Elephants shuttle to thermoregulate

1   **Maria Thaker[1*], Pratik R. Gupte[1,2], Herbert T. Prins[3], Rob Slotow[4], 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 must make decisions about
13   whether and where to move to avoid thermal stress. The movements of savanna elephants *Loxodonta*
14   *africana* have received much attention in the context of water dependence, yet ambient temperature
15   has seldom been invoked to explain them. We tracked 14 herds of elephants in Kruger National Park,
16   South Africa using GPS collars over a period of 2 years. We first quantified temperature differences
17   between the landscape types traversed by elephants, and confirmed that temperature loggers
18   (thermochrons) built into the GPS collars accurately reported ambient temperatures. We then
19   identified elephant visits to water, and studied elephant movement between successive visits to
20   water-sources.

21   We found that elephants in Kruger have characteristic intervals of visits to water that follow the
22   diurnal cycle. Elephants making day-long forays away from a water source are site-faithful, returning
23   to within a kilometre of the same source nearly half the time within a 24 hour period. Elephants are
24   closest to water during the hottest parts of the day, and move away from water as temperatures fall.
25   In contrast with other savanna ungulates, elephants move at their highest speeds as they approach and
26   leave water, and move at their slowest during the night. Temperature drives the relationship between
27   speed and distance to water, with elephants moving nearly twice as fast at upper temperature
28   extremes than at the daily mean temperature. These findings have implications for management that
29   seeks to control elephant ranges by altering the distribution of water sources.

30   **1   Introduction**
31   Animals faced with heat stress thermoregulate by altering their physiology and behaviour (Angilletta
32   2012). Most physiological responses to high temperatures, such as sweating in mammals, rely on
33   water evaporation to transfer heat away from the core-body. Many animals must complement

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

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

68   Savanna elephants are an excellent study system to examine the effects of temperature on movement
69   strategies in relation to water. Elephants lack a physiological means of thermoregulation, such as
70   sweating or panting, and therefore compensate by using thermoregulatory behaviours, such as ear-
71   flapping (Hiley 1975; Wright 1984; Wright and Luck 1984). At larger spatio-temporal scales,
72   elephants avoid thermal stress and the energetic costs of thermoregulation by shifting their activity
73   peaks to cooler times of the day, and select for thermally stable landscapes with lower variation in

74   daily temperatures(Johnson *et al.* 2002; Kinahan *et al.* 2007; Leggett 2010). Elephants are also
75   heavily water dependent and make periodic visits to water to hydrate and thermoregulate (Valls Fox
76   2015). Seasonal changes can have a significant effect on elephant movement, with individuals from
77   populations in Namibia and South Africa moving faster in the wet season than the dry season,
78   suggesting an effect of water availability on movement(Leggett 2010; Birkett *et al.* 2012). However,
79   in both these cases, the wet and dry seasons overlap with the hot and cool seasons, respectively,
80   opening up the possibility that differences in mean temperature between the seasons could contribute
81   to differences in movement. Testing this hypothesis requires both high-resolution position and
82   temperature data at each step of a movement track. Here, we characterise elephant movement in
83   relation to water sources and ambient temperature using data from traditional satellite telemetry,
84   coupled with instantaneous data from temperature loggers (thermochrons) borne by individuals, to
85   test the hypothesis that savanna elephants' movement is driven by temperature.

2   Methods

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. Collars
93   on elephants had transmitters and inbuilt thermochrons that were set to record half-hourly position
94   and temperature data, respectively. For this study, we selected location and temperature data from the
95   14 tagged elephants between August 2007 and August 2009, which we define as the study period,
96   and during which each elephant was tracked for on average 637 days (range: 436 – 731 per elephant).

97   We obtained the following landscape-level data: (1) a map (shapefiles) of all rivers, the locations of
98   active park waterholes, and 30m resolution terrain slope from Shuttle Radar Topography Mission V3
99   data (Farr *et al.* 2007); (2) polygon shapefiles of the landscape types of Kruger NP as defined by
100   Gertenbach 1983; (3) satellite imagery of the study area taken in the low-gain thermal infrared range
101   (Band 6 VCID 1: 10.40 – 12.50 μm) by the Enhanced Thematic Mapper + device aboard
102   LANDSAT-7 over the study period, which we converted to degree Celsius temperature data
103   (Chander *et al.* 2009); (4) satellite imagery of the study area from the same source as (3) taken in the
104   red and near infrared ranges (Band 3 (red): 0.63 - 0.69 μm, and Band 4 (near infrared): 0.77 - 0.90
105   μm), from which we calculated a two-year mean normalised difference vegetation index (NDVI) for
106   use as a mapping layer (see Fig. 2a) (Rouse Jr *et al.* 1974).

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

109

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. 2b), 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 represents the diurnal thermal landscape of Kruger NP (Fig. 2b). We tested for differences in LANDSAT-7 temperatures by landscape type using a simple GLM.

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. 2c). 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. 2c) 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, 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*.

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

146   linear distance between the two. Further, we computedthe actual distance moved along the segment

147   as the sum of the steplengths, i.e., distances between each successive point (pt_{xij} to pt_{xij+1}), and the

148   distance of each discrete position (pt_{xij}) from the nearest water source. Additionally, we obtained

149   thermochron temperature (t_{xij}) at each discrete position along the segment, and the steplength (v_{xij})

150   at each point.

