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## **Territorial movements of African lions: can waterholes shape multiple central-place territories in a savannah ecosystem?**

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## 19 HIGHLIGHTS

- 20 • Territorial movements are often conceptualized as animals patrolling along borders
- 21 • Here, we examine territorial movements in African lions (*Panthera leo*)
- 22 • Lions repeatedly moved along straight paths between waterholes
- 23 • Waterhole-oriented paths occurred both in territory core and periphery
- 24 • Both male and female lions defended “multiple central-place territories”

## 25 ABSTRACT

26 In territorial species, individuals need to regularly patrol their territory to display visual, auditory  
27 or olfactory signals, or to detect the presence of intruders. Although territorial movements are  
28 often conceptualized as animals travelling along the boundaries of their territories (‘border  
29 patrolling’ behaviour), the distribution of territorial cues could also match the distribution of  
30 resources when resources are spatially heterogeneous in their availability and found in stable  
31 patches, leading to the emergence of “multiple central-place territories”. Here, we explored how  
32 territoriality may shape the spatial behaviour of African lions (*Panthera leo*) in a savanna where  
33 waterholes are associated with aggregations of large herbivores throughout the year and are  
34 therefore well-known prey hotspots and key hunting sites for large carnivores. We hypothesized  
35 that male lions would be more likely to patrol a buffer area around the territory core to defend a  
36 core area where social interactions with groupmates occur, whereas female lions would more  
37 specifically patrol hunting sites, i.e. waterhole areas. However, we found that both female and  
38 male lions repeatedly moved along straight paths between the waterholes located both in the core  
39 and in the periphery of their territories, potentially to defend multiple central-place territories

40 driven by the distribution of waterholes in the landscape. These findings illustrate a case where  
41 territorial animals specifically mark feeding sites, increasing the renewal of territorial cues at  
42 these key places, potentially using long-distance territorial cues (i.e., vocalizations) to mark  
43 uncovered areas, and thereby reducing the cost of patrolling large territories. Overall, multiple  
44 central-place territories provide new insights on how the spatial distribution of resources shapes  
45 space use in territorial animals.

46 **Keywords:** African lion; animal movement; marking; sinuosity; territoriality; waterholes

47

48

## 49 INTRODUCTION

50 Territoriality may drive animals' movement decisions and thus shape patterns of animal space  
51 use. To secure resources or mating opportunities, territorial animals actively exclude  
52 conspecifics, often from the same sex, from spatial areas, using olfactory, visual or auditory cues  
53 (Brashares & Arcese, 1999; Krebs et al., 1978; Taylor et al., 2015). Theoretically, the avoidance  
54 of areas marked by conspecifics is sufficient for the emergence and maintenance of territories  
55 (Giuggioli et al., 2011). However, because visual and auditory signals are short-lived and scent-  
56 marks are also ephemeral, territorial animals need to regularly patrol their territories to renew  
57 these signals, as well as to detect incursion of intruders. For example, grey wolves (*Canis lupus*)  
58 keep track of space and time to patrol their territories, being more likely to revisit territorial  
59 borders not visited for a long time (Schlägel et al., 2017).

60 Animal territories are often conceptualized as a core territory intensively used and where,  
61 if any, social interactions mostly occur, buffered by a peripheral area that territorial animals  
62 patrol to prevent the intrusion of rivals. Such a pattern of territorial movements is well-known for  
63 some species. For example, chimpanzees (*Pan troglodytes*) move around the periphery of their  
64 territory, searching for signs of rivals without displaying auditory or olfactory signals (Mitani &  
65 Watts, 2005; Watts & Mitani, 2001). Other examples are grey wolf (*Canis lupus*) packs, that can  
66 form an “olfactory bowl” by specifically scent-marking all around their territorial borders (Peters  
67 & Mech, 1975) and Ethiopian wolves (*Canis simensis*) that more frequently scent-mark near  
68 territorial borders (Sillero-Zubiri & Macdonald, 1998). Here, we refer to this scenario as the  
69 “border-patrolling” hypothesis.

70           However, how territorial animals patrol their territories largely varies across species. In  
71 carnivores for example, strategies vary along a continuum from concentrating scent-marks in the  
72 territory core to scent-marking around the territorial borders (Macdonald, 1980). Marking  
73 borderlands or hinterlands is likely influenced by the energetic expenditure of patrolling large  
74 territories. For example, when spotted hyaenas (*Crocuta crocuta*) need to maintain large  
75 territories to ensure food supply, their scent-marks are concentrated in the hinterlands, whereas  
76 they are distributed in borderlands when resources are abundant enough to maintain small  
77 territories (Gorman & Mills, 1984). To trade-off the cost of patrolling, territorial animals may  
78 also integrate their territorial defences into foraging movements (Asensio et al., 2011) or adjust  
79 their territorial behaviours to the distribution and abundance of resources rather than patrolling  
80 along fixed boundaries (Harrison, 1983).

81           The distribution of territorial cues sometimes underlies the pattern of resource  
82 exploitation (Macdonald, 1980). In particular, when resources are heterogeneously distributed  
83 and found in stable patches, territorial animals may be expected to concentrate their territorial  
84 cues around some key places, such as reported for feral cats (*Felis catus*), wild cats (*Felis*  
85 *silvestris*) and red foxes (*Vulpes vulpes*) that specifically scent-mark in preferred hunting areas  
86 (Macdonald, 1980). Specifically marking feeding sites can increase the renewal of olfactory,  
87 visual and auditory signals around a limited number of key places. Because scent-marks may be  
88 dispersed by wind (for example wolves scent-mark elevated locations to facilitate wind dispersal  
89 of odours (Peters & Mech, 1975)) and because vocalizations may be heard at long distance (for  
90 example up to 8 km for lion vocalizations in the Serengeti ecosystem (Packer 2023)), specifically  
91 marking some key places may allow territorial animals to signal their presence in a radius large  
92 enough to cover the unvisited areas of their territories. Territories that are defended by animals

93 rotating between several feeding sites to exploit resources and patrol around these key places  
94 have been referred to as “multiple central-place territories” (Steingrímsson & Grant, 2008, 2011a,  
95 2011b). Here, we refer to this scenario accordingly.

96           Whether territorial animals patrol along territorial borders (“border-patrolling”  
97 hypothesis) or specifically focus on key places of their territories (“multiple central-place  
98 territories” hypothesis) could depend on the nature of the resources they are motivated to secure.  
99 In particular, animals defending the exclusive access to mobile resources, such as mating partners  
100 or prey, may be more willing to patrol along territorial borders to secure a buffer area around a  
101 territory core where interactions with mating partners and prey mostly occur (“border-patrolling”  
102 hypothesis). For example, male impalas (*Aepyceros melampus*) defend breeding territories which  
103 boundaries are not shaped by the distribution of resources (Oliver et al., 2007). On the contrary,  
104 animals defending stable patches of heterogeneously distributed resources may defend multiple  
105 central-place territories to increase the renewal of olfactory, visual and auditory signals around a  
106 limited number of key places, to reduce the cost of patrolling around long territorial borders, and  
107 should use long-distance marking signals to cover the unvisited areas of their territories  
108 (“multiple central-place territories” hypothesis).

109           Here, we analysed tracking data collected on 46 lions in Hwange National Park,  
110 Zimbabwe, a savanna ecosystem where surface water is a limited resource, with permanent  
111 waterholes unevenly distributed in the landscape (Chamaillé-Jammes et al., 2007) and associated  
112 with aggregations of large herbivores throughout the year, as herbivores come to these areas for  
113 drinking and for the foraging resources available in the open grasslands surrounding waterholes  
114 (Chamaillé-Jammes et al., 2009; Valeix, Loveridge, et al., 2009). In this ecosystem, waterholes  
115 can be considered prey hotspots throughout the year and therefore key hunting sites for lions

116 (Davidson et al., 2012; Valeix et al., 2010; Valeix, Fritz, et al., 2009). Because lions need to leave  
117 feeding sites to counter-balance the behavioural avoidance responses of prey following hunts  
118 (Valeix et al., 2011), the distribution of waterholes greatly determines lion ranging behaviour and  
119 lion territory size (Loveridge et al., 2009; Valeix et al., 2010, 2012). Since female lions compete  
120 against females from other prides for the exclusive access to stable, heterogeneously distributed,  
121 patches of food resources (e.g., prey aggregated around waterholes), here, we predicted that  
122 female lions would defend “multiple central-place territories” driven by the distribution and  
123 abundance of waterholes in the landscape (“multiple central-place territories” hypothesis) (Fig.  
124 1). On the contrary, since male lions compete against males from other coalitions for the  
125 exclusive access to females (Schaller, 1972), we predicted that they would defend a buffer area  
126 around a territory core to prevent the intrusion of rivals (“border-patrolling” hypothesis) (Fig. 1).  
127 To test these “multiple central-place territories” and “border-patrolling” hypotheses, we  
128 compared, for both sexes, lion trajectories to waterholes, including ones simulated from an  
129 individual-based model that controlled for the movement characteristics expected from resource-  
130 only selection.

## 131 **METHODS**

### 132 *Study area*

133 The study was carried out in the north-eastern area of Hwange National Park, Zimbabwe. In this  
134 semi-arid ecosystem, natural rain-fed pans dry during the dry season from May to October, and  
135 water remains available only in artificial permanent waterholes in which underground water is  
136 pumped (Chamaillé-Jammes et al., 2007). A GIS layer of all artificial permanent waterholes that

137 retain water throughout the dry season was available thanks to field observations conducted since  
138 the beginning of lion monitoring.

139 ***Ethical note***

140 Lion handling and care protocols were consistent with guidelines provided in the ‘Code of  
141 Practice for Biologists using Animals’, Department of Zoology, University of Oxford and  
142 approved by University of Oxford, Biomedical Sciences, Animal Welfare and Ethical Review  
143 Body. All procedures were undertaken with the permission of the Zimbabwe Parks and Wildlife  
144 Management Authority (Permit numbers: REF:DM/Gen/(T) 23(1)(c)(ii):713/12/01, 03/2002,  
145 07/2003, 20/2004, 01/2005, 01/2007, 03/2008, 03/2009, 25/2010, 06/2011, 12/2012, 08/2013,  
146 51/2014, 10/2015). Lion handling procedures were carried out by project staff trained and  
147 certified by the Zimbabwe Veterinary Association, Wildlife Group (Certificate  
148 numbers: Davidson: 09/03; Elliot: 9/10; Hunt: A11/04, 005/09, 5/14; Loveridge: 6/2000, 20/36  
149 (2007), 6/14; Stapelkamp: 34/2008) in accordance with Statutory Instrument 409 of 1999 (Clause  
150 21A to 21J) amending the Regulations of 1975 to the Dangerous Drugs Act, Zimbabwe. Initial  
151 training and refresher training (every five years) was undertaken through attendance at the  
152 Chemical and Physical Restraint of Wild Animals Course (run by Zimbabwe Veterinary  
153 Association, Wildlife Group and Government Veterinary Services Wildlife Unit).

