Journal of Arid Environments xxx (xxxx) 105612

Contents lists available at ScienceDirect

Journal of Arid Environments

journal homepage: www.elsevier.com/locate/jaridenv

Trophic niche partitioning in a carnivore community of a hyper-arid environment, the Sahara Desert

Carlos Sarabia [a,b], Jose María Gil-Sánchez [c,d,*], F. Javier Herrera-Sánchez [c], Javier Rodríguez-Siles [c], Miguel Ángel Díaz-Portero [c], Ángel Arredondo [c], Juan Manuel Sáez [c], Begoña Álvarez [b], Inmaculada Cancio [c], Joaquín Pérez [c], Jaime Martínez-Valderrama [c,e], Mariola Sánchez-Cerdá [a,c], Thomas Lahlafi [c], Jose Manuel Martín [c], Abdeljebbar Qninba [f], Emilio Virgós [g], Jennifer A. Leonard [a]

[a] *Conservation and Evolutionary Genetics Group, Estación Biológica de Doñana (EBD-CSIC), Avd. Americo Vespucio 26, Sevilla, 41092, Spain*
[b] *Center for Computational and Molecular Biology, Brown University, USA*
[c] *Harmusch, Association for the Study and Conservation of Wildlife, C/ San Antón 15, 1°, E, Almodóvar del Campo, Ciudad Real, 13580, Spain*
[d] *Departamento de Zoología, Universidad de Granada, Avda. de Fuente Nueva, s/n, Granada, 18071, Spain*
[e] *Estación Experimental de Zonas Áridas, CSIC, Crtra. Sacramento s/n, La Cañada de San Urbano, Almería, 04120, Spain*
[f] *Mohammed V University in Rabat, Institut scientifique, Laboratoire de Géo-Biodiversité et Patrimoine Naturel, Centre de Recherche GEOPAC, Av. Ibn Battota, B.P. 703, Agdal, Rabat, 10090, Morocco*
[g] *Escet, Departamento de Biología, Geología, Física y Química Inorgánica, Universidad Rey Juan Carlos, C/Tulipán, s/n, Madrid, E 28933, Spain*

ARTICLE INFO

Keywords:
Intraguild competition
Fecal DNA
Molecular barcoding
Trophic ecology
Canid
Felid

ABSTRACT

Lower primary productivity in more arid environments limits food resources to local animals and is particularly acute for taxa at higher trophic levels, such as carnivores. This selective pressure may drive intraguild competition in carnivore communities and directly impact survival and fitness of individuals, determining local population persistence. We have estimated the diet of a mesocarnivore community of the Sahara Desert composed of four species: African golden wolf (*Canis lupaster*), red fox (*Vulpes vulpes*), African wildcat (*Felis lybica*), and honey badger (*Mellivora capensis*). Interspecific exploitative competition was predicted to be intense in this stressful environment, which should drive high niche segregation. We studied diet overlap in two seasons to measure variation in niche segregation. African golden wolves had the broadest diet, which was based on domestic ungulates and a variety of items such as lagomorphs, small mammals, reptiles, arthropods, and fruit. Red foxes also fed on a wide range of species, mainly arthropods, small mammals, and reptiles. African wildcats were more specialized and consumed mostly small mammals, although with some consumption of reptiles and birds. Finally, honey badgers showed a strong preference for a single resource, the spiny-tailed lizard (*Uromastyx nigriventris*). As predicted, the four species showed relatively low diet overlap, with average seasonal Pianka's index ranging from 0.34 (SD = 0.17) in April to 0.43 (SD = 0.14) in December. This high level of niche segregation was relaxed in the wet season when more resources were available, further implicating the role of primary productivity in driving the ecology of the system.

1. Introduction

Understanding how the members of a guild interact and impact one another in ecosystems is crucial to understand the evolutionary pressures driving adaptation. Niche theory provides a framework to study how community structure in ecosystems is driven by species interactions and environmental factors (Chase and Leibold, 2003; Leibold and McPeek, 2006). One of the most prominent interactions shaping ecological communities is competition between species (Schoener, , 1974). Competitive interactions can profoundly change community assemblages, drive ecological specialization, and promote coexistence mechanisms (Schoener, , 1974; Hardin, 1960). While it is expected that two species can coexist if

---

* Corresponding author. Harmusch, Association for the Study and Conservation of Wildlife, C/ San Antón 15, 1°, E, Almodóvar del Campo, Ciudad Real, 13580, Spain.

E-mail address: jmgilsanchez@yahoo.es (J.M. Gil-Sánchez).

https://doi.org/10.1016/j.jaridenv.2026.105612
Received 25 June 2025; Received in revised form 12 February 2026; Accepted 31 March 2026

they differ enough in some niche dimension, if they share the same space and diet they should compete until the most successful one drives the other towards local extinction (competitive exclusion principle (Gause, , 1932)). Interspecific competition is especially strong when species in the same area are closely related phylogenetically (Webb et al., 2002; Violle et al., 2011) and they overlap in the use of limited resources with some fitness consequences for interacting individuals (Chesson, 2000). However, recent studies have found that in some cases species that are expected to interact negatively for resources (that is, compete) can also interact positively, where one facilitates the existence of the other, referred to as "coexistence theory" (Arsenault and Owen-Smith, 2002; Barrio et al., 2013; Hart and Marshall, 2013) (Arsenault and Owen-Smith, 2002; Barrio et al., 2013; Hart and Marshall, 2013). This is the case in inter-specific facilitation (Bruno et al., 2003; Moleón et al., 2014).

Although the original concept of competition for limiting resources within ecological niche theory predicts that overlap in niches should not be stable, observations suggest that the existence of specialized and non-overlapping niches is not absolutely necessary for coexistence. Coexistence among species can also be possible across time and space under conditions of high food availability and/or other potentially limiting resources combined with increased spatial heterogeneity (Alhajeri et al., 2018; Terry, , 2018). Overall, it has been shown that interactions between potentially competing species are very complex and depend upon a series of factors, including population density of both species, microhabitat availability within the landscape, selective occupancy of the territory, circadian and circannual rhythms, physiology, microhabitat diversity and selective specialization of resources (Pianka, , 1974).

