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

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HIGHLIGHTS

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

ABSTRACT

In territorial species, individuals need to regularly patrol their territory to display visual, auditory or olfactory signals, or to detect the presence of intruders. Although territorial movements are often conceptualized as animals travelling along the boundaries of their territories (‘border patrolling’ behaviour), the distribution of territorial cues could also match the distribution of resources when resources are spatially heterogeneous in their availability and found in stable patches, leading to the emergence of “multiple central-place territories”. Here, we explored how territoriality may shape the spatial behaviour of African lions (*Panthera leo*) in a savanna where waterholes are associated with aggregations of large herbivores throughout the year and are therefore well-known prey hotspots and key hunting sites for large carnivores. We hypothesized that male lions would be more likely to patrol a buffer area around the territory core to defend a core area where social interactions with groupmates occur, whereas female lions would more specifically patrol hunting sites, i.e. waterhole areas. However, we found that both female and male lions repeatedly moved along straight paths between the waterholes located both in the core and in the periphery of their territories, potentially to defend multiple central-place territories driven by the distribution of waterholes in the landscape. These findings illustrate a case where territorial animals specifically mark feeding sites, increasing the renewal of territorial cues at these key places, potentially using long-distance territorial cues (i.e., vocalizations) to mark uncovered areas, and thereby reducing the cost of patrolling large territories. Overall, multiple central-place territories provide new insights on how the spatial distribution of resources shapes space use in territorial animals.

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

INTRODUCTION

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

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

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

The distribution of territorial cues sometimes underlies the pattern of resource exploitation (Macdonald, 1980). In particular, when resources are heterogeneously distributed and found in stable patches, territorial animals may be expected to concentrate their territorial cues around some key places, such as reported for feral cats (*Felis catus*), wild cats (*Felis silvestris*) and red foxes (*Vulpes vulpes*) that specifically scent-mark in preferred hunting areas (Macdonald, 1980). Specifically marking feeding sites can increase the renewal of olfactory, visual and auditory signals around a limited number of key places. Because scent-marks may be dispersed by wind (for example wolves scent-mark elevated locations to facilitate wind dispersal of odours (Peters & Mech, 1975)) and because vocalizations may be heard at long distance (for example up to 8 km for lion vocalizations in the Serengeti ecosystem (Packer 2023)), specifically marking some key places may allow territorial animals to signal their presence in a radius large enough to cover the unvisited areas of their territories. Territories that are defended by animals rotating between several feeding sites to exploit resources and patrol around these key places have been referred to as “multiple central-place territories” (Steingrímsson & Grant, 2008, 2011a, 2011b). Here, we refer to this scenario accordingly.

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

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

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

METHODS

Study area

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

Ethical note

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

Lions were immobilized by chemicals. They were darted from the ground, using Dan Inject J.M.SP.25 CO2-powered dart guns to administer drugs by intramuscular injection (shoulder or rump). Lions received the dissociative anaesthetic Zoletil (dosage: 0.83e0.32 (range 0.53e1.38) mg/kg; manufacturer: Virbac RSA, Centurion, South Africa) and sedative medetomidine (Zalopine/Domitor; dosage 0.05e0.01 (range 0.04e0.06) mg/kg; manufacturer:

Novartis, Isando, South Africa or Orion Pharma, Turku, Finland). Once immobilized, lion eyes were covered and ear plugs fitted to reduce stimuli and stress, and the collars were fitted. We equipped lions with GPS collars from Televilt/Followit Positioning (AB, Lindesberg, Sweden) or African Wildlife Tracking (Pretoria, South Africa) or Sirtrack Ltd. (Havelock North, New Zealand). GPS collars weighed between 600 and 900 g, representing respectively 0.6 and 0.9% of the smallest individual captured (100 kg). Drugs were then reversed using Atipamezole (dosage: 1⁄4 0.18e0.07 (range 0.01e0.28) mg/kg; manufacturer: Farmos; Orion Corp., Espoo, Finland or Novartis). Once reversal drugs were injected, lions were monitored until their full recovery. Following collar deployments, all collared lions were located weekly to bimonthly from a vehicle or microlight aircraft to ensure that lions did not experience any adverse effects from the GPS collars. Collars were removed when batteries were flat or when they malfunctioned, and were usually replaced for long-term monitoring of the Hwange lion population. Collars were removed using the immobilization procedure described before. If not removed, collars would eventually fall off owing to deterioration of the collar material.