154         Lions were immobilized by chemicals. They were darted from the ground, using Dan  
155 Inject J.M.SP.25 CO<sub>2</sub>-powered dart guns to administer drugs by intramuscular injection  
156 (shoulder or rump). Lions received the dissociative anaesthetic Zoletil (dosage: 0.83e0.32 (range  
157 0.53e1.38) mg/kg; manufacturer: Virbac RSA, Centurion, South Africa) and sedative  
158 medetomidine (Zalopine/Domitor; dosage 0.05e0.01 (range 0.04e0.06) mg/kg; manufacturer:

159 Novartis, Isando, South Africa or Orion Pharma, Turku, Finland). Once immobilized, lion eyes  
160 were covered and ear plugs fitted to reduce stimuli and stress, and the collars were fitted. We  
161 equipped lions with GPS collars from Televilt/Followit Positioning (AB, Lindesberg, Sweden) or  
162 African Wildlife Tracking (Pretoria, South Africa) or Sirtrack Ltd. (Havelock North, New  
163 Zealand). GPS collars weighed between 600 and 900 g, representing respectively 0.6 and 0.9% of  
164 the smallest individual captured (100 kg). Drugs were then reversed using Atipamezole (dosage:  
165  $1/4 \cdot 0.18 \cdot 10^7$  (range  $0.01 \cdot 10^7$ ) mg/kg; manufacturer: Farnos; Orion Corp., Espoo, Finland or  
166 Novartis). Once reversal drugs were injected, lions were monitored until their full recovery.  
167 Following collar deployments, all collared lions were located weekly to bimonthly from a vehicle  
168 or microlight aircraft to ensure that lions did not experience any adverse effects from the GPS  
169 collars. Collars were removed when batteries were flat or when they malfunctioned, and were  
170 usually replaced for long-term monitoring of the Hwange lion population. Collars were removed  
171 using the immobilization procedure described before. If not removed, collars would eventually  
172 fall off owing to deterioration of the collar material.

### 173 ***Lion movement data***

174 From 2002 to 2016, 22 adult female lions and 21 adult male lions were monitored with GPS  
175 collars, collecting hourly or two-hourly locations over on average 22 months [quartile 1 = 12  
176 months; median = 17 months; quartile 3 = 27 months]. Because lion territories may change over  
177 time, especially for males, we used the segmentation method developed by Patin *et al.* (2020) and  
178 visual inspection of the derived segments to identify stationary periods of lion movements. We  
179 extracted 24 female and 27 male territories, potentially leading to non-independence between 6  
180 male territories and 2 female territories. We then used the 50% and 99% utilization distribution of  
181 a kernel-based home range estimate to describe the core territory and whole territory, using the

182 *adehabitatHR* package (Calenge, 2006). Hereafter, we distinguished waterholes located inside  
183 and outside the core territory, respectively named ‘core waterholes’ and ‘edge waterholes’.  
184 Because using a kernel approach, peripheral waterholes can fall in the centre of a lion range, we  
185 also used a Minimum Convex Polygon (MCP) to delineate the core and peripheral areas of a  
186 territory. Results using a MCP approach were similar to those obtained using a kernel approach  
187 (Supplementary file S1). Here, we therefore present results from the kernel-based home range  
188 estimate.

### 189 ***Definition of lion trips to waterholes***

190 As waterholes are known to shape lion space use in the study ecosystem (Valeix et al., 2010), we  
191 focused on how lions moved between visits to waterholes, using five metrics (see the following  
192 section) to test whether lions maintain multiple central-place territories – with waterholes being  
193 the central places – or patrol around territorial borders. To do so, for each location used by lions,  
194 we extracted the distance to the closest waterhole. We considered that lions were at a waterhole  
195 when this distance was shorter than 500 m. This distance was arbitrarily chosen, however, that  
196 distance was more restrictive than the 1 km and 2 km distance thresholds commonly employed to  
197 define a lion at a waterhole in the study ecosystem (Courbin et al., 2015; Davidson et al., 2013;  
198 Dejeante et al., 2024; Valeix et al., 2010; Valeix, Fritz, et al., 2009). Since lions may pass near a  
199 waterhole between two successive GPS points, we linearly interpolated lion trajectories to 30-min  
200 locations using the *redisltraj* function of *adehabitatLT* package in R (Calenge, 2006). We  
201 performed a linear interpolation so as not to influence the straightness of lion trips to waterholes  
202 (see the following section). We did not interpolate lion trajectories when the time interval  
203 between the two consecutive GPS points was longer than 2 hours. In the following analyses, we  
204 did not analyse lion trips when there was no GPS position recorded over more than 24 hours.

205 We defined a ‘trip between waterholes’ as a series of successive GPS positions between  
206 two waterholes. Despite lions may move away from a waterhole to visit other locations than  
207 waterholes, for instance and of interest here to patrol their territorial borders, because all lion  
208 movements necessarily end at a waterhole at some point, these segments of a lion path were still  
209 categorized as a trip between waterholes. However, it does not mean that these trips between  
210 waterholes were waterhole-oriented. Here, we therefore used five movement metrics (see below)  
211 to address whether – for each trip between waterholes – lions engaged in a movement directed  
212 towards the ending waterhole or not. We categorized trips between waterholes as follows: ‘core-  
213 to-core trips’ are segments of lion trajectories starting and ending at a waterhole located within  
214 the core territory of the lion (‘core waterhole’), ‘edge-to-edge’ trips are segments of lion  
215 trajectories starting and ending at a waterhole located outside the core territory of the lion (‘edge  
216 waterhole’) and ‘core-to-edge trips’ are segments of lion trajectories starting at a core waterhole  
217 and ending at an edge waterhole, or inversely. On average, we analysed  $90 \pm 15$  (mean  $\pm$  standard  
218 deviation) ‘core-to-core’,  $76 \pm 8$  ‘core-to-edge’ and  $32 \pm 5$  ‘edge-to-edge’ trips per lion territory.

### 219 ***Movement metrics***

220 For each lion territory encompassing multiple core waterholes (46 out of 51), we derived five  
221 movement metrics characterizing trips to waterholes. The combination of these five metrics  
222 allowed us to test whether male and female lions repeatedly navigated along straight trajectories  
223 between core and edge waterholes or patrol along territorial borders, and hence to test the  
224 “multiple central-place territories” and “border-patrolling” hypotheses (Table 1).

225 1. *Attraction index (core waterholes)* – the attraction index of core waterholes measures the  
226 attractiveness of core waterholes for lions. It was calculated by dividing the number of

227 core-to-core trips for which lions stayed in the core territory by the total number of core-  
228 to-core trips. If core waterholes are the focus of lion movements, we expect lions to rarely  
229 go outside the core area when travelling from one core waterhole to another. Additionally,  
230 because lion core territories, as delineated from kernel-based utilization distribution, may  
231 be the combination of multiple polygons, we considered that lions moved out of the core  
232 territory when they spent more time outside the core territory than expected from a  
233 straight path between the core waterholes. To determine this, we linearly interpolated 30  
234 min locations between the starting and ending core waterholes, and tolerated 20% of  
235 difference between the expected and observed time spent outside the core territory to  
236 identify when lions moved out of the core territory.

237 2. *Attraction index (edge waterholes)* – the attraction index of edge waterholes measures the  
238 attractiveness of edge waterholes in driving lions' excursions outside the core territory.  
239 This index is the ratio between the number of core-to-edge trips over the number of core-  
240 to-core trips for which lions moved out of the core territory, potentially marking the  
241 periphery of their territory but not at a waterhole. In the case that edge waterholes drive  
242 lion movement, we expect a high attraction index of edge waterholes.

243 3. *Straightness index (core to core)* – the straightness index measures how goal-oriented a  
244 path is by dividing the net displacement between the starting and ending waterholes (i.e.,  
245 straight path) by the total path length travelled along the trip. It can be seen as an indicator  
246 of whether the trip was specifically made to quickly reach the destination waterhole: the  
247 straightness index ranges between 0 (little goal-oriented, convoluted path) and 1  
248 (directional, goal-oriented path). We show examples of lion trips to waterholes with  
249 several straightness indices in Supplementary Figure S4. We measured the straightness

250 index of core-to-core trips not going outside the core territory. In the case that core  
251 waterholes drive lion movement, we expect high values of the straightness index.

252 4. *Straightness index (core to edge)* – We measured the straightness index of core-to-edge  
253 trips. In the case that edge waterholes drive lion movement, we expect high values of the  
254 straightness index.

255 5. *Straightness index (edge to edge)* – We measured the straightness index of edge-to-edge  
256 trips. In the case that edge waterholes drive lion movement, we expect high values of the  
257 straightness index.

258 This classification approach was sensitive to the threshold chosen to define “low” to “high”  
259 values for each metric. Therefore, to distinguish lions that would match predictions from the  
260 “multiple central-place territories” and “border-patrolling” hypotheses rather than the null  
261 hypothesis, we simulated the movement of individuals under the latter (i.e., under a resource-only  
262 model; see below), and used the movement metrics to identify lions whose trips had similar  
263 characteristics than the simulated ones (see “cluster analysis” section).

#### 264 ***Null-hypothesis simulation***

265 We used an individual-based model to simulate minimally oriented trips to core and edge  
266 waterholes (i.e., resource-only model, null hypothesis). For each lion territory encompassing  
267 multiple core waterholes, we first performed an integrated step selection analysis (iSSA) to  
268 simultaneously estimate movement and habitat selection (Avgar et al., 2016), using the *amt* R  
269 package (Signer et al., 2019). We included in the iSSA environmental variables known to impact  
270 lion habitat selection in the study system: distance to waterhole, habitat openness, and distance to  
271 home range centroid (Dejeante et al., 2024). We then used the coefficients estimated by the iSSA

272 to simulate lion trajectories within each lion territory over 20 000 time steps. To do so, for each  
273 time  $t$ , 30 potential steps were generated by randomly drawing step length and turning angle  
274 values from, respectively, the gamma and Von Mises distribution fitted to the empirical data. For  
275 each potential step ending in the lion territory, we then extracted the distance to waterhole, the  
276 habitat openness, and the distance to home range centroid. Finally, the location at time  $t+1$  was  
277 sampled among the 30 potential steps with probabilities proportional to the iSSA score.

