Elephants shuttle to thermoregulate

1 **Pratik R. Gupte[1,2], Herbert T. Prins[3], Rob Slotow[4], Maria Thaker1[1*], Abi T. Vanak[2]**

2 [1]Centre for Ecological Sciences, Indian Institute of Science, Bangalore, India

3 [2]Ashoka Trust for Research in Ecology and the Environment, Bangalore, India

4 [3]Wageningen University and Research (Alterra), Wageningen, The Netherlands

5 [4]University of Kwa-Zulu Natal, Durban, South Africa

6 *** Correspondence:**
7 Maria Thaker
8 mthaker@iisc.ac.in

11 **Abstract**

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

27 **1   Introduction**
28 Animals faced with heat stress thermoregulate by altering their physiology and behaviour (Angilletta
29 2012). Most physiological responses to high temperatures, such as sweating in mammals, rely on
30 water evaporation to transfer heat away from the core-body. Many animals must complement
31 physiological thermoregulation with behavioural mechanisms of losing heat. In general, behavioural
32 responses to overheating involve utilising heat-sinks to which excess body-heat may be transferred.

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

48   Animals must balance the energetic benefits of using water as a thermoregulatory aid against the
49   costs of negative interactions such as predation and competition at crowded waterholes (Cain *et al.*
50   2012; Owen-Smith and Goodall 2014). Individuals may attempt to avoid such costs by periodically
51   shuttling between water and more optimal foraging and resting sites, but this increases movement
52   costs and decreases time that could have been spent feeding (Johnson *et al.* 2002; Cain *et al.* 2012;
53   Owen-Smith and Goodall 2014; Giotto *et al.* 2015). Body size may mediate how a species reckons
54   with the costs and benefits of visiting water. Large species such as buffalo and eland *Taurotragus*
55   *oryx* that overheat more quickly are likely to be more water-dependent than smaller ones such as
56   sable antelope *Hippotragus niger,* and zebra *Equus quagga* (Cain *et al.* 2012; Shrestha *et al.* 2012;
57   Bennitt *et al.* 2014; Owen-Smith and Goodall 2014). Water-dependence can introduce periodicity to
58   an animal's movement, such as that corresponding to the diel or seasonal cycle (Giotto *et al.* 2015).
59   However, it is in turn affected by seasonal changes. For example, buffalo in the Okavango delta are
60   found farther from permanent water sources in the hot-wet season when they can use ephemeral
61   pools, and closer to water in the cool-dry season (Bennitt *et al.* 2014). Further, seasonal changes in
62   temperature and resource availability can affect the activity and movement of ungulates, changing
63   their distribution in relation to water (Leggett 2010; van Beest *et al.* 2012; Shrestha *et al.* 2012;
64   Owen-Smith and Goodall 2014). This sets up an interaction between environmental conditions such
65   as ambient temperature, an individual's physiological state, and its position in relation to water
66   sources.

67   Savanna elephants are an excellent study system to disentangle the effects of temperature on
68   movement strategies in relation to water. Elephants, lacking a physiological means of
69   thermoregulation, such as sweating or panting, must compensate by using behaviours such as ear-
70   flapping (Hiley 1975; Wright 1984; Wright and Luck 1984). At larger spatio-temporal scales,
71   elephants avoid thermal stress and the energetic costs of thermoregulation by shifting their activity
72   peaks to cooler parts of the day, and select for thermally stable landscapes with reduced variation in
73   daily temperatures (Johnson *et al.* 2002; Kinahan *et al.* 2007; Leggett 2010). Elephants, as expected
74   for mammals of their size, are heavily water dependent, making periodic movements to water that are

75 posited to be driven by temperature (Valls Fox 2015). Seasonal changes can have a significant effect
76 on elephant movement, with individuals from populations in Namibia and South Africa moving
77 faster in the wet season than the dry season, suggesting an effect of water availability on movement
78 (Leggett 2010; Birkett *et al.* 2012). However, in both these cases, the wet and dry seasons overlap
79 with the hot and cool seasons, respectively, opening up the possibility that differences in mean
80 temperature between the seasons could contribute to differences in movement. Testing this
81 hypothesis requires both high-resolution position and temperature data at each step of a movement
82 track. Here, we characterise elephant movement in relation to water sources and ambient temperature
83 using data from traditional satellite telemetry, coupled with instantaneous data from temperature
84 loggers (thermochrons) borne by individuals, to test the hypothesis that savanna elephants'
85 movement is driven by temperature.

86 ## 2   Methods

87 ### 2.1   Data collection

88 The study was conducted in the predominantly semi-arid savanna landscape of Kruger National Park
89 and adjacent private game reserves (extent: 31.06ºE – 32.0ºE, 23.9ºS – 25.4ºS) in South Africa,
90 where we have had 14 female African elephants – each from a different herd – fitted with GPS
91 logger-transmitter collars since 2007 (Fig. 1a, 1b). Details of the capture and collaring of these
92 elephants, including an ethics and permissions statement can be found in Birkett *et al.* 2012.
93 Transmitters and inbuilt thermochrons were set to record half-hourly position and temperature data,
94 respectively. For this study, we selected location and temperature data from our tagged elephants
95 between August 2007 and August 2009, during which each elephant was tracked for on average 637
96 days (range: 436 – 731) (see Fig. 13a).

97 To understand how ambient temperature is affected by environmental factors, specifically, the diel
98 cycle and vegetation type, we collected the following: First, images of the study site taken in the low-
99 gain thermal infrared range (Band 6 VCID 1: 10.40 – 12.50 μm) by the Enhanced Thematic Mapper
100 + device aboard LANDSAT-7, which we converted to degree Celsius temperature data (Chander *et*
101 *al.* 2009), and second, polygon shapefiles of the vegetation classes of Kruger NP as defined by
102 Gertenbach 1983.

103 To relate elephant movement to their landscape, we gathered shapefiles of the courses of park rivers,
104 the locations of active park waterholes, and 30m resolution terrain slope from SRTM data (Farr *et al.*
105 2007). To relate elephant movement to ambient temperatures, we sought to verify that thermochrons
106 reported the thermal landscape of elephants, and so we collected ambient temperature data from the
107 weather station tower at Kruger headquarters at Skukuza (24.98°S, 31.5°E) (Fig. 1b).

108 ### 2.2   Relating temperature to the landscape

109 We first sought to understand variation in ambient temperatures as a function of the landscape types
110 found over the study site (Gertenbach 1983). We mapped the mean temperature of Kruger NP logged

111   by LANDSAT-7 over the study period (see Fig. 11b), and created boxplots of the temperature in each
112   of 18 landscape types (see Fig. 12 *LANDSAT-7 temp.*). Since LANDSAT-7 (and most other
113   reflectance-based remote-sensors) makes passes only over the sunlit side of the earth, the reported
114   temperatures are only from the daytime. We took our temperature map (Fig. 11b) to represent the
115   diurnal thermal landscape of Kruger NP.

