Zoological Studies **64:**17 (2025)

Niche Segregation and Habitat Suitability of the Red Fox (*Vulpes vulpes*) and Asiatic Jackal (*Canis aureus*), Two Sympatric Canids in Northern Punjab (Pothwar Plateau), Pakistan

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(Received 6 November 2024 / Accepted 13 March 2025 / Published -- 2025)
Communicated by Jian-Nan Liu

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Red fox (*Vulpes vulpes*) and Asiatic jackal (*Canis aureus*) are sympatric in many areas of their distribution range. Knowledge of the spatio-temporal niche segregation and habitat status of the species is important for effective conservation planning and management. In the current study, we investigated comparative spatio-temporal patterns of distribution and modeling habitat suitability of red fox and Asiatic jackal, in the Pothwar Plateau. Camera trapping, direct field sighting, recovering dead bodies, den sightings, scats and bioacoustics surveys were conducted from November 2018 to October 2020 to record data from four districts of the Plateau. The time of photos captured from camera traps was used to calculate the coefficient of temporal niche overlap using the overlap package in R software. To model the suitability of habitat, a total of twenty-six types of variables including 19 bioclimatic and seven other environmental variables were used. Results revealed a coefficient of temporal niche overlap between the two canid species as $\hat{\Delta}_4 = 0.47$, 95% CI = 0.34-0.60. The red fox was found active during late night hours while the Asiatic jackal was found active during dawn and dusk, segregating their temporal niche. Habitat suitability modeling performed well in terms of AUC (0.844 and 0.802) and TSS (0.675 and 0.615) and identified land use and distance to poultry farms as major drivers of habitat suitability for both red fox and Asiatic jackal, respectively. Major factors determining habitat suitability of red fox and Asiatic jackal were land use cover and distance from poultry farms, respectively. Highly suitable habitats of red fox are present in the southern, central, and western parts of the study area while suitable habitat for Asiatic jackal is spread over the entire study area with few pockets of least suitable habitat. Furthermore, habitat suitability modeling revealed that 40.0% and 50.0% area of the Pothwar Plateau is highly suitable for red fox and Asiatic jackal, respectively. The study concludes that both canid species show temporal adjustments for their co-existence and suitable habitat for red fox is predominantly located on the southern side of the study area, whereas Asiatic jackal's suitable habitat is dispersed throughout the entire study area.

Keywords: Occurrence, Camera Trapping, Habitat Suitability Modeling, Niche segregation, Temporal niche segregation, MaxEnt

Citation: Farooq M, Mahmood T, Nadeem MS, Fatima H, Akrim F, Munawar N. 2025. Niche segregation and habitat suitability of the Red Fox (*Vulpes vulpes*) and Asiatic Jackal (*Canis aureus*), two sympatric canids in northern Punjab (Pothwar Plateau), Pakistan. Zool Stud **64:**17.

BACKGROUND

Red fox *(Vulpes vulpes*) and Asiatic jackal (*Canis aureus*) (hereafter, golden jackal) belong to the family Canidae. Globally, both species are categorized as "Least Concern" (Hoffmann et al. 2018; Hoffmann and Sillero-Zubiri 2021) but listed as "Near Threatened" in Pakistan, where they are facing various threats, like increased human settlements, cultivation, overgrazing and drought, local trade for tail, hunting, retaliatory killing and accidental mortality due to vehicle collision, etc. (Sheikh and Molur 2005). They have an important role in the biological control of pests, seed dispersal, predator and prey, vector of rabies, works as cleaner by providing ecosystem services and have top-down effects on the ecosystem by regulating the population of herbivores (Ćirović et al. 2016; Elmhagen and Rushton 2007; Juan et al. 2006; MacInnes et al. 2001).

Niche partitioning between two coexisting species with similar ecological requirements limits interspecific overlap by changing the extent of their use of a given resource to avoid or reduce competition. Numerous coexistence mechanisms have been proposed, including spatial segregation, variations in habitat use, behavioral adaptations and altered activity periods or movements, trophic segregation and specialization (Torretta et al. 2021).

Habitat suitability modeling is an important tool in ecology and biogeography and a typical method for combining specific species with niche factors (Elith and Leathwick 2009; Wang et al. 2020; Zhang et al. 2018). Although there are many habitat suitability models (Maxent, BIOCLIM, GARP, and Climex) that have been developed to predict the distribution of species (Zhu et al. 2013), the Maxent model is one of the most popular tools, utilizing the principle of maximum entropy on presence-only data to estimate a set of functions that relate environmental variables and habitat suitability to approximate the species' niche and potential geographic distribution (Phillips et al. 2006).

Red fox and golden jackal are sympatric with each other throughout their distribution range (Sillero-Zubiri and Switzer 2004). Both species utilize different mechanism to avoid competition such as spatial, temporal or trophic segregation of resource use (Carricondo-Sanchez et al. 2019; Shamoon et al. 2018a; Shamoon et al. 2018b; Shamoon et al. 2017; Torretta et al. 2021; Tsunoda et al. 2018; Tsunoda et al. 2020; Tsunoda et al. 2024). Numerous studies have been conducted on the spatio-temporal segregation of both species in other parts of the world. Such interactions between both species may also exist in Pothwar Plateau of Pakistan. However, knowledge is scarce about the spatio-temporal segregation of both species in Pothwar Plateau which is important for effective conservation and management of species. Therefore, we hypothesized that *(1)* red fox and golden jackal have different distribution patterns in the Pothwar Plateau. We also expect that *(2)* red fox and golden jackal have segregated their spatio-temporal niche for co-existence. We similarly expect that *(3)* red fox and golden jackal have different suitable habitat in Pothwar Plateau. Therefore, the current study was conducted to fill afore mentioned gaps in the Pothwar region.

MATERIALS AND METHODS

Study area

The current study was conducted in the Pothwar Plateau (32°10–34°9 N and 71°10–73°55 E) of the province of Punjab, Pakistan (Fig. 1). The eastern and western sides of the Plateau are flanked by the rivers Jhelum and Indus, respectively. To the north are the Margalla Hills and Kala Chita Ranges, and to the south are the Salt Ranges. The Pothwar Plateau comprises four administrative districts (Attock, Chakwal, Jhelum, and Rawalpindi) and encompasses an area of ~23,161 km^2. The sub-humid climate of the northern part of Pothwar gradually becomes drier as the distance from the sub-Himalayan region increases. The average rainfall varies from 1500 mm in the northeast to about 380 mm in the southwest (Rashid and Rasul 2011). Out of the total, about 80% of rain falls from July to October (Sarwar et al. 2016). The summer temperature ranges between 15°C and 40° C while the range of winter temperature is generally between 4°C and 25°C but it can occasionally drop (Amir et al. 2019). The middle of the Pothwar Plateau is occupied by the structurally down-warped basin of the Soan River. The general terrain of the basin consists of interlaced ravines, which are locally known as khadar's and are set deep in the soft Siwalik beds. The landscape is dissected and eroded by streams, which during the rains, cut into the land and wash away the soil. The streams are generally deep set and are of little or no use for irrigation (Britannica 2018). According to the 2017 census report by Pakistan Bureau of Statistics (PBS), 10,006,624 people are residing in the area (PBS 2017). Inhabitants of the area are mainly agrarian but many people are moving into industry and mining (Ali 2004).

