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ORIGINAL ARTICLE

Body size rules habitat selection and population declines after drought periods in a carnivore community of the Sahara Desert

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Abstract

Body size rules the distribution and abundance of species, affecting the composition of animal communities. Body size distributions may explain niche partitioning and have been used to quantify the relative resilience of communities to perturbations. Five hypotheses have been put forward to explain observed body mass patterns in animal communities (energetic, phylogenetic, biogeographical, textural discontinuity, and community interactions), offering a key framework for empirical studies. Hyper-arid regions provide ideal conditions to explore the hypotheses that explain community interactions and resilience and these regions are especially relevant in the scenario of global climate change. We conducted a field survey of mammalian carnivores (order Carnivora) in the Sahara Desert that was used: (1) to explore if habitat structure, resource availability (water and food), intra-guild competition, and human presence affect the body size composition of the Saharan carnivore communities; (2) to explore the relationship between body mass and species resilience to drought periods. Strong differences in the composition of carnivores were found at the landscape scale (first-order habitat selection), which were narrowly related to body mass since the larger species were restricted to areas with more predictable resources. Evidence of habitat partitioning was also detected at the third (home range) and fourth (food item) orders of selection. We discuss these results in the context of the framework offered by the above-mentioned hypotheses. Finally, although the smaller species exhibit more evolutionary adaptations to hyper-arid environments, this group tended to be more drought sensitive, which was probably related to increasing intra-guild competition during drought periods.

Keywords Body size distributions · Hyper-arid habitats · Intra-guild competition · Mammal diversity · Wildlife resilience

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Introduction

Body size is a key biological driver that rules the distribution and abundance of species, affecting the composition of animal communities (Peters 1983; Calder 1984). Body size distributions have been used to explore niche partitioning within a community (White et al. 2007) or character-wide displacement (Tamar and Simbeloff 2005), as well as to quantify the relative resilience of different communities to perturbations (Peterson et al. 1998). Five hypotheses try to describe the observed body mass patterns (see revision by Allen et al. 2006): (1) energetic hypothesis: a body mass distribution reflects the rate at which species can allocate energy to do reproductive work; (2) phylogenetic hypothesis: evolutionary processes constrain the distribution of body mass distributions within taxa and/or body mass distributions may be composed of faunas with different macro-evolutionary histories; (3) biogeographical hypothesis: body mass distributions are affected at mesoscales because of dispersal, history, and geography; (4) textural discontinuity hypothesis: habitat discontinuities produce a discontinuous distribution of species body masses, in which body mass aggregations are produced by the availability of resources at different scales; and (5) community interactions hypothesis: interactions involving exploitative or interference competition influence the distribution of body masses in a community. These five hypotheses try to explain the clustering in body distribution (Holling 1992; Kelt 1997) and make useful predictions at different spatial and temporal scales (Allen et al. 2006).

The Sahara Desert is an ancient, hyper-arid ecoregion that harbours a high biodiversity, due to three main reasons (see Brito et al. 2016). First, a long and relatively stable period has enabled speciation and adaptation to severe dry conditions; second, owing to its biogeographical position between two different biogeographic realms, the Palearctic and the Ethiopian, and, as a result the area contains faunal components from both biogeographic realms; and third, its geological diversity generates habitat heterogeneity and a high diversity of biogeographic refuges suitable to a wide range of species (Brito et al. 2016). In consequence, the Sahara has a surprisingly high diversity of mammalian carnivores (order Carnivora), with up to 16 species (Wilson and Mittermeier 2009). Many of them are currently endangered or even recently extinct because of human-related causes (Durant et al. 2018). As a major rule, all wildlife in the Sahara is exposed to harsh, hyper-arid conditions, a circumstance that affects the spatial and temporal variations of the composition of the communities (Whitford and Duval 2019). Due to several and severe limitations (Brito et al. 2018), very little attention has been paid to understanding the mechanisms that made the existence of this diverse community possible in such harsh habitat conditions. These features make the Sahara an interesting environment to explore the above-mentioned hypotheses that explain body-size community structure and how this affects community interactions, ecosystem processes, and resilience (Rosenzweig and Winakur 1969; Kotler and Brown 1988). It is especially relevant in the present scenario of global climate change, which probably will have knock-on impacts on the threatened wildlife of the Sahara and the other deserts of the Earth.

Small size is one of the main adaptations to aridity (Tattersall et al. 2012). Therefore, body size of Saharan carnivores should be a major driver of habitat selection in the hyper-arid conditions of this ecoregion. First, smaller species have lower food and water requirements than the larger ones (energetic hypothesis). Second, the smaller Saharan species (e.g. fennec fox *Vulpes zerda*, sand cat *Felis margarita*) bear specific adaptations to hyper-arid conditions (Wilson and Mittermeier 2009), whereas the larger species (e.g. striped hyena *Hyaena hyena*, African golden wolf *Canis lupaster*) are more physiologically constrained (phylogenetic hypothesis), in part due to their respective biogeographical origins (biogeographical hypothesis). Third, small carnivores should suffer from intra-guild predation from larger carnivores (Palomares and Caro 1999; Caro and Stoner 2003), which could produce spatial segregation that would affect the local composition of communities (community interactions hypothesis). And four, the habitat heterogeneity of the Sahara could be a key driver of the body size distributions for associated communities (textural discontinuity hypothesis), as some empirical studies have confirmed the effects of the habitat as a driver of body size distribution in birds and fish communities (Ashton 2002; Fischer et al. 2008; Nash et al. 2014). Moreover, the heterogeneity of habitats in the hyper-arid ecoregions can be affected by temporal variations, as in the case of the usual periodic droughts (or the emergent ones, e.g. due to Global Change), which should generate different responses by each Saharan carnivore species in relation to their body size (see Whitford 1976 or Abramsky 1988 for rodents). Thus, the species that have evolved in hyper-arid areas (as is the case for the smaller ones) will suffer less impact from drought periods, while the opposite effect will be observed for the species that evolved elsewhere (i.e. larger carnivores). The effect of climatic variations could have implications for body size distributions, with knock-on effects for community interactions, ecosystem processes, and resilience (Peterson et al. 1998; Gardner et al. 2011).

