Seasonal Dynamics Impact Habitat Preferences and Protected Area Use of the Critically Endangered Kordofan Giraffe (Giraffa camelopardalis antiquorum)

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RESEARCH ARTICLE

Seasonal dynamics impact habitat preferences and protected area use of the critically endangered Kordofan giraffe (*Giraffa camelopardalis antiquorum*)

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Understanding animals' habitat selection and movement behaviours relative to human activities is important for evaluating resource requirements and ensuring effective conservation management. The world's largest remaining population of Kordofan giraffe (*Giraffa camelopardalis antiquorum*) reside in Zakouma National Park, Chad. However, it is unclear whether the park boundaries sufficiently encompass the full range of this population's preferred habitats. We used GPS telemetry data from 17 female giraffe over multiple years to better understand landscape and seasonal factors that influence their home range patterns and habitat preferences at multiple spatial scales. Kordofan giraffe seasonal ranges and core seasonal ranges were larger during the wet season and core utilization distributions had greater overlap with the national park in the dry season. The importance of shifts in seasonal habitat use, attributed to the flooding and drying that occurs within the park, necessitates Kordofan giraffe to move beyond the park's boundaries. Kordofan giraffe selected for open grasslands (mean coefficient = 0.48, 95% CI [0.22,0.74]), and increased their tortuosity of movement in these areas (mean coefficient = –0.18, 95% CI [–0.23,–0.14]). Conversely, with *Vachellia* savannas as the reference level for land-cover variables, the giraffe avoided anthropogenic areas, barren lands, *Combretaceae* savannas and forests. We advise increased community-based co-learning projects and awareness of giraffe outside the park. In addition, by identifying key habitat types that giraffe selected, we advise enhanced monitoring in preferred giraffe habitats during the wet season to protect these areas from being encroached by human settlement or agricultural expansion, with the support of the legal framework of the Bahr Salamat Wildlife Reserve and other agreements that protect wet season wildlife corridors.

Keywords: habitat selection, Kordofan giraffe, integrated step selection.

INTRODUCTION

Habitat selection is the process in which animals aim to satisfy their resource requirements at different ecological scales among a variety of available spatiotemporally dynamic habitat types (Dupke *et al.*, 2017; Johnson, 1980; Van Moorter, Rolandsen, Basille & Gaillard, 2016). This process is well defined as hierarchical, and the behaviour of animals can vary between broad-scale and fine-scale selection (DeCesare *et al.*, 2012; Johnson,

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1980; Senft *et al*., 1987). Large herbivores often show varied patterns of behaviours, affecting their habitat selection at different spatial and temporal scales, including seasonal variation of resource distribution (Dupke *et al*., 2017). In tropical savanna ecosystems, many large-bodied herbivores adapt their food sources seasonally due to the increased need for quantity rather than quality of forage (Abraham, Hempson, Faith & Staver, 2022).

Human-induced landscape fragmentation has caused many wild animals to change their movement in order to gain access to natural resources (Doherty, Fist & Driscoll, 2019). Thus, protected areas play an important role in habitat conservation of many key flora and fauna species by providing intact habitat that is relatively undisturbed by humans. However, these protected areas are continually becoming smaller and more isolated, resulting in increasing biodiversity loss (Clerici *et al*., 2007; Pacifici, Di Marco & Watson, 2020).

Protected areas are predominantly gazetted around dry season resources (*e.g.* water), and often do not account for seasonal variation in resource requirements (Fynn & Bonyongo, 2011). Human–wildlife conflict outside of protected areas is a notable source of mortality for large mammals (Nyhus, 2016) and livestock incursions into protected areas, or wildlife excursions outside protected areas, can lead to potential conflicts with local communities through crop raiding, disease transmission, and livestock loss (Nyhus, 2016; Valls-Fox *et al*., 2018; Woodroffe & Ginsberg, 1998). Additionally, other human activities such as overexploitation, development of linear infrastructure, and habitat loss can also disrupt animal movement and habitat selection (Bolger, Newmark, Morrison & Doak, 2008; Tucker *et al*., 2018). Understanding the effects of anthropogenic activities on animal space use can allow for informed management decisions. Thus, incorporating anthropogenic factors and seasonality as drivers in habitat selection is a crucial step to developing effective conservation and management strategies, which depend on reliable data on habitat selection and use (Dakwa, Cuthill & Harris, 2020; Knüsel, Lee, König & Bond, 2019).

Giraffe (*Giraffa* spp.) are highly mobile, large-bodied browsers that require large quantities of woody vegetation to meet metabolic and reproductive requirements (Pellew, 1984a). They utilize different vegetation types, and the four species of giraffe inhabit diverse ecosystems across Africa (Brown & Bolger, 2020; Pellew, 1984a). These large herbivores are vital to ecosystem function through their role in seed dispersal, structuring open habitats and the stimulation of new forage growth (Miller, 1996; Pellew, 1984b; Strauss, Kilewo, Rentsch & Packer, 2015). Many giraffe populations are declining throughout Africa, and the species are now absent from much of their historical geographic range due to habitat loss, degradation of land, climate change and human pressures through illegal hunting (Brown *et al*., 2021; Fennessy & Marais, 2018). Ensuring sufficient access to resources in increasingly human-dominated landscapes is essential to the viability of key giraffe populations.

