RESEARCH ARTICLE



Interspecific Dietary Overlap Between Two Sympatric Wild Canids in Hirpora Wildlife Sanctuary, Northwestern Himalayas, India

Zakir Hussain Najar¹ · Bilal A. Bhat¹ · Iyaz Quyoom¹ · Riyaz Ahmad²

Received: 21 July 2023 / Revised: 24 May 2024 / Accepted: 10 July 2024 / Published online: 12 August 2024 © Zoological Society, Kolkata, India 2024

Abstract The red fox (*Vulpes vulpes*) and golden jackal (Canis aureus) frequently coexist and share resources. We investigated the dietary fluctuations of the red fox and the golden jackal over a two-year period to understand their dietary overlap and trophic relationship in Hirpora Wildlife Sanctuary, in the northwestern Himalayas of India. A total of 287 scat samples (red fox = 159 and golden jackal = 128) were analyzed. The scat analysis revealed 13 and 12 food items in the diet of red fox and golden jackal respectively. Domestic sheep contributed maximum in both the canid species with the relative occurrence of 12% in the diet of red fox and 8% in the diet of golden jackal. Livestock contributes maximum to the biomass of both species (red fox: 69% and golden jackal: 66%), while as the contribution of plant matter was negligible (red fox: 4% and golden jackal: 3%). The trophic niche breadth of the jackal (5.33) and red fox (6.29)suggests that both meso-carnivores are generalist feeders. The high level of dietary overlap suggests the presence of competition between the two species. However, their coexistence is facilitated by their preference for different altitudinal ranges within the study area, as well as by the plentiful availability of rodents and carrions. Findings of the present study are expected to act as baseline information on the trophic interactions and trophic overlap between the two meso-carnivores in the northwestern Himalayas, India.

Keywords Biomass consumption \cdot Dietary niche breadth \cdot Diet overlap \cdot Golden jackal \cdot Red fox

Riyaz Ahmad riyaz.cf@gmail.com

² National Centre for Wildlife, Riyadh, Saudi Arabia

Introduction

Competition among sympatric carnivores significantly influences their population dynamics and community structure by determining the extent to which they utilize available prey resources. This interspecific competition can shape the relative success of different carnivore populations within a shared habitat (Polis et al. 1989; Ritchie et al. 2012; Tsunado et al. 2017). Dietary overlap can lead to interference competition within trophic guilds, making niche differentiation crucial for coexistence of sympatric species (Palomares & Caro 1999; Tsunado et al. 2017). Various factors such as body size, body form and trophic overlap determine the degree of competition between the carnivore species (Donadio and Buskirk 2006). Interspecific competition among carnivores is taxonomically skewed but is prominent among in Canidae (Prugh and Sivy 2020). Studies focusing on resource use among the sympatric and closely related species such as canids especially in resource limited landscapes would provide critical information about the resource partitioning and coexistence of sympatric species.

Golden jackal (*Canis aureus*), has a body weight of 8–15 kg whereas red fox (*Vulpes vulpes*) is smaller with a body weight of 4–7 kg (Lanszki et al. 2006). Golden jackal is native to Asia, Europe, and Africa (Trouwborstet al. 2015; Lange et al. 2021). In Asia, its range extends from the southernmost tip of Sri Lanka to the easternmost regions of Myanmar, Thailand, Nepal, India, Pakistan, and certain provinces in China (Sillero-Zubiri et al. 2004; Jhala and Moehlman, 2008; Nadeem et al. 2018). In India, it is found in notheren and western parts of the country (Majumder et al. 2011; Chourasia et al. 2012; Singh et al. 2016). The IUCN (2023) Red List of Threatened Species currently lists the golden jackal as "Least Concern" (LC). The geographic

