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Ranging behaviours across ecological and anthropogenic disturbance gradients: a pan-African perspective of giraffe (*Giraffa* spp.) space use

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Animal movement behaviours are shaped by diverse factors, including resource availability and human impacts on the landscape. We generated home range estimates and daily movement rate estimates for 148 giraffe (*Giraffa* spp.) from all four species across Africa to evaluate the effects of environmental productivity and anthropogenic disturbance on space use. Using the continuous time movement modelling framework and a novel application of mixed effects meta-regression, we summarized overall giraffe space use and tested for the effects of resource availability and human impact on 95% autocorrelated kernel density estimate (AKDE) size and daily movement. The mean 95% AKDE was 356.4 km^2 and the mean daily movement was 14.1 km, both with marginally significant differences across species. We found significant negative effects of resource availability,

and significant positive effects of resource heterogeneity and protected area overlap on 95% AKDE size. There were significant negative effects of overall anthropogenic disturbance and positive effects of the heterogeneity of anthropogenic disturbance on daily movements and 95% AKDE size. Our results provide unique insights into the interactive effects of resource availability and anthropogenic development on the movements of a large-bodied browser and highlight the potential impacts of rapidly changing landscapes on animal space-use patterns.

1. Introduction

Emergent patterns in animal space use are the result of complicated interactions between environmental conditions, individual animals' internal states, social interactions and the capacity to move [1]. Evaluating sources of variation in space use and movement can better inform understandings of these interactions and remains a foundational research theme in ecology and conservation [2–4]. Space use strategies and variation in ranging behaviours are influenced by diverse factors, including body size [5], reproductive status [6], genetics/taxonomy [7,8], resource density/productivity [9,10], conspecific density [11], predation risk [12,13] and anthropogenic disturbance [10,14–16]. Despite this growing body of literature, empirical studies examining interactions between different drivers of movement across species' ranges remain largely underexplored (although see [14,16,17]). As human development increasingly alters ecological processes [18] and as climate change renders resource distribution spatiotemporally less predictable [19,20], understanding how animals respond to anthropogenic disturbance and bioclimatic variability is essential for informing conservation management strategies.

Maximizing resource acquisition relative to energy expenditure is a key trade-off in resource ecology across spatiotemporal scales. Exploitation theory predicts that increased efficiency in acquiring resources results in decreased overall space use [21]. Thus, animals in resource-rich environments generally exhibit more localized movement behaviours than those in resource poor environments [22,23]. Similarly, the spatio-temporal predictability of resource distribution strongly influences space use strategies, with highly predictable local resources supporting resident ranging behaviours and highly unpredictable resources resulting in nomadic movement behaviours [24]. In this way, both structural and functional heterogeneity impact animal space use at multiple scales, with increased spatio-temporal resource heterogeneity resulting in increased ranging behaviour and animals travelling greater distances to access dynamic resources. These movement behaviours are contingent upon relatively high degrees of functional landscape connectivity and increasingly studies show the impacts of anthropogenic disturbance on animal movements [10,14,15]. The direction and magnitude of anthropogenic effects on animal space use have varied across studies and taxa [25]. For instance, Tucker *et al*. [15] found general patterns across taxa of reduced displacement in areas of greater human footprint and Wall *et al*. [16] found significant negative effects of human activity on elephant space use across Africa. Conversely, Thompson *et al*. [26] found increased jaguar ranging behaviour in areas of increased human impact, representing differences in the ability of carnivores and herbivores to access variable resource gradients. Despite the growing body of space-use studies, additional research is needed to investigate how resource density and human disturbance interact to shape animal space use and movement patterns.

Understanding mechanisms for intrataxon variation of ranging behaviours provides insight into the ecological interactions driving movement decisions [27]. Historically, large scale comparative animal space use studies have been conducted via meta-analyses of disparate datasets that differ in data collection and analytical methods [28]. The lack of large volumes of uniformly collected data over broad ecological gradients has limited the potential for rigorous ecological studies of variation in ranging behaviours. The advent of relatively inexpensive miniaturized GPS tracking devices [29,30] and analytical frameworks to process the high volume of tracking data [31] have made systematic data collection and analyses more feasible. Additionally, increasingly accessible remotely sensed landscape-level data have enabled comparable environmental datasets to be developed across geographically diverse sites to test for the effects of bioclimatic covariates on movement [32]. Emerging analytical frameworks for highly autocorrelated and irregularly sampled tracking data, such as continuous time movement models (CTMMs), also enable statistically robust approaches for comparisons across disparately sampled populations. For widely distributed, highly mobile taxa, understanding environmental and life-history effects on the variation in space-use strategies for individuals offers new opportunities to understand ecological drivers of movement.

Giraffe (*Giraffa* spp.) are broadly distributed across sub-Saharan Africa, inhabiting a wide range of environments and bioclimatic conditions [33,34]. These habitats vary from hyper-arid deserts in northwest Namibia to mesic savannahs along the Nile River in Uganda. Throughout these areas, giraffe also inhabit distinctly varied human land-use and management systems, ranging across protected areas and national parks where people are largely absent [35] to agricultural land replete with human settlements [36]. Giraffe are widely considered to be aseasonal, asynchronous reproducers, effectively disassociating movement behaviours attributed to reproductive state and seasonal variation in environmental conditions [37]. As large-bodied ruminant browsers, giraffe can be highly mobile to access sufficient forage to meet metabolic requirements [38,39], moving across large landscapes to access spatio-temporally heterogeneous resources.

