

Elephants shuttle to thermoregulate

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Abstract

Overheating is a major concern for large mammals, and many species make landscape-scale movements to avoid thermal stress. The movements of savanna elephants *Loxodonta africana* have received much attention in the context of water dependence, yet temperature has seldom been invoked to explain them. We tracked 14 herds of elephants in Kruger National Park, South Africa using GPS collars over a period of 02 years. We quantified the extent to which elephants used the landscape in terms of total residence time, first passage time, and number of revisits. Using conservative criteria, we identified habitual water-points and studied elephant movement between successive visits to water. We found that elephants in Kruger are dependent on water sources, with more short trips away from water in the hot-wet season, and more long-distance forays in the cool-dry season. 80% of elephant movements between water-points are loops, ie, individuals returning to the water-point of origin. In a 24-hour period, elephants arrive at water-points when temperatures are highest (afternoon), and are farthest away when they are lowest (midnight). Elephant speed is highest when approaching and leaving water, ie, when ambient temperatures are high, which has implications for management decisions that alter water dependence to control their space use in a rapidly warming world.

1 Introduction

Animals faced with heat stress thermoregulate by altering their physiology and behaviour (Angilletta 2012). Most physiological responses to high temperatures, such as sweating in mammals, rely on

water evaporation to transfer heat away from the core-body. Many animals must complement physiological thermoregulation with behavioural mechanisms of losing heat. In general, behavioural responses to overheating involve utilising heat-sinks to which excess body-heat may be transferred. For example, the large ears of savanna elephants *Loxodonta africana* aid in rapid cooling by offering a large surface area that readily loses heat to the environment (Wright 1984). Thermal stress may also be avoided by temporal changes in activity. Most desert dwelling mammals are nocturnal, yet even in milder climates, ibex *Capra ibex* and elephants shift their activity peaks to earlier in the day in the hot season (Aublet *et al.* 2009; Leggett 2010). Occupying landscapes that promote heat loss, such as water sources or shade under dense vegetation constitutes another important class of behavioural responses to heat stress. For example, moose *Alces alces* seek refuge from high temperatures in shady coniferous forests in summer (Beest *et al.* 2012), while Arabian oryx *Oryx leucoryx* select for covered sites during the hottest part of the day (Hetem *et al.* 2012). Some landscapes, such as water sources, may promote both behavioural and physiological thermoregulation, as water is both a direct heat sink as well as a critical resource for evaporative water loss. This allows large tropical herbivores such as Cape buffalo *Syncerus caffer* and elephants to wallow and drink at water sources to cool down (Bennitt *et al.* 2014; Purdon 2016).

Animals must balance the energetic benefits of using water as a thermoregulatory aid against the costs of negative interactions such as predation and competition at crowded waterholes (Cain *et al.* 2012; Owen-Smith and Goodall 2014). Individuals may attempt to avoid such costs by periodically shuttling between water and more optimal foraging and resting sites, but this increases movement costs and decreases time that could have been spent feeding (Johnson *et al.* 2002; Cain *et al.* 2012; Owen-Smith and Goodall 2014; Giotto *et al.* 2015). Body size may mediate how a species reckons with the costs and benefits of visiting water. Large species such as buffalo and eland *Taurotragus oryx* that overheat more quickly are likely to be more water-dependent than smaller ones such as sable antelope *Hippotragus niger*, and zebra *Equus quagga* (Cain *et al.* 2012; Shrestha *et al.* 2012; Bennitt *et al.* 2014; Owen-Smith and Goodall 2014). Water-dependence can introduce periodicity to an animal's movement, such as that corresponding to the diel or seasonal cycle (Giotto *et al.* 2015). However, it is in turn affected by seasonal changes. For example, buffalo in the Okavango delta are found farther from permanent water sources in the hot-wet season when they can use ephemeral pools, and closer to water in the cool-dry season (Bennitt *et al.* 2014). Further, seasonal changes in temperature and resource availability can affect the activity and movement of ungulates, changing their distribution in relation to water (Leggett 2010; van Beest *et al.* 2012; Shrestha *et al.* 2012; Owen-Smith and Goodall 2014). This sets up an interaction between environmental conditions such as ambient temperature, an individual's physiological state, and its position in relation to water sources.

Savanna elephants are an excellent study system to examine the effects of temperature on movement strategies in relation to water. Elephants lack a physiological means of thermoregulation, such as sweating or panting, and therefore compensate by using thermoregulatory behaviours, such as ear-flapping (Hiley 1975; Wright 1984; Wright and Luck 1984). At larger spatio-temporal scales, elephants avoid thermal stress and the energetic costs of thermoregulation by shifting their activity

peaks to cooler times of the day, and select for thermally stable landscapes with lower variation in daily temperatures (Johnson *et al.* 2002; Kinahan *et al.* 2007; Leggett 2010). Elephants are also heavily water dependent and make periodic visits to water to hydrate and thermoregulate (Valls Fox 2015). Seasonal changes can have a significant effect on elephant movement, with individuals from populations in Namibia and South Africa moving faster in the wet season than the dry season, suggesting an effect of water availability on movement (Leggett 2010; Birkett *et al.* 2012). However, in both these cases, the wet and dry seasons overlap with the hot and cool seasons, respectively, opening up the possibility that differences in mean temperature between the seasons could contribute to differences in movement. Testing this hypothesis requires both high-resolution position and temperature data at each step of a movement track. Here, we characterise elephant movement in relation to water sources and ambient temperature using data from traditional satellite telemetry, coupled with instantaneous data from temperature loggers (thermochrons) borne by individuals, to test the hypothesis that savanna elephants' movement is driven by temperature.

2 Methods

2.1 Data collection

The study was conducted in the predominantly semi-arid savanna landscape of Kruger National Park and adjacent private game reserves (extent: 31.06°E – 32.0°E, 23.9°S – 25.4°S) in South Africa, where we have had 14 female African elephants – each from a different herd – fitted with GPS logger-transmitter collars since 2007 (Fig. 1a, 1b). Details of the capture and collaring of these elephants, including an ethics and permissions statement can be found in Birkett *et al.* 2012. Collars on elephants had transmitters and inbuilt thermochrons that were set to record half-hourly position and temperature data, respectively. For this study, we selected location and temperature data from the 14 tagged elephants between August 2007 and August 2009, which we define as the study period, and during which each elephant was tracked for on average 637 days (range: 436 – 731 per elephant).