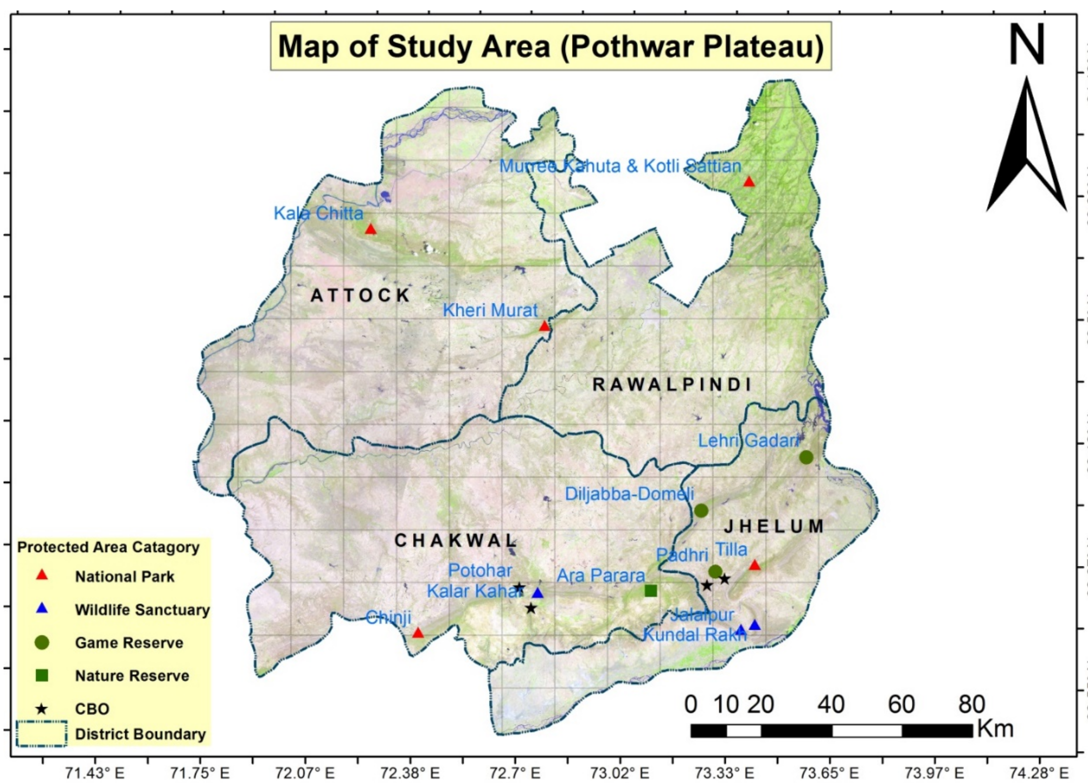

Fig. 1. Map of Study area: Map of Pakistan showing location of four administrative districts of the Pothwar Plateau (Attock, Rawalpindi, Chakwal and Jhelum), the study area.

Distribution patterns of red fox and golden jackal

Field surveys were conducted in the study area from November 2018 to October 2020 to record the presence of the red fox and golden jackal. Methods such as camera trapping, direct field sighting, recovering dead bodies, den sightings, and bioacoustics surveys were used. A detailed description of the camera trapping methodology is provided in the subsequent 'Temporal Niche Overlap' section.

Bioacoustics surveys were conducted for golden jackal by following the Harrington and Mech (1982) standard procedure. Stimulus howling was played by an mp3 player and was broadcast across the open environment from an elevated position with the help of a megaphone. Response calls of the jackals were recorded on a digital sound recorder (Sony ICD-PX470 Stereo Digital Voice) (Passilongo et al. 2015). The geographical coordinates of each observation were recorded using a handheld GPS device (Garmin 12-Channel GPS). Collected data was subjected to ArcGIS (Geographical Information System) software version 10.5 for generating distribution maps of each species. Kernel density was calculated to show the hotspots of distribution signs on map.

Temporal Niche Overlap

Camera trapping

Camera trapping was conducted at selected sampling sites in each district of the study area, based on direct and indirect signs of species presence. A total of seven infrared motion-triggered camera traps were used, although the number of cameras installed per night varied due to weather conditions and other disturbances. We employed three camera types: 1) Bushnell HD Trophy Camera Model-119537 (n = 2); 2) Bushnell HD Trophy Camera Model-119836 (n = 2); and 3) Browning Trail Camera Model-BTC-IXV (n = 3). Cameras were installed 30–40 cm above ground level (according to the breast height of animals) on tree trunks or bushes, approximately 1-2 meters apart from the expected passing route. The cameras were set to motion detect, rapid-fire, and photo mode, with a trigger speed of 0.2 seconds. We positioned the cameras to maximize the view of animals, enabling identification of individuals. Poultry offal, collected from butcher shops, was used as bait. A lure station was created by leveling the ground in front of the camera, approximately 1 meter away, and erecting a boulder with bait to maximize capture probability. Tall grass was removed from the trails in front of the camera to reduce false image captures. The trapping rate of the fox was calculated by dividing the total number of independent photo captures by the total number of trap nights. Cameras were installed for 5–7 consecutive days at each study site (Katuwal and Dahal 2013). Following Meek et al. (2014), pictures taken within two minutes were considered a single event. Time stamp was enabled on the photos to record the time and day of capture.

Analysis of Camera Trapping Data

The time of photos captured from camera traps was used to calculate the temporal niche overlap between the red fox and golden jackal in the study area. To estimate this overlap, we employed the kernel density function (Ridout and Linkie 2009). They defined the overlap coefficient (Δ) as the area under the overlapping curves of kernel density estimates from two samples. The coefficient values range from 0 (no overlap) to 1 (complete overlap).

$$\Delta(f, g) = \int min\{f(x), g(x)\}\, dx$$

Where *f(x)* and *g(x*) are density curves species *f* and *g* respectively.

In the present study, since both samples exceeded 75 observations, we employed the overlap coefficient $\hat{\Delta}_4$ (Dhat4) to estimate the overlap of activity patterns between the two species. We calculated the 95% confidence interval and mean of the overlap coefficients using 1000 bootstrap samples (Meredith and Ridout 2021). The extent of overlap can be classified into the following categories: low ($\Delta \leq 0.5$), moderately high ($0.5 < \Delta \leq 0.75$), and very high ($\Delta > 0.75$) (Monterroso et al. 2014). All statistical analyses were performed using the 'overlap' package (v. 0.3.4) in R statistical software (version 4.0.0) (Meredith and Ridout 2021).

Habitat Suitability Modeling

Initial Examination of the Observed Environmental Values

All statistical analyses and modeling were performed using R version 4.0.0, a widely used statistical software platform (R-Core-Team 2020). An initial examination of the observed environmental values for each species was carried out using the extract function from the 'raster' package (Hijmans et al. 2015). Environmental ranges of species were checked before running models in order to identify possible errors in the output.