¹ Department of Zoology, University of Kashmir, Srinagar, J and K, India

range of the red fox includes Asia, Europe, and some parts of North America (Sillero-Zubiri et al. 2004). In India, the red fox is distributed across the Himalayan and Trans-Himalayan ranges in the north, as well as the desert regions in the northwest (Ghoshal et al. 2016; Reshamwala et al. 2018). The red fox is currently classified as "Least Concern" (LC) on the IUCN (2023) Red List of Threatened Species. The golden jackal and the red fox exhibit omnivorous and opportunistic feeding behaviors, adapting to availability (Macdonald1979; Jedrzejewski and Jedrezejewka 1998; Lange et al. 2021). Studies have indicated that wild ungulates, livestock and small mammals form the main prey of golden jackal (Lamprecht 1978; Lanszki and Heltai 2010; Mukherjee et al. 2004; Lanszki et al. 2006; Lanszki et al. 2018). Additionally, they feed on fruits and vegetables, including seasonal berries, melons, and agricultural crops like grapes and nut (Lanszki et al. 2006; Lanszki et al. 2018; Lange et al. 2021). Red fox is an opportunistic generalist omnivore that consumes a wide range of foods, including small vertebrates, insects, reptiles, carrion, plant matter (fruits twigs, and seeds) and human excrement, (Jedrzejewska and Jedrzejewski 1998; Patalano and Lovari 1993; Jankowiak et al. 2008).

A few studies have been conducted on dietary ecology of red fox and jackal in India but studies on their interaction and resource partitioning are largely lacking. Himalayas harbor a rich assemblage of canids but little information is available on their resource partitioning and coexistence (Bhat et al. 2023). The current study is step forward to fill this gap and generate valuable information about the dietary overlap/partitioning of jackal and red fox in Hirpora Wildlife Sanctuary (HWS), a unique high-altitude protected area in Pir Panjal range of western Himalayas. We hypothesized that, the golden jackal, a socially adept predator with a larger body size, is likely to capture larger prey compared to the smaller red fox. We also hypothesis that differences in feeding habits will result in reduced trophic overlap among coexisting meso-carnivores, as resources will be segregated and partitioned (Rosenzweig 1966). In order to test these assumptions and have a finer understanding of trophic relations between them, we compared the diet composition, trophic overlap and dietary niche breadth of both the canid species.

Study Area

Hirpora Wildlife Sanctuary (HWS), nestled in Shopian District of Jammu and Kashmir, India with a total area of 341 km^2 ($33^\circ 29$ ' N and $74^\circ 30$ ' E). (Fig. 1). The elevation range of the area is 2557 m above sea level to 4666 m above sea level area with higher altitudes dominating the landscape (Najar et al. 2024). The climate is temperate with harsh winters and temperatures going down to -15 °C and snow accumulating to about 5 m (Kaul et al. 2014). The

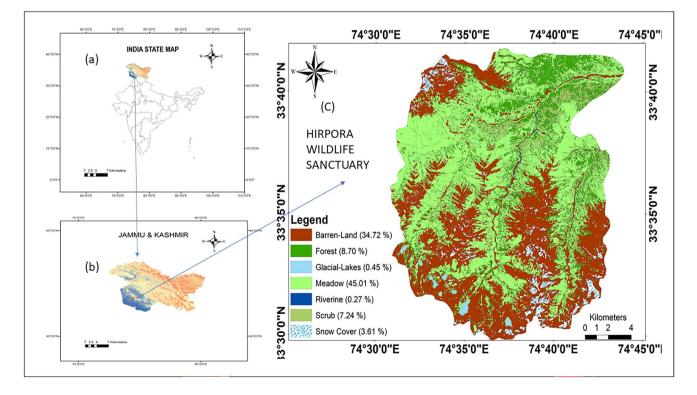


Fig. 1 Map of Hirpora Wildlife Sanctuary, Pir Panjal range of northwestern Himalayas, India

Sanctuary gets its name from the village Hirpora, a settlement on the protected area's western border. Historic Mughal Road which traverses the sanctuary and used by migratory herders from twin district of Jammu (Rajouri and Poonch) to enter Kashmir passes through this area (Ahmad et al. 2011; Kaul et al. 2014). This route has been recently developed into a highway which connects Kashmir with rest of the country (Ahmad et al. 2011; Kaul et al. 2014). Locals are agro-pastoralists but for last many years agriculture has been the main source of income. Among agricultural activities, potato and apple cultivation are major practices in the region, the area is famous for quality potato in Kashmir.