We obtained the following landscape-level data: (1) a map (shapefiles) of all rivers, the locations of active park waterholes, and 30m resolution terrain slope from Shuttle Radar Topography Mission V3 data (Farr *et al.* 2007); (2) polygon shapefiles of the landscape types of Kruger NP as defined by Gertenbach 1983; (3) satellite imagery of the study area taken in the low-gain thermal infrared range (Band 6 VCID 1: 10.40 – 12.50 μ m) by the Enhanced Thematic Mapper + device aboard LANDSAT-7 over the study period, which we converted to degree Celsius temperature data (Chander *et al.* 2009).

We also obtained ambient temperature data from the weather station tower at Kruger headquarters at Skukuza (24.98°S, 31.5°E) over the study period (Fig. 1b).

2.2 Variation in temperature across the landscape

We first sought to understand variation in ambient temperatures as a function of the landscape types found over the study area (Gertenbach 1983). We mapped the mean temperature of Kruger NP logged by LANDSAT-7 over the study period (see Fig. 11b), and created boxplots of the temperature in each of 18 landscape types (see Fig. 12 *LANDSAT-7 temp.*). Since LANDSAT-7 (and most other reflectance-based remote-sensors) makes passes only over the sunlit side of the earth, the reported temperatures are only from the daytime. Hence, this temperature map represent the diurnal thermal landscape of Kruger NP (Fig. 11b).

Further, we mapped the thermal landscape of the park as experienced by elephants, using an inverse distance interpolation (IDW) of the temperatures reported by elephant collar thermochrons (Fig. 11c). Similar to the LANDSAT-7 data, we created boxplots of the thermochron temperatures in each landscape type (see Fig. 12 *Elephant temp.*). As elephant thermochrons are active both during the day and night, the interpolated map (Fig. 11c) represents the preferred spatial positions of elephants at recorded thermochron temperatures.

Finally, we ran a generalised linear mixed model (GLMM, see Tab. 1) to test whether thermochron temperature was well predicted by LANDSAT-7 temperature, the landscape type, the hour of day, and season. We accounted for consistent individual variation between elephants by using elephant identity as a random effect. Since LANDSAT-7 data are restricted to the daytime, we restricted our analyses to thermochron data collected between 0600 and 1800 hours (6AM – 6PM) each day.

2.3 Thermochrons as accurate measures of ambient temperature

First, we tested the correlation of thermochron data with ambient temperatures from the Skukuza weather tower. For this, we used a subset of elephant positions ($n = 4,971$, 0.02% of total) within a 10km radius of the station (see Fig. 2c), computed mean temperature at each hour across individuals (hereon, thermochron temperature), matched these pooled data to hourly mean temperatures recorded at the station tower (tower temperature), and tested the correlation of elephant and ambient temperature separately in the hot-wet and cool-dry seasons as defined in Birkett *et al.* 2012.

2.4 Movement strategies between water points

To examine elephant movement in relation to water sources, we divided each individual's track into a set of segments between successive visits to water points, which we defined as positions within 500m of a water source. We chose this generous buffer distance so as to capture visits to water that occurred between GPS position fixes, and which thus went unrecorded (see Fig. 1c). Each segment thus began and ended within 500m of a water source. The last point pt_{nij} of each segment was immediately followed by the first point of the next segment pt_{0ij} , with $n-1$ points between the beginning and end of each segment j of each elephant i .

For each of these segments, we identified the first (pt_{0ij}) and last (pt_{nij}) points, and calculated the linear distance between the two. Further, we computed the actual distance moved along the segment

as the sum of the steplengths, i.e., distances between each successive point (pt_{xij} to pt_{xij+1}), and the distance of each discrete position (pt_{xij}) from the nearest water source. Additionally, we obtained thermochron temperature (t_{xij}) at each discrete position along the segment, and the steplength (v_{xij}) at each point.

We calculated the time difference between the two ends of a segment, and since each segment began and ended at water, this represented the interval between visits to water. To account for the cyclicity in ambient temperatures expected due to the diurnal cycle, we restricted further characterisation to track segments with a duration of 12 – 24 hours.

2.5 Movement speed as a function of the environment

To test whether temperature was a significant predictor of elephant speed, we ran a generalised additive mixed effects model (GAMM) using the entire data. The GAMM also included season, terrain slope, and the density of woody vegetation (see Bucini *et al.* 2010) as fixed effects, and individual identity as a random effect (see Tab. 1).

We acquired and handled the SRTM and LANDSAT-7 data using Google Earth Engine (Gorelick *et al.* 2017), and used the R statistical environment (R Core Team 2017) for all analyses, and specifically the *lme4*, *mgcv*, and *move* packages to implement the GLMM, GAMMs, and general movement data handling respectively (Wood 2013; Bates *et al.* 2015; Kranstauber and Smolla 2016; Bracis 2017).

3 Results

3.1 Elephant tracking

We obtained 283,737 total positions from 14 elephants, which we converted to movement tracks (Fig 1b). Elephants ranged on average 4005 km (range: 1854 km – 7074 km) across southern Kruger National Park over the tracking period, covering on average 7.2 km per day (range: 5 km – 9.9 km) at a mean speed of 398 m/hr (range: 304 m/hr – 470 m/hr). Individual positions were within 500m of water a mean 12% (range: 6% – 21%) and 11% (range: 3% – 17%) of the time in the cool-dry and hot-wet seasons respectively.

3.2 Landscape effects on temperature

We found that daytime thermochron temperatures were well predicted by the two-year mean LANDSAT-7 temperature ($z = -3.79$, $p = 0.000151$), the hour of day ($z = 26.01$, $p = 2 \times 10^{-16}$), and season ($z = 3.42$, $p = 0.000619$). We used Type II Wald chi-squared test to determine that within the

18 landscape types visited by elephants during the daytime, temperatures were significantly different ($X^2 = 1661.689$, $p = 2.2 \times 10^{-16}$). with z-values ranging from between -16.55 to 16.55.