### 278 *Cluster analysis*

279 We then aimed at identifying groups of lions (empirical or simulated) whose trips were similar,  
280 i.e., had similar values of the five movement metrics characterizing trips between waterholes. We  
281 did so by performing a principal component analysis (PCA) on the five metrics calculated on the  
282 empirical and simulated data, and then applying a hierarchical clustering on principal components  
283 using the R package *FactoMineR* (Lê et al., 2008). Since the five movement metrics were  
284 indexed between 0 and 1, we did not centre and scale them. The Ward's hierarchical clustering  
285 algorithm uses the Euclidean distance between pairs of points to identify clusters with minimum  
286 within-cluster variance, without requiring prior information on the number of clusters to detect.  
287 Because we performed the PCA on both simulated and empirical data, we could easily  
288 distinguish whether the studied lions had movement characteristics that differed greatly from  
289 simulated ones.

290       Because we expected male and female lions to exhibit differences in the way they  
291 navigate in the periphery of their territories (females specifically marking waterholes and males  
292 patrolling along territorial borders), we tested the influence of lion sex on the likelihood for lions  
293 to defend multiple central-place territories. We did so by fitting a generalized linear mixed model

294 with a logit link and a binomial distribution for errors, adding a random intercept with lion  
295 identity. Because we hypothesized that specifically marking feeding sites may be an efficient way  
296 to defend larger territories with a higher number of waterholes, we added multiplicative effects  
297 between the sex variable and the number of core and/or edge waterholes. We then compared  
298 model fit using AIC values and reported estimates from the most parsimonious model.

### 299 *Influence of the number of core and edge waterholes on lion movements*

300 Since the abundance of waterholes may impact both the straightness of lion movement paths and  
301 the propensity of lions to stay within their core territory or to visit their territorial borders, we  
302 specifically tested how the number of core and edge waterholes influenced each of the five  
303 movement metrics used in the cluster analysis. To do so, we used quasi-binomial regression for  
304 each metric since all ranged between 0 and 1. We tested the effect of the number of core  
305 waterholes (respectively edge waterholes) on the straightness of lion trips to core waterholes  
306 (respectively edge waterholes), and on the attractiveness of core waterholes (respectively edge  
307 waterholes). To address whether the potential effect of the number of core waterholes  
308 (respectively edge waterholes) on each of these variables was related to biological processes or  
309 mechanistic processes, we added a multiplicative effect between the number of core waterholes  
310 (respectively edge waterholes) and whether trips to waterholes were empirical or simulated.

## 311 **RESULTS**

### 312 *General information*

313 In general, 90% [46 out of 51] of lion's territories encompassed multiple core waterholes, ranging  
314 from 2 to 9 (Supplementary Figure S5). On average, male lions had 5 waterholes in their territory  
315 core [quartile 1 = 3; median = 4; quartile 3 = 6] and 13 waterholes in the periphery [quartile 1 =

316 10; median = 12; quartile 3 = 17]. Female lions had on average 4 waterholes in their territory core  
317 [quartile 1 = 2; median = 3; quartile 3 = 5] and 9 waterholes in the periphery [quartile 1 = 5;  
318 median = 8; quartile 3 = 12]. The number of core waterholes within lion territories was positively  
319 related to the size of the core territory (Pearson's correlation = 0.65) and, to a lesser extent, to the  
320 number of edge waterholes (Pearson's correlation = 0.36) (Supplementary Figure S6).

### 321 *Cluster analysis*

322 The first two principal components of the PCA explained 84% of the variance among the five  
323 metrics characterizing lions' trips to waterholes. Position of simulated and empirical lion  
324 trajectories along the first principal component (PC1; 63%) was mostly explained by the  
325 attraction index of core waterholes (contribution: 20%), and the straightness of trips to  
326 waterholes, both core to core (contribution: 20%), core to edge (contribution: 28%) and edge to  
327 edge ones (contribution: 25%) (Figure 2). Position along the second principal component (PC2;  
328 21%) was mainly related to the attraction index of edge waterholes (contribution: 64%) and the  
329 straightness of trips between core waterholes (contribution: 17%) (Figure 2).

330 The Ward's hierarchical clustering algorithm identified two clusters of lions' movements  
331 (Supplementary Figure S7). All simulated individuals belonged to cluster 0. Importantly, since  
332 one of these clusters corresponded to the null hypothesis (i.e., cluster 0), we did not find two  
333 separated clusters which could match the two tested hypotheses ("border-patrolling" hypothesis  
334 vs. "multiple central-place territories"). Additionally, by forcing the Ward's hierarchical  
335 clustering algorithm to identify 3 clusters of lions' movements, simulated movements from  
336 cluster 0 split into two groups, whereas empirical trajectories of lions from cluster 1 were still  
337 grouped together (Supplementary Figure S8). Cluster 1 grouped lions' movements characterized

338 by high values for the five movement metrics used in the PCA (Figure 3), and therefore  
339 corresponded to the expected trajectories of lions defending multiple central-place territories  
340 (Table 1). We show examples of trajectories collected on two lions identified as defending  
341 multiple central-place territories driven by waterholes (i.e., cluster 1) (Figure 4a-c), and examples  
342 of trajectories simulated under the null hypothesis within these territories (Figure 4b-d).

343         The movement of most lions was associated with cluster 1 (41 out of 46 trajectories).  
344 Therefore, it was not surprising that males and females had the same high likelihood of being  
345 associated with cluster 1 (Supplementary Table S1). Visual comparison of the five metrics for  
346 males and females did not allow us to identify a male subgroup and a female subgroup within  
347 cluster 1 (Supplementary Figure S9), which is not surprising since the Ward's hierarchical  
348 clustering algorithm did not identify more than two clusters. Only 5 lions' trajectories did not  
349 belong to cluster 1 and these were those from lions with territories with the fewest waterholes (on  
350 average 2 core and 4 edge waterholes) (Supplementary Table S2).

### 351 *Influence of the number of core and edge waterholes on lion movements*

352 Although most lions defended multiple central-place territories, it is interesting to note that the  
353 straightness of trips to core and edge waterholes increased, respectively, as the number of core  
354 and edge waterholes increased (Figure 5; Supplementary Table S3.a-b). Such patterns were  
355 detected for observed movements only and not for simulated movements (Figure 5;  
356 Supplementary Table S3.a-b), suggesting its biological relevance. We also noted that a higher  
357 number of edge waterholes increased the likelihood for lions to end at an edge waterhole when  
358 moving in the periphery of their territories (attraction index of edge waterholes), and that a higher  
359 number of core waterholes increased the likelihood for lions to stay within their core territory

360 when moving between core waterholes (attraction index of core waterholes) (Figure 5;  
361 Supplementary Table S3.c-d). As we found these patterns in both observed and simulated  
362 movements, we concluded that they did not reveal anything interesting in terms of space use  
363 strategies linked to territoriality.

## 364 **DISCUSSION**

365 Although knowledge has accumulated on territorial behaviour over the years (Potts & Lewis,  
366 2014), our understanding of how territorial animals actually move throughout their territory to  
367 patrol and maintain their exclusive access is lagging behind, perhaps excepted in the literature on  
368 chimpanzees (Mitani & Watts, 2005; Watts & Mitani, 2001) and grey wolves (Peters & Mech,  
369 1975). In this study, we found that lions of both sexes repeatedly move along straight, goal-  
370 oriented paths between the waterholes located in both the core and the periphery of their  
371 territories. Such movement patterns challenge the classic view of territorial movements being  
372 done along the border of the territory (Hansen et al., 2024; Peters & Mech, 1975; Watts & Mitani,  
373 2001). These territorial movement strategies lead to the emergence of “multiple central-place  
374 territories” structured by waterholes, which are key prey hotspots in the study system (Chamaillé-  
375 Jammes et al., 2009; Valeix, Loveridge, et al., 2009).

376 The concept of multiple central-place movements was first coined in the foraging  
377 literature. Multiple central-place foraging is conceptualized as the exploitation of multiple, well-  
378 identified and patchily distributed feeding sites. The pattern of visits to these sites is expected to  
379 be driven by the dynamics of resource depletion and growth, although it can be affected by other  
380 factors, such as the presence of a competitor. It was described in species as diverse as spider  
381 monkeys (*Ateles geoffroyi*) (Chapman et al., 1989), Lapland longspurs (*Calcarius lapponicus*)  
382 (McLaughlin & Montgomerie, 1989), Atlantic salmon (*Salmo salar*) (Steingrímsson & Grant,

383 2008, 2011a, 2011b) and African elephants (*Loxodonta africana*) (Valls-Fox et al., 2018). This  
384 framework has rarely been applied to predators, although it could be expected to adequately  
385 conceptualize their behaviour. Because prey adopt anti-predator responses following the presence  
386 of a predator, for example being more vigilant or moving away from the encounter site (Charnov  
387 et al., 1976; Courbin et al., 2015; Kotler, 1992), carnivores need to frequently leave feeding sites  
388 to counter balance this behavioural resource depression, i.e., lower availability of prey. This  
389 process was documented in African lions (Valeix et al., 2011) but also in other predators, such as  
390 mountain lions (*Puma concolor*) (Brown et al., 1999) or intermediate egrets (*Egretta intermedia*)  
391 (Amano & Katayama, 2009).

392         Valeix et al., (2010) already showed that lions adopt area-restricted search behaviour in  
393 the vicinity of waterholes, and Valeix et al., (2011) that lions tend to move to a different  
394 waterhole after a hunt near a waterhole. Our results extend these previous descriptions and bring  
395 two new insights: (1) lions alternate between multiple feeding sites along straight trajectories,  
396 minimizing the time spent away from waterholes and thus quickly reaching feeding sites where  
397 prey would be less wary; and (2) lions' movements are waterhole-oriented not solely in their  
398 territory core but also in the periphery of their territories. The latter observation suggests that  
399 multiple central-place territories do not solely emerge from the pattern of resource exploitation  
400 but potentially also from lion territorial behaviours. It could therefore support the idea that  
401 territorial animals integrate both territorial defence and foraging tactics in their movements  
402 (Asensio et al., 2011; Steingrímsson & Grant, 2011a).