The aim of the present study was to explore the factors affecting the carnivore community of the Sahara Desert in relation to body size (assessed in this paper via differences in body mass). We conducted a field survey of carnivores in the Atlantic Sahara with two complementary objectives in mind. First, we explored if habitat structure (e.g. following textural discontinuity hypothesis), resource availability (e.g. energetic hypothesis), and intraguild competition (e.g. community interactions hypothesis) affect the size composition of the Saharan carnivore communities. To reach this objective, we compared, at different spatial scales, two key Saharan habitats: the plains and the mountains. The environmental conditions of both habitats are quite different in terms of key resources like shelter, water and food availability, therefore creating an optimal scenario to study our objectives. We expected significant body-mass related differences in the composition and abundance of mammalian carnivores, with smaller taxa predicted to be better adapted to aridity conditions. We also evaluated whether our results aligned with each of the five hypotheses that describe the observed body mass patterns. Second, we explored the relationship between body mass and species resilience to drought periods. We predicted that the higher the body mass, the less resilient a species would be, based on the observation that desert-specific adaptions are mostly recorded in small Saharan carnivores.

Methods

Study area

We selected a region of ca. 20,000 km^2 located in the northern limit of the Atlantic Sahara (Morocco), just south of the Draa River (Fig. 1). Aligned with our goals, two of the most important features of this hyper-arid area (see a definition in Evenary et al. 1986) are (1) the presence of a diverse community of carnivores composed of 13 species (following Aulagnier et al. 2017; who used our data as reference), and (2) the presence of two different landscape types, namely djebels and regs. Djebels are mounts and hilly terrains dominated by rocky geology with elevation up to 790 m

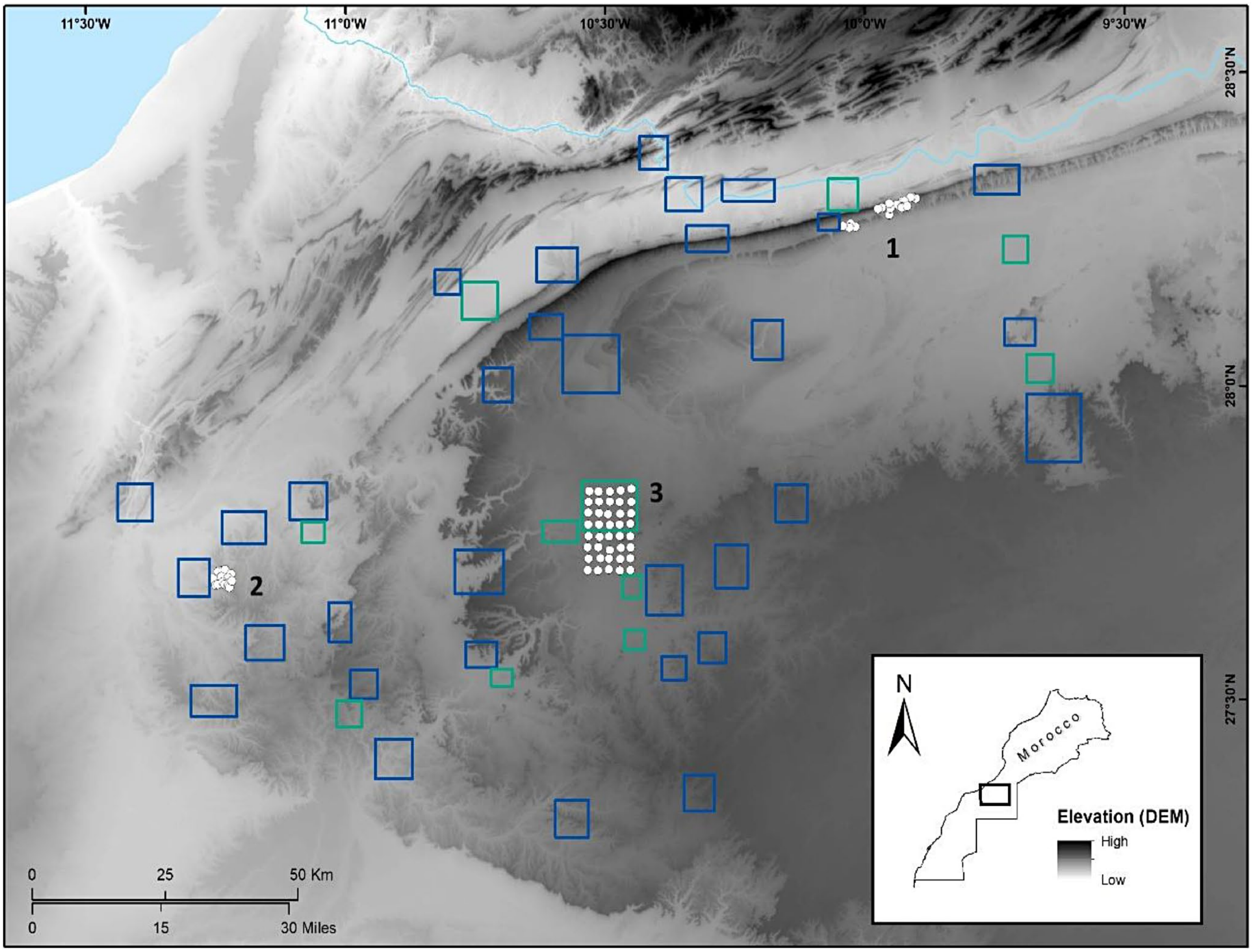


Fig. 1 Study area. Blue squares: walking surveys areas in djebels ($N=32$); green squares: walking surveys areas in regs ($N=11$). Dots: camera traps: 1 Djebel Ouarkziz, 2 Aydar mounts, 3 Reg Labyad

a.s.l. (Djebel Ouarkziz; Fig. 1), containing intricate webs of ravines (where seasonal waters persist even for months), frequent cliffs and dispersed water pits; this habitat joins the southernmost limit of the Macaronessian type vegetation (mostly restricted to ravines, as the argan tree *Argania spinosa*) with the northernmost limit of Saharan vegetation (where the acacias *Vachellia tortilis* and *V. ehrenbergiana* are the most representative trees). The regs are flat areas usually without dunes that extend far away from the southern slopes of the djebels towards the southern regions of the Atlantic Sahara, with two types: stony regs and graveled-sandy regs; the vegetation of regs is typically Saharan (included in the North Saharan Xeric Steppe and Woodland ecoregion; Olson et al. 2001), and permanent and seasonal water sources are much scarcer than in the djebels, usually limited to scattered oases. More details about climate, vegetation and human uses can be found in Herrera-Sánchez et al. (2022) and Gil-Sánchez et al. (2023).