3.3 Thermochron accuracy

Thermochrons fitted on elephant collars reported nearly identical mean daily temperatures of 27.68°C (range: 6°C – 47°C) and 27.62°C (range: 7°C – 44°C) in the cool-dry and hot-wet seasons respectively (Fig. 2a, 2b). Thermochron data from 3 elephants logged within 10km of Skukuza (see Fig. 13b) were well correlated with temperatures from the weather station at each hour in both seasons (mean hourly correlation, Pearson’s r: cool-dry = 0.66, hot-wet: 0.78). All correlations were significant, with $p < 0.05$. We henceforth consider thermochron temperatures to be equivalent to ambient temperatures.

3.4 Track segments between water points

Elephants were within 500m of water at 44,610 of 283,737 points ($\approx 16\%$), leading us to identify 44,622 track segments which began and ended at water. 40,347 ($\approx 90\%$) of these segments had a temporal duration of under 3 hours, with 89% lasting under an hour, i.e., indicating consecutive residence at water points. On excluding these “residence at water tracks” and segments with a duration above the 99th percentile (72 hours, $n = 445$), the remaining 3,754 ($\approx 8.4\%$) of segments had a multi-modal distribution of segment durations, with peaks between 12 – 24 hours, 36 – 48 hours, and at 72 hours (Fig. 3). We only retained 1,519 segments with durations between 12 and 24 hours for further characterisation.

3.5 Movement along track segments

Elephants began each 12 – 24 hour segment on average 311.42m (range: 1.3 – 499.9m) from a water source, and ended a mean 907.35 m (range: 500.14 – 4718.06m) from the next water source (Fig. 7a). 12 – 24 hour segments usually began at 14 – 19 hours (2PM – 7PM, SD = 4.84) and ended at 6 – 12 hours (6AM – 12 Noon, SD = 4.67), with elephants reaching the halfway point at 22 – 04 hours (10PM – 4AM, SD = 9.06) (Fig. 4). On average, elephants travelled 6,508 m (range: 526 – 20,326 m) along their path between visits to water points (Fig. 5), reaching a mean maximum distance of 2,462 m (range: 519 – 6,832 m) from the nearest water source. In $\approx 8\%$ and $\approx 30\%$ of segments respectively, elephants returned to within 500m and 1km of the position from which they began, with no difference between the seasons (Fig. 6). However, the midpoints of successive segments were within 500m and 1km of each other in only 3% and 9.8% of segments, respectively (Fig. 7). The distance travelled along a segment showed an increasing trend with an increasing linear distance between the start and end point of the segment (Fig. 8).

3.6 Temperature as a driver of movement

Elephants moving along 12 – 24 hour segments were initially moving away from water until about the halfway point, after which their distance from water diminished (Fig. 9a). Temperatures along segments initially decreased until halfway, and then climbed steadily (Fig. 9b). Elephant speed was

highest in the initial and final fifths of each segment (Fig. 9c), with the first and last speeds (716 m/hr and 667 m/hr respectively) in a segment nearly thrice as fast as the speed at the halfway point (242 m/hr). No seasonal difference was apparent.

Thermochron temperature was found to be a significant predictor of speed ($X^2 = 4410$, $p < 0.01$), and elephants moved faster in the hot-wet season ($X^2 = 312.97$, $p < 0.01$) but more slowly in denser woodland ($X^2 = 2347$, $p < 0.01$), and on steeper slopes ($X^2 = 16.64$, $p < 0.01$) (see Fig. 10).

4 Discussion

Discussion here on finalising methods and results.

5 Conflict of Interest

All financial, commercial or other relationships that might be perceived by the academic community as representing a potential conflict of interest must be disclosed. If no such relationship exists, authors will be asked to confirm the following statement:

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

6 Author Contributions

The Author Contributions section is mandatory for all articles, including articles by sole authors. If an appropriate statement is not provided on submission, a standard one will be inserted during the production process. The Author Contributions statement must describe the contributions of individual authors referred to by their initials and, in doing so, all authors agree to be accountable for the content of the work. Please see [here](#) for full authorship criteria.

MT, AV and RS designed the study and collected the primary data. HP did xxx. PG analysed the data, made figures, and PG and MT wrote the manuscript.

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9 Data Availability Statement

The datasets analysed for this study can be found on Movebank <http://www.movebank.org/>.

10 References

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11 Tables

No.	Type	Response	Fixed effects				Random effect	Sample size
1	GLMM	Thermochron temperature	LANDSAT-7 temperature	Season	Hour of day	Landscape type	Elephant identity	266,382
2	GAMM	Speed	Thermochron temperature	Season	Slope	Woody density	Elephant identity	275,129

