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Trophic Niche Partitioning between Two Desert Carnivores: Sand Cat *Felis margarita* Loche, 1858 (Felidae) and Rüppell's Fox *Vulpes rueppellii* (Schinz, 1825) (Canidae) in Central Iran

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Abstract: Most carnivore species are in constant competition with one another on common resources; their protection hinges upon identifying which mechanisms and to what degree they alleviate competition and facilitate coexistence between them. This study aimed at investigating niche overlap and divergence between two sympatric species, i.e. Rüppell's fox (*Vulpes rueppellii*) and sand cat (*Felis margarita*) in Rig-e-Jen area, Central Iranian desert. Totally, 73 and 61 scats were analysed belonging to Rüppell's fox and sand cat, respectively. Mammals were the most frequent food in the diet of both sand cat (86%) and Rüppell's fox (56%). Rüppell's fox tended to be a more flexible and opportunistic species with a more diverse diet. The niche breadth of the sand cat obtained by the standardised Levin's index (0.08) and Shannon-Wiener (0.36) was narrower than that of the Rüppell's fox (0.37 and 0.70, respectively). The trophic niche of sand cat and Rüppell's fox showed an overlap of 92%. Our findings in Rig-e-Jen area suggest that the larger diversity of prey type and size can promote sympatric living of sand cat and Rüppell's fox in Central Iran.

Key words: Rüppell's fox, sand cat, trophic niche, Rig-e-Jen, scat analysis, central Iran.

Introduction

Protecting mammalian species requires developing an in-depth knowledge about their various ecological characteristics such as habitat selection and diet. These characteristics are highly influenced by the inter- and intra-species interactions that a species has with its coexisting species. Identification of these interactions also serves as a perquisite for laying out effective strategies for mammal protection. Specifically, most carnivore species are in a constant competition with one another on common resources (Davis et al. 2018) and their protection hinges upon identifying which mechanisms and to what degree they alleviate the competition and facilitate the coexistence between these species (Caro & Stoner 2003, Broekhuis et al. 2013).

According to the competitive exclusion principle (Gause's law), the species coexistence urges the discrimination between common resources, i.e. niche differentiation (MacArthur & Levins 1967, Schoener 1974). Niche differentiation between carnivores is enforced by various mechanisms based on the level of competition, morphological differ-

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ences and environmental conditions; one or more mechanisms contribute simultaneously in reducing competition and facilitating coexistence (Davis et al. 2018). The type and body size of the preferred prey and the spatiotemporal pattern of habitat use are among the most important mechanisms underlying niche differentiation (Scognamillo et al. 2003, Vieira & Port 2007, Davis et al. 2019).

Ecological niche has three dimensions: spatial, temporal and trophic (Pianka 1975). Among these dimensions, the trophic niche has been frequently regarded as the most important niche dimension among most carnivores because prey availability is a fundamental determinant of carnivore distributions (Rich et al. 2017, Davis et al. 2018). In addition, diet has a remarkable influence on the growth, survival and reproduction (Preez et al. 2017) and even on forming other niche dimensions of carnivores (Broekhuis et al. 2013, Davis et al. 2018). Studies in this field showed that the competition between two or more coexisting carnivores may lead to a change in the diet and feeding habits of recessive carnivores (Andheria et al. 2007).

Accurate identification of the carnivores' dietary habits has always been a challenge due to their low abundance, large home ranges, nocturnal activity and secretive behaviour that collectively hinder their direct observation in the environment (Klare et al. 2011, Farhadinia et al. 2018). To compensate for this problem, a growing interest has emerged among ecologists regarding the indirect analysis of the dietary habits of carnivores, notably scat analysis (Hosseini-Zavarei et al. 2013, Tourani et al. 2014).

Feeding habits of small-sized carnivores have been extensively determined by scat analysis because these species often spend a short time to capture and eat a prey and in most cases, consume all parts of the body, leaving no sign of the eaten prey in the environment (Trejo 2012). E.g., this method was utilised to investigate the dietary partitioning of the sand cat *Felis margarita* Loche, 1858 (Felidae) and the Rüppell's fox *Vulpes rueppellii* (Schinz, 1825) (Canidae) in some parts of the Saudi Arabian desert (Lenain et al. 2004) and the dietary habits of corsac fox *V. corsac* Linnaeus, 1768 and red fox in Mongolia (Murdoch et al. 2010).