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

122   Finally, we ran separate generalised linear models (see Tab. 1) to test whether landscape type
123   influenced either the LANDSAT-7 temperature or the thermochron temperature. In the case of
124   LANDSAT-7 temperature we sampled 10,000 random points with a minimum distance of 30m
125   between points within the extent of the study site. When testing for an effect on thermochron
126   temperature, we accounted for consistent individual variation between elephants by using elephant
127   identity as a random effect, making for a mixed model (GLMM). We further added time of day as a
128   fixed effect to test the influence of the diurnal cycle on temperature, especially in comparison with
129   landscape type.

2.3   Thermochrons as accurate measures of ambient temperature

131   First, we tested the correlation of thermochron data with ambient temperatures from the Skukuza
132   weather tower. For this, we used a subset of elephant positions (n = 4,971, 0.02% of total) within a
133   10km radius of the station (see Fig. 2c), computed the pooled mean temperature at each hour across
134   individuals (hereon, thermochron temperature), matched these pooled data to hourly mean
135   temperatures recorded at the station tower (tower temperature), and tested the correlation of elephant
136   and ambient temperature separately in the hot-wet and cool-dry seasons as defined in Birkett *et al.*
137   2012.

2.4   Characterising movements between water points

139   To examine elephants' movements in relation to water sources, we divided each individual's track
140   into a set of segments between successive visits to water points, which we defined as positions within
141   500m of a water source. We chose this generous buffer distance so as to capture visits to water that
142   occurred between GPS position fixes, and which thus went unrecorded (see Fig. 1c). Each segment

143   thus began and ended within 500m of a water source. The last point pt_{nij} of each segment was

144   immediately followed by the first point of the next segment pt_{0ij}, with *n-1* points between the
145   beginning and end of each segment *j* of each elephant *i*.

146   For each of these segments, we identified the first (pt_{0ij}) and last (pt_{nij}) points, and calculated the

147   linear distance between the two. Further, we computed the distance moved along the segment as the

148   sum of the distances between each successive point (pt_{xij} to pt_{xij+1}), and the distance of each

149   discrete position (pt_{xij}) from the nearest water source. Additionally, we obtained thermochron

150   temperature (t_{xij}) at each discrete position along the segment, and the transmitter-reported speed

151   (v_{xij}) at each point.

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

156   ## 2.5   Relating movement to temperature

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

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

166   # 3   Results

167   ## 3.1   Elephant tracking

168   We obtained 283,737 total positions from 14 elephants, which we converted to movement tracks (Fig
169   1b). Elephants ranged on average 4005 km (range: 1854 km – 7074 km) across southern Kruger over
170   the tracking period, covering on average 7.2 km per day (range: 5 km – 9.9 km) at a mean speed of
171   398 m/hr (range: 304 m/hr – 470 m/hr). Individual positions were within 500m of water a mean 12%
172   (range: 6% – 21%) and 11% (range: 3% – 17%) of the time in the cool-dry and hot-wet seasons
173   respectively.

174   ## 3.2   Landscape effects on temperature

175   We found a significant influence of landscape type on the two-year daytime temperature recorded by
176   LANDSAT-7, and a analysis of deviance using a Wald II chi-squared test showed landscape type

177   overall to be significant predictor of temperature (X^2 = 482.46, p < 0.01). Similar analyses using the
178   elephant movement and thermochron data revealed landscape type to be a significant predictor of
179   thermochron temperatures (X^2 = 5252.4, p < 0.01, Wald II chi-squared test). However, hour of day
180   was a stronger predictor of thermochron temperatures (X^2 = 7149.9, p < 0.01, Wald II chi-squared
181   test).

182   **3.3   Thermochron accuracy**

183   Thermochrons fitted on elephant collars reported nearly identical mean daily temperatures of
184   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
185   respectively (Fig. 2a, 2b). Thermochron data from 3 elephants logged within 10km of Skukuza (see
186   Fig. 13b) were well correlated with temperatures from the weather station at each hour in both
187   seasons (mean hourly correlation: cool-dry = 0.77, hot-wet: 0.81), with all hourly correlations ≳ 0.6
188   (fig 3b). We henceforth consider thermochron temperatures to be equivalent to ambient temperatures.

189   **3.4   Track segments between water points**

190   Elephants were within 500m of water at 44,610 of 283,737 points (≈ 16%), leading us to identify
191   44,622 track segments which began and ended at water. 40,347 (≈ 90%) of these segments had a
192   temporal duration of under 3 hours, with 89% lasting under an hour, i.e., indicating consecutive
193   residence at water points. On excluding these and segments with a duration above the 99th percentile
194   (72 hours, n = 445), the remaining 3,754 (≈ 8.4%) of segments had a multi-modal distribution of
195   segment durations, with peaks between 12 – 24 hours, 36 – 48 hours, and at 72 hours (Fig. 3). We
196   only retained 1,519 segments with durations between 12 and 24 hours for further characterisation.

197   **3.5   Movement along track segments**

198   Elephants began each 12 – 24 hour segment on average 314m (range: 1.3 – 2346m) from a water
199   source, and ended a mean 907 m (range: 500 – 718m) from the next water source (Fig. 7a). 12 – 24
200   hour segments usually began at 14 – 19 hours (2PM – 7PM, SD = 4.84) and ended at 6 – 12 hours
201   (6AM – 12 Noon, SD = 4.67), with elephants reaching the halfway point at 22 – 04 hours (10PM –
202   4AM, SD = 9.06) (Fig. 4). On average, elephants travelled 6,508 m (range: 526 – 20,326 m) along
203   their path between visits to water points (Fig. 5), reaching a mean maximum distance of 2,462 m
204   (range: 519 – 6,832 m) from the nearest water source. In ≈8% and ≈ 30% of segments respectively,
205   elephants returned to within 500m and 1km of the position from which they began, with no
206   difference between the seasons (Fig. 6). However, the midpoints of successive segments were within
207   500m and 1km of each other in only 3% and 9.8% of segments, respectively (Fig. 7). The distance
208   travelled along a segment showed an increasing trend with an increasing linear distance between the
209   start and end point of the segment (Fig. 8).

210   **3.6   Temperature as a driver of movement**

211 Elephants moving along 12 – 24 hour segments were initially moving away from water until about
212 the halfway point, after which their distance from water diminished (Fig. 9a). Temperatures along
213 segments initially decreased until halfway, and then climbed steadily (Fig. 9b). Elephant speed was
214 highest in the initial and final fifths of each segment (Fig. 9c), with the first and last speeds (716 m/hr
215 and 667 m/hr respectively) in a segment nearly thrice as fast as the speed at the halfway point (242
216 m/hr). No seasonal difference was apparent.

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

4   Discussion

221 Discussion here on finalising methods and results.

5   Conflict of Interest

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

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

6   Author Contributions

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

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

7   Funding

237 Details of all funding sources should be provided, including grant numbers if applicable. Please
238 ensure to add all necessary funding information, as after publication this is no longer possible.

8   Acknowledgments

240 This is a short text to acknowledge the contributions of specific colleagues, institutions, or agencies
241 that aided the efforts of the authors.

242 We thank SANParks for providing weather data from the Skukuza weather station, and for providing
243 shapefiles of geographic features of Kruger. We thank xxx for xxx.