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12 Figures

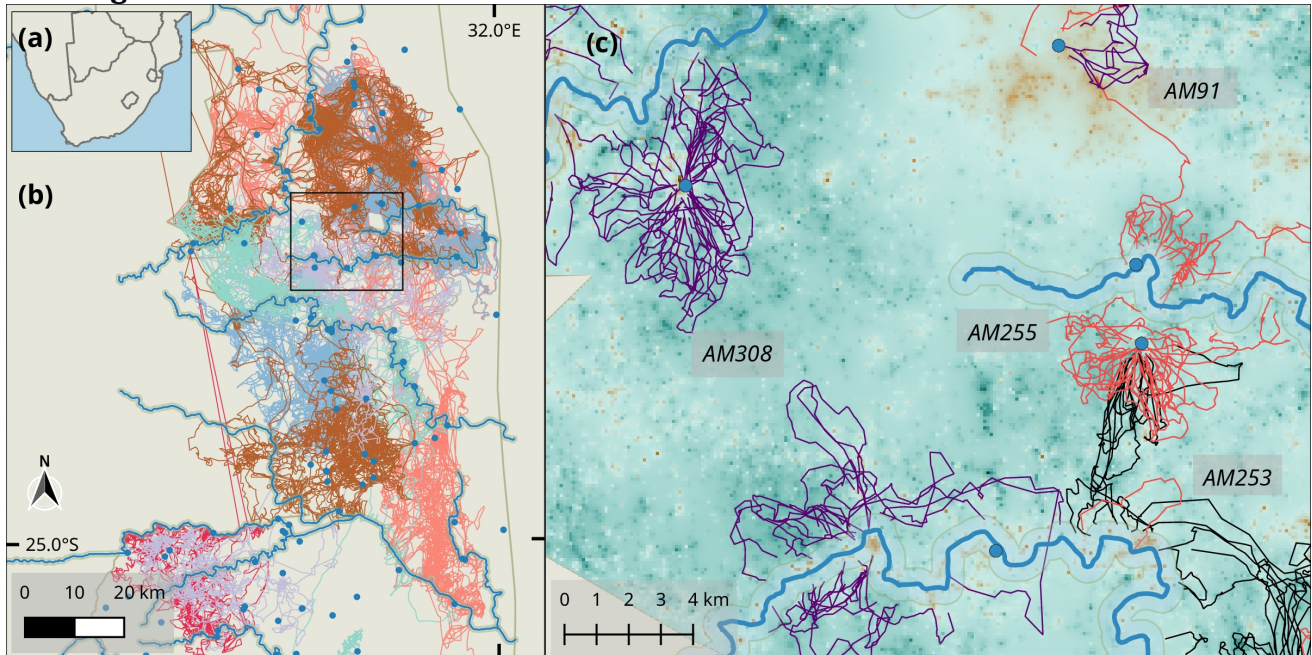


Fig. 1: (a) Study site in Kruger National Park, South Africa (red star), showing (b) park boundary (dashed grey line), major rivers (solid blue lines), open waterholes (blue dots), and raw elephant tracks (coloured lines, $n = 14$). (c) Inset showing 12 – 24-hour long track segments between water sources (blue dots and lines), coloured by representative elephant ID ($n = 4$). The riparian zone along rivers (500m from river centre) is shaded in blue. Background shows inverse distance interpolated values of woody density (see Bucini et al. 2010).

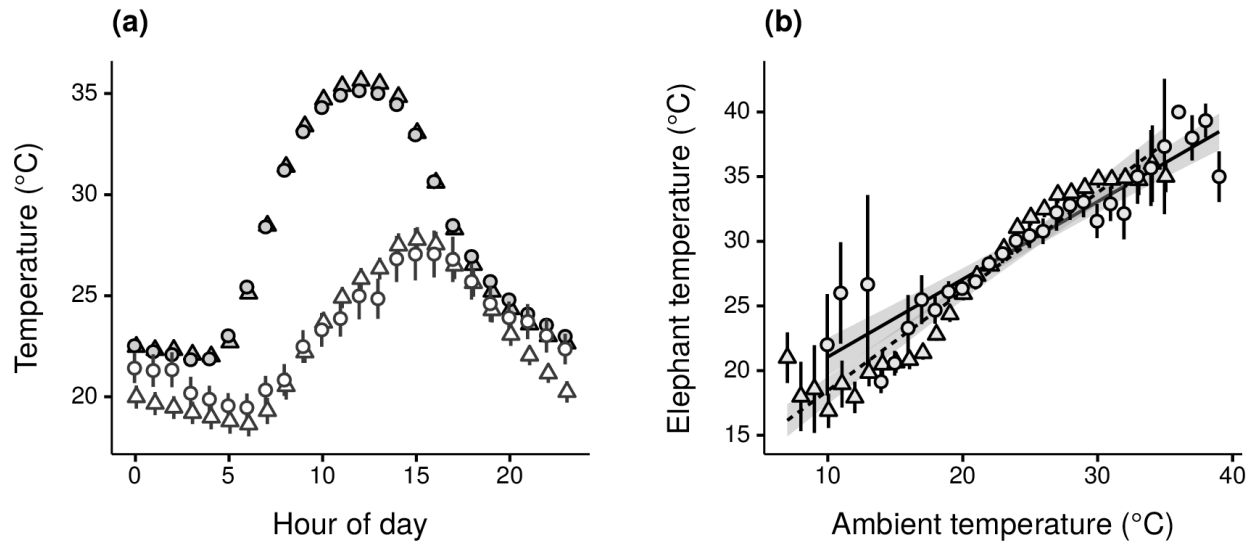


Fig. 2: (a) Mean thermochron temperature (coloured points: cool-dry = blue, hot-wet = red) and measured ambient temperature (outline points: cool-dry = circles, hot-wet = triangles) at each hour of day in each season across the study period (and (b) GLM fits (lines) in each season (cool-dry: blue circles & lines, hot-wet: red triangles & lines). Vertical lineranges and shaded areas (coloured by season) indicate 95% confidence intervals at each point.