One way to understand the complexity of competitive interactions is through the study of predator communities. Due to their high metabolic requirements and competition with other members of the guild, carnivores are generally the species most affected by both abiotic and biotic changes in the ecosystem such as desertification, loss of top predators, or disappearance of certain prey (O'Connell et al., 1975; Menge et al., 1994). The existence of abundant prey potentially reduces exploitative competition between carnivores, which specialize in different prey (White et al., 1995; Zalewski et al., 1995; Lanszki et al., 2019). When carnivores of roughly similar size and dietary preferences coexist in an area, those populations tend to specialize in diet or space, which makes them extremely vulnerable to subtle changes in habitat (Creel, 2001; Schuette et al., 2013).

In hyper-arid environments, strong habitat partitioning of carnivores is impractical due to low prey density and patchiness of water (Gil-Sánchez et al., 2024). In such a competitive scenario, dietary niche partitioning becomes a key ecological mechanism to enable inter-specific coexistence through the relaxing of exploitative competition, as has been suggested for some desert mesocarnivores (Scheinin et al., 2006; Karssene et al., 2019). However, dietary generalism should be advantageous in arid environments, permitting continuous exploitation of temporally and spatially patchy food sources (Fisher and Dickman, 1993). Thus, one might expect that mesocarnivores exhibit broad diets in arid environments and overlap between species would be higher than where specialization carries less energetic cost to foragers.

Here we tested the niche segregation hypothesis that allows coexistence (exclusion principle *sensu* Gause's principle) in this arid environment. This predicts that trophic overlap is low in the Sahara Desert mesocarivore community. As an alternative hypothesis, we state mesocarnivores exhibit broad diets, resulting in higher overlapping. We use diet data from feces of four species of mesocarnivores (range of sizes: 4.4-8.1 kg) and then calculate dietary overlap per season. In addition, we provide novel information on the largely understudied carnivores in the largest hyper-arid region of the world, where wildlife has suffered a severe collapse in the last century due to overhunting and habitat destruction (Durant et al., 2014; Brito et al., 2018).

2. Materials and methods

2.1. Study area

The study area is situated in the Atlantic Sahara of Morocco, between the lower Draa River and the basin of Sequiat al Hamra, forming a rough ellipse of around 20,000 km^2 between latitudes 11°30′W and 9°30′W and longitudes 28°30′N and 27°0′N (Fig. 1). The climate is arid and hot and corresponds to a low-latitude subtropical desert in the Köppen-Geiger classification – Bwh (Beck et al., 2018). Mean temperature ranges from 22.7 °C in the west to 23.2 °C in the eastern inland areas with annual precipitation averaging from 59 mm to 138 mm, respectively, with strong seasonality in precipitation (climate stations at Smara: 26°46′ N, 11°31′ W, 460 m.a.s.l. and Tindouf: 27°40′ N, 8 °7′ W, 401 m.a.s.l.; see Fig. S1 for more details on local rainfalls). The area falls inside the North Saharan Xeric steppe and woodland ecoregion with prolonged droughts and irregular rainfalls (Olson et al., 2001). The landscape is heterogeneous and rocky, with patches of elevated plains (*hamadas*) and long gravel plains (*regs*) situated between 290 and 770 m above sea level (m.a.s.l.). Seasonal ponds collect in dry riverbeds and two rivers, the Draa and Chebeica, have permanent water pools (*gueltas*). Regional vegetation is scarce and irregular except in the dry riverbeds, where local savanna-like forests of horn trees (*Vachellia tortilis* subsp. *Raddiana* and *V. flava*), Egyptian balsam (*Balanites aegyptiaca*), and Sodom apple (*Calotropis procera*) coexist with *Searsia tripartita* bushes and some scattered argan trees (*Argania spinosa*) in valleys and ravines.

The carnivore community is composed of 12 species from 6 families (Gil-Sánchez et al., 2024): 4 species of canids (African golden wolf *Canis lupaster*; red fox *Vulpes vulpes*; Ruppell's fox *V. ruepellii;* fennec *V. zerda*), 3 species of felids (African wildcat *Felis lybica*; sand cat *F. margarita;* caracal *Caracal caracal*), 2 mustelids (honey badger *Mellivora capensis*, Saharan striped weasel *Ictonyx libyca*), 1 viverrid (common genet *Genetta genetta*), 1 herpestid (Egyptian mongoose *Herpestes ichneumon*), and 1 hyenid (striped hyaena *Hyaena hyaena*).

2.2. Field survey

Fecal samples were collected in 10 expeditions (from April 2011 to April 2017). Sixty-eight plots were surveyed within the area (Fig. 1) searching for carnivore signs along 1 - 4 transects each. In total 2490 km of accumulated search effort was made (12.08 ± 0.72 km per walking survey). A total of 518 carnivore fecal samples were found and georeferenced with a portable GPS. A field identification was made based on fecal size and morphology, after which they were put in paper bags. Environmental conditions were dry enough to preserve the samples without need of desiccants, since dryness is suitable for long term preservation of fecal material. Two sampling periods were targeted with higher and lower primary productivity but also avoiding the hottest months: December-January (hereafter December) and March-April (hereafter April). Aside from fecal samples collected in this study, previously identified scats of honey badger from the same transects but reported in a previous publication (Gil-Sánchez et al., 2020) were included for studies of trophic niche overlap (n = 107).

2.3. Genetic barcoding of feces

Genetic analyses were used to identify the samples at the species level. After collection, feces were left to dry in paper bags at ambient temperature for approximately 10 days until the field sampling was completed. Samples were sent to Estación Biológica de Doñana (Sevilla, Spain), and stored at −80 °C immediately upon arrival for three weeks. After this time, samples were held at −20 °C until extractions were done. Fecal DNA extractions and other pre-PCR steps were performed in a dedicated laboratory for low quality DNA in hoods with particle filters. All surfaces where fecal processing was done were first cleaned with 20% bleach and 30 min of UV-irradiation to ensure there was no DNA contam-

