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Research Article

Modeling the habitat suitability for sympatric small and medium-sized felids and investigating the spatiotemporal niche overlapping in Maduru Oya National Park, Sri Lanka

Dulan Jayasekara and[1,2], Wanigatunga Arachchige Dharshani Mahaulpatha[1]*

[1]Department of Zoology, Faculty of Applied Sciences, University of Sri Jayewardenepura, Gangodawila, Sri Lanka
[2]Faculty of Graduate Studies, University of Sri Jayewardenepura, Gangodawila, Sri Lanka
*Email: mahaulpatha@sjp.ac.lk

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Abstract

Habitat suitability modeling and identification of spatiotemporal niches help in understanding the ecological requirements of faunal guilds. Small and medium-sized felids of wild Sri Lanka include three cat species; fishing cat (*Prionailurus viverrinus*), jungle cat (*Felis chaus*), and, rusty-spotted cat (*Prionailurus rubiginosus*). These felids are hyper-carnivorous elusive predators that play important ecological roles in a variety of habitats. We conducted this study to identify the habitat associations of sympatric small and medium-sized felids and model the habitat suitability of Maduru Oya National Park (MONP), Sri Lanka. Spatiotemporal niche overlapping and partitioning was also investigated. Species occurrence data were obtained based on the camera trap capture events, direct observations, and roadkill records. Modeling was conducted based on the maximum entropy algorithm (MaxEnt) using the software package Maxent (version 3.4.3). The predictive accuracies (ROC) of the selected models were evaluated to be greater than 0.80 (AUC). Distance to water resources (44.9%), Bio1-mean annual temperature (33.6%), and habitat type (Dense dry-mixed forest; 79.8%) were identified as the most important variables contributing to habitat suitability for fishing cats, jungle ,cats and rusty-spotted cat respectively. We further identified that spatial variation in habitat use facilitates these three species to coexist in MONP despite the significant temporal (activity) overlapping. The outcome of this research will contribute to future conservation and management. The findings will be useful in comparative studies in Sri Lanka as well as elsewhere in the world.

Keywords: Felidae, MaxEnt modeling, ecological niche, resource partitioning, small carnivores

Introduction

Family Felidae is represented in Sri Lanka by four wild species. The apex predator of Sri Lanka's forests and the only 'big cat' of the island (Yapa & Ratnavira, 2013) is the Sri Lankan Leopard (*Panthera pardus kotiya*). The remaining three felids can be considered medium to small-sized cats (Nowell & Jackson, 1998; Sunquist & Sunquist, 2002), all of which fall into the category of meso-carnivores (Hoffmann et al., 2010; Parker et al., 2012). They are fishing cat (*Prionailurus viverrinus*), jungle cat (*Felis chaus*), and rusty-spotted cats (*Prionailurus rubiginosus*) (Wijeyeratne, 2008; Yapa & Ratnavira, 2013; Miththapala, 2018). These sympatric felids are hyper carnivorous elusive predators and may sometimes fill the role of apex predator in habitats where the leopard is absent (Prugh et al., 2009). However, their nocturnal activity and discreet nature have made it difficult to study their natural behaviors in wild habitats. In recent years, there has been increased research interest in small and medium-sized felids of the country (Miththapala, 2018). Past and ongoing research work and publications have identified the distribution of these felids on the island (Nekaris, 2003; Wijeyeratne, 2008; Miththapala, 2018; Scar.lk, 2021). However, the available data regarding their fine-scale spatial distribution and behavioral patterns in natural habitats is limited (Miththapala, 2018). Furthermore, the development of knowledge on the spatial ecology of these species would facilitate the conservation of a great number of related species and management planning. Furthermore, the development of knowledge on the spatial and habitat requirements of these species would facilitate the conservation of a great number of related species and management planning. As an initiation of predicting the distribution, habitat suitability and identifying the habitat conditions required for small and medium-sized felids, we conducted this study in Maduru Oya National Park (MONP), Sri Lanka. The primary sampling methodology was based on a camera trap-based field approach and a maximum entropy-based analysis framework. We also evaluated the spatial and temporal overlap between the species of concern.

The fishing cat (*P. viverrinus*) is a medium-sized felid (mean body weight: 6.8 kg) (Nowell & Jackson, 1998; Sunquist & Sunquist, 2002) and the largest of the three focal felids. It is a habitat specialist and associated with water/wetlands most of the time (Nowell & Jackson, 1998; Miththapala, 2018). Fishing cat is assessed as endangered (EN) locally and Vulnerable (VU) globally in the IUCN Red Lists (MOE, 2012; IUCN, 2021). This species is distributed in South and Southeast Asia. A jungle cat (*F. chaus*) is a small felid (mean body weight: 5.4 kg) (Nowell & Jackson, 1998), often the size of a domestic cat (may grow larger), but with distinct morphological characteristics (Miththapala, 2006). In other parts of the world, jungle cats are known to utilize a variety of habitats (Nowell & Jackson, 1998) while in Sri Lanka it is more of a dry zone species (Nekaris, 2003; Wijeyeratne, 2008; Miththapala, 2017). This is the species with the broadest distribution among the focal felids but occurs in patches (IUCN, 2021). The IUCN

Red List status is Near Threatened (NT) locally (MOE, 2012) and Least Concern (LC) globally (IUCN, 2021). The rusty-spotted cat is known as the smallest cat in the world (mean body weight: 1.4 kg) (Nowell & Jackson, 1998), generally smaller than a domestic cat, found only in some parts of India and throughout Sri Lanka (Nowell & Jackson, 1998; Miththapala, 2017). It is known as a forest species (Nowell & Jackson, 1998; Wijeyeratne, 2008; with some arboreal activity (Nowell & Jackson, 1998; Yapa & Ratnavira, 2013), but observations are not very common. Rusty-spotted cat has been categorized as Endangered (EN) locally (MOE, 2012) and Near Threatened globally (IUCN, 2021).

Models that establish relationships between environmental variables and species occurrence are widely used with many applications in wildlife conservation and management-related fields (Rushton et al., 2004; Hirzel & Le Lay, 2008). The early models were mainly developed for presence-absence data modeling. However, due to the bias and the limited availability of absence data, modeling approaches based on presence-only data have been proposed. The ecological niche theory (Phillips et al., 2006; Hirzel & Le Lay, 2008) is an important concept around which most of these models have been built. Ecological-niche-based models generally define a function that links the fitness of individuals to their environment (Hirzel & Le Lay, 2008). Therefore, using these models, ecologists can identify the habitat characteristics required by a species. Ultimately, the ecological niche of the species can be rebuilt from the environmental variables describing its habitat (Hirzel & Le Lay, 2008; Redon & Luque, 2010).