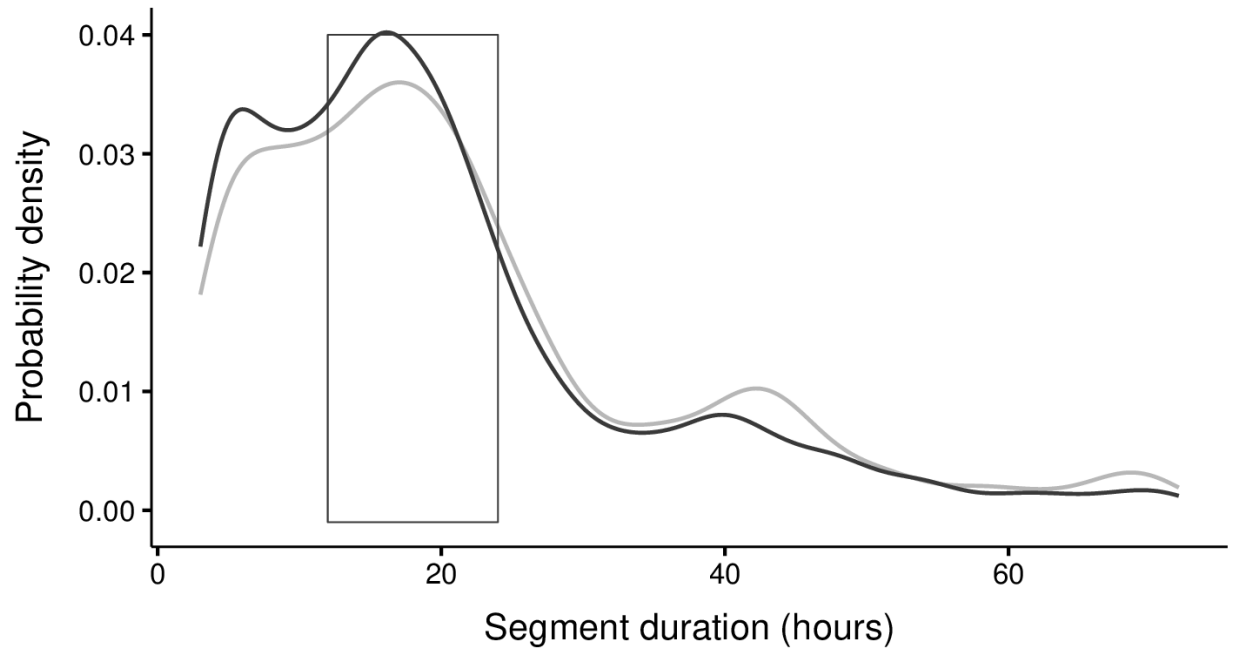


Fig. 3: Probability density plot of segment durations (in hours) segments between water points. Seasons are represented by lines (cool-dry: grey, hot-wet: black). Upper and lower limits in both seasons have been set at 72 and 3 hours, respectively. The rectangle shows the peak representing segments of a duration between 12 and 24 hours, which were used for all further characterisation.

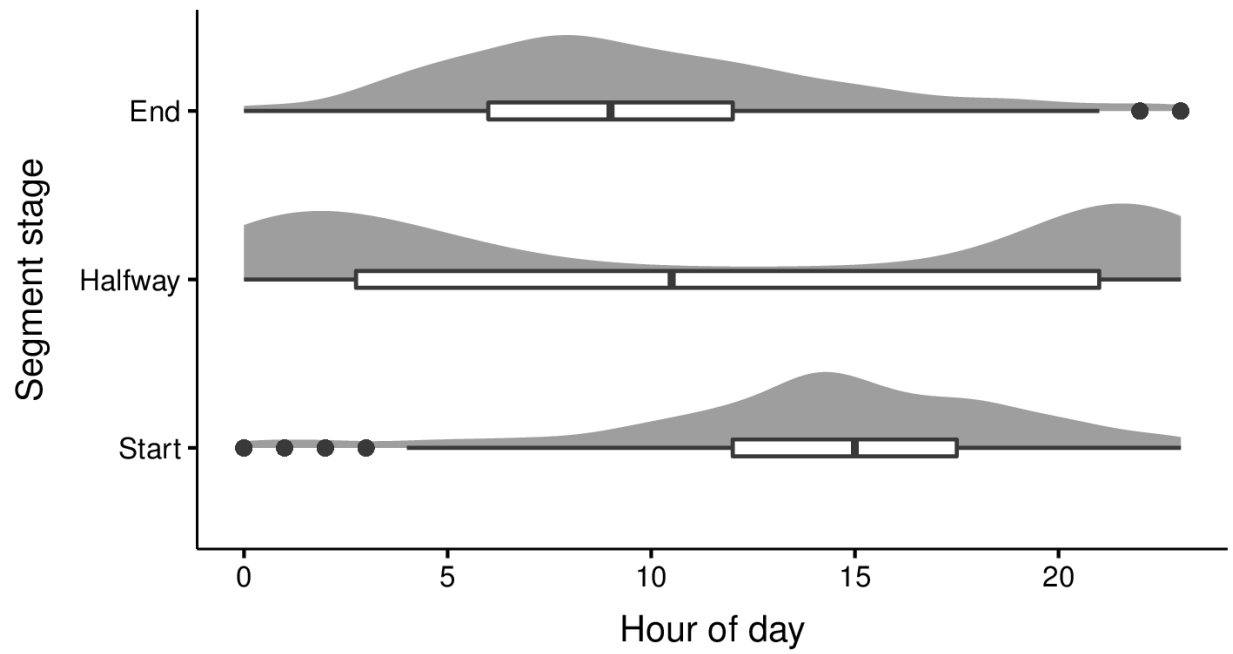


Fig. 4: Boxplots and probability distributions (half-violins) of the hour of day of the three main stages of a 12 – 24 hour segment between water points.

