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WILDLIFE RESEARCH

Habitat use strategies of African elephants under different seasonal and ecological constraints

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ABSTRACT

Context. Habitat selection is a fundamental process that shapes animal spatial ecology. Species with wide geographic distribution that occupy diverse habitats have to adapt their resource acquisition strategies to maximise their effectiveness under local ecological constraints, leading to intraspecific behavioural variability. Identifying environmental determinants of habitat use pattern and regional intraspecific differences advances our understanding of the ecological underpinnings of animal behaviour and is important in strategising effective conservation and management of free-ranging populations. **Aims.** The aim of this study was to assess individual heterogeneity of habitat selection and use by African elephants under different seasonal and ecological constraints, in order to better understand the processes underlying their spatial behaviour. **Methods.** We investigated the habitat selection pattern of 19 African elephants equipped with satellite-linked GPS-collars in two different ecosystems, resource-rich bushveld bordering Kruger National Park, South Africa (six individuals) and arid savannah of Etosha National Park, Namibia (13 individuals). By constructing individual-specific and population-level resource selection functions (RSFs), we examined seasonal differences of elephant habitat use pattern to identify the underlying ecological mechanisms. **Key results.** Elephants were attracted to surface water in both study areas; but when water availability decreased in arid environment, they showed individual-specific preference in using natural vs artificial water sources. Road networks enabled efficient travel among resource patches, but its use differed between individuals. Areas with higher and more predictable vegetation productivity were generally preferred by elephants in dry season, but in more competitive arid savannah system there were individual/group-specific seasonal differences in resource selection patterns, likely reflecting the social dynamics among individuals. At population-level, the habitat selection pattern was less apparent due to considerable intra-population variability. **Conclusions.** The substantial differences in model coefficients within and between our study populations demonstrate the spatio-behavioural plasticity of elephants under various environmental conditions and suggest that population-level RSFs may over-simplify elephants' socio-ecological complexity. **Implications.** Within the resource competition paradigm, individual-specific habitat selection may be as essential in maintaining population resilience as is the population-level pattern of resource use. Consequently, spatio-behavioural heterogeneity within and between populations should be accounted for in resource selection studies and all subsequent conservation management policies.

Keywords: behavioural plasticity, habitat use strategy, individual heterogeneity, *Loxodonta africana*, resource selection function (RSF), southern Africa, surface water, vegetation productivity.

Introduction

Daily movement of animals is shaped by ecological constraints and resource selection process at different spatial scales (James 1970; Johnson 1980; Getz 2022). The climate and biome impose restrictions on the geographic range of a species (first-order selection; e.g. Peterson 2001; Rotenberry *et al.* 2006; Kanagaraj *et al.* 2019), within which individuals establish their home ranges (second-order selection; e.g. Willems *et al.* 2009;

Vanderwel *et al.* 2012; Yiu *et al.* 2017) that contain preferred habitat patches (third-order selection; e.g. Karczmarski *et al.* 2000; Bennitt *et al.* 2014; Roffler *et al.* 2018). Individuals then exploit the latter by maximising effective resource acquisition within available patches (fourth-order selection; e.g. Zalewski 1997; Menzel *et al.* 2002). Therefore, the spatial behaviour of individuals can vary among and even within populations under different environmental conditions. From the animal's perspective, its habitat use pattern may be viewed as an emergent structure that arises from a series of behavioural decisions motivated by the needs to acquire resources, avoid threats and search for mates (fourth-order) in preferred habitat patches (third-order) that collectively constitute its home range (second-order) within a habitable landscape (first-order). From this 'bottom-up' viewpoint, it becomes apparent that spatio-behavioural variation among individuals, i.e. heterogeneity, either sex-specific or due to ontogenetic stage of life history (Cransac *et al.* 1998; Melzheimer *et al.* 2018), reproductive stage (Long *et al.* 2009; Luisa Vissat *et al.* 2023), body condition (Heithaus *et al.* 2007), social rank (Murray *et al.* 2007; Akbaripasand *et al.* 2014) or personality trait differences (Getz *et al.* 2015; Schirmer *et al.* 2019) can significantly influence individual space use pattern, and ultimately population processes and evolutionary traits of species (Bolnick *et al.* 2011; Dall *et al.* 2012; Getz *et al.* 2016).

Resource selection function (RSF) methods that assess the probability of individuals to use particular types of habitat relative to its availability (Manly *et al.* 2002), have been applied in numerous studies to better understand adaptive resource use of various species (e.g. Leclerc *et al.* 2016; Gedir *et al.* 2020; Reddell *et al.* 2023). One of the most common RSF modelling approaches applies the use-availability study framework, where the environmental/predictor variables (fixed effects) of habitat patches that animals visited (used points) and those of randomly selected locations (available points) are fitted with logistic regression (Boyce *et al.* 2002; Manly *et al.* 2002). To account for among-individual (or among-group) variation, random effects such as individual identity are often included in resource selection studies (Lesmerises and St-Laurent 2017; Fattebert *et al.* 2018; Muff *et al.* 2020) using generalised linear mixed models (GLMM). Most RSF studies include only random intercepts which, although has the advantage of simpler parametrisation, addresses only the baseline differences among individuals (or groups of animals) while assuming they respond to environmental variables in the same way (Ranglack and du Toit 2015; Roffler *et al.* 2018). On the other hand, while the inclusion of random coefficients allows the RSF models to reveal behavioural heterogeneity among individuals (if it exists), the number of model parameters and computational demand increase rapidly with the number of fixed and random effects. Constructing individual-specific RSFs with generalised linear model (GLM) is a simpler and more direct alternative that captures individual behavioural heterogeneity, yet delivers similar results compared to population-level models that include individual identify as random effect (Murtaugh 2007). Individual-specific coefficients also help in addressing behavioural variations that underscore the complexity of animal resource selection (Bastille-Rousseau and Wittemyer 2022).

African elephants (*Loxodonta africana*) are widely distributed across sub-Saharan Africa (de Boer *et al.* 2013) and their spatial behaviour may differ, at times substantially, between populations and ecosystems (Shannon *et al.* 2008*a*; Mramba *et al.* 2017, 2019) as a result of varying resource and habitat choices (Loarie *et al.* 2009; Young *et al.* 2009; Fishlock *et al.* 2016). Elephant interactions with their environment can modify local habitats (Pringle 2008; Nasseri *et al.* 2011), changing vegetation structure and composition (Baxter and Getz 2005, 2008; Guldemond *et al.* 2017) by affecting the recruitment and survival of various plant species (Lombard *et al.* 2001; Jacobs and Biggs 2002). These effects can interact with abiotic factors such as fire (Baxter and Getz 2008; Moncrieff *et al.* 2008) and drought (O'Connor *et al.* 2007), further amplifying the impacts on the habitat.

