



Influence of seasonality on lion movement in the Greater Zakouma Ecosystem, Chad

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Abstract

Lions are threatened, especially in West and Central Africa, with conflict as key factor, especially outside core protected areas. Using GPS satellite collars, we studied the movement of 15 lions in Chad's Greater Zakouma Ecosystem (GZE), and specifically its core area Zakouma National Park. We analysed their home range and core range sizes, and compared movement patterns during the wet and dry seasons, between 2020 and 2023. In the dry season, lions in the eastern part of Zakouma National Park mainly ranged within the boundaries of the park, where wild prey concentrated around remaining waterholes. In the wet season lions shifted their home ranges to areas outside the park, resulting in very large total home range sizes. Outside the park, lions exhibited increased nocturnal activity and travelled over considerably greater distances, however this strategy did not prevent human-lion conflict. We conclude that lions in the GZE regularly use areas outside the national park, suggesting that conservation efforts within the park alone are insufficient for the species' conservation. Mitigating conflicts in surrounding community areas is crucial to prevent a population decline and ensure landscape connectivity.

Keywords *Panthera leo* · Home range · Activity pattern · Satellite tracking · Land use · Protected area

Introduction

With fewer than 25,000 lions (*Panthera leo*) remaining in Africa, the species is listed as Vulnerable on the IUCN Red list, and regionally as Critically Endangered in West Africa

and Regionally Endangered in Central Africa (Nicholson et al. 2023). Lions currently occupy approximately 7.4% of their historical range, with a 36% range decline over the last two decades (Nicholson et al. 2023) and with an estimated 38% of their range falling outside Protected Areas (PA) (Bauer et al. 2018). PAs are particularly important for wildlife conservation, especially for large species posing a threat to people. Outside PAs lions are more affected by threats such as human-lion conflict, prey depletion and habitat loss (Bauer et al. 2022). Lion strongholds all have a PA in their core (Riggio et al. 2013), and effective management of PAs is an important factor in lion survival (Bauer et al. 2015).

When conflict is not managed on the outskirts of PAs, it can negatively impact populations within, and in extreme cases also lead to extinctions by setting an 'ecological trap' (Woodroffe and Ginsberg 1998; Van Der Meer et al. 2013). This is a phenomenon where perceptible cues like prey or water attract animals to an area where their survival is low, often due to anthropogenic factors (Schlaepfer et al. 2002; Battin 2004). An example is when lions are attracted to livestock in an area where they are at risk of retaliatory killing.

In order to avoid human encounters in human-dominated areas, species adjust their spatio-temporal use of the

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landscape (Oriol-Cotterill et al. 2015). Many carnivores adapt by becoming more nocturnal and this has been noted in leopards *Panthera pardus* (Odden et al. 2014), grey wolves *Canis lupus* (Smith et al. 2024; Sunde et al. 2024), pumas *Puma concolor* (Abernathy et al. 2023), black bears *Ursus arctos* (Procko et al. 2023) and lions (Jansson et al. 2024). A shift to more nocturnal activity is often not enough to avoid conflict with humans. Well managed mitigation and compensation schemes can be effective in preventing retaliatory lion killings and promoting carnivore conservation and coexistence outside PAs (Hazzah et al. 2014; Sibanda et al. 2021). Such programs involve community members in lion conservation and in mitigating livestock predation and have proven to reduce lion killings within the communities involved (Hazzah et al. 2014; Dolrenry et al. 2016). Identifying critical habitats, corridors, sink areas and conflict hotspots is critical for directing effective conservation efforts, especially where PAs are not fenced and wildlife is free to move between protected and human dominated areas. For example, lion space use was analysed in the Kavango-Zambezi Transfrontier Conservation Area (KAZA) and surrounding landscapes, ranking the relative importance of dispersal areas, corridors and conflict areas to identify areas for priority conservation actions (Cushman et al. 2018).

A home range (HR) is the area where an animal finds the necessary resources to carry out its natural activities of feeding, mating and rearing its young (Burt 1943). Generally, home range size decreases when prey biomass increases (Van Orsdol et al. 1985; Loveridge et al. 2009). For females, pride size is also a driver of home range size, while for males an important driver is access to females (Loveridge et al. 2009). These differences generally causes males to have larger home ranges than females (Tumenta et al. 2013), but not always (Zehnder et al. 2018).

In regions with marked wet and dry seasons, seasonal changes in lion home ranges have been observed (Bauer and de Iongh 2005), as water drives prey dispersion and predictability, thus influencing lion ranging behaviour (Loveridge et al. 2009). In other areas, home range size does not vary seasonally (Van Orsdol et al. 1985), although lions may be more dispersed in their range during periods of food shortage (Schaller 1972). Lions in Hwange National Park (NP), Zimbabwe, respond to changes in food abundance on an annual timescale, and home ranges were smaller when annual rainfall was lower, determined by dispersion of prey in the environment rather than just abundance of prey (Loveridge et al. 2009). Tarangire NP in Tanzania retains water throughout the year thanks to the presence of the perennial Tarangire river, and serves as refuge to wildlife in the dry season when water is scarce, while in the wet season grass and water are widely available and prey species are more widely distributed, including in the surrounding community

areas (Laizer et al. 2014). Lions there had smaller home ranges inside park boundaries in the dry season, while in the wet season they had larger home ranges and used the area outside the PA more (Laizer et al. 2014). A similar pattern has been observed in Waza NP in Cameroon (Tumenta et al. 2013) and is suspected in Zakouma NP in Chad.

