Movement patterns and athletic performance of leopards in the Okavango Delta

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Abstract

Although leopards are the most widespread of all the big cats and are known for their adaptability, they are elusive and little is known in detail of their movement and hunting energetics. We used high-resolution GPS/IMU (inertial measurement unit) collars to record position, activity and the first high speed movement data on four male leopards in the Okavango Delta, an area with high habitat diversity and habitat fragmentation. Leopards in this study were generally active and conducted more runs during the night, with peaks in activity and number of runs in the morning and evening twilight. Runs were generally short (<100 m) and relatively slow (maximum speed 5.3 ms^{-1}, mean of individual medians) compared to other large predators. Average daily travel distance was 11 km and maximum daily travel distance was 29 km. No direct correlation was found between average daily temperature and travel distance or between seasons and travel distance. Total daily energy requirements based on locomotor cost and basal metabolic rate varied little between individuals and over time. This study provides novel insights into leopards' movement patterns and athletic performance through quantitative high-resolution measurement of the locomotor, energetic, spatial and temporal movement characteristics. The results are unbiased by methodological and observational limitations characteristic of previous studies and demonstrate the utility of applying new technologies to field studies of elusive nocturnal species.

Introduction

Leopards are the most widespread and numerous of the large cats with a distribution ranging widely across Africa and Asia (1). They occupy a wide variety of habitats including deserts,

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savanna grasslands, rainforests and high mountain ranges. They are thought to be the most adaptable of the large cats (2), modifying their behaviour, prey selection and ranging patterns according to conditions. However, despite this versatility, like many other species, their numbers have declined dramatically (3), with anthropogenic impact on the environment, poaching, trophy hunting, human conflict, habitat fragmentation and loss and reduced prey availability all contributing factors. An estimated 28-51% of leopard range has been lost in southern Africa (4), whilst globally leopards have lost 69-75% of their historic range (4). Conservation of the leopard and other vulnerable species requires insight into how they utilise their environment: for example, how territory size, movement patterns and hunting strategies correlate with habitat and season. Understanding these issues requires long term data sets; often gathered by observation(5-9), with the help of VHF collars (1, 10-16) or more recently sourced from GPS collars(17-21). GPS collars can record data 24/7 for months or even years, in any terrain or conditions, at lower cost and without the bias inherent with observational studies. However, the limitation of collar battery life means that most studies use a sample schedule that prolongs collar life at the expense of high resolution data collection, often relying on daily or hourly measurements and recording no data on the most fine-scale and high speed movements such as hunting or escape events which are often essential for survival. These limitations have been overcome by a new generation of solar rechargeable GPS/IMU collars, which are able to dynamically switch sample rate based on the animals' activity to provide long-term high-resolution movement monitoring including very detailed data on high-speed events. Such detailed data enables insight into daily locomotor costs, habitat use, hunting strategies and factors that impact hunting success (22-25) and enables investigation of intra- and interspecies interaction between collared individuals (26). In this study, we obtained the first measurements of athletic performance of leopards and used high resolution movement data to estimate energetic cost of daily locomotion and analyse territory use.

The leopard's solitary and nocturnal lifestyle and preference for rugged terrain and dense vegetation (5) make direct observations of their hunting and movement difficult (15, 21). Consequently, detailed descriptions of their movement and behaviour often include some type of methodological bias towards spatial or habitat-specific observations. Habitat, sex, age and prey density influence home range size (5). Adult male leopards are reported to occupy home ranges from 13 km^2 (27) to 800 km^2 (6). The most comprehensive study of the African leopard reports variation between 16.4 and 96.1 km^2 in habitats associated with the Kruger National Park (5). Leopards are primarily nocturnal in most areas, while the dominant form of activity during the day is resting (5). However, all predominantly nocturnal activities such as walking, feeding, hunting and courting have been observed during daylight hours, and in

some African forest mountain areas leopards are reported to be relatively diurnal (1, 13, 14). Leopards rely on sight and sound during hunting (5, 28, 29), but avoid hunting in the open (30, 31). They are known to either stalk or ambush prey with only short chases (mean 5 m to 10 m (11, 30); mean 10.3 m, range 0-117 m, (15)). However, observations of leopards in the Kalahari (12) suggest, when hunting in more open habitats, chases can be considerably longer (mean±s.d 52.3±79.9 m, range 5-450 m). Maximum speed reported for leopards is 60 kmh^{-1} (2). Males travel further than females and distance travelled per day is thought to correlate to size of the territory (1, 13); however, this is not always the case (19). Mean distance travelled is reported to be typically between 2.3 and 4.2 km (1, 5, 13, 19, 21), with the exceptions of Stander et al. (15) reporting a mean daily distance travelled of 12.2 km and Bothma et al (12) of 14.3 km and a maximum distance of 33.0 km for male leopards in the Kalahari. Most leopard studies relied on direct observation and radio telemetry or spoor tracking and few have GPS collar data with at most daily or hourly sample rates. Here we use high temporal and spatial resolution GPS data on four male leopards in the Okavango Delta in order to (a) determine daily activity and distance travelled (b) estimate the energetic locomotor costs, (c) investigate movement spatially with reference to territory boundaries, and (d) quantitatively characterise high speed locomotion and evaluate athletic performance.