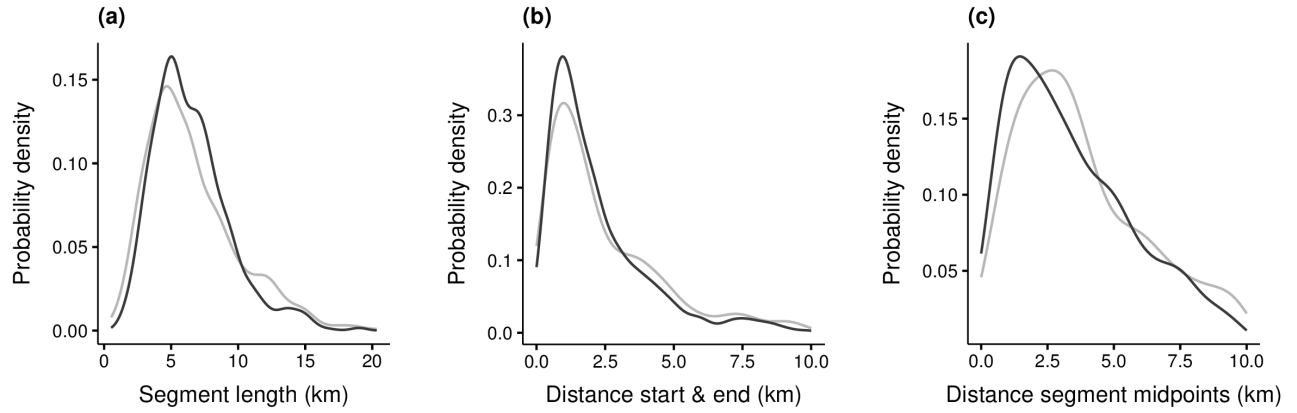
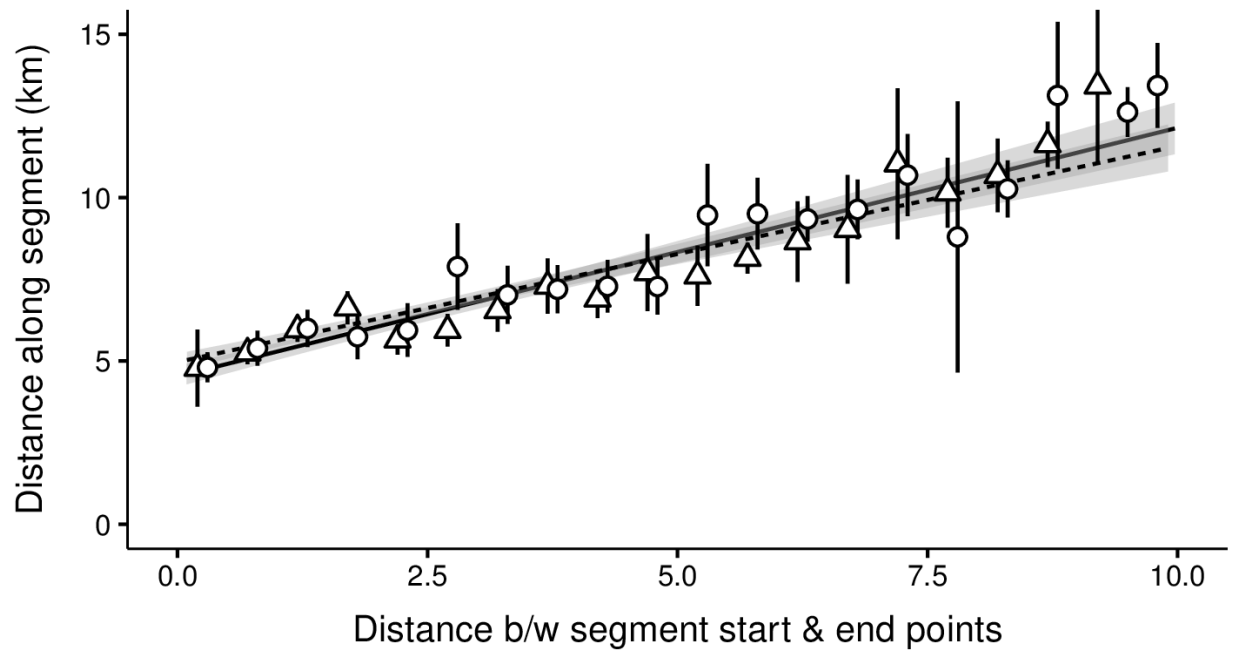
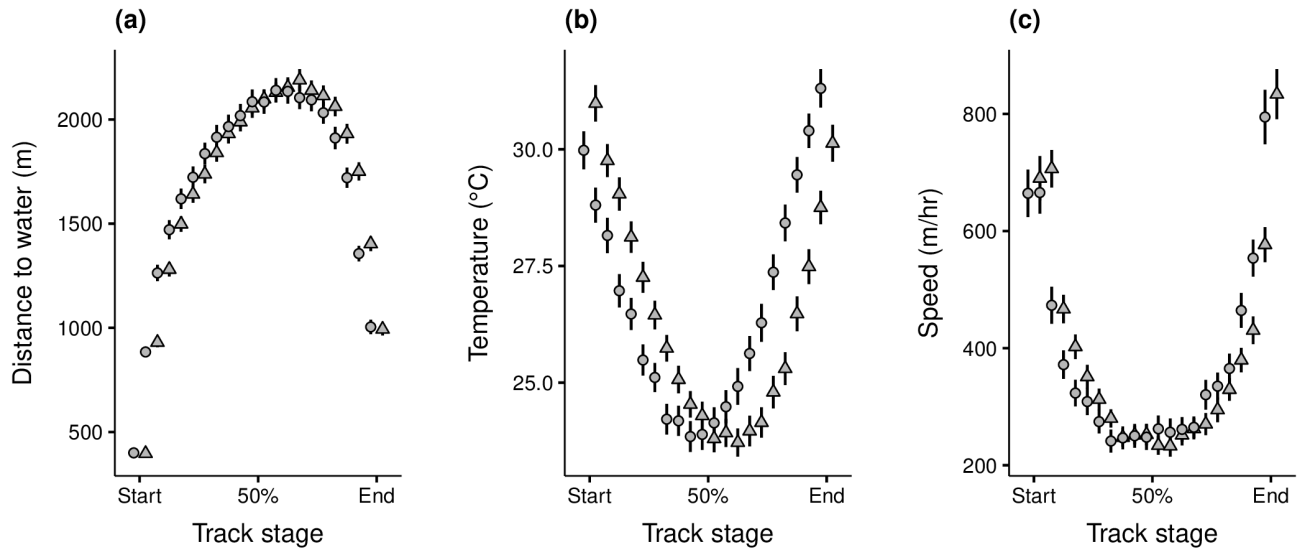


Fig. 5: Probability density plots of (a) Actual distances travelled by elephants along 12 -- 24 hour track segments between water points, (b) Linear distances between start and end points of 12 -- 24 hour track segments between water points, and (c) Linear distance between the midpoints (defined by temporal duration) of successive 12 -- 24 hour segments in each season. Seasons are represented by lines (cool-dry: grey, hot-wet: black).