Even within populations, elephant habitat use pattern is subject to physiological and socio-behavioural differences between sexes (Shannon *et al.* 2008*a*, 2013; Evans and Harris 2012). Male elephants leave natal groups and became solitary after reaching sexual maturity, while females stay with family units in a fission-fusion society (Lee *et al.* 2011; Moss and Lee 2011). Shaped by complex social dynamics between individuals and social units (Wittemyer *et al.* 2007; O'Connell-Rodwell *et al.* 2011), elephant spatial dynamics are similarly complex leading to intra-population heterogeneity in movement and habitat use pattern. Several recent studies (e.g. Bastille-Rousseau and Wittemyer 2019, 2022; Beirne *et al.* 2021) suggest that ecological footprint of elephants can differ substantially among individuals, with some being more impactful than others. Unravelling individual differences in elephant habitat selection can support conservation planning by advancing our understanding of elephant flexibility and resilience in using landscapes. This in turn may assist in identifying key habitats and prioritising conservation areas, or priority zones within larger conservation areas (Johnson *et al.* 2004; Squires *et al.* 2013; Zeller *et al.* 2017), thus aiding in conservation management and mitigation of human-elephant conflict.

In this study, we investigate habitat selection of elephants in two different African ecosystems, the bushveld environment of the Associated Private Nature Reserves (APNR) at the central-western perimeter of Kruger National Park (KNP), South Africa; and the arid savannah system of the Etosha National Park (ENP), Namibia. We constructed seasonal RSFs separately for each satellite-tracked elephant to examine their third-order habitat selection pertaining to surface water, road network and habitat productivity, and how that may vary among individuals. By quantifying the influence of different environmental factors on individual elephant habitat use patterns across seasons and study areas, we assess their resource selection and habitat use strategies under different

seasonal and ecological constraints. We also discuss the potential processes behind the spatio-behavioural intricacies and individual heterogeneity of elephant habitat selection pattern.

Materials and methods

Study areas

The Associated Private Nature Reserves (APNR) encompass a bushveld habitat located at the central-western boundary of the Kruger National Park (KNP) in South Africa (Fig. 1*a*). Since 1993, most fences within and between the APNR and KNP were removed, facilitating free movement of wildlife (Prins *et al.* 2012). Natural rivers and abundant artificial waterholes in APNR create a water-rich environment even in dry season (Henley 2014). A mosaic of tourist camps and lodges, and human settlements are interconnected via a dense network of gravel roads. A variety of woody and herbaceous vegetations, including *Senegalia* (*Acacia*) *nigrescens*, *Combretum apiculatum*, *Colophospermum mopane*, *Urochloa mosambicensis*, *Bothriochloa radicans*, *Digitaria eriantha* and *Panicum maximum* provide abundant supply of forage resources for elephants in the area (van der Waal *et al.* 2011).

The Etosha National Park (ENP) is an arid savannah system in the north of Namibia (Fig. 1*b*). Several large natural pans at the centre and northeast of the park provide seasonal surface water, while sparsely distributed man-made waterholes offer perennial water supply for the wildlife. Road network connects campsites with lodges and waterholes throughout the park. The ENP is dominated by grassland and steppe species such as *Leucosphaera baenesii*, *Salsola tuberculate* and *Monechma genistifolium*, as well as shrub and tree savannah species such as *Colophospermum mopane*, *Catophractes alexandri*, *Vachellia* (*Acacia*) *nebrownii* and *Terminalia prunioides* (du Plessis 1999).

Elephant spatial data

Location data of six elephants (three males; three females) in APNR and 13 elephants in ENP (five males; eight females), each fitted with satellite-linked global positioning system (GPS) collars (Africa Wildlife Tracking™, South Africa; Henley 2014; Tsalyuk *et al.* 2019), were collected from August 2009 to August 2016 and from October 2008 to March 2014 in APNR and ENP, respectively. All collared male elephants were sexually mature adults that have left their natal groups, and female elephants were from different family groups (Supplementary Table S1). All tracking data were regularised at 4-h fix interval, and subset into 4-month seasonal tracks representing wet and dry season, based on rainfall records provided by the South African Weather Services (for APNR)

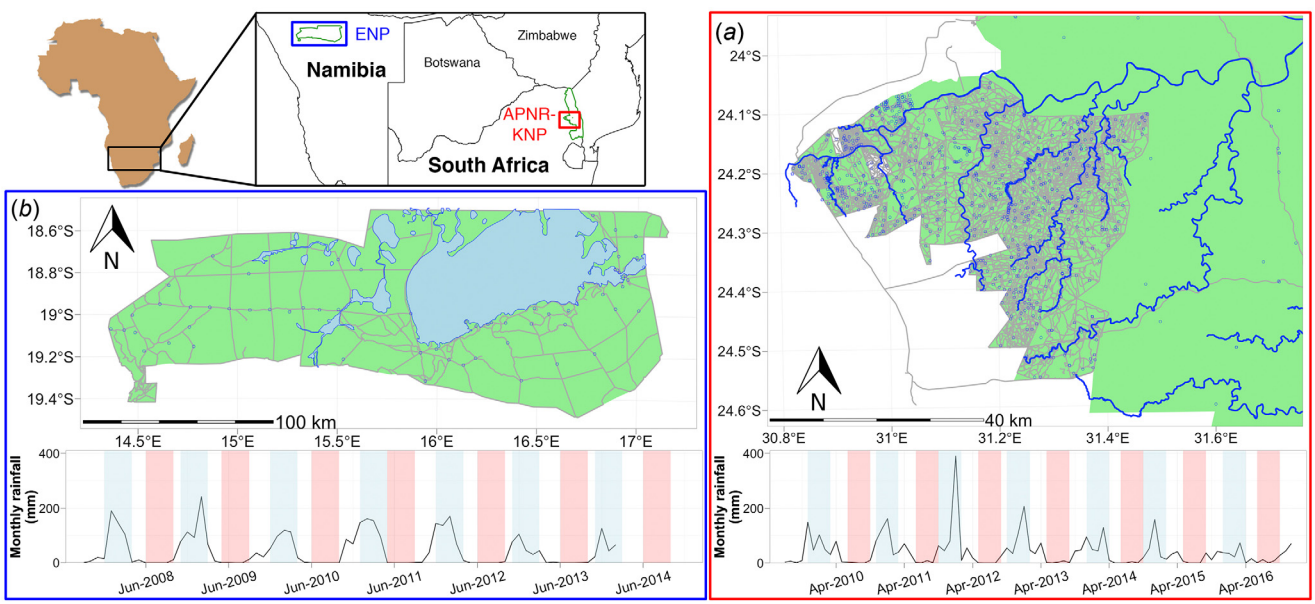


Fig. 1. Location of two study areas, (*a*) the Associated Private Nature Reserves (APNR) at the western perimeter of the Kruger National Park (KNP), South Africa and (*b*) the Etosha National Park (ENP), Namibia. Blue lines and blue areas on the maps represent rivers and pans in the APNR and ENP, respectively; blue circles indicate the location of artificial waterholes; grey lines indicate the road network. Rainfall records in the APNR, from July 2009 to December 2016, were sourced from the South African Weather Services. Rainfall records in the ENP were collected and averaged from eight stations across the park from September 2007 to February 2014 (as records were not available beyond February 2014, part of the 2014 wet and dry seasons were projected based on previous rainfall pattern). The wet season (indicated with blue bars) is defined as the 4 consecutive months with the highest rainfall; the dry season (indicated with pink bars) is defined as the 4-month period with the lowest rainfall. As the onsets of wet and dry seasons are governed by the rainfall, the specific date marking the beginning of the seasons may vary slightly from year to year, but the duration is fixed in this study at 4 months.

and collected from eight stations in the ENP (Fig. 1). Collars of some elephants (primarily in the APNR) required battery replacement during the study period, which resulted in occasional gaps in the tracking data. To ensure an accurate representation of elephant habitat use pattern, only tracks with 70% or above successful fix rate (i.e. number of GPS fixes *successfully recorded* divided by number of GPS fixes *expected* in a 4-month period) were used for subsequent analyses.