Methods

Leopards

Four male leopards (CHK, GSE, CAL, LPM) were immobilized by free darting from a vehicle and collared (approved by RVC Ethics & Welfare Committee and under Botswana Department of Wildlife and National Parks research permit EWT8/36/4), in the region of the Okavango Delta in Northern Botswana. The leopards were monitored over different time periods by researchers from the Botswana Predator Conservation Trust as part of an ongoing study. One individual (GSE) was collared three times. Collars were operational for five to eight consecutive months. Data were recorded over a total of 33.5 months (1007 days) at five minute intervals, with acceleration triggering the collars/data collection into high resolution mode (5 Hz GPS/50 Hz IMU) for a total of 19 weeks in order to capture run occurrence and performance. CHK and GSE provided data from April – October 2012 (CHK 03.04.-20.10.12, GSE 04.04.-02.09.12) and CAL and GSE from September 2015-April 2016 (CAL 05.09.15-29.4.16, GSE 05.09.15-20.4.16). LPM was recorded between November 2016 - May 2017 (15.11.16-25.05.17). GSE provided additional running data for June 2017 (16.05.17-30.06.17), but five minute data were not used due to the short period of data collection.

Two research assistants followed CAL and GSE in October 2015, to the best of their abilities, and recorded kill and mating sites.

Data logged on the collars were retrieved opportunistically via UHF radio link from a vehicle. Expected battery life of the deployed data logging collars was one year, but collars did not last that long due to physical damage from fighting and/or mechanical factors.

Data recording and analysis

Collars used in this study were designed, engineered and assembled at the RVC (24, 25). They were equipped with a GPS module (M8N GPS module; u-Blox AG, Thalwil, Switzerland), a 6-axis Inertial Measurement Unit incorporating a 3-axis accelerometer and a 3-axis gyroscope (MPU-6050, TDK-Invensense, San Jose, California), a separate low power 3-axis accelerometer (MMA8652, NXP Semiconductors, Eindhoven, Netherlands) and an ambient light sensor (TSL2591, Ams AG, Unterpremstaetten, Austria). Solar charging panels (25) were integrated to increase battery life. Collars were able to switch dynamically between three operating states (22, 23, 25) (resting, moving and running) determined by the animal activity level (based on accelerometer measurements). Switching between different states enabled optimisation of power use between relatively low steady-state power consumption and quantity and resolution of data during focal activities. Collars logged GPS position and instantaneous velocity data at five minute intervals when the animal was moving and hourly when the animal was stationary. A higher resolution data regime was enabled opportunistically to record for a period up to 32 days, based on accessibility of the leopard and collar battery charge. The high resolution program increased the 12 fix/hr GPS rate (0.0033Hz) when moving to five fixes/second (5.0 Hz for GPS and 250 Hz (later changed to 50 Hz) for accelerometers), when acceleration peaks were greater than $\pm$ 3g, a conservative threshold indicator of running. Only GPS position and instantaneous velocity data were used for the analysis of movement, energetics and boundary patrol. The GPS module provides an accuracy estimate for each position and instantaneous velocity data point collected (median GPS horizontal position error 1.93 m, median instantaneous velocity error 0.4 ms^{-1}). For analysis of runs, higher accuracy speed and position data were obtained by using Kalman filtering to fuse GPS and IMU data (25).

Activity data

Continuous 24-hour activity records were recorded with 50 Hz acceleration data. Maximum change in acceleration was calculated on each axis (X, Y, Z) at two-second intervals and an activity record was stored every 30 seconds consisting of: 1) the largest peak-peak acceleration seen in any of the 15 x 2-second windows for each axis; 2) the mean of the mean peak-peak accelerations calculated in each of the 15 x 2-second windows, for each axis.

Movement data

GPS position data with a horizontal accuracy estimate greater than 15 m were excluded from the analysis. Distance moved per day was calculated based on the cumulative distance between consecutive GPS positions. A 99th percentile cut off was applied to the distance moved per day to exclude outliers. Distances travelled per day were averaged for each animal over the different seasons and subsequently a mean and s.d. for the season calculated.