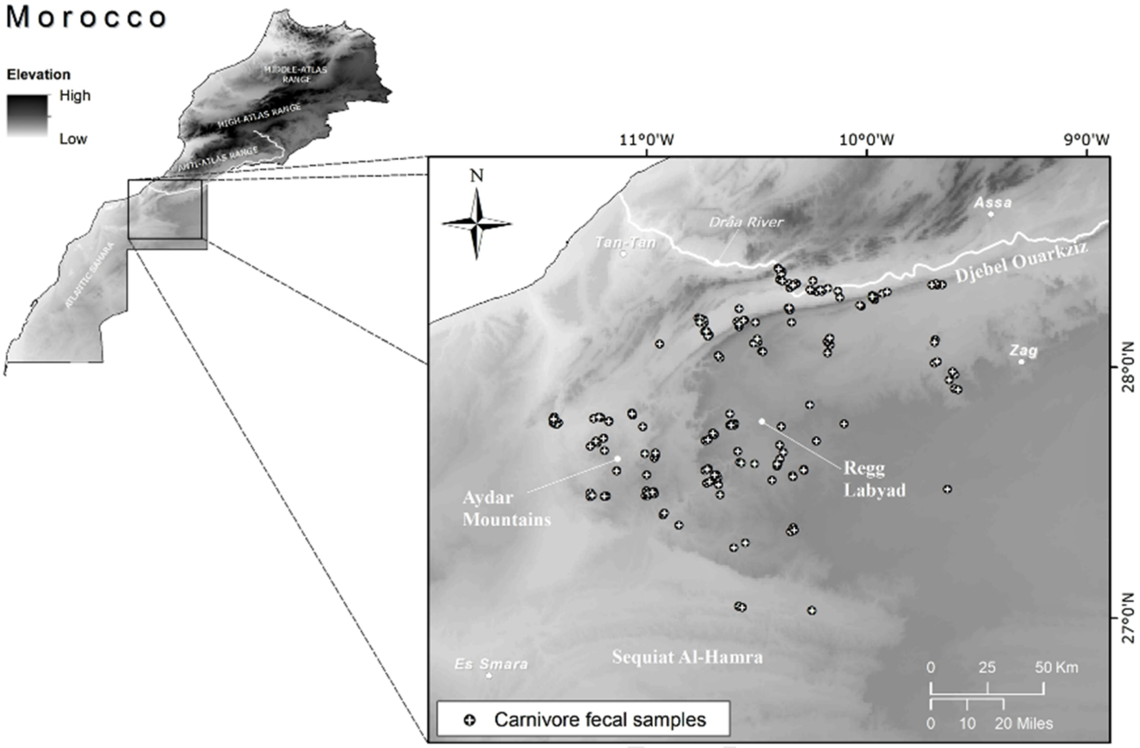

Fig. 1. Location of the study area and key topological names. The Drâa River marks the northern limit of the Saharan bioclimatic zone. Dots mark the collection sites of the carnivore fecal samples which were genetically identified for diet analysis.

ination. Aerosol-resistant pipette tips and isolation suits were also used. All DNA extractions and PCR amplifications included negative controls to monitor for contamination. We peeled fecal samples with a blade and used 180-200 mg by weight of scat per extraction.

We considered carefully the challenge of amplifying DNA from suboptimal sources such as feces from dry, intensely UV-radiated environments such as the Sahara desert. We followed an adaptive procedure until we found the most efficient DNA extraction method for our samples. We applied three different extraction methods: the QIAmp DNA extraction kit following manufacturer's recommendations (Qiagen, Hilden, Germany), a CTAB/PCI/SPRI beads-based method which was efficient in a recent study of carnivore scats (Sarabia et al., 2020), and a silica beads-based method (Kohn et al., 1995) (to different groups of scats. Whenever a method did not work for DNA extraction after three PCRs attempts, we would try another.

Barcode regions were amplified from DNA extracts using TaqGold polymerase® (ThermoFisher Scientific, Waltham (MA), USA) following manufacturer's protocol in 12 μL reactions with 2.5 mM $MgCl_2$, 0.25 mM of each dNTP, 0.6 μM of each primer (Table S1), 0.4 mM bovine serum albumin (BSA) and 3 μL of DNA extract. PCR conditions were: 95 °C for 8"; 45 cycles of 95 °C for 30″, 55 °C for 30″, and 72 °C for 60″ and a final extension time of 7'. Products were visualized in 2% agarose gels with a 100-1500 bp ladder and visualized with the ImageLab v5.2.1 software in a Gel Doc™ EZ Gel transilluminator (Bio Rad, Hercules, CA, USA). Following the adaptive procedure, first longer, then shorter Cyt *b,* then control region (CR) fragments were tested if necessary (Table S2; Fig. S2). Since it is not possible to differentiate red fox from Ruppell's fox with the targeted fragment of Cyt *b* (Leite et al., 2015), samples with this sequence were further evaluated for a CR fragment which can differentiate these two species (Table S1–S2, Fig. S3–S5).

After amplification, all PCR products were purified using Sera Mag SPRI beads (Rohland and Reich, 2012). Cleaned PCR products were Sanger sequenced (Macrogen, Madrid, Spain). Primers and low-quality sequences were trimmed using Geneious v11.0.5 and reads were BLASTed using the blastn algorithm implemented in Geneious (Altschul et al., 1990). Only fragments with sequence identity higher than 98% were accepted as identification of the species. Sequence identity was approximated by similarity in the whole database (Table S1) and then confirmed by phylogenetic analyses. A neighbor-joining phylogeny was constructed in Geneious with default parameters to confirm the phylogenetic position of each scat. In total, 268 out of 518 scats yielded successful genetic identification, from which 234 scats could be identified as belonging to either African golden wolf, wildcat or red fox. To these samples, 107 scats of honey badger (see Field survey subsection) were added to a total of 341 scats (see "Barcoding results" below).

2.4. *Diet composition*

All scats were dry-preserved with silica-gel after being subsampled for DNA analysis. Feces were broken up and food items were identified by examining the undigested material. Prey remains such as claws, bones, hairs, molars and reptile scales were compared to a personal reference collection and bibliography (rodent teeth (Aulagnier et al., 2017):). We also used identification by hair microscopy. Hair was isolated from the remaining material and their microstructure (hair medulla and cuticular scales) was compared to our personal collection and published atlases (References S1). Seeds, fruits and arthropods were identified with our reference collection or specialists were consulted. The percentage of the volume of each identified item per scat was estimated visually (Putman, 1984).

2.5. *Data analyses*

For each carnivore species we calculated relative frequency of occurrence (Fr) and percentage of volume (%V) of each dietary item identified in the feces. Fr is the number of occurrences of an item divided by the total number of occurrences of all prey items multiplied by 100 (Putman, 1984). The %V is an estimation of each prey type divided by the total estimated volume of the feces multiplied by 100. We assigned all dietary items to one of ten categories: domestic ungulates, lagomorphs, small mammals, spiny-tailed lizard, reptiles, birds, arthropods, fruits, other organic unidentified material, and waste. In order to account for the extreme dietary specialization of honey badgers (Gil-Sánchez et al., 2020) and to make a separate niche overlap estimation for this new dataset, we excluded spiny-tailed lizards from the reptile category and placed them into their own.