Seasonal variation in giraffe movement is likely linked to phenology of vegetation and forage productivity. Giraffe modify their diet by selecting for high quality forage to maintain increased levels of protein and energy, or to maximize efficiency of foraging and movement (Caister, Shields & Gosser, 2003; Pellew, 1984b). Across many populations, giraffe show foraging preference for *Acacia sensu lato* (*i.e. Vachellia* and *Senegalia*) species, although they exhibit flexibility in their feeding ecology through efficient digestive processes (Mandinyenya, Monks, Mundy, Sebata & Chirima, 2019; Pellew, 1984a). The abundance and palatability of *Vachellia* and other preferred forage species vary seasonally (Brown & Bolger, 2020; Milewski & Madden, 2006; Pellew, 1984b). Therefore during the dry season, the feeding ecology of giraffe is highly flexible in order to maintain adequate nutritional uptake, which is thought to have driven their spread across Africa (Berry & Bercovitch, 2017; Milewski & Madden, 2006; Pellew, 1984a,b). Maintaining access to seasonally-varying resources is critical for sustaining populations of giraffe and limiting the impacts of density-dependent population regulation in seasonally variable environments (Brown & Bolger, 2020). In addition to seasonal variation in both the quantity and palatability of forage, changes in accessibility can occur during the wet season causing animals to modify their behaviour and distribution in ways that change food availability, such as moving to areas of higher elevation due to flooding (Gathuku, Chiawo, Warui, Gichuki & Ngare, 2021).

The northern giraffe (*G. camelopardalis*) has an estimated population of fewer than 6000 individuals, and is the least numerous of the four giraffe species (Brown *et al*., 2021; Coimbra, Winter, Mitchell, Fennessy & Janke, 2022; Fennessy *et al*., 2016; Winter, Fennessy & Janke, 2018). The

Kordofan giraffe (*G. c. antiquorum*), a subspecies of the northern giraffe (Brown *et al.*, 2021; Coimbra *et al.*, 2022; Fennessy *et al.*, 2016; Winter *et al.*, 2018), was once widespread across Central Africa, with an estimated population of >13 500 in the 1980s, but now has a small and fragmented distribution across northern Cameroon, Central African Republic, southern Chad, northern Democratic Republic of Congo (DRC) and South Sudan (Brown *et al.*, 2021; D'haen, Fennessy, Stabach & Brandlová, 2019; O'Connor *et al.*, 2019). The current population estimate of 2300 individuals represents a significant decline, resulting in their listing as 'critically endangered' on the IUCN Red List (Brown *et al.*, 2021; Fennessy & Marais, 2018). In central and southern Chad, the Kordofan giraffe once occurred widely but habitat loss and fragmentation, illegal hunting, and drought greatly impacted them, with the largest surviving population located in and around Zakouma National Park (ZNP) (Brown *et al.*, 2021). As such, ZNP is a critical population and priority landscape for their long-term conservation.

Using GPS telemetry and a multi-scale space use analysis, including second-order seasonal home range formation and third-order integrated step selection analysis (iSSA), we evaluated seasonal variation in: (1) broad-scale habitat use within and surrounding ZNP; (2) fine-scale habitat selection and movement of the female giraffe; and (3) potential conflicts with local communities surrounding ZNP. We examined the effects of ecological (habitat type and elevation), anthropogenic (inside or outside the national park) and temporal (wet or dry season) factors on habitat selection and movement.

We predicted that wet season flooding in ZNP results in seasonal variation in giraffe movement and habitat selection, with giraffe selecting for higher elevation and increased use of areas outside the park. We also predicted that giraffe use and select for habitats that are distant to anthropogenic areas such as human habitation and agricultural land. Previous studies identified the importance of human activities, such as poaching and land conversion for agriculture as factors affecting giraffe range and distribution (Knüsel *et al.*, 2019). These conflicts may be reflected in their movement behaviours as they move through these areas. We describe key habitat features that require protection for the giraffe in and around ZNP, and quantify the impacts of humans on their seasonal movements.

MATERIAL AND METHODS

Study area

Zakouma NP is located in southeastern Chad and is the core of the Greater Zakouma Ecosystem (Fig. 1), surrounded by the Bahr Salamat Wildlife Reserve, a lower level protected area according to the IUCN Protected Area Management Categories (Dudley, 2008). Covering an area of more than 3000 km^2 and situated between the Sahara Desert and the rainforest regions of Central Africa, ZNP contains important populations of West and Central African savanna biodiversity, including the country's largest population of African savanna elephant (*Loxodonta africana*) and over two-thirds of the world's remaining Kordofan giraffe (Brown *et al.*, 2021; Granjon *et al.*, 2004). The Sudano-Sahelian climate of the park receives between 800–900 mm of rainfall annually between May and October (wet season) (Appendix 1), resulting in approximately half of the park flooding due to the high water-retention of the soil (Calenge, Maillard, Gaillard, Merlot & Peltier, 2002; Granjon *et al.*, 2004). The flooding results in many areas of the park becoming inaccessible to terrestrial animals (Granjon *et al.*, 2004). The dry season is divided into two periods – cool season (November to January) and hot season (February to April) (Dolmia, Calenge, Maillaird & Planton, 2007). Due to the aforementioned high water-retention of the soil, this study extended the wet season to between May and November, and thus the dry season is categorized as December to April. The park's vegetation varies from the north to the south along a rainfall gradient, with *Vachellia seyal* savannas dominating in the north, *Combretaceae* savannas in the central areas and *Caesalpiniaceae* savannas in the south (Calenge *et al.*, 2002; Poilecot, Saidi & N'Gakoutou, 2009).

Due to strong pressures from illegal hunting in the area, driving species such as the black rhinoceros (*Diceros bicornis*) to local extinction, and the African savanna elephant and the Kordofan giraffe to the edge of local extirpation, the Chadian government declared Zakouma a national park in 1963 (Poilecot, N'Gakokutou & Taloua, 2010). In 2010, the government signed a private–public partnership agreement with African Parks Network (APN) for the long-term rehabilitation and management of ZNP, in partnership with the government and working collaboratively with local communities (African Parks, 2023).