The sanctuary hosts significant animal and plant species. Mammals such as Kashmir markhor (Capra falconeri cashmiriensis), Kashmir musk deer (Moschus cupreus), Himalayan brown bear (Ursus arctos isabellinus), leopard (Panthera pardus), and Himalayan black bear (Ursus thibetanus) inhabit the area (Kaul et al. 2014). The Himalayan black bear, leopard, and Himalayan wolf are currently classified as "Vulnerable" (VU), whereas the Kashmir markhor, Kashmir musk deer, and Himalayan brown bear are currently listed as "Near Threatened" (NT), "Endangered" (EN), and "Critically Endangered" (CR), respectively, on the IUCN (2023) Red List of Threatened Species. In addition to that, the area is home to 129 different bird species (Kaul et al. 2014; Najar et al. 2022; Najar et al. 2024). The flora of the area is dominated by blue pine (Pinus wallichiana), spruce (Picea smithiana) and silver fir (Abies pindrow), Himalayan indigo (Indigofera heterantha), Himalayan viburnum (Viburnum grandiflorum), Kashmir elder (Sambucus wightiana), Juniper (Juniperus spp.) and Rhododendron (Rhododendron spp.). Important medicinal plants in the area include snow lotus (Saussurea atkinsonii), common wormwood (Artemisia absinthium), Himalayan sage (Phlomis bracteosa), Govan's corydalis (Corydalis govaniana), Himalayan snowberry (Gaultheria trichophylla), yam (Dioscorea deltoidea), and blue poppy (Meconopsis aculeate) are found in the study area (Kaul et al. 2014).

Methods

Scats of golden jackals and red foxes were collected along well-established trails (n = 36) across the various habitats for interspecific dietary comparison. Scats of golden jackal and red fox were distinguished based on their odor, size, and morphology (Macdonald 1980). Since jackal faeces are sub divided into many parts with blunt ends, commonly occur in piles (Vanak and Mukherjee 2008; Markhov and Lanszaki 2012; Nadeem et al. 2012), each pile within a circle (1–1.5 m diameter) was collected (Macdonald 1979). Red fox scats are more elongated and generally divided

into two parts (Aryal et al. 2010; Ahmad et al. 2018). Once collected, the scats were kept in paper bags labelled with date, trail name, GPS coordinates, age (fresh or old) and habitat type. Scats samples were first sun dried at the camping site and then dried in an oven at 60 °C to avoid fungal damage before processing. Furthermore, there were no stray dogs in the vicinity except few guarding dogs of migratory herders especially in the alpine region, which reduced the confusion in identification of scats.

Scats were immersed in water for approximately 12 h, then washed under flowing tap water in a sieve (mesh size of 0.5–0.6 mm). After that the remnants were dried. The prey items, especially the hair, were washed in alcohol and then cleared in xylene. Reference collections were made in the Wildlife Research Laboratory as well as from the scientific literature (Oli 1993; Mahmood et al. 2013) were used to identify the prey species, based on their medullary and cuticular patterns of scales. The diets of the two meso-predators were represented in three different ways (Table 1), viz; frequency of diet item in total scats (F), relative frequency of occurrence (RO) and percentage of biomass consumed (B%). Dietary overlap (O), and dietary niche breadth (B) were also evaluated. To compute RO, the number of food type occurrences for *i*th food item was divided by the summation of occurrences of all food items and multiplied by 100. To calculate the amount of biomass consumed, each dry food remnant was first weighed and then multiplied by an appropriate coefficient of digestibility. The coefficient of digestibility is given for livestock (118), small mammals (23), birds (35), insects (5), and plant material (14) (Goszezyinski 1974, Jedrezejewska and Jedrezewski 1998; Nadeem et al. 2012). The trophic overlap between the two meso-carnivores was estimated using the Pianka index (1974).

$$O_{jk} = \frac{\sum_{i}^{n} p_{ij} p_{ik}}{\sqrt{\sum_{i}^{n} p_{ij}^2 + \sum_{i}^{n} p_{ik}^2}}$$

where as_{ij} is the proportion of *i*th food item in the total diet of predator *j*, and p_{ik} is the proportion of *i*th food item in the total diet of predator *k*.

The Levins index (Levins 1968) was used to determine the dietary niche breadth:

$$\mathbf{B} = \frac{1}{\sum_{Pi}^{2}}$$

where *pi* represents the relative frequency of food items eaten by the predator p

To compare the differences in the diets of the golden jackal and red fox, the data were first subjected to the Shapiro–Wilk test to check normality in R Statistical Software (R Core team 2023). We then performed the Mann–Whitney U test in R software (R Core team 2023) to determine the significant differences in the relative occurrence (RO) of prey items consumed by the two canid species.

Results

Diet spectrum

A total of 159 red fox scats and 128 golden jackal scats were analyzed. The analysis revealed 13 and 12 food items in golden jackal and red fox, respectively. Both canids' diets included animal and plant remains. The animal matter consisted of both wild prey (such as rodents, pikas, insects, and birds) and domestic prey species (including sheep, goats, cows, horses, and buffalo) (Table 1). Furthermore, there were minimal quantities of unidentifiable items, human artefacts (cloth, polythene), and soil debris also present.