Field surveys

We carried out 14 expeditions of 9 days each, encompassing the four seasons of the year, where we deployed two complementary types of non-invasive surveys. First, scat surveys were used to obtain information on carnivore presence and relative abundance at the regional level, following Barea-Azcón et al. (2007). Once the study area had been surveyed through scat sampling, we selected three representative zones (see below) where we carried out camera-trapping surveys following Monterroso et al. (2020), to obtain more detailed information on carnivore relative abundance and habitat use.

We carried out two types of scat surveys: (A) Systematic walking surveys at 43 study sites, 32 located in djebels and 11 in regs (Fig. 1); the differences in the sampling size between both habitats were due to poor results obtained in regs that prevented us to increase effort (see Results). We carried out 1–3 walking surveys per study site (one person each), with 3–23 walked km per survey (mean = 11.1 km, SE = 0.51 km), resulting in 69 walking surveys in djebels (745 km in total), and 17 in regs (209 km in total). This type of sampling was carried out during winter and spring to avoid harsh conditions for the field staff, between 2011 and 2014. (B) Nonsystematic sampling of scats, opportunistically collected during other activities during the expeditions (installation of camera traps, night camps, resting sites, or focal sampling of honey badger scats [Gil-Sánchez et al. 2020a]), and during all seasons between 2011 and 2017. The scats were identified to the species level through genetic analysis (see Suppl. Materials text S1).

The camera-trapping surveys were designed to capture most of the spatial and weather variability through sampling three representative areas (Fig. 1) during rainy and during drought periods (see Fig. 2a): (A) djebels: with two study sites, one located in the Djebel Ouarkziz (inland), and another one in the *Aydar* mounts (nearer to the Atlantic coast); (B) Reg Labyad (one of the most important inland regs of the region). We used three models of passive infrared (PIR) camera devices: Bushnell Trophy Cam Essential E2™ and Moultrie 880™ equipped with infrared LEDs, and BolyGuard SG562-C™ cams equipped with white LEDs. Both illumination types are battery-saving, a mandatory condition for our long-term surveys. Cameras were programmed to take 1–3 pictures per event, with 0–5 s of PIR interval, lured with Iberian lynx urine (Monterroso et al. 2020; Gil-Sánchez et al. 2023), deployed separated by 1 to 2 km, and always installed by the same two persons on wild animal paths in the djebels and close to scrubs in the regs (where paths are absent, see Gil-Sánchez et al. 2023 for details). Sampling design consisted in: (1) Djebel Ouarkziz and Aydar mounts: two surveys (Fig. 2a), one between January and April 2017 (10 cameras/study site) and another one between September 2017 and September 2018 (14 and 16 cameras/study site, including replaced devices) with lure, memory cards and batteries replaced every four months. The total effort was 4171 camera-days for Djebel Ouarkziz and 3171 camera-days for *Aydar* mounts (7342 camera-days together). Ten camera traps were stolen and replaced at nearby locations, which were considered as new cameras in the data analyses. The camera arrays extended over 36.7 km^2 (Djebel Ouarkziz) and 35.7 km^2 (Aydar mounts), respectively. (2) Reg Labyad: two surveys (Fig. 2a), one during 2019 (January–April) with 20 cameras, and another one in 2020 (January–May) with 40 cameras (adding 20 cameras to the sampling design of 2019); the camera arrays extended over 48 km^2 and 112 km^2 respectively, with a total effort of 6757 camera-days.

Statistical analyses

We used three indexes to describe the carnivore community: (A) Kilometric abundance index KAI of scats per species (Long et al. 2008), (B) relative abundance index RAI (O'Connell et al. 2011), calculated per species, with camera station as sampling unit, and (C) in the case of the genus *Felis*, we determined the minimum number of individuals through the stripped individual patterns (Gil-Sánchez et al. 2020b, 2023). We did not use corrected RAI for imperfect detection (see N-Mixture models, Royle 2004) since: (1) RAI is related to the abundance of small carnivores at the landscape level when a homogeneous sampling strategy is used (Jiménez et al. 2017; Gil Sánchez et al. 2020b), (2) our preliminary exploration of data showed strong differences in the community composition at landscape level from RAI,