Environmental predictor variables

To ensure the comparability of the modelling results, we used the same set of five environmental variables available in both study areas. These are the distance to the nearest rivers (*river_ldist*)/water pans (*pans_ldist*) and waterholes (*wtpt_ldist*), distance to the nearest roads (*road_ldist*), median seasonal vegetation productivity (*ndvi_median*) and within-season productivity variability (*ndvi_var*). Rivers and water pans were considered natural water sources in the APNR and ENP, respectively and were differentiated from artificial water sources (waterholes) because elephants respond to natural and artificial water sources differently (Smit *et al.* 2007*a*). The distance to roads was included as a proxy for potential vehicle/human disturbance to elephants (Gaynor *et al.* 2018). All distances were measured in metres using environmental feature shapefiles of the APNR and ENP with Universal Transverse Mercator (UTM) zone 36S and UTM zone 33S coordinate system projections, respectively, in R ver. 3.5.2 (R Core Team 2018). The distance was then log transformed, i.e. log(distance + 1 m), to underscore the influence of the features at close range while balancing the magnitude of the effect with increasing distance.

Moderate Resolution Imaging Spectroradiometer (MODIS) 16-day 250 m × 250 m Normalised Difference Vegetation Index (NDVI) was used to estimate vegetation productivity. Composites of MODIS images were compiled for each wet and dry season, defined by rainfall pattern (Fig. 1), to capture the changes of productivity over time. The median NDVI (*ndvi_median*) was calculated for each pixel in each 4-month season to represent the seasonal vegetation productivity at the 250 m × 250 m habitat scale. The variance of NDVI (*ndvi_var*) for each pixel in each wet and dry season was calculated to denote the within-season variability of productivity (Bastille-Rousseau *et al.* 2020). MODIS data was downloaded from NASA EARTHDATA website (https://search.earthdata.nasa.gov/search).

The effect of collinearity of the predictor variables was estimated using the variance inflation factor (VIF). All five variables were retained and used in subsequent modelling as VIF was <5 (Graham 2003; Leclerc *et al.* 2016).

Resource selection functions

To quantify the importance of various environmental factors on elephant habitat selection, we built seasonal RSFs within a use-availability analytical framework (Manly *et al.* 2002). Because we are interested in individual-specific responses to environmental variables, as opposed to the population-level responses, seasonal RSFs were constructed separately for each elephant. As the duration of GPS collar deployment varied among individuals, with some being collared for less than a year, we did not include year as a random effect for result comparability. Thus, generalised linear models (GLMs) were used. Seasonal home ranges of individuals were constructed and defined as the 95% utilisation distributions using 4-hourly location fixes with Time-scaled Local Convex Hull (T-LoCoH) method with R-package '*tlocoh*' (Lyons *et al.* 2013). The number of points used for local hull construction was determined as the square root of the number of location fixes in each seasonal track, i.e. $k = \sqrt{n}$ (Getz *et al.* 2007), and the time-scaling factor, *s*, was set at a value that equalised the weightings of spatial distance and temporal distance between fixes 1 day apart for each seasonal track (Lyons *et al.* 2013). Location fixes within individual's seasonal home range were considered as used points. Available points were randomly sampled within the seasonal home range at 1:10 used-to-available point ratio (Fieberg *et al.* 2021).

The five environmental predictor variables (indicated above) were modelled as fixed effects. For temporally sensitive variables (i.e. *ndvi_median* and *ndvi_var*), values at the used and available points were extracted from the same composite of MODIS images of that season. All environmental variables were standardised, i.e. centred by subtracting mean value and scaled by dividing by standard deviation (Schielzeth 2010). The wet and dry season RSFs were constructed for each individual using the '*glm*' function in R ver. 3.5.2.

A set of six *a priori* candidate models (Table 1) was tested. The Akaike information criterion (AIC) and Akaike weights (*w*) were calculated to identify the best-fitting models, i.e. *w* higher or equal to 0.95 (Buckland *et al.* 1997; Burnham and Anderson 2002). In case of model uncertainty, i.e. equivocal models with $\Delta AIC \leq 6$ (Richards 2005) and cumulative Akaike weight added up to 0.95 (acc $w \geq 0.95$; Symonds and Moussalli 2011), multi-model inference was performed by model averaging. The averaged coefficient estimates, weighted by Akaike weight (*w*) of the equivocal models, and adjusted standard error (Buckland *et al.* 1997) were calculated using R-package '*MuMIn*' ver. 1.43.17 (Bartoń 2009).

To evaluate the population-level seasonal resource selection pattern for each study site, the coefficient estimate and standard error of each environmental variable were calculated as the weighted average of the individual-specific RSF results, where the weight is proportional to the reciprocal of individual standard error (Murtaugh 2007). We refer to this as the '*averaged*' model. Generalised linear mixed models (GLMMs) were also constructed using the '*glmer*' function in R-package '*lme4*' (Bates *et al.* 2015) with logit link function. Elephant IDs were set as random effects to allow for individual-specific response to each environmental variable, i.e. the inclusion of random intercept and random coefficient (random slope). We refer to this as the '*glmm*' model. For comparison, another

Table 1. Six *a priori* candidate models used to construct resource selection functions (RSFs).

a	Predictor variables[A]				
	river_ldist/pans_ldist[B]	*wtpt_ldist*	*road_ldist*	*ndvi_median*	*ndvi_var*
Model 1 (global model)					
Water + road + productivity and variability	✓	✓	✓	✓	✓
Model 2					
Water + productivity and variability	✓	✓		✓	✓
Model 3					
Water + productivity	✓	✓		✓	
Model 4					
Water	✓	✓			
Model 5					
Productivity and variability				✓	✓
Model 6					
Productivity				✓	

b	APNR		ENP	
	Wet	Dry	Wet	Dry
Model 1	0.85 (0.24–1.00)	0.65 (0.26–1.00)	0.81 (0.33–1.00)	0.53 (0.24–1.00)
Model 2	0.08 (0.00–0.34)	0.33 (0.00–0.73)	0.13 (0.00–0.55)	0.36 (0.00–0.73)
Model 3	0.06 (0.00–0.38)	0.02 (0.00–0.09)	0.04 (0.00–0.22)	0.11 (0.00–0.49)
Model 4	0.01 (0.00–0.04)	0.00 (0.00–0.00)	0.00 (0.00–0.00)	0.00 (0.00–0.00)
Model 5	0.00 (0.00–0.00)	0.00 (0.00–0.00)	0.01 (0.00–0.14)	0.00 (0.00–0.00)
Model 6	0.00 (0.00–0.00)	0.00 (0.00–0.00)	0.00 (0.00–0.01)	0.00 (0.00–0.01)