Lion movement data

From 2002 to 2016, 22 adult female lions and 21 adult male lions were monitored with GPS collars, collecting hourly or two-hourly locations over on average 22 months [quartile 1 = 12 months; median = 17 months; quartile 3 = 27 months]. Because lion territories may change over time, especially for males, we used the segmentation method developed by Patin *et al.* (2020) and visual inspection of the derived segments to identify stationary periods of lion movements. We extracted 24 female and 27 male territories, potentially leading to non-independence between 6 male territories and 2 female territories. We then used the 50% and 99% utilization distribution of a kernel-based home range estimate to describe the core territory and whole territory, using the *adehabitatHR* package (Calenge, 2006). Hereafter, we distinguished waterholes located inside and outside the core territory, respectively named ‘core waterholes’ and ‘edge waterholes’. Because using a kernel approach, peripheral waterholes can fall in the centre of a lion range, we also used a Minimum Convex Polygon (MCP) to delineate the core and peripheral areas of a territory. Results using a MCP approach were similar to those obtained using a kernel approach (Supplementary file S1). Here, we therefore present results from the kernel-based home range estimate.

Definition of lion trips to waterholes

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

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

Movement metrics

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

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

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

2. *Attraction index (edge waterholes)* – the attraction index of edge waterholes measures the attractiveness of edge waterholes in driving lions' excursions outside the core territory. This index is the ratio between the number of core-to-edge trips over the number of core-to-core trips for which lions moved out of the core territory, potentially marking the periphery of their territory but not at a waterhole. In the case that edge waterholes drive lion movement, we expect a high attraction index of edge waterholes.
3. *Straightness index (core to core)* – the straightness index measures how goal-oriented a path is by dividing the net displacement between the starting and ending waterholes (i.e., straight path) by the total path length travelled along the trip. It can be seen as an indicator of whether the trip was specifically made to quickly reach the destination waterhole: the straightness index ranges between 0 (little goal-oriented, convoluted path) and 1 (directional, goal-oriented path). We show examples of lion trips to waterholes with several straightness indices in Supplementary Figure S4. We measured the straightness

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

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

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

Null-hypothesis simulation

We used an individual-based model to simulate minimally oriented trips to core and edge waterholes (i.e., resource-only model, null hypothesis). For each lion territory encompassing multiple core waterholes, we first performed an integrated step selection analysis (iSSA) to simultaneously estimate movement and habitat selection (Avgar et al., 2016), using the *amt* R package (Signer et al., 2019). We included in the iSSA environmental variables known to impact lion habitat selection in the study system: distance to waterhole, habitat openness, and distance to home range centroid (Dejeante et al., 2024). We then used the coefficients estimated by the iSSA to simulate lion trajectories within each lion territory over 20 000 time steps. To do so, for each time *t*, 30 potential steps were generated by randomly drawing step length and turning angle values from, respectively, the gamma and Von Mises distribution fitted to the empirical data. For each potential step ending in the lion territory, we then extracted the distance to waterhole, the habitat openness, and the distance to home range centroid. Finally, the location at time *t+1* was sampled among the 30 potential steps with probabilities proportional to the iSSA score.

Cluster analysis

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

Because we expected male and female lions to exhibit differences in the way they navigate in the periphery of their territories (females specifically marking waterholes and males patrolling along territorial borders), we tested the influence of lion sex on the likelihood for lions to defend multiple central-place territories. We did so by fitting a generalized linear mixed model with a logit link and a binomial distribution for errors, adding a random intercept with lion identity. Because we hypothesized that specifically marking feeding sites may be an efficient way to defend larger territories with a higher number of waterholes, we added multiplicative effects between the sex variable and the number of core and/or edge waterholes. We then compared model fit using AIC values and reported estimates from the most parsimonious model.

Influence of the number of core and edge waterholes on lion movements

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

RESULTS

General information

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

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

Cluster analysis

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

The Ward's hierarchical clustering algorithm identified two clusters of lions' movements (Supplementary Figure S7). All simulated individuals belonged to cluster 0. Importantly, since one of these clusters corresponded to the null hypothesis (i.e., cluster 0), we did not find two separated clusters which could match the two tested hypotheses ("border-patrolling" hypothesis *vs.* "multiple central-place territories"). Additionally, by forcing the Ward's hierarchical clustering algorithm to identify 3 clusters of lions' movements, simulated movements from cluster 0 split into two groups, whereas empirical trajectories of lions from cluster 1 were still grouped together (Supplementary Figure S8). Cluster 1 grouped lions' movements characterized by high values for the five movement metrics used in the PCA (Figure 3), and therefore corresponded to the expected trajectories of lions defending multiple central-place territories (Table 1). We show examples of trajectories collected on two lions identified as defending multiple central-place territories driven by waterholes (i.e., cluster 1) (Figure 4a-c), and examples of trajectories simulated under the null hypothesis within these territories (Figure 4b-d).