151   We calculated the time difference between the two ends of a segment, and since each segment began

152   and ended at water, this represented the interval between visits to water. To account for the cyclicity

153   in ambient temperatures expected due to the diurnal cycle, we restricted further characterisation to

154   track segments with a duration of 12 – 24 hours.

2.5   Movement speed as a function of the environment

156   To test whether temperature was a significant predictor of elephant speed, we ran a generalised

157   additive mixed effects model (GAMM) using the entire data. The GAMM also included season,

158   terrain slope, and the density of woody vegetation (see Bucini *et al.* 2010) as fixed effects, and

159   individual identity as a random effect (see Tab. 1).

160   We acquired and handled the SRTM and LANDSAT-7 data using Google Earth Engine(Gorelick *et*

161   *al.* 2017), and used the R statistical environment (R Core Team 2017) for all analyses, and

162   specifically the *lme4*, *mgcv,* and *move* packages to implement the GLMM, GAMMs, and general

163   movement data handling respectively(Wood 2013; Bates *et al.* 2015; Kranstauber and Smolla 2016;

164   Bracis 2017).

3   Results

3.1   Elephant tracking

167   We obtained 283,737 total positions from 14 elephants, which we converted to movement tracks (Fig

168   1b). Elephants ranged on average 4005 km (range: 1854 km – 7074 km) across southern Kruger

169   National Park over the tracking period, covering on average 7.2 km per day (range: 5 km – 9.9 km) at

170   a mean speed of 398 m/hr (range: 304 m/hr – 470 m/hr). Individual positions were within 500m of

171   water a mean 12% (range: 6% – 21%) and 11% (range: 3% – 17%) of the time in the cool-dry and

172   hot-wet seasons respectively.

3.2   Landscape effects on temperature

174   We found significant variation in the mean daytime temperatures recorded by LANDSAT-7 from the

175   different landscape types in the study area (see Fig. 3 *LANDSAT-7 temp.*). For example, the lowveld

176   sour bushveld of Pretoriuskop (Fig. 3, vegetation type 12) found in the south-west of Kruger NP

177   (approximately 31.25ºE, 25.14ºS) had a mean temperature 1.5ºC cooler than the study area mean (z =

178   -3.398, p = 0.000678), while two contiguous landscapes in the north-east of the study area, the Bangu

179   rugged veld and the dwarf *Acacia nigriscens* savanna (Fig. 3, vegetation types 2 and 9, respectively),

180   had mean temperatures 1.5ºC and 2.5ºC warmer than the study area mean (Bangu veld: z = 28.622, p

181   = 2×10^{-16}; dwarf *Acacia nigriscens* savanna: z = 44.324, p = 2×10^{-16}).

182   We found that daytime thermochron temperatures were well predicted by the two-year mean

183   LANDSAT-7 temperature (z = -3.79, p = 0.000151), the hour of day (z = 26.01, p = 2×10-16), and

184   season (z = 3.42, p = 0.000619). We used Type II Wald chi-squared test to determine that within the

185   18 landscape types visited by elephants during the daytime, temperatures were significantly different

186   (X^2 = 1661.689, p = 2.2×10^{-16}). with z-values ranging from between -16.55 to 16.55.

187   3.3   Thermochron accuracy

188   Thermochrons fitted on elephant collars reported nearly identical mean daily temperatures of

189   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

190   respectively (Fig. 4a). Thermochron data from 3 elephants logged within 10km of Skukuza (Fig. 4b)

191   were well correlated with temperatures from the weather station at each hour in both seasons (mean

192   hourly correlation, Pearson's r: cool-dry = 0.66, hot-wet: 0.78). All correlations were signficant, with

193   p < 0.05. We henceforth consider thermochron temperatures to be equivalent to ambient

194   temperatures.

195   3.4   Track segments between water points

196   Elephants were within 500m of water at 44,610 of 283,737 points (≈ 16%), leading us to identify

197   44,622 track segments which began and ended at water. 40,347 (≈ 90%) of these segments had a

198   temporal duration of under 3 hours, with 89% lasting under an hour, i.e., indicating consecutive

199   residence at water points. On excluding these "residence at water tracks" and segments with a

200   duration above the 99th percentile (72 hours, n = 445), the remaining 3,754 (≈ 8.4%) of segments had

201   a multi-modal distribution of segment durations, with peaks between 12 – 24 hours, 36 – 48 hours,

202   and at 72 hours (Fig. 6a). We only retained 1,519 segments with durations between 12 and 24 hours

203   for further characterisation.