Acquisition and Processing of Data

Bioclimatic data comprising 19 variables (Table 1) were downloaded from the WorldClim database by using the 'raster' package (Hijmans et al. 2005), and collinearity among the variables was assessed using Variation Inflation Factors (VIF). After collinearity assessment, three bioclimatic variables were selected for further analysis: bio_01 (annual mean temperature), bio_07 (temperature annual range) and bio_12 (annual precipitation). Normalized Difference Vegetation Index (NDVI) was calculated from the Landsat 8 images which were downloaded from the GloVis-USGS website (https://glovis.usgs.gov/) by applying the filter of the 0 to 20% cloud cover. Digital Elevation Model (DEM) was retrieved from the USGS earth explorer database (https://earthexplorer.usgs.gov/) and was used to generate Vector Ruggedness Measure (VRM) via the *terrain* function in the ‘raster’ package (Hijmans et al. 2017). The land use cover was downloaded from the Esri website (https://livingatlas.arcgis.com/landcover/). To assess the collinearity with the other variables, the categorical land cover data was converted into proportional data (continuous data) by decreasing resolution to 3 × 3 km and calculating the proportion of each high-resolution cell (10 m resolution) within the coarser 3 × 3 km resolution cells. Local shape files for human settlements and roads were downloaded from the Humanitarian Data Exchange website (https://data.humdata.org/). A shape file for water bodies was obtained from the DIVA GIS website (https://www.diva-gis.org/), and data on poultry farm locations were collected directly in the field. These shape files were used to calculate Euclidean distances using the fasterVectToRastDistance function from the 'fasterRaster' package (Smith 2018). Subsequently, all environmental variables were resampled to a 0.5 arc-minute resolution using the bilinear method and then masked to the shape file of the Pothwar Plateau. The explanatory variables were then stacked and tested for multicollinearity using the vifstep and vifcor functions from the 'usdm' package, with a threshold VIF of 10 and an absolute correlation coefficient threshold of 0.7 (Naimi 2015); we excluded predictors that were strongly correlated but less relevant for modeling both canid species compared to other variables. Additionally, variables were also selected depending on the ecology of red fox and golden jackal (Charaspet et al. 2019; Honghai et al. 1999; Khattak et al. 2022; Krim et al. 1990; Mukherjee et al. 2018).

Table 1. Variables used for Maxent: List of Bioclimatic (N = 19) and other environmental variables (N = 7) that were analyzed for the habitat suitability modeling of the two sympatric red fox and golden jackal in the current study

Sr. No.	Variable	Description
1	bio_1 (Annual Mean Temperature)	Average temperature across an entire year at a specific location

2	bio_2 (Mean Diurnal Range)	Average difference between the monthly maximum and minimum temperatures throughout a year
3	bio_3 (Isothermality)	How large the day- to-night temperatures oscillate
4	bio_4 (Temperature Seasonality)	Standard deviation of the monthly mean temperature multiplied by 100
5	bio_5 (Max Temperature of Warmest Month)	Highest temperature recorded during the hottest month of the year at a specific location
6	bio_6 (Min Temperature of Coldest Month)	Lowest average temperature recorded during the coldest month of the year at a specific location
7	bio_7 (Temperature Annual Range)	Difference between the average temperature of the hottest month and the average temperature of the coldest month in a given location
8	bio_8 (Mean Temperature of Wettest Quarter)	Average temperature during the quarter of the year with the highest precipitation
9	bio_9 (Mean Temperature of Driest Quarter)	Average temperature during the quarter with the lowest precipitation throughout the year
10	bio_10 (Mean Temperature of Warmest Quarter)	Average temperature during the three-month period with the highest average temperature in a year
11	bio_11 (Mean Temperature of Coldest Quarter)	Average Temperature of the Coldest Quarter
12	bio_12 (Annual Precipitation)	Annual precipitation
13	bio_13 (Precipitation of Wettest Month)	Total amount of precipitation recorded during the single month with the highest rainfall in a given location throughout the year
14	bio_14 (Precipitation of Driest Month)	Total amount of precipitation recorded during the single driest month of the year at a given location
15	bio_15 (Precipitation Seasonality)	Calculated using the coefficient of variation to measure the variation in monthly precipitation totals over a year.
16	bio_16 (Precipitation of Wettest Quarter)	Total amount of precipitation received during the three-month period with the highest rainfall in a given location each year.
17	bio_17 (Precipitation of Driest Quarter)	Total amount of precipitation received during the driest three-month period of the year at a given location
18	bio_18 (Precipitation of Warmest Quarter)	Total amount of precipitation received during the three warmest months of the year in a given location
19	bio_19 (Precipitation of Coldest Quarter)	Total amount of precipitation received during the coldest three months of the year at a given location
20	NDVI (Normalized Difference Vegetation Index)	Measures of health and density of vegetation
21	Distance from settlements	Euclidian distance from settlements
22	Distance from road	Euclidian distance from road
23	Distance to water body	Euclidian distance from water body
24	Distance from poultry farms	Euclidian distance from poultry farms
25	Land use cover	Physical characteristics of what is on the Earth's surface, including vegetation, water bodies, bare soil, and human-made structures
	VRM (Vector Ruggedness Measure)	Quantification of ruggedness or complexity of terrain

Model Fitting and Tuning

Maxent is a piece of software (Phillips et al. 2006) running a specific SDM algorithm on the supplied data and user-specified (or default) settings. It can also be seen as an algorithm itself. A range of environmental variables, which are crucial for understanding species distribution and abundance, are integrated into the model, ultimately contributing in conservation efforts (Debinski et al. 1999; Kaky et al. 2020). Habitat suitability model was developed for this study using following guidelines on Maxent parameterization (Feng et al. 2017; VanDerWal et al. 2009). Species occurrence records were spatially thinned to a single point per raster cell, minimizing spatial biases and ensuring data independence. Subsequently, Maxent models were generated utilizing the 'dismo' package, which provides a software wrapper for the Maxent algorithm (Hijmans et al. 2017). Bias correction 'bias_con' file was created by following the guidelines of Young et al. (2011). We generated 2,000 geographically randomized background points. Models were tuned using the ENMeval function from the 'ENMeval' package (Muscarella et al. 2014). This involved identifying the most informative feature selection variables and regularization multiplier (beta-multiplier) values, which were selected based on the lowest delta Akaike Information Criterion (AIC_c) using five random k-folds.

Evaluation of Model Performance

The Maxent datasets were split into training (75%) and testing (25%) subsets using a 4-way partitioned k-fold approach. The final models included linear and quadratic (lq) features, with the regularization multiplier (beta-multiplier) initially varied between 1 and 2 for sensitivity analysis and ultimately set to 1 for the finalized model. We selected these features for the final Maxent models for each species based on the statistics we used to validate our model: area-under-the-curve (AUC) values within receiver-operating characteristic (ROC) curves and the true skill statistic, TSS = TP+TN-1, where TP = proportion of true positive predictions and TN = proportion of true negative predictions. AUC_{Diff} values were also computed to check either model is over fitting or under fitting. The Jackknife procedure was implemented for the percentage contribution of each variable in determining the habitat suitably. Models were replicated with replacement using the bootstrap method. True skill statistics is defined based on the components of the standard confusion matrix representing matches and mismatches between observations and predictions (Fielding and Bell 1997). Model outputs were defined as habitat suitability on a 0–1 probability scale (1 = highest suitability; 0 = lowest suitability) (Fig. 2). Finally, the habitat suitability index (HSI) map was reclassified into three distinct categories: highly suitable, moderately suitable, and least suitable by using 'raster' package.

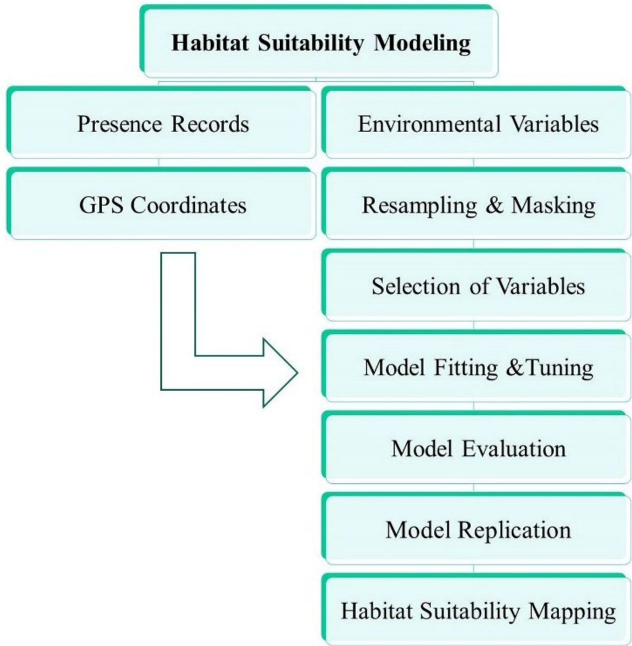

Fig. 2. Flow Chart of Habitat Suitability Modeling: Flow Chart of Habitat Suitability Modeling of red fox and golden jackal in study area.