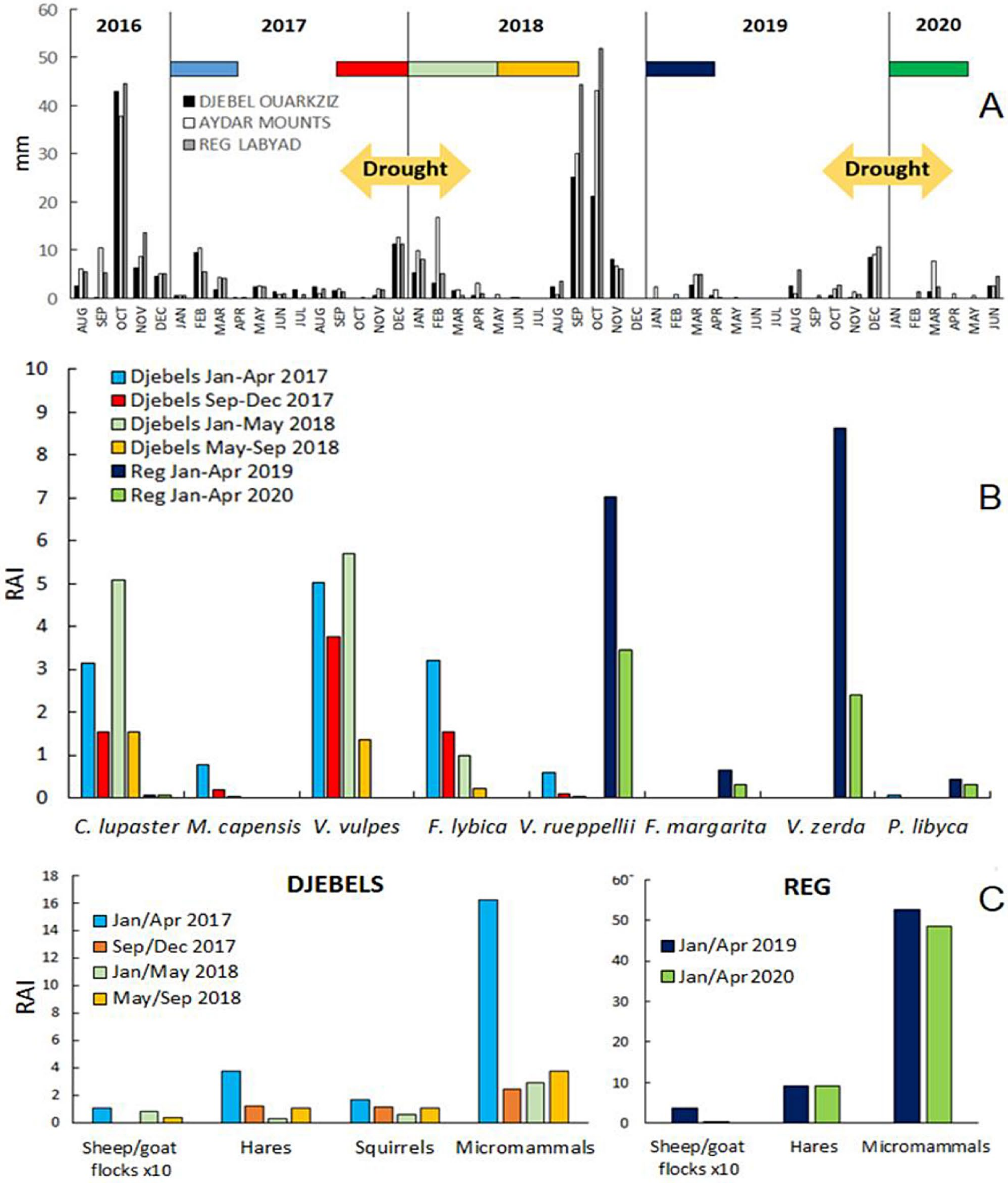


Fig. 2 (**a**) Camera-trapping sampling periods (horizontal bars) and monthly precipitations at the three camera-surveyed areas (taken from Ventusky, https://www.ventusky.com); drought periods are highlighted. (**b**) Decline in carnivore abundance. (**c**) Changes in prey abundance after two drought periods (each colour corresponds with sampling periods in (**a**) and (**b**)

and (3) for the case of micro-habitat selection analyses, RAI was used as a proxy for the intensity of space use but not as abundance index (we assumed absence when a species was not detected by a camera). Data from both djebel study sites were pooled since no differences in RAI at the species level were detected. We followed Monterroso et al. (2020) for the independence criteria of camera captures.

We first carried out a first-order habitat selection analysis (which can be defined as the selection of geographical range of a species, Johnson 1980), through intra-specific pairwise comparisons (using nonparametric Mann-Whitney *U* tests) between regs and djebels, using RAI and KAI as proxies for habitat selection. We explored if these habitat comparisons were related to body mass (i.e. if the bigger taxa were more linked to one habitat and the smaller ones to the other habitat), through visually comparing the RAI and KAI outputs (note that further analyses were not necessary, see Results section). We also conducted pairwise habitat comparisons (Table 1; *U* tests) between the reg and djebels of environmental variables related to water availability (water holes were detected after deep exploration of each sampling area), relief, accessibility to humans, vegetation, and food abundance (Table 1), including that of spiny lizard *Uromastyx nigriventris* (data from Gil-Sánchez et al. 2020a). On the basis of the results of the first-order habitat selection analysis, we plotted the relative abundance (Y-axis) and the body mass (X-axis) separately for djebels and the reg, to explore the body size distribution in each of them (Allen et al. 2006).

Table 1 Explanatory variables taken for every camera trap. Fruits were berries of *Lycium Shawii*, *Nitraria retusa*, *Ziziphus lotus*, *Searsia Tripartita*, and dates of *Phoenix dactylifera*

Variable / unit	Descriptor of
Distance (km) to the nearest permanent water hole	Water availability
Distance (km) to the nearest seasonal water hole	Water availability
Slope, as altitudinal range (m) within a 0.5 km radius	Refuge
Number of cliffs (> 10 m vertical height) within a 0.5 km radius	Refuge
% of bush cover within a 0.1 km radius	Refuge
% trees within a 0.1 km radius	Refuge
Distance (m) to the nearest 4×4 trail	Human impact
Accessibility by 4×4 (yes = 1, no = 0)	Human impact
Presence (1) or absence (0) of plant species with mature fruits within a 0.1 km radius	Food availability
RAI of sheep/goat flocks	Food availability, human impact
RAI of hares	Food availability
RAI of small mammals (rodents and macroscelids)	Food availability
RAIs of the other carnivores	Competition/predation risk/facilitation