We described the inter-specific patterns of diet and calculated the overlap between pairs of species. First, we determined the niche breadth (Ba) of each species applying a correction of Levins' formula of niche breadth that considers the number of dietary categories:

$$\mathrm{Ba} = (\mathrm{nB_n}-1)\Big/(\mathrm{n}-1);\ \text{or}\ \mathrm{Ba} = \left[\left(1\Big/\left(\sum \mathrm{P_i^2}\right)\right)-1\right]\Big/[\mathrm{n}-1]$$

where n is the total number of dietary categories and $\mathrm{P_i}$ is the contribution of each item in the total diet of each species, calculated from Fr. Ba ranges from 0, when the species uses only one resource, to 1 (or n/n), when the species uses all resources available. Second, we calculated the equitability index:

$$\mathrm{E'} = -\Sigma\ \mathrm{Pi}\ \ \ln(\mathrm{Pi})\Big/\ln(\mathrm{n})$$

which is based on the Shannon and Weaver's Diversity Index Σ Pi ln(Pi); this index varies from 0 (dietary specialist) to 1 (dietary generalist). Third, we calculated the Pianka's dietary overlap index for the six possible pairs of species as:

$$\mathrm{O_{jk}} = \frac{\sum_i^n p_{ij}p_{ik}}{\sqrt{\sum_i^n p_{ij}^2 \sum_i^n p_{ik}^2}}$$

where $\mathrm{O_{jk}}$ is the trophic niche overlap between species j and species k, $\mathrm{p_{ij}}$ is the percentage of volume of food item in species j, and $\mathrm{p_{ik}}$ is the percentage of volume of food item i in species k. $\mathrm{O_{jk}}$ ranges from 0 (no overlap) to 1 (complete overlap). Seasonal variations in each index were studied by grouping the samples into two periods: feces collected during April and feces collected during December. December represents the period of maximum local primary production after the autumn rainfalls, while April represents the period of decreasing primary production after the rainy season (Fig. S1). To further estimate whether there were significant differences between relative frequencies of dietary items between species in the same season, and between relative frequencies of dietary items within the same species in different seasons, we applied a series of paired Fisher's Exact Tests with 99% confidence intervals. To account for false discovery rates, a Benjamini-Hochberg (BH) post-hoc correction was applied. All statistical analyses were performed in Rv4.0.1 (Team and R. R Core Team, 2010).

3. Results

3.1. Barcoding results

We genetically identified 268 out of 518 scats from all expeditions, of which 220 were replicated at least twice and were chosen for further dietary analyses: 80 for African golden wolf (44 April, 36 December), 92 for wildcat (41 April, 51 December), 39 for red fox (26 April, 13 December), 3 for fennec, and 6 for Ruppell's fox, with a mean ID success of 52%. To these fecal samples we added the 107 honey badger scats (44 April, 63 December) from Gil-Sánchez et al. (2020). Twenty-two scats could be identified only to *Vulpes*, because the control region failed to amplify. Some other carnivores were also identified: 2 scats of striped hyaena (each replicated twice), 2 scats of common genets (replicated once), and 6 scats of domestic dogs (Table S3). Therefore, 4 sympatric mesocarnivore species were included in the study: 2 canids (African golden wolf and red fox), 1 felid (African wildcat) and 1 mustelid (honey badger). They represented the mesocarnivore community of the study area, excluding caracals, which were very rare in Atlantic Sahara. The samples of these four species were well distributed throughout the study area (Fig. S6), thus, local effects of environmental conditions or resources surrounding the locations where feces were collected could be considered of minor importance. However, our samples were biased towards the driest years of the entire study period (Fig. S1), a circumstance that must be taken into account for this study, as it affects the annual food resource availability.

3.2. Diet composition and overlap

We found key differences in the diet composition of the four target species (Fig. 2; Table S4; Table S5). African golden wolves had the broadest trophic niche according to both the Equitability index and Levins' Ba in December followed by the red fox in April. (Table 1). African golden wolves mainly fed on anthropogenic resources such as goats but also on lagomorphs, small mammals, reptiles, arthropods, and fruits (Fig. 2), resources which they consume significantly more than other carnivores of the assemblage both in April and December (Fig. 3B and C). Red fox fed on a variety of resources such as arthropods, small mammals, and reptiles, indicating a very diverse diet with the second highest values of niche breadth after African golden wolves in April (Fig. 3B and C, Table 1). African wildcats consumed mainly small mammals (around 44 - 77% volume of their diet, Fig. 3), with some consumption of reptiles and birds. In December they had the most restricted niche breadth (Table 1), which could be due to a strong specialization in small mammals in this season, which they consume significantly more than other carnivores (Fig. 3C). Honey badgers show a strong preference for a single resource, the spiny-tailed lizard (Figs. 2 and 3B, C), yielding the lowest values of niche breadth in April and the second lowest value in December (Table 1). These dietary differences resulted in low values of trophic niche overlap between the four studied mesocarnivores (Table 2). High $\mathrm{O_{jk}}$ values were observed for the two species of the same family (canids), and for the two smaller species (red fox and African wildcat; Table 2, Fig. 3). The minimum $\mathrm{O_{jk}}$ values were observed for African golden wolf and Africa wildcat in December, and African golden wolf and honey badger in April (Table 2), the latter due to high consumption of spiny lizards (Fig. 3B and C).

Overall, the diets of three species changed between seasons (the exception was the red fox, but its sample size in December was low, Figs. 2 and 3; see data in Table S5). African golden wolves feed on more goats in April than in December, resulting in a reduced trophic niche breadth in this season (Fig. 2, Table 1). Contrary to the reduction of niche breadth in African golden wolves in April, African wildcats tend to have less diverse diets in April than in December (Table 1) when consumption of small mammals increased (Figs. 2 & 3A). Honey badgers consumed fewer spiny-tailed lizards in December, which were compensated for in the diet by small mammals (Fig. 3A). These seasonal changes affected diet overlaps (Fig. 3, Table 2), which were generally lower in April (average values = 0.34) than in December (average values = 0.43).

4. Discussion

Our results support the niche segregation hypothesis that allows coexistence. Through our study of dietary patterns in a mesocarnivore community in an arid environment based on genetically identified fecal samples (the first of its kind carried out in North Africa), we found that in the Sahara Desert most carnivore species showed low values of diet overlap, and only the most related species had more similar niches (Webb et al., 2002; Violle et al., 2011). This agrees with the conclusions of Steneck (Steneck et al., 2005), who suggested that in deserts, where resources are scarcer, they become more limiting to species, particularly in the ecological context of carnivores. Under such a stressful scenario, competition together with abiotic stress can drive the system, overriding other inter-specific interactions (Menge et al., 1994).