244 **9 Data Availability Statement**

245 The datasets analsyed for this study can be found on Movebank http://www.movebank.org/.

246 **10 References**

Aublet J-F, Festa-Bianchet M, Bergero D, and Bassano B. 2009. Temperature constraints on foraging behaviour of male Alpine ibex (Capra ibex) in summer. *Oecologia* **159**: 237–247.

Bates D, Mächler M, Bolker B, and Walker S. 2015. Fitting Linear Mixed-Effects Models Using lme4. *J Stat Softw* **67**: 1–48.

Beest FM van, Moorter BV, and Milner JM. 2012. Temperature-mediated habitat use and selection by a heat-sensitive northern ungulate. *Anim Behav* **84**: 723–35.

Bennitt E, Bonyongo MC, and Harris S. 2014. Habitat Selection by African Buffalo (*Syncerus caffer*) in Response to Landscape-Level Fluctuations in Water Availability on Two Temporal Scales. *PLOS ONE* **9**: 1–14.

Birkett PJ, Vanak AT, Muggeo VMR, *et al.* 2012. Animal Perception of Seasonal Thresholds: Changes in Elephant Movement in Relation to Rainfall Patterns. *PLOS ONE* **7**: 1–8.

Bracis C. 2017. recurse: Computes Revisitation Metrics for Trajectory Data.

Bucini G, Hanan N, Boone R, *et al.* 2010. Woody fractional cover in Kruger National Park, South Africa: remote-sensing-based maps and ecological insights. *Ecosyst Funct Savannas Meas Model Landsc Glob Scales*: 219–238.

Cain JW, Owen-Smith N, and Macandza VA. 2012. The costs of drinking: comparative water dependency of sable antelope and zebra. *J Zool* **286**: 58–67.

Chander G, Markham BL, and Helder DL. 2009. Summary of current radiometric calibration coefficients for Landsat MSS, TM, ETM+, and EO-1 ALI sensors. *Remote Sens Environ* **113**: 893–903.

Farr TG, Rosen PA, Caro E, *et al.* 2007. The Shuttle Radar Topography Mission. *Rev Geophys* **45**.

Gertenbach WPD. 1983. Landscapes of the Kruger National Park. *Koedoe* **26**.

Giotto N, Gerard J-F, Ziv A, *et al.* 2015. Space-Use Patterns of the Asiatic Wild Ass (*Equus hemionus*): Complementary Insights from Displacement, Recursion Movement and Habitat Selection Analyses. *PLOS ONE* **10**: 1–21.

Gorelick N, Hancher M, Dixon M, *et al.* 2017. Google Earth Engine: Planetary-scale geospatial analysis for everyone. *Remote Sens Environ* **202**: 18–27.

Hetem RS, Strauss WM, Fick LG, *et al.* 2012. Activity re-assignment and microclimate selection of free-living Arabian oryx: responses that could minimise the effects of climate change on homeostasis? *Zoology* **115**: 411–6.

Hiley P. 1975. HOW the ELEPHANT KEEPS ITS COOL. *Nat Hist* **84**: 34–41.

Johnson CJ, Parker KL, Heard DC, and Gillingham MP. 2002. Movement parameters of ungulates and scale-specific responses to the environment. *J Anim Ecol* **71**: 225–235.

Kinahan AA, Pimm SL, and Aarde RJ van. 2007. Ambient temperature as a determinant of landscape use in the savanna elephant, *Loxodonta africana*. *J Therm Biol* **32**: 47–58.

Kranstauber B and Smolla M. 2016. move: Visualizing and Analyzing Animal Track Data.

Leggett K. 2010. Daily and hourly movement of male desert-dwelling elephants. *Afr J Ecol* **48**: 197–205.

Owen-Smith N and Goodall V. 2014. Coping with savanna seasonality: comparative daily activity patterns of African ungulates as revealed by GPS telemetry. *J Zool* **293**: 181–191.

Purdon A. 2016. Environmental determinants of the movement patterns of elephants in the Kruger National Park.

R Core Team. 2017. R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing.

Shrestha AK, Wieren SE van, Langevelde F van, *et al.* 2012. Body temperature variation of South African antelopes in two climatically contrasting environments. *J Therm Biol* **37**: 171–8.

Valls Fox H. 2015. To drink or not to drink? The influence of resource availability on elephant foraging and habitat selection in a semi-arid savanna.

Wood SN. 2013. Generalized Additive Models: An Introduction with R. Chapman and Hall/CRC.

Wright P. 1984. Why do elephants flap their ears? *South Afr J Zool* **19**: 266–269.

Wright C and Luck C. 1984. Do elephants need to sweat? *South Afr J Zool* **19**: 270–274.: 270–274.

247 **11 Tables**

Model	Type	Response	Fixed effects				Random effect	Sample size
1	GLM	LANDSAT-7 temperature	Landscape type (Gertenbach 1983)					10,000
2	GLMM	Thermochron temperature	Landscape type (Gertenbach 1983)	Hour of day			Elephant identity	266,382
3	GAMM	Speed	Thermochron temperature	Season	Slope	Woody density	Elephant identity	275,129