Zakouma NP and the surrounding community land is considered one of the most important PAs in Central Africa (Scholte et al. 2022). It host 15% of the known extant Northern lions and is the second largest population after the W-Arly-Pendjari Complex (Benin, Burkina Faso, Niger) (Funston et al. 2023), but the ranges of these lions and the connectivity with other PAs is still little understood. Satellite collars were first used in Zakouma NP in 2013 on three female and one male lion (Olléová and Dogringar 2013). Unfortunately, only two collars (1 female; 1 male) were operational for a full year, recording a female home range of 135 km² and a male home range of 978 km² (African Parks, unpublished data) and the data collected was insufficient to extrapolate seasonal patterns.

Here we report the results of a more extensive collaring program in Zakouma NP, aimed at monitoring lion movements as part of a conflict mitigation strategy. We investigated the influence of seasonality on lion home range and inter range habitat use. We tested the following sets of hypothesis: (1) lions respond to seasonal changes, including changes in prey abundance (Fraticelli et al. 2024), by increasing their home range; (2) male and female lions differ in their home range response to seasonality, including both in changes of home range use and overlap of used range; (3) lions are more nocturnal when in a human-dominated landscape. Finally, we also investigated the relative use of the PA across seasons. We expected lions to have significantly larger ranges in the wet season, extending beyond Zakouma NP boundaries, where we expected them to shift to more nocturnal behaviour to reduce encounters with humans.

Materials and methods

Study area

The GZE, located in the Sudano-Sahelian ecosystem in south east Chad, is a mosaic of PAs with different degrees of protection. The core PA of the GZE is Zakouma NP, a 3,054 km² PA created in 1963. Since 2010, Zakouma NP has been managed, in partnership with the Chadian government by African Parks, an organisation engaged in the long-term delegated management of PAs in multiple African countries (African Parks 2023). Zakouma NP is surrounded by the Bahr Salamat Faunal Reserve, designated in 1964. Siniaka-Minia Wildlife Reserve is a second core PA of the GZE;

established in 1965, it was upgraded to National Park in 2024 (African Parks 2023). North of Siniaka Minia NP is the Melfi-Roukoum hunting domain, a privately managed hunting concession. In 2017 African Parks' mandate was extended to the full GZE. Human settlements are present throughout the GZE with the exception of the core PAs of Zakouma NP and Siniaka Minia NP, but can be found in the immediate vicinity of these parks. Human presence in the GZE includes both permanent settlements with livestock and agriculture, and seasonal nomadic herders with large herds of cattle and camels.

No area of the GZE is fenced, and wildlife roams across borders. Wildlife in the GZE includes lion, leopard, spotted hyaena (*Crocuta crocuta*), elephant (*Loxodonta africana*), buffalo (*Syncerus caffer*), giraffe (*Giraffa camelopardalis*), roan antelope (*Hippotragus equinus*), hartebeest (*Alcelaphus buselaphus*), tiang (*Damaliscus lunatus*), waterbuck (*Kobus ellipsiprymnus*) and olive baboon (*Papio anubis*), as well as a range of smaller herbivores and carnivores.

Rainfall is focused in the months between May and October, but the first rains usually fall as early as April (Clark et al. 2023). The morphology of the territory and several large seasonal rivers flowing into Zakouma NP from the periphery, cause the flooding of large part of the park, especially the eastern side. The rainy season is followed by a cold dry season (average temperatures 27 °C, range 13–42 °C) until February and a hot dry season (average temperatures 33 °C, range 19–45 °C), when surface water is only present in a few permanent pans in the east. As a result, the eastern half of Zakouma NP has the highest wildlife densities in the dry season; this area is most intensively managed and has most infrastructure. Throughout this paper, we use the term dry season for January–June and wet season for July–December; this corresponds with available surface water, which remains after the rains end.

Data collection

Between February 2020 and December 2023, satellite GPS collars were deployed on 15 lions (9 females; 6 males) in Zakouma NP (Government of Chad collaring permits: N°100/MEEP/DG/DGTRFFP/DCFAP/2019 and N°107/PCMT/PMT/MEPDD/SG/DGRFFP/DFAP/2022). The lions were selected from different prides with home ranges near park boundary. Starting in 2020, each lion encountered in Zakouma NP was identified by its unique features (Pennyquick and Rudnai 1970) and assigned a unique code, thus the codes of the collared lions are not always sequential, but they all start with LM for males and LF for females.

Lions were chemically immobilized by qualified personnel with combination of Zoletil (100 mg for males and 80 mg for females) and Medetomidine (6/8 mg for males

and 4/5 mg for females) deployed with a Dan-Inject gas powered dart gun. Once immobilized, lions were fitted with satellite GPS collars (African Wildlife Tracking, Pretoria, South Africa; Followit Tellus, Lindesberg, Sweden). All operations followed African Parks' Standard Operating Procedures for Animal Handling and Care (African Parks 2020). Over the course of the four years, two lions were collared three times, six lions were collared two times, and seven lions were collared once.

In 2020 collars were set to record and send a GPS location every 4 h. From 2021 this was changed and collars were set to send a GPS location every 2 h, with occasional changes to 4 h intervals for logistical reasons. When collars were retrieved, the additional data points that were recorded but not sent due to missed connection to satellites or other errors were downloaded directly from the collars and integrated into the dataset.

Data analysis

The GPS data downloaded via the web-based platforms of the respective collar manufacturers (www.tracker.africawildlifetracking.com for African Wildlife Tracking; <https://wildlifegeo.followit.se/> for Followit). Data were subsequently cleaned from invalid coordinates and merged in a single dataset. Data were filtered to exclude all points taken less than 2 h apart, but with a 5 min buffer to compensate eventual delays in connecting to the satellites.