Energy calculation

Minimum daily energy expenditure was calculated based on the mass-dependent basal metabolic rate (BMR (32, 33)) and a minimum locomotor cost dependent on distance travelled and cost of transport (COT). The COT estimate was calculated based on (34) $COT=10.7*mass^{-0.316}$. Leopard mass varied between 63-68.5 kg and the average of 65.8 kg was assumed for one individual whose body mass was unknown. COT is most likely underestimated, since potential high speed manoeuvring costs were ignored and preferred speed travel assumed. Additionally, energy cost of locomotion is higher when mammals move across soft surfaces such as sand, snow and wet areas (35-37). Energy expenditure increases 1.2 times for reindeer when walking on wet instead of dry tundra (36) and humans walking on sandy surfaces have a 2.5 times higher COT (37). Due to the lack of more appropriate studies we used the conservative human factor of 2.5 to give a higher COT estimate.

Territory boundaries and size

The outline of the territory was calculated in Matlab (The Mathworks Inc., MA, USA) using a convex hull, basic alpha shape (38) with a probe radius of 800-1000 m. This is comparable to using the local convex hull (LoCoH) method (39) in the free GIS software OpenJUMP HoRAE 1.7.1 (Jump Open source Mapping Platform, http://www.openjump.org) (Supplementary material SF1). Polygon boundary reduction was performed using perl (perl.org) including a perl CPAN module, (Math:Clipper (http://search.cpan.org)), that implements a wrapper around the C++ Clipper library (https://sourceforge.net/projects/polyclipping). Polygon offsets were generated by parameterised calls representing negative distance (100, 200 and 500 meters), using the function's default nonzero fill strategy, thus shrinking the polygons inward. Five minute position and instantaneous velocity data were used to compare movement speeds inside the 500 m wide strip from the boundary lines with the rest (outside of the boundary area) of the territory. One hour data (indicating lack of movement) were excluded and 5 Hz fixes down sampled to five minutes. In order to assure independence of the samples the data were then

down-sampled to 15 minutes based on autocorrelation analysis (Supplementary material SF2). A Wilcoxon rank sum test was performed to test for significant differences between speeds within and outside the territory boundary lines at a significance level of 0.05.

Running data

Runs were characterised by extracting speed, tangential acceleration (fore–aft) and centripetal acceleration. In order to reduce noise, improve precision and increase temporal resolution in the position and velocity data, GPS and IMU measurements were fused as previously described (22, 23, 25) using a 12-state extended Kalman filter (40) followed by a Rauch-Tung-Striebel smoother (41) written in Matlab. The accuracy of fused data was estimated from the known error characteristics of the inertial sensors and GPS position and velocity accuracy data for each fix. GPS horizontal position error (median stridewise SD) was reduced by data fusion from 1.93 m (pure GPS data) to 0.23 m in the fused data. Speed error was reduced from 0.4 ms^{-1} to 0.18 ms^{-1} (Supplementary material SF3).

Stride timing (beginning and end of a gait cycle) was derived from vertical IMU acceleration data and speed was derived from the Kalman-filtered velocity averaged over strides (from here on referred to as stride speed) in order to remove the effects of speed fluctuation through the stride and collar oscillation relative to the centre of mass. Tangential acceleration and centripetal (turning) acceleration between strides were computed from the change in stride speed and the time between mid-strides. Stride accelerations were weighted by taking the previous and following stride into account (22, 23, 25) and triggered data were classified as runs when they contained at least three strides with one stride exceeding a speed threshold of 3 ms^{-1}. Of the 2398 trials that were triggered 422 trials passed the Kalman filter and contained at least three strides. On multiple occasions trials were triggered in short succession and we combined trials that occurred within 5 minutes to a single event. This resulted in 270 trials with 162 of those trials exceeding the three strides and >3 ms^{-1} criterion and being classified as runs.

Results

Leopards were predominantly nocturnal, but activity was bimodal with peaks in daylight during the early morning near sunrise and evening after sunset (Figure 1a,b). Slow locomotion and periods of resting were interspersed by relatively infrequent runs. Over a period of 134 days, three male leopards ran a total of 162 times with speeds exceeding 3 ms^{-1} (mean± s.d: 1.2±0.09 runs per day). Few runs occurred between 9:00 and 17:00 local time (Figure 1b).

Data were collected spanning three periods loosely defined by season, but not all individual data sets covered all seasons. We distinguished between dry (post rainy season) cold season (1 April-31 July), dry hot season (1 Aug-30 Nov) and the wet (rainy) season (1 Dec-30 March). Daily travel distances varied within individuals (Figure 2a-e), with all individuals reaching up to 20 km per day. During the dry cold season, leopards in this study travelled an average (mean±s.d.) of 12.0±7.3 km and a maximum distance of 28.7±2.6 m. During the dry hot season average travel distance was slightly less, 10.2±5.6 km with a maximum distance of 21.7±2.2 km. During the wet season, average travel distance was 10.6±6.3 km with a maximum distance of 19.4±0.6 km. The difference in the collective average travel distance between season is not significant (Figure 2f), although one individual (GSE) showed a significant difference between seasons (ANOVA, SPSS Statistics v24, IBM, Chicago, Illinois, USA; GSE: $p=0.003$; LPM; $p=0.283$; CAL: $p=0.913$; CHK: $p=0.147$). While the difference in travel distance between seasons is non-significant, there is notable variation in the distances travelled per month (Figure 2g). Interestingly, the leopards that were recorded at the same time period show very similar trends in rise and fall of the average distance travelled. No direct correlation was detected between daily distance travelled and average daily temperature (GLMM, SPSS; individual as random effect, $p=0.598$).