248

249   **12   Figures**
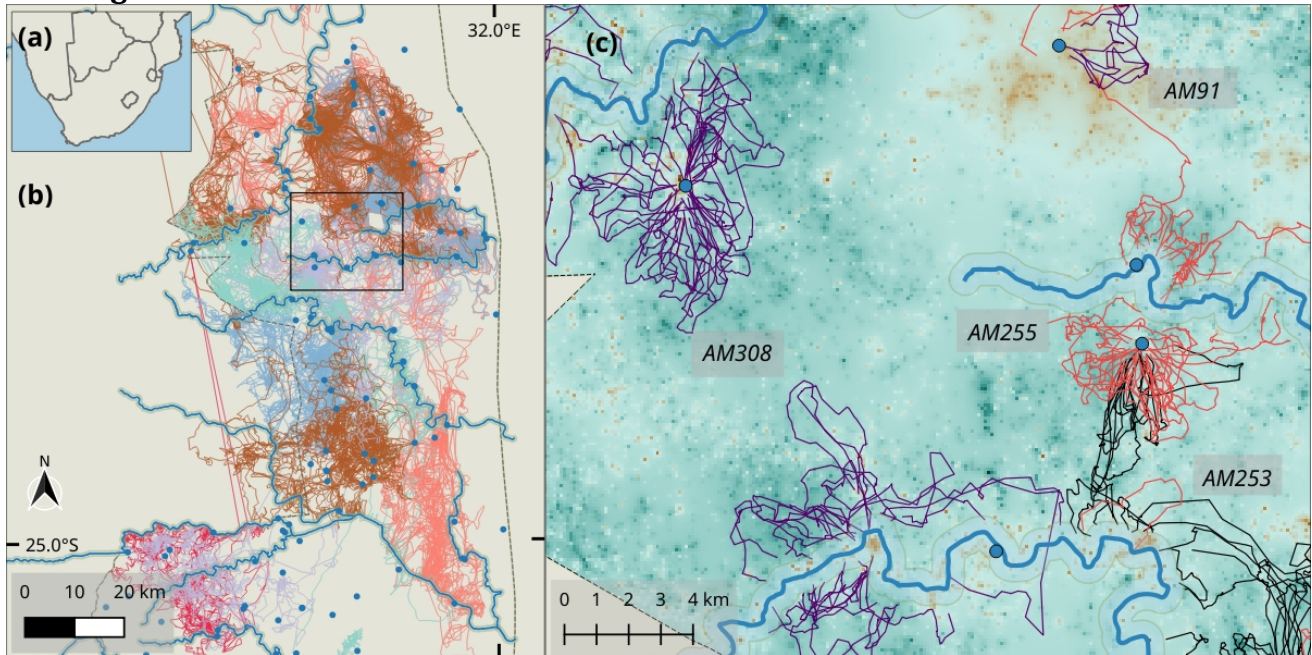
Fig. 1: (a) Study site in Kruger National Park, South Africa (red star), showing (b) park boundary (dashed grey line), major rivers (solid blue lines), open waterholes (blue dots), and raw elephant tracks (coloured lines, n = 14). (c) Inset showing 12 – 24-hour long track segments between water sources (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).
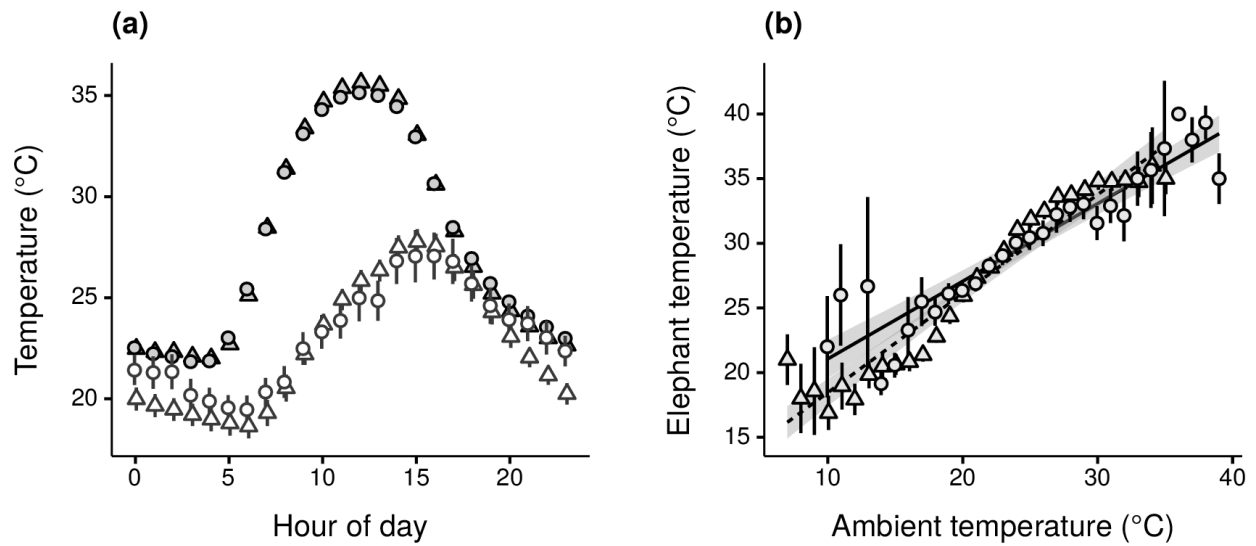
Fig. 2: (a) Mean thermochron temperature (coloured points: cool-dry = blue, hot-wet = red) and measured ambient temperature (outline points: cool-dry = circles, hot-wet = triangles) at each hour of day in each season across the study period (and (b) GLM fits (lines) in each season (cool-dry: blue circles & lines, hot-wet: red triangles & lines). Vertical lineranges and shaded areas (coloured by season) indicate 95% confidence intervals at each point.