Previous giraffe ranging behaviour studies largely focused on site-specific space-use. These studies indicated that giraffe exhibit a wide range of space-use behaviours across habitat types with larger home ranges reported in more arid environments and smaller home ranges in more mesic savannas [40–43]. Some studies also suggested intraspecific variation of space use and habitat selection within populations [38,44]. These studies, however, investigated the movement behaviour of individual populations or species. Earlier efforts at comparative literature evaluations of giraffe space use across populations have been complicated by different data collection schemes, inconsistent space use metrics and disparate analytical techniques [43,45]. No systematic analyses of giraffe ranging behaviour have been conducted across all four species of giraffe [46,47] at the continental scale.

In this study, we incorporated GPS telemetry data systematically collected on all four species of giraffe—northern giraffe (*Giraffa camelopardalis*), Masai giraffe (*G. tippelskirchi*), reticulated
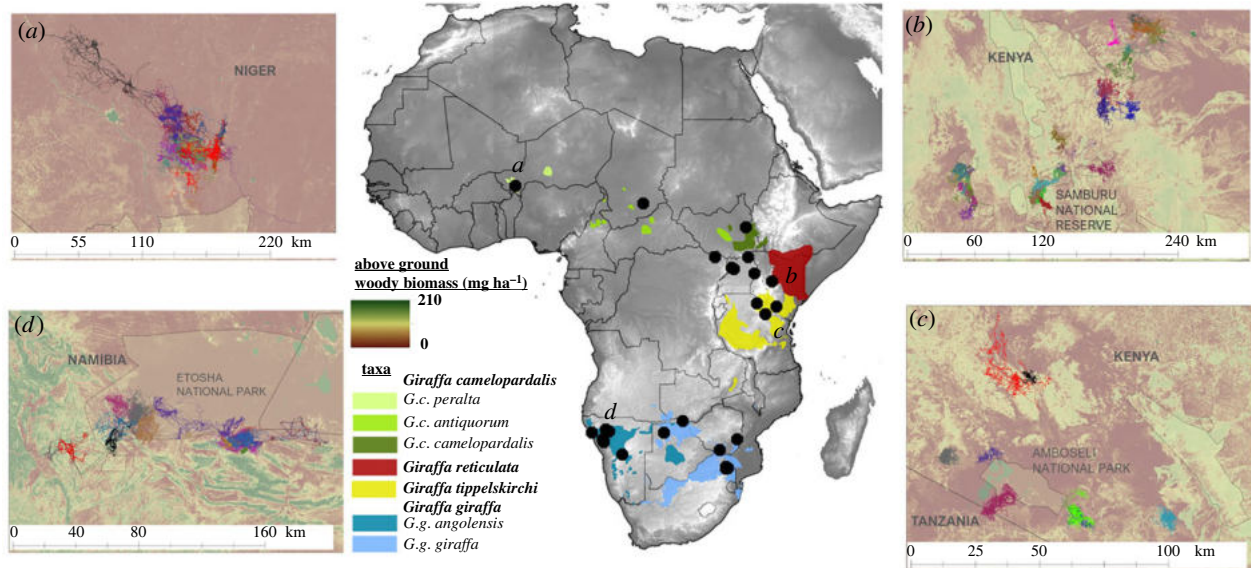
Figure 1. Distribution of giraffe tracking study sites across Africa. We deployed tracking units in 30 distinct populations across 11 countries over most of the known geographical range of giraffe. Black dots represent individual study sites. Outset maps represent focal giraffe trajectories from selected populations from each of the four species: (a) *Giraffa camelopardalis peralta* in the Giraffe Zone of Niger, (b) *Giraffa reticulata* in northern Kenya, (c) *Giraffa tippelskirchi* in the Amboseli ecosystem of Kenya and (d) *Giraffa giraffa angolensis* in the greater Etosha ecosystem of Namibia. The background of outset maps shows aboveground woody biomass derived from Bouvet *et al.* [52] and the range map is derived from O'Connor *et al.* [34] and Brown *et al.* [33].

giraffe (*G. reticulata*) and southern giraffe (*G. giraffa*) [46,48]—across the majority of giraffe geographical distribution to (1) describe overall trends of space use, and (2) evaluate the effects of environmental conditions and anthropogenic pressures on giraffe ranging behaviour. We analysed these data in the CTMM framework [49,50] and used a novel application of mixed effect meta-regression analysis to incorporate uncertainty of space use metrics in evaluating the impacts of ecological variation and anthropogenic disturbance on giraffe spatial ecology across Africa. We predicted a negative effect on home range size and daily movement rates when measures of productivity (NDVI, above-ground woody biomass) increased, aligning with previous research along smaller ecological gradients [42] and based on the principle that higher densities of reliably accessible resources reduce the need to range across large spatial extents [11,23,51]. Additionally, we expected increased variation in productivity to be associated with increased home range size, as spatio-temporally heterogeneous environments may require increased movement to access patchy resources in dynamic environments [24,38]. Lastly, we predicted a negative effect of human footprint and a positive effect of protected area overlap on home range size and daily movement rates. Protected areas represent relatively intact, unfragmented landscapes with limited barriers to movements, providing large unimpeded systems for giraffe to move. Conversely, higher levels of human footprint may limit connectivity and restrict movements [15]. We explore these effects within the context of understanding how giraffe alter space use and movement behaviour across a gradient of landscape productivity and human land use in an era of rapid landscape change.