403         In our study, we found that both male and female lions defended multiple central-place  
404 territories driven by the distribution of waterholes. We did not reveal any border-patrolling  
405 behaviour for male lions, as was initially expected for territorial animals defending the exclusive

406 access to social mates. Because male lions are more likely to spend time with pride females near  
407 waterholes (Dejeante et al., 2024), and because female lions repeatedly alternate between  
408 waterholes linked by straight paths, male lions' movements possibly reflect female movements.  
409 By specifically marking waterholes rather than patrolling around territorial borders, male lions  
410 could therefore prevent the intrusion of rivals directly where females spend most of their time  
411 (Dejeante et al., 2024), potentially helping females to compete against other prides [such as  
412 suggested by results from Mosser and Packer (2009)]. Besides, the long-distance vocalizations of  
413 lions (up to 8 km in the Serengeti ecosystem; Packer 2023) may also allow them to signal their  
414 presence in a radius large enough to cover the unvisited areas between waterholes, similarly to  
415 wolves scent-marking elevated locations to facilitate wind dispersal of odours (Peters & Mech,  
416 1975). In another ecosystem, Wijers et al., (2021) showed that lions vocalize as frequently in the  
417 core as in the periphery of their territory, and that they are more likely to repeatedly roar once  
418 close to waterholes. Territorial animals using long-distance marking signals at multiple central  
419 places could reinforce the renewal of territorial cues at some key places and passively indicate  
420 their presence over a large area. Doing so, territorial animals should reduce the cost of patrolling,  
421 relative to moving along the border of their territory, since (1) lions reach more quickly  
422 unmarked key places and (2) long-distance marking signals allow them to cover the unvisited  
423 places between multiple central places.

424         If specifically marking some key places of their territories provides several benefits to  
425 territorial animals (i.e., reduced travel costs, increased renewal of territorial cues at key places,  
426 coverage of unvisited areas through long-distance cues), then why do not territorial animals  
427 always defend multiple central-place territories? A first key condition for the emergence of  
428 multiple central-place territories is that territorial animals live in landscapes where resources are

429 spatio-temporally heterogeneous in their availability, which leads them to regularly return to  
430 patchily distributed feeding sites (Macdonald & Johnson, 2015). Lions in Hwange National Park  
431 live in a highly heterogeneous landscape with spatially-stable patches of resources (i.e., prey  
432 aggregated around waterholes) that is evidently not representative of the diversity of ecosystems  
433 territorial animals live in. However, in other ecosystems, resources may be found in stable,  
434 heterogeneously distributed patches. For example, in Prince Albert National Park (Canada),  
435 plains bison (*Bison bison*) move within a mosaic of discrete meadows (Harvey & Fortin, 2013)  
436 that could lead grey wolves to maintain multiple central-place territories driven by the  
437 distribution of these patches. A second condition to investigate the emergence of multiple central-  
438 place territories is likely related to the size of an animal's territory. Here, the rare lions that did  
439 not maintain multiple central-place territories had only a small number of waterholes to defend.  
440 Additionally, we found a strong correlation between the number of waterholes, the size of lion  
441 territories and the straightness of trips between waterholes, suggesting a gradient between lions'  
442 territorial strategies: lions defending larger territories may need to move more rapidly in  
443 straighter goal-oriented movements to efficiently mark their whole territory. Because the size of  
444 lion territories is inversely related to the density of waterholes and to the prey biomass  
445 (Loveridge et al., 2009), our results suggest that multiple central-place territories are more likely  
446 to emerge when territorial animals live in landscape where resources are rare. Interestingly,  
447 multiple central-place territories were described in wild young-of-the-year Atlantic salmon  
448 (*Salmo salar*) (Steingrímsson & Grant, 2008, 2011a, 2011b), making it clear that multiple  
449 central-place territories are not restricted to our study system. Therefore, investigating whether  
450 territorial animals from other ecosystems similarly defend multiple central-place territories, and  
451 the environmental conditions under which such territories emerge, is appealing. Generally, it

452 should allow ecologists to gain new insights on how the spatial distribution of resources shapes  
453 space use in territorial animals.

454 **DATA AVAILABILITY STATEMENT**

455 Data available from the figshare repository: <https://doi.org/10.6084/M9.FIGSHARE.26004463>

456 **DECLARATION OF INTEREST**

457 The authors declare that they have no conflict of interest.

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466

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622  
623

624 **TABLE**

625 **Table 1.** Hypotheses and associated predictions for the five movement metrics characterizing  
 626 lion trips to waterholes.

Movement metrics	H0	‘Multiple central-place territories’ hypothesis	‘Border-patrolling’ hypothesis
Attraction index (core waterhole)	low	high	high
Attraction index (edge waterhole)	low	high	low
Straightness index (core-to-core)	low	high	high
Straightness index (core-to-edge)	low	high	low
Straightness index (edge-to-edge)	low	high	low

627

628 H0 refers to the null hypothesis: lions select for areas close to waterholes but do not exhibit  
 629 waterhole-oriented trips. In the case that lions defend “multiple central-place territories”, we  
 630 expect that lions frequently move between core and edge waterholes to exploit these resource  
 631 patches and specifically mark these key feeding sites of their territories. Here, we predict such a  
 632 pattern for female lions. The “border-patrolling” hypothesis refers to the case whereby lions  
 633 solely move between core waterholes to exploit resources but move around territorial borders to  
 634 patrol their territory, i.e., we expect that lions’ movements in the periphery of their territory are  
 635 not waterhole-oriented. We predict such a pattern for male lions. The five movement metrics  
 636 range between 0 and 1.

637

638 **FIGURE LEGENDS**

639 Figure 1. Schematic representation of (a) the “border-patrolling” and (b) the “multiple central-  
640 place territories” hypotheses. In the case that lions defend “multiple central-place territories”, we  
641 expect that lions frequently rotate between core and edge waterholes to exploit resources and  
642 specifically mark key feeding sites of their territories. Here, we predict such a pattern for female  
643 lions. The “border-patrolling” hypothesis refers to the case whereby lions solely rotate between  
644 core waterholes to exploit resources but move along territorial borders to patrol their territories,  
645 i.e., we expect that lions’ movements in the periphery of their territory are not waterhole-  
646 oriented. We predict such a pattern for male lions.

647

648 Figure 2. Scatterplot of lion clusters based on PCA-defined axes. Cluster 0 (blue) groups  
649 individuals characterized by little oriented trips to core and edge waterholes, i.e., validating the  
650 null hypothesis. Cluster 1 (red) groups individuals characterized by very oriented trips to core and  
651 edge waterholes, i.e., validating the “multiple central-place territories” hypothesis. Square dots  
652 represent simulated individuals, circular dots represent lions tracked with GPS collars. Star  
653 symbols show individuals for which we did not record any trips between edge waterholes. For  
654 those individuals, we performed the PCA analysis from the four other movement metrics and  
655 with the average straightness index of edge-to-edge trips. ‘Attraction’ refers to the attraction  
656 index and ‘Si’ to the straightness index.

657

658 Figure 3. Scatterplot of lion clusters overlaid on four of the five movement metrics used in the  
659 PCA analysis. Cluster 0 (blue) groups individuals characterized by little oriented trips to core and  
660 edge waterholes, i.e., validating the null hypothesis. Cluster 1 (red) groups individuals

661 characterized by oriented trips to core and edge waterholes, i.e., validating the “multiple central-  
662 place territories” hypothesis. Square dots show simulated individuals, circular dots show lions  
663 tracked with GPS collars. Star symbols show individuals for which we did not record any trips  
664 between edge waterholes. For those individuals, we performed the PCA analysis from the four  
665 other movement metrics and with the average straightness index of edge-to-edge trips.

666

667 Figure 4. Illustration of multiple central-place territories (a, c) and associated computer  
668 simulations (b-d). Blue dots show waterholes located in the core of the lion territory and red dots  
669 waterholes in the periphery of the lion territory. The shaded area represents the 99% utilization  
670 distribution of a kernel-based home range estimate.

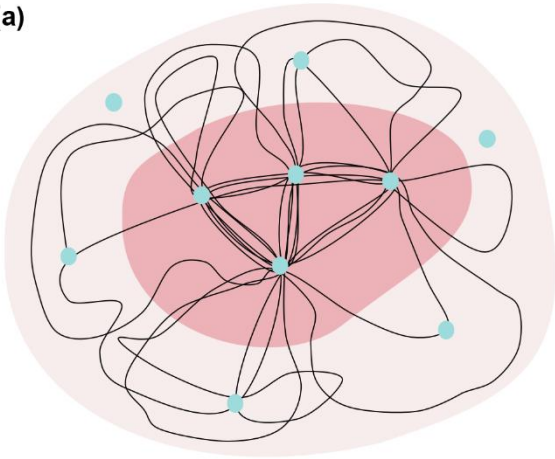
671

672 Figure 5. Importance of the number of waterholes in the core and the periphery of lion territories  
673 on (a) the straightness of lion trips between core and edge waterholes, (b) the straightness of lion  
674 trips between core and edge waterholes, (c) the attraction index of core waterholes, and (d) the  
675 attraction index of edge waterholes. Square dots (blue) show simulated individuals, circular dots  
676 (red) show lions tracked with GPS collars.

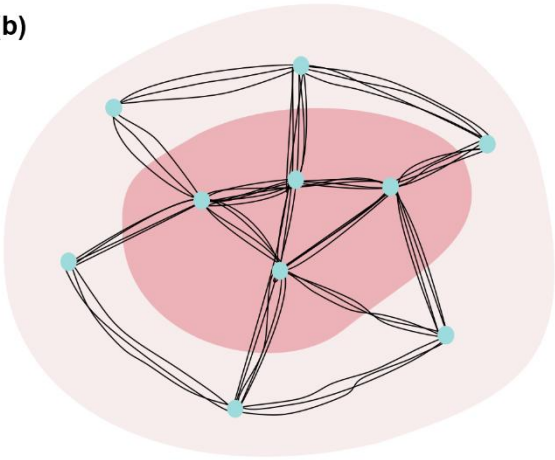
677

678 **FIGURES**

(a)

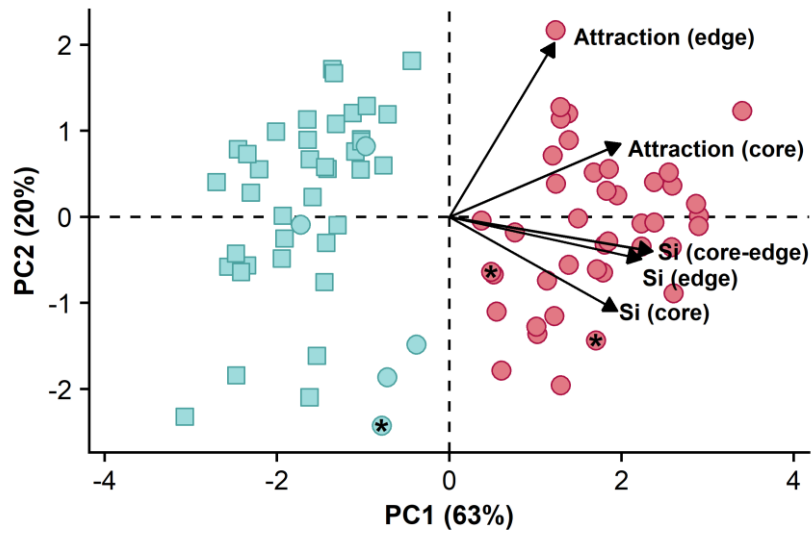


(b)