For each individual we calculated the overall and the monthly (based on calendar months) 100% minimum convex polygon (MCP), home range (HR; 95% kernel density estimate - KDE) and core range (CR; 50% KDE) with reference smoothing factor href using the package adehabitatHR (Calenge 2006) in R (R Core Team 2024). For analyses based on monthly data we only included months with locations recorded in at least 27 days to ensure comparability between months. Monthly home range size was log-transformed to achieve a normal distribution of the data. We compared male and female total range size and seasonal range size using t-tests. When analysing range overlap between wet and dry season, we removed the first and last month of each season to avoid including the data from the transition periods, so that the dry season goes from February to May and wet season from August to November. Time spent inside or outside of the park was calculated as percentage of GPS fixes inside or outside per lion per month. We compared male and female range size and wet season and dry season range size using Mann-Whitney U test.

For analyses based on distance moved we used package adehabitatLT (Calenge 2006) to calculate the metric distance between GPS points logged 2 h apart. If a GPS fix was not recorded and thus the temporal distance was > 2 h

apart, this distance was excluded from the analysis. To create a smoother activity curve and render data comparable, we calculated the movement rate per hour by dividing each distance record (meters) in two and assigning them to each of the two hours during which the movement was recorded (Lashley et al. 2018; Wolfson et al. 2023).

We log transformed the movement rate data to achieve a normal distribution, then we used an ANOVA to analyse how the distance moved by lions was related to sex, time of day (day/night) and location (inside/outside the park). To analyse effect of location we only considered females as we didn't have a large enough sample size for males and we analysed data from the wet season (July to December). Six females were included in this analysis, as the data recorded by the other three females did not cover a complete wet season.

Results

Home range

We collared 15 lions in Zakouma NP, including 13 lions in the east (9 females and 4 males) and two males in the west (LM106 and LM117) of the park (Fig. 1 for females; Fig. 2 for males). Duration of tracking for each lion was variable and ranged from 33 days to 1330 days (637 ± 448 days). Four of the 15 collared lions died during the study. These included two lions (LM03 male, LF04 female) which died of natural causes within the national park, and two lions which died outside of the national park. Of the latter, the collar of female LF61 was found cut and buried 7.5 km north of Zakouma NP, the body was never found; male LM117 was poached and found buried less than 1 km north of the park boundary.

There was evidence for size difference between both HR and CR size between males and females (Table 1), both when analysing the overall (females=5, males=5; excluding lions that do not have at least 3 months in each the dry

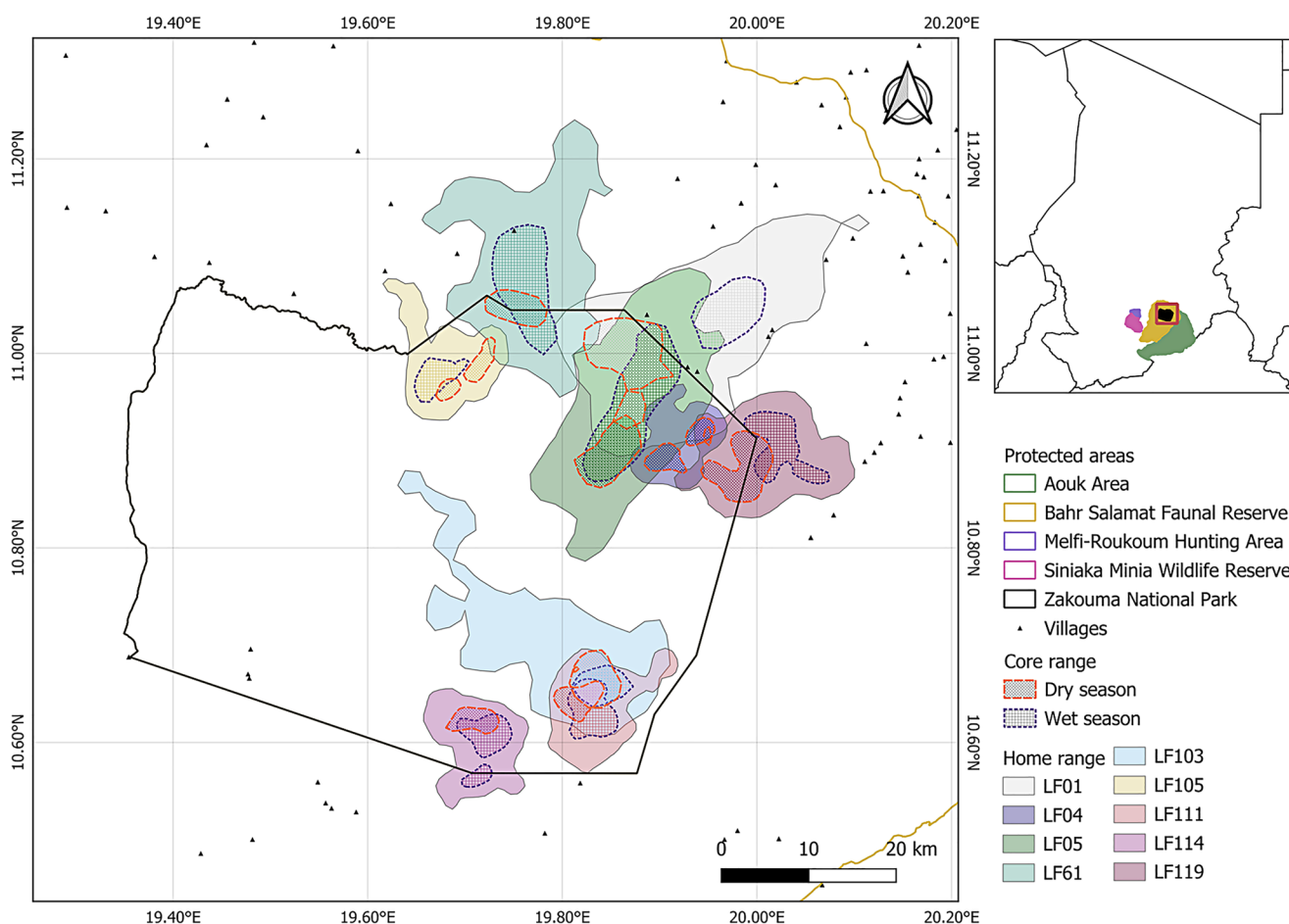


Fig. 1 Total home range of female lions in the Greater Zakouma Eco-system (Chad) calculated as 95% KDE (kernel density estimate), with dry season (orange border) and wet season (blue border) core range

calculated as 50% KDE, showing the size of the home range and the shift in space use between the dry and wet season