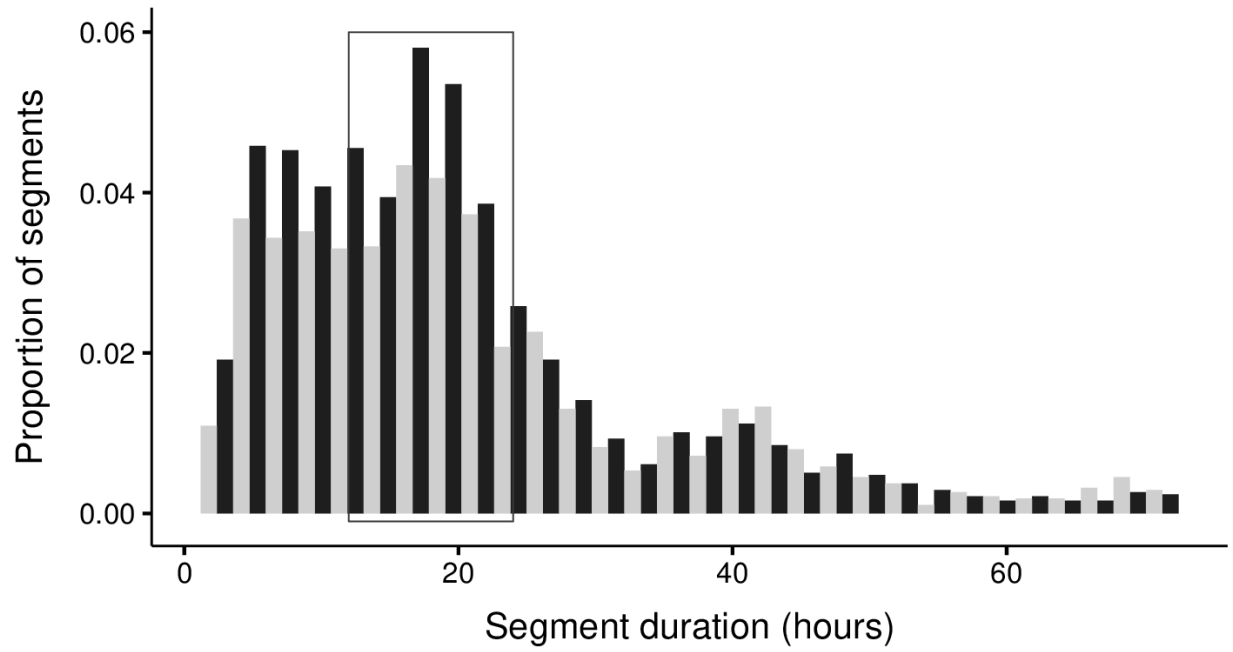
Fig. 3: Histogram of segment durations (in hours) for segments between water points. Seasons are represented by shaded bars (cool-dry: grey, hot-wet: black). Upper and lower limits in both seasons have been set at 72 and 3 hours, respectively. The rectangle shows the peak representing segments of a duration between 12 and 24 hours, which were used for all further characterisation.
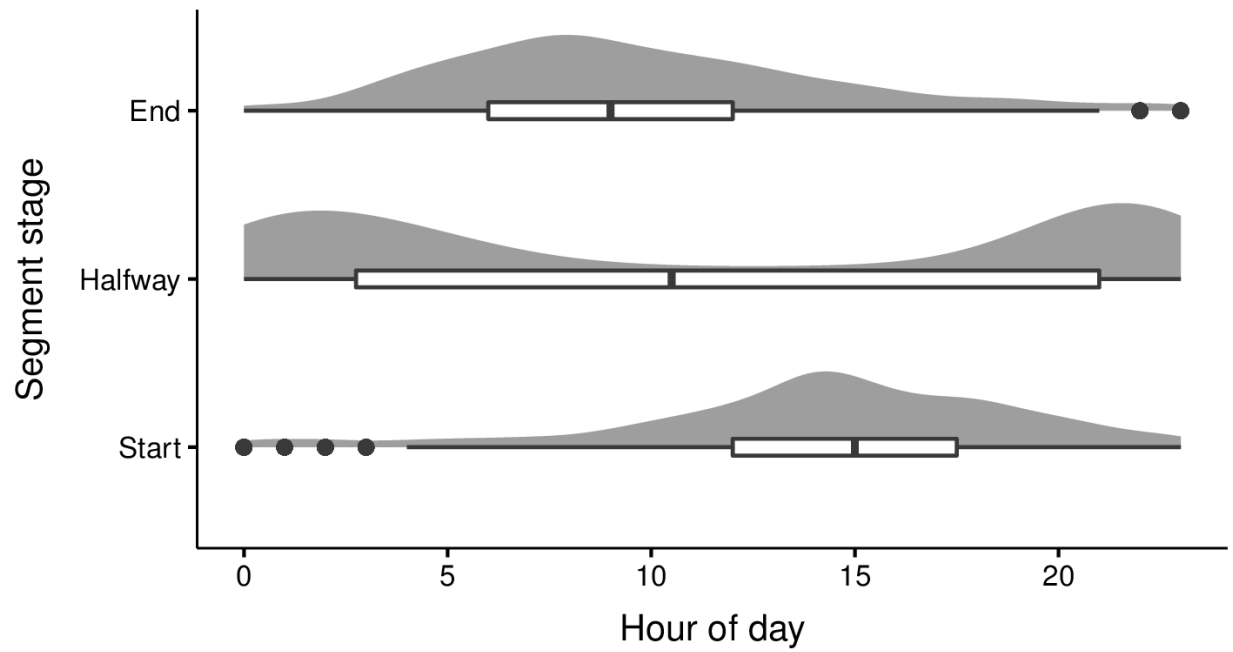
Fig. 4: Boxplots and probability distributions (half-violins) of the hour of day of the three main stages of a 12 – 24 hour segment between water points.
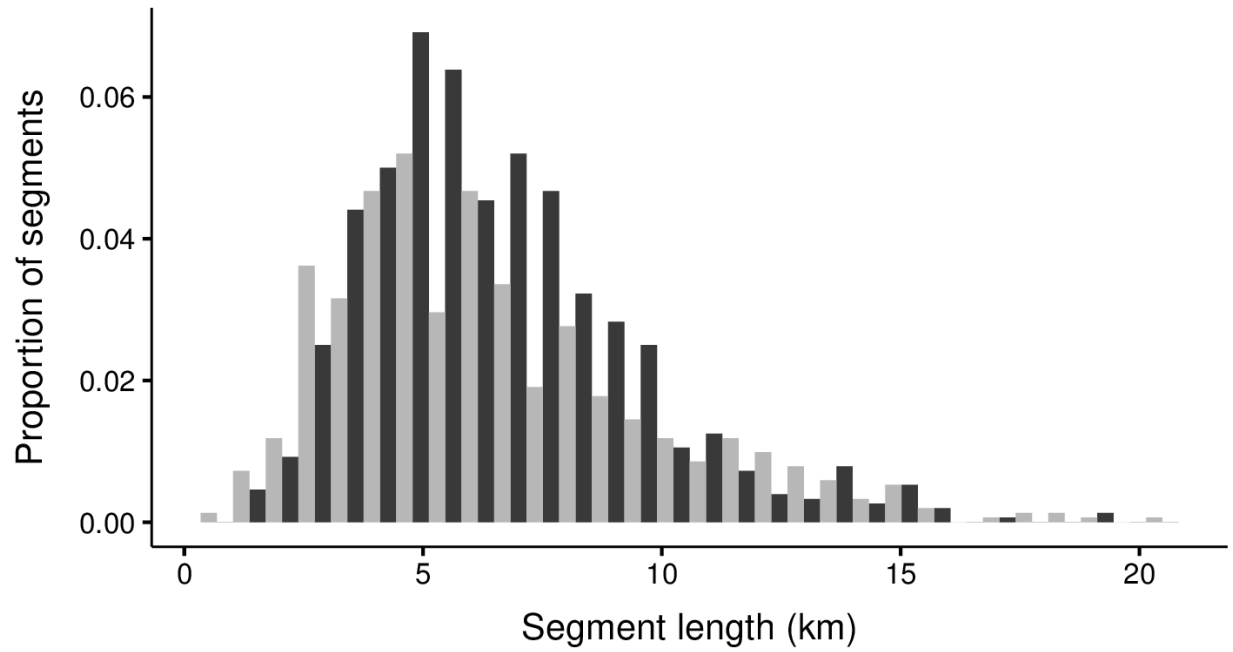
Fig. 5: Histogram of distances travelled by elephants along 12 -- 24 hour track segments between water points. Seasons are represented by shaded bars (cool-dry: grey, hot-wet: black).
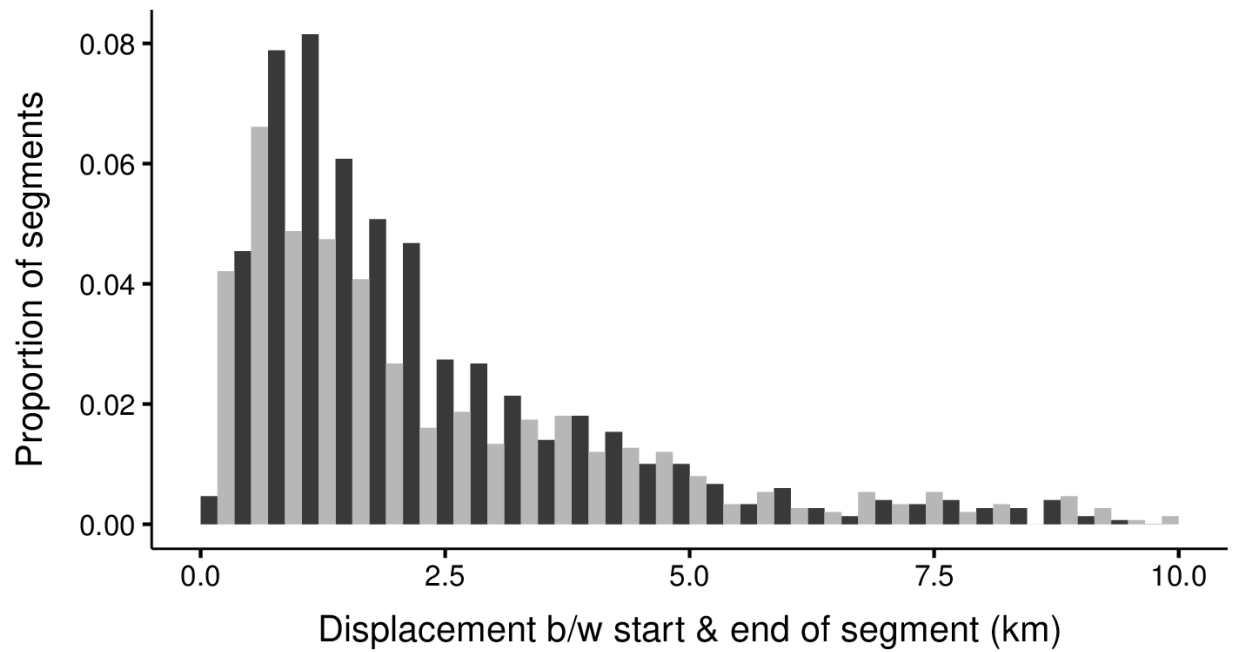