2. Methods

To evaluate variation in giraffe space use, we assembled the largest dataset of GPS telemetry data ever collected on giraffe throughout their range. This dataset is comprised of coordinate fixes collected from 220 GPS units deployed on unique individuals from all four

giraffe species and their constitutive subspecies in 30 distinct populations across 10 countries between September 2011 and January 2022 (figure 1) (electronic supplementary material, table S1). The distribution of tracking data encompasses much of the geographical distribution of giraffe, most taxonomic groups (excluding the Luangwa giraffe, *G. t. thornicrofti*) and most biome types where giraffe exist (figure 1). Technology for tracking giraffe has evolved considerably over the past two decades [29,30]. As a result, we used data collected from four different GPS device manufacturers, each with of a different method for device attachment: head harnesses developed by African Wildlife Tracking (AWT) (see [42,45,53]), solar charged ossicone and tail-mounted GPS units manufactured by Savannah Tracking (ST) (see [29,30,34,38]), ear tag units developed by the Max Planck Institute of Animal Behaviour, and solar charged ear tag units developed by Ceres (electronic supplementary material, figure S1). Aside from the Ceres tags, which were programmed to record a position every 6 h, we programmed the GPS units to record coordinate fixes predominantly at hourly intervals. For solar charged units, the fix rate and regularity of sampling was heavily influenced by voltage profiles, with units deactivating below predetermined voltage levels and resuming normal function after sufficient recharge. Thus, some of the individual giraffe trajectories were irregularly sampled with gaps in data collection. All tracking devices transferred data remotely, minimizing post-tagging human interaction with tracked individuals.

For tracking device deployment, giraffe were chemically immobilized using a variety of immobilization drugs (e.g. etorphine, thiafentanil, or a combination thereof) remotely delivered through darts from either the ground or a helicopter, at the discretion of the local wildlife veterinarians. Once physically restrained, giraffe were immediately administered the reversal drug(s) and fitted with a GPS tracking device before being released. We deployed tracking devices predominantly on female giraffe (female = 177; male = 32). All research was conducted with permits or approvals from each range state (electronic supplementary material, table S2).

We used the CTMM framework [49] to quantify space use and movement for each giraffe. CTMM was the preferred method for estimating ranging behaviour since it accounts for inherent serial autocorrelation in high temporal resolution GPS telemetry data.

The framework is robust to gaps in data collection and effectively calculates confidence intervals for home range and movement estimates [31,54].

We consolidated data from all tracking devices and filtered each trajectory to remove aberrant and biologically implausible GPS coordinate fixes. We first excluded points collected within 24 hours of the capture date and prior to the last recorded location based on recommendations in Northrup, Anderson & Wittemyer [55]. We then used the outlie() function included in the CTMM workflow to exclude points resulting from a sustained velocity of greater than 3.0 m per second [50]. To ensure giraffe were tracked across multiple seasons at all study sites to account for potential seasonal variation in range residency, only individuals that were tracked for at least five months were included in analyses.

We fitted a suite of continuous-time stochastic movement models to each filtered individual giraffe trajectory. These included: (1) an independent identically distributed (IID) process model that assumed uncorrelated positions and velocities; (2) an Ornstein–Uhlenbeck (OU) model that combined Brownian diffusion models with a central place tendency [56,57]; and (3) an OU foraging (OUF) process that incorporated correlated velocity and area restricted space use [54]. Models were fitted for each of these candidate models using maximum-likelihood approaches. The best model for each individual was selected based on AICc [49]. For each individual giraffe trajectory, we visually inspected the variogram to (1) assess the autocorrelation structure of each dataset, and (2) evaluate if animals met the range residency assumption, indicated by the estimated semi-variance reaching an asymptote. After generating CTMM models, animals that did not meet the range residency assumption (23 giraffe) were removed from further analyses [54].

For each giraffe trajectory, we used the best-fitting movement model to generate the 95% autocorrelated kernel density estimates (AKDE) for home range. We summarized the average daily distance travelled from parameters estimated from each movement model, providing insights into the movement behaviour of each giraffe. All analyses were conducted in the R environment for statistical computing v. 4.1.2 [58] using the ctmm package [49].

To test our hypotheses on the effects of environmental productivity, environmental variability, and human disturbance on giraffe space use and movement, we developed a series of environmental covariates for each individual giraffe (table 1). To ensure that covariates were consistently collected and comparable across all study sites, we restricted candidate covariates to global or continental spatial datasets with temporal coverage over the duration of the GPS telemetry study. For each individual giraffe, we extracted environmental covariate values associated with all coordinate fixes. For temporally dynamic datasets (i.e. 16-day composite NDVI imagery), we associated the location of the giraffe with the environmental conditions closest to its position in space and time. We extracted temporally dynamic environmental covariates using Google Earth Engine accessed through the Rgee package in R, following instructions described by Crego et al. [61,62]. We calculated the mean and standard deviation for each continuous variable extracted at giraffe point locations to provide a single synthetic metric associated with the trajectory-based response variables (e.g. home range area, daily movement rate) for each giraffe. In addition to NDVI, we used above-ground woody biomass as a proxy for habitat type [52]. This product, which provides a 25 m resolution estimate (Mg ha^{-1}) derived from the 2010 ALOS PALSAR mosaic, has been independently assessed for savannah ecosystems and shown to be an effective measure of available woody vegetation cover for ungulate browsers [63]. To develop a protected area intersection index, we overlaid giraffe coordinate fixes on the World Database on Protected Areas and assigned each giraffe an index value based on the percentage of total coordinate fixes that fell within a designated protected area class [59]. We also recorded the species taxonomic identity and study site (table 1).