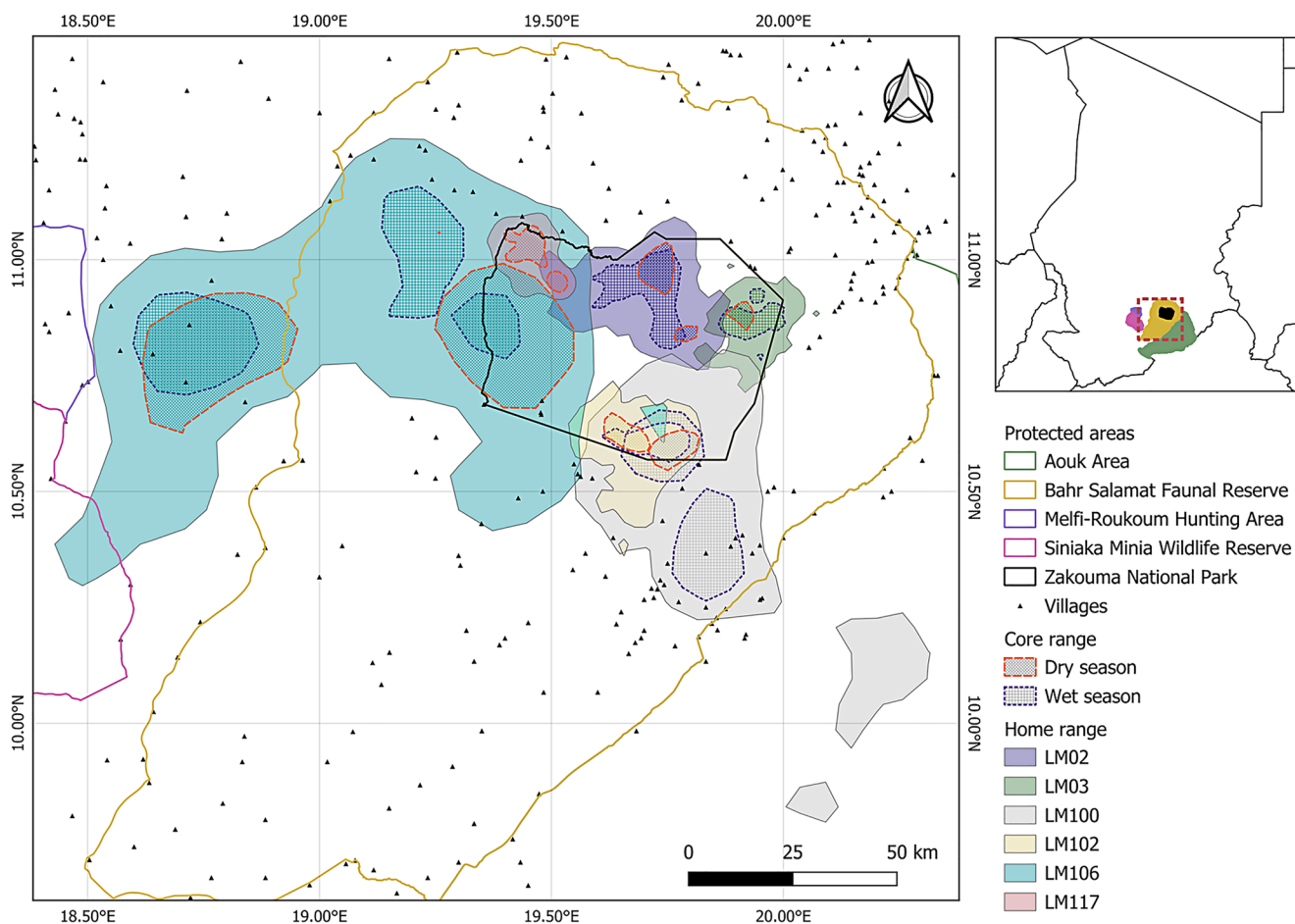


Fig. 2 Total home range of male lions in the Greater Zakouma Ecosystem (Chad), calculated as 95% KDE (kernel density estimate), with dry season (orange border) and wet season (blue border) core range

calculated as 50% KDE, showing the size of the home range and the shift in territory between the dry and wet season

Table 1 Summary of home and core ranges as 100% MCP (minimum convex polygon), 95% KDE (kernel density estimate) and 50% KDE for male and female lions in the greater Zakouma ecosystem (Chad), considering all data, dry season only (January - June) and wet season only (July - December). For males we report the cumulative ranges, but also separate between East and West of Zakouma National park, in the West we colored two lions but only report data for one as the second one was collared for only a month. Females were only collared in the East of Zakouma National park

	Sex	All data Mean±SD (km ²)	Mean monthly All Mean±SD (km ²)	Mean monthly Dry season Mean±SD (km ²)	Mean monthly Wet season Mean±SD (km ²)
Home range 100% MCP	Females (n=9)	370±267	79±62	87±68	74±57
	Males (n=5)	3306±3590	374±450	342±581	403±287
	Males east (n=4)	2596±2433	282±217	211±165	349±240
	Male west (n=1)	9232	1085±927	1672±1320	743±330
Home range 95% KDE	Females (n=9)	226±141	111±100	113±101	110±100
	Males (n=5)	1964±2524	586±953	541±1276	627±521
	Males east (n=4)	1179±1062	401±380	262±247	533±434
	Male west (n=1)	6780	2007±2169	3373±3145	1210±650
Core range 50% KDE	Females (n=9)	43±30	27±26	25±23	28±28
	Males (n=5)	347±508	139±243	127±326	149±130
	Males east (n=4)	158±106	94±98	57±60	129±114
	Male west (n=1)	1369	484±563	839±821	277±157