The contribution of small mammals was the highest with RO: 30.14%, whereas large mammals, were represented by 20.35% in the red fox scats (Table 1). Additionally, birds, invertebrates, and plant matter collectively accounted for 39.78%. The relative occurrence (RO) of domestic prey items in the red fox diet was 20.35%, while wild prey items accounted for 69.92%. Among domestic prey, sheep contributed the most (RO: 12.1%). Rodents were the most represented wild prey (RO: 28.2%), followed by insects and birds (RO: 15.5% and 7.28%, respectively) (Table 1).

The contribution of animal matter to the biomass of the red fox diet was the highest at 96.1%, while plant matter contributed very little at 3.87%. Domestic prey items were the most significant, contributing 69.1%, followed by wild prey items at 27.01%. The proportion of domestic sheep

in the red fox's diet in terms of biomass was the highest at 43.57%. The rest was contributed by rodents (19.6%), cows (14.1%), domestic goats (8.46%), birds (7.8%), pikas (2.06%), and insects (1.09%) (Table 1). The contribution of different food categories to the biomass of the red fox is presented in Fig. 2.

Analysis of golden jackal scat revealed that animal matter accounted for a significant portion (RO: 74.49%), while plant matter made up a smaller proportion (RO: 13.9%). Within the animal matter, small mammals were the most prevalent (RO: 36.8%) in the diet. Large mammals (livestock) collectively accounted for 15.92% of the diet (Table 1). Large mammals contributed the most to the

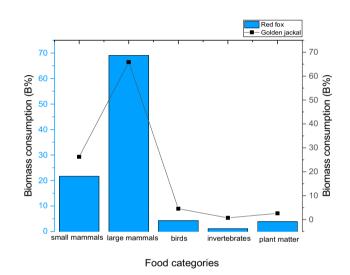


Fig. 2 Shows percent biomass (B%) of different food categories consumed by red fox and golden jackal in Hirpora Wildlife Sanctuary

Table 1Contribution of fooditems to the diet of red foxand golden jackal in terms offrequency of prey item in totalnumber of scats (F), relativeoccurrence of prey items (RO)and biomass (B%) consumptionof prey item

S. No	Food Categories	Prey items	Red fox $(n=159)$			Golden jackal $(n = 128)$		
			F	RO	B%	F	RO	B%
1	Small mammals	Rodent	58	28.2	19.6	72	35.8	25.04
		Pika	4	1.94	2.06		1	1.22
2	Large mammal	Sheep	25	12.1	43.57	16	7.96	33.4
		Goat	6	2.91	8.46	3	1.49	7.30
		Cow	9	4.37	14.1	8	3.9	16.12
		Horse	0	0	0	1	0.5	2.1
		Buffalo	2	0.97	2.96	4	1.99	6.96
3	Birds	Bird	15	7.28	4.26	15	7.46	4.54
4	Invertebrates	Insect	32	15.5	1.09	29	14.4	0.7
5	Plant matter	Plant matter	35	17	3.87	28	13.9	2.61
6	Human artefacts	Human artefacts	4	1.94	0	10	4.98	0
7	Soil and debris	Soil and debris	7	3.4	0	8	3.98	0
8	Unidentified	Unidentified	9	4.37	0	5	2.5	0
Total			206	100	100	201	100	100

biomass of golden jackals (65.8%), followed by small mammals (26.26%) (Fig. 2). Among large mammals, domestic sheep made up the majority (33.4%), followed by cows (16.12%), whereas among small mammals, rodents contributed the most (25.04%) to the biomass. Birds, insects, and plant matter combined contributed 7.86% to the biomass of jackals (Table 1).

Shapiro–wilk test revealed there was no normal distribution in Relative Occurrence (RO) of both the mesopredators. Mann Whitney U test revealed there was no significant difference in the consumption of different prey species (w = 84, p = 1).

Dietary Overlap and Trophic Niche Breadth

The dietary overlap between these two meso-carnivores was (0.97), with rodents, domestic sheep, insects, and birds being the primary contributors to this overlap. The trophic niche breadth was B = 5.33 for the jackal and B = 6.29 for the red fox.