Environmental predictor variables in each candidate model are listed in (*a*), including log distance to the nearest rivers (*river_ldist*), log distance to the nearest pans (*pans_ldist*), log distance to the nearest waterholes (*wtpt_ldist*), log distance to the nearest roads (*road_ldist*), seasonal median of NDVI (*ndvi_median*) and within-season variance of NDVI (*ndvi_var*). The averaged Akaike weights (*w*) of each candidate model across the individual-specific seasonal resource selection functions are presented in (*b*), with the minimum and maximum Akaike weights (*w*) of each candidate model given in parentheses.

[A]All predictor variables were standardised (centred and scaled).

[B]*river_ldist* was used in APNR models, *pans_ldist* was used in ENP models.

population-level RSF was constructed in each study area by combining all data points (used and available) regardless of individual identity using GLM, referred to as the '*combined*' model. Multi-model inference was carried out by model averaging using R-package '*MuMIn*' (Bartoń 2009) as described above, when equivocal models were identified.

Ethics approval

All field work and collaring operations in APNR were carried out under SANParks permit (SANParks ID: judith1547.22), and in ENP under the Ministry of Environment and Tourism (MET) permit (permit no.: 1220/2007).

Results

A total of 12 individual-specific seasonal RSFs were constructed with the APNR dataset (wet: 6; dry: 6), and 24 RSFs were constructed with the ENP dataset (wet: 13; dry: 11). The global model (model 1) was the unequivocal best-fitted model ($w \geq 0.95$) for the majority of cases (41.67%; Tables S2 and S3). The remaining had equivocal best-fitted models ($\Delta AIC \leq 6$, acc $w \geq 0.95$) consisting of either model 1 and 2 (30.56%) or model 1, 2 and 3 (22.22%).

In the APNR, the coefficient estimates of *river_ldist* (Fig. 2*a*), *wtpt_ldist* (Fig. 2*b*) and *road_ldist* (Fig. 2*c*) were predominantly negative, indicating that the probability of selection generally decreased as the habitat was further away from rivers, waterholes and roads. For each individual, the coefficient estimates of *river_ldist* and *wtpt_ldist* in wet season were less negative than those in dry season, and the magnitude of the seasonal change was greater in males than females (Fig. 2*a*, *b*). Elephants generally selected areas near road network, but more so males than females (Fig. 2*c*). The coefficient estimates of seasonal vegetation productivity (*ndvi_median*) were generally small and close to zero in wet season but increased in dry season (Fig. 2*d*). The coefficient estimates of within-season

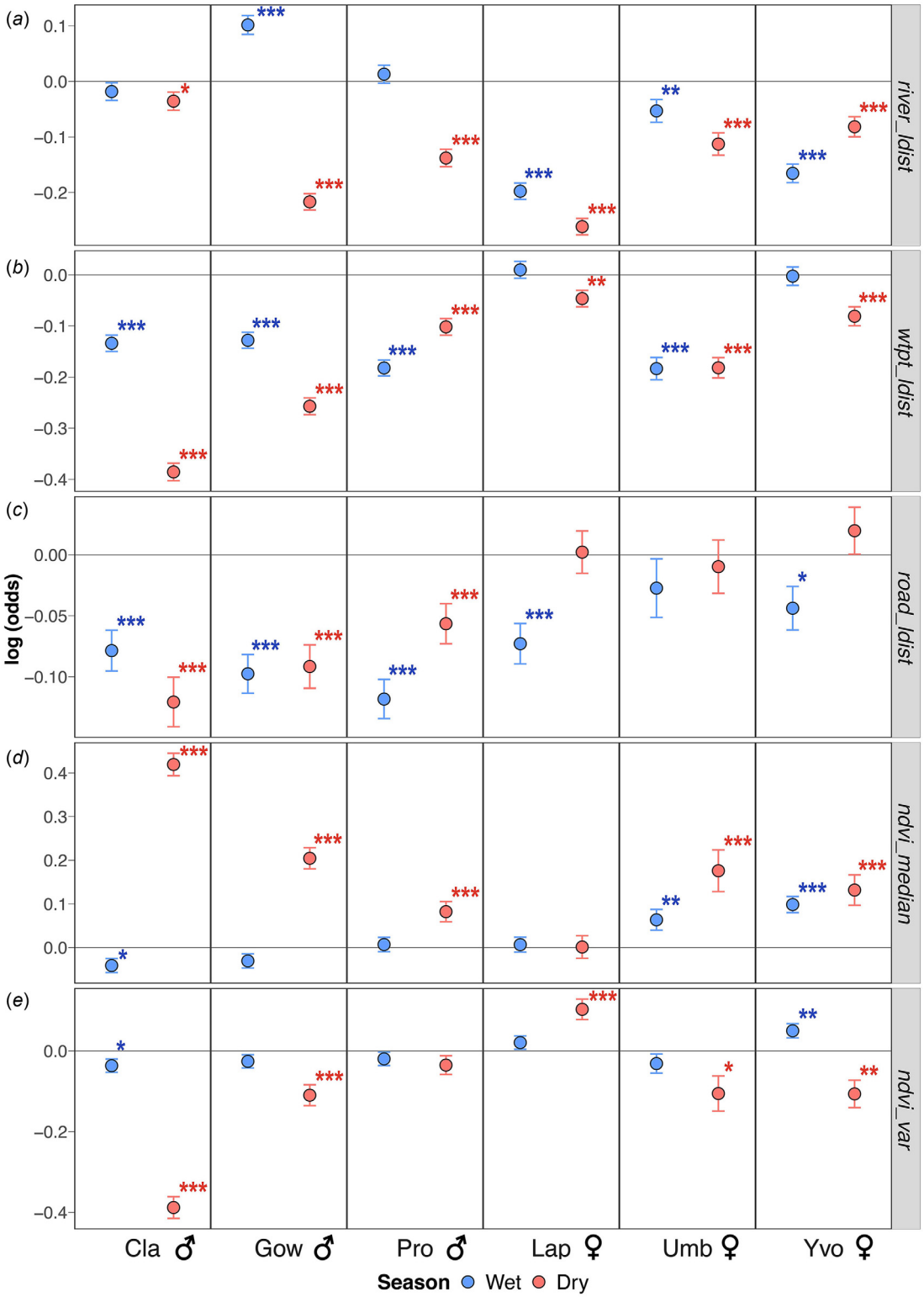


Fig. 2. The coefficient estimates and standard error bars of the environmental variables in individual-specific RSFs of the APNR elephants (male: Cla, Gow, Pro; female: Lap, Umb, Yvo). Variables include (*a*) log distance to rivers (*river_ldist*), (*b*) log distance to water points (*wtpt_ldist*), (*c*) log distance to roads (*road_ldist*), (*d*) seasonal vegetation productivity (*ndvi_median*) and (*e*) within-season variability of productivity (*ndvi_var*). Asterisks indicate the significant *P*-value of the predictor variables (*P*-value < 0.001 '***'; <0.01 '**'; <0.05 '*').

productivity variability (*ndvi_var*) were similarly small in wet season but became negative in dry season for both sexes (with only one exception; Fig. 2*e*).