679

680 **Figure 1**

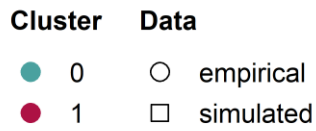
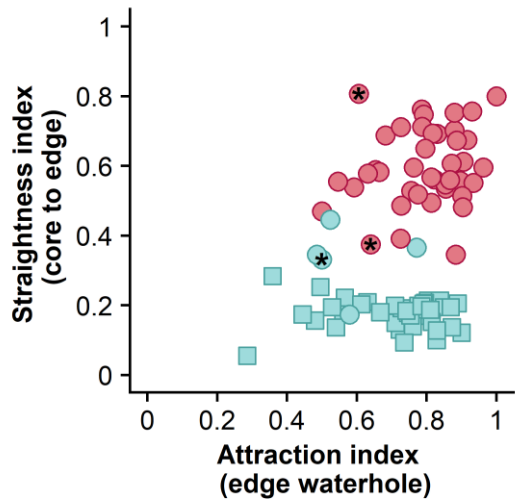
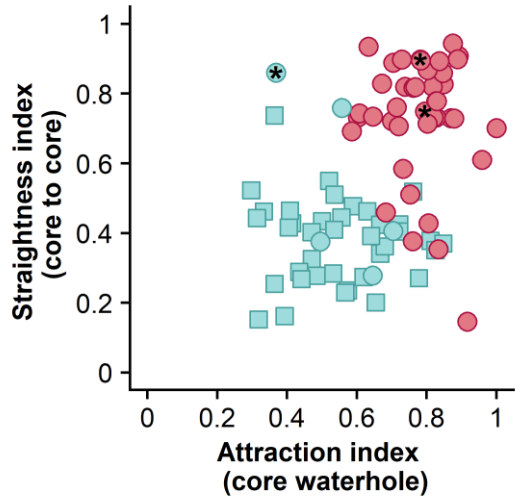


Data	cluster
○ empirical	● 0
□ simulated	● 1

681

682 **Figure 2**

683

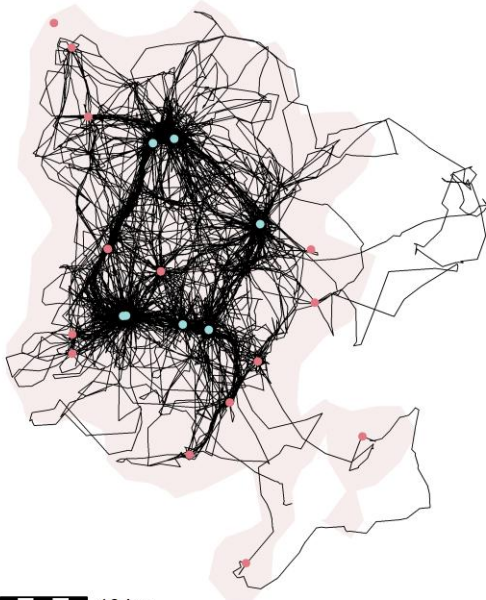


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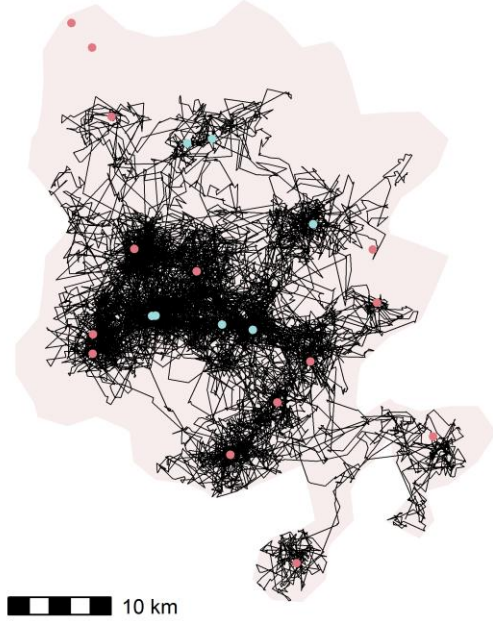
685 **Figure 3**

686

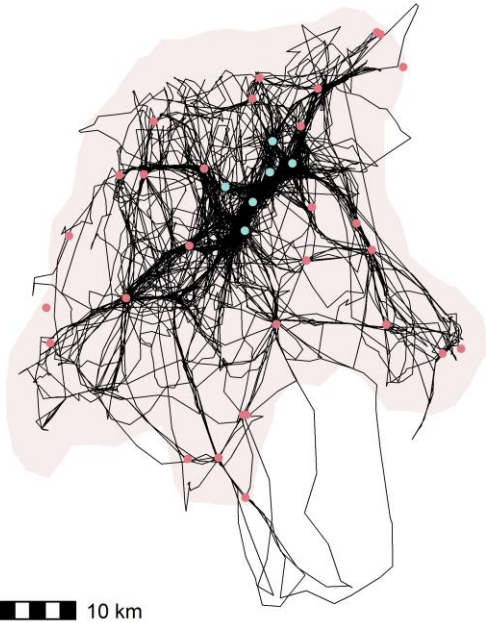
(a)



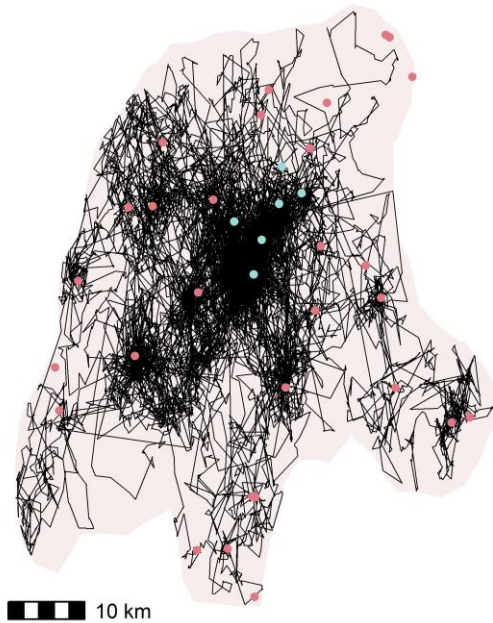
(b)



(c)

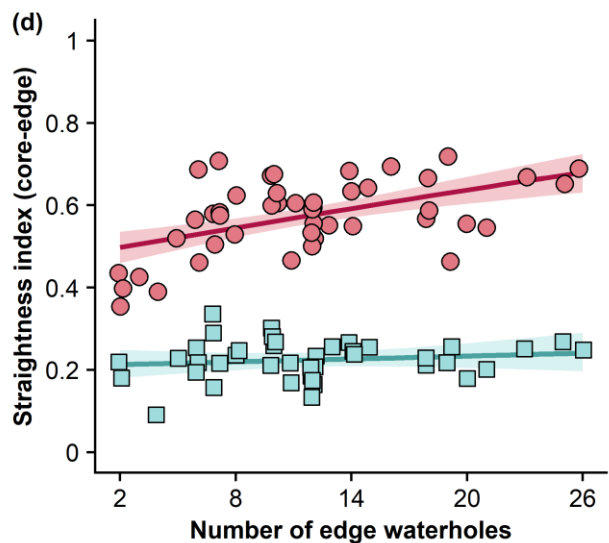
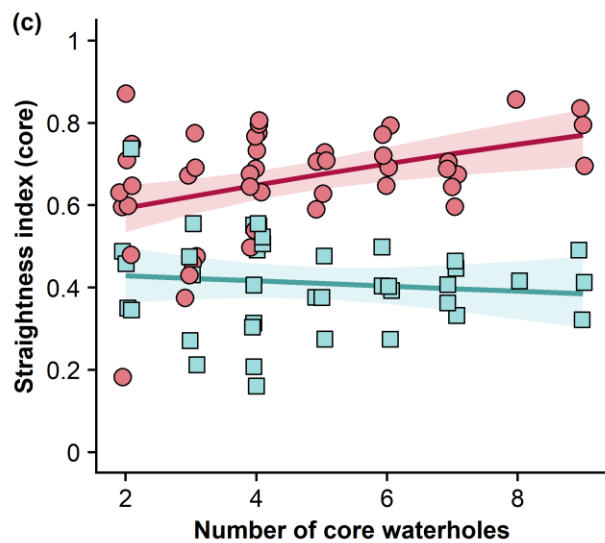
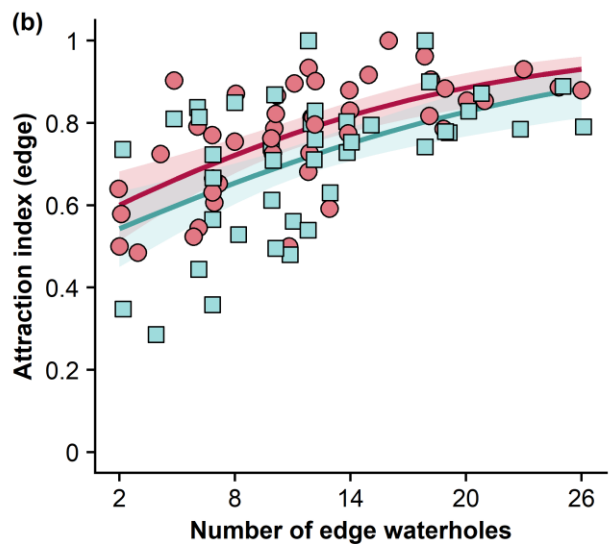
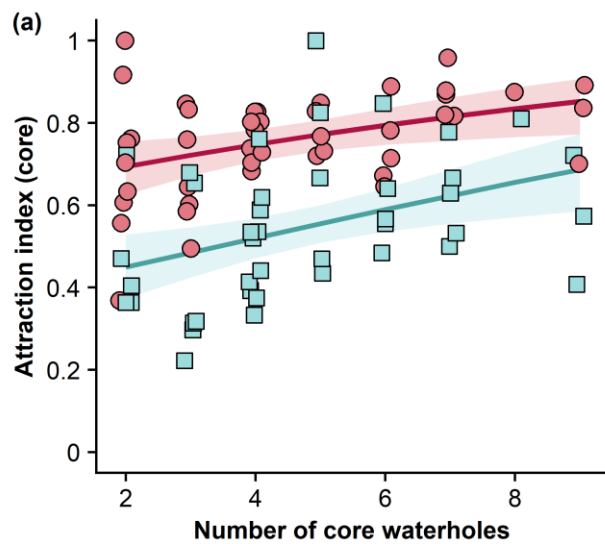