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

Influence of the number of core and edge waterholes on lion movements

Although most lions defended multiple central-place territories, it is interesting to note that the straightness of trips to core and edge waterholes increased, respectively, as the number of core and edge waterholes increased (Figure 5; Supplementary Table S3.a-b). Such patterns were detected for observed movements only and not for simulated movements (Figure 5; Supplementary Table S3.a-b), suggesting its biological relevance. We also noted that a higher number of edge waterholes increased the likelihood for lions to end at an edge waterhole when moving in the periphery of their territories (attraction index of edge waterholes), and that a higher number of core waterholes increased the likelihood for lions to stay within their core territory when moving between core waterholes (attraction index of core waterholes) (Figure 5; Supplementary Table S3.c-d). As we found these patterns in both observed and simulated movements, we concluded that they did not reveal anything interesting in terms of space use strategies linked to territoriality.

DISCUSSION

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

The concept of multiple central-place movements was first coined in the foraging literature. Multiple central-place foraging is conceptualized as the exploitation of multiple, well-identified and patchily distributed feeding sites. The pattern of visits to these sites is expected to be driven by the dynamics of resource depletion and growth, although it can be affected by other factors, such as the presence of a competitor. It was described in species as diverse as spider monkeys (*Ateles geoffroyi*) (Chapman et al., 1989), Lapland longspurs (*Calcarius lapponicus*) (McLaughlin & Montgomerie, 1989), Atlantic salmons (*Salmo salar*) (Steingrímsson & Grant, 2008, 2011a, 2011b) and African elephants (*Loxodonta africana*) (Valls-Fox et al., 2018). This framework has rarely been applied to predators, although it could be expected to adequately conceptualize their behaviour. Because prey adopt anti-predator responses following the presence of a predator, for example being more vigilant or moving away from the encounter site (Charnov et al., 1976; Courbin et al., 2015; Kotler, 1992), carnivores need to frequently leave feeding sites to counter balance this behavioural resource depression, i.e., lower availability of prey. This process was documented in African lions (Valeix et al., 2011) but also in other predators, such as mountain lions (*Puma concolor*) (Brown et al., 1999) or intermediate egrets (*Egretta intermedia*) (Amano & Katayama, 2009).

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

In our study, we found that both male and female lions defended multiple central-place territories driven by the distribution of waterholes. We did not reveal any border-patrolling behaviour for male lions, as was initially expected for territorial animals defending the exclusive access to social mates. Because male lions are more likely to spend time with pride females near waterholes (Dejeante et al., 2024), and because female lions repeatedly alternate between waterholes linked by straight paths, male lions' movements possibly reflect female movements. By specifically marking waterholes rather than patrolling around territorial borders, male lions could therefore prevent the intrusion of rivals directly where females spend most of their time (Dejeante et al., 2024), potentially helping females to compete against other prides [such as suggested by results from Mosser and Packer (2009)]. Besides, the long-distance vocalizations of lions (up to 8 km in the Serengeti ecosystem; Packer 2023) may also allow them to signal their presence in a radius large enough to cover the unvisited areas between waterholes, similarly to wolves scent-marking elevated locations to facilitate wind dispersal of odours (Peters & Mech, 1975). In another ecosystem, Wijers et al., (2021) showed that lions vocalize as frequently in the core as in the periphery of their territory, and that they are more likely to repeatedly roar once close to waterholes. Territorial animals using long-distance marking signals at multiple central places could reinforce the renewal of territorial cues at some key places and passively indicate their presence over a large area. Doing so, territorial animals should reduce the cost of patrolling, relative to moving along the border of their territory, since (1) lions reach more quickly unmarked key places and (2) long-distance marking signals allow them to cover the unvisited places between multiple central places.