Fig. 3 Monthly core range (50% Kernel Density Estimate) and home range (95% KDE) size differences in dry season (January - June) and wet season (July - December) for lions in the Greater Zakouma Ecosystem (Chad), separating females ($n=9$), males in the east of Zakouma National Park ($n=4$) and male in the west of Zakouma National Park ($n=1$, LM117 excluded). Note that the y-scale is different between the three graphs

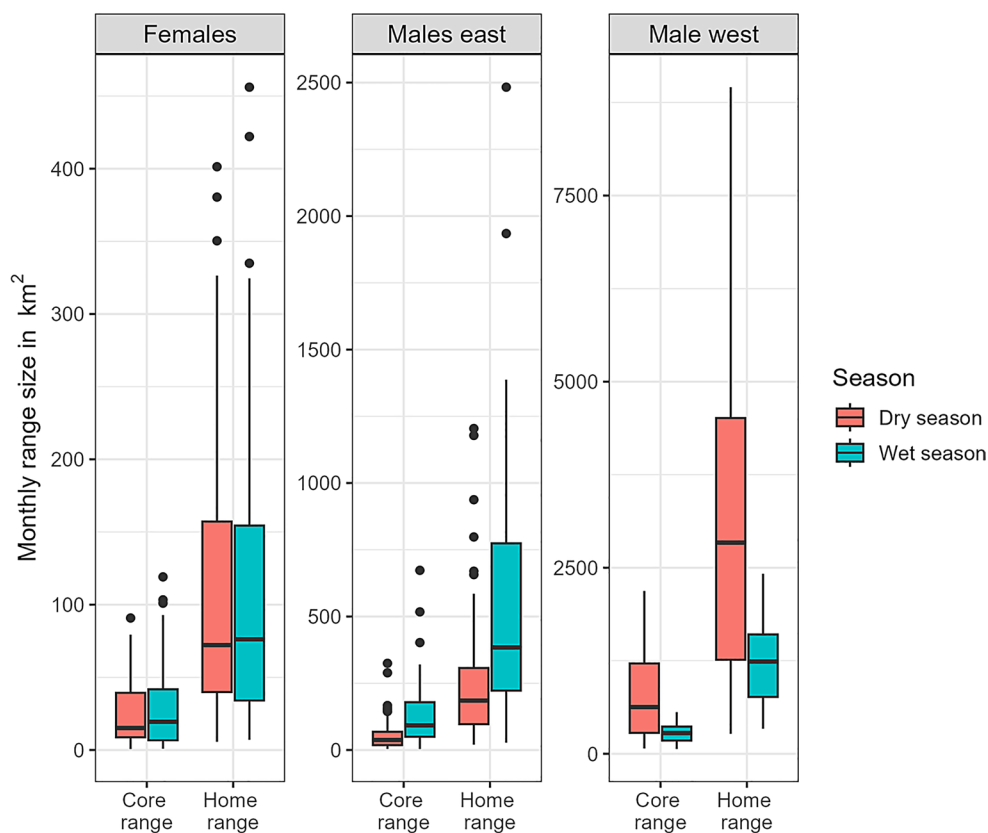
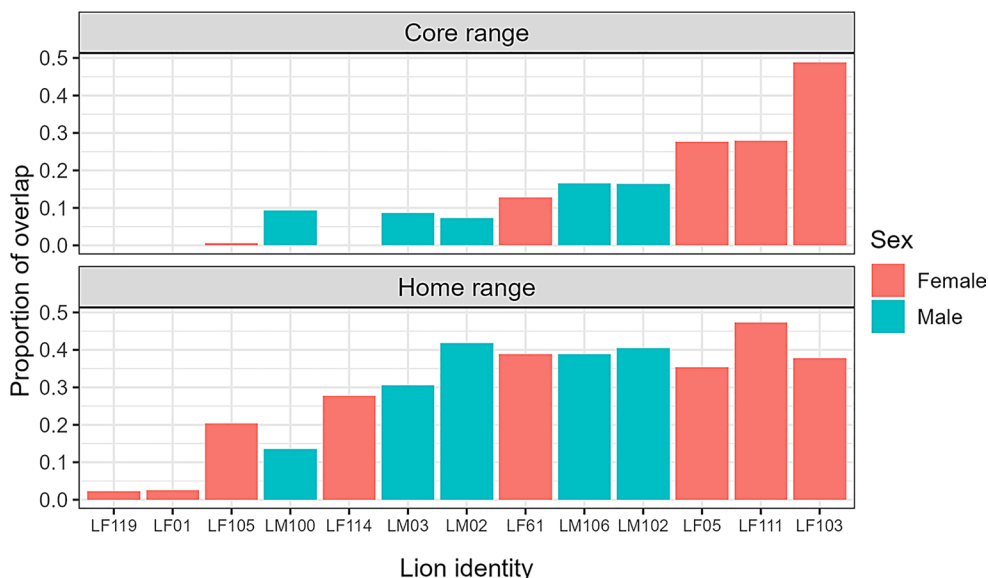


Fig. 4 Proportion of overlap between each lion's dry season (February - May) and wet season (August - November) core range (50% Kernel Density Estimate; top) and home range (95% KDE; bottom) in the Greater Zakouma Ecosystem (Chad), with females in red and males in blue. Ordered by smaller to larger proportion of overlap



and wet season) HR ($t = -2.75$, $df=5.87$, $p=0.034$) and CR ($t = -2.48$, $df=6.21$, $p=0.046$) and when comparing mean monthly (females=9, males=5) HR ($t = -12.42$, $df=295.04$, $p<0.001$) or CR ($t = -11.12$, $df=291.17$, $p<0.001$).