In the ENP, the selection pattern for water pans was highly inconsistent between individuals and seasons (Figs 3*a* and 4*a*); and similarly so for the coefficient estimates of log distance to waterholes (*wtpt_ldist*) in wet season, while those in dry season were generally negative or close to zero (Figs 3*b* and 4*b*). The selection for roads was generally positive but weak and varied among individuals (Figs 3*c* and 4*c*). Higher vegetation productivity (*ndvi_median*) was generally preferred by elephants in both seasons, but the direction and magnitude of the seasonal change of this preference differed between individuals (Figs 3*d* and 4*d*). The seasonal change of the *ndvi_var* and *ndvi_median* coefficients for each ENP elephant seemed interrelated, but the pattern differed between sexes. Among males, individuals that displayed higher *ndvi_median* coefficients in dry season also had higher *ndvi_var* coefficients, and *vice versa* (Fig. 3*d*, *e*); while females with higher *ndvi_median* coefficients in dry season had lower coefficients of *ndvi_var* when the productivity declined (Fig. 4*d*, *e*), similarly as females in APNR.

The '*averaged*', '*glmm*' and '*combined*' population-level RSF models generally yielded similar results in both seasons and study areas (Fig. 5, Tables S4 and S5). The '*glmm*' model, however, provided additional means to estimate individual responses (as random coefficients) that the other approaches did not. In the APNR, elephants selected for habitat near water, both natural and artificial, in both seasons; and in the ENP they were more likely to use habitat patches near waterholes in dry season. Road network was selected for in both study areas. Areas of high vegetation productivity were used more often in dry season than wet season. In the APNR, elephants preferred habitat with less variable productivity in the dry season, while the ENP elephants generally did not show any preference. The population-level standard error of the coefficient estimates for most environmental variables was generally small in all three models (Fig. 5). In the mixed models '*glmm*' where individual elephants were included as random effects, the random coefficients suggested considerable variations among individuals which agreed with the results of the individual-specific models (Figs 2–4). However, because of the intra-population differences, the coefficient values in these population-level RSFs, including the mixed models, were much closer to zero when compared with individual RSFs.

Discussion

The individual-specific resource selection functions (RSFs) of elephants in two different African ecosystems revealed that elephant habitat selection pattern differs not only between seasons and study areas, but also among individuals within the same population. The results underscore elephant's diverse habitat-use strategies and highlight their complex behavioural responses to environmental features – such as surface water, road network, vegetation productivity and its variability – under different seasonal ecological regimes.

Surface water is one of the most important environmental features in elephant habitat use (de Beer and van Aarde 2008; Purdon and van Aarde 2017; Valls-Fox *et al.* 2018), especially during the dry season (Smit *et al.* 2007*a*; Bastille-Rousseau *et al.* 2020). In both study areas, elephants were generally attracted to water sources, more so in the dry than in wet season (Figs 2*a*, *b*, 3*a*, *b* and 4*a*, *b*). This can be attributed to their daily water requiremnts (Chamaillé-Jammes *et al.* 2013; Polansky *et al.* 2015). As calves have high water turnover rate and are susceptible to dehydration (Beuchat 1990), and lactating females are under water stress to maintain milk production (Parrot 1996), family groups may need to prioritise water accessibility throughout the year, resulting in smaller seasonal differences in their selection of habitats close to water. Males on the other hand, are more tolerant of water stress and thus capable of roaming further from water sources in search of food and mates (Stokke and Du Toit 2002).

Artificial waterholes were generally preferred over natural water sources in both study areas. While this seems to disagree with findings that elephants prefer riverine areas for additional resources, such as shade and higher quality forage (Ntumi *et al.* 2005; Smit *et al.* 2007*a*), there is also a body of evidence suggesting that elephants utilise artificial waterholes as primary or supplementary water source when those become available (Smit *et al.* 2007*b*; Purdon and van Aarde 2017; Wilson *et al.* 2021). In the APNR, high abundance of artificial waterholes and rich vegetation likely reduces elephant's attraction to seasonal rivers and the surrounding riparian zone compared with their conspecifics in the Kruger National Park (Smit *et al.* 2007*a*, 2007*b*; Purdon and van Aarde 2017). On the other hand, given the seasonal fluctuation and patchy distribution of natural water pans in the ENP, elephants likely favour a stable supply of water from the relatively easy-to-access waterholes (Leggett 2006).

It is apparent that the differences in surface water availability between the two study areas affect the elephants' dependence on water and their pattern of habitat selection. In the APNR, natural rivers and artificial waterholes provide a stable supply of surface water (Henley 2014) that enables relatively free movement of elephants year-round. Hence their selection for habitat close to water was relatively stable across seasons and the wet-to-dry seasonal change was consistent and comparable among individuals (Fig. 2*a*, *b*). In the arid environment of ENP, however, the seasonal selection for different types of water source (natural pans vs artificial waterholes) differed considerably between individuals (Figs 3*a*, *b* and 4*a*, *b*). Elephants that displayed strong preference for natural pans in the dry season were less affected by the change of seasons in their use of artificial waterholes