RESULTS

Distribution patterns of red fox and golden jackal

Data revealed that red fox and golden jackal occur in all four districts of the Pothwar Plateau. A total of N = 341 field signs of the occurrence of both canid species were recorded at 45 different locations including N = 131 field signs of red fox and N = 210 for golden jackal (Table 2). Red fox was recorded at 36 of the 45 sampling sites surveyed in the study area, with an altitudinal range of 235-923 m above sea level (asl). High abundances of red fox signs were recorded at Ara Basharat (*n* = 10), Jalal Pur Sharif (*n* = 9), Sarkal (*n* = 8), Moorat Mor (*n* = 6), Lawa (*n* = 6), and Ahmadabad (*n* = 5) (Fig. 3a and b; Table 2). In contrast, direct and indirect signs of golden jackal were found at 42 of the 45 surveyed sites, with an altitudinal range of 194-904 m asl. Notably, high density of golden jackal signs was recorded at Jatli (*n* = 15), Dhurnal (*n* = 15), Khairi Murat (*n* = 13), Sayed Kasran (*n* = 12), Lawa (*n* = 12), and Ara Basharat (*n* = 10) (Fig. 3c and d; Table 2).

Table 2. Field signs red fox and golden jackal: Direct and indirect signs of Red fox and golden jackal recorded in four districts of the Pothwar Plateau

Sr. No.	Site Name	Latitude	Longitude	Elevation (m)	Scats		Camera Trapping		Howling	Den		Direct Field Sighting		Foot Prints		Road Kill/Dead Body	
					Red fox	Golden Jackal	Red fox	Golden Jackal	Howling	Red fox	Golden Jackal	Red fox	Golden Jackal	Red fox	Golden Jackal	Red fox	Golden Jackal
Attock District																	
1	Dhoke Pathan	33.12421	72.34756	441	2	5	+	-	+	-	-	+	+	-	-	-	-
2	Gali Jahangir	33.42368	72.63858	523	-	7	+	+	-	-	-	-	-	-	-	-	-
3	Dhoke Afghan	33.93554	72.41761	477	3	8	+	-	-	-	-	-	-	-	-	-	-
4	Makhad Shareef	33.12115	71.74447	517	-	3	+	+	-	-	-	-	-	-	-	-	-
5	Moorat Village	33.47991	72.88713	477	1	2	+	-	+	-	-	-	-	-	-	-	-
6	Ganda Kas	33.64954	72.14657	405	-	-	-	+	+	-	-	-	-	-	-	-	-
7	Ratwal	33.51771	72.69780	423	-	7	+	+	+	-	-	-	-	-	-	-	-
8	Ikhlas Pindi Gheb	33.25423	72.30924	420	-	-	+	-	+	-	-	-	+	-	-	-	-
9	Ahmadal	33.28663	72.47887	533	-	-	-	+	+	-	-	-	-	-	-	-	-
10	Fate Ullah	33.77718	72.57200	655	-	-	-	+	+	-	-	-	-	-	-	-	-
11	Moorat Mor	33.49688	72.90563	441	4	6	-	+	-	-	-	+	-	+	+	-	-
12	Basal	33.55228	72.23705	638	2	2	+	-	+	-	-	+	+	-	-	-	-
13	Khairi Murat	33.46367	72.78375	904	1	12	-	+	-	-	-	+	-	-	-	-	-
Chakwal District																	
14	Dhermond	32.93083	72.21575	426	2	-	-	-	+	-	-	-	+	-	-	-	-
15	Sarkal	33.14803	72.90467	510	6	-	+	-	+	-	-	+	+	-	-	-	-
16	Ara Baharat	32.78206	73.08862	510	8	8	+	-	+	-	-	-	-	+	-	-	+
17	Chumbi Surla	32.78719	72.79134	420	-	-	+	+	-	-	-	+	-	-	-	-	-
18	Dhoke Fateshah	32.92398	72.15728	391	4	8	+	+	-	-	-	-	-	-	-	-	-
19	Dhurnal	32.74083	72.13212	199	-	13	-	+	+	-	-	-	-	-	-	-	-
20	Mutan Khurd	32.99256	72.01190	494	2	8	+	+	+	-	-	-	-	-	-	+	-
21	Sarkal Kasar	33.19077	72.72844	442	3	5	-	+	-	-	-	-	-	-	-	-	-
22	Saghar	32.92575	72.25561	428	-	1	-	-	-	-	+	-	-	-	-	-	-
23	Thoa Mehram Khan	32.83335	72.23482	640	-	-	+	-	+	-	-	-	-	-	-	-	-
24	Lawa	32.67763	71.96703	310	5	10	-	+	+	-	-	+	-	-	-	-	-
Jhelum District																	
25	Ahmadabad, Graveyard	32.49867	72.83253	194	-	-	-	-	+	-	-	-	-	-	-	-	-
26	Andhri	32.79037	73.32580	424	-	1	+	-	-	-	-	-	-	-	-	-	-
27	Goorha Atum Singh	33.02134	73.30945	525	2	-	+	-	-	-	-	+	-	-	-	-	-
28	Jalal Pur Sharif	32.66531	73.42029	565	6	-	+	-	-	-	-	+	-	-	-	-	-
29	Mal Maira	32.83738	73.29863	411	2	1	+	-	-	-	-	-	-	+	-	-	-
30	Potha	32.80794	73.25960	430	2	-	-	+	-	+	-	-	-	+	+	-	-
31	Rakh Parial	32.84432	73.15923	425	4	-	+	-	+	-	-	-	+	-	-	-	-
32	Rehana Munda	32.98432	73.59257	257	-	-	-	+	-	-	-	-	-	-	-	-	-

33	Ahmadabad	32.52200	72.86322	235	4	9	+	+	-	-	-	-	-	-	-	-	-
34	Kotila	32.76208	73.28798	292	3	1	+	-	+	-	-	-	-	-	-	-	-
35	Mal Maira	32.83738	73.29863	411	4	-	-	+	-	-	-	-	-	-	-	-	-
36	Sohawa	33.12883	73.42798	529	-	-	-	+	+	-	-	-	-	-	-	-	+
37	Dina	33.03630	73.55748	554	-	-	-	+	-	-	+	-	-	-	-	-	-
Rawalpindi District																	
38	Bhangali Shareef	33.24203	73.10698	529	-	1	+	-	+	-	-	-	-	-	-	-	+
39	Dera Abbas	33.19248	73.31375	638	-	-	-	+	+	-	-	-	-	-	-	-	-
40	Dhala	33.43101	72.91279	565	-	-	+	-	+	-	-	-	-	-	-	-	-
41	Koont farm	33.12038	73.01442	517	2	5	-	-	+	+	-	-	-	+	-	-	+
42	Jatli	33.18445	73.09298	542	-	14	+	-	+	-	-	-	-	-	-	-	-
43	Keral	33.65702	73.44326	923	-	-	+	-	-	-	-	-	-	-	-	-	-
44	Mari Janjir	33.24677	73.14604	550	2	-	-	+	+	-	-	-	-	-	-	-	-
45	Sayed Kasran	33.11560	73.02741	485	4	10	-	+	+	-	-	-	-	+	-	-	-
	Total signs (N=341; red fox=131, golden jackal=210)				78	147	34	24	25	2	2	10	6	6	2	1	4