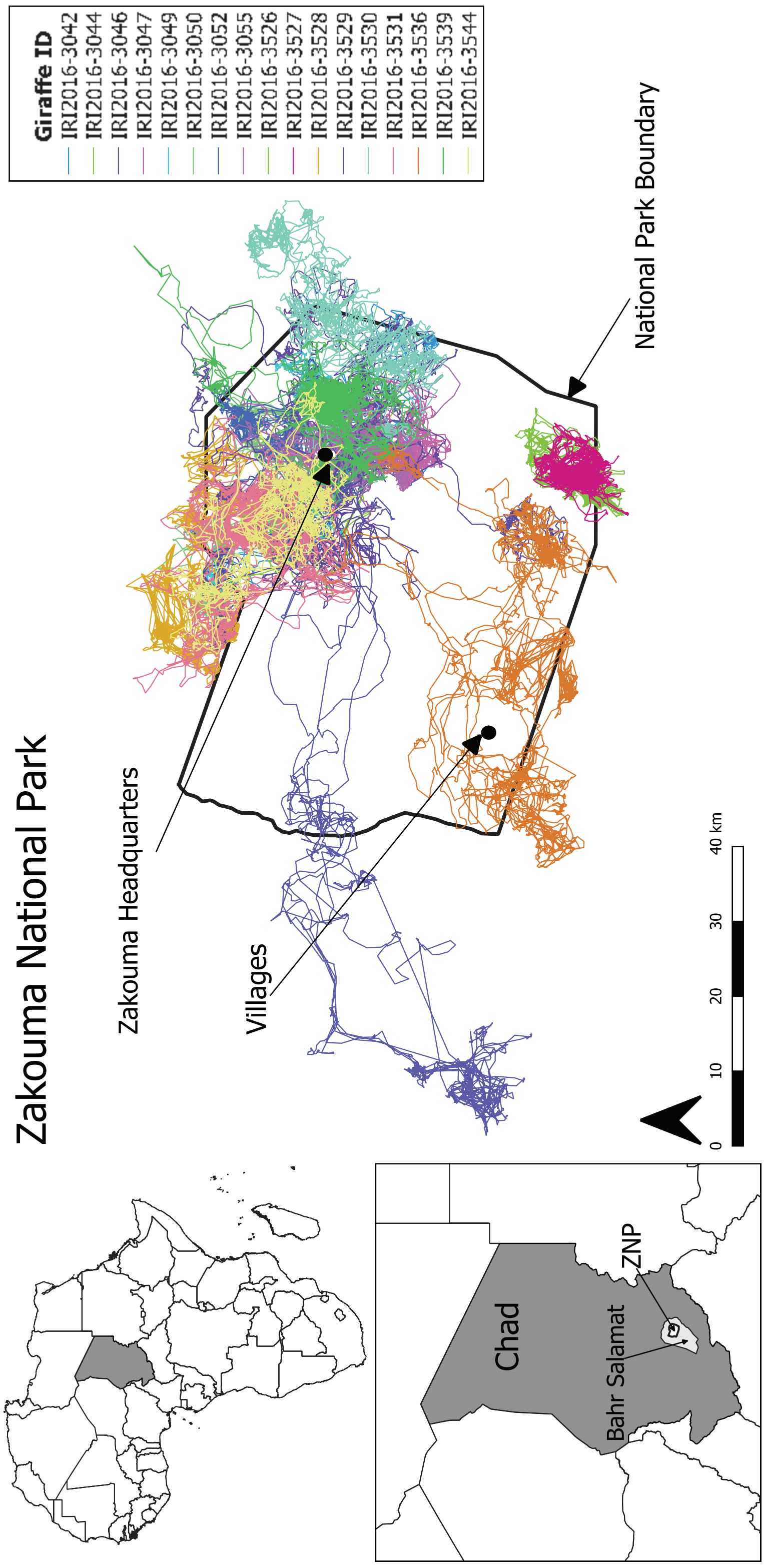

Fig. 1. Giraffe trajectories in and around Zakouma National Park. Movement trajectories, generated from spatial coordinates for 17 female Kordofan giraffe between January 2019 and February 2022 in and surrounding Zakouma National Park, situated in southeastern Chad, Africa. The national park boundary is outlined as well as areas of human habitation (black).

GPS telemetry data

We deployed GPS satellite tracking units on 17 adult female Kordofan giraffe to collect locational data between January 2019 and February 2022, recording their spatial coordinates at hourly intervals, with an overall precision error of 12.79 m (Hart *et al.*, 2020). The 180 g Savannah Tracking units were mounted to the giraffe's ossicone (Hart *et al.*, 2020) through a collaboration between the government of Chad, APN and the Giraffe Conservation Foundation (GCF) under the guidance of experienced wildlife veterinarians and capture team. Male giraffe tend to remain solitary or in bachelor herds, and movements are driven by mating behaviour, whereas females are more responsive to resource requirements (Bercovitch & Berry, 2018). Therefore, females were chosen for GPS tracking allowing for population and spatial movement data to be collected which primarily focused on habitat utilization and selection. We filtered all points to generate regularly sampled trajectories (Fig. 1) by limiting step duration to 60 minutes with a 5-minute tolerance using the 'amt' package in R (version 4.2.1) (R Core Team, 2022; Signer, Fieberg & Avgar, 2019). Animal immobilizations were conducted under the authorization of African Parks and its partnership with the government of Chad and GCF, and approved by the Institutional Animal Care and Use Committee (IACUC) at GCF.

Data analysis

We quantified second-order seasonal ranges (total area used at seasonal timescale) and third-order (resource use at the hourly timescale) habitat selection (Johnson, 1980) to better understand the landscape characteristics influencing giraffe space use and resource selection at multiple scales. We made broad-scale seasonal range comparisons, and conducted fine-scale integrated step selection analysis (iSSA), which distinguishes the effects of environmental covariates on movement and habitat selection processes of individuals (Avgar, Potts, Lewis & Boyce, 2016) to examine factors impacting giraffe space use and habitat selection.