(d)

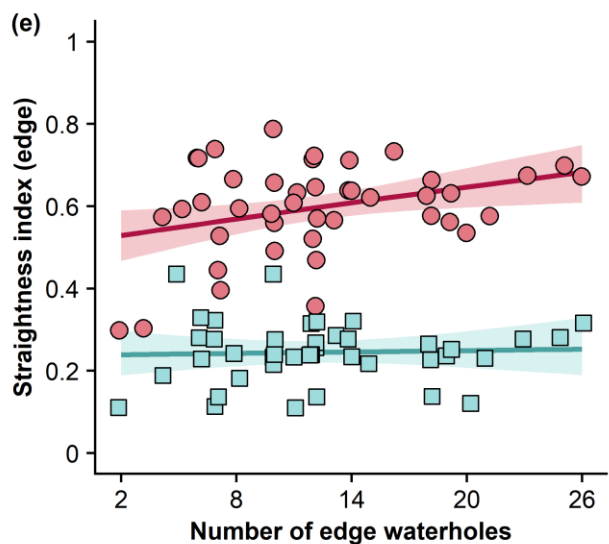


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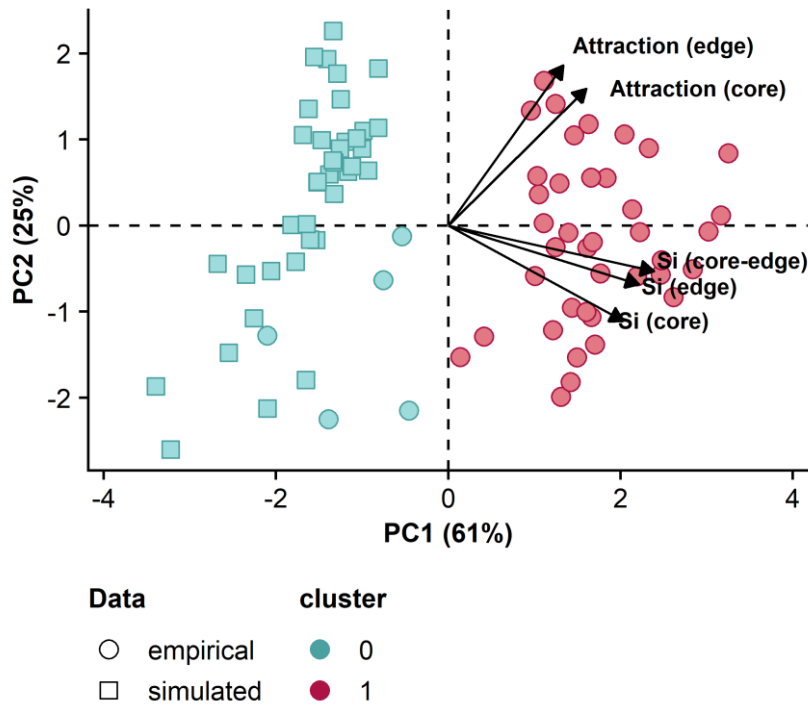
688 **Figure 4**



**Data**  
● empirical  
■ simulated

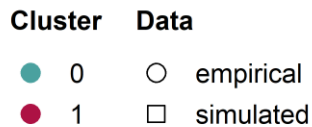
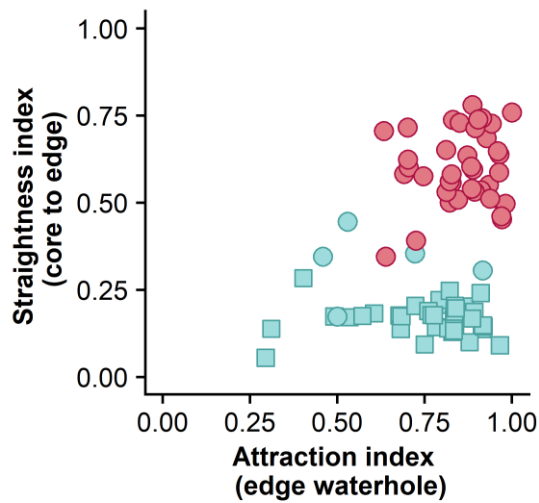
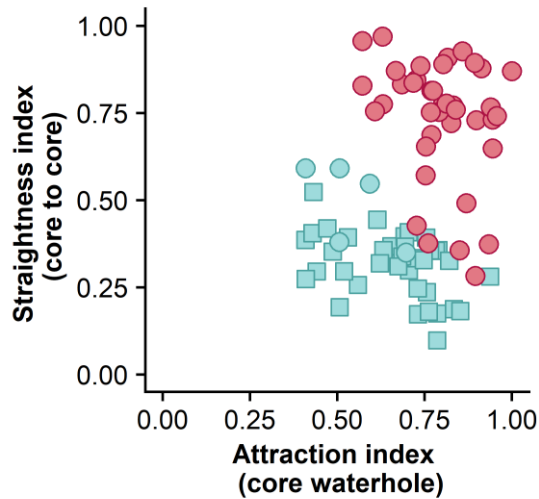


690 **Supplementary file S1. Supplementary analyses – Minimum convex polygons**



691

692 Figure S1. Scatterplot of lion clusters based on PCA-defined axes. Cluster 0 (blue) groups  
 693 individuals characterized by little oriented trips to core and edge waterholes, i.e., validating the  
 694 null hypothesis. Cluster 1 (red) groups individuals characterized by very oriented trips to core and  
 695 edge waterholes, i.e., validating the “multiple central-place territories” hypothesis. Circular dots  
 696 represent simulated individuals, and square dots represent lions tracked with GPS collars. Core  
 697 and edge waterholes were located respectively inside and outside the core area of lions’ home  
 698 ranges, as delineated from a Minimum convex polygons approach.



699

700 Figure S2. Scatterplot of lion clusters overlaid on the four metrics used in the PCA analysis.

701 Cluster 0 (blue) groups individuals characterized by little oriented trips to core and edge

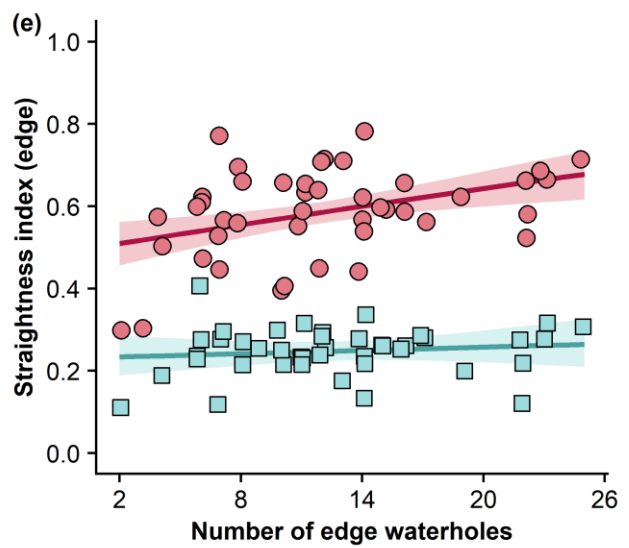
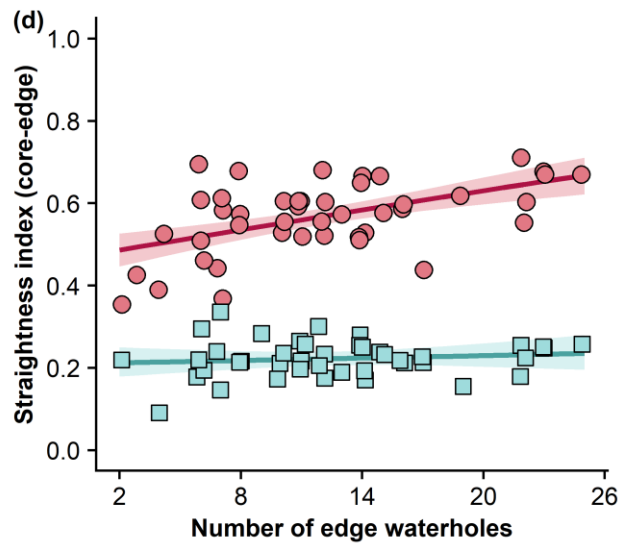
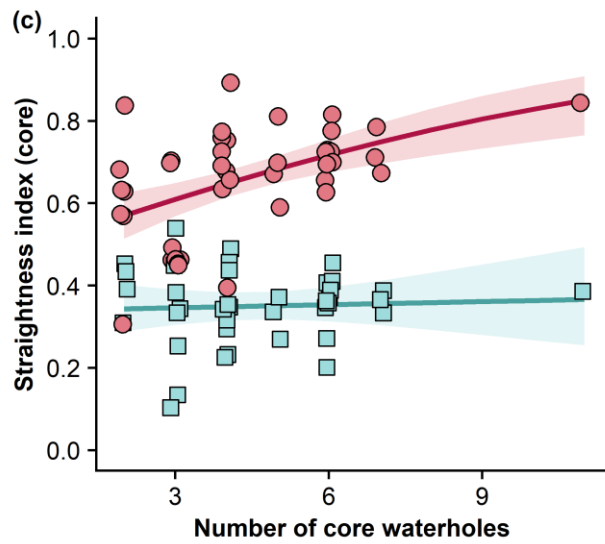
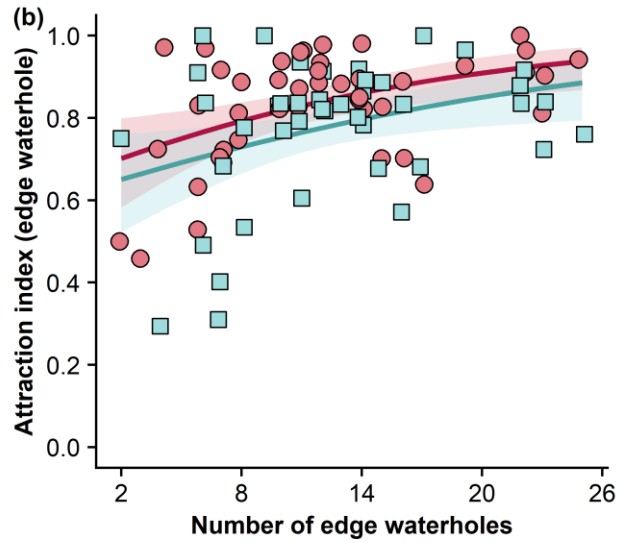
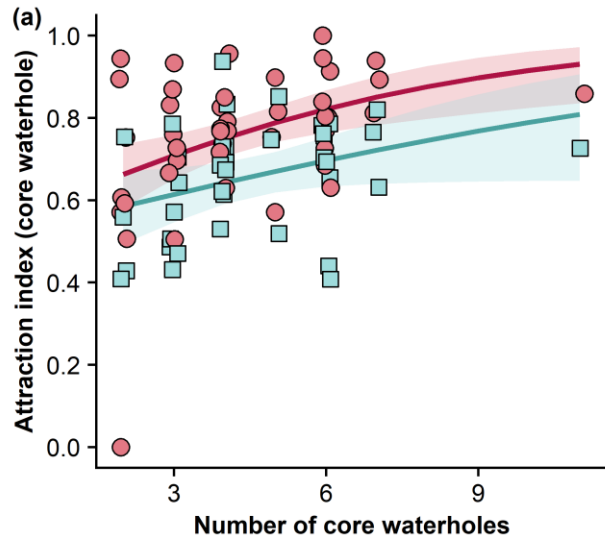
702 waterholes, i.e., validating the null hypothesis. Cluster 1 (red) groups individuals characterized by