If specifically marking some key places of their territories provides several benefits to territorial animals (i.e., reduced travel costs, increased renewal of territorial cues at key places, coverage of unvisited areas through long-distance cues), then why do not territorial animals always defend multiple central-place territories? A first key condition for the emergence of multiple central-place territories is that territorial animals live in landscapes where resources are spatio-temporally heterogeneous in their availability, which leads them to regularly return to patchily distributed feeding sites (Macdonald & Johnson, 2015). Lions in Hwange National Park live in a highly heterogeneous landscape with spatially-stable patches of resources (i.e., prey aggregated around waterholes) that is evidently not representative of the diversity of ecosystems territorial animals live in. However, in other ecosystems, resources may be found in stable, heterogeneously distributed patches. For example, in Prince Albert National Park (Canada), plains bison (*Bison bison*) move within a mosaic of discrete meadows (Harvey & Fortin, 2013) that could lead grey wolves to maintain multiple central-place territories driven by the distribution of these patches. A second condition to investigate the emergence of multiple central-place territories is likely related to the size of an animal's territory. Here, the rare lions that did not maintain multiple central-place territories had only a small number of waterholes to defend. Additionally, we found a strong correlation between the number of waterholes, the size of lion territories and the straightness of trips between waterholes, suggesting a gradient between lions' territorial strategies: lions defending larger territories may need to move more rapidly in straighter goal-oriented movements to efficiently mark their whole territory. Because the size of lion territories is inversely related to the density of waterholes and to the prey biomass (Loveridge et al., 2009), our results suggest that multiple central-place territories are more likely to emerge when territorial animals live in landscape where resources are rare. Interestingly, multiple central-place territories were described in wild young-of-the-year Atlantic salmon (*Salmo salar*) (Steingrímsson & Grant, 2008, 2011a, 2011b), making it clear that multiple central-place territories are not restricted to our study system. Therefore, investigating whether territorial animals from other ecosystems similarly defend multiple central-place territories, and the environmental conditions under which such territories emerge, is appealing. Generally, it should allow ecologists to gain new insights on how the spatial distribution of resources shapes space use in territorial animals.

DATA AVAILABILITY STATEMENT

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

DECLARATION OF INTEREST

The authors declare that they have no conflict of interest.