The maximum entropy (MaxEnt) model is an ecological niche model, which is widely used to assess species distributions (Clements et al., 2012; Bai et al., 2018). MaxEnt models were originally designed to estimate the presence density of a target species across a landscape (Phillips et al., 2006). However, these models have been applied to model species distribution and environmental niches to identify important species-habitat relationships. Considering only the "presence" data and environmental covariates, avoid bias and often lead to accurate results (Phillips et al., 2006; Pearson et al., 2007; Redon & Luque, 2010; Merow et al., 2013; Merow & Silander, 2014). The application of MaxEnt models has been generally focused on larger geographic distributions considering mostly the global bioclimatic variables. However, there are certain studies that have applied this modeling approach to fine-scale situations with considerable success (Massaro et al., 2018; Segal et al., 2021). An important factor to consider in this regard is taking into account the fine-scale environmental covariates associated with small geographic areas. In our study we, focused on Maduru Oya National Park in Sri Lanka (588 km^2) as our study area and analysis was concentrated both on bioclimatic variables as well as fine-scale habitat covariates associated with the parking area and focal felid species. Moreover, to further understand the temporal niche of small and medium-sized felids of MONP, we analyzed activity data obtained through camera traps during our study.

Our study aimed to: (1) assess the potential distribution and habitat covariates associated with small and medium-sized felids in MONP, (2) identify spatial and temporal overlap between species, and (3) identify critical areas for felid conservation within MONP.

Materials and methods

Study site

The study site was Maduru Oya National Park (MONP) situated in the dry zone of Sri Lanka (Fig. 1). The park is considered the third-largest national park in the country. The park is forged around the large Maduru Oya reservoir and several other reservoirs are situated within the park. The main habitat types identified in the park are shrublands, grasslands, and the dense forests of climax dry-mixed evergreen forests (Jayasekara et al., 2021a). Rocky outcrops can be observed in patches, scattered throughout the park. The reservoir areas can be identified as aquatic/wetland habitats (Jayasekara et al., 2021a). Most of the grasslands and shrublands are a result of slash and burn cultivation practiced over the years until the area was declared a national park in 1983 (Green, 1990). The grasslands assume characteristics of savannas in some areas, whereas the reservoir perimeter is surrounded by seasonal grasses that grow during the dry season (late January-October).

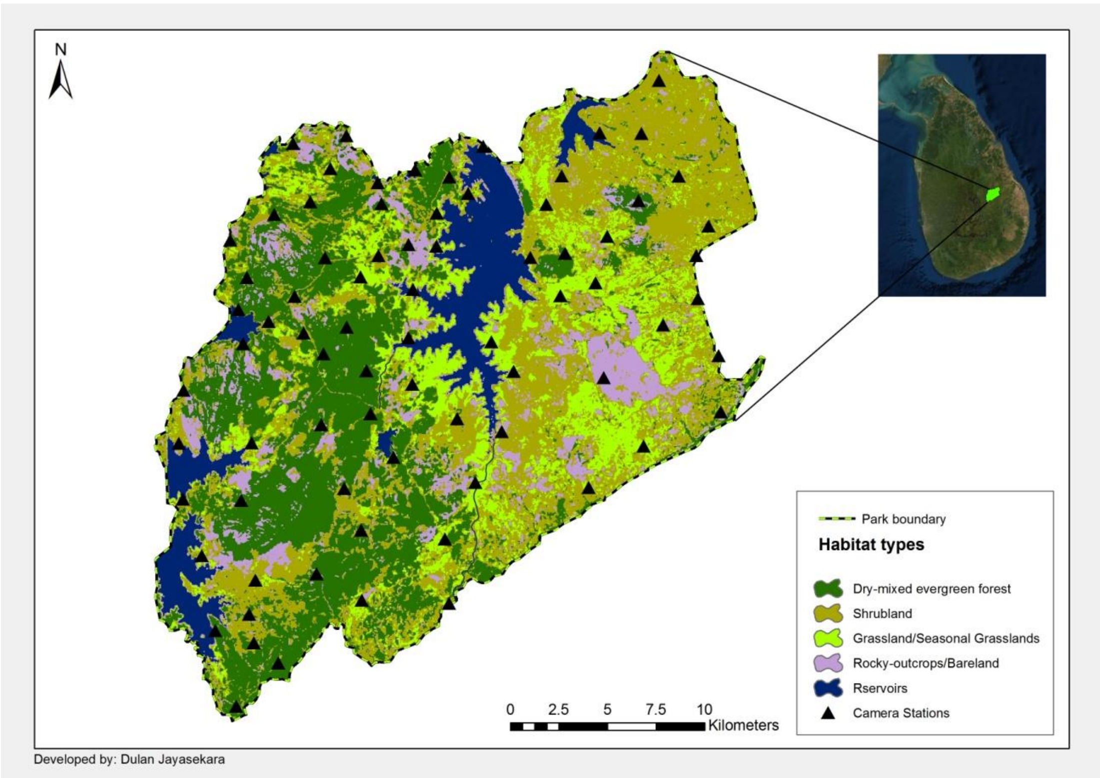

Figure 1. Habitat map of Maduru Oya with camera trap locations (Map adapted from Jayasekara et al., 2021a)

Collection of presence data of small and medium-sized felids

The park area was divided into 2*2km^2 plots using the 'grid index feature' tool in ArcMap version 10.4.1 (Esri, Redlands, USA). We established 75 camera stations following a stratified random approach, covering all available habitat types within the park. Camera trapping was conducted from January 2019 to January 2021. We used four infra-red-triggered camera models: Browning Strike Force HD Pro (n=10, low glow flash); Browning Dark OPS HD Pro (n=15, no glow flash); Browning Strike Force 850 (n=5) (Browning, USA,) and Bushnell Aggressor (n=10, low glow flash) (Bushnell, USA). All cameras were without the white flash to cause minimum interference to the animals. Camera placement was at a height of 25cm usually attached to a tree or a log. To maximize the detection some cameras were placed in probable locations of felid activity identified based on pugmarks and feces. No baits were used. Cameras were active 24 hours per day for approximately 40 days on average at a single station. All browning cameras were set to video mode and Bushnell cameras were set to hybrid mode to capture both photos and videos of animals that trigger the sensors.

To complement the camera trapping presence data, we conducted ground (32km) and vehicle (1280km) transects. Additionally, GPS coordinates for road-killed felids (on the main road that goes bisecting the park) were recorded after species identification. Repeated location data were removed by thinning to assign only one presence coordinate for each 1km^2. This supplementation of presence records does not violate the modeling assumptions since MaxEnt modeling is based on presence-only data (Phillips et al., 2006; Proosdij et al., 2016). Furthermore, for species such as rusty-spotted cats and jungle cats which have low prevalence (Jayasekara et al., 2021b), a small sample size would perform reasonably well within a small geographical area like MONP (Pearson et al. 2007; Proosdij et al., 2016).

Environmental covariates

We obtained 19 bioclimatic variable raster maps from WorldClim (www.worldclim.org) data and extracted them for the park area using a mask in Arc GIS. Additionally, we prepared raster maps of normalized difference vegetation index (NDVI) using Landsat 8 multispectral images for two different months of the year (March and June), elevation (based on a digital elevation model [DEM]) and Euclidean distance to water sources (generated using Euclidean distance tool) as continuous variables and habitat type (adapted from vegetation/land cover map of Jayasekara et al., 2021a) as a categorical variable (Table 1). The raster maps with different spatial extents and resolutions were resampled to match the parameters of 19 bioclimatic variables (30 seconds~1km^2) (Phillips et al., 2006). After accounting for multicollinearity (>75%), the number of covariates considered for the final analysis was 10.