204   3.5   Movement along track segments

205   Elephants began each 12 – 24 hour segment on average 311.42m (range: 1.3 – 499.9m) from a water

206   source, and ended a mean 907.35 m (range: 500.14 – 4718.06m) from the next water source. 12 – 24

207   hour segments usually began at 14 – 19 hours (2PM – 7PM, SD = 4.84) and ended at 6 – 12 hours

208   (6AM – 12 Noon, SD = 4.67), with elephants reaching the halfway point at 22 – 04 hours (10PM –

209   4AM, SD = 9.06). On average, elephants travelled 6,508 m (range: 526 – 20,326 m) along their path

210   between visits to water points (Fig. 6b), reaching a mean maximum distance of 2,462 m (range: 519 –

211   6,832 m) from the nearest water source. In ≈8% and ≈ 30% of segments respectively, elephants

212 returned to within 500m and 1km of the position from which they began, with no difference between
213 the seasons (Fig. 6c). However, the midpoints of successive segments were within 500m and 1km of
214 each other in only 3% and 9.8% of segments, respectively (Fig. 6d). The distance travelled along a
215 segment showed an increasing trend with an increasing linear distance between the start and end
216 point of the segment (Fig. 7).

3.6 Temperature as a driver of movement

218 Elephants moving along 12 – 24 hour segments were initially moving away from water until about
219 the halfway point, after which their distance from water diminished (Fig. 8a). Temperatures along
220 segments initially decreased between the segment start and the segment midpoint, and then climbed
221 steadily until the segment end (Fig. 8b). Elephant speed was highest in the initial and final fifths of
222 each segment (Fig. 8c), with the first and last speeds (716 m/hr and 667 m/hr respectively) in a
223 segment nearly thrice as fast as the speed at the halfway point (242 m/hr). No seasonal difference was
224 apparent.

225 Thermochron temperature was found to be a significant predictor of speed ($F = 4410.4$, $p = 2 \times 10^{-16}$),
226 and elephants moved faster in the hot-wet season ($t = 17.69$, $p = 2 \times 10^{-16}$), but more slowly in denser
227 woodland ($t = -46.9$, $p = 2 \times 10^{-16}$), and on steeper slopes ($t = -4.08$, $p = 4.51 \times 10^{-5}$) (see Fig. 9).

4 Discussion

229 Discussion here on finalising methods and results.

5 Conflict of Interest

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

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

6 Author Contributions

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

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

7 Funding

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

8   Acknowledgments

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

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

9   Data Availability Statement

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

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.

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.

Rouse Jr J, Haas R, Schell J, and Deering D. 1974. Monitoring vegetation systems in the Great Plains with ERTS.

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.

255 **11 Figures**
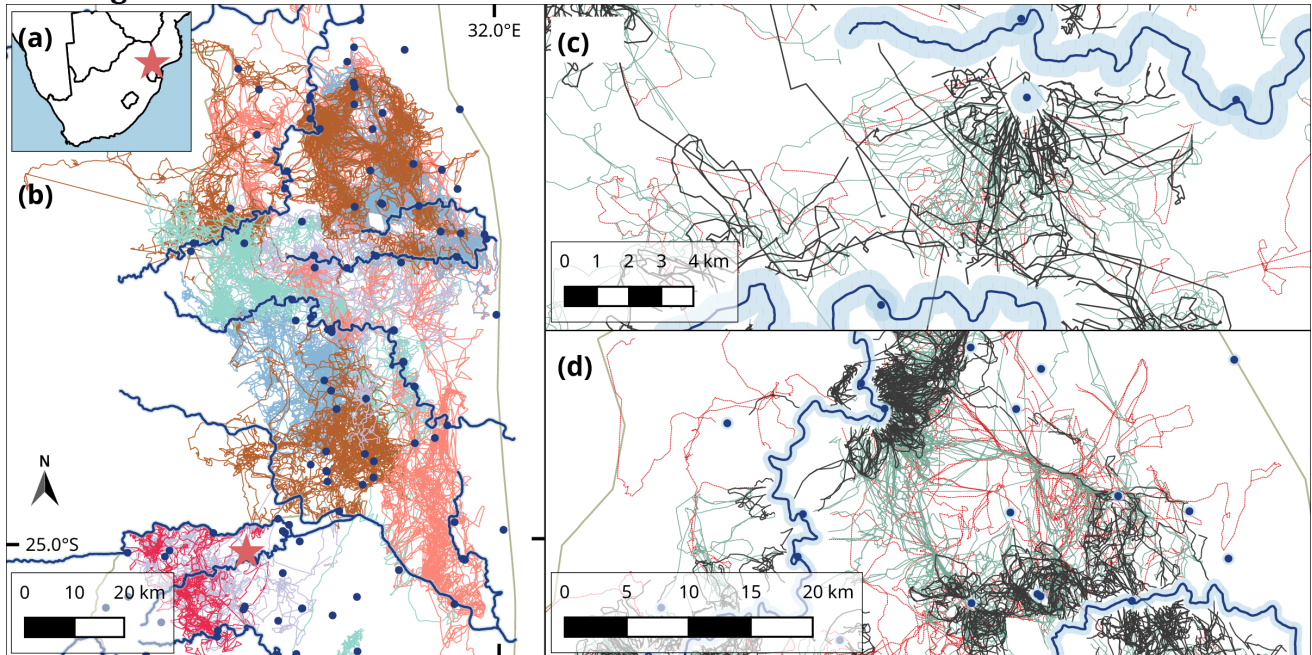
Fig. 1: (a) Study site in Kruger National Park, South Africa (red star), showing

(b) park boundary (dashed grey line), major rivers (solid blue lines), open waterholes (blue dots),
and raw elephant tracks (coloured lines, n = 14).