703 oriented trips to core and edge waterholes, i.e., validating the “multiple central-place territories”

704 hypothesis. Circular dots show simulated individuals, square dots show lions tracked with GPS

705 collars. Core and edge waterholes were located respectively inside and outside the core area of

706 lions’ home ranges, as delineated from a Minimum convex polygons approach.

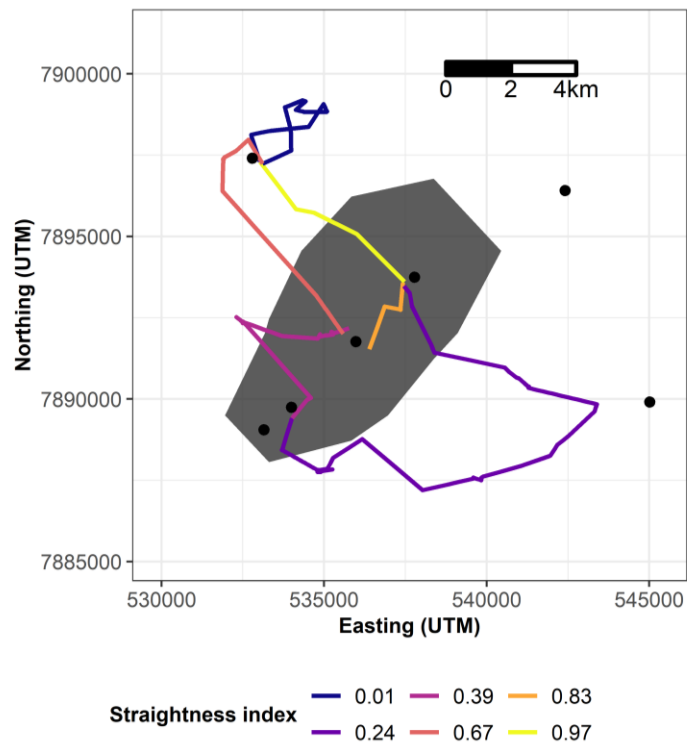


**Data**  
● empirical  
■ simulated

708 Figure S3. Importance of the number of waterholes in the core and the periphery of lion  
709 territories on (a) the straightness of lion trips between core and edge waterholes, (b) the  
710 straightness of lion trips between core and edge waterholes, (c) the attraction index of core  
711 waterholes, and (d) the attraction index of edge waterholes. Circular dots (blue) show simulated  
712 individuals, square dots (red) show lions tracked with GPS collars. Core and edge waterholes  
713 were located respectively inside and outside the core area of lions' home ranges, as delineated  
714 from a Minimum convex polygons approach.

715 **Supplementary file S2. Supplementary figures**

716

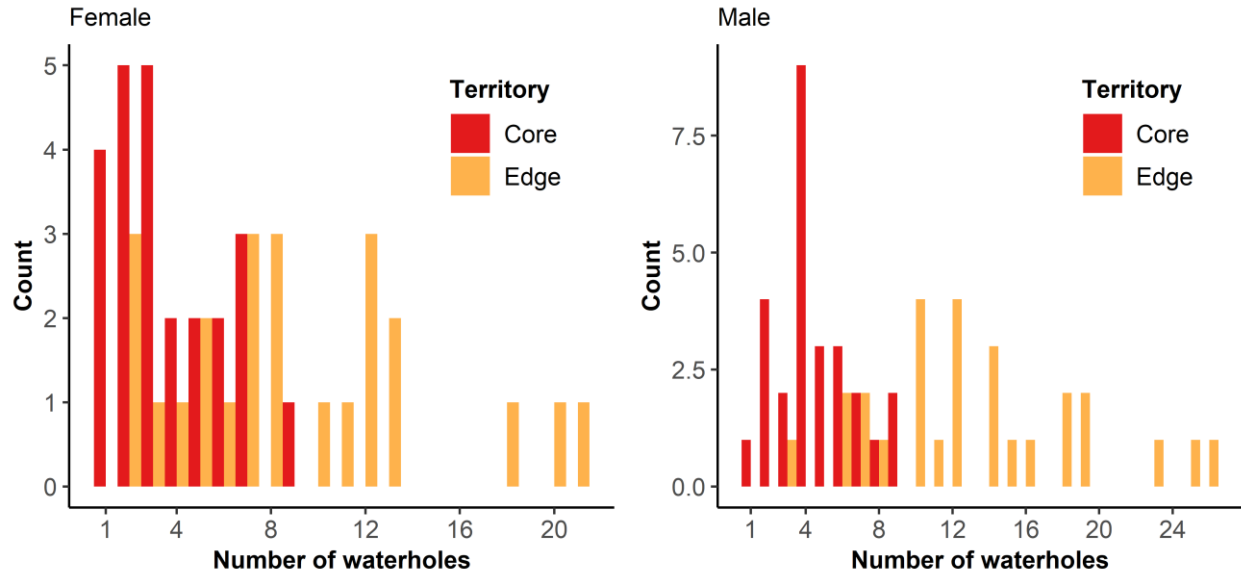


717

718 Figure S4. Illustration of lion trips to waterholes colored by the straightness index of each trip.

719 The straightness index measures how much a trip between two waterholes (dark points) is  
720 following a straight trajectory (index close to 1), or is tortuous (index close to 0).

721



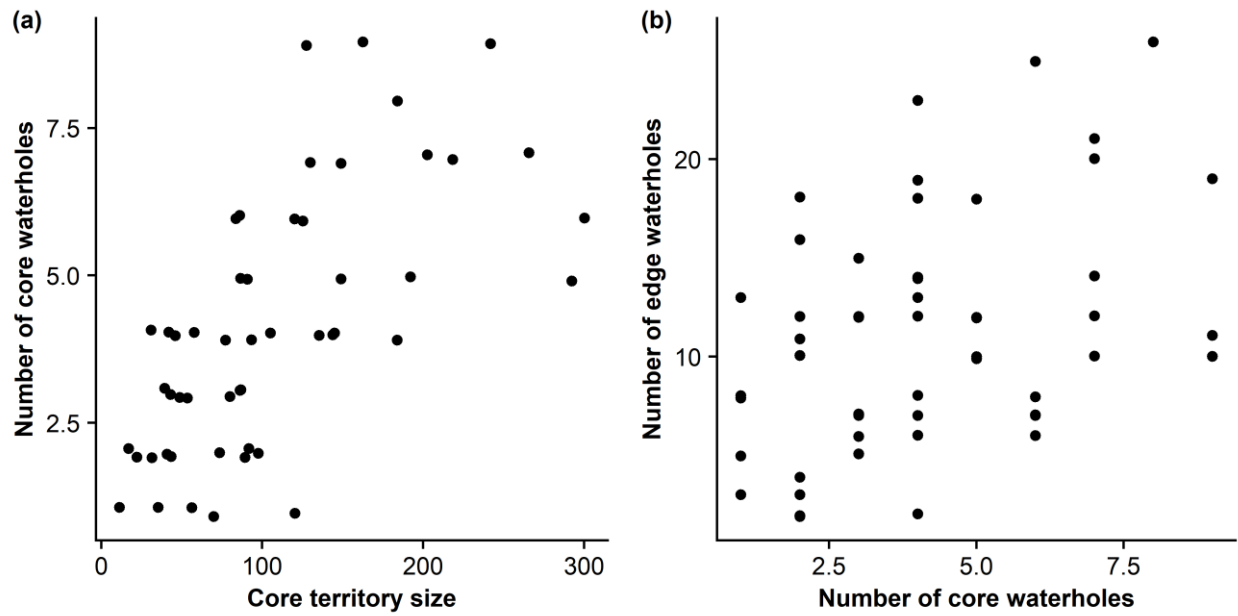
722

723 Figure S5. Distribution of the number of waterholes within the core (red) and edge (orange)

724 territories of male and female lions.

725

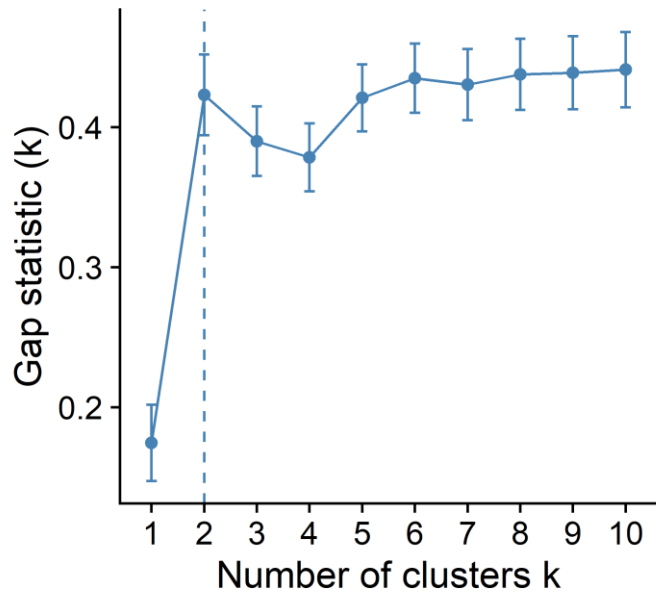
726



727  
728

729 Figure S6. Relationship between (a) the number of waterholes in lion core territories and the size  
730 of core territory and (b) between the number of waterholes in the periphery of lion territories and  
731 the number of waterholes in their core territory.