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TABLE

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

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

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

FIGURE LEGENDS

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

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

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

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

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

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

FIGURES

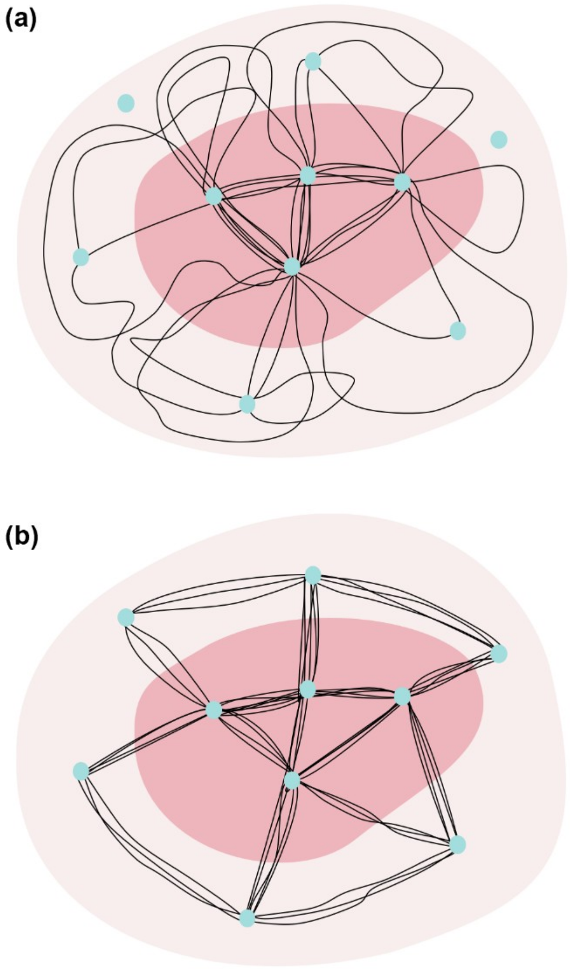


Figure 1

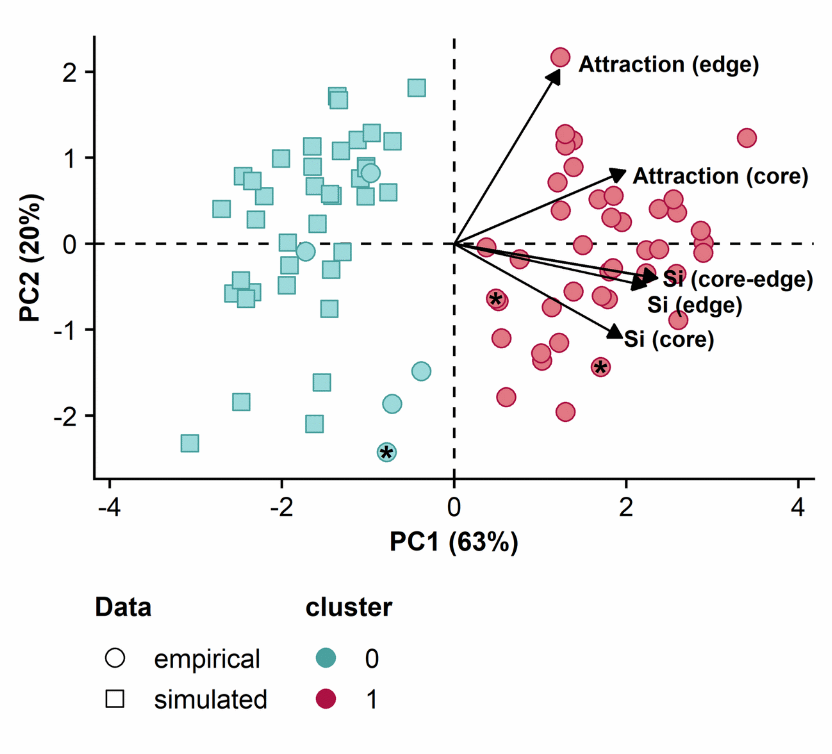

Attraction (edge)
Attraction (core)
Si (core-edge)
Si (edge)
Si (core)
2
1
0
-1
-2
PC2 (20%)
-4
-2
0
2
4
PC1 (63%)
*
Data
○ empirical
□ simulated
cluster
● 0
● 1

Figure 2

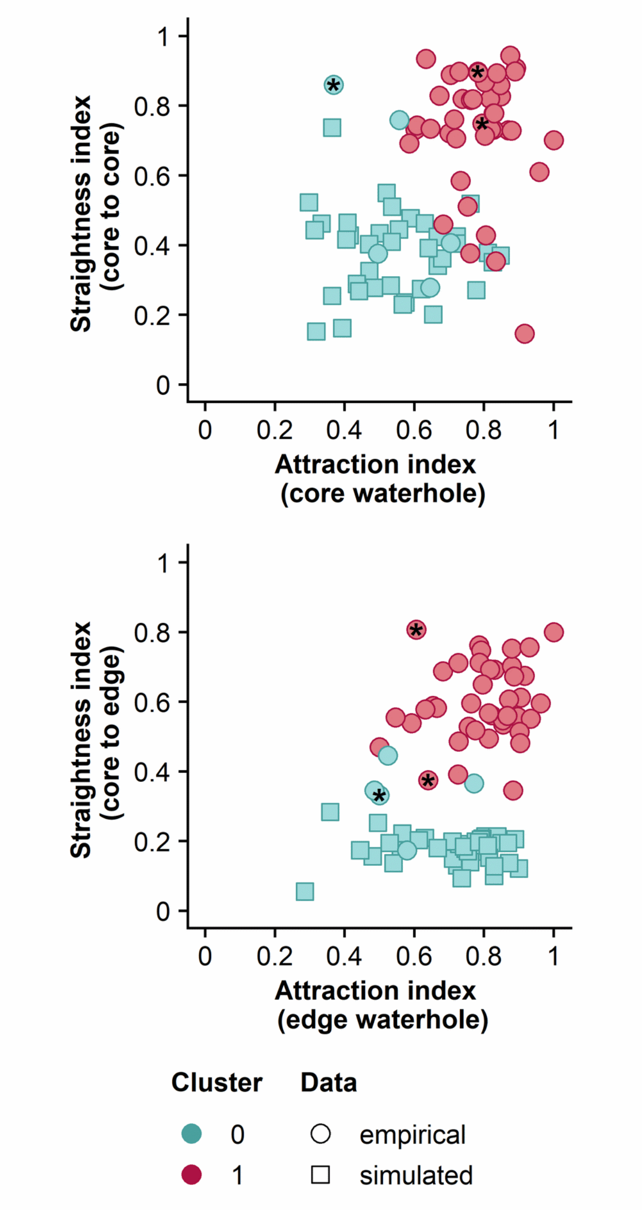

Straightness index
(core to core)
Attraction index
(core waterhole)
0
0.2
0.4
0.6
0.8
1
Straightness index
(core to edge)
Attraction index
(edge waterhole)
Cluster
0
1
Data
empirical
simulated