(c) and (d) Insets showing 3 – 72-hour long track segments between water sources (blue dots and
lines), coloured by duration class (12 – 24 hours: black lines, 24 – 48 hours: green, 48 – 72 hours:
red). The 500m buffer from river and waterhole centres is shaded in blue.

264   r
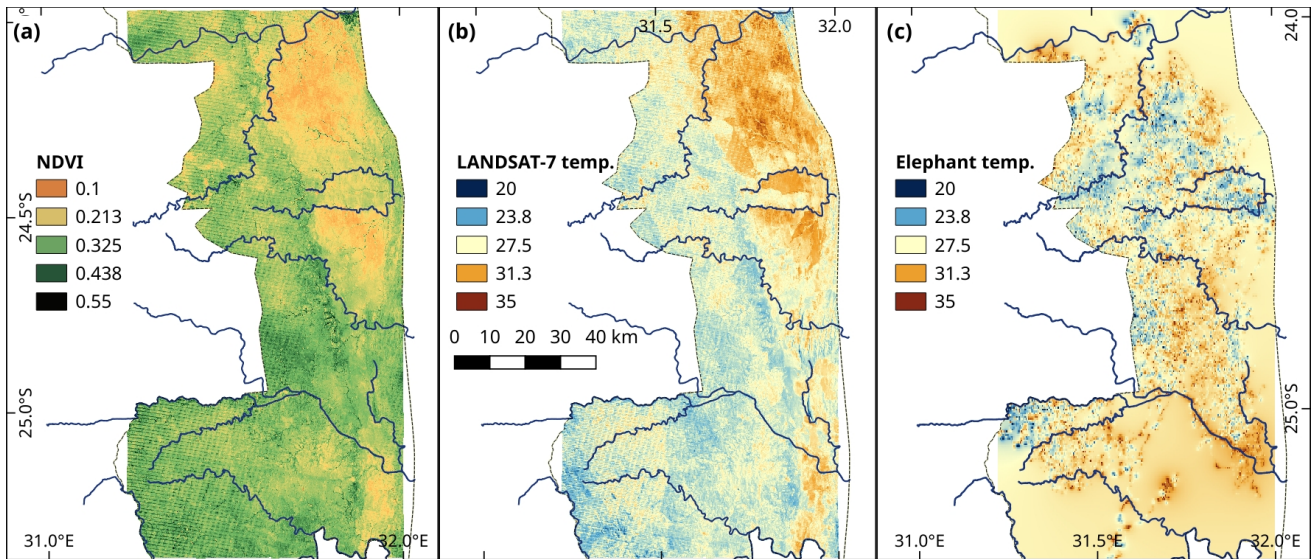
Fig. 2: (a) Two year mean NDVI in Kruger National Park over the study period August 2007 – August 2009.

(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.

Map (c) created as an inverse distance interpolation of values from elephant position and thermochron data, respectively
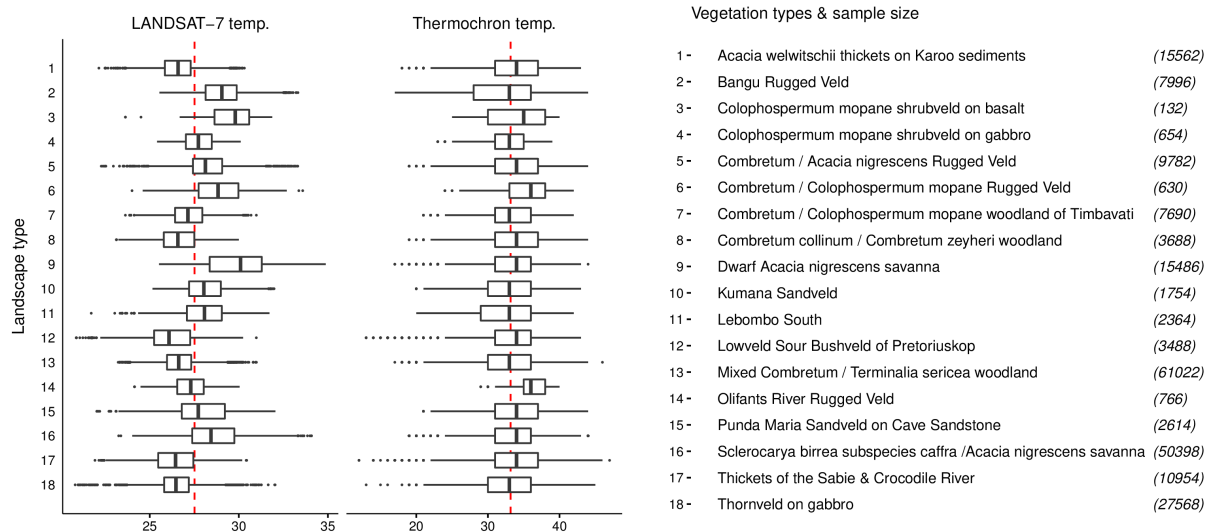
Fig. 3: Boxplots of the mean daytime temperature over the two-year long study period (August 2007 – August 2009) derived from LANDSAT-7, and the ambient daytime temperature reported by elephant-borne thermochrons over the the two-year study period, in each of 18 vegetation types reported in the data (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.