In addition to the strong niche partitioning identified overall, finer scale seasonal analysis of data also supports the niche partitioning hypothesis. Seasonality in the diet of wild carnivores in North Africa has also been identified in other studies (Karssene et al., 2019; Amroun

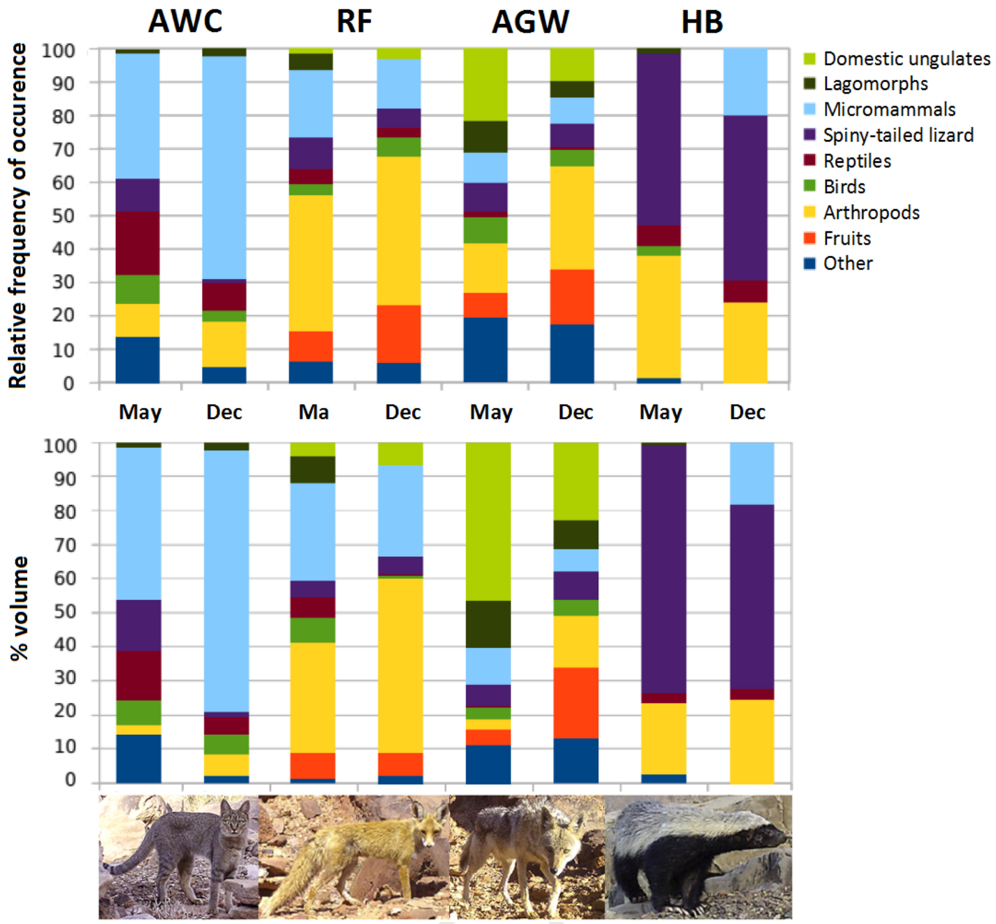

Fig. 2. Diet composition and seasonal variations for the four studied species in the Sahara Desert. African wildcat (AWC), red fox (RF), African golden wolf (AGW) and honey badgers (HB). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 1
Trophic niche breadth of African wildcat (AWC), red fox (RF), African golden wolf (AGW), and honey badgers (HB) according to the Equitability index (E′), and Levin's trophic niche breadth (Ba). All indexes were calculated using volume of each dietary category.

	Season	Equitability E′	Levins's Ba
AWC	April	0.7	0.41
AWC	December	0.42	0.18
RF	April	0.82	0.52
RF	December	0.61	0.32
AGW	April	0.76	0.42
AGW	December	0.89	0.71
HB	April	0.35	0.19
HB	December	0.5	0.29

et al., 2014; Eddine et al., 2017). We detected higher overlap during the period of maximum productivity after the peak of annual rains in the autumn. Plants and animals in deserts are adapted to rapid demographic responses to rains, an important but unpredictable, short, and very irregular resource ((Whitford and Duval, 2019) and Fig. S1). Such particular life history strategies probably affect our target species in the form of rapid functional responses that affect diet composition and, therefore, seasonal variations of niche overlap. For example, an increase in primary production quickly results in demographic explosions of rodents in arid biomes (Auffray et al., 2009), which could explain the higher contribution of small mammals to diets in the December sample by African wildcats and honey badgers, favouring a seasonal scenario that diminishes the exploitative competition between them and red foxes. A similar case could be the higher contribution of arthropods to the red fox diet in the December sample. In the case of domestic ungulates, autumn rains are followed by the traditional arrival of nomadic shepherds to our study area, but the effects on the African golden wolf diet were higher in the April sample, probably due to the accumulation of carcasses through the period when herds are present in the area. The contribution of reptiles decreased in the December sample in three of the four carnivores (wolves were the exception, but this item was very rare in the diet); probably more related to strongly reduced activity of the ectotherm reptiles in the winter (December) when temperatures can fall to 0° Celsius.

Theoretically, the most significant competition should happen between the most phylogenetically related members of the carnivore guild (Webb et al., 2002; Violle et al., 2011). Hence, diet segregation should be expected in scenarios of coexistence. In our dataset the most phylogenetically related species are the African golden wolf and red fox. In richer environments, foxes and medium-sized carnivores have high niche overlap (Lanszki et al., 2019; Lanszki and Heltai, 2002), which is also observed in the Saharan case, where red foxes have little significant differences in feeding preferences with African golden wolves. Other studies have found that members of large omnivorous families, such as Canidae, coexist with a greater proportion of potential competitors due to their broader trophic niches (Donadio and Buskirk, 2006; Hunter and Caro, 2008), and we did find them to have broader trophic niches. In a competitive context, high overlap might occur, but if resources are plentiful, or obtained in different localities, exploitative competition should be reduced thus allowing for coexistence. In the case of the Sahara Desert, high spatial overlapping between African golden wolves and red foxes has been observed (Gil-Sánchez et al., 2024), while food availability could be assumed as not plentiful. Therefore, the observed overlapping between both canids deserves further research. Since they