Table 1: Variables considered for modeling (Variables used for modeling indicated by 'X' mark)

Abbreviation	Variable	Description	Model Usage
Bio1	Bio1 (Annual mean temperature)	Continuous	X
Bio2	Bio2 (Mean diurnal range)	Continuous	X
Bio3	Bio3 (Isothermality)	Continuous	X
Bio4	Bio4 (Temperature seasonality)	Continuous	
Bio5	Bio5 (Max temperature of the warmest month)	Continuous	
Bio6	Bio6 (Min temperature of the coldest month)	Continuous	
Bio7	Bio7 (Temperature annual range)	Continuous	
Bio8	Bio8 (Mean temperature of wettest quarter	Continuous	
Bio9	Bio9 (Mean temperature of the driest quarter)	Continuous	
Bio10	Bio10 (Mean temperature of the warmest quarter)	Continuous	
Bio11	Bio11 (Mean temperature of the coldest quarter)	Continuous	
Bio12	Bio12 (Annual precipitation)	Continuous	
Bio13	Bio13 (Precipitation of the wettest month)	Continuous	X
Bio14	Bio14 (Precipitation of the driest month)	Continuous	
Bio15	Bio15 (Precipitation seasonality) (Coefficient of variation)	Continuous	X
Bio16	Bio16 (Precipitation of the wettest quarter)	Continuous	
Bio17	Bio17 (Precipitation of the driest quarter)	Continuous	X
Bio18	Bio18 (Precipitation of the warmest quarter)	Continuous	
Bio19	Bio19 (Precipitation of the coldest quarter)	Continuous	
Habitat type	1. Dry-mixed evergreen forest 2. Shrubland 3. Grassland 4. Rocky outcrops 5. Reservoir/Wetlands	Categorical	X
edw	Euclidean distance to water	Continuous	X
ele	Elevation	Continuous	X
NDVIj	Normalized difference vegetation index June	Continuous	X
NDVIm	Normalized difference vegetation index March	Continuous	

MaxEnt modeling and simulation procedure

We used the software package MaxEnt (v 3.4.3) for our analysis. For each species, the presence coordinates and environmental variables were fed into MaxEnt software adapting to the format requirements (Phillips et al., 2006). Each replicated run type was set to "Cross-validate" with a replicate value of one less than the total occurrence points. Response curves were created and jack-knife tests of variable importance were generated along with random seed and plot data. Jackknife estimator was used to detecting the importance of each variable. The maximum number of iterations was set to 1000. Regularization multipliers of 0.5, 1, 1.5, and 2 were tested to obtain the best fit model. Model evaluation was based on the receiver operating characteristic (ROC) curves (reviewed in Merow et al., 2013).

We exported the output results to ArcGIS 10.4 for reclassification in order to identify the suitable habitat distribution map for each species. The 'Focal statistics' tool in ArcMap was used to smooth the raster map to obtain the felid distribution maps in MONP (Bai et al., 2018).

We used the 10-percentile training presence rule (Phillips et al., 2006; Escalante et al., 2013; Kamyo & Asanok, 2020) to reclassify the averaged model results for each species into binary maps representing suitable (1) or less suitable habitat (0). The binary presence/absence maps were then used to determine the total area of suitable habitat for each species.

We utilized the 'cell statistics' tool in ArcGIS 10.4 to generate a felid species spatial overlapping map based on the binary maps and calculated the percentage spatial overlap between species.

Activity overlap analysis

Based on the species-specific time stamp data from camera trap records, we generated radian time datasets. The activity time data were analyzed following the methods of (Ridout & Linkie, 2009) using the R package '*overlap'* (Meredith & Ridout, 2021) in R version 4.0.3 (R Core Team 2013) bootstrapping with 1000 iterations from the original data to obtain confidence intervals. Activity overlap was estimated by pairwise felid activity comparison (Hearn et al., 2018). The measure of overlap between felids was calculated using the coefficient of overlapping ($\Delta 1$) (for sample size <75); 0 (no overlap), 1 (complete overlap) (Ridout & Linkie, 2009; Hearn et al., 2018; Meredith & Ridout, 2021). Activity graphs were generated based on non-parametric von Mises kernel density (Ridout & Linkie, 2009; Meredith & Ridout, 2021).

Results

Presence data of species

Our camera trap survey yielded 132 captures of fishing cats (Fig. 2a), 8 captures of jungle cats (Fig. 2b), and 7 captures of rusty-spotted cats (Fig. 2c). Additionally, two road kills of fishing cats (Fig. 3a) and three road kills of jungle cats (Fig. 3b) were recorded during the study period. Possible pugmark sites of 47 fishing cats, two jungle cats, and one rusty-spotted cat were observed during ground surveys. We recorded direct visual observations of 14 fishing cats, two jungle cats, and two rusty-spotted cats during transect observations. When repeated occurrences within 1km^2

were excluded, 22 occurrence points for fishing cats, 12 occurrence points for jungle cats, and nine occurrence points for rusty-spotted cats were taken as input for MaxEnt presence data.

Species distribution and suitable habitats with associated environmental covariates

The ROC results yielded >0.80 area under the receiver operating curve (AUC) values for all three felid species considered (fishing cat-0.804; jungle cat-0.856; rusty-spotted cat-0.819) indicating good prediction values for MaxEnt models. Based on the habitat suitability maps that were generated, we identified that habitats adjacent to the reservoirs were a high presence probability for fishing cats (Fig. 4a). Jungle cats mostly preferred drier shrubland and grassland areas of the park and it was distributed with a higher probability in park areas with close proximity to agricultural fields outside of the park boundary (Fig. 4b). The rusty-spotted cat was showing a high affinity to areas with an abundant forest cover of dry-mixed evergreen forest (Fig. 4c).