280
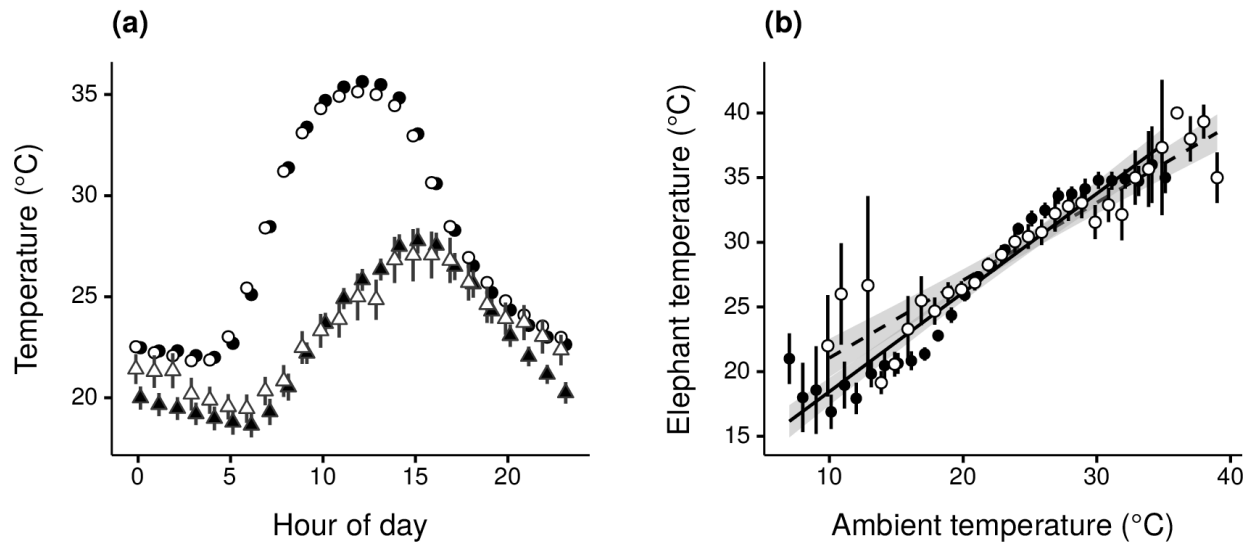
282 *Fig. 4: (a) Mean thermochron temperature (circles) and measured ambient temperature (triangles)*
283 *at each hour of day in each season (cool-dry: open symbols, hot-wet: filled symbols) across the study*
284 *period.*

285 *(b) GLM fits (lines) in each season (cool-dry: open circles & dashed lines, hot-wet: red triangles &*
286 *lines). Vertical lineranges and shaded areas (coloured by season) indicate 95% confidence intervals*
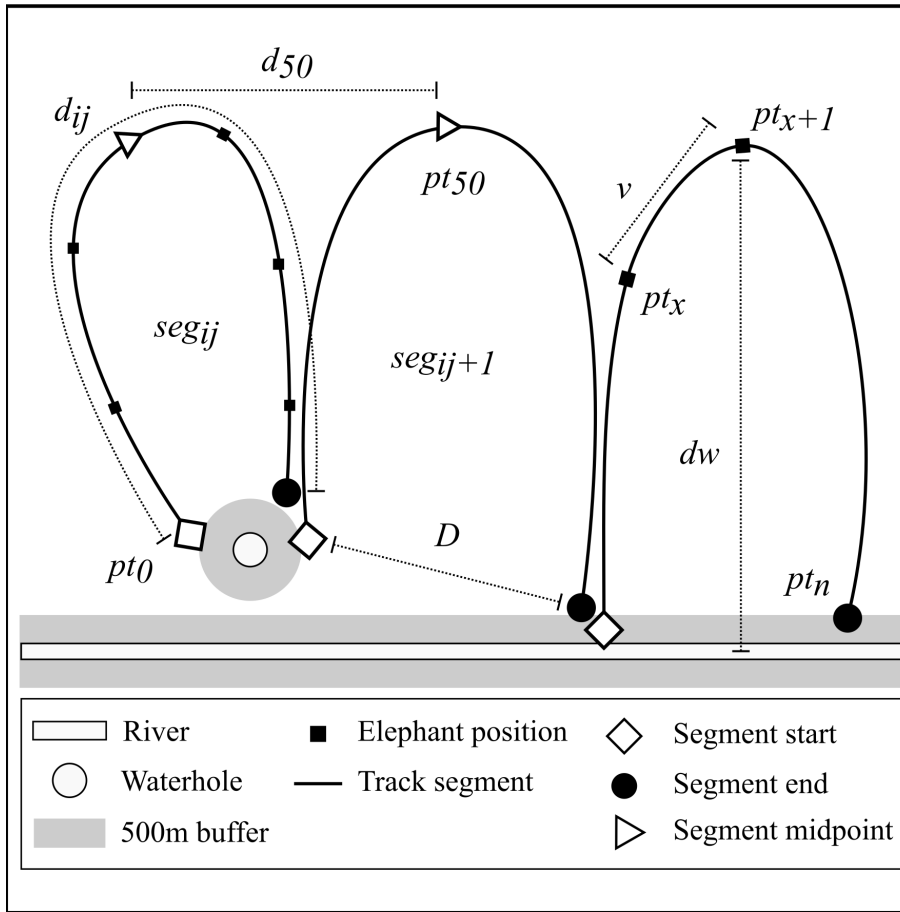287 *at each point.*

Fig. 5: Schematic of elephant track segments between water points. We collected elephant positions (filled squares, denoted by pt_x) using GPS transmitters. Positions within 500m (shaded grey area) of a water source (river: open rectangle, waterhole: open circle) were identified as water points.