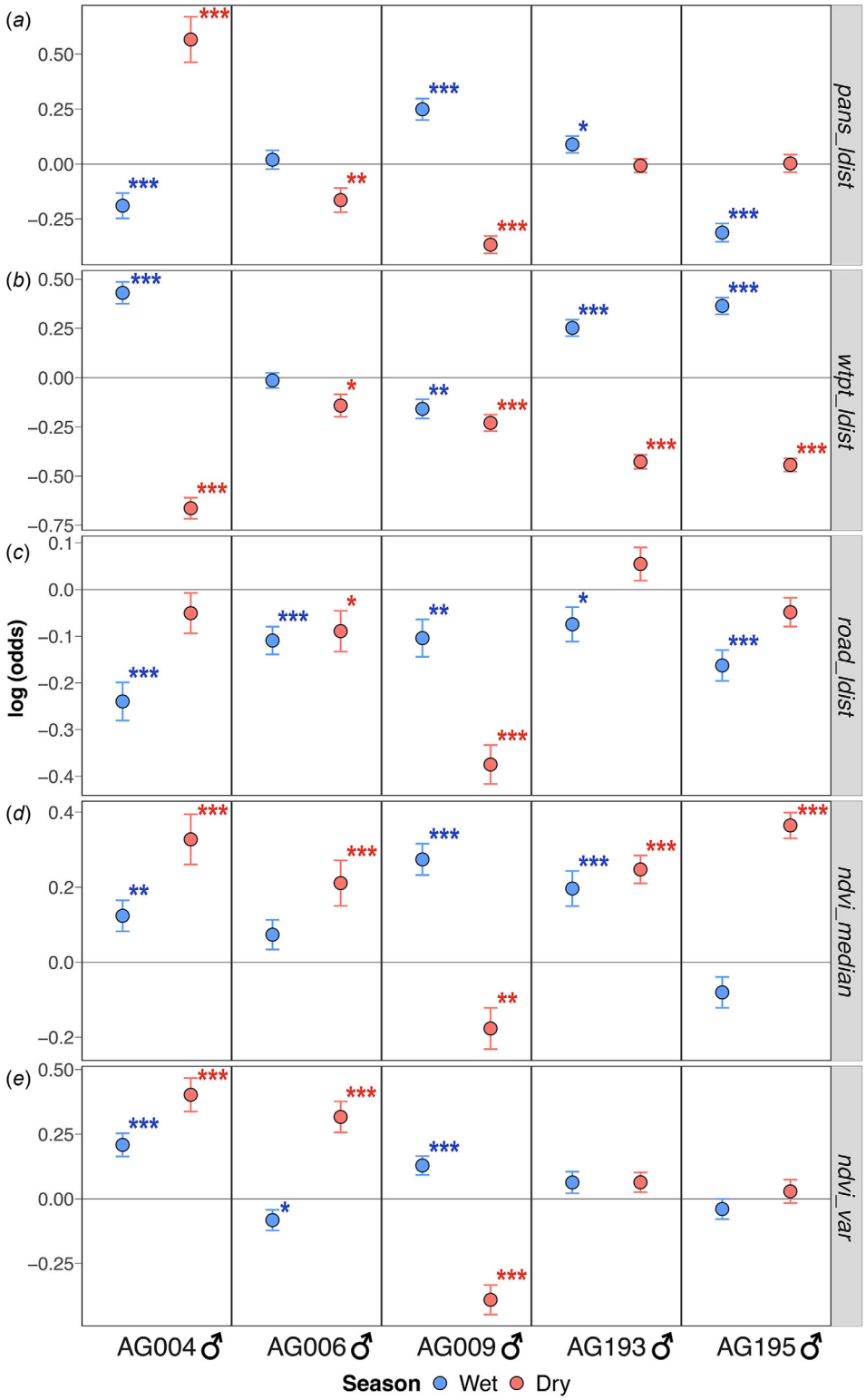


Fig. 3. The coefficient estimates and standard error bars of the environmental variables in individual-specific RSFs of the ENP male elephants. Variables include (*a*) log distance to pans (*pans_ldist*), (*b*) log distance to water points (*wtpt_ldist*), (*c*) log distance to roads (*road_ldist*), (*d*) seasonal vegetation productivity (*ndvi_median*) and (*e*) within-season variability of productivity (*ndvi_var*). Asterisks indicate the significant *P*-value of the predictor variables (*P*-value < 0.001 '***'; <0.01 '**'; <0.05 '*').

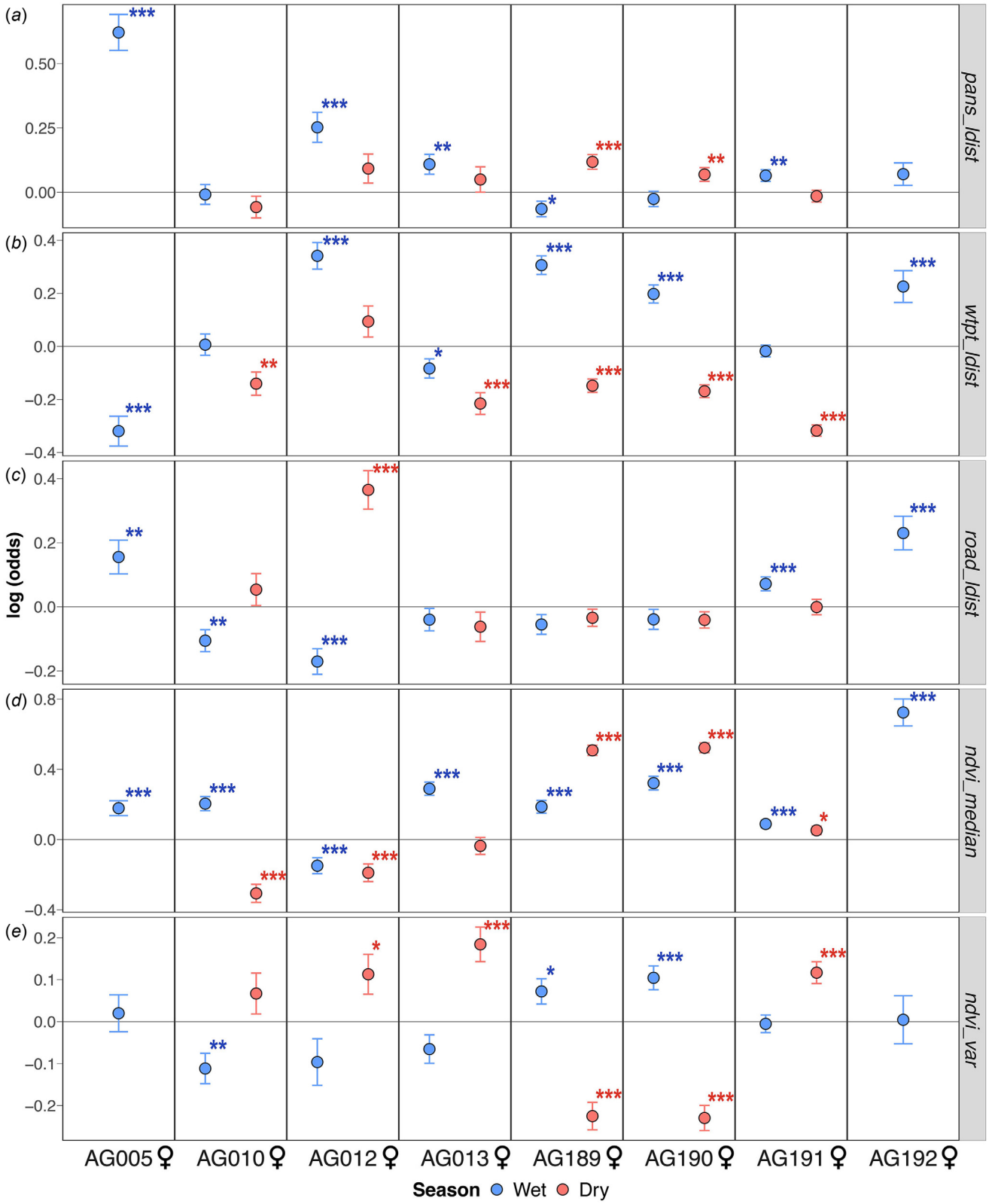


Fig. 4. The coefficient estimates and standard error bars of the environmental variables in individual-specific RSFs of the ENP female elephants. Variables include (*a*) log distance to pans (*pans_ldist*), (*b*) log distance to water points (*wtpt_ldist*), (*c*) log distance to roads (*road_ldist*), (*d*) seasonal vegetation productivity (*ndvi_median*) and (*e*) within-season variability of productivity (*ndvi_var*). Asterisks indicate the significant *P*-value of the predictor variables (*P*-value < 0.001 '***'; <0.01 '**'; <0.05 '*').