Second, we carried out a third-order and fourth-order habitat selection analysis for each species (third-order selection describes the usage of habitat components within the home range, and fourth-order is the selection of food items, Johnson 1980), with the goal of (A) looking for possible explanations to the first-order habitat selection patterns, (B) exploring possible differences between the larger taxa (honey badger *Mellivora capensis* and African golden wolf in the djebels, and Rüppell's fox *Vulpes rueppellii* and sand cat in the reg) and the smaller taxa (red fox *V. vulpes* and African wildcat *F. lybica* in the djebels, and fennec fox and Saharan striped polecat *Poecilictis libyca* in the reg), with respect to the number and type of limiting factors affecting each species in relation to body mass. The sampling unit was each camera trap station, and this habitat selection approach was separately conducted in the djebels and in the reg, following first-order habitat selection results. The response variables were the RAI of each species, measured as camera records / 100 camera-days, while we used 12 explanatory variables describing the key environmental features (Table 1), and 8 variables corresponding to each inter-specific RAI (as describing intra-guild competition, predation risk or facilitation). The food availability descriptors were selected after a diet analysis of the collected scats (see Suppl. Materials text S2). We fitted Linear Mixed Models (LMM) separately for djebels and reg, to test the effect of explanatory variables on the different RAI values as response variables. Discrete explanatory variables were used as fixed factors and the study period and the camera model as random factors to control for potential effects on the models. We used Gaussian errors with a log link. Backward stepwise models were run until four variables were selected from all possible combinations. We inspected diagnostic graphs to assess normality and homoscedasticity of residuals (Suppl. Materials text S3). We used R base functions (version 3.6.1, R Core Team 2019) and specialized packages (lme4 v.1.1–21 for GLMMs: Bates et al. 2020).

Since we assumed that data from the camera survey described abundance at first order level (see above), we also assumed that we were able to detect numeric responses to environmental changes. We were confident that our data at first order level showed numerical rather than behavioural responses because the spatial scale of camera surveys was congruent with the spatial ecology for most of the targeted species (see Wilson and Mittermeier 2009). Therefore, the resilience to drought of each target species was estimated through the change rate in RAI (CR) after drought periods. These periods were determined after detecting significant reductions in rainfalls (Fig. 2a) that severely affected the vegetation. We used the normalized CR: (b - a) / (b + a); where CR = -1 when b = 0 and CR = 1 when a = 0 (a = RAI after bigger rains and b = RAI at the end of drought, see

Fig. 2b). For each species, we took as "a" the highest RAI index and as "b" the lowest RAI index. We fitted logarithmic regressions to the plotted body mass and CR with species a sampling unit. This analysis was separately conducted between djebels and reg. Species average body mass values were taken from Wilson and Mittermeier (2009). In the case of the Reg Labyad, we exclusively used the data belonging to the same period (January–April) for both survey years (2019 and 2020). We also analyzed the reductions in prey abundance (RAI) after drought through comparing the variations of the RAI registered for each sampling period at first order level. Finally, note that we described responses to a short-duration drought period, i.e. lasting for a single year (note than in the study area the drought can extend for more than a year).

Results

Camera-trapping, scat surveys, and diet description

We detected ten species belonging to five carnivore families (Hyenidae, Canidae, Felidae, Mustelidae, and Viverridae; Table 2). One more species, the Egyptian mongoose *Herpestes ichneumon* (Herpestidae), could be confirmed by clear footprints found during two surveys carried out along the banks of two rivers with permanent water (Oued Draa and Oued Chevica); and the caracal *Caracal caracal*, was doubtfully detected by one camera (Djebel Ouarkziz) and one footprint track (NW Aydar Mounts). Our surveys suggested the regional extinction of the cheetah *Acynonix jubatus*, in agreement with Durant et al. (2022). Most species were widely distributed, except the striped hyena, the common genet *Genetta genetta*, and the Egyptian mongoose. Scat surveys resulted in very low detection rate in the reg despite the high relative abundance registered by the remote cameras (Fig. 3), probably in relation to the effects of the frequent winds (Gil-Sánchez et al. 2023). We genetically identified 286 out of 536 scats, which allowed to adequately describe the diet of four species (Fig. S1). The key resources for the carnivore community were micromammals, arthropods, domestic ungulates, spiny lizards, and fruits (Fig. 3).

First-order habitat selection and body size distribution

The carnivore communities in the djebels and the reg were totally different (Fig. 3) and were composed by the larger and the smaller species, respectively. Additionally, there were some key differences in the habitat descriptors at the landscape level, highlighting slope, seasonal water, accessibility to humans, and most food items (Fig. S2). Both Saharan carnivore communities showed a close to log-normal pattern in body mass distribution, right skewed in the case of djebels and left skewed in the case of the reg (Fig. 3).

Third-order and fourth-order habitat selection and body size

Habitat variables showed 9 significant outputs in the reg out of 44 cases (20.4%, 2.2 significant variables per species on average), and 14 in the djebels out of 55 cases (25.4%, 2.8 significant variables per species; see Fig. 4 and see Supplementary information text S3 for models). In both habitats, each species showed exclusive patterns of habitat selection that were apparently related to body mass: (A) for the case of habitat descriptors, in the djebels the larger species tended to be influenced by more variables (African golden wolf and honey badger: 3 and 4 variables, respectively) than the smaller species (red fox, African wildcat and Rüppell's fox: 0, 0, and 2 variables respectively), while the same was observed in the reg (Rüppell's fox and sand cat: 3 and 2

Table 2 Summary of the field survey results

Survey type	Camera-trapping			Scat surveys			
Species	Independent captures	Detection ($N=68$ cameras)	% detection	Systematic (N scats)	Detection ($N=86$ surveys)	% detection	Detection Nonsystematic (N scats)
Hyaena hyaena	0	0	0	1	1	1.16	1
Canis lupaster	220	27	41.53	73	30	34.88	7
Vulpes vulpes	291	21	30.88	17	12	13.95	22
Vulpes rueppellii	349	36	52.94	4	4	4.65	2
Vulpes zerda	197	25	36.76	1	1	1.16	2
Felis lybica	98	20	29.41	56	26	30.23	36
Felis margarita	21	13	19.11	0	0	0	0
Mellivora capensis	18	10	14.70	66*	5	5.81	41*
Poecilictis libyca	18	12	17.64	0	0	0	0
Genetta genetta	2	2	2.94	1	1	1.16	1
	1214			153			71