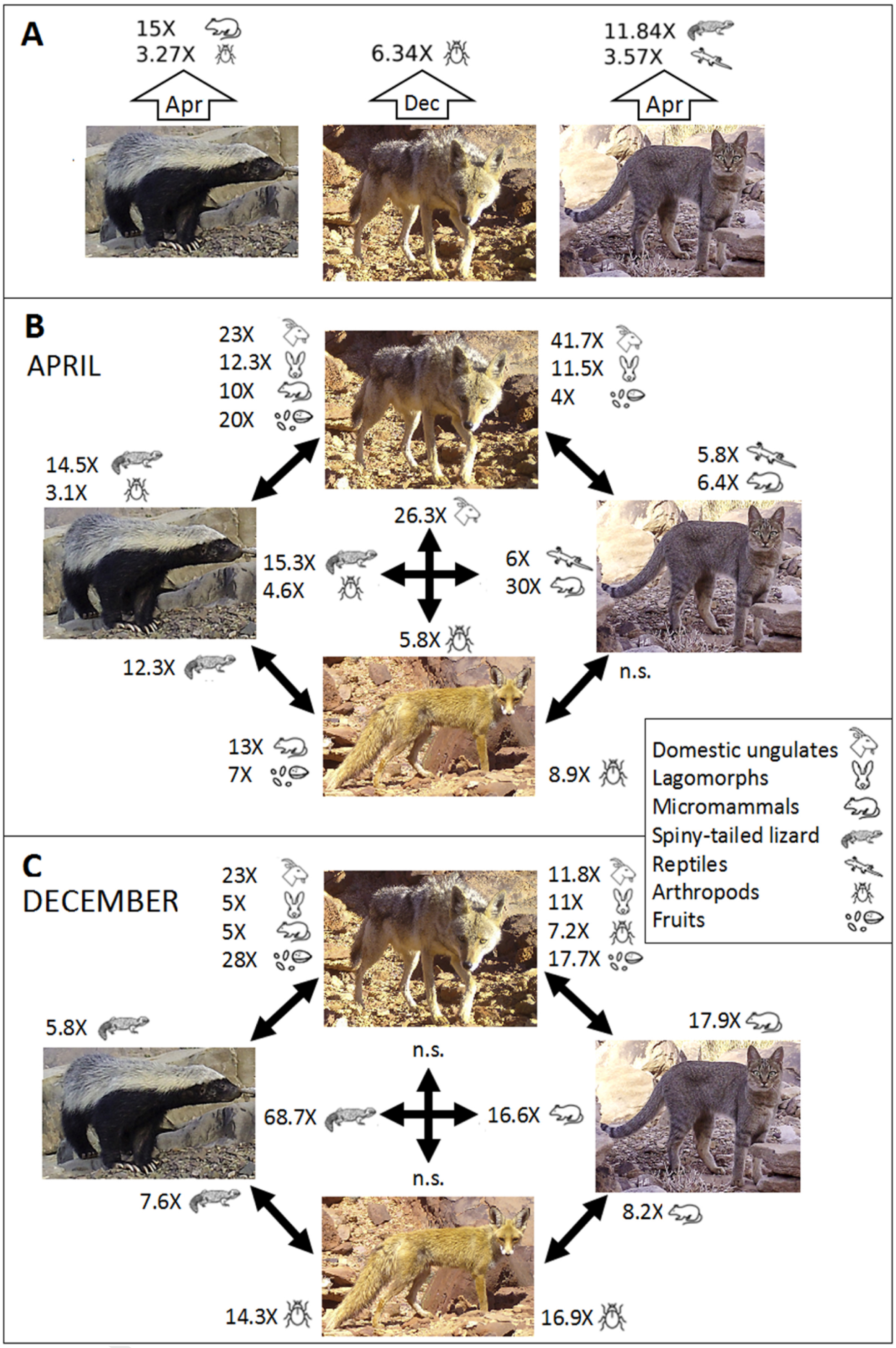

Fig. 3. Conceptual figures of significant dietary differences in relative frequencies after Fisher's exact tests and Benjamini-Hochberg post-hoc corrections ($P < 0.01$). A) Significant differences within the same predator species and between seasons (honey badger, African golden wolf and African wildcat, April vs December). B) Significant odds ratio of food categories between all four carnivores in April (honey badger, African golden wolf, African wildcat and red fox). C) Significant odds ratio of food categories between all four carnivores in December. Numbers indicate fold changes in resource consumption between seasons (A) or species within season (B and C), except when the difference is not significant (n.s.). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

appear to coexist through niche partitioning other than diet and spatial ecology, diel activity patterns become an interesting alternative to study.

Our study of inter-specific relationships suggests a mechanism related to niche partitioning that allows the coexistence of interacting species within a stressful environment where exploitative competition must play a key role. Interestingly, our results were different from those in other ecological systems (Barrio et al., 2013; Lesser et al., 2020), in that we found evidence of stronger competition through the observation of stronger niche partitioning. This highlights the importance of empirical field studies covering a range of species and ecosystems. In the current situation where large ecological field studies face a crisis (Ríos-Saldaña et al., 2018), it is worth mentioning that we were able to successfully carry out an important field effort that had to be designed and implemented in a harsh and remote area, the Sahara Desert. There wildlife has suffered a severe collapse during the last century, due to overhunting and habitat destruction (Durant et al., 2014), and where very little research effort has been developed, partially due to hostile conditions that imply high levels of insecurity for researchers

Table 2
Diet overlap (Pianka's index) between different predators per season (higher numbers higher overlap, lower numbers lower overlap). AWC: Africa wild cat, RF: red fox, AGW: African golden wolf, HB: honey badger. Pairwise diet overlap between species for feces collected in April over the diagonal, and December below the diagonal.

	April			
	AWC	RF	AGW	HB
AWC	-	0.67	0.3	0.31
RF	0.52	-	0.33	0.3
AGW	0.23	0.58	-	0.14
HB	0.35	0.55	0.38	-
	December			

(Brito et al., 2018). Despite the risks and costs, an understanding of the ecology of arid environments is an important objective for science in order to face the current climatic change scenario there and elsewhere (Brito et al., 2021).