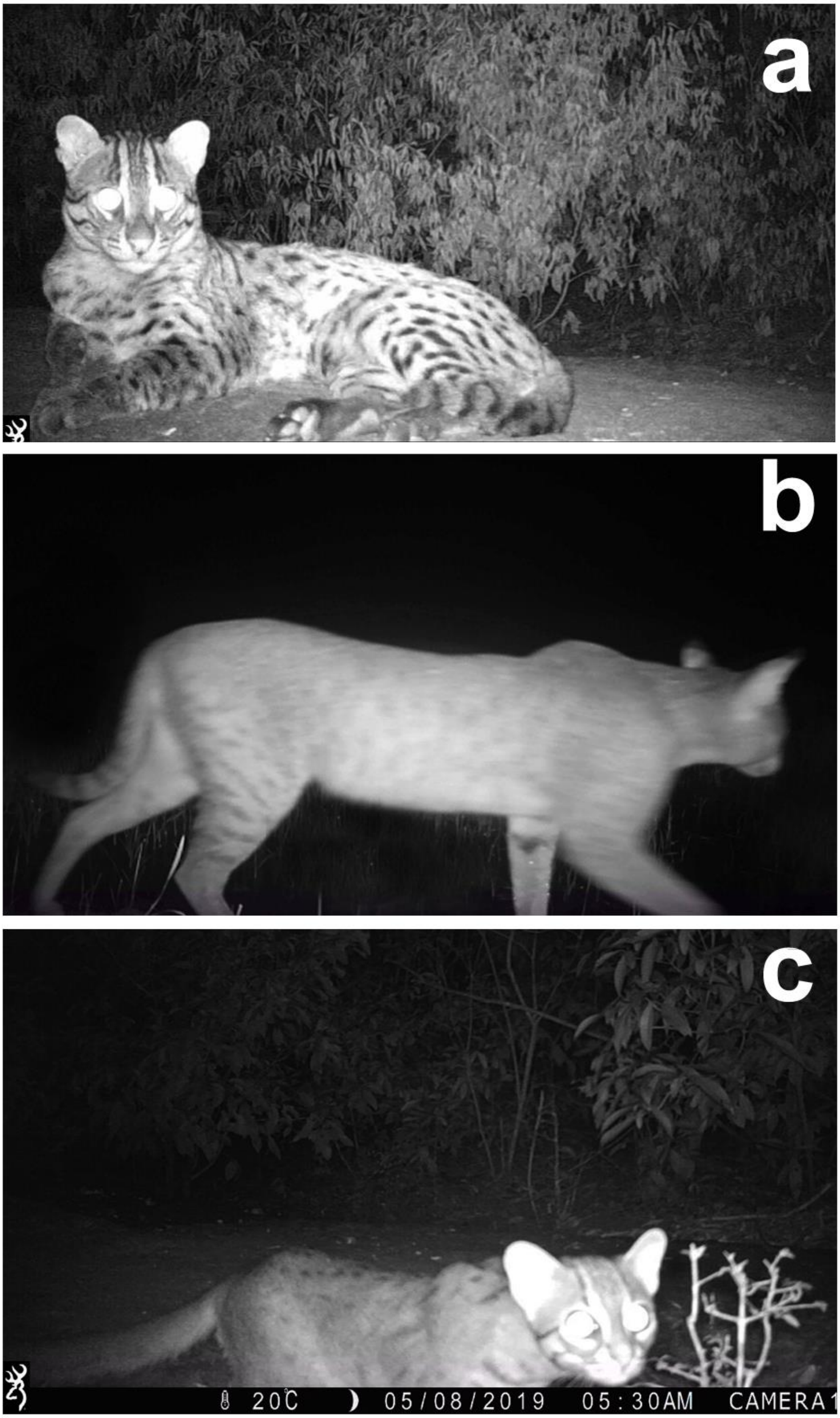

Figure 2. (a) Fishing cat, (b) Jungle cat, and (c) Rusty-spotted cat recorded in our cameras

Figure 3. Road kills of (a) a fishing cat and (b) a jungle cat (Photo credits: Chathuranga Dharmarathne)

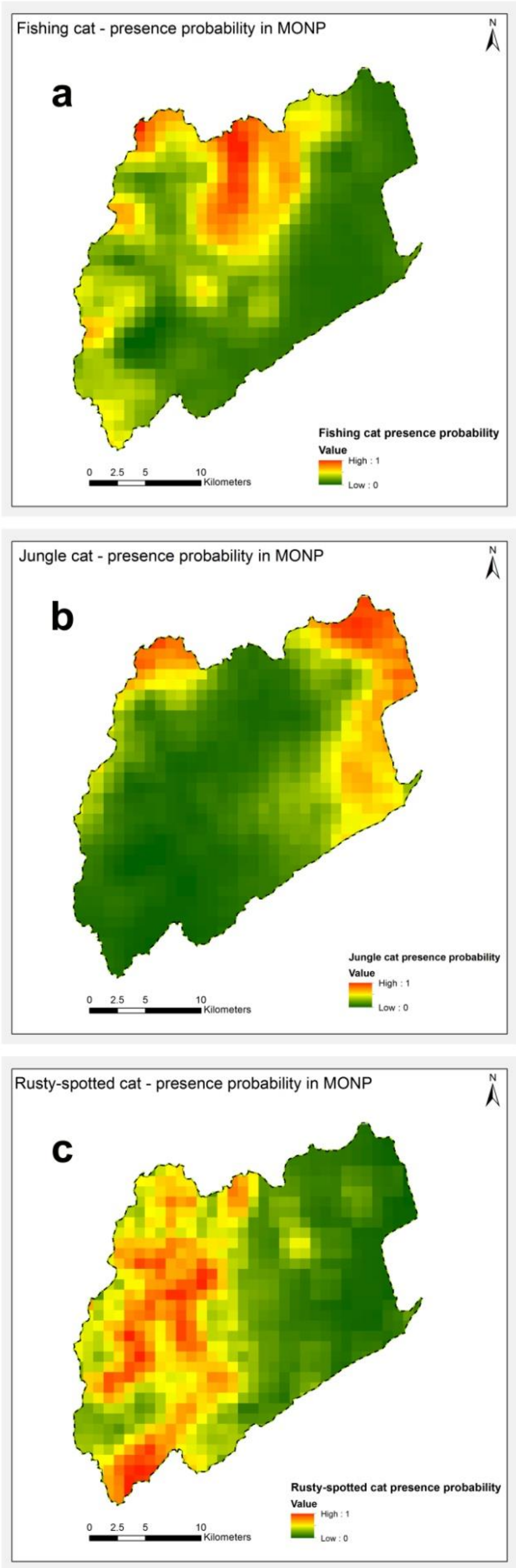

Figure 4. Modeled species distribution maps for small and medium-sized felids in MONP

Table 2. Contribution and permutation importance values of environmental variables

Variable	% contribution	Permutation Importance
Fishing Cat		
Euclidean distance to water	44.9	37.8
Bio2	19.3	10.5
Habitat type	13.7	6.4
NDVIj	7.5	10.2
Jungle Cat		
Bio1	33.6	64.7
Habitat type	28.5	14.6
Bio2	25.7	3.4
Bio17	4.9	2.8
NDVIj	4.4	13.2
Rusty-spotted Cat		
Habitat type	79.8	47.1
Euclidean distance to water	7.7	28.1
elevation	4.5	11.2