There was no evidence for a size difference between dry season and wet season HR or CR size for females or for the male in the west, but values were significantly higher in

the dry season for males in the east (Fig. 3; HR: $t = -5.50$, $df=140.26$, $p<0.001$; CR: $t = -5.81$, $df=141.81$, $p<0.001$).

Range overlap

HR overlap between dry season and wet season range was $29\% \pm 15\%$ (range: 2–47%; Fig. 4) with no significant difference between males and females ($t = -1.18$,

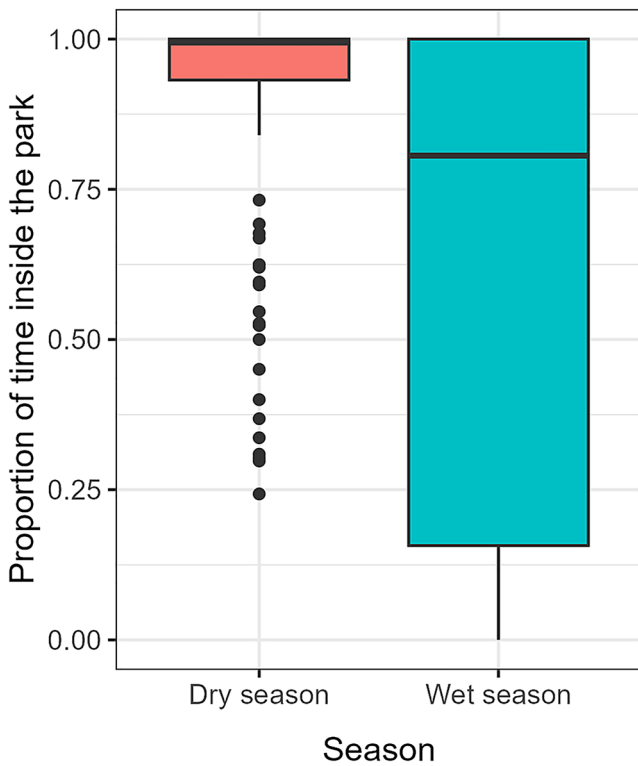


Fig. 5 Proportion of time each month spent inside Zakouma National Park during the dry season (January - June) and wet season (July - December) for lions, excluding LM106

$df=9.67, p=0.267$). CR overlap between seasons was $9\% \pm 14\%$ (range: 0–49%; Fig. 4) with no significant difference between males and females ($t=0.45, df=8.26, p=0.663$).

Use of protected areas

Lions in the east of Zakouma NP spent most of the dry season inside the park, but spent considerable time outside the park in the wet season (Fig. 5). There was no evidence for a difference in the proportion of time spent inside of the park between males and females ($W=11692, p=0.522$) but there is very strong evidence for difference in the amount of time spent inside of the park during the wet and dry seasons ($W=15664, p<0.001$).

Activity patterns

A comparison of average hourly distance moved for males and females in the dry and wet season is shown in Fig. 6. There was a significant difference in distance moved between males and females ($F_1=1177, p<0.001$), as well as significant interaction between time of day and sex ($F_1=6157, p<0.001$), with male lions moving more at night than females. There was no significant difference in the hourly distance moved by males at night in the two seasons while all other pairwise comparisons were significant.

Comparison of the activity patterns in the wet season for six females showed that three individuals (IDs: LF103, LF105, LF111) spent the majority of their time inside the

Fig. 6 Average hourly distance moved (and 95% Confidence Interval) for males (blue) and females (red) in the dry (circles) and wet (triangles) season in the Greater Zakouma Ecosystem (Chad). Vertical lines indicate sunrise and sunset