The Rig-e-Jen area is one of the most important and richest habitats for the populations of the sand cat and the sand fox in the central Iranian desert. To outline the effective strategies for conservation and management of these species, it is initially essential to illuminate which factors and to what degree alleviate the competition and facilitate their coexistence (Ghafaripour et al. 2017, Akbari et al. 2018). Many ecological aspects of these species are still unknown, and they resemble each other in terms of the amount of energy consumed and criteria influencing habitat selection. Therefore, relying on scat analysis, the present study aimed at investigating niche overlap and divergence between these two sympatric carnivore species in Rig-e-Jen area. The results are expected to derive useful insights on basic ecology, which can enhance our knowledge on coexisting patterns between sympatric carnivores in desert ecosystems.

Materials and Methods

Study area

This study was carried out in eastern and central parts of Rig-e-Jen Desert in Northeastern Isfahan Province. This region (hereafter referred to as Rig-e-Jen) contains one of the most prominent and most notorious sand dune habitats in the central Iranian plateau. With an area of about 160,900 ha, Rig-e-Jen area spans over 33°31′ – 33°52′ N longitude and 53°30′ – 54°28′ E latitude (1). The altitude range of the study area varies between 700 to 900 m a. s. l. The annual temperature varies between -9 and 47°C. Due to its arid and desert climate, Rig-e-Jen receives a very low amount of rain (Akbari & Jalalpour 2011).

The flora of the region is dominated by white saxaul *Haloxylon persicum*, *Calligonum comosum*, *Haloxylon aphyllum* and *Stipagrotis plumosa* (Akbari & Jalalpour 2011). The wide diversity of habitats in this region includes sand dunes, plains, floodplains, streams and considerable vegetation covers such as *Haloxylon* spp. and *Calligonum comosum.* Age-old forest patches across the region, pristine conditions, existence of small farmlands near the south-eastern boundary and proximity to some of the most important and rich in animal diversity protected areas in Central Iran such as Abbas-Abad Wildlife Refuge are among the main factors endowing a rich and unique biodiversity to Rig-e-Jen.

Besides sand cat and Rüppell's fox, this region is home to some other carnivores such as common fox (*Vulpes vulpes*), golden jackal (*Canis aureus*), wolf (*Canis lupus*) and caracal (*Caracal caracal*). Lagomorph and rodent species include hare (*Lepus capensis*), grey dwarf hamster (*Cricetulus migratorius*), Indian gerbil (*Tetra indica*), Persian jird (*Meriones persicus*), Baluchistan gerbil (*Gergilluse nanus*), great gerbil (*Rhombomys opimus*), Blanford's jerboa (*Jaculus blanfordi*), small five-toed

jerboa (*Allactaga elater*), short-tailed bandicoot rat (*Nesokia indica*) and house mouse (*Mus musculus*). Likewise, the area is home to MacQueen's bustard (*Chlamydotis macqueenii*), Pleske's ground jay (*Podoces pleskei*), Greater hoopoe-lark (*Alaemon alaudipes*), Crested lark (*Galerida cristata*) and Crowned sandgrouse (*Pterocles coronatus*) (Akbari et al. 2009).

Scat sampling

Scat sampling was undertaken on foot along several transects with a total length of 175 km during 6 months from early winter 2015 to late spring 2016. The team's prior knowledge about the shape and structure of the species scats and the location of active dens was used to distinguish between the scats of both species accurately. Each newly-found scat was also compared with the previously collected samples, especially those who were surely appeared to belong to a species, to ensure their accurate separation. In total, 81 and 67 scats were collected for Rüppell's fox and sand cat, respectively, and refined to 73 and 61 after the exclusion of suspicious samples. Each sample was kept in a plastic bag labelled with its geographic location and transported to the laboratory.