Discussion

Our results suggest that the large and small -sized mammals constituted a significant portion to the diet of red fox and jackal in the HWS. Both the species consumed livestock carrion which indicates their scavenging behavior by opportunistically feeding large sized domestic livestock. This is in agreement with the findings from a study conducted in Pakistan (Akrim et al. 2019). Feeding on livestock carcasses is probably due to presence of large number of livestock available in and around the study area. Domestic animals provided more than half of the biomass devoured by both the carnivores. Apparently, the motorable road that traverses through the sanctuary is the main route for migratory herders to enter and exit Kashmir valley for seasonal grazing. During migration some of their livestock dies because of bad weather, road accidents or disease. Furthermore, much of the carrion comes from the livestock that stays within the sanctuary during summer, portion of this livestock dies due to diseases, predator attacks rock hits. Carrion is beneficial as it provides a nutrient rich food supply without the energy expense on hunting and chasing prey species (Wilson and Wolkovich 2011). Similar observations have been reported by Ahmad et al. (2018) while investigating dietary spectrum of two sympatric canids in Trans-Himalayas.

The two species consumed a variety of prey items from insects to large mammals highlighting their wide dietary spectrum. Despite our assumptions of body sizes and social structure, we found that small mammals formed a significant proportion of the diet, of both species. Our results are in line with several previous studies (Basuony et al. 2005; Ahmad et al. 2018; Bhat et al. 2023). The consumption of birds and invertebrates could be to compensate protein requirements as reported by Pakalniske (2012). The occurrence of rodents was highest in golden jackal diet despite its larger body size than red fox. This may be because the settlements in and around the HWS engage in substantial agricultural practices especially potato and apple production, which probably made this area conducive for rodents. Both species are known to prefer rodents when they are available in plenty (Lanszki and Heltai 2010), and their trophic niches change in response to changes in rodent populations (Lanszki et al. 2006). This suggests that the availability of local resources may be a major factor in trophic overlaps. This is supported by the study conducted in Hungry where rodents dominated the diet of golden jackal and red fox (Lanszki et al. 2016).

Both red fox and golden jackal in HWS had trophic niches more or less the same, indicating their opportunistic feeding behavior of. The niche breadth of red fox was slightly greater than golden jackal, which could be because red fox is more widespread in the HWS. This is in contrary with the study conducted in Pakistan (Akrim et al. 2019) where jackals had wider niche breadth than foxes. It has been suggested that carnivores behave as generalists when prey is scarce and specialists when prey is abundant (Mac Arthur and Pianka 1966).

The dietary overlap between the two carnivores was expected while sharing the same geographic area (Ahmad et al. 2018) and if large part of the different prey is available as carrion. Thus, golden jackal and red fox in HWS had a significant trophic overlap, which is consistent with some previous studies (Soe et al. 2017; Tsunoda and Saito 2020). Both species consumed livestock carrion, rodents, insects and birds in considerable amount. But due to the altitudinal and habitat differences and readily available large amounts of livestock carrion, the two species probably avoid competition as red foxes uses all the available altitudinal ranges and more open areas, while jackals prefer lower altitudinal ranges and forested habitats. In contrary, Tsunoda et al. (2017a, b) documented trophic separations where red foxes fed on rodents, and golden jackals scavenged livestock or wild ungulate carrions.

In conclusion, this study establishes a baseline for the dietary overlap between the two canid species found in the Western Himalayas and elsewhere in the Indian Himalayan Region. Given that both species inhabit the same geographical range, a certain degree of dietary overlap is expected. The study reveals that both species overlap in the consumption of four species: domestic sheep, rodents, insects and birds. This high level of overlap suggests the presence of competition between the two species. However, their coexistence is facilitated by their preference for different altitudinal ranges within the study area, as well as by the plentiful availability of rodents and livestock carcasses.

Potential Limitations

Although traditional scat-based dietary assessment methods used in the current study is simple and inexpensive, this method has important shortcomings: 1) a high degree of uncertainty is associated with the specieslevel identification of closely related prey remains; and 2) dietary items composed of soft and highly digestible tissues are not detected and the presence of other prey may be underestimated. The identification of consumed prey using DNA analysis can overcome some limitations of morphology- based diet assessments. Addressing this limitation in future research could enhance the understanding of interspecific interactions and contribute to the conservation strategies for these species in changing environments.

Acknowledgements We are highly thankful to Department of Wildlife Protection for providing necessary permission to carry out field work in Hirpora Wildlife Sanctuary. The first author acknowledges the University Grants Commission for providing financial assistance as Junior Research Fellowship under UGC NET-JRF Scheme.