For each individual elephant i, we identified track segments j (solid lines, denoted seg_{ij}) as the path joining all positions chronologically between successive water points. Each segment began at a water point (open rhombi, pt_0), and ended at the point immediately preceding the starting point of the next segment (filled circle, denoted by pt_n).

We calculated the time-difference between each segment's start and end points as the segment time (t_{seg}), and identified the segment's midpoint (open triangle, denoted pt_{50}) as the elephant position when half the segment time had elapsed ($t_{seg}/2$).

We computed the distance travelled between successive positions ($pt_x \rightarrow pt_{x+1}$) in a segment as the steplength (denoted by v), and the sum of all v in a segment as the distance travelled along the segment (denoted d_{ij}). We calculated the displacement (linear distance, denoted D) between each segment's start and end points, and the displacement (linear distance, denoted d_{50}) between the midpoints of successive segments.

Finally, we obtained the linear distance from each elephant position to the nearest water source (denoted dw), and the thermochron temperature at each position (T_x).
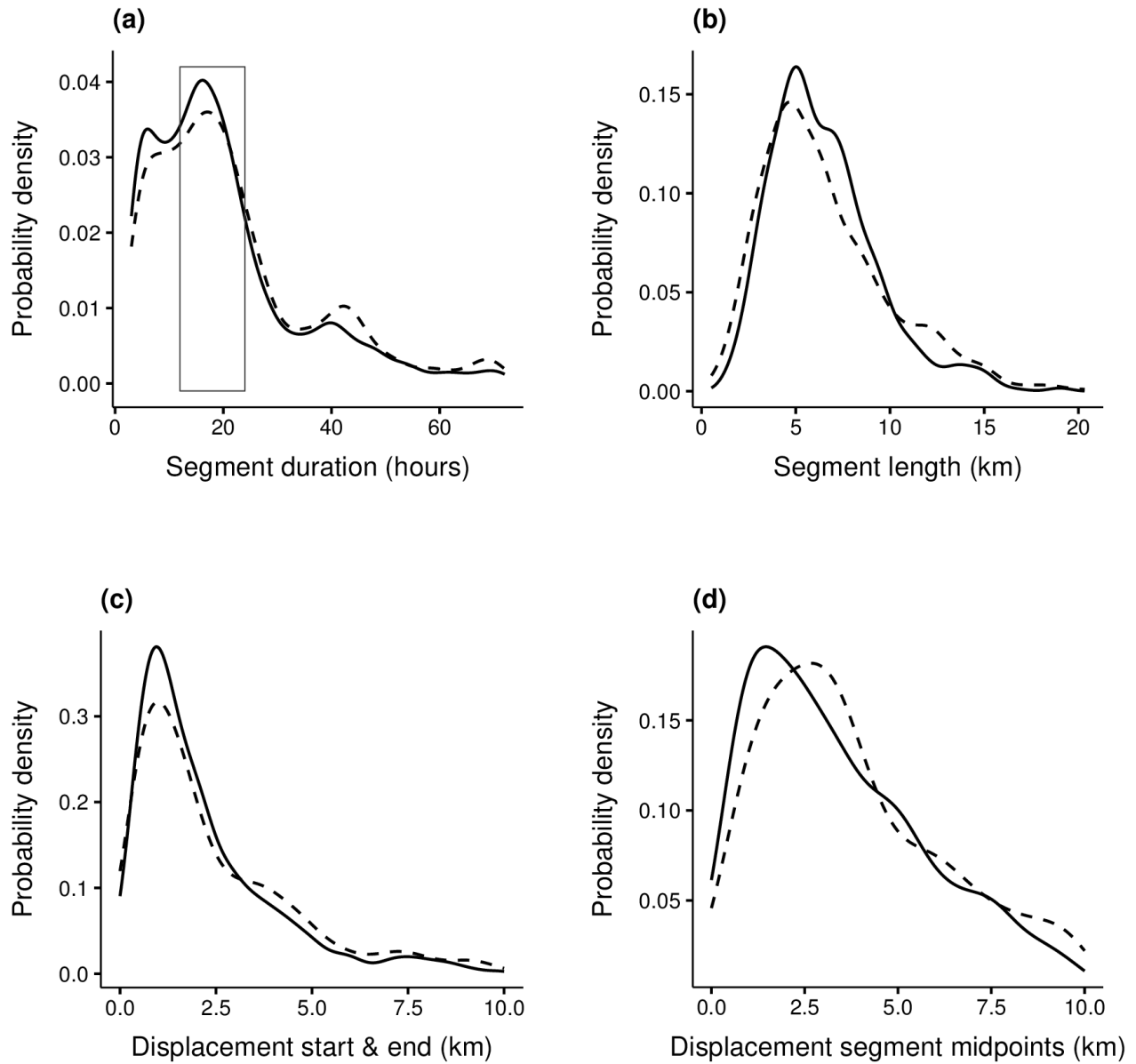
310   *Fig. 6: (a) Probability density plot of segment durations (in hours) between water points. Lower and*
311   *upper limits of segment durations in both seasons have been set at 3 and 72 hours, respectively. The*
312   *rectangle denotes the peak representing segments of a duration between 12 and 24 hours, which*
313   *were used for all further characterisation.*

