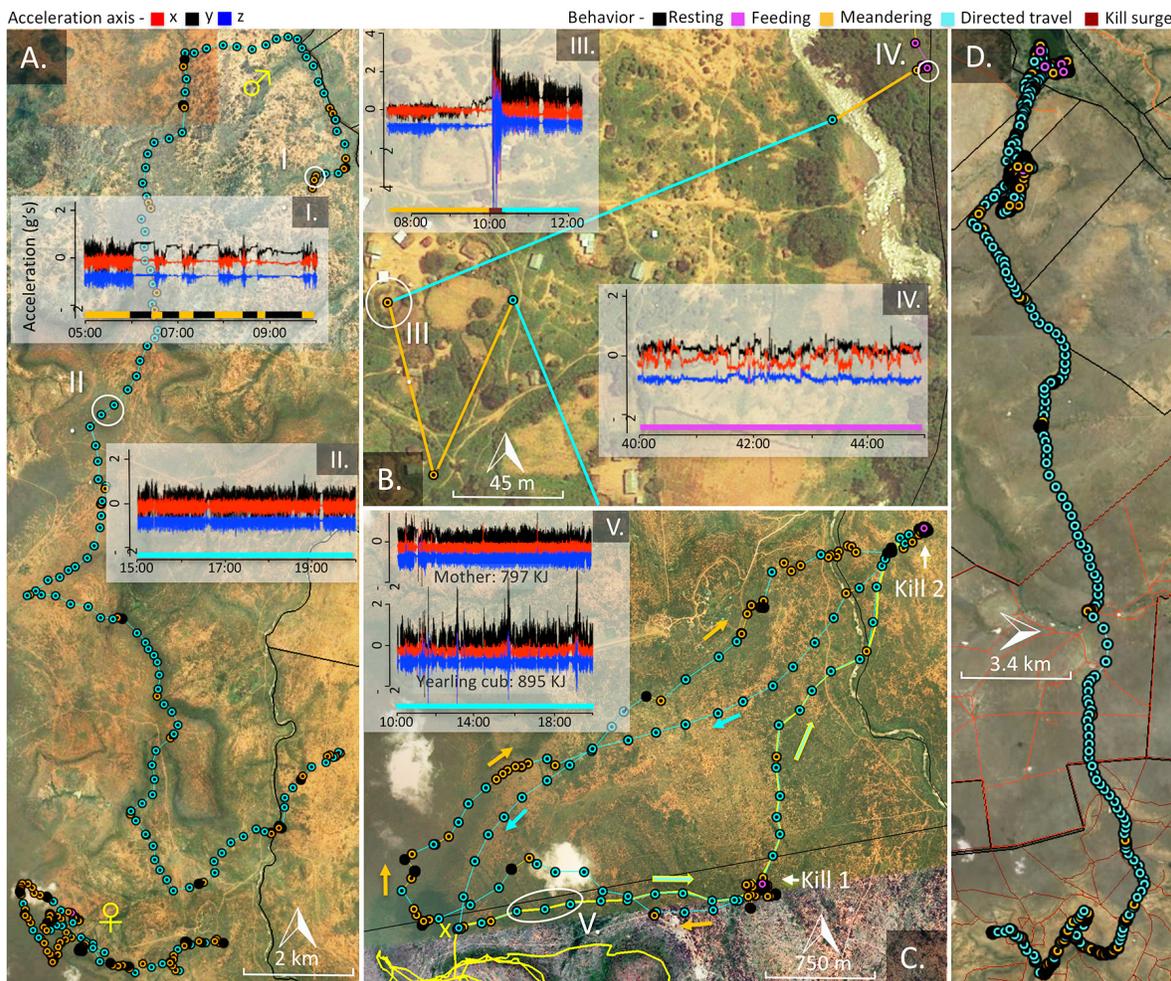


Fig. 4. Five-minute GPS locations are color-coded according to the behaviors identified in Fig. 2 and overlaid on a satellite image of the study area. Examples of raw tri-axial accelerometer data corresponding to certain circled GPS locations that are plotted over five- or 10-minute increments. Color bands below the accelerometer data correspond to the behaviors listed in the legend. (A) Representative 24-h movement pattern for the adult male (top) and adult female with cub (bottom). Characteristic accelerometer traces corresponding to I. meandering and II. directed travel are also plotted. (B) GPS track of the adult male as he kills a goat inside a boma and then carries it across a river to feed. Accelerometer trace III. shows the kill surge as he enters the boma at 10 min after the hour followed by directed travel. IV. shows feeding behavior. (C) The adult female with cub kills and feeds on an aardwolf at kill 1, then meanders to kill 2 where she kills an impala. She then travels toward her cub (cub is depicted by the yellow line) in a directed manner and meets up with him at the yellow x. She then brings him to feed at kill 1 followed by kill 2. Accelerometer traces represent 10 min of mother and cub moving together. (D) Track of the dispersal-aged male leopard as he made a foray outside of his normal home range.

et al. 2002, Laundre and Hernandez 2003). Likewise, the adult female with cub spent an extra 8.3% of her daily energy expenditure on directed travel in comparison with the female without cubs, representing an average of 1634 kJ/d in

extra energy expenditure that she devoted to parental care. These differences in energy expenditure between the individuals in our study provide the first putative estimates of the energetic costs to large carnivores of engaging in reproductive