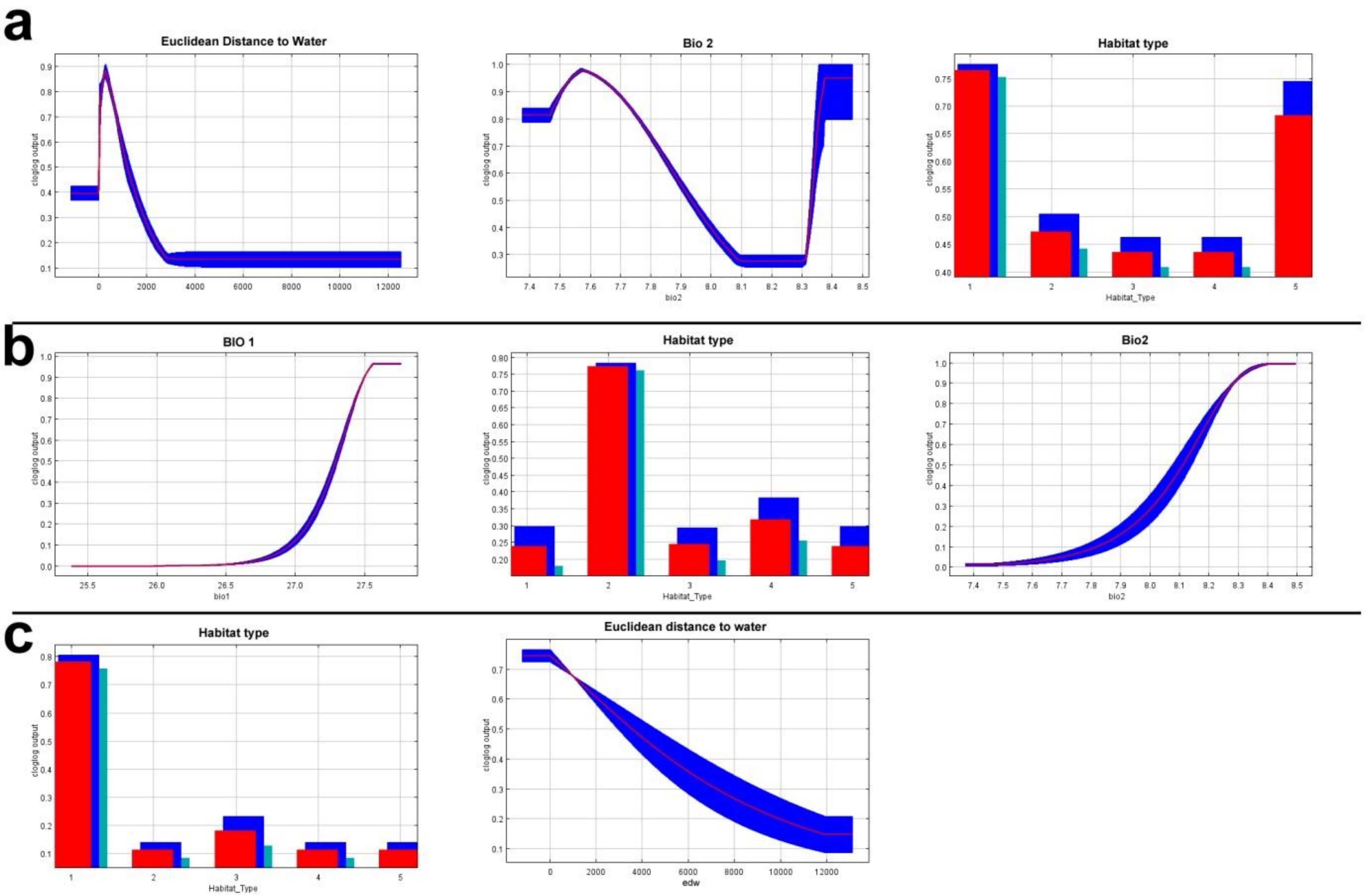

Figure 5. The response curves of selected variables for a) Fishing cat b) Jungle cat c) Rusty-spotted cat

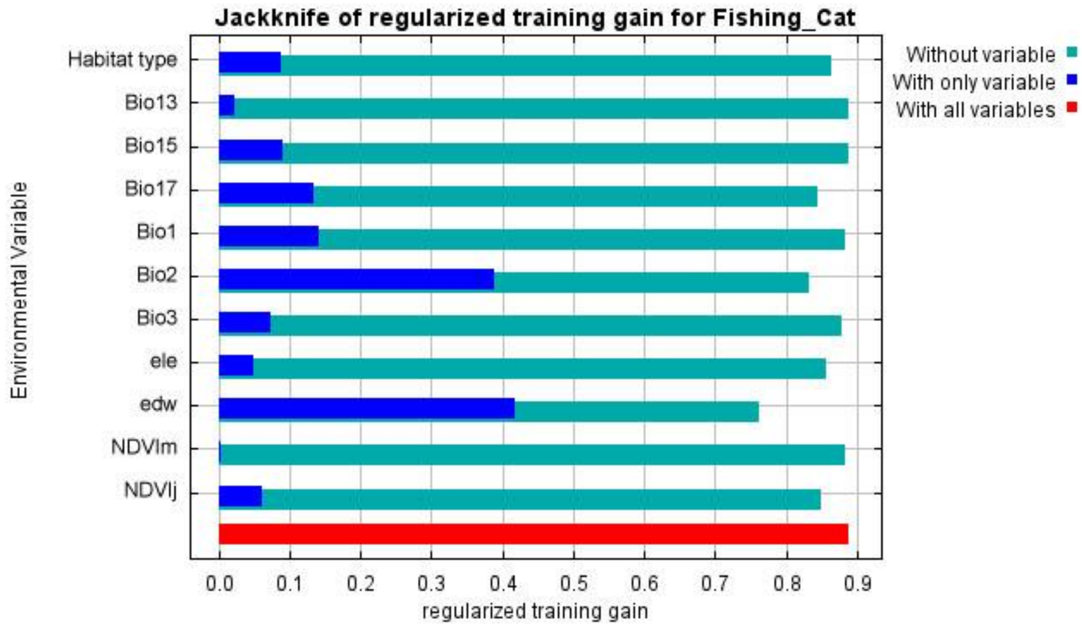

Figure 6. Jackknife test of environmental variables in training data for Fishing cat

The jackknife test of training gain (Fig. 6) showed that Euclidean distance to water (44.9%), Bio2 (19.3%), habitat type (13.7%), and ndvij (7.5%) were the main factors contributing to fishing cat habitat selection. The permutation importance rates in the MaxEnt model prediction indicated that Euclidean distance to water, elevation, and bio17 as the main factors affecting the model (Table 2). The response curves further confirm the above, indicating that fishing cat occurrence decreases with increasing distance from water. Bio2 was also showing a negative relationship (Fig. 5).

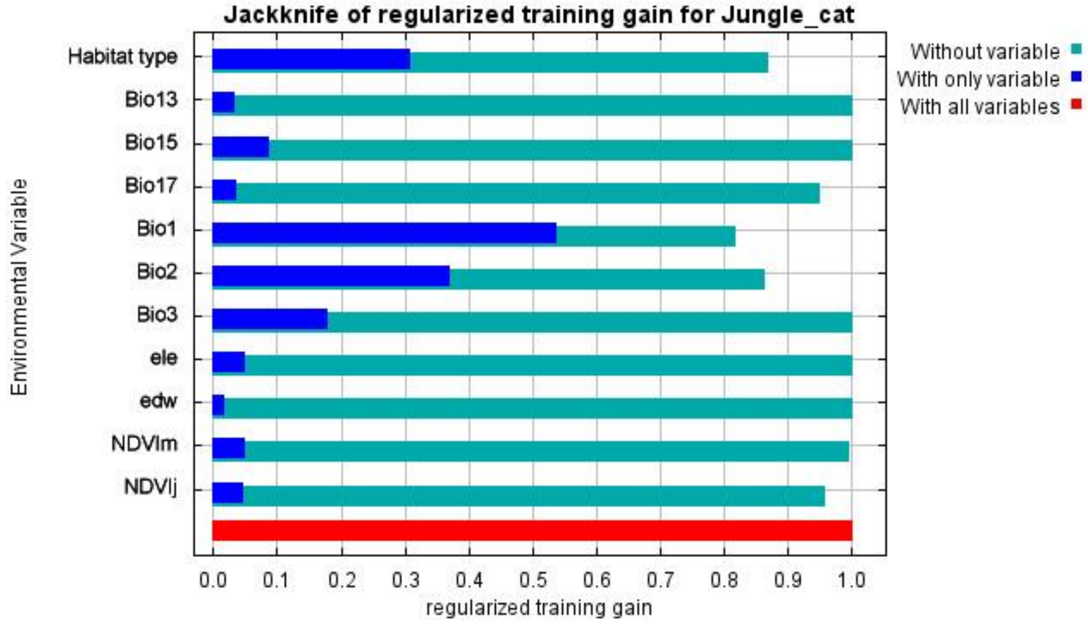

Figure 7. Jackknife test of environmental variables in training data for Jungle cat