* Collected at six independent latrines

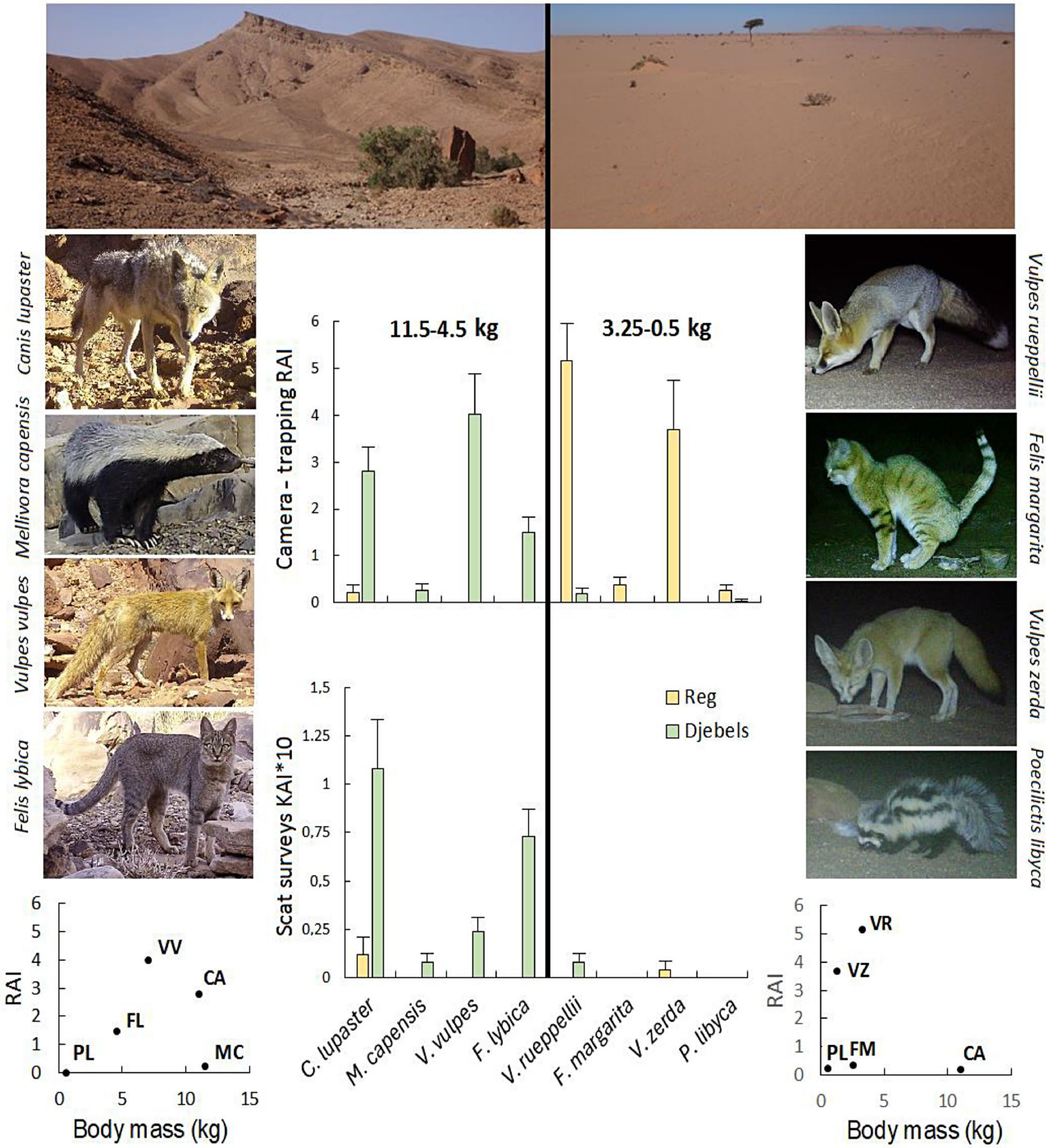
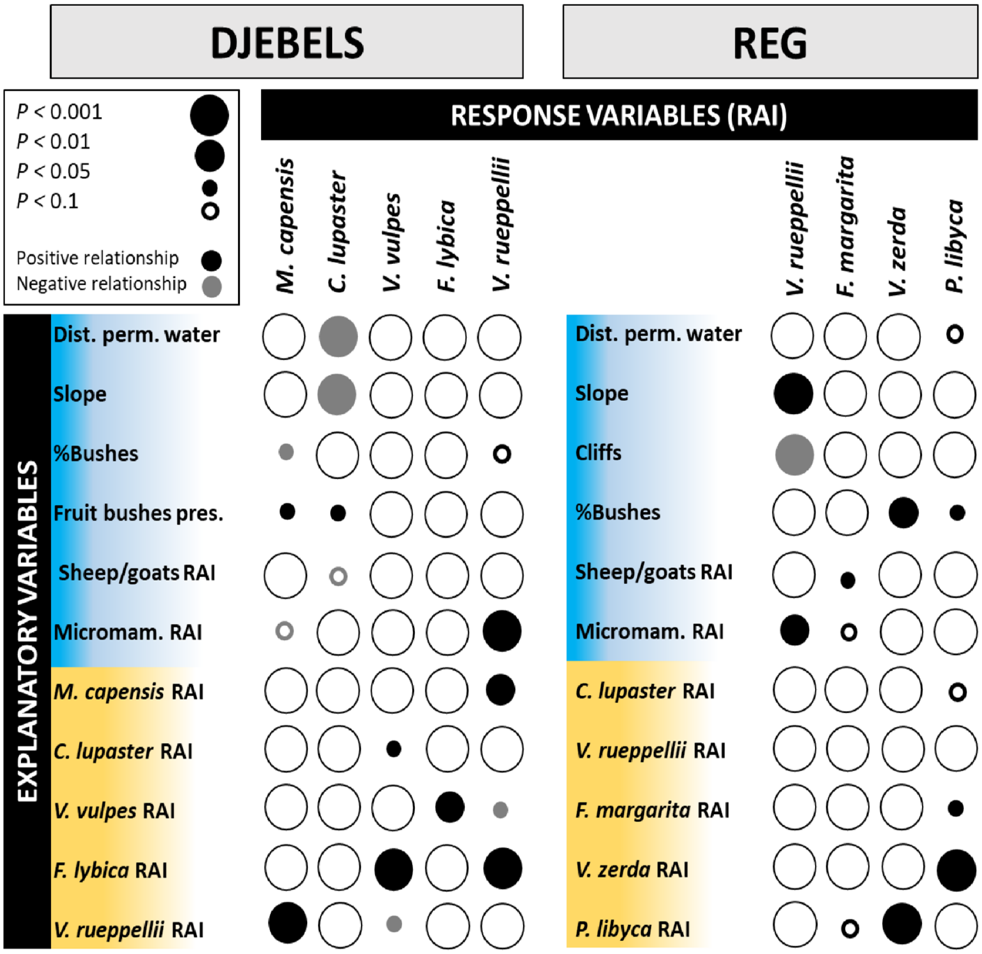