Minimum daily energy expenditure is shown in Figure 2h-l, accounting for BMR and locomotor cost, which was based on preferred speed estimates and a possible increase through sandy conditions, but neglecting potential high speed and manoeuvring costs. Daily locomotor cost varied little with month and individual. Assuming preferred speed and optimal conditions, the contribution of locomotor cost to daily expenditure is on average (mean±sd) 23±4%; while unfavourable sandy conditions might increase it to 42±5%.

The territories of GSE and CHK shared a boundary, even overlapping slightly, in 2012, while GSE and CAL territories were close in 2015/16, but there was a gap between their borders (Figure 3). Territory size is fairly consistent among individuals (Table 1). GSE's territory changed only slightly between the two observation periods.

We compared the instantaneous velocity values of movement fixes situated within the 500 m boundary strip with those inside the territory (Figure 3b-f). Movement within the boundary area occurred at significantly higher velocities (mean±sd, averaged over individuals): 0.90 ± 0.09 ms^{-1} *vs* 0.85 ± 0.09 ms^{-1} in all but one example (Wilcoxon rank sum test; Figure 3b: $p<0.001$; 3c: $p=0.031$; 3d: $p<0.001$; 3e: $p<0.001$; 3f: $p=0.381$).

Faster movements (indicated by triggered and Kalman-filtered trials which did not exceed 3 ms^{-1} threshold) and runs were widely distributed over the territories (Figure 4), but there were areas of the territory where they were more tightly clustered.

The median distance covered 5 min before the run was 56 m, and 78 m when 10 min before the run were taken into account (figure 5). In comparison, when walking at their preferred speed of 1 ms^{-1} (based on speed histogram of steady state walking strides, extracted according to(42)), leopards are predicted to move 300 m in 5 min, while the histogram of distances travelled within 5 min peaks at 200 m (mode: 204 m). Both measures indicate a much slower stalking mode before the run.

Run performance was analysed by extracting duration and distance as well as stride parameters for each run. Data included maximum stride speed, maximum tangential acceleration (fore-aft acceleration and deceleration) and maximum centripetal acceleration, and mean heading rate as an indicator of manoeuvrability (Supplementary material ST1, Supplementary dataset 1,2). Maximum speed recorded by a single individual was 11.4 ms^{-1}, all three individuals reached 9.4 ms^{-1}. Median maximum speeds varied between 4.6-5.8 ms^{-1} (Figure 6a), with a mean of medians of 5.3±0.8 ms^{-1}. All three individuals reached maximum tangential accelerations of 3.7 ms^{-2} and decelerations of -7.4 ms^{-2} (average medians: 1.3±0.1 ms^{-2} and -1.7±0.6 ms^{-2}), maximum centripetal acceleration of 7.6 ms^{-2} (average medians: 1.2±0.3 ms^{-2}) and maximum (stride averaged) heading rate of 66º (average medians: 15.5±3.1º). Average median run distance was 58.5±16.3 m with a duration of 26.4±4.4 seconds. Five run events (by two individuals, stitched together from consecutive runs) exceeded distances of 600 m (not shown in figure).

Discussion

The estimated territory size of these Okavango Delta leopards lies between 77.9 and 130.6 km^2, putting them at the upper end of the territory sizes measured in the Kruger National Park area (5). Their activity pattern of mainly nocturnal movement and resting during the day is in agreement with previous observations for leopards in the Kalahari desert (6) and Kruger National Park (5). The detailed analysis of their activity patterns and run times shows a notable peak in their activity around sunrise and sunset (Figure 1a,b) that corresponds with a substantial increase/decrease in light levels. Cats are known for their night vision (43), and being nocturnal hunters it can be assumed leopards can see well at night. However, we are unaware of specific scientific literature about leopards' eyesight. Unlike domestic cats and other, smaller ambush predators, leopards' pupils are round instead of showing the vertically slit configuration associated with ideal night vision(44). The peak in hunting activity in the

early morning and evening hours might indicate that during times when temperatures are low but light levels are significantly higher than night levels, conditions are ideal for spotting and pursuing prey that might be more vulnerable on account of the dim light or their activity pattern (45, 46). Leopards are less active and fewer runs occur during daytime (Figure 1a,b).