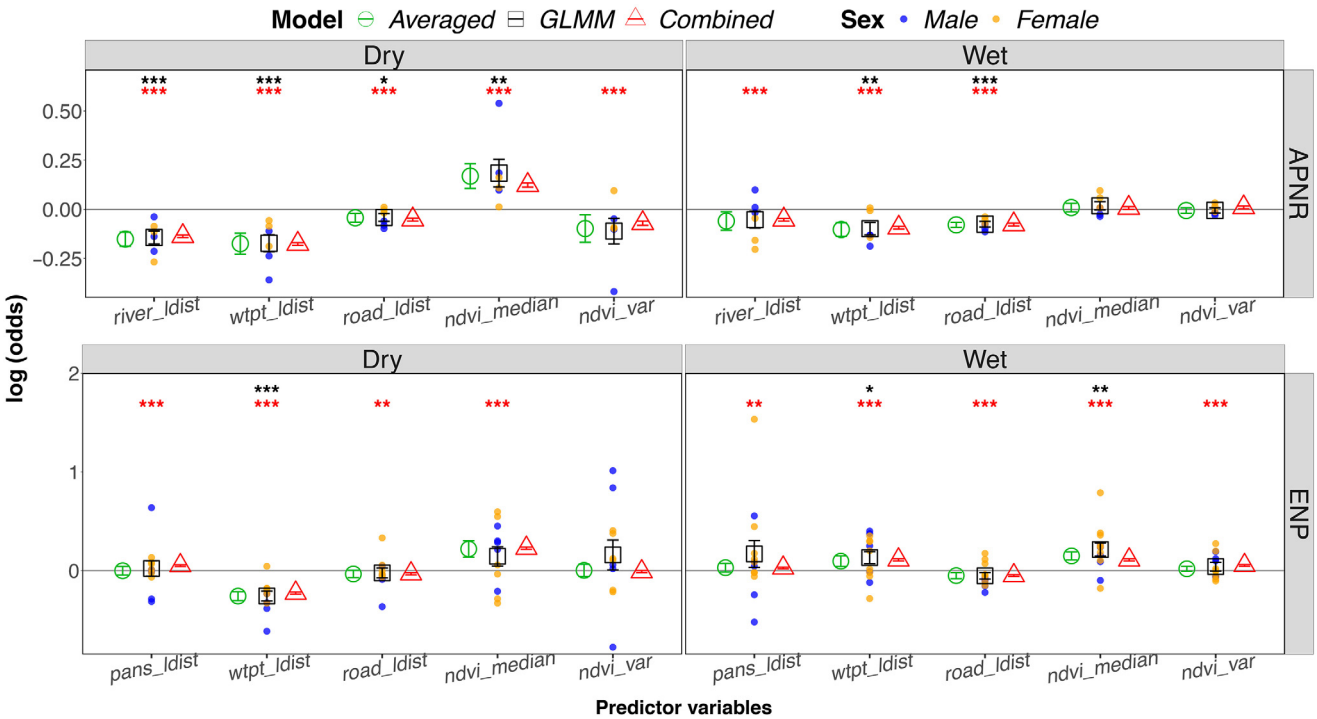


Fig. 5. The population-level RSF coefficient estimates calculated by taking the average of the individual-specific model results ('*averaged*' model; green circles), mixed effect model with individual elephants as random effect ('*glmm*'; black squares) and '*combined*' model (red triangles) of the APNR and ENP elephants. Asterisks indicate the significant *P*-value of the '*glmm*' and '*combined*' model predictor variables (*P*-value < 0.001 '***'; <0.01 '**'; <0.05 '*'). Blue and orange dots represent the random coefficient estimates of individual elephants for each predictor variable in the '*glmm*' model (blue = males; orange = females). For further details, see Table S4 and S5 in Supplementary material available online.

(e.g. AG006, AG009, AG012), i.e. smaller seasonal decrease of *wtpt_ldist* coefficient; while those that only infrequently used natural pans displayed strong selection for waterholes in the dry season (e.g. AG004, AG189, AG191). The seasonal differences in the selection for the types of water source among the ENP elephants are likely individual-specific behavioural responses to the scarcity of surface water in arid environment. Individuals and family groups adjust behaviourally (O'Connell-Rodwell *et al.* 2011; Ferry *et al.* 2016) and spatially (Wittemyer *et al.* 2007, 2008) their utilisation of scarce resources and habitats to minimise intraspecific competition and to avoid potential conflicts. The seasonal utilisation of pans versus waterholes seems to be complementary of one another in response to their availability during dry season, where elephants always stay in close proximity to one of the water sources, underscoring the importance of surface water in elephant's day-to-day habitat use.

In both study areas, elephants were generally attracted to the road network (Figs 2*c*–4*c*). This was evident despite the fact that the proximity of roads may cause disturbance (Blake *et al.* 2008) and pose a risk of injury, even death, and is therefore often avoided by animals (Dussault *et al.* 2012; Prokopenko *et al.* 2017), especially those targeted by hunters and poachers (Stokes *et al.* 2010; Muposhi *et al.* 2016). In the APNR and ENP, however, ivory poaching is not as severe as in other reserves across Africa (Wittemyer *et al.* 2014), while the connection between various resource patches that the road network offers may lower the energetic costs of movement (Gaynor *et al.* 2018; Tsalyuk *et al.* 2019) especially in areas with either none or minimal risk (Chibeya *et al.* 2021). Our study elephants are also habituated to human and vehicle presence by the long history of human settlement in the APNR and tourism in both areas. Speed limits (30–50 km/h in the APNR, 60 km/h in the ENP) and the type of traffic (primarily wildlife safari) further reduce the chance of incidental injury by traffic as vehicles often slow down or stop when elephants are around. However, this does not imply that vehicles and tourists pose no disturbance to elephants (Weibull and Eriksson 1998; Szott *et al.* 2019). In fact, the different response to roads that we noted between sexes (Fig. 2*c*) and among individuals (Figs 3*c* and 4*c*) may be a combined result of previous exposure to vehicles, varying tolerance to disturbance, and perhaps personality traits (e.g. such as boldness, neophobia, etc.) of individuals or family groups (Dammhahn and Almeling 2012).