Author Contributions The first author collected all the data and analysed it. He also prepared the first draft of the paper. The 2nd author and the corresponding authors designed the study and provided comments on the first draft to refine it. The 3rd and corresponding authors also accompanied the first author in the field for few times.

Declarations

Conflict of interest The authors declare no conflict of interest.

References

- Ahmad, R., P. U., S. I., S. Haq, S. Querishi, M. Puri, and R. Kaul. 2011. The lost Markhor of Pirpinjal; Assessing the distribution of markhor (*Capra falconeri*) and other important fauna along with southern slopes of Pirpanjal with special reference to resource competition with local grazier communities, in Hirpora WLS, Jammu and Kashmir. Wildlife Trust of India, Delhi.
- Ahmed, T., A. Khan, and P. Chandan. 2018. Dietary spectrum of two sympatric canid species in Ladakh, India. *In Proceedings of the Zoological Society* 71: 320–326.
- Aiyadurai, A., and Y.V. Jhala. 2006. Foraging and habitat use by golden jackals (*Canis aureus*) in the Bhal region, Gujarat. *India Journal Bombay Natural History Society* 103: 1–10.
- Akrim, F., T. Mahmood, M.S. Nadeem, T. Dhendup, H. Fatima, and S. Andleeb. 2019. Diet composition and niche overlap of two sympatric carnivores: Asiatic jackal (*Canis aureus*) and Kashmir hill fox (*Vulpes vulpesgriffithii*), inhabiting Pir Lasura National Park, northeastern Himalayan region, Pakistan. *Wildlife Biology* 2019: 1–9.

- Aryal, A., S. Sathyakumar, and B. Kreigenhofer. 2010. Opportunistic animal's diet depend on prey availability: Spring dietary composition of the red fox (*Vulpes vulpes*) in the Dhorpatan hunting reserve. *Nepal Journal of Ecology and the Natural Environment* 2 (4): 59–63.
- Basuony, M., Saleh, M., Riad, A., and W. Fathy. 2005. Food composition and feeding ecology of the red fox *Vulpes vulpes* (Linnaeus, 1758) in Egypt. *Egyptian Journal of Biology* 7: 96–102.
- Bhat, K.A., B.A. Bhat, B.A. Ganai, A. Majeed, N. Khurshid, and M. Manzoor. 2023. Food habits of the red fox *Vulpes vulpes* (Mammalia: Carnivora: Canidae) in Dachigam National Park of the Kashmir Himalaya. *India Journal of Threatened Taxa* 15 (1): 22364–22370.
- Bhat, R.A., H. Tak, B.A. Bhat, M.F. Fazli, H.M. Wani, and R. Ahmad. 2019. Livestock Helminth Infestation as a potential threat to wild ungulates in hirpora wildlife sanctuary. *Journal Himalayan Ecol Sustain Dev* 14: 71–78.
- Chourasia, P., K. Mondal, K. Sankar, and Q. Qureshi. 2012. Food habits of golden jackal (*Canis aureus*) and striped hyena (Hyaena hyaena) in Sariska Tiger Reserve. Western India World Journal of Zoology 7 (2): 106–112.
- Donadio, E., and S.W. Buskirk. 2006. Diet, morphology, and interspecific killing in carnivora. American Naturalist 167: 524–536.
- Ghoshal, A., Y.V. Bhatnagar, C. Mishra, and K. Suryawanshi. 2016. Response of the red fox to expansion of human habitation in the Trans-Himalayan mountains. *European Journal of Wildlife Research* 62: 131–136.
- Goszczynski, J. 1974. Studies on the food of foxes. *Acta Theriologica* 19: 1–18.
- Hoffmann, M., and C. Sillero-Zubiri. 2016. Vulpes vulpes. The IUCN red list of threatened species 2016: e. T23062A46190249. IUCN https://doi.org/10.2305/IUCN
- IUCN. 2023. The IUCN Red List of threatened species. Retrieved Jan 2024, from https://www.iucnredlist.org.
- Jankowiak, L., M. Antczak, and P. Tryjanowski. 2008. Habitat use, food and the importance of poultry in the diet of the red fox (*Vulpes vulpes*) in extensive farmland in Poland. *World Applied Sciences Journal* 4 (6): 886–890.
- Jhala, Y. V., and P.D. Moehlman. 2008. *Canis aureus*. The IUCN red list of threatened species 2008: eT3744A10054631.
- Jedrzejewska, B., and W. Jedrzejewski. 1998. Predation in vertebrate communities, 450. The Bialowieza Primeval Forest as a case study: Springer-Verlag, Berlin.
- Kaul R., R. Ahmad, T. Bhatacharya. S. Bhodankar, MA. Tak and I. Suhail. 2014. Management Plan for Hirpora Wildlife 118.
- Lamprecht, J. 1978. On diet, foraging behaviour and interspecific food competition of jackals in the Serengeti National Park, East Africa. *Zeitschrift fur Saugetierkunde* 43: 210–223.
- Lange, P.N., G. Lelieveld, and H.J. De Knegt. 2021. Diet composition of the golden jackal (*Canis aureus*) in south-east Europe–a review. *Mammal Review* 51 (2): 207–213.
- Lanszki, J., and M. Heltai. 2010. Food preferences of golden jackals and sympatric red foxes in European temperate climate agricultural area (Hungary). *Mammalia* 74: 267–273.
- Lanszki, J., A. Kurys, L. Szabo', N. Nagyapa'ti, L.B. Porter, and M. Heltai. 2016. Diet composition of the golden jackal and the sympatric red fox in an agricultural area (Hungary). *Folia Zoologica* 65 (4): 310–322.
- Lanszki, J., G. Giannatos, A. Dolev, G. Bino, and M. Heltai. 2010. Late autumn trophic flexibility of the golden jackal (*Canis aureus*). *Acta Theriologica* 55: 361–370.
- Lanszki, J., M. Heltai, and L. Szabo'. 2006. Feeding habits and trophic niche overlap between sympatric golden jackal (*Canis aureus*) and red fox (*Vulpes vulpes*) in the Pannonian ecoregion (Hungary). *Canadian Journal of Zoology* 84: 1647–1656.