Samples were dried using an oven and weighted with an accuracy of 0.01 g. They were then diluted in water to a volume of 300 ml and soaked for 15 days. Next, samples were washed with distilled water and passed through 0.5 mm sieve. Samples were dried using paper towels and then were weighed. All of the remaining prey body parts (hair, feather, bone and scale, separately for mammals, reptiles, birds, insects; plant tissues), grouped to the order or the family levels, were analysed. Hair samples were taken for lab investigation based on a reference hair collection (Rezaei 2014).

Scat analysis

The scat samples were first analysed using the Frequency of Occurrence (FO) to determine the consumption rate and importance of each prey for both study species (Fox et al. 2014). This index was calculated by dividing the number of observations from species i (n_i) by the total number of scats (N) (Eq. 1) (Klare et al. 2011). Although this method leads to useful and practical information, it may produce biased results by giving higher importance to small prey when the consumed prey has different body sizes (Sharbafi et al. 2016). Accordingly, studies in this field showed a greater tendency to Percentage of Occurrence (PO %). The performance of this index was also found to be higher when more than one species exist in each scat (Loveridge & Macdonald 2003). PO% was calculated by adding the number of observations obtained from species i (C_i) to the total number of observations (C) (Eq. 2).

$$FO_i = ({}^{n_i}/_{N}) \times 100$$

$$PO_i = {}^{c_i}/_{C} \times 100$$

FO and PO overestimate the presence of small prey species such as insects and lizards and thus lower the importance of larger prey in the species diet (Klare et al. 2011). Hence, the Relative Volume (RV %) was used to provide a robust analysis and comparison of the consumed items between the study species. This index was measured using both the graduated cylinder and the graph paper methods and calculated numerically by dividing the number of occupied cells by item i (n_i) by the total number of occupied cells (N) and then multiplying by 100 (Eq. 3).

$$Rv_i = ({}^{n_i}/_{N}) \times 100 Rv_i = ({}^{n_i}/_{N}) \times 100$$

Niche breadth refers to the range of resources used by a species and is assessed spatially, dietary and temporally. Moreover, the fundamental niche refers to the full range of resources that a species uses in the absence of competitors (an ideal situation), whereas the realised niche indicates the range of resources narrowed down due to the presence of competitor (Davis et al. 2018). Each concept could be measured using various indices, which are all sensitive to the number of prey items and their relative frequencies (Hass 2009). In this study, the standardised Levin's and Shannon-Wiener indices were used to measure the trophic niche breadth of the study species. The Shannon-Wiener index provides a non-dimensional measure of diversity along with results biased toward rare and less-consumed species. Eq. 4 shows the Shannon-Wiener niche breadth (H), where p_j is the ratio of the consumed prey j. This index obtains values ranging from 0 to 1 (the maximum possible niche breadth) (Krebs 1999).

In order to avoid the bias of Shannon-Wiener results towards overestimating rare species, the Levin's index (L) was also measured as a complementary index. This index is a measure of uniform distribution of various preys in the species diet and is not sensitive to rare prey species (Krebs 1999). Eqs. 5 and 6 represent the simple (L) and the standardised (L_s) Levin's index (L). Similar to the Shannon-Wiener, this index obtains values between 0 and 1 (Krebs 1999).

$$H = -\sum P_i (\ln P_i)$$

$$L = {}^{1}/_{\sum P_i^2}$$

$$L_s = L - 1/n - 1$$

The Pianka (1974) index (Eq. 7) was used to estimate the trophic niche overlap between the Rüppell's fox and the sand cat where α_{kj} is the amount of overlap between species k and j; P_{ij} is the percentage of prey i consumed by species j and P_{ik} is the percentage of prey i consumed by species k. This index shows the effect of segregation and utilization of resources as well as dietary divergence and convergence of two species in response to changes in the diversity of foods (Krebs 1999). Pianka Index provides a symmetric measure of niche overlap, meaning that the niche overlap of species k over species j is equal to that of species j over species k. In reality, however, niche overlap between species may be asymmetric, in which the overlap of the winner species is quite larger than that of the defeated one. In this case, the asymmetric MacArthur & Levins (1967) index (Eq. 8) was also measured to realise which species exert the larger overlap with the other species.