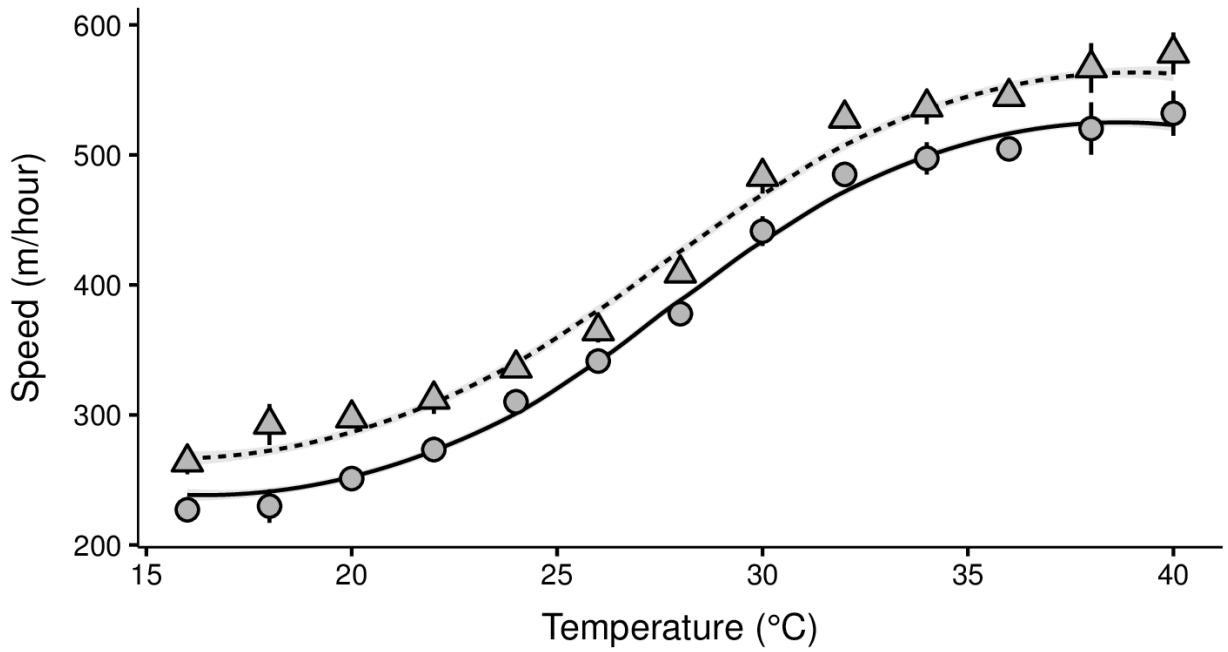


278 *Fig. 6: Distance moved along 12 – 24 hour segments as a function of the linear distance between the*
 279 *beginning and end of the segment, in each season. Data were grouped and averaged in 500m*
 280 *increments of the distance between segment start and end points. Seasons are represented by*
 281 *symbols (cool-dry: circles, hot-wet: triangles). Vertical lines represent 95% confidence intervals*
 282 *about each point.*

283



285 *Fig. 7: Elephant movement variables along 12 – 24 hour track segments between water points at 5%*
 286 *intervals of segment duration (time): (a) Minimum distance to water (in metres), (b) Thermochron*
 287 *temperature, and (c) Speed (in m/hr). Points are separated by season (cool-dry = circles, hot-wet =*
 288 *triangles), and offset from each other to avoid overlap. Vertical lineranges show 95% confidence*
 289 *intervals about each point.*



290 *Fig. 8: Elephant speed (points) at 2°C temperature intervals in each season (cool-dry: blue circles,*
 291 *hot-wet: red triangles). GAMM fit (lines), data error intervals (linerranges), and fit error intervals*
 292 *(shaded areas) are shown.*

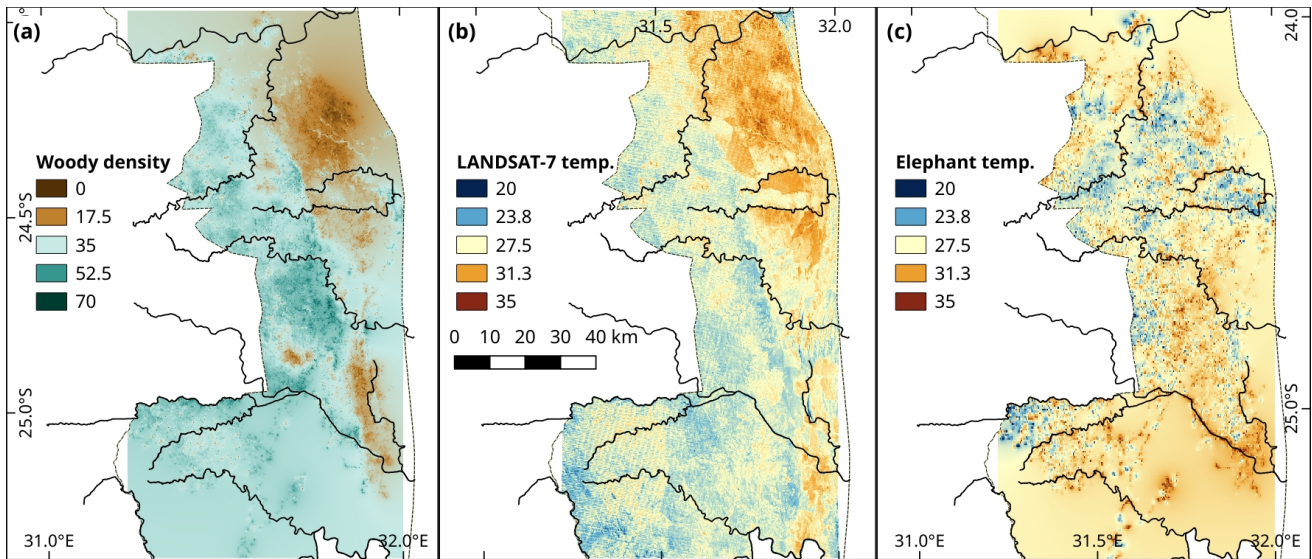


Fig. 9: (a) Woody densities at points traversed by elephants ($n = 14$), in Kruger National Park over the period August 2007 – August 2009. (b) LANDSAT-7 derived mean daytime temperature in Kruger NP over the study period, and (c) Ambient temperature as reported by elephant-borne thermochrons over the study period. Maps (a) and (b) created as inverse distance interpolations of values from elephant movement and thermochron data, respectively.