Fig. 6: Histogram of displacements along 12 -- 24 hour track segments between water points. Seasons are represented by shaded bars (cool-dry: grey, hot-wet: black). Elephants return to within 500m of the start of a track around 8% of the time, and to within 1km of the start around 30% of the time.
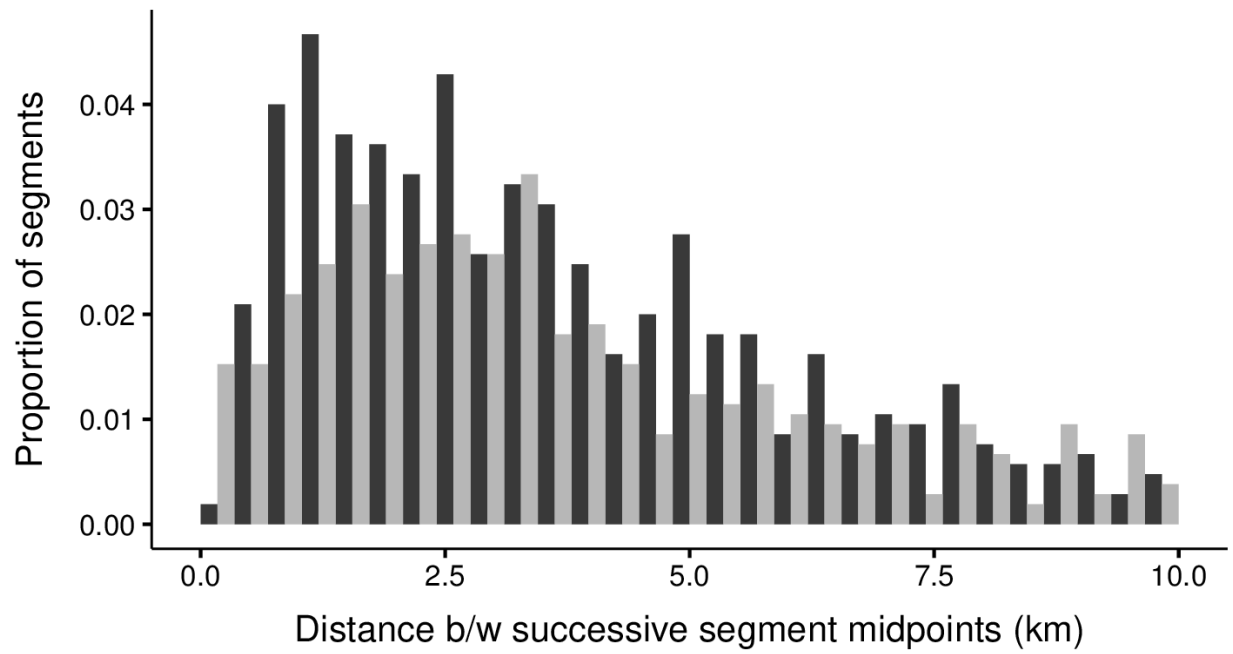
Fig. 7: Histogram of the linear distance between the midpoints (defined by temporal duration) of successive 12 – 24 hour segments in each season. Seasons are represented by shaded bars (cool-dry: grey, hot-wet: black).
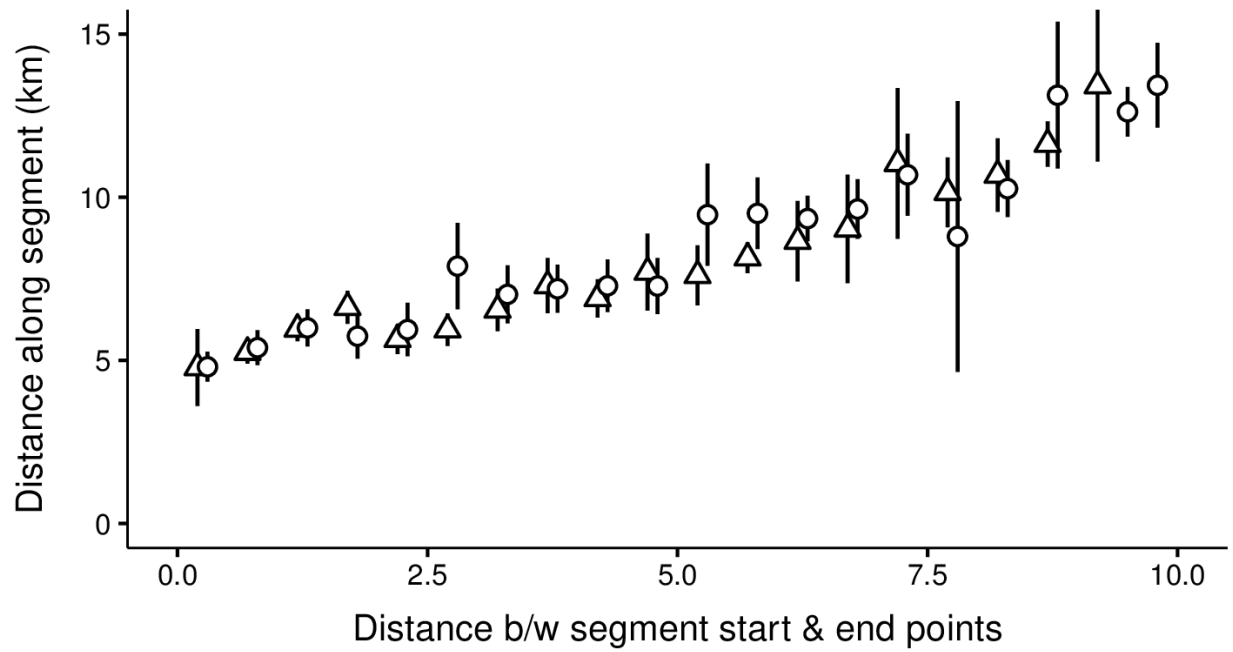
Fig. 8: Distance moved along 12 – 24 hour segments as a function of the linear distance between the beginning and end of the segment, in each season. Data were grouped and averaged in 500m increments of the distance between segment start and end points. Seasons are represented by symbols (cool-dry: circles, hot-wet: triangles). Vertical lines represent 95% confidence intervals about each point.