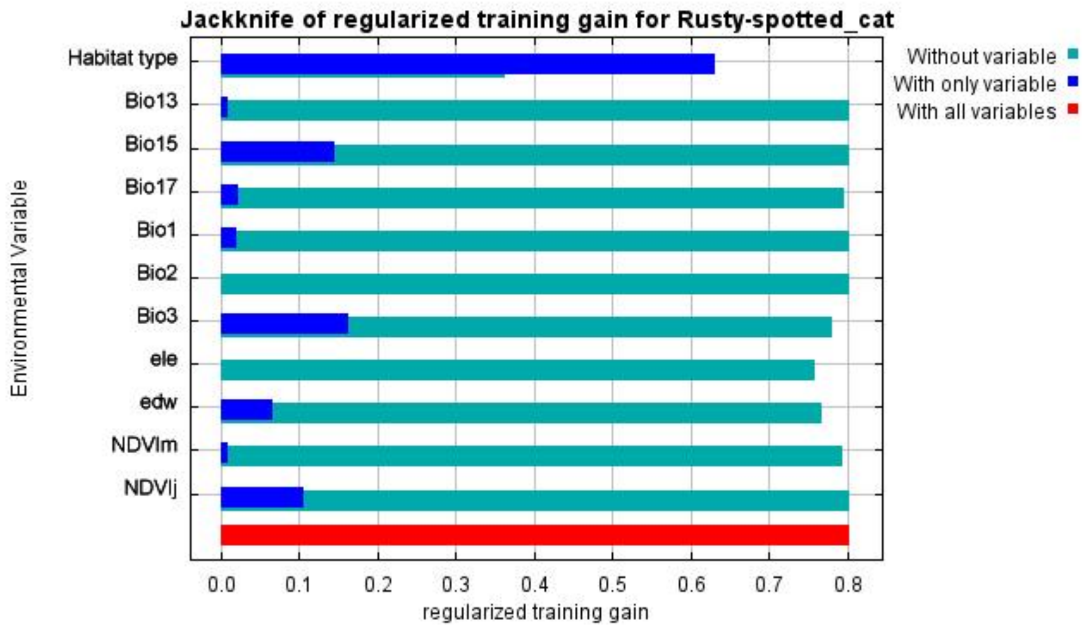

Figure 8. Jackknife test of environmental variables in training data for Rusty-spotted cat

Bio1 (33.6%), habitat type (28.5%), and bio2 (25.7%) were the main factors contributing to jungle cat habitat suitability. The permutation importance rates in the MaxEnt model prediction indicated that Bio1, habitat type, and NDVIj as the main factors affecting the model (Table 2, Fig. 8). The response curve clearly shows the positive association of jungle cats with BIO1 and Bio2 (Fig. 5). Habitat type (79.8%) was highly contributing to the rusty-spotted cat habitat suitability followed by Euclidean distance to water (7.7%). The same two parameters were with the highest permutation importance (Table 2, Fig. 8).

Spatial overlap between species

According to the maps of fig. 9, the suitable area percentage for all three felid species considered was lower than 30% of the total area in MONP (fishing cat-21.33%; jungle cat-21.13%; rusty-spotted cat-27.73%). When spatial overlap between the species was considered, we observed the highest overlap of 21.48% between fishing cats and rusty-spotted cats. Jungle cat was overlapping in lower spatial area percentages of 7.2% and 1.7% respectively with fishing cat and rusty-spotted cat. The area, where all three species were overlapping, was extremely low accounting only for 0.67% of the total suitable areas (Fig. 9d).

Temporal (activity) overlap

The activity graphs indicate that all three species were mostly nocturnal. However, the jungle cat was observed to be exclusively nocturnal while the fishing cat and rusty-spotted cat were active to some extent during the daytime also. When species activity was compared pairwise, there was a significant temporal overlap between of three felids. The highest overlap was between fishing cats and jungle cats recording a $\Delta 1$ value of 0.67 (0.51-0.97). The lowest activity overlap was between rusty-spotted cat and jungle cat ($\Delta 1$: 0.52) (Fig. 10/).