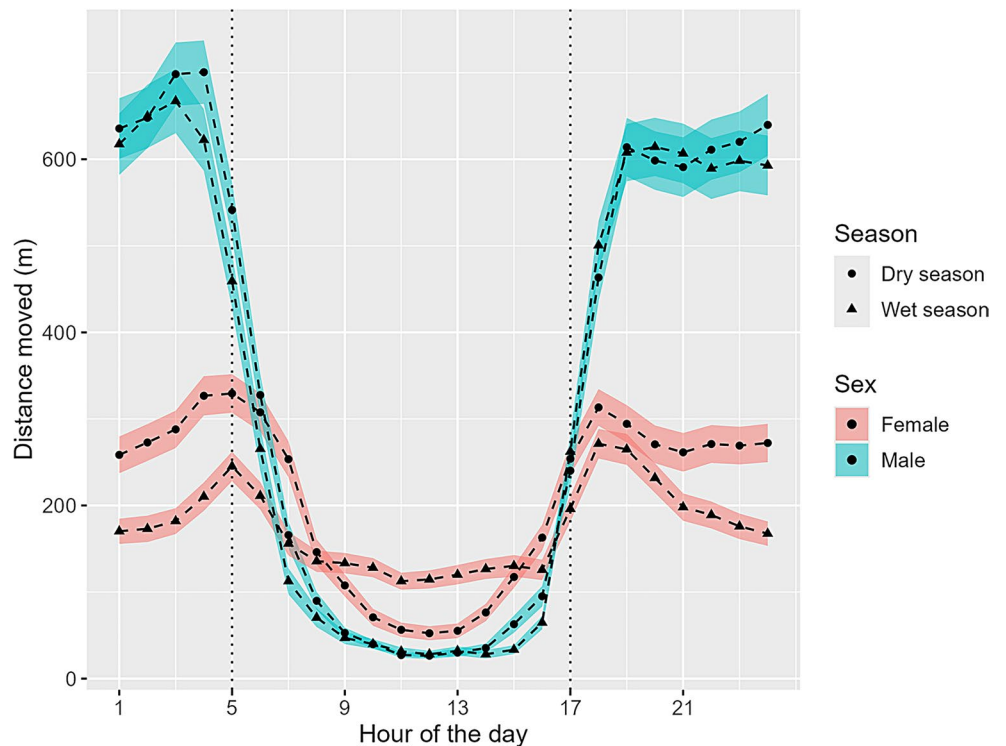
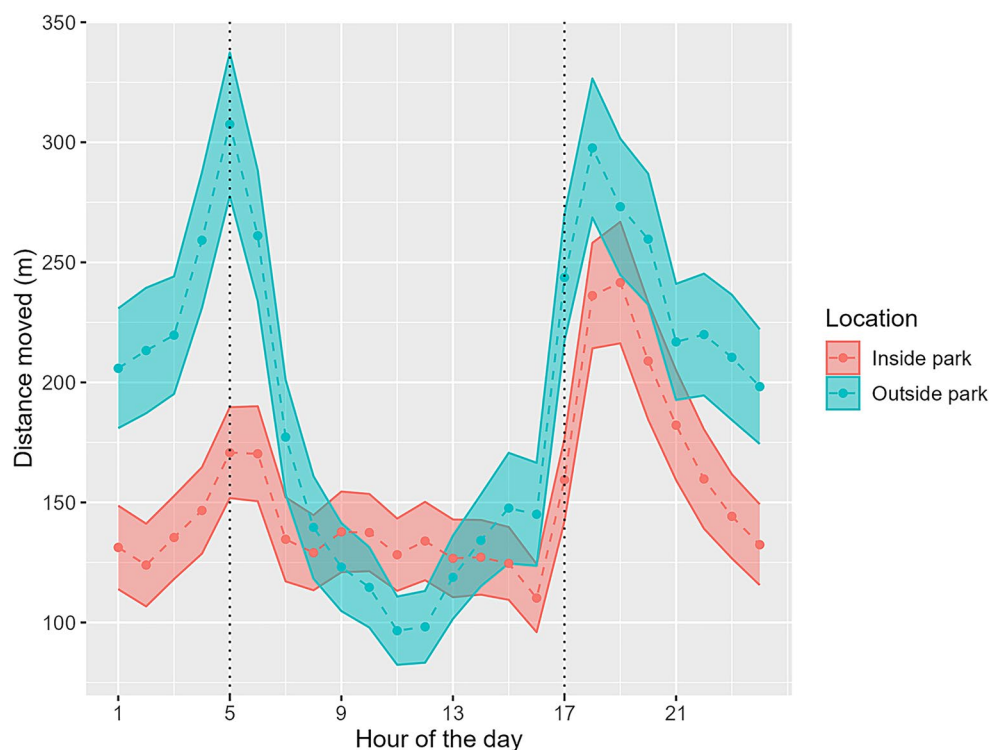


Fig. 7 Average hourly distance moved (and 95% Confidence Interval) by 6 females in the wet season months (July - December) with LF103, LF105 and LF111 who spent more than 80% of the time inside Zakouma National Park considered as Location=Inside park and LF01, LF61 and LF119 who spent more than 80% of the time outside of Zakouma National Park considered as Location=Outside park. Vertical lines indicate sunrise and sunset



park while other three females (IDs: LF01, LF61, LF119) spent most of their time outside of the park. We found independent significant effects of time of day ($F_1=148.26$, $p<0.001$) and location ($F_1=164.85$, $p<0.001$), which showed that in the wet season all lions moved significantly more at night than during the day, and that lions outside of the park moved significantly longer distances daily compared to lions inside of the park. The model also reported a significant interaction between time of day and lion location on distance moved ($F_1=94.64$, $p<0.001$), and a Tukey post-hoc test revealed that lions outside the park moved significantly longer distances and mostly during the night, compared to lions inside the park (Fig. 7; Out: night vs. In: day, $p<0.001$; Out: night vs. Out: day, $p<0.001$; Out: night vs. In: night, $p<0.001$).

Discussion

Our results show that lions in Zakouma NP have large home ranges and adapt to seasonal changes in the environment by increasing the size of their range and by shifting to use more the area outside of the NP, with different responses between males and females. Male ranges in particular were comparable to those of lions in drier environments such as Kgalagadi Transfrontier Park or the Kalahari (Botswana), and Etosha NP (Namibia) (Funston 2011; Stander 1991; Zehnder et al. 2018). Two of the male lions showed exceptional ranges, with LM100 in the south east having a home

range of 2739 km² over 33 months and LM106 in the west having a home range of 6780 km² over 19 months (95% KDE) or 9232 km² when calculated as 100% MCP, which is larger than lion home ranges reported in Africa, with the largest to date being 7337 km² (100% MCP) in the Kunene Region (Stander 2006).

The movements of LM106 and LM100 were biologically important, as they showed connectivity between Chad's PAs, with LM106 moving back and forth between Zakouma NP and Siniaka Minia NP, through an area that is an officially zoned wildlife corridor; and LM100 moving between Zakouma NP and the Aouk project area. In both cases the movement was not considered dispersal or exploration, as the lions moved between the different areas more than once.