Figure 3

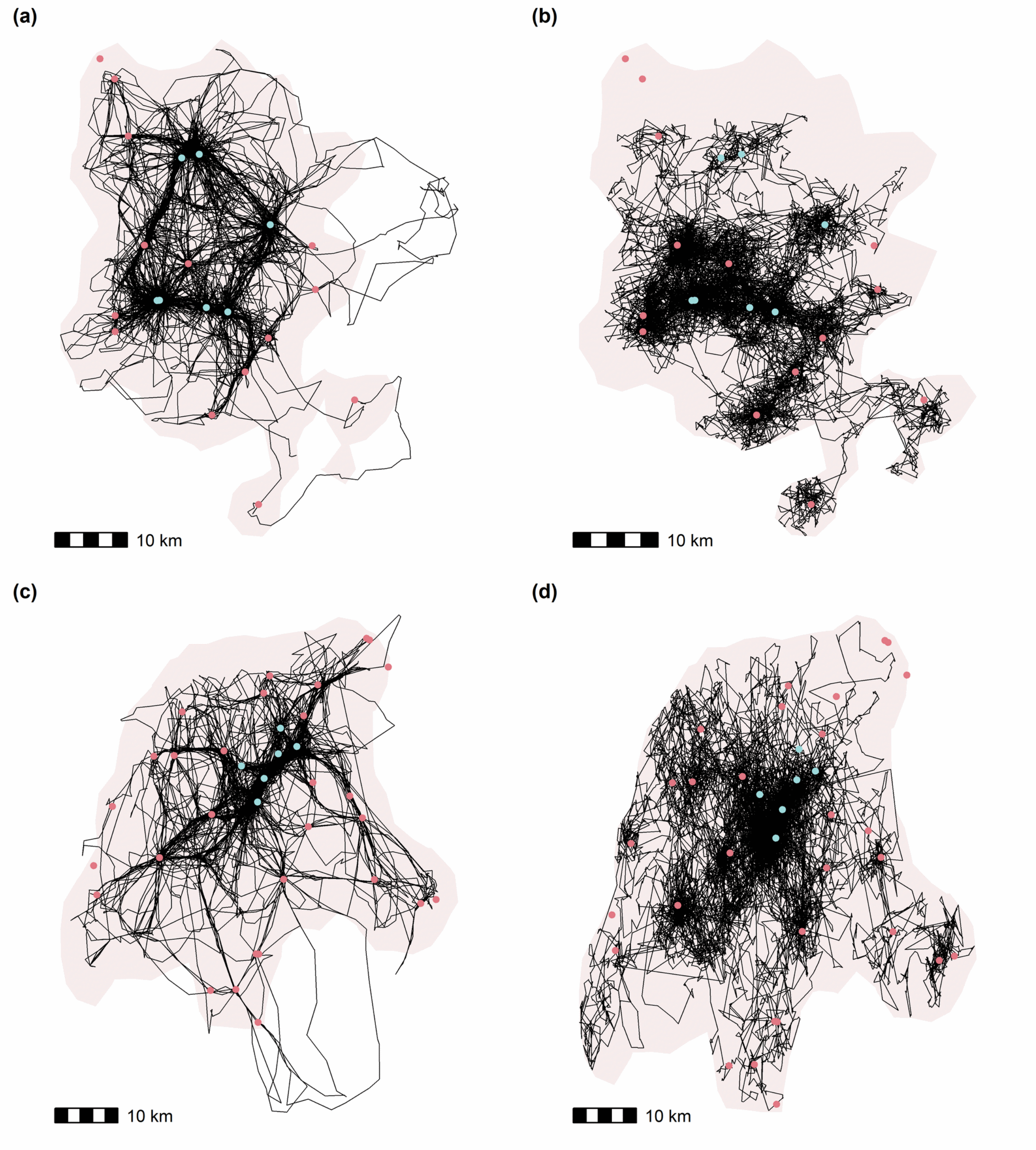
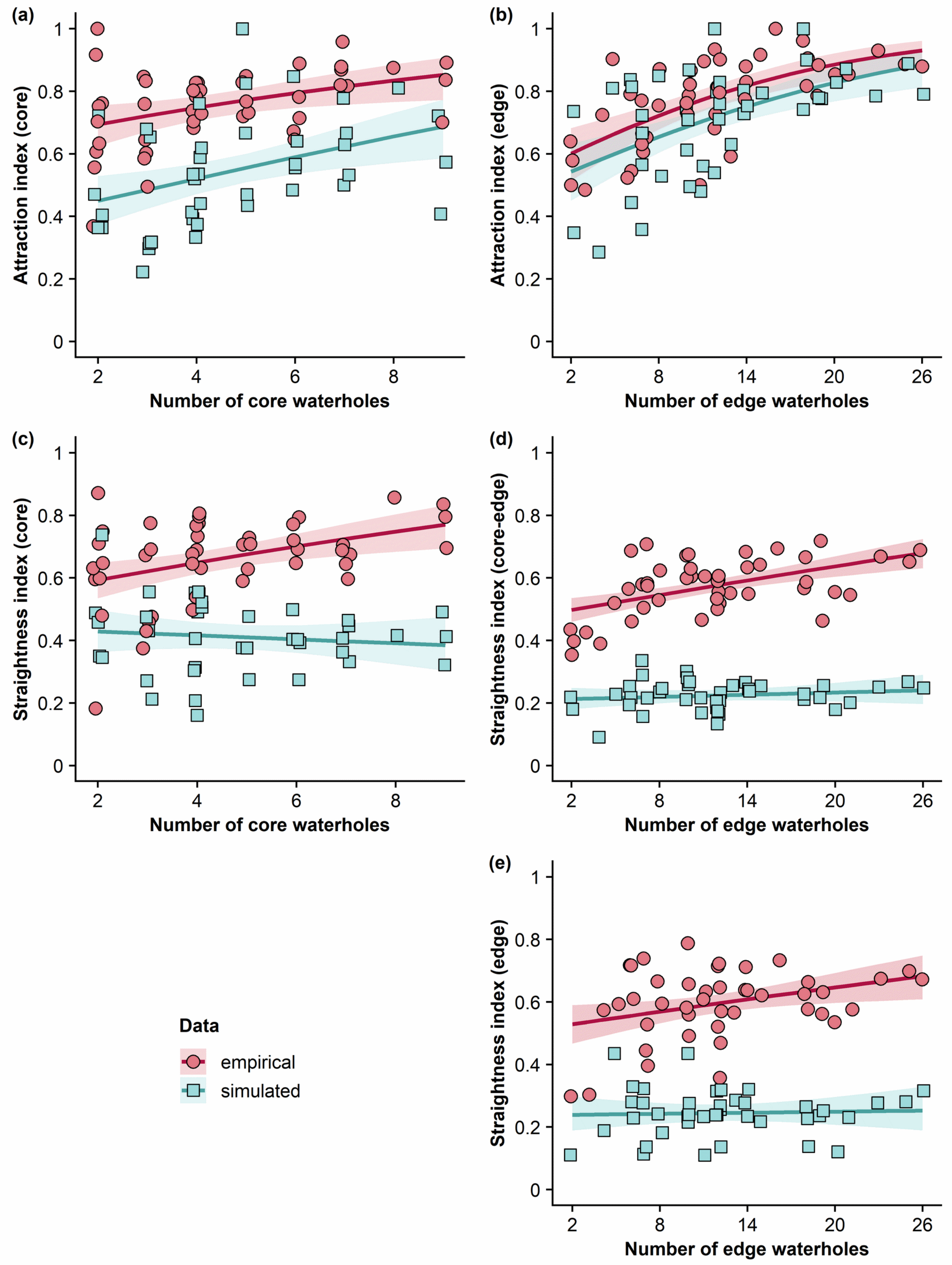


Figure 4


(a)
Attraction index (core)
Number of core waterholes
(b)
Attraction index (edge)
Number of edge waterholes
(c)
Straightness index (core)
Number of core waterholes
(d)
Straightness index (core-edge)
Number of edge waterholes
(e)
Straightness index (edge)
Number of edge waterholes
1
0.8
0.6
0.4
0.2
0
2
4
6
8
8
14
20
26
Data
empirical
simulated

689