Second order: seasonal ranges and protected area overlap

To evaluate second-order seasonal space use in relation to protected areas, we created seasonal range models using Kernel Density Estimators (KDE) (Worton, 1989). We subset each giraffe's movement data by season and calculated both the 95% (seasonal range) and 50% (core seasonal range) isopleths with a reference bandwidth using the adehabitatHR package (Calenge & Fortmann-Roe, 2023) in R (R Core Team, 2022). We then calculated the percentage of the seasonal range and seasonal core within the national park to compare overall seasonal space use, and seasonal use of the park (de la Torre *et al.*, 2022).

Third order: habitat selection and movement behaviours

To evaluate third-order habitat selection, we used an iSSA approach which incorporates movement parameters into resource selection functions. Here, step length was defined as a straight line between two consecutive locations, sampled from a gamma distribution from the telemetry data, and turning angles were the angular deviations between two consecutive steps, sampled from a von Mises distribution (Signer *et al.*, 2019). These distributions were derived from the individual-level trajectory such that the distribution represents actual movements of each giraffe. For each used step, 20 random available steps were generated from these step length and turn-angle distributions for analysis.

Environmental covariates

We developed a series of environmental covariates to test how the giraffe select for these different features over space and time. Land-cover classifications for the study area, generated by APN through a supervised classification of SPOT imagery (10 m spatial resolution) with ground survey ground truthed test locations, were used to define 19 different habitat types (Poilecot *et al.*, 2009). These habitat types were then combined into broader classifications to reduce the number of habitat factors in modelling (Appendix 3). In addition to different habitat types, there are anthropogenic areas which include human habitation and agricultural land (Appendix 4). The minimum, median and mean area of each patch (m^2) were calculated to ensure that, on average, patch sizes exceeded the average precision error of the GPS tag (Appendix 5). We used the park boundary to determine whether the giraffe moved between, inside and outside of the park. We extracted elevation values for locations using the 'elevatr' package in R (Hollister, 2021).

Model fitting and inference

To assess third-order habitat selection and behavioural responses to habitat, we developed a series of models using iSSA, which distinguishes the effects of environmental covariates on movement and habitat selection processes of individuals, by inferring the speed that animals travel through different habitats (Avgar *et al.*, 2016). A conditional logistic regression model, with binomial error, was fitted to each individual separately using the '*fit_issf*' function in the 'amt' package (Signer *et al.*, 2019) in R (R Core Team, 2022), with the step ID as the strata for the models. The model included all aforementioned environmental covariates, with additional movement parameters (step length, log step length and cosine of the turning angle (cos(turning angle)) as continuous fixed effects in the model to evaluate the speed and the tortuosity of movement. Interactions between season and all other fixed effects were included within the model to investigate seasonal variation in selection. Step length, and log step length are indicators of movement velocity, whereas cos(turning angle) is an indicator of directional persistence, with positive values representing directional persistence and negative values representing more tortuous movements (Avgar *et al.*, 2016). Importantly, interactions between land cover and log step length and cos(turning angle) were also included as well as interactions between protected area use (inside/outside national park) and the step length/turning angle covariates to investigate differences in movement. For example, higher movement rates (given by higher log step length) may suggest rapid movement through unfavourable habitat types, and less directional movement behaviours (given by a negative cos(turning angle)) may suggest increasing time in favourable habitats. In the models, we assumed that all individuals were independent from one another. Due to one individual remaining within the boundary of the park throughout the duration of the study (IRI2016-3047), this individual was removed during iSSA so that interactions between protected area type and the other covariates could be explored. We fitted the full model to all individuals and calculated the mean and 95% confidence intervals across individuals for each of the model parameters.

RESULTS

Second order: seasonal ranges and protected area overlap

Kordofan giraffe wet season ranges (mean = 412.1 km^2, S.D. = 424.6) were significantly larger than dry season ranges (mean = 225.3 km^2 , S.D. = 228.5) ($V = 19$, $P < 0.01$) (Fig. 2A). Similarly, wet season core areas (mean = 80.5 km^2, S.D. = 75.0) were significantly larger than dry season core areas (mean = 47.5 km^2, S.D. = 51.8) ($V = 26$, $P = 0.015$) (Fig. 2B).

In evaluating the percentage of seasonal use overlap with park boundaries, we found no significant difference between dry season (mean = 87.5% , S.D. = 17.9) and wet season (mean= 77.1%, S.D. = 21.7) ($V = 102$, $P = 0.24$) (Fig. 2C). However, dry season core area overlap (mean = 91.1%, S.D. = 17.3) was significantly greater than wet season core area overlap (mean = 66.7%, S.D. = 33.0) ($V = 137$, $P < 0.01$) (Fig. 2D), indicating greater use of the park in the dry season.

Third order: habitat selection

Giraffe significantly avoided anthropogenic areas (which included human habitation and agricultural land), barren areas (which included burned, barren dry, and barren habitats), *Combretaceae* savannas (which included savanna woodland terminalia, short grass *Balanites* and *Anogeissus* stands), and forests, relative to *Vachellia* savannas as the reference level (Fig. 3). The strongest avoidance was for barren habitat types. Open grassland was the only habitat significantly selected for at this scale when compared to *Vachellia* savannas; however, the strength of selection was small (Fig. 3). Lower elevations were selected for across the study period at this scale.

No other habitats were significantly avoided or selected for, and no seasonal variation in habitat selection (*i.e.* interactions) was apparent at the fine-scale hourly step duration. The selection for the protected area was not significant, although this result was close to significance (Appendix 2).

Third order: movement behaviours

Interactions between movement parameters (log step length and cos(turning angle)) were investigated with land-cover classes and protected area type. With *Vachellia* savanna as the reference for the land-cover variables, we found that giraffe moved significantly faster through barren areas, *Combretaceae* savannas and forests (Fig. 4), and showed directional persistence while travelling through forest habitats and the park. The only habitat that giraffe tended for more tortuous movements, with a negative coefficient for cos(turning angle), was open grassland (Fig. 4). Full model results can be found in Appendix 2.