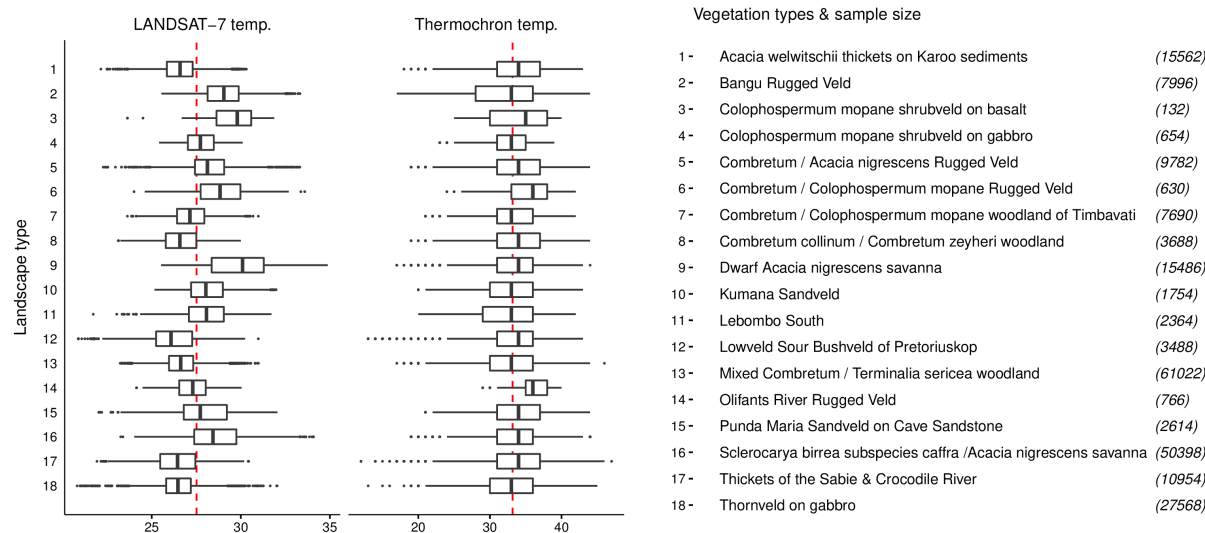


Fig. 10: Boxplots of the mean daytime temperature over the two-year long study period (August 2007 – August 2009) derived from LANDSAT-7, and the ambient daytime temperature reported by elephant-borne thermochrons over the the two-year study period, in each of 18 vegetation types reported in the data (right hand side). Numbers in brackets next to the vegetation types represent the number of elephant positions in each vegetation type. Data are not divided by season.

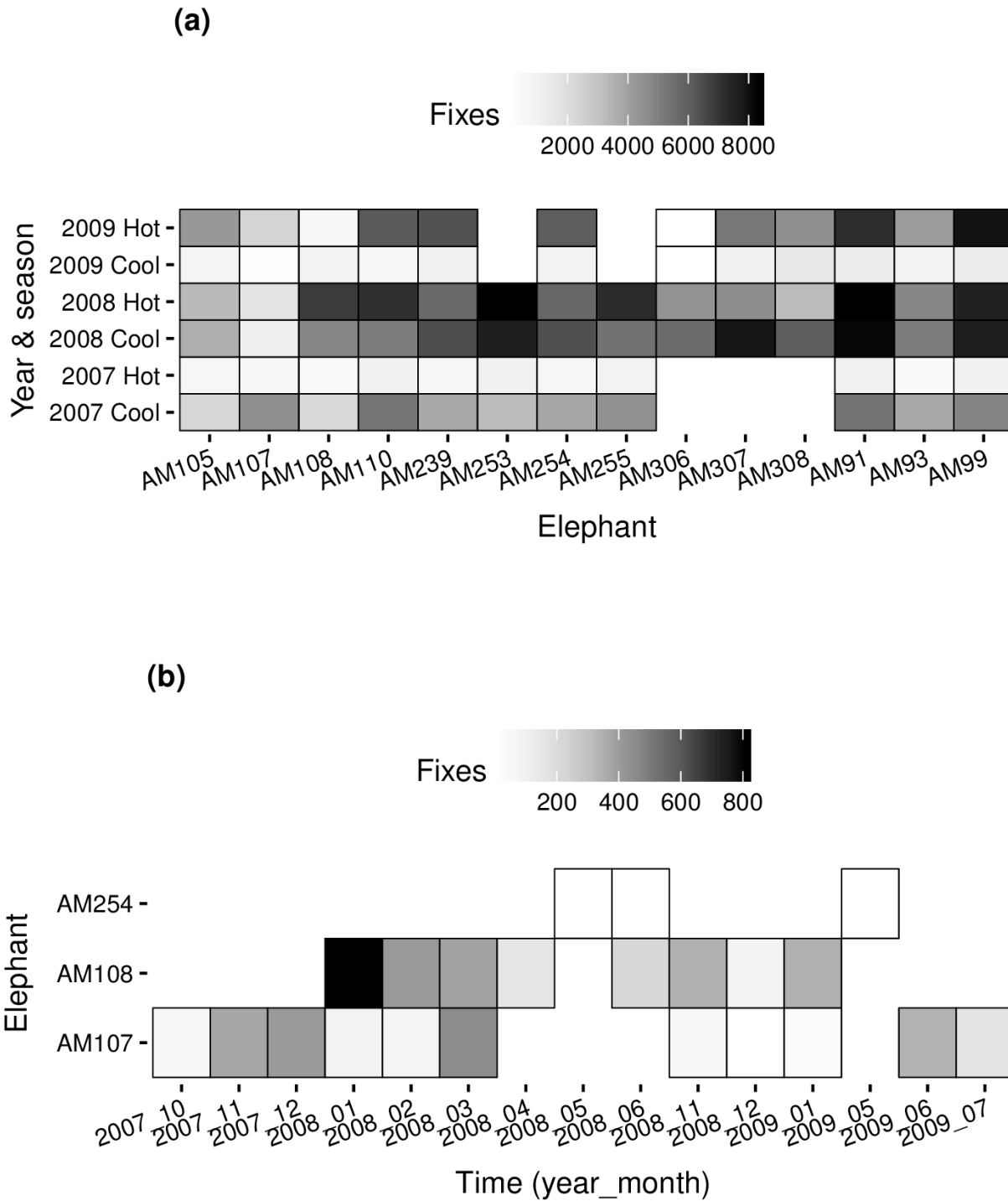


Fig. 11: Numbers of GPS fixes for each elephant in discrete intervals of the tracking period. (a) GPS fixes per individual ($n = 14$) per season per year, and (b) GPS fixes within 10km of the weather station at Skukuza per individual ($n = 3$) in each month of the tracking period. Data shown in (b) were used to assess the accuracy of thermochrons as accurate measures of ambient temperature.