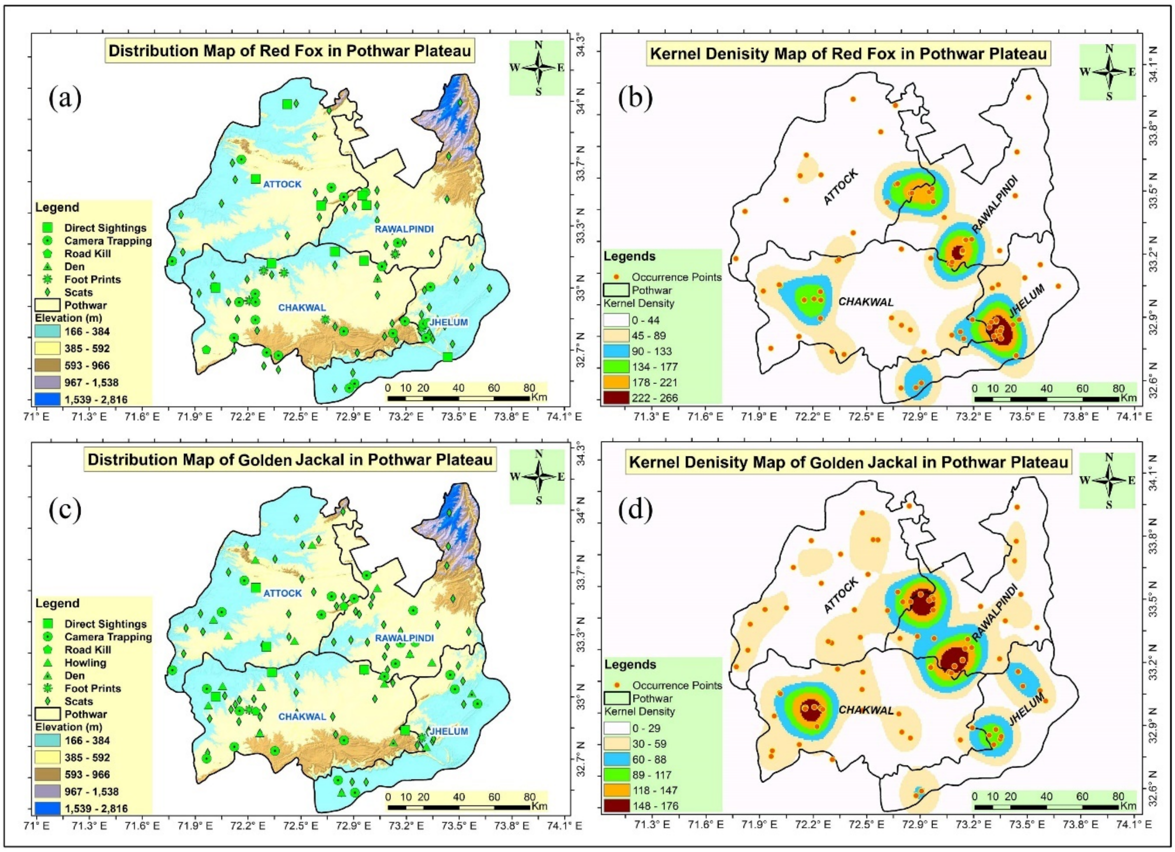

Fig. 3. Distribution and Kernel density maps: GIS-based map showing (a and c), comparative distribution of red fox and golden jackal in the Pothwar Plateau and (b and d), Kernel density analysis of their field signs.

Temporal niche overlap

Temporal niche overlap was calculated by using *the overlap* package in R by using camera trapping data. A total of 79 capture events of red fox and 81 capture events of golden jackal were used in the analysis (Table 3; Fig. 4). Both of these samples were more than 75 observations, so the $\hat{\Delta}_4$ estimate, Dhat4 was used. Our results showed that the red fox was found active during the late night while golden jackal was found active during dawn and dusk (Fig. 5). The coefficient of overlap ($\hat{\Delta}_4$= 0.47, 95% CI = 0.34-0.60) showed that the degree of diel activity overlap between the red fox and golden jackal was low, indicating a 47% temporal overlap between the two species.

Table 3. Camera trapping effort of Red fox and Asiatic jackal recorded in four districts of the Pothwar Plateau

District	Nights	camera station	Photo capture	Photo Captured of Non-target species	False triggered	Trap event (Red fox)	Trap event (Golden jackal)	Trap nights
Attock	25	14	150	25	92	25	31	350
Chakwal	22	10	132	27	92	13	19	220
Jhelum	16	10	198	21	70	18	15	160
Rawalpindi	12	5	114	12	55	23	16	60
Total	75	39	594	85	309	79	81	790

Fig. 4. Camera trapped photos: Photos of (a), red fox and (b), golden jackal captured by camera trap in the study area.

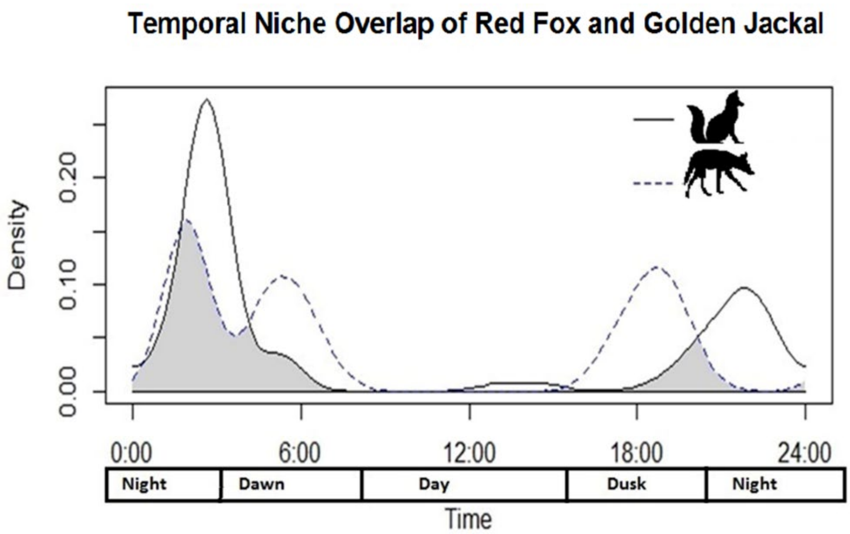

Fig. 5. Temporal Niche overlap: Temporal activity patterns of Red fox and golden jackal in Pothwar Plateau. Solid line shows the activity of red fox while the dotted line shows the activity of golden jackal in 24 hours. The shaded area shows the overlapping.

Habitat Suitability Modeling

Initially, 26 variables, comprising 19 bioclimatic and 7 other environmental variables were considered for habitat suitability modeling. After assessing collinearity by using the Variance Inflation Factor (VIF) and considering the ecological requirements of both species, we removed 16 variables and retained only 10 variables for our model. Habitat suitability modeling performed well in terms of AUC (0.844 and 0.802) and TSS (0.675 and 0.615) (Fig. 6). In terms of AUC_{Diff} value, the model was better fitted for the red fox (0.0213) compared to the golden jackal (0.0973).