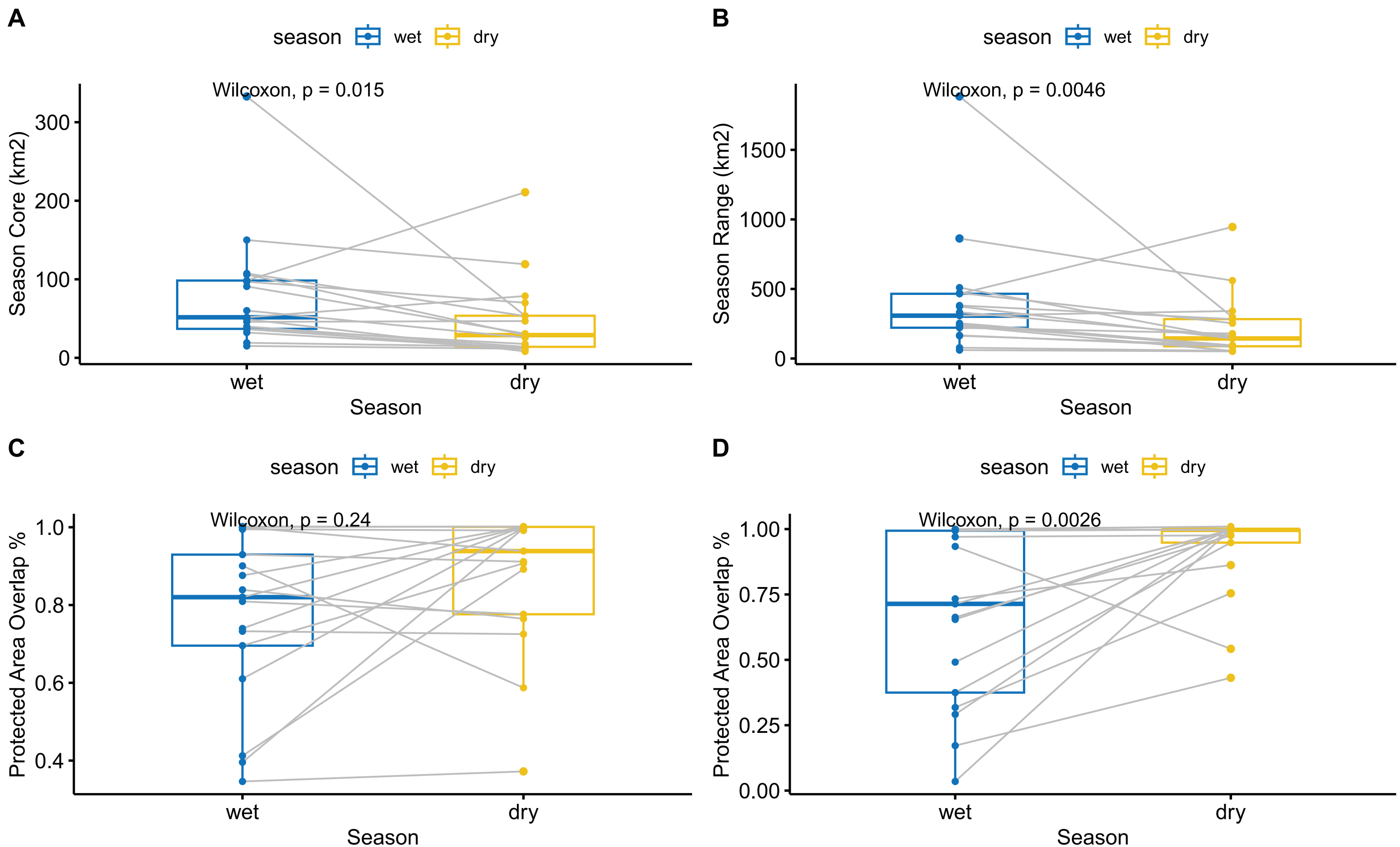

Fig. 2. Comparison of seasonal range and core areas and overlap with Zakouma National Park, Chad. **A**, 50% KDE (seasonal core) area; **B**, 95% KDE (seasonal range) area comparisons; **C**, 95% KDE protected area overlap; **D**, 50% KDE protected area overlap comparisons. Grey lines represent paired comparisons of 17 individual giraffe across the wet and dry seasons. Wilcoxon sign rank test results indicate significant differences across seasons.

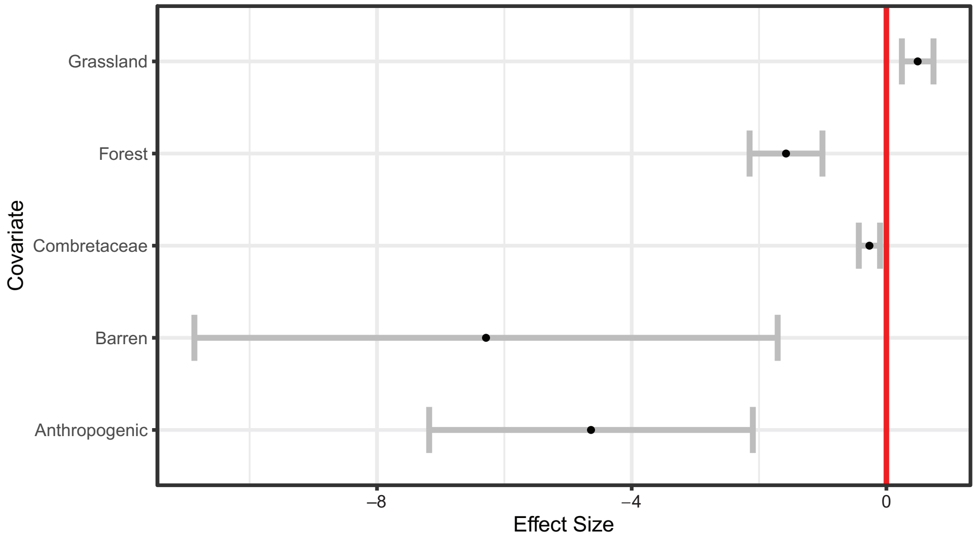

Fig. 3. Model results for fine-scale habitat selection of Kordofan giraffe in Zakouma National Park, Chad. Statistically significant coefficients for habitats using an integrated step selection approach, with the black dot representing the mean (±95% CI) value of estimated coefficients across 16 individuals. *Vachellia* savanna habitat was the reference level for land-cover variables (Grassland, Forest, Combretaceae, Barren and Anthropogenic).