The four leopards travelled considerable daily distances (mean 11 km), much further than the 1.5 km reported by (5) and comparable only with those reported by Stander et al (15) and Bothma et al.(12), who previously reported maximum travel distances of up to 33 km in Kalahari landscapes compared to ours with 29 km. Seasonal changes in average travel distance per day were non-significant. However, average distance travelled varied between month and the fluctuation in distance travelled per month is similar for the respective leopard pairs and might suggest that external factors such as weather or prey abundance influence travel distance. No correlation was found between daily travel distance and average daily temperature, possibly due to the predominant travel during the night when temperatures are lower.

Locomotor energy expenditure varies with total distance travelled and per month, but overall was very similar in all individuals and measurement periods. Despite the extensive travelling, the main source for the daily energetic expense is the basal metabolic rate. Depending on the factors assumed to influence COT such as sandy surfaces, we calculated the locomotor costs to be a minimum of 26% and a maximum of 65% of the basal metabolic rate, without taking additional costs for running into account or any post-exercise BMR increase. However, we predict both effects to be relatively small.

Like many cats, leopards patrol and scent mark their territory and boundaries (2, 5, 29). With an average travel distance of 11 km and at most 29 km per day and taking territory size into account, patrolling borders requires several days of travel, raising the question about efficiency of patrolling a large perimeter. We tested the hypothesis that leopards might move more quickly in the outer parts of their territory, moving more purposefully and minimising time spent on the task or the risk of direct encounters with neighbouring leopards. Excluding running and resting data, we found a small but significant increase in average speed within 500 meters of the territory boundaries in all four cases. It is important to note that average speed does not only include purposeful walking, which might occur at preferred speeds independent of location, but also any other kind of movement such as stalking and searching for females, suggesting that leopards might focus more on patrolling close to the boundaries of their territory than on other tasks such as hunting.

Runs and faster movements are widespread over the territories (Figure 4), but seem to cluster in some areas eg CAL often runs along the water's edge (Figure 4a). The habitat is a mixture of grassland with shrubs and open spaces, mixed woodland, and swamp. Overlaying run positions on Google Earth (available historical images from 12/2015 and 12/2016 respectively) shows that few runs occurred in open areas. Leopards mostly ran in areas with vegetation cover, along the edge of open areas or along the river.

Interspecific competition is common in large predators (47-49). Leopards in the Moremi area compete for resources with hyena, lion, cheetah and African wild dogs. Here we compare their athletic performance with two of their competitors, based on studies in the same area. We recorded an average of 1.2 runs per day. Leopards (L) run approximately as often as cheetah (C) (1.3 runs/day (25)), but less often than African wild dogs (AWD) (2.4 runs/day (22)). However, the number of runs is considerably lower than the 2.7 hunts per day reported for male leopards in the more open Kalahari by (7). Compared with stride performance data from cheetah and African wild dogs (25) (23), and with the requirement that the value must be reached by at least three individuals, leopards show considerably lower maximum stride speeds (L: 9.4 ms^{-1}, C: 22 ms^{-1}, AWD: 19 ms^{-1}) and fore-aft accelerations (L: 3.7 ms^{-2}, C: 9.8 ms^{-2}, AWD: 8 ms^{-2}). Deceleration (L: -7.4 ms^{-2}, C: -15.2 ms^{-2}, AWD: -8 ms^{-2}) and turning performance (centripetal acceleration, L: 7.6 ms^{-2}, C: 13 ms^{-2}, AWD: 8 ms^{-2}) are about half of those in cheetah, but comparable to those in African wild dogs. The maximum speed measured (11.4 ms^{-1}, from a single individual) was slower than the estimated ±60 km/h (16.7 ms^{-1}) found in (2) which is cited in (50, 51) and given in many mainstream reports. However, the measurement method and accuracy of this value are not known.

Reported hunting success rates in leopards vary considerably between 38% in Namibia (15), 20% in South Africa (10), 13.6-27.9% in the Kalahari (7) and 16% in Kruger National Park (5). Aside from location, success rate varies with sex, the necessity to feed cubs and prey size (7). We do not know how many of our recorded runs were actual hunting events. Running could be triggered by interactions with other carnivores and/or conspecifics. However, in Kruger National Park leopards eat about one impala per week (5) and with a corresponding success rate of 16% the number of hunts conducted over a period of time can be estimated. With a total of 162 runs recorded (from three leopards) over a total period of 19 weeks, an estimate of 119 runs were actual hunts (19*(1/16*100)), assuming that hunting is always accompanied by at least a short run. The distance covered in the time leading up to the run is very short (Figure 5). Leopards only moved a median distance of 56 m in the five minutes before the run, while cheetah and African wild dogs move considerably further, 235 m and 473 m respectively (22). This shows a substantial difference in hunting style, where leopards actually more often stalk or ambush their prey as chance encounters arise, perhaps waiting in

key prey locations, instead of relying on finding prey as they move around their territory. A study on puma indicates a notable reduction in hunting costs when using the stalk and pounce tactic (52).