- Lanszki, J., M.W. Hayward, and N. Nagyapáti. 2018. Feeding responses of the golden jackal after reduction of anthropogenic food subsidies. *PLoS ONE* 13: 12-e0208727.
- Levins, R. 1968. *Evolution in changing environments*, 132. Princeton N.J.: Princeton University Press.
- MacArthur, R.H., and E.R. Pianka. 1966. On optimal use of a patchy environment. *American Naturalist* 100: 603–609.
- Macdonald, D.W. 1979. The flexible social system of the golden jackal, *Canis aureus. Behavioral Ecology and Sociobiology* 5: 17–38.
- Macdonald, D.W. 1980. Patterns of scent marking with urine and faeces amongst carnivore communities. In Symposia of the Zoology Society of London 45: 107–139.
- Mahmood, T., F. Niazi, and M.S. Nadeem. 2013. Diet composition of asiatic jackal (*Canis aureus*) in margallah hills national park, Islamabad, Pakistan. *The Journal of Animal and Plant Sciences* 23 (2): 444–456.
- Majumder, A., K. Sankar, Q. Qureshi, and S. Basu. 2011. Food habits and temporal activity patterns of the Golden Jackal Canis aureus and the Jungle Cat Felis chaos in Pench Tiger Reserve, Madhya Pradesh. *Journal of Threatened Taxa* 26: 2221–2225.
- Markov, G., and J. Lanszki. 2012. Diet composition of the golden jackal, *Canis aureus* in an agricultural environment. *Folia Zoologica* 61: 44–48.
- Mukherjee, S., S.P. Goyal, A.J.T. Johnsingh, and M.L. Pitman. 2004. The importance of rodents in the diet of jungle cat (*Felis chaus*), caracal (*Caracal caracal*) and golden jackal (Canis aureus) in Sariska Tiger Reserve, Rajasthan. *India Journal of Zoology* 262 (4): 405–411.
- Nadeem, M.S., N.A.Z. Ruqqya, S.I. Shah, M.A. Beg, A.R. Kayani, M. Mushtaq, and T. Mahmood. 2018. Season-and locality-related changes in the diet of Asiatic jackal (*Canis aureus*) in Potohar. *Pakistan Turkish Journal Zoology* 36: 798–805.
- Najar, Z.H., B.A. Bhat, R. Ahmad, and M. Javid. 2024. Assessing current and future habitat suitability for the Himalayan wolf in the Hirpora Wildlife Sanctuary. *Journal of Wildlife and Biodiversity* 8(2): 150–164.
- Najar, Z.H., B.A. Bhat, and R. Ahmad. 2022. First record of Small Minivet *Pericrocotuscinnamomeus* (Aves: Passeriformes: Campephagidae) from Kashmir India. *Journal of Threatened Taxa* 14 (2): 20680–20682.
- Oli, M.K. 1993. A key for the identification of the hair of mammals of a snow leopard (*Panthera uncia*) habitat in Nepal. *Journal of Zoology* 231: 71–93.
- Pakalniske, M. 2012. The feeding habits of the Red fox (Vulpes vulpes Linnaeus, 1758) in different landscapes and seasons in Latvia. Acta Biologica Universintis Dqugavpiliensis 12 (2): 167–173.
- Palomares, F., and T.M. Caro. 1999. Interspecific killing among mammalian carnivores. *American Naturalist* 153: 492–508.
- Patalano, M., and S. Lovari. 1993. Food habits and trophic niche overlap of the wolf (*Canis lupus*, L. 1758) and the red fox (*Vulpes vulpes*, L. 1758) in a Mediterranean mountain area. *Revue Ecology* 48: 23–38.
- Pianka, E.R. 1973a. The structure of lizard communities. *Annual Review Ecology Systematics* 4: 53–74.
- Pianka, E.R. 1973b. The structure of lizard communities. Annual Review of Ecology and Systematics 4 (1): 53–74.
- Polis, G.A., C.A. Myers, and R.D. Holt. 1989. The ecology and evolution of intraguild predation: Potential competitors that eat each other. *Annual Review Ecology Systematics* 20: 297–330.