CRediT authorship contribution statement

Carlos Sarabia: Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Writing – original draft. **Jose María Gil-Sánchez:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Supervision, Validation, Writing – review & editing. **F. Javier Herrera-Sánchez:** Data curation, Investigation, Methodology, Resources, Validation, Visualization. **Javier Rodríguez-Siles:** Data curation, Project administration, Validation, Visualization. **Miguel Ángel Díaz-Portero:** Data curation, Investigation, Resources, Validation, Visualization. **Ángel Arredondo:** Data curation, Investigation, Validation, Visualization. **Juan Manuel Sáez:** Data curation, Validation, Visualization. **Begoña Álvarez:** Data curation, Investigation, Validation. **Inmaculada Cancio:** Data curation, Investigation, Validation, Visualization. **Joaquín Pérez:** Data curation, Validation, Visualization. **Jaime Martínez-Valderrama:** Data curation, Validation, Visualization. **Mariola Sánchez-Cerdá:** Data curation, Investigation, Validation, Visualization. **Thomas Lahlafi:** Data curation, Investigation, Validation, Visualization. **Jose Manuel Martín:** Data curation, Validation, Visualization. **Abdeljebbar Qninba:** Project administration, Resources, Supervision, Validation, Visualization. **Emilio Virgós:** Conceptualization, Investigation, Methodology, Validation, Visualization, Writing – review & editing. **Jennifer A. Leonard:** Funding acquisition, Investigation, Resources, Software, Supervision, Validation, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We sincerely thank Jesús de Lucas, Gerardo Valenzuela, Jose M. Martín, Emil McCain, Salvador Castillo, Luis García-Cardenete, Aitor Rincón-García, Jesús Rodríguez-Osorio, Luis Llaneza, Ugo Melone, and Marcos Mallo for their assistance in the field, Anna Cornellas for her assistance in the lab, and the consevol group for comments and suggestions which improved this manuscript. We are especially grateful to the members of the association Tabia Biladohoud of Assa for their hospitality and support. The Département des Eaux et Forêst of Morocco authorized these wildlife surveys. Logistical support was provided by the Laboratorio de Ecología Molecular (LEM-EBD) and Doñana ICTS-RBD. Funding was provided by the Junta de Andalucia Frontera grant P18-FR-5099 to JAL.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jaridenv.2026.105612.

Data availability

Data will be made available on request.

References

Alhajeri, B.H., Steppan, S.J., 2018. Community structure in ecological assemblages of desert rodents. Biol. J. Linn. Soc. 124, 308–318.
Altschul, S.F., Gish, W., Miller, W., Myers, E.W., Lipman, D.J., 1990. Basic local alignment search tool. J. Mol. Biol. 215, 403–410.
Amroun, M., Oubellil, D., Gaubert, P., 2014. Écologie trophique du chacal doré dans le parc national du Djurdjura (Kabylie, Algérie). Revue d'Écologie 69 (3-4), 304–317.
Arsenault, R., Owen-Smith, N., 2002. Facilitation versus competition in grazing herbivore assemblages. Oikos 97, 313–318.
Auffray, J.C., Renaud, S., Claude, J., 2009. Rodent biodiversity in changing environments. Kasetsart J./Nat. Sci. 4 (3), 83–93.
Aulagnier, S., Cuzin, F., Thévenot, M., 2017. Mammifères sauvages au Maroc. Peuplement, répartition, ecologie. Société Française Pour L'Etude Et La Protection Des Mammifères.
Barrio, I.C., Hik, D.S., Bueno, C.G., Cahill, J.F., 2013. Extending the stress-gradient hypothesis. Is competition among animals less common in harsh environments? Oikos 122, 516–523.
Beck, H.E., Zimmermann, N.E., McVicar, T.R., Vergopolan, N., Berg, A., Wood, E.F., 2018. Present and future köppen-geiger climate classification maps at 1-km resolution. Sci. Data 5, 1–12.
Brito, J.C., del Barrio, G., Stellmes, M., Plkegezuelos, J.M., Saarinen, J., 2021. Drivers of change and conservation needs for vertebrates in drylands: an assessment from global scale to Sahara-Sahel wetlands. Eur. Zoological J. 88, 1103–1129.
Brito, J.C., Durant, S.H., Pettorelli, N., Newby, N., Canney, S., Algadafi, W., Rabei, T., Crochet, P.-A., Pleguezuelos, J.M., Wacher, T., de Smet, K., Gonçalves, D.V., Ferreira da Silva, M.J., Martínez-Freiría, F., Abáigar, T., Campos, J.C., Comizzoli, P., Fahd, S., Fellous, A., Garba, H.H.M., Hamidou, D., Harouna, A., Hatcha, M.H., Nagy, A., Silva, T.L., Sow, A.S., Vale, C.G., Boratyński, Z., Rebelo, H., Carvalho, S.B., 2018. Armed conflicts and wildlife decline: challenges and recommendations for effective conservation policy in the Sahara-Sahel. Conserv. Lett. 11, 1–13.
Bruno, J.F., Stachowicz, J.J., Bertness, M.D., 2003. Inclusion of facilitation into ecological theory. Trends Ecol. Evol. 18, 119–125.
Chase, J.M., Leibold, M.A., 2003. Ecological Niches. Linking Classical and Contemporary Approaches. University of Chicago Press.
Chesson, P., 2000. General theory of competitive coexistence in spatially-varying environments. Theor. Popul. Biol. 58, 211–237.
Creel, S., 2001. Four factors modifying the effect of competition on Carnivore population dynamics as illustrated by African wild dogs. Conserv. Biol. 15, 271–274.
Donadio, E., Buskirk, S.W., 2006. Diet, morphology, and interspecific killing in carnivore. Am. Nat. 167, 524–536.
Durant, S.M., Wacher, T., Bashir, S., Woodroffe, R., de Ornellas, P., Ransom, C., Newby, J., Abaigar, T., Abdelgadir, M., El, Alqamy, et al., 2014. Fiddling in biodiversity hotspots while deserts burn? Collapse of the Sahara's megafauna. Divers. Distrib. 20, 114–122.
Eddine, A., Mostefai, N., de Smet, K., Klees, D., Ansorge, H., Karssene, Y., Nowak, C., van der Leer, P., 2017. Diet composition of a newly recognized canid species, the African golden Wolf (*Canis anthus*), in Northern Algeria. Ann. Zool. Fenn. 54, 347–356.
Fisher, D.O., Dickman, C.R., 1993. Diets of insectivorous marsupials in arid Australia: selection for prey type, size or hardness? J. Arid Environ. 25 (4), 397–410. https://doi.org/10.1006/jare.1993.1072.
Gause, G.F., 1932. Experimental studies on the struggle for existence. J. Exp. Biol. 9, 389–402.
Gil-Sánchez, J.M., Herrera-Sánchez, F.J., Rodríguez-Siles, J., et al., 2024. Body size rules habitat selection and population declines after drought periods in a carnivore community of the Sahara Desert. Mamm. Biol. 105 (1), 69–81.
Gil-Sánchez, J.M., Herrera-Sánchez, F.J., Rodríguez-Siles, J., Sáez, J.M., Díaz-Portero, M.A., Arredondo, A., Álvarez, B., Cancio, I., de Lucas, J., Castillo, C., et al., 2020. Feeding specialization of honey badgers in the Sahara desert: a trial of life in a hard environment. Diversity 12, 59.
Hardin, G., 1960. The competitive exclusion principle. Science 131, 1292–1297.
Hart, S.P., Marshall, D.J., 2013. Environmental stress, facilitation, competition, and coexistence. Ecology 94, 2719–2731.
Hunter, J., Caro, T., 2008. Interspecific competition and predation in American carnivore families. Ethol. Ecol. Evol. 20, 295–324.
Karssene, Y., Chammem, M., Li, F., Eddine, A., Hermann, A., Nouira, S., 2019. Spatial and temporal variability in the distribution, daily activity and diet of fennec fox (*Vulpes zerda*), red fox (*Vulpes vulpes*) and African golden wolf (*Canis anthus*) in southern Tunisia. Mamm. Biol. 95, 41–50.
Kohn, M., Knauer, F., Stoffella, A., Schröder, W., Pääbo, S., 1995. Conservation genetics of the European brown bear- a study using excremental PCR of nuclear and mitochondrial sequences. Mol. Ecol. 4, 95–103.
Lanszki, J., Heltai, M., Kövér, G., Zalewski, A., 2019. Non-linear relationship between body size of terrestrial carnivores and their trophic niche breadth and overlap. Basic Appl. Ecol. 38, 36–46.