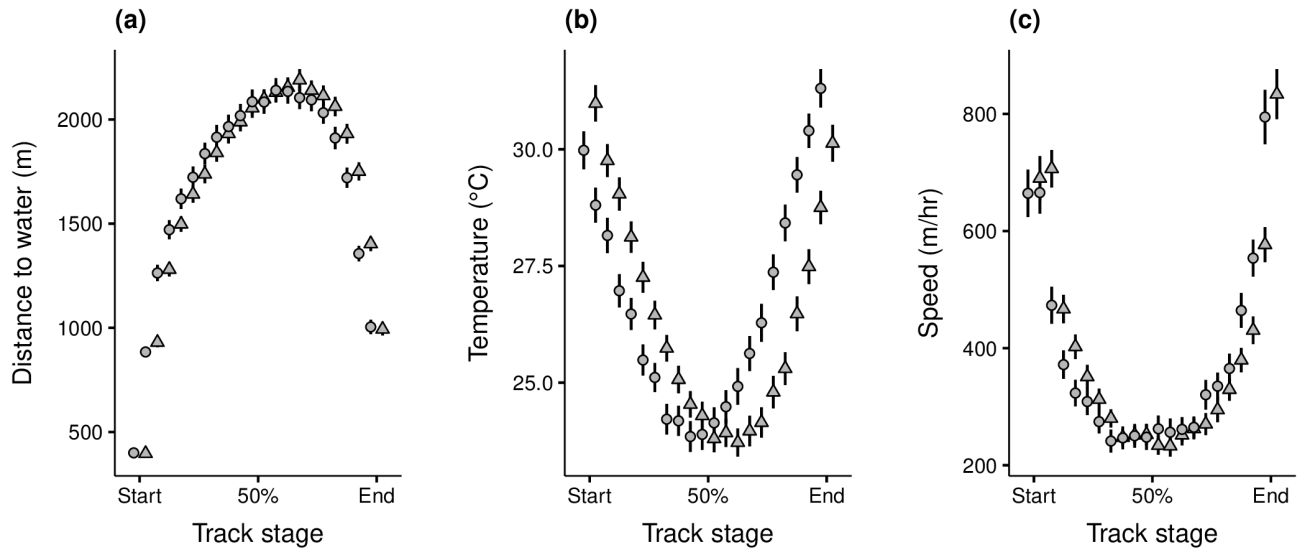
Fig. 9: Elephant movement variables along 12 – 24 hour track segments between water points at 5% intervals of segment duration (time): (a) Minimum distance to water (in metres), (b) Thermochron temperature, and (c) Speed (in m/hr). Points are separated by season (cool-dry = circles, hot-wet = triangles), and offset from each other to avoid overlap. Vertical lineranges show 95% confidence intervals about each point.
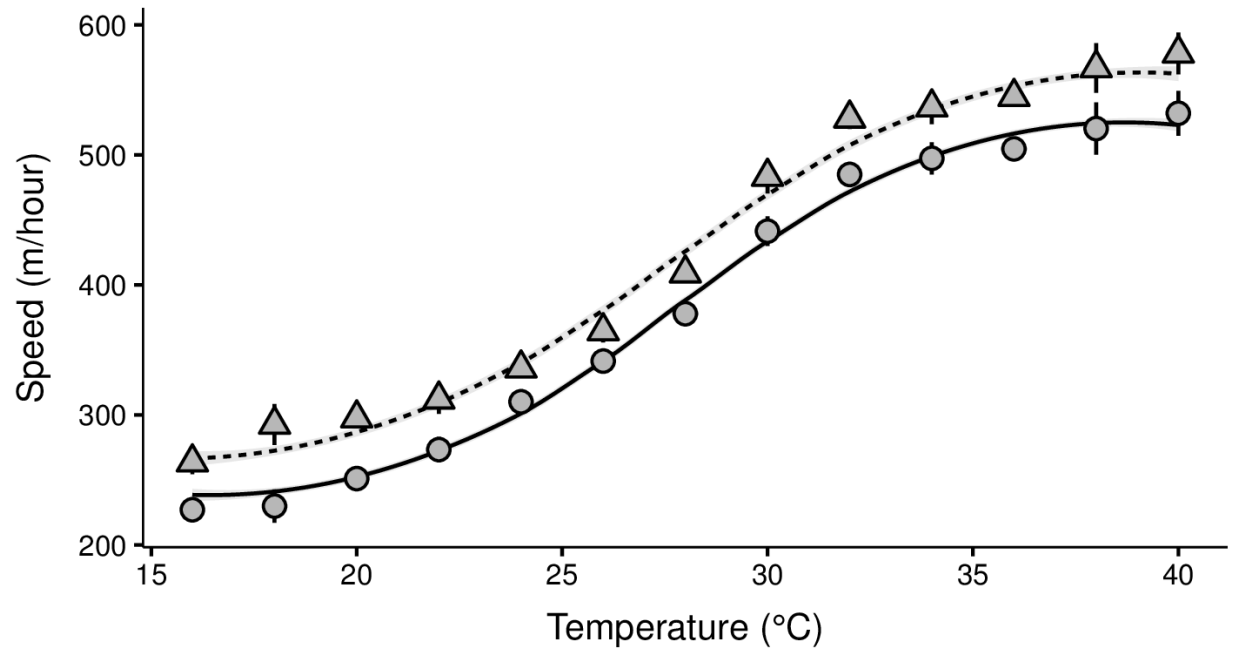
Fig. 10: Elephant speed (points) at 2°C temperature intervals in each season (cool-dry: blue circles, hot-wet: red triangles). GAMM fit (lines), data error intervals (lineranges), and fit error intervals (shaded areas) are shown.
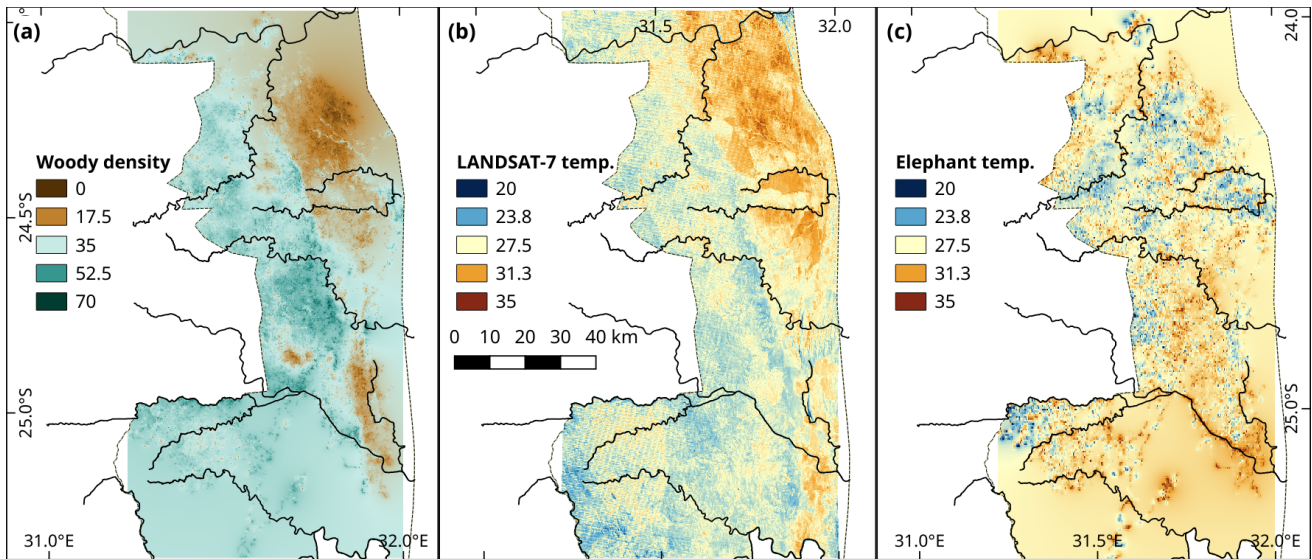