- Prugh, L.R., and K.J. Sivy. 2020. Enemies with benefits: Integrating positive and negative interactions among terrestrial carnivores. *Ecology Letters* 23: 902–918.
- R Core Team. 2023. RA language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Ritchie, E.G., B. Elmhagen, A.S. Glen, M. Letnic, G. Ludwig, and R.A. McDonal. 2012. Ecosystem restoration with teeth: What role for predators? *Trends in Ecology and Evolution* 27: 265–271.
- Rosenzweig, M.L. 1966. Community structure in sympatric Carnivora. Journal of Mammalogy 47: 606–612.
- Sillero-Zubiri, C., M. Hoffmann, and D.W. Macdonald. eds. 2004. Canids: foxes, wolves, jackals and dogs: status survey and conservation action plan. Gland and Cambridge: IUCN/SSC Canid Specialist Group.
- Singh, A.A., S. Dookia. Mukherjee, and H.N. Kumara. 2016. High resource availability and lack of competition have increased population of a meso-carnivore—a case study of golden jackal in Keoladeo National Park, India. *Mammal Research* 61: 209–219.
- Soe, E., J. Davison, K. Suld, H. Valdmann, L. Laurimaa, and U. Saarma. 2017. Europe-wide biogeographical patterns in the diet of an ecologically and epidemiologically important mesopredator, the red fox *Vulpes vulpes*: A quantitative review. *Manmal Review* 47: 198–211. https://doi.org/10.1111/mam.12092.
- Trouwborst, A., M. Krofel, and J.D.C. Linnell. 2015. Legal implications of range expansions in a terrestrial carnivore: The case of the golden jackal (*Canis aureus*) in Europe. *Biodiversity and Con*servation 24: 2593–2610.
- Tsunoda, H., and M.U. Saito. 2020. Variations in the trophic niches of the golden jackal Canis aureus across the Eurasian continent associated with biogeographic and anthropogenic factors. *Journal* of Vertebrate Biology 69: 20056–20061.
- Tsunoda, H., E.G. Raichev, C. Newman, R. Masuda, D.M. Georgiev, and Y. Kaneko. 2017a. Food niche segregation between sympatric golden jackals and red foxes in central Bulgaria. *Journal of Zoology* 303 (1): 64–71.
- Tsunoda, H., E.G. Raichev, C. Newman, R. Masuda, D.M. Georgiev, and Y. Kaneko. 2017b. Food niche segregation between sympatric golden jackals and red foxes in central Bulgaria. *Journal of Zoology* 303: 64–71. https://doi.org/10.1111/jzo.12464.
- Vanak, A.T., and S. Mukherjee. 2008. Identification of scat of Indian fox, jungle cat and golden jackal based on morphometrics. *Journal of the Bombay Natural History Society* 105: 212.
- Wilson, E.E., and E.M. Wolkovich. 2011. Scavenging: How carnivores and carrion structure communities. *Trends in Ecology and Evolution* 26 (3): 129–135.

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.