$$\alpha_{jk} = \sum P_{ij}P_{ik} \Big/ \sqrt{\sum P_{ij}^2 P_{ik}^2}$$

$$\alpha_{jk} = \sum P_{ij}P_{ik} \Big/ \sum P_{ik}^2$$

$$\alpha_{kj} = \sum P_{ik}P_{ij} \Big/ \sum P_{ij}^2$$

Results

The results of scat analysis showed 161 food items in 73 Rüppell's fox scat samples (mean 2.2 items per scat) and 111 food items in 61 sand cat scats (mean 1.8 ± 0.2 species per scat). Both species consumed a variety of different types of mammals, insects, snakes and lizards, birds, seeds, various parts of plants and, in rare cases, livestock. Due to such high prey diversity and the difficulty of inaccurate identification of scat contents, prey remains were categorised into five classes of mammals, birds, reptiles, insects and plants (Tables 1 and 2). Most scats of both species contained species from more than one prey class.

The relative comparison of items identified from scat samples showed that rodents from the mammal class with PO% of 41.63 % and 54.96 % and relative volume percentage of 56.20 % and 86.08 % ranked first and had the highest frequency in the diet of Rüppell's fox and sand cat, respectively. Rüppell's fox had a high tendency to feed on Baluchistan gerbil, Blanford's jerboa, Persian jird and hare. Moreover, finding the remains of livestock (especially goat) in the Rüppell's fox scats, although it occurred in very few samples (n=3) with a low frequency, corroborates its scavenging behaviour. Small five-toed jerboa, Blanford's jerboa, Baluchistan gerbil and grey dwarf hamster were the most common prey species for the sand cat. Insects with PO% of 33.55 % and 26.58 % and relative volume percentage of 23.43 % and 6.06 % were listed as the second most taken prey by Rüppell's fox and sand cat, respectively. Hymenoptera, Coleoptera and Orthoptera were the most frequently-observed orders of insects in the Rüppell's fox scats, while the majority of insects found in the sand cat scats belonged to the orders Orthoptera, Coleoptera and Hymenoptera as well as to the Scorpionida.

Plant materials, particularly seeds were frequently consumed by Rüppell's fox. Various plant parts such as leaves, stems, seeds and fruits were observed in most scats. Among them, we detected seeds of bitter cucumber (*Citrullus colocynthis*), watermelon (*Citrullus lanatus*), date palm (*Phoenix dactylifera*), common sunflower (*Helianthus annuus*), sacred fig (*Ficus religiosa*), cucumber (*Cucumis* spp.), *Calligonum comosum* and saxaul (*H. persicum*).

The fourth most important pray type of Rüppell's fox was the group of reptiles in terms of relative volume and birds according to RV%. Based on the corrected FO, the least important classes are the birds and reptiles, respectively. It was also possible to distinguish between the scales of snakes and lizards in the scats of both species, even if they simultaneously occurred in one scat. Based on the results of all indices, insects and reptiles were the third and fourth most important pray types in the diet of the sand cat, respectively.

The standardised Levin's and Shannon-Wiener indices were measured to be 0.37 and 0.7 for Rüppell's fox and 0.08 and 0.36 for the sand cat, respectively. The Pianka's measure of niche overlapping between the two species was 92%. The results of asymmetric MacArthur and Levins index showed that the amount of competition that sand cat exerts over and receives from Rüppell's fox was 1.26 and 0.86, respectively.

Table 1. Frequency of occurrence and relative volume of prey species found in the scats of the Rüppell's fox in Rig-e-Jen area, Central Iran (mean prey items per scat=2.2)

No.	Prey type	FO	Corrected FO	PO (%)	RV (%)
1	Rodents	0.92	0.4612	41.63	56.20
2	Birds	0.12	0.0388	5.6	3.85
3	Reptiles	0.01	0.0502	6.22	1.98
4	Insects	0.74	0.3380	33.55	26.58
5	Plants	0.29	0.1118	13	11.38
Total		**2.21**	**1**	**100**	**100**