Fig. 11: (a) Woody densities at points traversed by elephants (n = 14), in Kruger National Park over the period August 2007 – August 2009. (b) LANDSAT-7 derived mean daytime temperature in Kruger NP over the study period, and (c) Ambient temperature as reported by elephant-borne thermochrons over the study period. Maps (a) and (b) created as inverse distance interpolations of values from elephant movement and thermochron data, respectively.
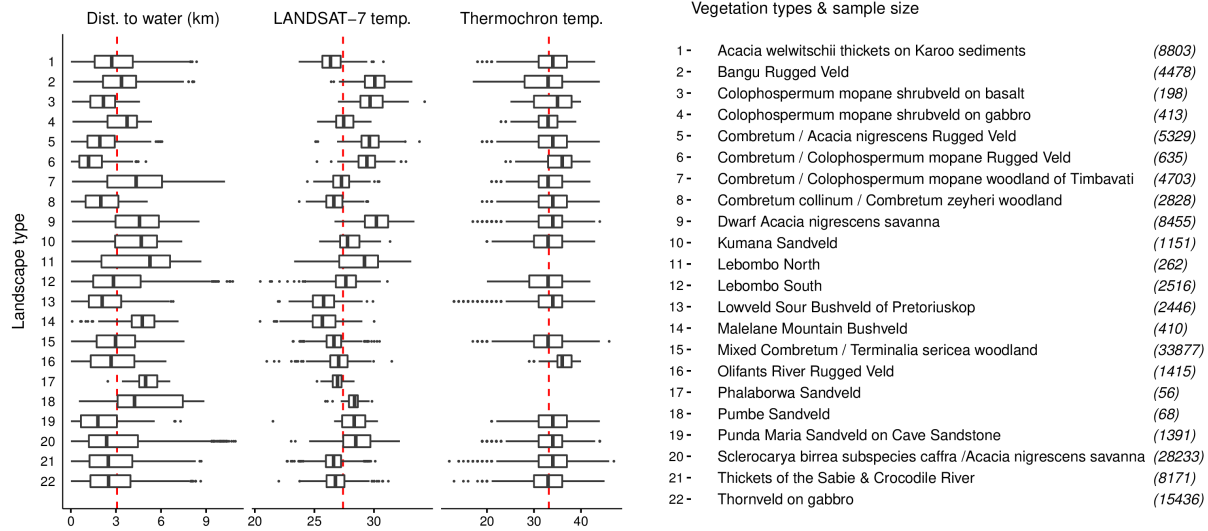
Fig. 12: Boxplots of the minimum distance to water (in km), the mean daytime temperature over the two-year long study period (August 2007 – August 2009) derived from LANDSAT-7, and the ambient daytime temperature reported by elephant-borne thermochrons over the the two-year study period, in each of 18 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. Missing boxplots in column 3 indicate insufficient data.
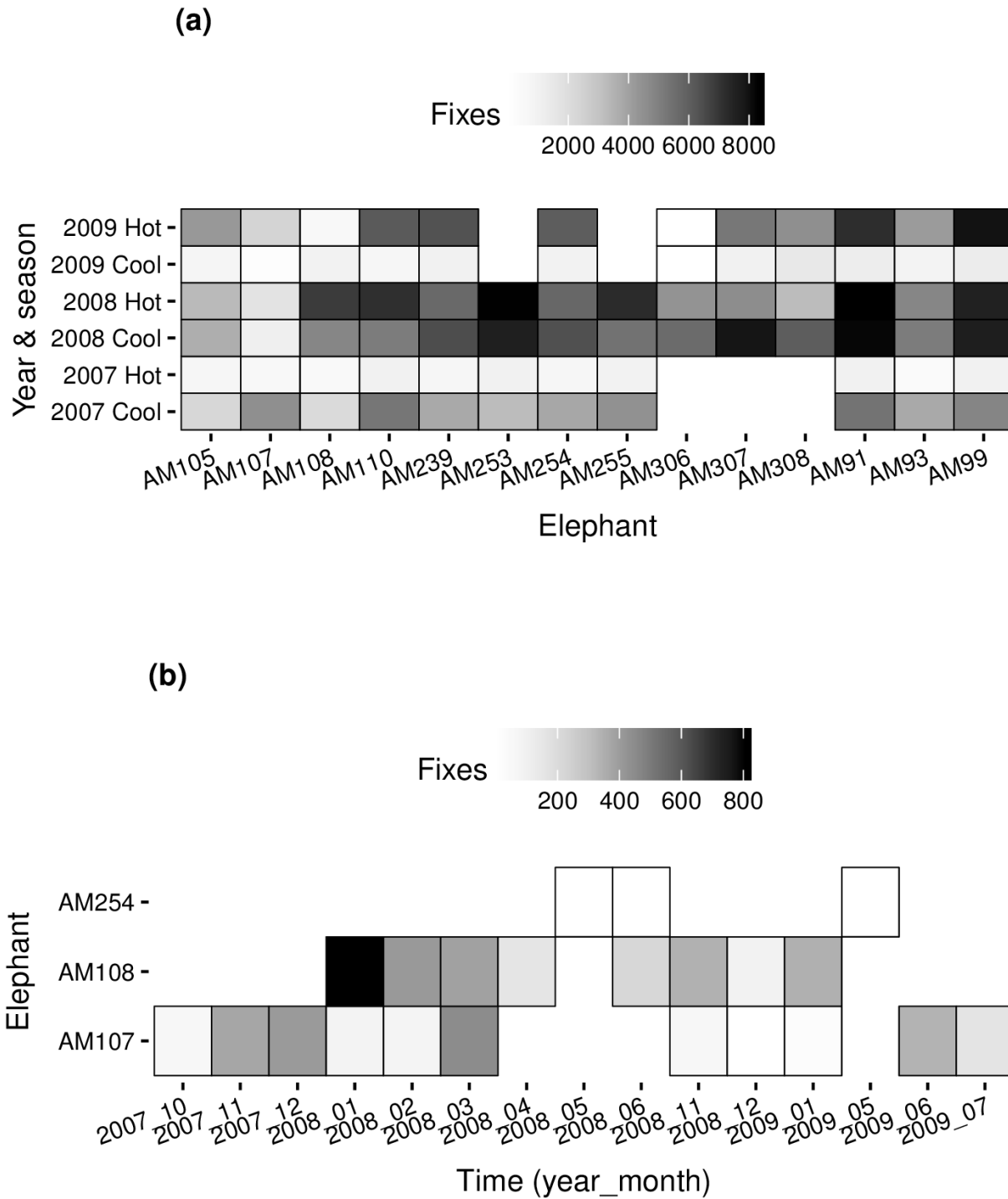
(a)

(b)

Fig. 13: 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.