When food resources are rich and abundant, elephants are less selective and generally opt for a more diverse diet for nutritional balance over pure energy gain (Codron *et al.* 2012; Pretorius *et al.* 2012). On the contrary, they are less

explorative and prefer habitats with more predictable food supplies when resources are scarce (Young *et al.* 2009; Tsalyuk *et al.* 2019). In our study, elephants in the bushveld environment of APNR were generally less selective of highly productive areas during wet season but were drawn to habitat with high vegetation productivity in dry season (Fig. 2*d*). Such tempered effect of vegetation productivity on elephant movement was also observed elsewhere in a productive ecosystem when resources are relatively abundant (Wall *et al.* 2024). The selection pattern of within-season productivity in the APNR was similar for all individuals – elephants were more selective of habitat with higher temporal stability of NDVI (i.e. woodlands; Archibald and Scholes 2007) in dry season than in wet season (Fig. 2*e*). While it could be argued that elephants use woodlands for shade and thermoregulation, it is not likely in our case as the selection for woodlands increased in dry season, and the dry season occurs in winter in both APNR and ENP. Instead, the seasonal change in selectivity may reflect their forage strategy in response to resource availability (Pretorius *et al.* 2012) and the shift from graze-dominated to browse-dominated diet in dry season (Codron *et al.* 2006; Kos *et al.* 2012; Okello *et al.* 2015). The increased utilisation of woodlands, which provide stable resource supply for elephants in the APNR-KNP region in dry season (Jacobs and Biggs 2002; Shannon *et al.* 2008*b*), likely explains the observed avoidance of habitats that have unpredictable productivity in the dry season.

In the ENP however, low vegetation productivity (du Plessis 1999), particularly in the dry season, appears to give rise to a varying pattern of habitat selection and use by individuals across seasons. When resources are abundant during the wet season, vegetation productivity had a positive effect on the probability of elephant presence similarly across most individuals. However, when competition for forage increases in the dry season, individuals responded differently to habitat productivity and its variability. The sociality of elephants can play a role in the observed behavioural differences where the interactions among individuals and social units may influence their movement (Wittemyer *et al.* 2007; Allen *et al.* 2020). However, all collared elephants in our study were either independent adult males or females from distinct social units, thus the observed spatial pattern cannot be attributed to intra-group (herd) dynamics. On the other hand, although we were not able to examine the dominance hierarchies of the ENP elephants, it cannot be ruled out that the variations arose from the social dynamics of their hierarchical society (Wittemyer and Getz 2007). Even though elephants are not territorial, when resources become limited, dominant individuals are known to outcompete subordinates in the access to resources (O'Connell-Rodwell *et al.* 2011) and utilise areas with higher habitat quality that minimises the cost of movement (Wittemyer *et al.* 2007, 2008). Correspondingly, it is possible that females AG189, AG190, and their family groups were able to use more productive and nutritionally stable areas at the time of scarce resources because they were dominant over family groups of females AG010 and AG013 who had to resort to using less productive and more variable habitat (Fig. 4*d*, *e*). Similarly, access to more productive areas by males AG004 and AG195 in the dry season (Fig. 3*d*, *e*) could be a result of higher ranking males outcompeting lower ranking males (presumably AG009, AG193), while their high dietary tolerance would have relaxed the need for predictable productivity (Shannon *et al.* 2006, 2013).

While the above scenario remains speculative, substantial differences among individuals in their selection of habitat in terms of its productivity and variability are evident in both study areas, especially in the dry season in ENP. This suggests that elephant spatio-behavioural plasticity along with their transitive dominant hierarchy (Wittemyer and Getz 2007) may contribute to lowering intraspecific competition and overt conflicts (Wittemyer *et al.* 2007; O'Connell-Rodwell *et al.* 2011). This also resonates with the observed seasonal differences in the use of water sources among the ENP elephants, where some individuals/groups (presumably dominant) retain access to a stable water supply at artificial waterholes and a more productive habitat in the dry season, while other individuals (presumably low ranking) have to resort to suboptimal habitats. As elephants' selection for productive habitat is subject to the availability of water in the environment (Bastille-Rousseau *et al.* 2020; Beirne *et al.* 2020), when surface water becomes the limiting factor (as in the dry season in ENP), they may prioritise water access over food acquisition, resulting in the observed resource use pattern of some individuals.

This study demonstrates that elephant habitat selection pattern varies in response to seasonal ecological differences of local environments, and that individual differences (i.e. intra-population heterogeneity) can be substantial, a phenomenon commonly reported in fine-scale behavioural studies of elephants (Bastille-Rousseau and Wittemyer 2019, 2022; Hertel *et al.* 2020; Beirne *et al.* 2021) and other large mammals (Leclerc *et al.* 2016; Lesmerises and St-Laurent 2017; Hertel *et al.* 2021). While the physiological (Kinahan *et al.* 2007) and dietary (Codron *et al.* 2006; Kos *et al.* 2012; Pretorius *et al.* 2012) tolerance of elephants are important biological precursors of their behavioural plasticity, other aspects of their behavioural ecology – such as environmental memory, personality traits and social structure – may explain the considerable differences among individuals and their spatial patterns (Polansky *et al.* 2015; Beirne *et al.* 2021; Bastille-Rousseau and Wittemyer 2022). This, however, has often been overlooked in habitat and resource studies that focus mainly on spatio-ecological responses at the population level. For example, our population-level RSFs ('*averaged*', '*glmm*' and '*combined*' models) suggested substantially weaker and less pliable selection for surface water – an important environmental determinant of elephant habitat use pattern – compared to individual-specific models, unless relevant fixed and random coefficients are incorporated and evaluated. The

effects are especially pronounced in the dry season and arid environment, where intense competition for water and food likely prompts individuals to adopt different resource use strategies. Because of these behavioural variations, constructing accurate resource selection function of elephants, even of one single population, is challenging as the effects of environmental features can be obscured by individual heterogeneity (Bastille-Rousseau and Wittemyer 2022). The inclusion of individual-specific selection pattern as random coefficients, and evaluation of the effects are, therefore, crucial for unravelling behavioural complexity and plasticity in populations (Bastille-Rousseau *et al.* 2020; Beirne *et al.* 2021; Kaszta *et al.* 2021).

Understanding the habitat selection pattern of a species is crucial to its conservation and habitat management, and population-level RSF analyses represent a valuable research tool with important conservation management implications (e.g. de la Torre *et al.* 2022). However, direct application of a generalised population-level response in management planning, without an adequate understanding of the behavioural ecology of the target population with its inherent individual-specific behavioural heterogeneity, should be avoided. This is important not only for elephants, but also other behaviourally complex species (e.g. Yamagiwa and Karczmarski 2014) where individual-specific habitat selection may be as essential in maintaining population resilience as is the population-level pattern of resource use. For this reason alone, greater understanding of the behavioural processes behind intra-population differences in resource, habitat, or niche partitioning is important, perhaps even instrumental for conservation success.

Supplementary material

Supplementary material is available online.

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Data availability. The data of this study will be shared upon reasonable request to the 1st corresponding author (SYSC).

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