314   *Probability density plots of (b) Actual distances travelled by elephants along 12 -- 24 hour track*
315   *segments between water points, (c) Linear distances between start and end points of 12 – 24 hour*
316   *track segments between water points, and (d) Linear distance between the midpoints (defined by*
317   *temporal duration) of successive 12 – 24 hour segments in each season. Data are separated by*
318   *season (cool-dry: dashed lines, hot-wet: solid lines).*
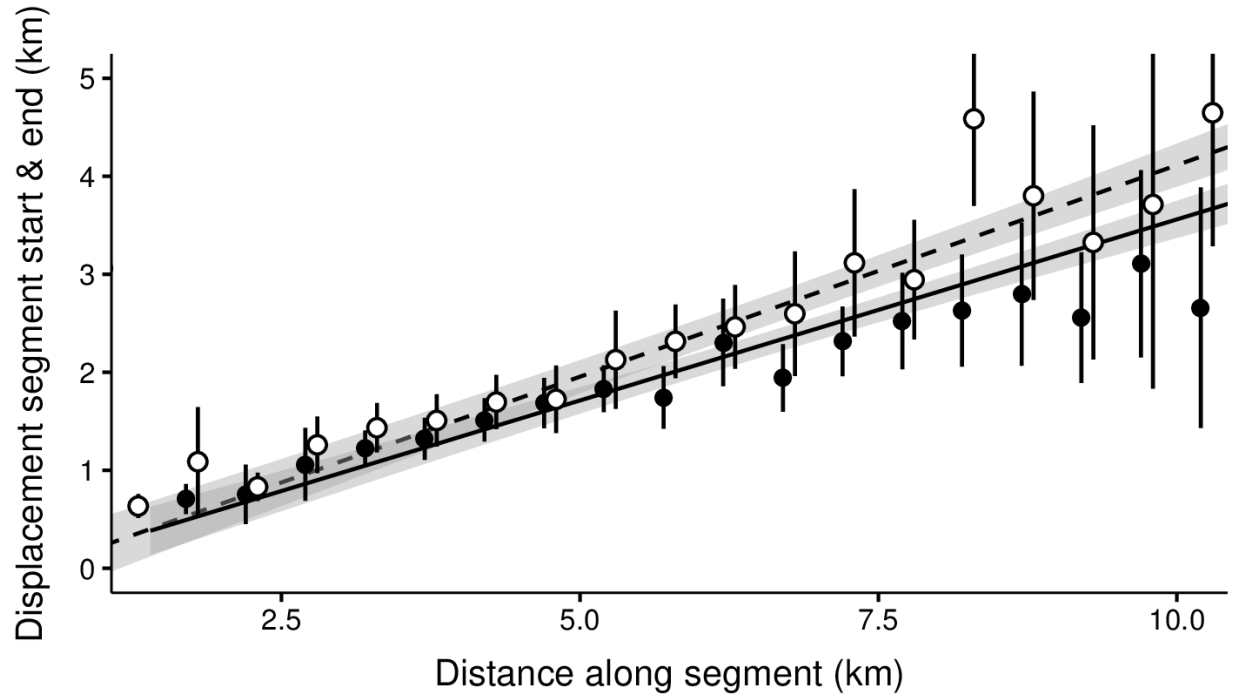
319   *Fig. 7: Displacement (linear distance) between the beginning and end of 12 – 24 hour segments*
320   *between water points, as a function of the distance moved along the segment, in each season. Data*
321   *were grouped and averaged in 500m increments of the distance along segments. GLM fit line for*
322   *each season is shown. Seasons are represented by symbols and lines (cool-dry: open circles &*
323   *dashed line, hot-wet: filled circles & solid line). Vertical lines represent 95% confidence intervals*
324   *about each point.*