Average run distance was 129±202 m (mean±s.d., all runs), considerably longer than runs previously recorded (12, 15). The results might be biased due to a few very long runs. The median value is 63 m (all runs) and when removing the seven runs over 450 m (longest running distance measured by (12)) the mean drops to 94±89 m (mean±s.d., all runs), which fits better with the previously observed distances. Differences could also be caused by the variation in methods between studies; tape measure or pace *vs* collar GPS data, and the potential error due to missed tortuosity in the former. The seven longest runs (events) contained alternating segments with slower and faster speeds and were highly directional (Supplementary material SF4).

Conclusion

The results provide useful insights into leopards' movement patterns and athletic performance in a habitat characterised by seasonal flooding, open areas and mixed woodland and scrub. The detailed analysis of activity and run occurrence shows similar levels of activity throughout the night hours with distinct spikes in the morning and evening twilight hours. Despite seasonal changes in temperature, daily travel distance and consequently energy expenditure did not change significantly. However, different leopards showed notably similar patterns in average monthly travel distances over time, suggesting that external factors such as vegetation/grass height, local flooding or food availability may influence residents' movements to similar extents. In terms of athletic performance, leopards were considerably slower than cheetah and African wild dogs and have lower acceleration; however, their manoeuvring performance, while considerably surpassed by cheetah, is comparable to that of African wild dogs. Comparisons of territory size, hunting style and frequency between these leopards and those inhabiting the broadly similar habitats of Kruger National Park and entirely different habitats in other study areas reinforces the view that leopard are highly adaptable to their environment.

The collar technology deployed for this study has enabled the first measurements of athletic performance of wild leopard, and the most detailed measurements of activity and locomotory behaviour. The recording of such high-resolution activity and behavioural data could provide an efficient way of gaining unbiased insights into animal behaviour, delivering benefits for wildlife management. This knowledge can be used to tailor conservation efforts for specific species and to reduce human-wildlife conflict.

Author Contributions

AMW, TYH, KAG and JWM. conceived and designed the methods and study. KAG and KR established, maintained and monitored the study population and directed and conducted field data collection. TYH analysed and interpreted the data and wrote the paper with input from all authors.

Competing financial interests

The authors declare no competing financial interests.

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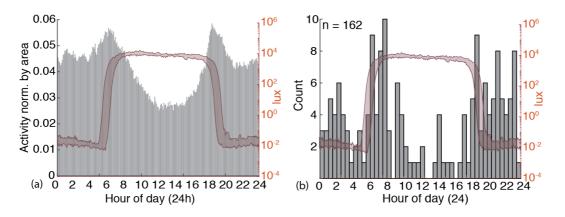carnivores. J Anim Ecol. 1998;67(3):370-86.

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Figures

Figure 1: (a) Leopard activity versus time of day. Figure based on max peak to peak acceleration over 30 seconds in fore-aft direction. Data averaged over timeslots before being averaged over days. Data normalized by area and averaged over all individuals. (b) Histogram of the time of day when runs above 3 ms^{-1} occur. (a, b) red shaded area represents light level measured by collar, bandwidth reveals the variation over the measurement period.
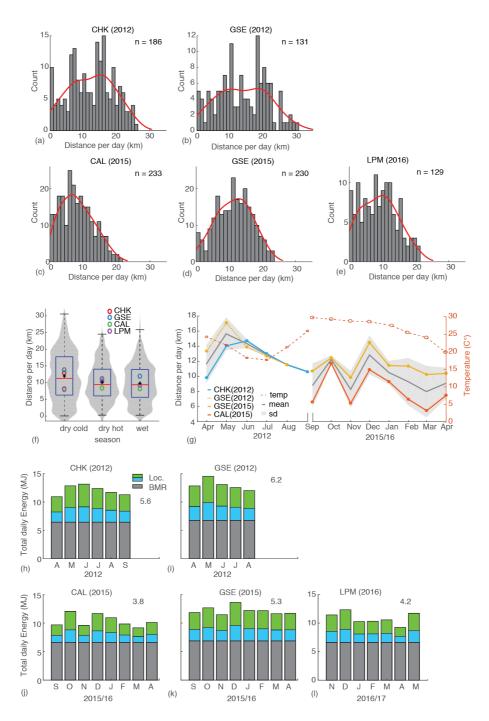
Figure 2: Energy expenditure and distance travelled per day after removal of the 99th percentile for four individuals. (a,b) April-Oct. 2012, (c,d,e) Sep. 2015-April 2016). (e) Nov. 2016-April 2017. Abscissa is cut off at 99th percentile. Red line: kernel density estimate, n: number of days for each individual. GSE was recorded in 2012 and 2015. (f) Boxplots showing distance per day *vs* season (Median, Q_1, Q_3), including the average values for each individual (g) Distance per day averaged per month for each leopard and sd and mean for the respective leopards. (h-l) Energy expenditure due to locomotion (Locomotion cost: blue: min. COT, blue+green: COT*2.5) and basal metabolic rate (BMR) separated by month and individual; (h,i) dry season (April-Sept 2012), (j,k) dry hot - wet season (Sep 2015-April 2016) (l) wet season (Nov 2016-Mar 2017).
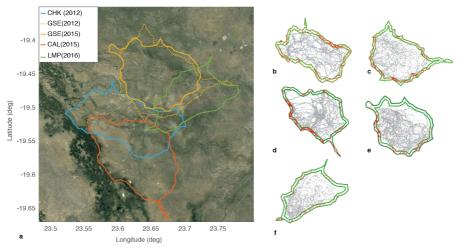
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Figure 3: Movement/range use by resident leopards. (a) Territory boundaries for the four leopards during the three collaring periods (April-Oct 2012, Sep 2015-Feb 2016, Nov 2016-April 2017). (b-f) Positions (for moving animals) and territory boundaries. Boundary strip with 500 m band width located between green lines, red: positions within the boundary strip, grey: positions in the inner range of the territory. a) CHK (2012), b) GSE (2012), c) GSE (2015/16), d) CAL (2015/16), e) LPM (2016/17).
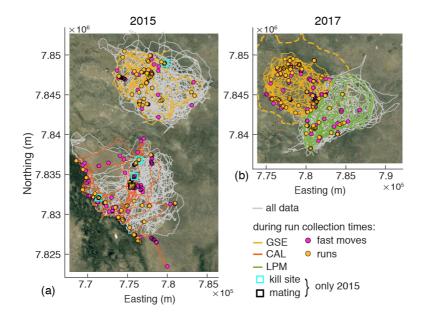