We used a meta analytic framework to account for estimate uncertainty associated with CTMM space use metrics [64] to (1) summarize space use patterns of the different giraffe species, and (2) evaluate the effects of environmental/anthropogenic covariates on giraffe space-use and movement. These techniques weight point estimates by the variance components of the estimates, which is simultaneously estimated with regression coefficients, providing more credibility and thus more weight to samples with smaller variance. We used a log transformation on response variables (95% AKDE and daily movement rate) to better satisfy Gaussian model assumptions. To ensure that the variance components conformed to the transformed response variables, we developed variance estimates for the log-transformed 95% AKDE (1/degrees of freedom for AKDE estimate) and daily movement (1/4 × degrees of freedom for movement estimate). To provide global estimates for mean 95% AKDE size (hereafter referred to as home range size) and daily movement rates, we first fit an intercept only model for each of the response variable. To generate species-specific summary statistics of space-use metrics, we evaluated differences in home range area and daily movement across species, using taxonomic identity as the fixed moderator for each response variable. We next evaluated the effects of environmental and human disturbance on home range size and daily movement, by developing candidate models with every permutation of covariates as fixed effects. We included study site as a random effect in candidate models to account for lack of independence in local covariates within the hierarchical structure of the data. We also evaluated the interaction between mean NDVI and anthropogenic covariates (HFI, and protected area overlap) to examine the relationships between primary productivity and human impact on giraffe space use and movement (see electronic supplementary material, figure S2 for plotted covariates space for both models). We did not include taxonomic identity as a random effect since it is associated with geographical location. We used restricted maximum likelihood as a heterogeneity variance estimator for all models [65,66]. We assessed statistical heterogeneity using a Q-test [67] and the I^2 statistic [68]. The I^2 statistic represents the percentage of total variation across effect size estimates that is due to heterogeneity rather than chance [69]. To ensure effect sizes were comparable, we applied a z-score transformation and scaled all moderators by mean and standard deviation before fitting models. We inspected all moderators for collinearity and checked that all bivariate correlations were less than 0.75 for all covariates included in the candidate models. We used (AICc) to determine the models best supported by the data and conducted all analyses using the metafor package [64] in R.

3. Results

We analysed 148 giraffe trajectories (G. camelopardalis = 63; G. giraffa = 55; G. reticulata = 18; G. tippelskirchi = 12) from 22 different study sites after filtering trajectories that did not meet a priori duration thresholds or did not exhibit range residency assumptions (i.e. modelled semi-variance did not reach an asymptote) (electronic supplementary material, table S1). Of these giraffe, the majority of individuals exhibited OUF anisotropic movement (n = 142), with fewer individuals exhibiting OU anisotropic (n = 2), OU isotropic (n = 1) and OUF isotropic (n = 3) movements. OUF movement processes are characterized by area restricted space use and autocorrelated velocities, and are often suitable for modelling finely sampled, longer duration telemetry datasets that are characteristic of this study [49].

Table 1. Candidate model covariate descriptions.

covariate	description	source	rationale/predictions
species	giraffe species	[48]	species-specific summary statistics are provided for movement and space use metrics
study site	description of location where giraffe was tagged		study site is incorporated as a random effect to account for hierarchical structure of data sampling
NDVI (mean)	mean spatio-temporally explicit NDVI estimate for each focal giraffe (250 m).	MODIS 16 day composite	as mean measures of environmental productivity increase, AKDE size and daily movements will decrease since available resources are denser and require less movement to access
NDVI (s.d.)	standard deviation of spatio-temporally explicit NDVI estimates for each focal giraffe (250 m)	MODIS 16 Day composite	as measures of environmental heterogeneity increase, AKDE size and daily movements will increase since relatively resource quality varies over space and time, resulting in more movements to access spatio-temporally varying resources
protected area intersection	percent intersection of range area with a Protected Area from the World Database on Protected Areas 2013 database	IUCN and UNEP-WCMC [59]	as the relative amount of time giraffe spend in protected areas increases, AKDE size and daily movement will increase since protected areas represent intact, unfragmented landscape
human footprint index (mean)	mean human footprint index for each giraffe (1 km)	[60]	as mean HFI increases, the AKDE size and daily movement rates will decrease as matrix permeability around suitable habitat patches decreases and restricts potential for movement
human footprint index (s.d.)	standard deviation of human footprint index for each giraffe (1 km)	[60]	as standard deviation in HFI increases, AKDE size and daily movement rates increase since giraffe navigate a matrix of human influenced landscape and wild landscape
woody vegetation availability (mean)	mean above-ground woody vegetation biomass of African savannahs and woodlands (25 m)	[52]	as availability of woody biomass in giraffe habitat increases, AKDE size and daily movement rates decrease since resource availability is more reliable
woody vegetation availability (s.d.)	standard deviation of above-ground woody vegetation biomass of African savannahs and woodlands (25 m)	[52]	as availability of woody vegetation in giraffe habitat becomes more spatio-temporally heterogeneous, AKDE size and daily movement will increase since giraffe need to cover greater areas to access patchily distributed resources