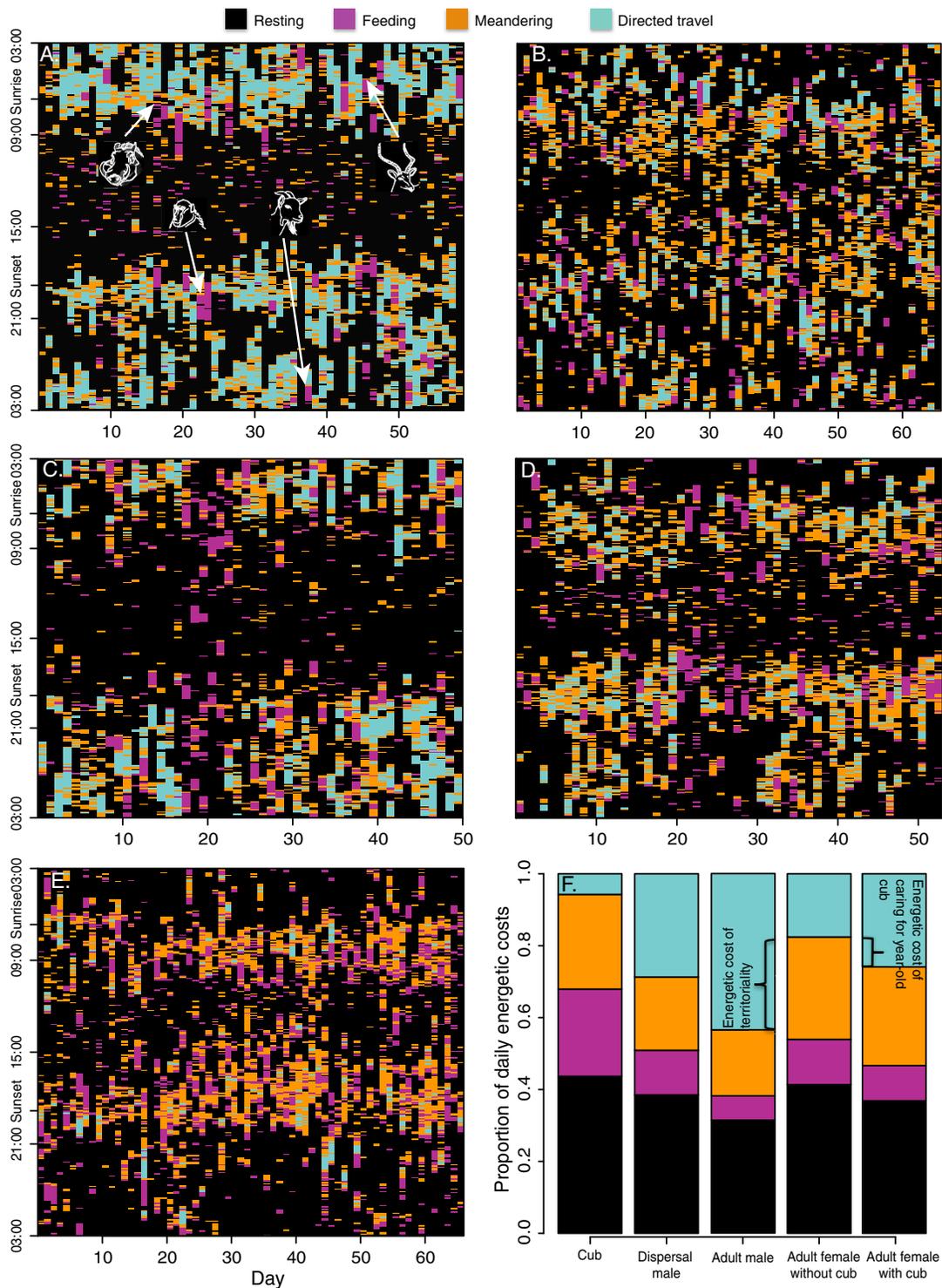


Fig. 5. (A–E) Actograms displaying the temporal sequence of behaviors over the course of the study. Each column represents one day and each color slice represents the behavior over a five-minute period derived from the speed by energetics relationships detailed in Fig. 2 for the (A) adult male with a sample of species killed depicted

(Fig. 5. Continued)

by line drawings, (B) adult female with cub, (C) dispersal-aged male, (D) adult female without cubs, and (E) yearling cub. (F) The proportion of energy consumed by day averaged over the study period for each leopard.

behaviors and suggest that these costs may be a major contributor to the drive to kill.

Accelerometers are increasingly being used to estimate the energetics of freely roaming wild animals (Curry 2014) to test new questions in animal ecology (Wilmers et al. 2015). This often involves a laboratory to field approach by which accelerometers are calibrated on animals in captivity and then deployed on wild counterparts (e.g., Williams et al. 2014). Accelerometers can also be fit to movement patterns using techniques from machine learning to estimate underlying behaviors such as walking, running, and resting (Watanabe et al. 2005, Wang et al. 2015). Our

approach here of combining energetics with GPS-derived animal velocity through two-dimensional histograms reveals new features of cryptic natural history that allow for generating hypotheses about the underlying drivers of predator killing behavior, which was not possible to understand using these previous approaches.

Although the sample size in this study was too small to test for general patterns of the influence of life history on energetics, our results provoke a new conceptual framework that links behaviors to ecological outcomes (including kill rate, prey selection, and indirect effects) through the currency of energy expenditure (Fig. 6). According