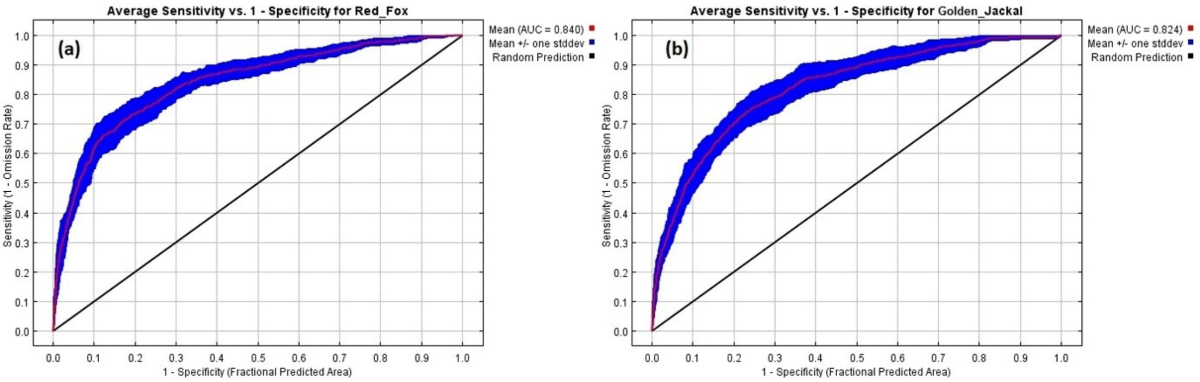

Fig. 6. Average training AUC: ROC verification of distribution of suitable habitat for (a), red fox and (b), golden jackal in the Pothwar Plateau.

Major factors determining habitat suitability

Jackknife tests of variable importance for the red fox showed that land use cover made the greatest contribution (24.6%), followed by annual precipitation (bio_12, 23.2%), Vector Ruggedness Measure (14.2%), distance from human settlements (7.8%), distance from water bodies (7.3%), temperature annual range (bio_07, 7.1%), distance from roads (5.0%), distance from poultry farms (4.2%), annual mean temperature (bio_01, 4.2%), and vegetation cover (NDVI, 2.5%) (Fig. 7a; Table 4). Land use cover showed the highest contribution in determining the habitat suitability of the red fox. Level-11 (rangeland or scrub forest) of land use cover had a peak value of 0.60. The habitat suitability for the red fox increased with increasing annual precipitation (bio_12) and reached a peak value of 0.65 at values ranging from 400 to 800. Habitat suitability for the Vector Ruggedness Measure peaked at 8.1 and then decreased as the ruggedness value increased (Fig.8a).

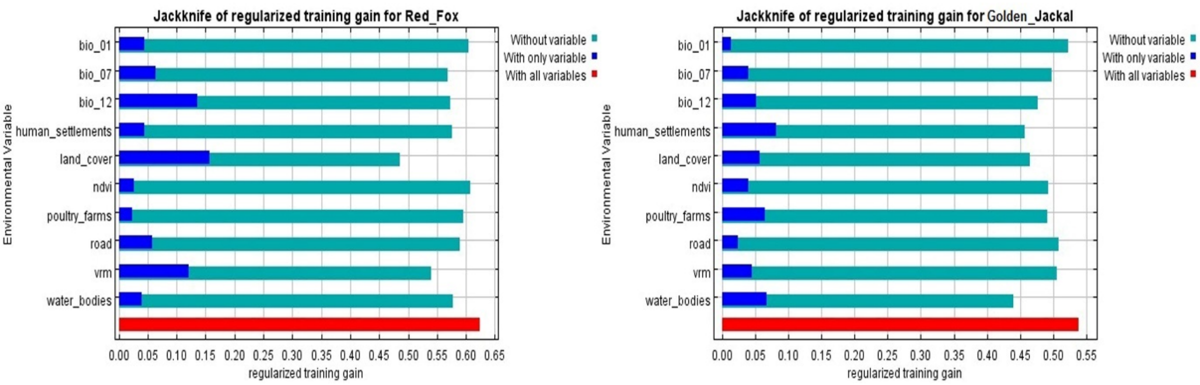

Fig. 7. Jackknife test of variable importance: Jackknife test of regularized training gain of variables tested in habitat suitability model for red fox (a) and golden jackal (b).

Similarly, Jackknife tests of variable importance for the golden jackal showed that the contribution of distance from poultry farms was the greatest (16.2%), followed by land use cover (15.1%), distance from human settlements (14.2%), distance from water bodies (13.5%), annual precipitation (bio_12, 11.8%), temperature annual range (bio_07, 7.8%), vegetation cover (NDVI, 6.8%), Vector Ruggedness Measure (6.8%), distance from roads (5.2%), and annual mean temperature (bio_01, 2.6%) (Fig. 7b; Table 4). The habitat suitability of the golden jackal increases as the distance from poultry farms decreases. The peak value of habitat suitability for distance from poultry farms is 0.50 at 2,500m (2.5 km). Land cover level-2 (trees) and level-11 (rangeland or scrub forest), both contribute highly (0.53) to determine the habitat suitability of the golden jackal. However, habitat suitability of the golden jackal decreases as the distance from human settlements increases. The peak value (0.65) of suitability of habitat is found within distances below 1 km (Fig. 8b).

Table 4. Predictors contribution: Percentage contribution of variables in determining the habitat suitability of red fox and golden jackal in the Pothwar Plateau

Species	Sr. No.	Variable	Percent contribution	Permutation importance
Red fox	1	land_cover	24.6	30.5
	2	bio_12	23.2	11.8
	3	vrm	14.2	8.7
	4	human_settlements	7.8	8.7
	5	water_bodies	7.3	3.4
	6	bio_07	7.1	16.7
	7	road	5	5.9
	8	poultry_farms	4.2	6
	9	bio_01	4.2	5.7
	10	ndvi	2.5	2.8
Golden jackal	1	poultry_farms	16.2	6.5
	2	land cover	15.1	24.7
	3	human_settlements	14.2	5.4
	4	water_bodies	13.5	11.8
	5	bio_12	11.8	14.9
	6	bio_07	7.8	12.4
	7	ndvi	6.8	8.9
	8	vrm	6.8	6
	9	road	5.2	3.5
	10	bio_01	2.6	5.8