The mean home range size for all giraffe was 356.4 km^2 (CI = 301.3–421.5 km^2) with maximum-likelihood estimates ranging from 13.4 km^2 (a female southern giraffe tagged in Etosha Heights Private Reserve in Namibia) to 3859.2 km^2 (a female northern giraffe tagged in Niger). According to the Q-test, the true home range sizes were heterogeneous ($QE_{144} = 11\,172.20$, $p < 0.01$); ($I^2 = 98.32\%$); ($QM_3 = 4.41$, $p = 0.22$), indicating differences in total space use across giraffe. G. giraffa exhibited the largest average home range size (392.1 km^2; CI = 298.0–516.0.6 km^2), followed by G. camelopardalis (379.1 km^2; CI = 293.6–489.5 km^2), G. reticulata (308.9 km^2; CI = 191.6–498.1. km^2 and G. tippelskirchi (205.2 km^2; CI = 114.2–369.6 km^2) (figure 2a). Post hoc tests indicated a marginal difference between G. camelopardalis / G. giraffa and G. tippelskirchi ($p = 0.06$).

The mean average daily distance travelled for all giraffe was 14.1 km (CI = 13.6–14.6 km) with maximum-likelihood estimates ranging from 5.1 km (a female northern giraffe translocated into southern Murchison Falls NP, Uganda) to 24.1 km (a female northern giraffe tagged in the Giraffe Zone in Niger). Daily movement rates were heterogeneous and varied across species ($QE_{147} = 121\,215.2$, $p < 0.001$); ($I^2 = 99.9\%$); ($QM_3 = 12.86$, $p < 0.01$). G. camelopardalis exhibited greatest daily movement rates of 15.1 km day^{-1} (CI = 14.3–16.0 km day^{-1}), followed by G. giraffa (13.7 km; CI = 12.9–14.5 km day^{-1}), G. reticulata (13.5 km day^{-1}; CI = 12.1–15.0 km day^{-1}) and G. tippelskirchi (12.1 km day^{-1}; CI = 10.6–13.7 km day^{-1}) (figure 2b). Post hoc tests showed a significant difference between G. camelopardalis and G. tippelskirchi ($p < 0.01$), and a marginal difference between G. camelopardalis and G. reticulata ($p = 0.07$).