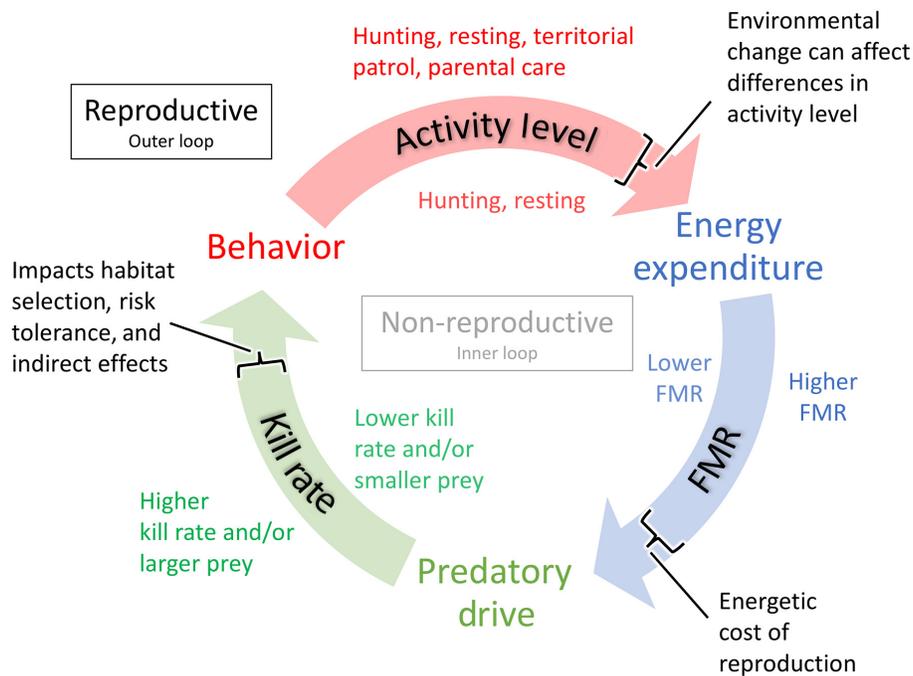


Fig. 6. Conceptual diagram illustrating the interaction between behavior, energy expenditure, and the drive to kill (predatory drive). Reproductive individuals exist along the outer loop of the figure and are predicted to have higher activity levels, field metabolic rate (FMR), and kill rates than non-reproductive individuals (inner loop) because of the increased behavioral demands of reproducing. The thickness of the arrows (as indicated by the brackets) illustrates the difference in activity levels, FMR, and kill rates between the two life history stages. As such, the thickness of the arrows determines the energetic cost of reproduction and the corresponding impact of this increased cost on ecological variables such as habitat selection, risk tolerance, and indirect effects. Environmental change can impact the thickness of the arrows through its influence on leopard behavior (e.g., navigating fencing might increase the cost of territorial patrol).

to this framework, non-reproductive individuals (Fig. 6, inside loop) will primarily rest and hunt to meet their daily maintenance requirements. These individuals will have a comparatively low FMR and as a result should kill less often or kill smaller, less risky prey, potentially resulting in relatively weak top-down effects. In order to reproduce (Fig. 6, outside loop), males will need to disperse to find a territory and patrol it once they have found one, both energetically costly behaviors because of the increased directed travel required to accomplish them. Reproductive females will need to hunt more often and engage in increased directed travel to unite offspring with food sources, thus incurring a higher energetic burden. When individuals switch from being non-reproductive to being reproductive, the resulting increase in FMR due to these changes in behavior (represented by the width of the arrow in Fig. 6) will lead them to seek a higher kill rate and/or larger riskier prey. This might result in a change in habitat selection if larger prey occupy different habitats or if attaining a higher kill rate requires hunting in riskier habitats, such as