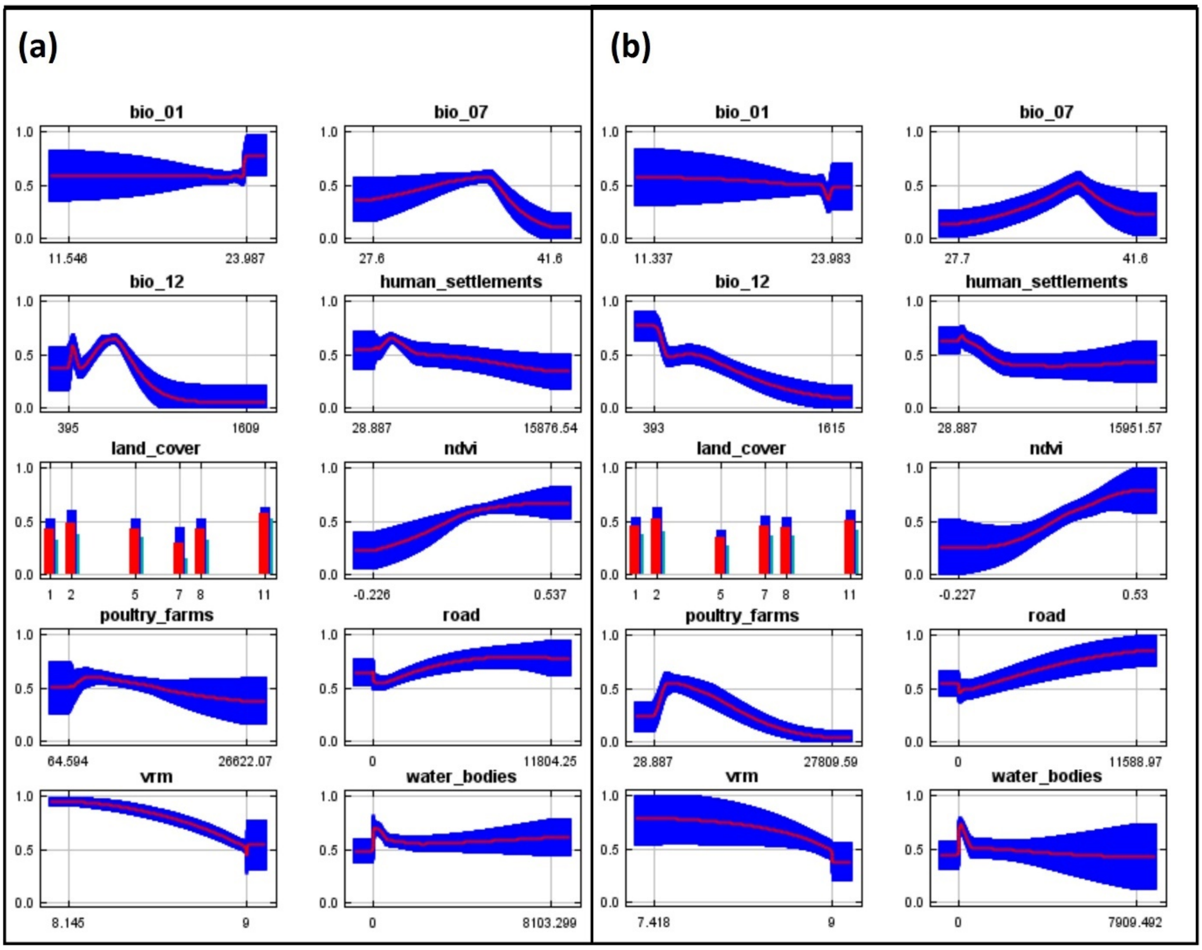

Fig. 8. Predictors Response curves for red fox and golden jackal: Response curves of predictors for (a), red fox and (b), golden jackal occurrence in the Pothwar Plateau. The curves show the mean response of the 15 replicate Maxent runs (red) and the mean +/- one standard deviation (blue, two shades for categorical variables). The predicted value of habitat suitability (logistic output) is shown on the Y-axis, while the range of the environmental predictors is shown on the X-axis.

Distribution of suitable habitat for red fox and golden jackal

The habitat suitability map of red fox showed that highly suitable habitats of red fox are present in the southern, central, and western parts of the Pothwar Plateau. The areas of Salt Range (Chakwal), Kala Chitta Range (Attock), and Kheri Murat National Park (Fateh Jang, Attock) are present in these areas which are the designated protected areas for fauna and flora (Fig. 1 and Fig. 9a). Moderately suitable habitats of red fox are restricted in the central parts of the Plateau. On the other hand, least suitable habitats are located in some central and western parts of the Plateau where vegetation cover is low. Results obtained by processing the reclassified maps revealed that overall, approximately 40% (9264 km^2) habitat of the total area of the Pothwar Plateau falls under the “highly suitable” habitat, followed by approximately 25% of the area that represents moderately suitable habitat while approximately 35% of the area of the Pothwar Plateau represents “least suitable” habitat for distribution of the red fox (Fig. 9a).

For the golden jackal, the suitable habitat is spread across the whole study area with few pockets of less suitable habitat. This includes both protected as well as non-protected areas in the Pothwar Plateau (Fig. 1 & Fig. 9b). A total of approximately 50% (11581 km^2) area of the Plateau represents a "highly suitable" habitat for the golden jackal, followed by approximately 21% "moderately suitable" and the remaining 29% "least suitable habitat for distribution of the golden jackal in the Pothwar Plateau (Fig. 9b).

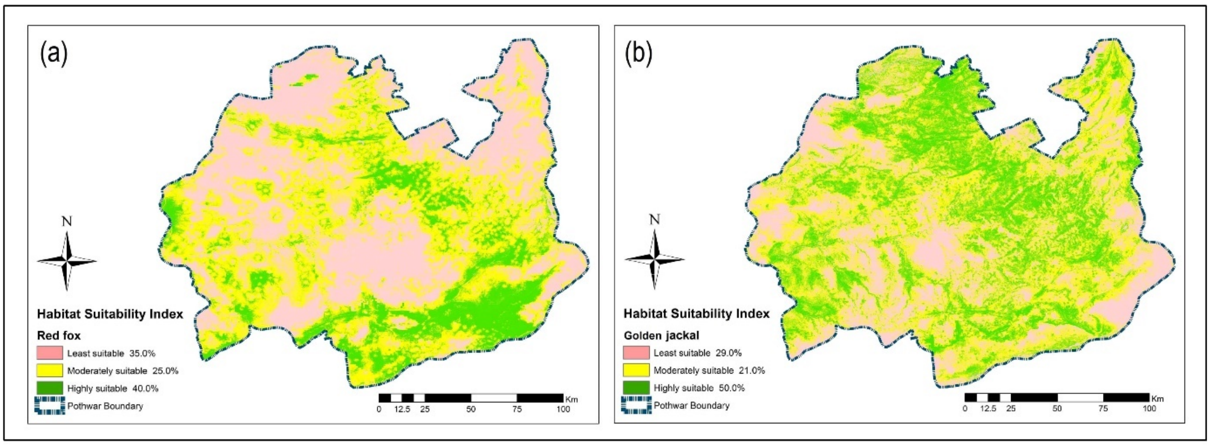

Fig. 9. Habitat Suitability indices: Percentage and distribution of suitable habitat for red fox (a) and golden jackal (b) in the study area based on Maxent modeling.

DISCUSSION

In this study, we showed that red fox and golden jackal are present throughout the Pothwar Plateau. Our study also showed that the temporal niche of red fox and golden jackal segregate in the study area. We also revealed that red fox and golden jackal have different distributions of suitable habitats in the Pothwar plateau. The current study focused on the distribution, temporal niche overlap, and habitat suitability modeling of red fox and golden jackal. The study on distribution and habitat suitability modeling was conducted at a large spatial scale, covering the entire study area, and utilized all presence signs, both direct and indirect. In contrast, the study on temporal niche overlap relied solely on camera trap data from selected study sites.

The finding of the current study clearly showed that red fox and golden jackal are occurring sympatrically, throughout the Pothwar plateau of Pakistan. However, the kernel density of red fox is higher in the southern side of the study area, which has a good cover of rangeland or scrub forest. The red fox is an omnivore and a generalist feeder that lives in all of the possible golden jackal habitats (Gittleman 1985; Lloyd 1980). According to the study conducted by Akrim et al. (2019), the proportion of domestic prey was lower in the diet of red fox as compared to golden jackal. In remote areas like the Salt Range, red fox density is high because it can cope by utilizing wild prey.

According to wildlife staff responsible for protecting the Punjab urial (*Ovis vignei punjabiensis*) in the Salt Range, red foxes have been reported to prey on Punjab urial lambs, whereas no such cases have been reported for golden jackals (M. Farooq, pers. comm.). Our study concluded that the red fox and golden jackal are living sympatrically throughout the study area but the density of red fox is high in remote areas like Salt Range.

The current study reveals that red foxes and golden jackals in the Pothwar Plateau segregate their temporal niches, facilitating coexistence. Specifically, our findings indicate that red foxes are predominantly active during dark hours, whereas golden jackals exhibit peak activity during twilight hours, namely dawn and dusk. This temporal partitioning is consistent with previous studies, which have shown that red foxes are nocturnal, with a consistent seven-hour activity period at night regardless of the time of year (Doncaster and Macdonald 1997). In contrast, golden jackals have been found to exhibit bimodal activity patterns, with peaks in the early morning and nighttime hours (Majumder et al. 2011). Our study highlights the importance of temporal niche segregation in allowing these two species to coexist in the same habitat.