Fig. 3 Species abundance at first-order habitat selection and distribution of body sizes (reg right, djebels left). Photographs from our camera-trap surveys in the study area

variables respectively *versus* fennec fox and striped polecat: 1 variable each); (B) for the case of inter-specific relationships, both in djebels and in the reg the smaller species tended to be more influenced by other carnivore species (2.2 species on average for the pooled red fox, African wildcat, Rüppell's fox in djebels, fennec fox and striped polecat) than the larger ones for (0.5 species on average for the pooled Rüppell's fox in the reg, sand cat, African golden wolf and honey badger), with both negative and positive relationships (Fig. 4). Rüppell's fox showed different patterns

Fig. 4 Third-order / fourth-order habitat selection of the target species (in blue habitat descriptors, in beige abundance of other carnivores)



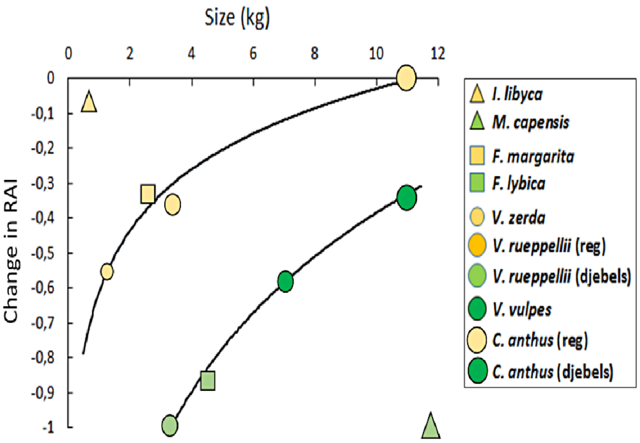


Fig. 5 Relationships (logarithmic adjustments with $P < 0.05$) between species resilience to drought and body mass

in the djebels and in the reg, except for the abundance of micromammals (Fig. S2). For the case of the period (see Supplementary information text S3), we did not detect any clear effect of body size, with the most affected species the African golden wolf and African wildcat in the djebel and the fennec fox and Rüppell's fox in the reg.

Species resilience and body size

Camera-trapping detected a reduction after droughts for most species (Fig. 2b); in the case of felids, we detected a strong decline in the number of individuals for African wildcat (from 12 to 2), while the same number of sand cats were detected after the drought (2 individuals, considering the same sampling area for both periods). In the djebels, a decline of prey (especially micromammals) after the first survey was detected, while in the reg prey remained stable (Fig. 2c). We found a positive relationship of CR with body mass if mustelids were excluded (Fig. 5). The species inhabiting the reg were less impacted (lower CRs) by drought than the species inhabiting the djebels (Fig. 5). Mustelids showed a negative relationship, with the honey badger being apparently the most impacted species in the carnivore community.

Discussion

Patterns of habitat selection and resilience to drought

We detected evidence of strong habitat partitioning within the carnivore community, as is predicted in stressful habitats where food resources are reduced and become a limiting factor, resulting in competition driving the system (Menge et al. 1994; Steneck 2005). On the other hand, we found interspecific differences in relation to resilience to drought periods which is related not only to the physiological characteristics of each species, but also to behavioural patterns that determine habitat selection. For a better understanding of the results, we discuss each species separately in Suppl. Materials text S4.

Habitat selection and body size

The log-normal pattern in body mass distribution of both Saharan carnivore communities has been observed in other communities and other habitats (Maurer 1999; Gaston and Blackburn 2000). The right skewed distribution of the case of djebels has been explained by an energetic/evolutionary model of body mass (Brown et al. 1993), while the left skewed distribution in the case of reg is rarer (but see Gaston et al. 2001). However, it is important to highlight that nowadays the targeted community is incomplete, for the bigger species (30–200 kg) were locally driven to extinction by humans during the 20th century (lion *Panthera leo*, leopard *P. pardus*, and cheetah; Aulagnier et al. 2017) or have been reduced to an ecologically non-functional level (striped hyaena). Thereby, the size distribution of the former community likely was bimodal (i.e. clustered).

Beyond the body mass distribution patterns (unimodal / clustered) within a given community, our results support that body size is a key biological driver that rules the final taxonomic composition of the Saharan carnivore communities, affecting the niche partitioning within the community. Our new results are relevant to the five hypotheses that describe the body mass patterns (Allen et al. 2006).