Lanszki, J., Heltai, M., 2002. Feeding habits of golden jackal and red fox in south-western Hungary during winter and spring. Mamm. Biol. 67, 129–136.

Leibold, M.A., McPeek, M.A., 2006. Coexistence of the niche and neutral perspectives in community ecology. Ecology 87, 1399–1410.

Leite, J.V., Álvares, F., Velo-Antón, G., Brito, J.C., Godinho, R., Alvares, F., Velo-Anton, G., Brito, J.C., Godinho, R., 2015. Differentiation of North African foxes and population genetic dynamics in the desert: insights into the evolutionary history of two sister taxa, *Vulpes rueppellii* and *Vulpes vulpes*. Org. Divers. Evol. 15, 731–745.

Lesser, J.S., James, W.R., Stallings, C.D., Wilson, R.M., Nelson, J.A., 2020. Trophic niche size and overlap decreases with increasing ecosystem productivity. Oikos 129, 1303–1313.

Menge, B.A., Berlow, E.L., Blanchette, C.A., Navarrete, S.A., Yamada, S.B., 1994. The keystone species concept: variation in interaction strength in a rocky intertidal habitat. Ecol. Monogr. 64, 249–286.

Moleón, M., Sánchez-Zapata, J.A., Selva, N., Donázar, J.A., Owen-Smith, N., 2014. Inter-specific interactions linking predation and scavenging in terrestrial vertebrate assemblages. Biol. Rev. 89, 1042–1054.

O'Connell, J., 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiment. In: Cody, M.L., MacArthur, R.H., Diamond, J. (Eds.), Ecology and Evolution of Communities. Harvard University Press, pp. 460–490.

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., et al., 2001. Terrestrial ecoregions of the world: a new map of life on Earth. Bioscience 51, 933–938.

Pianka, E.R., 1974. Niche overlap and diffuse competition. Proc. Natl. Acad. Sci. 71, 2141–2145.

Putman, R.J., 1984. Facts from faeces. Mamm Rev. 14, 79–97.

Rohland, N., Reich, D., 2012. Cost-effective, high-throughput DNA sequencing. Genome Res. 22, 939–946.

Ríos-Saldaña, C., Delibes-Mateos, M., Ferreira, C., 2018. Are fieldwork studies being relegated to second place in conservation science? Glob. Ecol. Conserv. 14, e00389.

Sarabia, C., Salado, I., Cornellas, A., Fernández-Gil, A., Vilà, C., Leonard, J.A., 2020. Towards high–throughput analyses of fecal samples from wildlife. Anim. Biodivers. Conserv. 43, 271–283.

Scheinin, S., Yom-Tov, Y., Motro, U., Geffen, E., 2006. Behavioural responses of red foxes to an increase in the presence of golden jackals: a field experiment. Anim. Behav. 71, 577–584.

Schoener, T.W., 1974. Resource partitioning in ecological communities: research on how similar species divide resources helps reveal the natural regulation of species diversity. Science 185, 27–39.

Schuette, P., Wagner, A.P., Wagner, M.E., Creel, S., 2013. Occupancy patterns and niche partitioning within a diverse carnivore community exposed to anthropogenic pressures. Biol. Conserv. 158, 301–312.

Steneck, R.S., 2005. An ecological context for the role of large carnivores in conserving biodiversity. In: Ray, J.C., Redford, K.H., Steneck, R., Berger, J. (Eds.), Large Carnivores and the Conservation of Biodiversity, pp. 9–33.

Team, R. R Core Team, 2010. European environment agency. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing.

Terry, R.C., 2018. Isotopic niche variation from the Holocene to today reveals minimal partitioning and individualistic dynamics among four sympatric desert mice. J. Anim. Ecol. 87, 173–186.

Violle, C., Nemergut, D.R., Pu, Z., Jiang, L., 2011. Phylogenetic limiting similarity and competitive exclusion. Ecology 14, 782–787.

Webb, C.O., Ackerly, D.D., McPeek, M.A., Donoghue, M.J., 2002. Phylogenies and community ecology. Annu. Rev. Ecol. Evol. Syst. 33, 475–505.

White, P.J., Ralls, K., White, C.A.V., 1995. Overlap in habitat and food use between coyotes and San Joaquin Kit foxes. Southwest. Nat. 40, 342–349.

Whitford, W., Duval, B., 2019. Ecology of Desert Systems, second ed. Academic Press.

Zalewski, A., Jedrzejewski, W., Jedrzejewski, B., 1995. Pine marten home ranges, numbers and predation on vertebrates in a deciduous forest (Bialowieza National Park, Poland). Ann. Zool. Fenn. 32, 131–144.