325

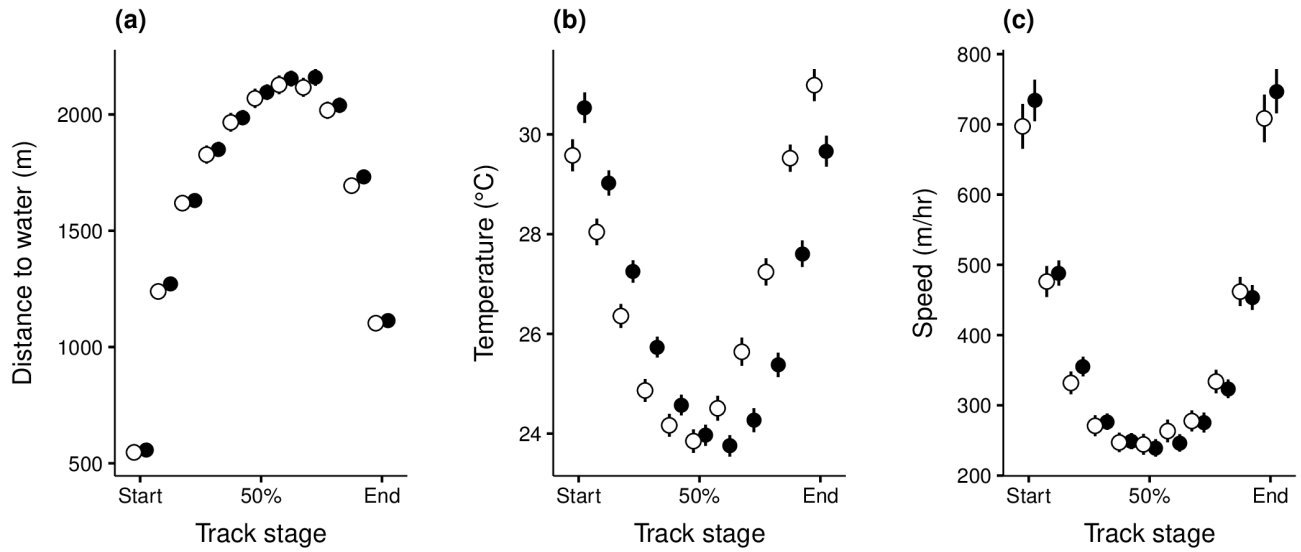327 *Fig. 8: Elephant movement variables along 12 – 24 hour track segments between water points at*
328 *10% intervals of segment duration (time):*

329 *(a) Minimum distance to water (in metres),*

330 *(b) Thermochron temperature, and*

331 *(c) Speed (in m/hr). Points are separated by season (cool-dry = open circles, hot-wet = filled*
332 *circles), and offset from each other to avoid overlap. Vertical lineranges show 95% confidence*
333 *intervals about each point.*
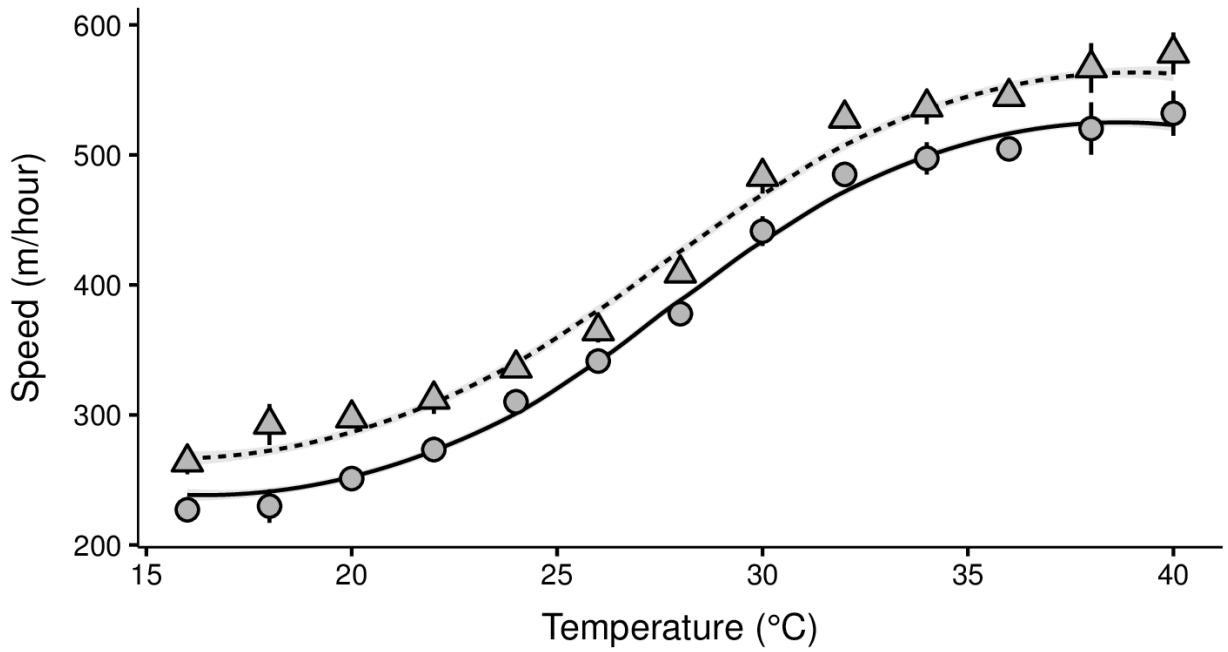
334   *Fig. 9: Elephant speed (points) at 2°C temperature intervals in each season (cool-dry: blue circles,*
335   *hot-wet: red triangles). GAMM fit (lines), data error intervals (lineranges), and fit error intervals*
336   *(shaded areas) are shown.*