Figure 4: Locations of fast moving instances and runs. Display of GPS path for the whole of data collection time (grey) and when the collar was allowed into chase mode (colour-coded by individual). (a) GSE and CAL 2015/16. During Oct. 2015, when collars where in chase mode, leopards were followed for prolonged periods of time and one mating and four kill sites were recorded. (b) LPM and GSE, with GSE providing running data for June 2017. GSE previous territory from 2015/16 outlined in (b) with dashed yellow line. Fast moves: triggered trials that passed the Kalman filter, contained three strides, but did not exceed the 3 ms^{-1} threshold.
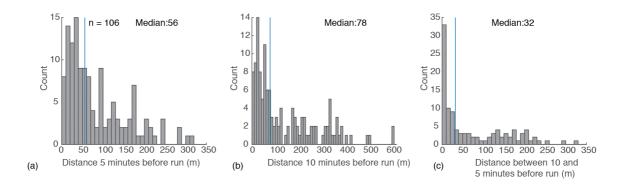
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Figure 5: Histogram of distance travelled before run. (a) Five minutes before, (b) ten minutes before, (c) between five and ten minutes before. Line: median, n: number of runs used for a-c.
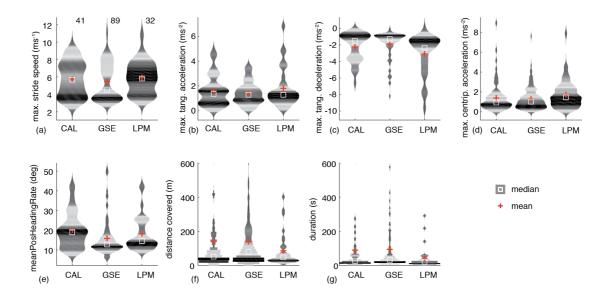

Figure 6: Stride parameters for three individuals displayed as violin plots (combining box plot and kernel density plot). Number of runs analysed: n=162. Violin plots show the density distribution of the values, with each histogram normalised to the same maximum bin width in order to compare distribution shape. The total number of parameter values per individual is given in (a), with the exception of (d) where left and right turns are combined, doubling the count; red cross - mean; white box - median. (a-d) Maximum value for the respective parameter extracted from each trial (a) Maximum stride speed, (b) maximum tangential (fore-aft) acceleration and (c) deceleration, (d) maximum centripetal (turning) acceleration (right+left). (e) mean absolute heading rate (degree/stride), (f) run distance and (g) run duration.

Table 1: Territory size and probe radius for all individuals based on alpha hull calculation.