those closer to human settlements. Increasing predatory drive might cause changes in hunting behavior and/or risk taking that could then cascade through the food chain due to either the density (e.g., Estes and Palmisano 1974) or behaviorally (e.g., Suraci et al. 2016) mediated effects that large carnivores have on their prey. These differences in hunting are driven by the increased energetic demands of fitness-enhancing behaviors, which until now were impossible to measure in free-living terrestrial carnivores.

Environmental change, in this framework, can be conceived as impacting the width of the arrows. For instance, habitat fragmentation or fencing might increase the energy required to patrol a territory or provide parental care, thus leading to either altered kill rates, indirect effects, and/or human-wildlife conflict (as a result of increased risk taking), or decreased population viability if individuals cannot increase kill rates on wild prey. By measuring energy use by large carnivores at the appropriate temporal and spatial scales, we can now link environmental change, through the filter of life history and behavior, to energetics. Understanding the energetic demands of individuals then allows us to better understand their drive to kill and its ecological consequences.

ACKNOWLEDGMENTS

This work was supported by NSF Grant DBI-1255913 (C.C.W. and T.M.W.) and NSF Grants BCS 99-03949 and BCS 1266389, the L.S.B. Leakey Foundation, and the University of California, Davis, Committee on Research (L.A.I.). We thank Dairen Simpson, Steve Ekwanga, and Mathew Mutinda for assistance with leopard capture; Marc Napao for assistance in finding kill sites; and Chris Carbone, Robin Freeman, Justin Suraci, and Jim Estes for comments on discussion about the analyses. Photograph in Fig. 1 was taken by John Armstrong. Animal handling procedures were approved by the UCSC and UCD IACUCs and approved in Kenya by the Kenya Wildlife Service and National Commission for Science, Technology, and Innovation. Electronic copies of the data are stored on servers at UCSC and available by request from CCW.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1850/full>