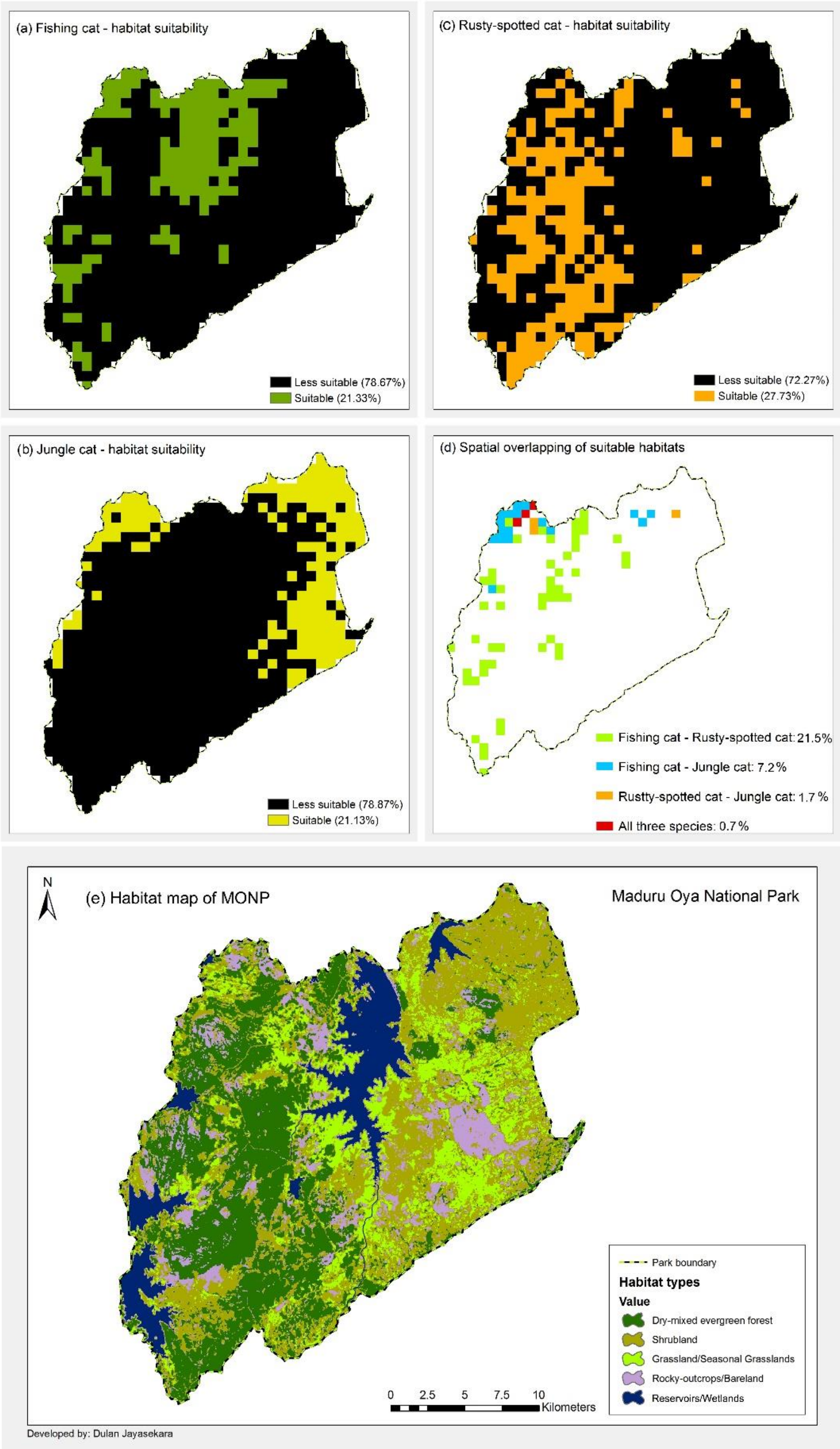

Figure 9. Habitat suitability maps for a) Fishing cats b) Jungle cats c) Rusty-spotted cats. d) Map showing the spatial overlapping of suitable habitats of three felids (e) Habitat map of MONP

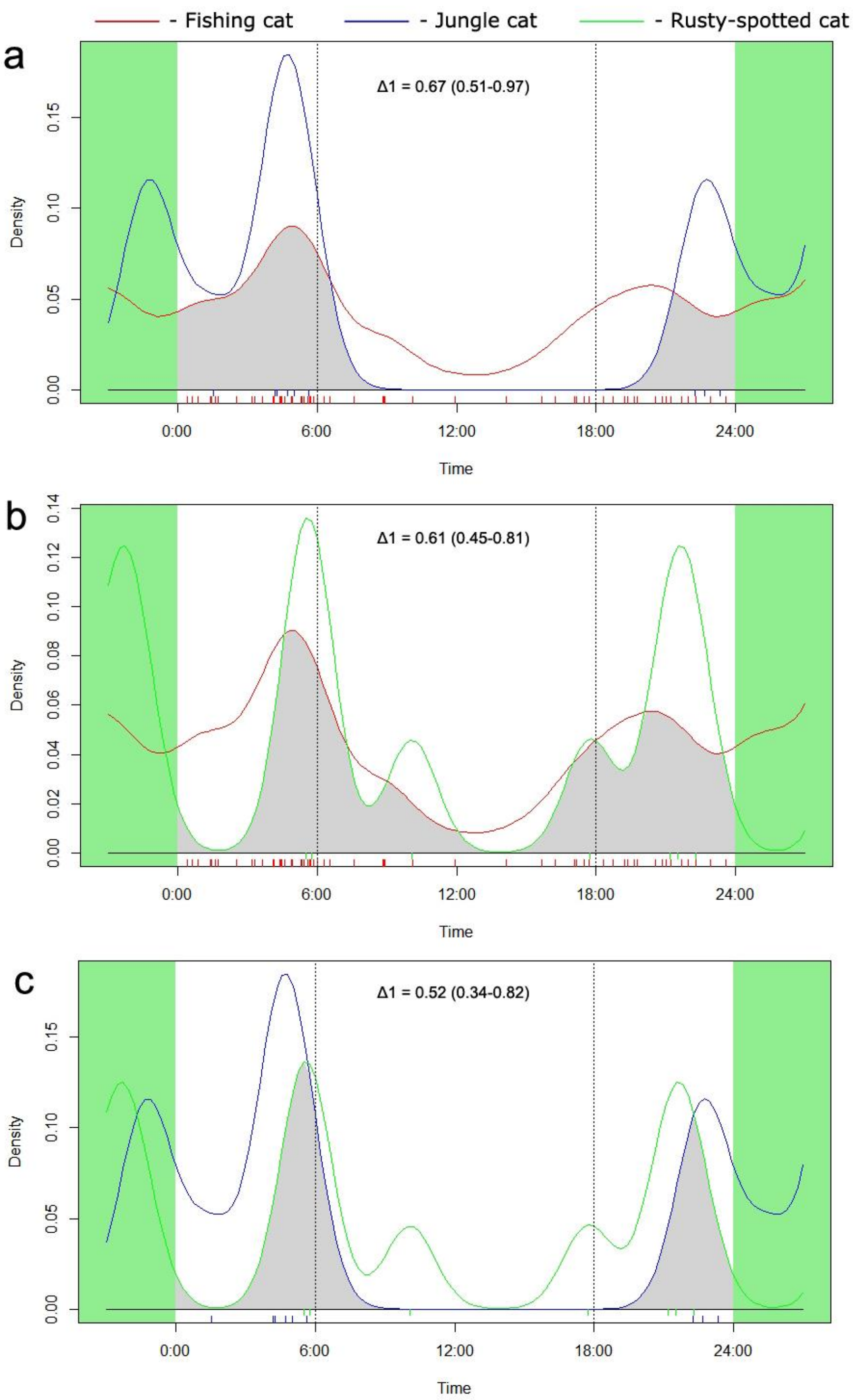

Figure 10. Activity overlaps between the three felid species. Red line indicates a fishing cat, Greenline indicates a Rusty-spotted cat and the blue line indicates a Jungle cat (The coefficient of overlap (Δ1) is shown by the grey shaded areas which represent the overlap periods, green-shaded are the area outside the concerned time frame)

Discussion

This is one of the first studies in Sri Lanka to apply MaxEnt modeling approach to study the distribution of small and medium-sized felids in a protected area in Sri Lanka. The distribution of jungle cats has been assessed based on citizen science data by Miththapala et al. (in press) very recently. The spatiotemporal overlapping of the focal species has not been investigated in detail previously in the island (Miththapala, 2018).