For models evaluating home range size, we found a large variance component attributed to heterogeneity across study sites ($QE_{138} = 7027.6$, $p < 0.01$) (see electronic supplementary
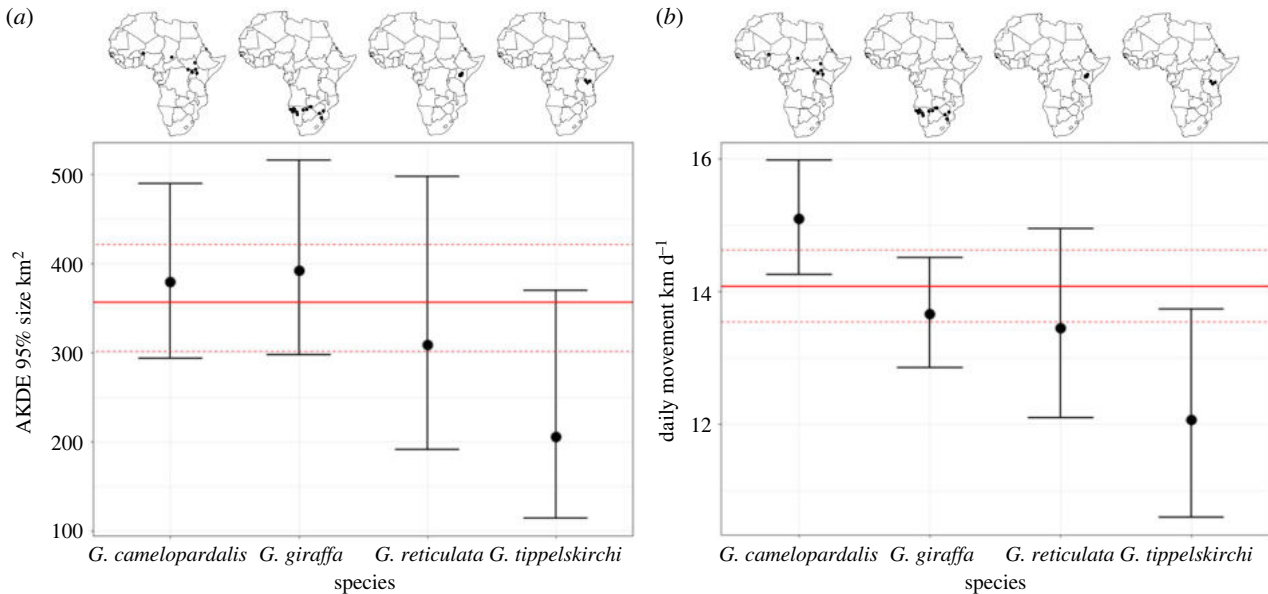
Figure 2. (*a*) Mean 95% AKDE and (*b*) mean daily distance travel for each giraffe species. Error bars represent upper and lower 95% confidence intervals. The solid red line represents the global mean value for all giraffe with the dashed lines representing upper and lower 95% global confidence limits.
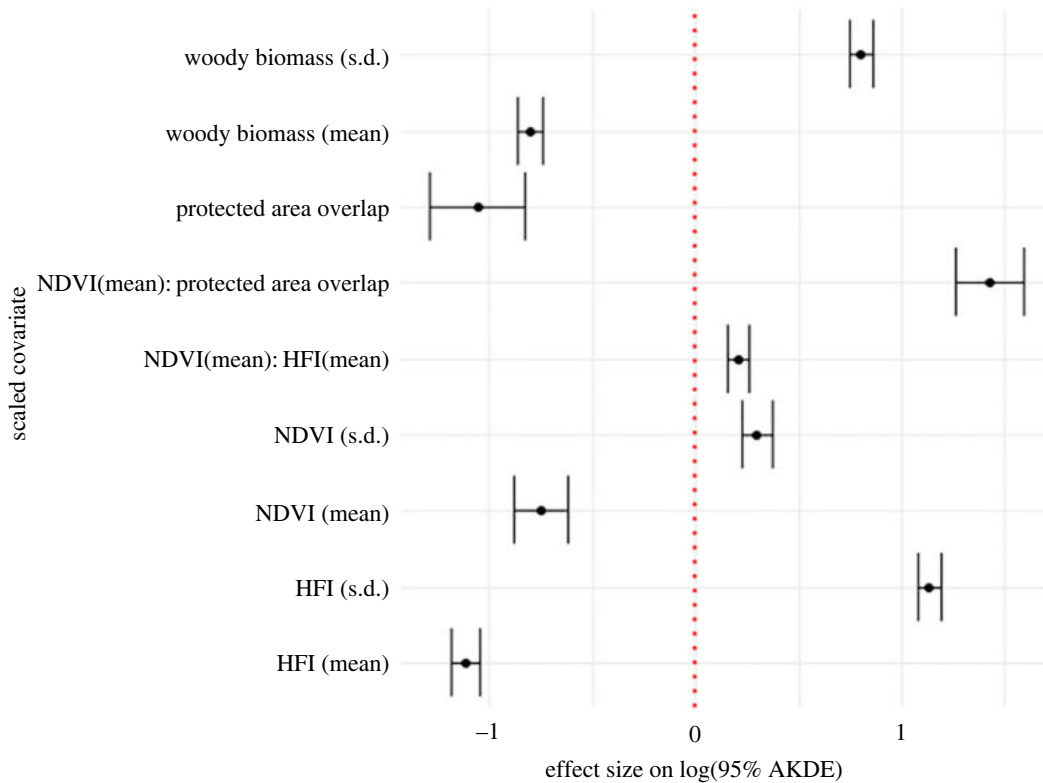

Figure 3. Standardized model coefficients and confidence intervals from the best supported model evaluating environmental and anthropogenic influences on home range size (95% AKDE). Coefficients indicate the influence of each covariate on giraffe space use, with larger magnitude suggesting greater importance.

material, table S4 for study site random intercepts for 95% AKDE models). The omnibus test for multivariate analyses of moderators was significant (QM_{DF9}: 3058.1, $p < 0.01$). The best-supported model had significant positive effects of NDVI (SD) ($p < 0.01$), woody biomass (SD) ($p < 0.01$) and HFI (SD) ($p < 0.01$) on log(95%AKDE) ($p < 0.01$) (figure 3). We found negative effects of NDVI (mean) ($p < 0.01$), protected area overlap ($p < 0.01$), and HFI (mean) ($p < 0.01$) (figure 3). Giraffe in low NDVI areas (fourth quartile of NDVI (mean) values) had home ranges 278% larger than giraffe in high NDVI areas (first quartile of mean NDVI