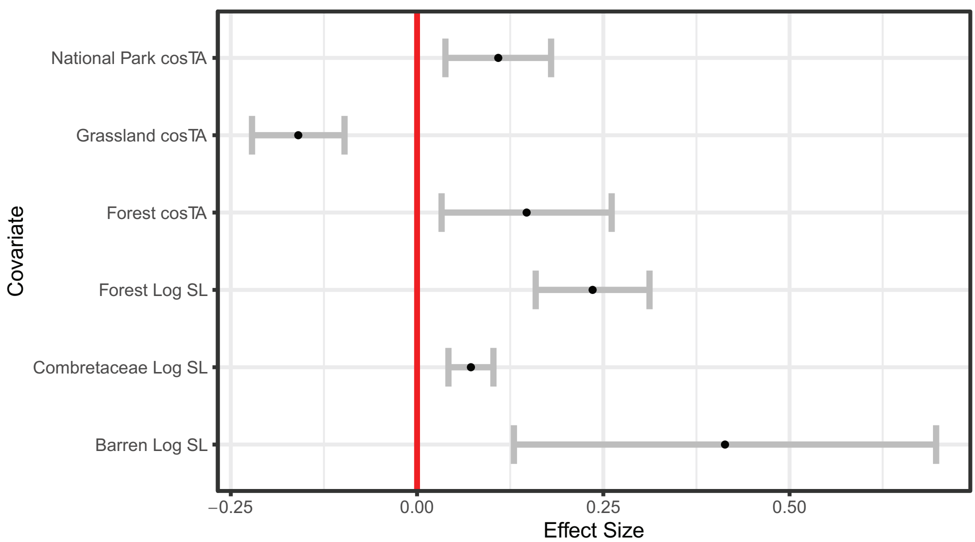

Fig. 4. Model results for movement covariates of Kordofan giraffe in Zakouma National Park, Chad. Statistically significant movement coefficients, using an integrated step selection approach, for log step length (Log SL) and the cos(turning angle) (cosTA) in interactions with landcover and protected area status. Here, the black dot represents the mean (±95% CI) value of estimated coefficients across the 16 individuals. *Vachellia* savanna habitat was the reference level for land-cover variables (Grassland, Forest, Combretaceae and Barren).

DISCUSSION

This first-ever study on the seasonal range and habitat selection of female Kordofan giraffe in ZNP identified that their wet season range was significantly larger than the dry season, yet their season core ranges overlapped with the park more in the dry season than in the wet season. These findings support our original predictions and suggest that seasonal flooding and potential phenological shifts in ZNP result in giraffe habitat becoming inaccessible, thus limiting forage availability, and driving giraffe beyond the boundaries of the national park. This finding is supported by evidence that African savanna elephant within ZNP also move outside the park during the wet season (Dolmia *et al*., 2007; Labuschagne, 2014), suggesting that seasonal shifts in habitat suitability cause the giraffe to move into areas beyond the park boundaries, and thus limits park management's abilities to enforce wildlife protection laws. Many protected areas in Africa do not cover an area large enough to encompass the full range of resource requirements for large ungulate populations, particularly those that seasonally flood (Fynn & Bonyongo, 2011). The seasonal variation in range size found within ZNP contrasts that of other giraffe populations that reside outside protected areas. West African giraffe (*G. c. peralta*) home ranges in Niger were larger in the dry season, compared to the wet season (Pendu & Ciofolo, 1999); similarly in South African giraffe (*G. g. giraffa*) home ranges were smaller in the wet season compared to the dry season (Deacon & Smit, 2017), while Angolan giraffe (*G. giraffa angolensis*) in northwestern Namibia exhibited no seasonal variation in their movements (Fennessy, 2009).

At the finer spatial scale (*i.e.* third-order selection), we incorporated movement metrics along with the environmental covariates (land-cover types, elevation, park use and seasonality) in an iSSA to distinguish and characterize movement and habitat selection behavioural responses. While giraffe do not often show large-scale seasonal migrations, they can show fine-scale seasonal movements (Brown & Bolger, 2020; Pellew, 1984b). Compared to *Vachellia* savannas, giraffe avoided anthropogenic and barren areas, as well as *Combretaceae* savanna and forest habitats (Fig. 4). Conversely, they selected for open grasslands. This observed habitat selection is consistent with female Luangwa giraffe (*G. tippelskirchi thornicrofti*) selecting for open areas to forage on forbs and samplings in the herbaceous layer, and to allow for greater visibility to detect predators (Bercovitch & Berry, 2018). Likewise, Masai giraffe (*G. t. tippelskirchi*) avoid areas of human habitation and agriculture (Bond, Lee, Ozgul & König, 2019). Similar avoidance of dense areas, such as forests was observed in South African giraffe (*G. g. giraffa*) (Deacon & Smit, 2017). Additionally, giraffe selected for lower elevations but the strength of this did not vary seasonally as expected. Indeed, seasonal variation in habitat selection was not apparent in our fine-scale analysis, suggesting that, while giraffe shift ranges seasonally, their preferences for habitat types within those ranges do not change. Due to the seasonal differences in palatability of *Vachellia* and other forage, the feeding ecology of giraffe is highly flexible to maintain adequate nutritional uptake (Berry & Bercovitch, 2017; Levi, Lee, Bond & Treydte, 2022; Milewski & Madden, 2006; Pellew, 1984a,b), and we had expected to observe seasonal variation in fine-scale preferences.