Table 2. Frequency of occurrence and relative volume of prey species found in the scats of the sand cat in Rig-e-Jen area, Central Iran (mean prey items per scat=1.8)

No.	Prey type	FO	Corrected FO	PO (%)	RV (%)
1	Rodents	1	0.64	54.95	86.08
2	Birds	0.09	0.04	5.4	2.38
3	Reptiles	0.21	0.09	11.72	4.16
4	Insects	0.43	0.19	23.43	6.06
5	Plants	0.82	0.04	4.5	1.32
Total		**1.82**	**1**	**100**	**100**

Discussion

Diet

Mammals were the dominant food items in the diet of both carnivores. Rüppell's fox showed to be a more flexible and opportunistic species with a more diverse diet. These findings align with the results of a concurrent study on their habitat classification in Abbas-Abad and Rig-e-Jen (Akbari et al. 2018). Sand cat primarily selects dune habitats covered with dense *Haloxylon* spp. and *Calligonum comosum*, with vertebrate diversity consisting mainly of rodents. Such a difference in habitat selection can be associated with differentiation in dietary habits (Akbari et al. 2018).

Studies on small-sized carnivores showed that small mammals (mostly rodents) form the main part of their diets across various habitats such as forests (Mukherjee et al. 2003), mountains (Napolitano et al. 2008) and arid lands (Murdoch et al. 2010, Ross et al. 2010) as well as agricultural and residential areas (Rajaratnam et al. 2007). It seems that sand cat has a higher preference to small mammals and rodents compared to Rüppell's fox. Another study in Southeastern Iran found that jerboas, jirds and gerbils comprise a significant proportion of the sand cat diet (Ghafaripour et al. 2017). Ghadirian et al. (2016) also reported similar taxa as the main food for sand cats in Iran. A great deal of research, in this case, confirmed that cats are dependent on hunting small animals (Mukherjee et al. 2003, Ross et al. 2010, Farhadinia et al. 2016, Moqanaki et al. 2016), whereas similar sized smaller canids such as red fox, Rüppell's fox and golden jackal tend to be more omnivorous and opportunistic feeders.

Many studies showed that sand cat usually feeds on small rodents residing in sand dunes (Sunquist & Sunquist 2002, Ghadirian et al. 2016). These studies also showed that the sand cat is a specialist evolved to hunt rodents and small mammals as large as young hares. The Rüppell's fox, on the other hand, tends to feed uniformly on a wider range of food items compared to the sand cat. In most studies, rodents represent the main part of the Rüppell's fox diet (Mukherjee et al. 2004, Silva-Pereira et al. 2011, Bianchi et al. 2011). Nevertheless, it is a flexible and opportunistic species with the ability to change its diet according to the existence and availability of food sources (Larivière & Seddon 2001). In Morocco, where the mammalian diversity is low, sand cat feeds on insects (Serra et al. 2007, Sillero-Zubiri et al. 2004). Similarly, following mammals, insects and other invertebrates such as scorpions and millipedes were identified as the second most crucial group of prey for the sand cat. The specific behaviour of sand cat and its ability to switch prey were further corroborated by finding some of its scats exclusively contained the remains of insects and invertebrates.

A study on the diet of the Rüppell's fox in the Rub'al Khali desert (Saudi Arabia) has shown that it feeds on large insects (locusts, crickets and cockroaches) as well as on reptiles (*Romastyx aegyptia*, *Cerastes gasperettii* and lizards of the genus *Ere-*

mias) from early spring to mid-summer; in winter, it switches to rodents (Murdoch et al. 2010). Sand cat uses insects and reptiles as a complementary food source to rodents. Other studies also showed that besides consuming rodents and other mammals, cats tend to feed on insects and reptiles only as complementary food items (Rajaratnam et al. 2007). The presence of the remains of beetles in the scats of cat species was attributed to their scavenging behaviour. This behaviour was further corroborated in this research by finding livestock hairs in the scats of the sand cat.