The large size of the home range of lions of the GZE is plausibly explained by the extreme seasonal changes in the environment that force lions to adjust their ranging behaviour between the wet and dry seasons. The two sides of Zakouma NP significantly differ in terms of water and prey availability in the different seasons (Fraticelli et al. 2024). The eastern side of Zakouma NP is a basin that maintains several pans of permanent water in the dry season, where wildlife gathers, while in the wet season it collects water from the nearby rivers and often floods, thus dispersing wildlife and making extensive areas uninhabitable. The western side does not maintain standing water in the dry season leading to very low prey densities, whereas it becomes lush dryland in the wet season (Vanherle 2011). These differences in water and prey availability, which are

known to be key drivers of predator distribution and ranging behaviour (Van Orsdol et al. 1985; Loveridge et al. 2009) likely explain differences in lion movements.

During our study, only two lions were located and collared in the west of Zakouma NP, and unfortunately one was tracked for only a month after collaring before it was killed, so it is hard to make inferences. The ranging behaviour of the lion collared in the west differed evidently both in size and in seasonality from the lions in the east, but we can only speculate that this was due to the difference in environment and not the individuality of LM106.

The males residing in the east of Zakouma NP had larger home ranges in the wet season, when prey is less readily available, which is similar to other studies (Loveridge et al. 2009; Tumenta et al. 2013). Lions in Zakouma NP prey mostly on buffalo, waterbuck, giraffe, warthog (*Phacochoerus africanus*) and hartebeest (Fratlicelli et al. 2024). In the dry months, prey is abundant and clustered around water, easy to locate. After the onset of the rains in April and May prey start to disperse. In June/July the migratory antelopes such as hartebeest and tiang, leave the park for their wet season range 30–180 km north of Zakouma NP (African Parks, unpublished data; Poilecot 2006). Giraffes also spent significantly more time outside of the park than inside in the wet season (Clark et al. 2023). Overall, most of the favoured prey species of lions either migrate out of the park, or disperse within the park, thus being less available and making predator-prey encounters less predictable. In November prey species start to come back (African Parks, unpublished data) and receding water means in January the prey is once again abundant and easy to find around water.

Zehnder et al. (2018) found no seasonal variation, but rather temporal variation, in home range size for lions in the Kalahari (Botswana). In Waza NP, home range size increased by almost 60% between 2000 and 2010, probably due to prey declines (Tumenta et al. 2013). In Zakouma NP, despite a 58% increase in prey biomass, there did not seem to be any difference in lion range size between the results of the 2013–2014 (Olléová and Dogringar 2013) study and the current study, although sample size is too small to be conclusive.

While females do not adjust to the wet season conditions by increasing their range, both females and males shift between a dry season range and a wet season range. All lions showed <50% overlap between their home range and core ranges in the two seasons, and LF01 and LF119 completely shifted their wet season range from their dry season range (0% core range overlap, 3% and 2% home range overlap, respectively) with their wet season range fully outside Zakouma NP. Interestingly, this cannot be caused by the inaccessibility of the dry season range due to the floods, as this area is used by other lions during the wet season.

Both males and females spent significantly more time outside of the national park in the wet season compared to the dry season, with no significant differences between sexes. Only three lions out of 15 in this study did not spend time outside of the national park, but one of these was tracked for less than two months. In Waza NP, two out of three collared females shifted their core range outside of the PA during the wet season (Bauer and de Jongh 2005), and in Tarangire NP lions also spent much of their time outside park boundaries in the wet season (Laizer et al. 2014). Similar ranging behaviour was observed in Nairobi NP, where male lions had larger home ranges and travelled longer distances than females (Lesilau et al. 2021). There, both males and females roamed outside of the PA more often and for longer duration during the wet season compared to the dry season, and mostly at night, when human activity was lower (Lesilau et al. 2021). Comparing the activity patterns of female lions outside and inside of Zakouma NP in the wet season revealed that lions outside of the park moved significantly longer distances and mostly during the night.

In many cases though, a shift from diurnal to nocturnal activity is not enough though to avoid conflict with humans, with direct poaching for body parts, poaching bycatch and preventive or retaliatory killing tied to livestock depredation as potential threats encountered in the human-dominated landscape (Bauer et al. 2022). In Zakouma NP lions moved out of the park in the wet season, and anecdotal evidence suggests conflict is indeed a major issue and further work on this topic is forthcoming (African Parks, unpublished data). During our study two collared lions were killed outside of the park, and after the end of this study LM106 was poisoned and died in the corridor between Zakouma NP and Siniaka Minia NP in March 2024 (Zayed A. A., personal communication). This illustrates the risks that lions face outside of well-managed PAs, especially in Central Africa (Aebischer et al. 2020) and the importance of protecting corridors and dispersal areas.

Considering that lions in Zakouma NP are below carrying capacity when considering available prey biomass (Fratlicelli et al. 2024), it is unlikely to be the density of lions inside the PA that push lions to disperse outside (push factor; Loveridge et al. 2007), but rather the area outside of Zakouma NP could be a wet season ecological trap. Conflict mitigation was essential for the lion population to increase and maintain connectivity in Kenya (Dolrenry et al. 2020). With the amount of prey available in Zakouma NP (Fratlicelli et al. 2021) and with conservation actions aimed to restore wild prey in Siniaka Minia NP, the lion population of the GZE has the potential to become a regional stronghold in Central Africa. To allow this to occur, conservation efforts need to be effective across the landscape and covering the

full yearly ranges of lions, and not solely focused on core protected areas.

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Data availability The GPS data that support the findings of this study is available from African Parks upon reasonable request, but restrictions apply due to sensitivity reasons.

Declarations

Ethical approval Collaring operations were authorized by the Government of Chad (permits: N°100/MEEP/DG/DGTRFFP/DCFAP/2019, N°107/PCMT/PMT/MEPDD/SG/DGRFFP/DFAP/2022). African Parks' Standard Operating Procedures for Animal Handling and Care (African Parks 2020) were followed during all operations.

Conflict of interest The authors have no competing interests to declare that are relevant to the content of this article.

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