Zakouma NP giraffe moved faster through barren areas, *Combretaceae* savannas and forests and with significant directional persistence through forest areas (Fig. 4). This movement behaviour was to be expected due to the avoidance of these habitat types (Fig. 3). Interestingly, giraffe also moved with significant directional persistence through ZNP in the fine-scale analysis (Fig. 4). Such movement behaviour may be attributed to their ability to move more easily in the park, thus facilitating opportunities for greater long-distance, straight-line movement. In contrast, we expected that grasslands would have a negative coefficient for the cos(turning angle) suggesting that when selecting for and encountering open grassland areas, giraffe spend more time there by increasing their tortuosity of movement, and may be seeking open areas to allow for increased vigilance while resting and ruminating during non-feeding periods (Van Moorter *et al*., 2016).

In the third-order iSSA models, the individual giraffe were assumed to be independent of each other to allow for simple population level inferences to be made about habitat selection and movement. This may have some limitations within a giraffe population due to the well-recognized fission–fusion herd structure of these animals, which involves the splitting and joining of loose social groups within an overall larger network (Aureli *et al*., 2008; Wolf *et al*., 2018). This dynamic population structure may allow for groups to respond to seasonal fluctuations in forage availability and predator risk (Bond *et al*., 2019). It has also been found that ungulates tend to congregate together in open environments, and conversely, disperse into smaller groups in more dense landscapes (Bond *et al*., 2019; Hart *et al*., 2020; Muller, Cuthill & Harris, 2018). Nonetheless, many movements were independent of one another (Fig. 1) and the approach provided detailed population-level inferences on space use in ZNP. Predator–prey interactions were not included in the analysis for this study. This may be an important relationship to explore in future studies as predation risk likely varies by habitat type and seasons (Lee, Kissui, Kiwango & Bond, 2016). Lions (Panthera leo) are the major predator of giraffe (Dagg, 2014; Foster & Dagg, 1972; Strauss & Packer, 2013), and lion populations within ZNP have been thriving (African Parks, 2023; Scholte *et al*., 2021), so consequently may be an important driver of habitat selection, particularly when giraffe calves are present. We found that giraffe select for open grassland and increase their time spent within these areas, which could infer a response to predator avoidance, and this is supported within the literature from other giraffe populations (Young & Isbell, 1991). In addition, no information was available on the presence of calves within this population due to a lack of any detailed population assessment. Giraffe with calves show marked differences in their habitat use and selection as well as influencing group dynamics (Bond *et al*., 2019). Females with calves may select open habitats in order to increase their visibility of predators, while others may select for more dense habitats in order to hide neonatal calves during their first one to three weeks of life (Bond *et al*., 2019; Wolf *et al*., 2018). Understanding the differences in habitat selection of pregnant giraffe and those with calves may prove crucial to understand what habitat types require the most protection for the continued growth of the Kordofan giraffe population in ZNP.

Open grasslands are key habitats selected by giraffe, and the importance of *Vachellia* savannas can be inferred through the strong avoidance of other habitats by comparison. We identified a significant avoidance of the park during the wet season, and the impact of the flooding environment in modifying their behaviour. Identifying seasonal movements and variation in habitat selection of giraffe has important consequences for long-term conservation and management of this critically endangered taxon. Most interesting is the identification of key times and areas that giraffe move beyond park boundaries. Across their range, giraffe are susceptible to human–giraffe conflict (Fennessy, 2009), particularly illegal hunting. However various giraffe populations do coexist with humans with relatively limited levels of conflict (Ciofolo, 1995). Intensive illegal hunting incidents in/around ZNP historically drove local populations of giraffe to near extinction (Poilecot *et al*., 2010). Our results suggest that giraffe have higher risks of interactions with humans during the wet season when their range extends beyond the park boundaries, and the habitat in ZNP may be insufficient to support giraffe foraging needs when the park is flooded. Additionally, anthropogenic areas were avoided by giraffe at the finer spatial scale, further emphasizing the importance of managing potential human–giraffe relationships between local communities and giraffe through appropriate future land-use planning. At this time, ongoing monitoring and targeted conservation co-learning projects between communities and park management is essential to maintain positive human–giraffe relationships and lead to positive outcomes both for communities and conservation. By integrating multi-scale understandings of movement behaviour into management practices, future conservation efforts can better incorporate spatiotemporal dynamics of habitat requirements into more effective landscape-level strategies.

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Appendix 1. Rainfall data to define seasons for study system.

Rainfall data from the years 2018–2021 were generated from CHIRPS rainfall data accessed through Google Earth Engine to define the wet and dry season for the study period.

Appendix 2. Full iSSA model results with the 'Mean' column as the mean beta coefficient for 16 giraffe.