Remains of birds were low in the scats of both species. It seems that the ability of birds to fly makes them an unpredictable and unstable source of food for both species; hunting on birds can only be achieved by surprising them randomly based upon luck (Pires et al. 2011). *Alaemon alaudipes, Galerida cristata, Oenanthe hispanica, Ammoperdix griseogularis* and *Pterocles coronatus* are among the most frequent bird species hunted by sand cat and Rüppell's fox (Sunquist & Sunquist 2002, Ghadirian et al. 2016). Through the field surveys of this research, we also observed an immature houbara bustard hunted by a sand cat.

Niche breadth

The results of this study showed that the niche breadth of the sand cat obtained by the standardised Levin's index of 0.08 and Shannon-Wiener 0.36 were much narrower than that of the Rüppell's fox with the standardised Levin's and Shannon-Wiener indices of 0.37 and 0.70, respectively. Other studies also found that canids occupy a more extensive niche breadth compared to their sympatric felids (Carvalho & Gomes 2004, Mukherjee et al. 2004). Canids such as red fox, Rüppell's fox and jackal are highly flexible with unique adaptive abilities, enabling them to feed on a wide variety of food resources (Sillero-Zubiri et al. 2004).

According to a concurrent study, it was found that Rüppell's fox is not selective about its habitat and occupies the majority of habitats in the region, including sand dunes, open plains, foothills and hilly areas (Akbari et al. 2018). It seems that such an ability has helped Rüppell's fox to exploit a broader trophic niche. Sand cat, on the other hand, prefers only sand dunes and plain areas (Akbari et al. 2018). Thus, the species can supply its food by focusing on species found in sand dune habitats.

Consistent with our previous research, this study showed that *Haloxylon* spp. and *Calligonum comosum* covering sand dunes support the greatest diversity and frequency of rodents and other small mammals selected by the sand cat (Akbari et al. 2009, Hemami et al. 2010, Akbari & Jalalpour 2011). The high specialisation of the sand cat made it vulnerable against carnivores with a broader niche breadth because the survival of this species in the region now entirely hinges upon the abundance of sand- and desert-living rodents.

Trophic niche overlap

The trophic niche of sand cat and Rüppell's fox showed an overlap of 92%. This indicates a fierce competition between these species, which has not been previously observed between small canids and felids (Mukherjee et al. 2004, Bianchi et al. 2011). The Gause's law denotes that sympatric species with a high ecological niche overlap should evolve mechanisms facilitating coexistence and reducing interference and exploitative competition (Caro & Stoner 2003, Broekhuis et al. 2013). Our findings showed that rodents account for the most preferred prey of the sand cat, whereas Rüppell's fox feeds on a more various diet. The specialist behaviour of sand cat made it occupying a narrow niche. In contrast, the breadth niche of Rüppell's fox was found to be much broader due to feeding almost equally on a high diversity of food resources.

The specialist and generalist behaviours of sand cat and Rüppell's fox, respectively, can be regarded as one of the mechanisms helping them to coexist with each other in the region. Furthermore, the diversity and frequency of prey in Rig-e-Jen and temporal segregation of nocturnal activities are other causes and mechanisms contributing to their coexistence (Akbari & Jalalpour 2011, Akbari et al. 2018). The results of one-way MacArthur and Levins index showed that Rüppell's fox, despite having a broader ecological niche, was the suppressed species in its competition with sand cat. This indicates that the length of niche breadth does not necessarily reflect the availability of suitable food resources. According to the optimal diet theory, a defeated species extends its niche space to achieve its nutrient requirements from various possible food sources (Caughley & Sinclair 1994, Azevedo 2008).

The results of the present study and those previously conducted in Rig-e-Jen suggest that rodents comprising the diet of sand cat and, in part, of Rüppell's fox, have evolved to survive and live in this region. The diversity of prey type, age and size could facilitate higher coexistence between sympatric carnivores (Davis et al. 2018).

Further studies are needed to understand prey selectivity among rodents in different habitat types by these small carnivores. What is certain is that

these sensitive sand and desert habitats and their unique biodiversity faced the heightened risk of degradation. Its main drivers are severe drought events, excessive exploitation of underground water for agricultural purposes, uncontrolled tourism, overgrazing of vegetation by livestock during winter and spring. These pressures require special attention to ensure the sustainability of this ecosystem and its associated species over time.

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