values). Similarly, giraffe in areas of higher HFI (first quartile of mean HFI values) had 72% smaller home ranges than giraffe in areas with lower HFI (fourth quartile of mean HFI values). We also found significant interactions between NDVI (mean): woody biomass (mean) ($p < 0.01$), and NDVI (mean): HFI (mean), and NDVI (mean): protected area overlap (figure 3). The standard deviation of HFI, the standard deviation of woody biomass, the mean woody biomass, mean NDVI, protected area overlap were the most important predictors in the model as indicated by the relative magnitude of the standardized coefficients (figure 3).
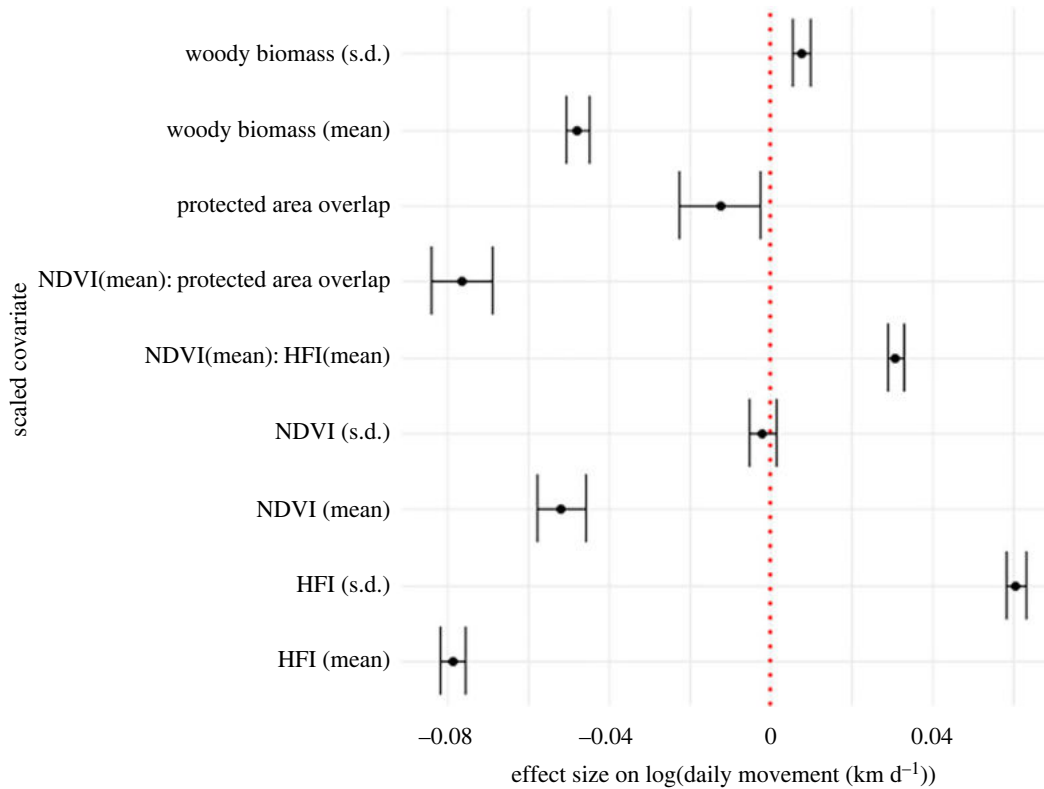
Figure 4. Standardized model coefficients and confidence intervals from the best supported model evaluating environmental and anthropogenic influences on daily movement. Coefficients indicate the influence of each covariate on giraffe space use, with larger magnitude suggesting greater importance.

For models evaluating daily movement rates, we also found a large variance component attributed to heterogeneity across study sites ($Q_{138} = 105\,257.52$, $p < 0.01$) (electronic supplementary material, tables S3 and S5 for random intercepts for study sites). The omnibus test for multivariate analyses for moderators was significant (Q_{DF9}: $14\,223.20$, $p < 0.01$). The best-supported model had significant positive effects of woody biomass (SD) ($p < 0.01$), and HFI (SD) ($p < 0.01$) on log(95% AKDE) ($p < 0.01$) (figure 4). There were significant negative effects of NDVI (mean) ($p < 0.01$), protected area overlap ($p < 0.01$) woody biomass (mean) ($p < 0.01$), and HFI (mean) on daily movements ($p < 0.01$) (figure 4). Giraffe in low NDVI areas (fourth quartile of NDVI (mean) values) had daily movement rates 133% greater than giraffe in high NDVI areas (first quartile of NDVI (mean) values. Similarly, giraffe in areas of higher HFI (first quartile of HFI (mean)) had 41% lesser daily movements than giraffe in areas with lower HFI (fourth quartile of HFI (mean). We also found significant interactions between NDVI (mean): HFI (mean) and NDVI (mean): protected area overlap (figure 4). When evaluating the relative importance of the standard deviation of HFI, the standard deviation of woody biomass, the mean woody biomass, mean NDVI, protected area overlap were the most important predictors in the model as indicated by the relative magnitude of the standardized coefficients (figure 4).

4. Discussion

We used novel applications of CTMM outputs with meta-regression analyses to provide overall space use descriptions for all giraffe species and to evaluate the effects of resource productivity and anthropogenic disturbances on giraffe ranging behaviours at the continental scale. Our systematic study of giraffe ranging behaviours using GPS telemetry data provided home range estimates larger than most other previously reported across all giraffe taxa [36,40,42,43,70–74]. Compared to other large-bodied herbivores, these giraffe home range estimates are generally smaller than African bush elephants (*Loxodonta africana*) across a wide range of systems [75], but larger than reported home range values for African buffalo (*Syncerus caffer*) [76], greater kudu (*Tregelaphus strepsiceros*) [72] and significantly larger than home range size reported for the temperate red deer (*Cervus elaphus*) [77–79]. Moreover, we found significant ecological and anthropogenic effects on space use across their range.