Covar	Mean	S.D.	Upper_CI	Lower_CI
Landcover2Anthropogenic	–4.86	5.29	–2.18	–7.53
Landcover2Barren	–6.61	9.57	–1.77	–11.45
Landcover2Combretaceae	–0.27	0.35	–0.09	–0.45
Landcover2Forest	–1.53	1.19	–0.93	–2.14
Landcover2Grassland	0.48	0.52	0.74	0.22
Landcover2Other.Woodland	0.02	0.51	0.28	–0.24
Landcover2Wetland	–2811.49	10486.85	2495.59	–8118.57
elevation	–0.04	0.03	–0.03	–0.06
PA_typeParc.National	1.59	5.06	4.15	–0.96
seasonwet	0.00	0.00	0.00	0.00
sl_	–0.00	0.00	0.00	–0.00
log_sl_	–0.04	0.19	0.05	–0.14
cos_ta_	–0.01	0.21	0.09	–0.12
Landcover2Anthropogenic.seasonwet	1.84	5.56	4.65	–0.98
Landcover2Barren.seasonwet	1.79	6.17	4.91	–1.33
Landcover2Combretaceae.seasonwet	0.05	0.29	0.20	–0.10
Landcover2Forest.seasonwet	0.05	0.66	0.39	–0.28
Landcover2Grassland.seasonwet	–0.08	0.25	0.05	–0.21
Landcover2Other.Woodland.seasonwet	0.00	0.28	0.14	–0.14
Landcover2Wetland.seasonwet	–15.88	47.86	8.34	–40.10
PA_typeParc.National.seasonwet	0.41	5.51	3.20	–2.38
elevation.seasonwet	0.02	0.06	0.05	–0.01
seasonwet.cos_ta_	0.01	0.16	0.09	–0.07
seasonwet.log_sl_	–0.01	0.10	0.05	–0.06
seasonwet.sl_	0.00	0.00	0.00	–0.00

Continued on p. 133

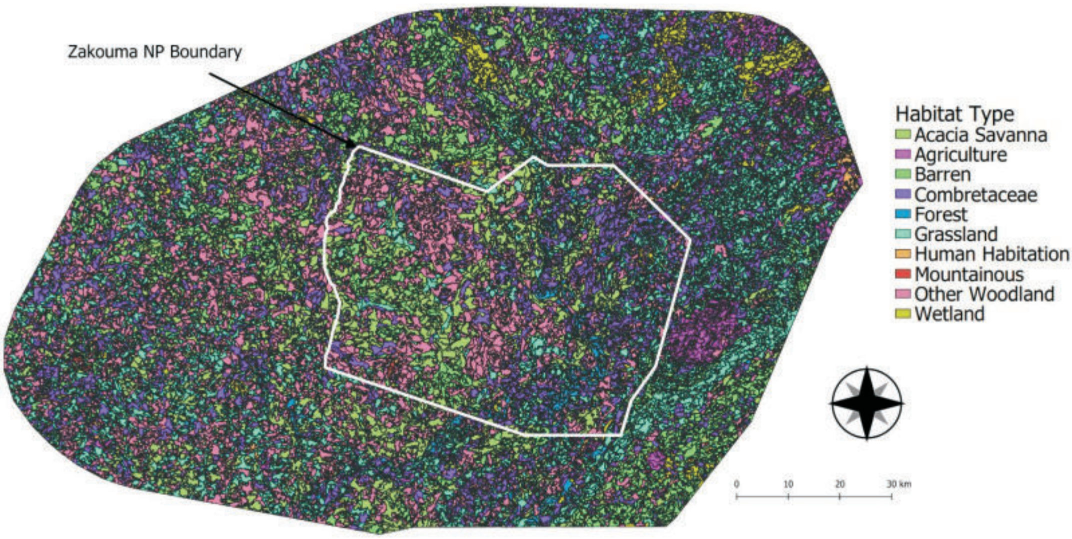
Appendix 2 (continued)

Covar	Mean	S.D.	Upper_CI	Lower_CI
Landcover2Anthropogenic.log_sl_	0.11	0.37	0.30	–0.08
Landcover2Barren.log_sl_	0.44	0.59	0.74	0.14
Landcover2Combretaceae.log_sl_	0.06	0.05	0.09	0.04
Landcover2Forest.log_sl_	0.23	0.16	0.31	0.15
Landcover2Grassland.log_sl_	–0.03	0.08	0.01	–0.07
Landcover2Other.Woodland.log_sl_	0.00	0.07	0.04	–0.03
Landcover2Wetland.log_sl_	36.09	129.87	101.81	–29.63
Landcover2Anthropogenic.cos_ta_	0.32	1.28	0.97	–0.32
Landcover2Barren.cos_ta_	1.82	6.49	5.11	–1.47
Landcover2Combretaceae.cos_ta_	–0.02	0.09	0.03	–0.07
Landcover2Forest.cos_ta_	0.15	0.24	0.27	0.02
Landcover2Grassland.cos_ta_	–0.18	0.09	–0.14	–0.23
Landcover2Other.Woodland.cos_ta_	–0.02	0.11	0.04	–0.07
Landcover2Wetland.cos_ta_	2584.92	9667.48	7477.34	–2307.50
PA_typeParc.National.log_sl_	0.06	0.16	0.14	–0.02
PA_typeParc.National.cos_ta_	0.11	0.14	0.18	0.04

Appendix 3. Simplified landcover classifications.

Simplified land-cover classification	Original land-cover classification
Acacia savanna	*Acacia seyal*
Wetland	Floodplain Water Swamp Wetland
Grassland	Open Grassland
Mountainous	Inselberg
Barren	Burned Barren Dry Barren
Forest	Riverine Gallery Forest Palm Forest
Combretaceae	Savanna Woodland Terminalia Short Grass *Balanites* *Anogeissus* stand
Other Woodland	Marula Woodland Mixed Woodland
Anthropogenic	Human Habitation Agriculture

Appendix 4. Habitat map of Zakouma National Park (white border) and surrounding area.



Appendix 5. Minimum, mean and median patch size of land-cover type.

Habitat type	Minimum (m^2)	Mean (m^2)	Median (m^2)
Acacia savanna	533.496	1779385.1	1406665
Anthropogenic	0.012	747218.3	450900
Barren	5400	1206372.7	837900
Combretaceae	3319.34	1280832.9	937800
Forest	15.476	1136776	848700
Grassland	111.479	1379944.2	1009800
Mountainous	2.416	183221.2	74464.6
Other woodland	7393.32	1593030.6	1211400
Wetland	1294.25	805181.2	475200