1) The energetic hypothesis, focusing upon limits of available resources and the optimal body mass for resource utilization (Allen et al. 2006), was supported by: (A) the observed first-order habitat selection for the species restricted to djebels (honey badger and African golden wolf, red fox, and African wildcat), where they found optimal refuge within such a stressful desert landscape (i.e. more food and permanent water) since they are the most water and food demanding species within this community due to their larger body size; and (B) by the observed third-order and fourth order habitat selection for the bigger species of djebels (honey badger and African golden wolf), and reg (Rüppell's fox and sand cat), which, in agreement with the previous result, were more influenced by environmental variables.
2) The phylogenetic hypothesis, which emphasizes the role of the limits of evolutionary constraints upon body forms, focusing upon the role of historical contingency (Allen et al. 2006), was supported by the observed first order habitat selection for the four typically Saharan species (Rüppell's fox, fennec fox, sand cat and Saharan striped polecat), which are the smaller species of the target carnivore community. These taxa exhibit specific anatomic, physiological and behavioural adaptations to hyper-arid environments, since they evolved in deserts, therefore resulting e.g. in large ears for thermoregulation, marked fossorial behavior that is favored by soft soils of reg, or haired paws adapted to walking in sandy soils (Wilson and Mittermeier 2009).
3) The biogeographical hypothesis emphasizes the role of the limits of geographical constraints upon dispersal and species mixing, focusing also upon the role of historical contingency (Allen et al. 2006). It was supported by the observed first order habitat selection for the four Saharan species, which are restricted to regs, and also maybe for the four species having Eurasian or Sub-Saharan origins (honey badger, African golden wolf, red fox, and African wildcat; Wilson and Mittermeier 2009), which are restricted to the djebels, since they do not have any specific adaptation to hyper-arid regions (Wilson and Mittermeier 2009).
4) The textural discontinuity hypothesis was supported by all species in both habitats at first order selection, where the bigger taxa are restricted to the topographically complex djebels and the smaller ones to the largely homogeneous flat regs. Like the energetic hypotheses, it emphasizes interactions with resource availability and distribution.
5) The community interactions hypothesis was supported by the smaller species in both habitats at: (A) third order and fourth order habitat selection (red fox, African wildcat, Rüppell's fox in djebels, fennec fox, sand cat, and Saharan striped polecat), which are more affected by interspecific descriptors, and (B) maybe at first order selection, where habitat-opportunistic smaller species (Rüppell's fox, Saharan striped polecat) would avoid djebels to minimize intra-guild killing (Caro and Stoner 2003; Palomares and Caro 1999; Vissia and Van Langevelde 2022) by the larger species that inhabit this habitat. Unlike the other hypotheses, the community interaction hypothesis is focused upon interspecific interactions.

It's important to highlight that this study could not be used to test if one hypothesis should be favoured / is more likely to drive the found pattern, compared to the other hypotheses, because of the fact that all five of them can explain the same pattern. We did not find any evidence against any one of these hypotheses, but we recognize that the higher human-caused mortality risk (accessibility by four-wheel drive vehicle) in the reg could (partially) be an alternative interpretation for our results, particularly affecting the abundance and distribution of the larger species (African golden wolf and honey badger). The support for this hypothesis is clear for the African golden wolf, although it is evident that this canid finds more resources (food and water) and shelter against insolation in the djebels. In the case of honey badgers, its strong regional dependence for spiny lizards (Gil-Sánchez et al. 2020a) should be sufficient to explain its first-order habitat selection. The other species of the djebels, the red fox and the African wildcat, have a body size close to Rüppell's fox in magnitude order, therefore the human-caused mortality risk hypothesis is not supported.

Species resilience and body size

We found that, contrary to our predictions, the smaller carnivores of the Sahara tended to be more drought sensitive, except mustelids, which are variable. As mentioned above, this unexpected result was probably related to increasing intra-guild competition during drought periods, which would affect the smaller taxa (e.g. the cases of Rüppell's foxes over fennecs in the reg, and red foxes over Rüppell's foxes in the djebels). In general, djebels are topographic refuges where permanent water and primary production are less affected by droughts (Herrera-Sánchez et al. 2023), favouring the persistence of the larger species, which would increase their negative effects on the smaller ones during the more stressing periods. A few anecdotal observations in this line include two African golden wolves trying to chase a red fox, and a camera trap photo of a wolf carrying a fresh red fox head. In the case of regs, and once the cheetah became extinct (last records during the 1990s, Aulagnier et al. 2017), Rüppell's fox became the apex predator after the very rare African golden wolf. Despite being a small canid, it could exert a negative impact of the much smaller fennec fox when environmental stress increased. Interestingly, rodents in the reg did not decline after the drought, and they could be an important prey for this poorly known desert-dwelling canid (Sillero-Zubiri 2009). The reg community of rodents was dominate by the lesser Egyptian jerboa *Jaculus jaculus* and Tarabul's gerbil *Gerbillus tarabuli* (70.2% and 26.9%% of records respectively, $N=2791$), both being species than store food underground (Aulagnier et al. 2017), which allows for resilience during short droughts. Therefore, the availability of alternative food could benefit Rüppell's fox during such stressing periods. In line with our results, recent theory highlights the higher sensitivity of small carnivores to environmental changes, including intraguild competition exerted by the larger species (Marneweck et al. 2022; Do Linh San 2024, Jachowski et al. 2024).

Conclusions

Our study supports body size as a key biological driver that determines the composition of the Saharan carnivore community. We found multiple lines of evidence supporting each of the five hypotheses (energetic, phylogenetic, biogeographical, textural discontinuity, and community interactions hypotheses) put forward to explain the observed body size patterns in the targeted carnivore community. One of the most relevant results was the strong habitat partitioning at the landscape level. This favours a very rich carnivore community at the regional level despite the hyper-arid conditions of this region. Djebels play a key role as a refuge for the larger taxa less adapted to deserts. The resilience to droughts also showed a relationship with body size, exhibiting the opposite result as that expected (except for mustelids), where the bigger taxa were the more resilient, probably due to a synergic effect of intra-guild competition and the above-mentioned refuge effect of djebels, but further research is necessary.

Finally, we offer novel information on the ecology of such a very poorly known and diverse carnivore community, which is of interest not only for ecologists but also for conservationists and practitioners, being specifically useful for designing and managing protected areas. Unfortunately, field studies are suffering a dramatic global reduction (Ríos-Saldaña et al. 2018) that particularly affects remote areas, like the paradigmatic case of the Sahara, where the ecosystem has suffered a recent collapse due to the loss of its mega-fauna from over hunting (Durant et al. 2014; Gil-Sánchez and Sánchez-Cerdá 2023). Hence, studies like ours are essential to obtain the necessary knowledge for a better conservation of such poorly understood and largely threatened ecosystems.

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Data availability Data are available from the Dryad Digital Repository: (URL to be added upon publication).

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