732



733

734 Figure S7. Investigation of the optimal number of clusters that lions' movements belonged to.

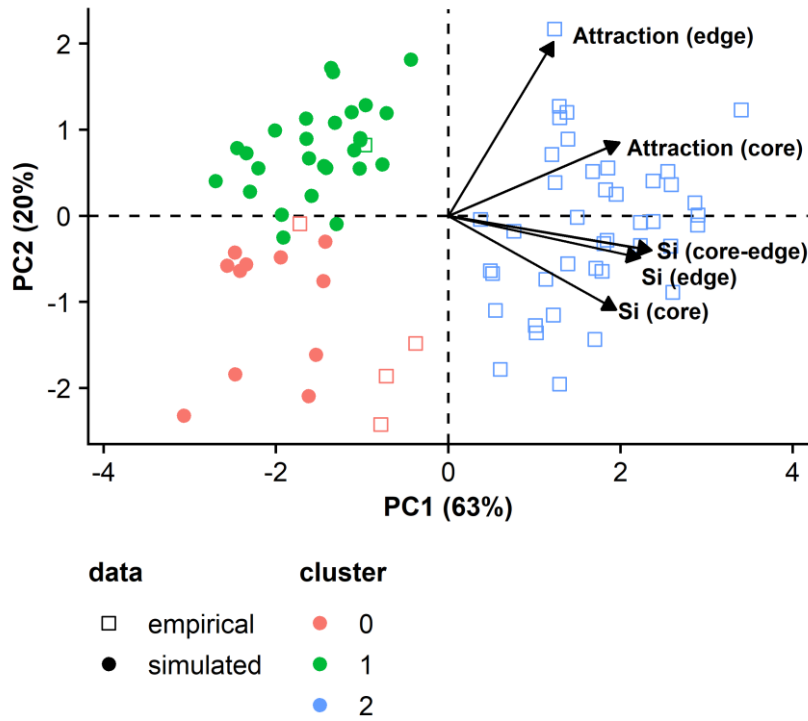
735 The gap statistic compares the variations within each cluster with the value expected from the

736 random distribution of points. Adding more than two clusters does not reduce the gap between

737 the total within intra-cluster variation and the expected variations under the null hypothesis.

738

739



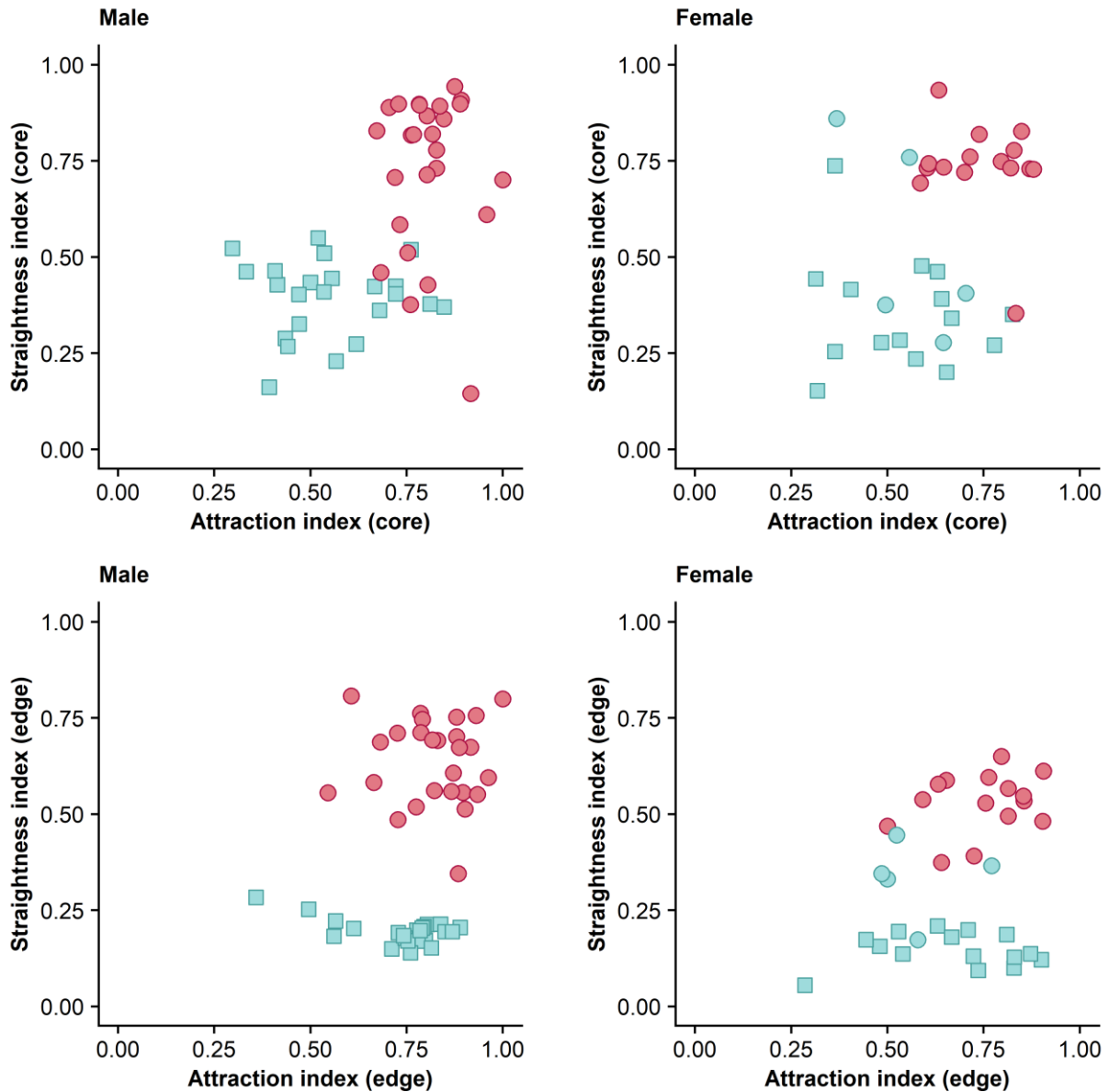
740

741 Figure S8. Scatterplot of lion clusters based on PCA-defined axes. Circular dots show simulated  
742 individuals, and square dots shows lions tracked with GPS collars. Adding a third cluster does not  
743 allow us to find subgroups between empirical lions' movements, but on the contrary to find  
744 subgroups between the simulated trajectories.

745

746

747



Cluster	Data
● 0	○ empirical
● 1	□ simulated

748  
 749 Figure S9. Scatterplot of male and female lion clusters overlaid on the four metrics used in the  
 750 PCA analysis. Cluster 0 (blue) groups individuals characterized by little oriented trips to core and  
 751 edge waterholes, i.e., validating the null hypothesis. Cluster 1 (red) groups individuals  
 752 characterized by oriented trips to core and edge waterholes, i.e., validating the “multiple central-

753 place territories” hypothesis. Circular dots show simulated individuals, square dots show lions  
754 tracked with GPS collars.

755 **Supplementary file S3. Supplementary tables**

756

757 Table S1. Model selection procedure to investigate the importance of the number of core  
758 waterholes, edge waterholes and of lion sex on the probability that lions use waterholes as  
759 multiple central places (i.e., that a lion was grouped within the cluster 1 in the cluster analysis).  
760 The selected model is indicated in bold letters.

761

762

763

Models	k	AIC	$\Delta$ AIC
Core waterholes + Edge waterholes	3	19.9	0.0
<b>Edge waterholes</b>	<b>2</b>	<b>21.2</b>	<b>1.3</b>
Core waterholes $\times$ Sex	4	23.2	3.3
Edge waterholes $\times$ Sex	4	23.5	3.5
(Core waterholes + Edge waterholes) $\times$ Sex	6	26.1	6.1
Core waterholes	2	26.3	6.3
Sex	2	26.8	6.9

764 Table S2. Coefficients ( $\beta$ ) and standard errors (SE) for the logistic regression testing the effect of  
765 the edge waterholes on the likelihood that lions' movements belonged to cluster 1.

766

Models	$\beta$	SE	z-value	p-value
(Intercept)	-2.20	1.41	-1.56	0.12
Edge waterhole	0.61	0.25	2.47	<0.05

767 Table S3. Coefficients ( $\beta$ ) and standard errors (SE) for the quasi-binomial regression testing the  
 768 effect of the number of core waterholes, edge waterholes and whether trips to waterholes were  
 769 empirical or simulated on the four metrics used in the cluster analysis.

Models	$\beta$	SE	z-value	p-value
<b>(a) Straightness index – trips between core waterholes</b>				
(Intercept)	0.14	0.19	0.72	0.47
Core waterhole	0.12	0.04	2.99	<0.01
Simulated trip	-0.37	0.28	-0.84	0.19
Core waterhole $\times$ Simulated trip	-0.15	0.06	-3.05	<0.05
<b>(b) Straightness index – trips between core and edge waterholes</b>				
(Intercept)	-0.07	0.09	-0.81	0.42
Edge waterhole	0.03	0.01	4.55	<0.001
Simulated trip	-1.25	0.15	-8.41	<0.001
Edge waterhole $\times$ Simulated trip	-0.03	0.01	-2.26	<0.05
<b>(c) Straightness index – trips between edge waterholes</b>				
(Intercept)	0.06	0.15	0.42	0.67
Edge waterhole	0.03	0.01	2.47	<0.05
Simulated trip	-1.22	0.23	-5.41	<0.001
Edge waterhole $\times$ Simulated trip	-0.02	0.02	-1.43	0.16
<b>(d) Attraction index (edge waterhole)</b>				
(Intercept)	0.23	0.21	1.06	0.29
Edge waterhole	0.09	0.02	4.84	<0.001
Simulated trip	-0.21	0.31	-0.68	0.50

Edge waterhole × Simulated trip	-0.01	0.03	-0.52	0.61
<b>(e) Attraction index (core waterhole)</b>				
(Intercept)	0.55	0.24	2.26	<0.05
Core waterhole	0.13	0.05	2.53	<0.05
Simulated trip	-1.03	0.35	-2.98	<0.01
Core waterhole × Simulated trip	0.01	0.07	0.11	0.92

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