	CHK 2012	*GSE 2012*	*CAL 2015/16*	*GSE 2015/16*	*LPM 2016/17*
Area (km²)	128.5	116.2	130.6	108.1	77.9
Probe radius (km)	0.8	0.8	1	0.8	0.8

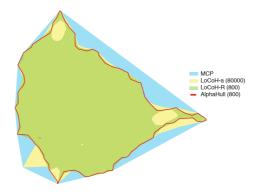18

Supplementary Material:

Figure S1: Comparison of territory size for GSE (2012) using different methods: minimum convex polygon (MCP) method, local convex hull method (LoCoH-R, radius in meter; LoCoH-a distance in meter) and alpha hull method (radius in meter). MCP and LoCoH were calculated using OpenJUMP HoRAE 1.7.1. Alpha Hull was calculated using MATLAB. Values in brackets in meter.
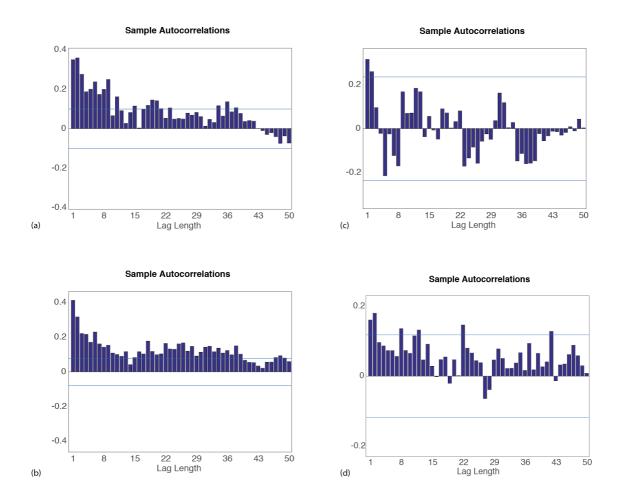

Figure S2: Four examples of autocorrelation within movement data. Based on two trials with 30 second fixes (a,b), and two trials with 5 minute fixes (c,d).
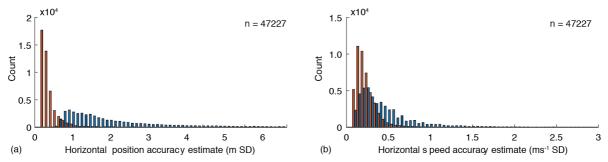
Figure S3: Summary of GPS performance in the field. Horizontal position accuracy standard deviation estimate from the GPS module for the stand alone GPS data (blue) and from the Kalman smoother once GPS and IMU data have been fused (red). The estimation algorithm inherently gives error covariances of each parameter for each sample based on the measurement error calculated for each fix by the GPS module and IMU errors from lab testing. (a) GPS horizontal position error (median stridewise SD) was reduced by data fusion from 1.93 m (pure GPS data) to 0.23 m in the smoothed solution. (b) Equivalent plot to (a) for horizontal speed. Speed error was reduced from 0.4 ms^{-1} to 0.18 ms^{-1}. n: number of datapoints.
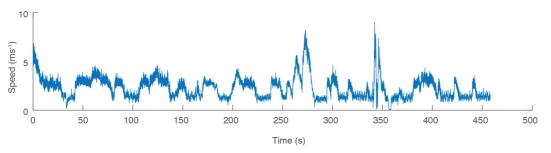

Figure S4: Speed versus time in an example for runs longer than 450 m.

Table S1: Summary of mean and median stride parameter values for all individuals. Values are based on all strides (steady state and non-steady state included).

	Max. stride speed (ms^{-1})	Max. centrip. Acceleration (ms^{-2})	Max. tang. Acceleration (ms^{-2})	Max. tang. deceleration (ms^{-2})	Mean pos. headingrate (deg.)	Run distance (m)	Run duration (s)
Mean from individual mean (±std)	5.7±0.2	1.5±0.2	1.6±0.2	-2.4±0.6	18.1±2.0	122.1±31.8	74.8±29.6
CAL mean±std	5.8±2.0	1.4±1.1	1.6±1.2	-2.2±1.7	20.1±9.0	142.9±281.8	89.5±174.4
GSE mean±std	5.5±2.2	1.3±0.8	1.4±0.9	-1.9±1.7	16.0±9.3	138.0±185.4	94.1±170.3
LPM mean±std	5.9±1.8	1.7±1.0	1.8±1.6	-3.1±2.4	18.3±8.7	85.6±96.3	40.6±62.3
Mean from individual median (±std)	5.3±0.8	1.2±0.3	1.3±0.1	-1.7±0.6	15.5±3.1	58.5±16.3	26.4±4.4
CAL median (LQ,UQ)	5.7 (3.8,7.3)	1.1 (0.8,1.6)	1.4 (0.7,2.1)	-1.5 (-3.6,-0.9)	19.0 (13.3,23.9)	51.5 (30.2,136.3)	27.0 (16.6,71.6)
GSE median (LQ,UQ)	4.4 (3.5,7.4)	1.0 (0.7,1.8)	1.3 (0.8,1.9)	-1.2 (-2.1,-0.8)	12.9 (11.0,16.9)	77.1 (34.4,185.5)	30.6 (17.3,84.5)
LPM median (LQ,UQ)	5.8 (4.3,7.2)	1.5(1.1,2.2)	1.3 (0.8,2.1)	-2.3 (-4.4,-1.4)	14.5 (12.2,24.5)	46.9 (28.2,105.4)	21.8 (11.4,33.5)