Home range size in giraffe is tightly linked to spatio-temporal variation and heterogeneity in resource availability. Home ranges were small in areas with high mean productivity (i.e. high NDVI and woody biomass) as evident in the home ranges in the mesic savannahs of Uganda's Murchison Falls NP. Similarly, giraffe in Garamba NP in the Democratic Republic of Congo had relatively high mean woody biomass metrics and exhibited among the smallest reported home range sizes (electronic supplementary material, figure S3). Conversely, giraffe home ranges were relatively large in more arid and less woody environments such as the hyper arid deserts of Northwest Namibia (electronic supplementary material, figure S3). These trends support the prediction that relatively high landscape productivity and resource availability maintain smaller ranging behaviours and less daily movement. These results suggest bottom-up impacts related to consistent abundance and quality of forage resources with increased acquisition efficiency of spatio-temporally predictable resources reduce the need for long-distance movements [51,80,81]. Conversely, higher productivity and resource heterogeneity, as measured through the standard deviation of NDVI and woody biomass, were

associated with more expansive home ranges, as evident in the relatively larger home range size and daily movement rates in the spatio-temporally heterogeneous savannahs of Zakouma NP in Chad (electronic supplementary material, figure S3). As resource availability becomes more variable in space and time, giraffe cover larger areas and increase their daily movement rates. For temporally dynamic covariates, such as NDVI, this metric of resource variation incorporates both spatial and temporal heterogeneity. Thus in spatially heterogeneous environments (such as the hyperarid deserts of Northwest Namibia [41] and seasonably variable environments, such as the savannahs of northeastern Uganda [38], this patchy distribution of resources over time necessitates that giraffe move greater distances and range over greater areas to meet resource requirements. Understanding the consequences of environmental variability on giraffe movement behaviours has the potential to improve strategic planning initiatives aimed at restoring giraffe habitat by clarifying space-use requirements associated with local ecological and anthropogenic conditions.

As expected, anthropogenic influences on the landscape also strongly impacted giraffe space use patterns as indicated by the relative magnitude of the standardized coefficient for mean HFI in the 95% AKDE model. At larger scales, HFI had a significant negative effect on home range size and movement rates, suggesting that human-dominated landscapes present important barriers to movements and may limit giraffes' potential to access spatially dispersed resources. For instance, southern giraffe in Zimbabwe's Save Valley Conservancy exhibited small home range sizes and had among the highest reported mean HFI values due to the developed areas at the Conservancy's peripheries (electronic supplementary material, table S1). This finding is consistent with studies that demonstrated reduced movements of wide ranging taxa in anthropogenic dominated landscapes [15]. Contrary to our initial predictions, we found a significant negative effect of protected area overlap on 95% home range size, suggesting that giraffe have smaller home ranges in more protected area landscapes. This effect may potentially be attributed to access to higher quality resources within protected areas limiting the need to cover larger areas of land. Alternatively, hard boundaries associated with human development and fencing on the peripheries of protected areas may restrict giraffe movement and limit ranging capacity [82–86].

There was a strong positive effect of HFI (SD) on home range size and daily movement rates, with relatively high model importance, suggesting that giraffe in landscapes with more spatially heterogeneous human impacts move over greater areas at greater rates potentially because of semi-permeable mixed human-use landscapes between quality habitat patches. The anthropogenic effects on space use are consistent with movement behaviours of other megaherbivores across the continent: including African elephants (*Loxondonta africana* and *Loxodonta cyclotis*) [16], black rhinoceroses (*Diceros bicornis*) [87] and African buffalos (*Syncerus caffer*) [88]. These impacts of anthropogenic disturbance were mediated by the effects of environmental productivity, as indicated by the significant positive interaction between NDVI (mean): HFI (mean) and the significant interactions between NDVI (mean): protected area overlap. As environmental productivity increases, the negative effect of HFI (mean) on home range size increases. Conversely, as environmental productivity increases there is an increasingly negative effect of protected area overlap

daily movements, and an increasingly positive effect on home range size suggesting that in protected areas with productive environments, giraffe daily movements decrease, while overall home range sizes increase. Other studies indicate that larger-bodied animals were more strongly impacted by these negative effects of HFI on space use, suggesting that giraffe, with adult body mass often exceeding 1000 kg, are more strongly adversely impacted by these developments relative to smaller-bodied herbivores [89].

Methodologically, we presented a workflow for evaluating intrataxon variation of animal ranging behaviours using GPS telemetry, CTMM analyses, remotely sensed environmental covariates, and mixed effects meta-regression analyses. This novel application of mixed effects meta-regression analysis incorporates the estimated variability of space use parameter estimates into subsequent models. Previous efforts to evaluate environmental effects on CTMM space use metrics have used point estimates in subsequent linear models without effectively incorporating the variance components of these estimates [10,14,26]. These variance components for individual space use metrics, depending on their magnitude, can be consequential for subsequent inferences (see electronic supplementary material, figure S4). As such, the most technically appropriate methods for their analyses incorporate the variance components of these estimates. We applied available tools commonly used in meta-analyses frameworks to address these issues in a workflow which allowed for the inclusion of study site as a random effect [64]. Our work emphasizes the value of this approach to integrate uncertainty of space use metric inherent to CTMM within the modelling outputs. By using spatio-temporally explicit covariate extraction, we effectively incorporated the environmental conditions experienced by each giraffe at each location in space and time.

Our study shows that environmental and anthropogenic impacts shape giraffe space use and ranging behaviour. Furthermore, our findings support the growing body of evidence that spatio-temporal heterogeneity in resource distribution and anthropogenic disturbances alter animal movement and generally lead to increased ranging behaviours to access necessary resources [90]. Current climate change scenarios project more uncertainty in bioclimatic conditions and significant impacts on biodiversity [91,92]. Additionally, increasing human populations across sub-Saharan Africa, particularly on the peripheries of protected areas may potentially exacerbate fragmentation threats in these areas [86,93]. Using the environmental variability afforded by range-wide studies to model these effects is instrumental in guiding landscape-level conservation initiatives across Africa.

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