The temporal activity patterns of red foxes and golden jackals are influenced by various factors, including prey activity, presence of other predators, and habitat disturbance. Red foxes, as crepuscular and nocturnal hunters, rely heavily on their sense of hearing (Österholm 1964). In a study conducted by Giannatos et al. (2005) in Fokida, Greece, both species avoid each other. Foxes occurred permanently only on the fringes of the jackal territories. However, in the winter season, few individual foxes can penetrate within jackal territories. Scheinin et al. (2006) found that foxes spatially avoided jackals, a reasonable outcome given that larger species typically dominate smaller ones in direct encounters. The extent of niche segregation or overlap determines the degree to which different species can either coexist or competitively exclude each other (Carvalho and Gomes 2004; Pianka 1973). This segregation or overlap is influenced by each species' physical ability to obtain food (Owen-Smith and Mills 2008; Radloff and Du Toit 2004) and also by variation in the spatial and temporal availability of food (Azevedo et al. 2006). For distinct carnivore guilds, different mechanisms may be involved, such as different body sizes of predators (Carvalho and Gomes 2004) and prey species (Juarez and Marinho-Filho 2002; Karanth and Sunquist 2000) activity patterns (Loveridge and Macdonald 2003) and microhabitat use (Johnson and Franklin 1994). Our study reveals that these two species segregate their temporal niches, allowing them to coexist. This segregation is achieved through adjustments in their activity patterns, with red foxes avoiding the activity periods of golden jackals.

We used the occurrence data of each species for habitat suitability modeling. Our results showed that land use cover is the major contributing factor in determining the suitability of red fox. Level 11 (rangeland or scrub forest) of land cover had the highest significant contribution for red fox (Fig. 8a). Interestingly the highly suitable areas predicted by Maxent in our study area comprised scrub forest. Red fox avoids dense forest but can be found in any type of open country. In Pakistan, it prefers extensive uncultivated tracts with sand dunes in the Indus plains (Roberts 1997). The diet of red fox is comprised is food items, including small mammals, birds, insects, serpents, arachnids, and many plant materials, including cereals and fruits (Basuony et al. 2005). The second most influential factor in determining the habitat suitability of red fox is Annual precipitation (BIO-12). Results of our study showed that red fox prefers to exist in annual moderate precipitation. Except for the northern part of the Pothwar Plateau, which receives relatively high rainfall (around 1500 mm), the region as a whole receives moderate precipitation which makes the second most important predictor in determining the habitat suitability of red fox.

Our study reveals that the most suitable habitats for red foxes are concentrated in the southern, central, and western regions of the Pothwar Plateau, largely due to the presence of designated protected areas in these zones (Fig.1; Fig. 9a). Whereas moderately suitable habitats of red fox are restricted in the central parts of the Plateau. On the other hand, less suitable habitats are in some central and western parts of the Plateau where croplands are predominant. A study on red fox, conducted by Khattak et al. (2022) in Pakistan, revealed that highly suitable areas for red fox comprised the protected areas (PAs) and their buffer zones; however, the moderately suitable areas mainly occurred in the peri-urban zones and were avoided by red fox. Global land cover and poultry were the most influential factors associated with habitat suitability of red fox. According to study in Shigar valley, Pakistan, conducted by Zaman et al. (2020), the number of red fox dens is positively correlated with shrubs, Indian pika burrows, and negatively influenced by forest and distance to road. Similarly, we concluded that land cover, especially, scrub forest is the major contributing factor in determining the habitat suitability of red fox. The increased human population pressure in the Pothwar Plateau also affects the rangelands by converting them into agricultural land and housing societies. Scrub forest is only intact in protected areas of the plateau (Islam et al. 2022).

Our finding showed that distance from poultry farms had the highest contribution in determining the habitat suitability of golden jackal. Open-type poultry houses in the study area, where maintaining the internal environment is economically challenging, experience high bird mortality. These dead birds are the major source of food for the golden jackal. Bino et al. (2010) found a similar case in red foxes, where reducing anthropogenic waste of dead/discarded chicken in the area resulted in increased home range size and decreased survival rates. But in our results in Pothwar Plateau distance from poultry farm has the least contribution in determining the habitat suitability of red fox. This may be due to disturbance in habitat and presence of its other competitors like feral dogs and jackals as discussed earlier that red fox avoids spatially to golden jackal. The second most contributing factor in determining the habitat suitability of golden jackal is land use cover. Level 2 (trees) and Level 11 (rangeland or scrub forest) of land cover had the highest significant contribution to golden jackal habitat suitability. It is a highly adaptable species, capable of thriving in a wide range of environments, from grasslands and rangelands to agricultural areas and forests (Hoffmann et al. 2018). Notably, the Pothwar Plateau, with its predominantly rangeland cover type, provides an ideal habitat for this species. The highly suitable habitat of the golden jackal spreads across the whole study area with just a few pockets of less suitable habitat. This includes both protected as well as non-protected areas in the Pothwar Plateau.

The area of highly suitable habitat (40%) for red fox is comparatively less than that for golden jackal (50%). Keeping in view the results obtained from the Maxent modeling, we believe that red fox prefers to exist in remote areas where the scrub forest is intact which is also evident from the occurrence records of red fox in the study area. On the other hand, the golden jackal seems to prefer the neighborhood of poultry farms, maybe mainly because of the easy availability of poultry birds as its food.

Several limitations should be acknowledged when interpreting the results of this study. The use of different signs (*e.g.*, scats, foot prints) of species presence for Maxent Modeling may have introduced variability in detection probabilities, affecting species distribution model. The limited sample size (n_1 = 79, n_2 = 81) and large study area (23,161 km^2) may have reduced statistical power and increased uncertainty in estimates of temporal overlap. Additionally, integrating camera trap data was challenging due to environmental and weather variations, non-uniform sampling effort across seasons, and unquantified disturbances. Future studies should address these gaps by accounting for environmental variations, uniform sampling, and investigating disturbance impacts. Furthermore, one notable limitation of this study is the lack of direct assessment of spatial overlap between the two species. To fully understand the spatial relationships between the species, future studies should consider calculating overlap indices using occupancy modeling approaches.

CONCLUSIONS

This study concludes that both canid species, red fox and golden jackal, show temporal adjustments for their co-existence. The suitable habitat for red fox is mostly located on the southern side of the study area while the suitable habitat for golden jackal is dispersed over the whole study area. A highly suitable area for red fox is less available as compared to golden jackal. Further studies are required on the population status, threats, and ecological role of red fox and golden jackals in regulating the community structure of the ecosystem.

Acknowledgments: We thank the staff of the Punjab Wildlife & Parks Department and Mammalian Ecology & Conservation Lab, Department of Zoology, Wildlife and Fisheries, PMAS Arid Agriculture University. The authors received no financial support for this work.

Authors' contributions: MF: Field surveys and data collection, Methodology, Software, Writing- Original draft preparation. TM: Conceptualization, Methodology, Supervision, Writing original draft. MSD: Conceptualization. FA: Writing- Reviewing and Editing. HF: Data curation. NM: Data Analysis.

Competing interests: The authors hereby declare they have no financial or any other competing interests.

Availability of data and materials: The data will be made available on reasonable request.

Consent for publication: On behalf of all the co-authors, the corresponding author hereby gives consent for publication of this manuscript in the Zoological Studies.

Ethics approval consent to participate: Not applicable because we conducted this observational and non-invasive study.

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