Based on the MaxEnt modeling output, the fishing cat presence probability was highest around the reservoirs that are found within MONP. However, their distribution was more skewed towards the western flank of the park where dense forest habitat cover is greater. The affinity of fishing cats to areas adjacent to water sources has been previously identified (Mukherjee et al., 2016; Miththapala, 2018; Hunter, 2019; Ganguly & Adhya 2020; Scar.lk, 2021). The habitat specialist nature of the species described by Miththapala 2017 was verified by our results. This was especially visible in the jackknife estimator results where the highest contribution for the MaxEnt model was from the euclidean distance to water. Fishing cat occurrence was highest nearby the water edge of the reservoirs and it was decreasing as the distance to water increased. Therefore, fishing cats were showing high adaptability to forest habitats adjacent to water. The contributions of the diurnal temperature range (Bio2), habitat type, and green forest cover indicated by NDVIj for fishing cat presence show that fishing cats preferred relatively moist (less dry) areas of the park. They did not prefer the drier western flank of the park dominated by shrubland and grassland habitats. However, fishing cats were observed in all habitat types in varying extents. This may be because of their diversification of prey species which also include terrestrial species (Thudugala & Ranawana 2015; Miththapala, 2017) in addition to the prey associated to aquatic habitats (Ganguly & Adhya, 2020; Hunter, 2019; Cutter, 2015; Kitchener et al., 2010; Haque & Vijayan, 1993). There is the possibility of male fishing cats with larger territories crossing the forest patches via shrublands, about which very little is known. Even though the species is mostly nocturnal according to Philips (1935) and as mentioned by Miththapala (2018), we recorded several daytime observations both on cameras and while on ground transects. Therefore, in addition to nocturnal activity, some activity was present in the morning and evening periods which confirms the observations of Wijeyeratne (2008).

The distribution of jungle cats was most prominent in the shrubland and grassland areas and close to the peripheral area of the park adjacent to the agricultural lands. The highest affinity was shown to the shrubland habitat and interestingly most of the environmental covariates preferred by the jungle cat were the opposite of the other two species. The presence probability was positively increased with annual mean temperature (Bio1) and diurnal temperature range (Bio2) indicating the preference of this species for dry, hot and humid conditions. Yapa & Ratnavira (2013) described the adaptability of this species to different environments including very harsh conditions. The competition and predation (Wijeyeratne, 2008; Yapa & Ratnavira 2013) by larger counterparts such as fishing cats and leopards could be one reason for this species drifting away from the resource-rich habitats. All our activity records were almost completely nocturnal for this species. Wijeyeratne (2008) records some daytime activity (early morning and evening) in undisturbed habitats elsewhere.

When a rusty-spotted cat is concerned, the distribution was highly concentrated to the densely forested areas of the park. Hence, the presence probability was highest in the western flank of the park which sustains the majority of the remaining dense forests of climax dry-mixed evergreen type. This was visible in the jackknife estimators followed by the contribution of Euclidean distance to water which was the second most important parameter. The affinity to densely forested habitats in Sri Lanka has been identified by the earlier work of Kittle & Watson (2004) and described by Langle (2019). Displaying some affinity to areas close to the water sources could be related to the dryness of the area in general where resources are abundant as it gets close to the water. Even though rusty-spotted cats are generally considered nocturnal animals (Kittle & Watson, 2004; Miththapala, 2018), their activity records in MONP suggest that they were active sometimes during day time as well. While conducting ground transects, we unexpectedly observed one rusty-spotted cat possibly hunting for frogs and trapped fish at a seasonal pond nearby the main Maduru Oya reservoir during the late wet season. Yapa & Ratnavira (2013) predict such diurnal activity in the absence of threats, which was the case in MONP (until it was disturbed by the authors' presence).

According to Philips (1935), as mentioned by Miththapala (2018), fishing cats are described as 'savage and ferocious' and some villagers fear the animal and consider it a danger. There are reports of conflicts with humans for attacks on poultry by fishing cats and jungle cats (Wijeyeratne, 2008, Yapa & Ratnavira, 2013). Snares intended for other species such as wild boar may potentially kill especially the fishing cats (Yapa & Ratnavira, 2013). Chathuranga Dharmarathne (Personal communication) indicates that the local hunters would not hesitate to take them (felids) as bushmeat if they get the opportunity. Moreover, based on our experience of encounters with all three species in the field, we identified that they are quite elusive and shy. In almost all situations, they fled to refuges and distanced away from humans as soon as they felt the human presence.

There was a clear spatial niche partitioning in MONP between the three felids considered in the study which was illustrated in the habitat suitability maps. The highest spatial overlap was between fishing cats and rusty-spotted cats which were 21.48%. However, it cannot be considered a considerable overlap. The spatial overlapping between fishing cat-jungle cat and jungle cat-rusty-spotted cat was minimal. Interestingly, the proportion of area suitable for mutual use by all three species was extremely low (0.67%). We identified ring-tailed civet/small Indian civet (*Viverricula indica*) as a nocturnal species that co-occur with these felids in almost all habitats. Contrastingly, a significant temporal niche (activity) overlap was observed between the three felid species where the highest being the fishing cat vs. jungle cat. Moreover, there could be a possible foraging niche overlap between the species despite the diversity of prey they consume (Wijeyeratne, 2008; Yapa & Ratnavira, 2013). Therefore, in MONP the competition has been largely reduced by the spatial niche petitioning of small and medium-sized felids, facilitating them to utilize overlapping temporal and foraging niches, to coexist within this protected area. The availability of diverse habitats is one important characteristic of MONP which assists to provide shelter for not only small and medium-sized felids but also the leopard. It is important to mention that the number of leopards recorded during the survey was relatively low when the park area is considered. However, the focus of the methodologies followed was on small and medium-sized felids which are meso-carnivores at a trophic level below the apex predator. High hunting pressure (Gabadage et al., 2015) on ungulates and leopards by the poachers may have resulted in low population numbers of leopards as well as larger prey. Therefore, the high abundance of the fishing cat (which is next in line after the leopard) could be similar to the observations of Prugh et al. (2009) where they describe "the rise of a mesopredator". The high population density of fishing cats and low densities of rusty-spotted cats and jungle cats in the western flank of the park has been recently recorded by Jayasekara et al. (2021b).

The suitable area for each felid species was less than one-third of the parking area indicating the importance of specific habitats. We identify the reservoirs and associated canal networks associated with the park are highly important for the fishing cats. The remaining area of dense forest (dry-mixed evergreen) is vital along with the habitat enrichment by the large Maduru Oya reservoir for both fishing cats and rusty-spotted cats. Therefore, the highest conservation priority should be given to densely forested habitats of MONP. These habitats are vulnerable to some amount of illegal logging due to the availability of timber plants with rich economic value. Moreover, we observed a number of manmade forest fires set by the poachers in shrublands/grasslands that got spread into the forested habitats. Unlike the fire-adapted tree species of some of the park areas (Gunatilleke et al., 2008), the forest trees are vulnerable to such fires. Therefore, we highlight these fires as one important management issue that prevails at MONP. Despite the continuous efforts of park management with limited availability of personnel to regularly apprehend illegal activists, there is a need of increasing the staff capacity to help law enforcement. Even though the shrubland and some grassland habitats of the park are relatively degraded habitats due to past anthropogenic activities, there is still a reasonable refuge for species like jungle cats and which are also foraging grounds for Asian elephants. Miththapala (2018) identified habitat loss and forest cover loss as one of the major threats for the felids of the island highlighting the importance of conservation measures.

With the expansion and uplifting of the road network of the country, the number of road-killed felids increased at a considerable rate. A major road that connects two adjacent towns, one to the North (Aralaganwila) and the other to the South East (Maha Oya) of the park, can be identified as a concern due to road kills. This road (that goes through the park) had been closed for several years and after the reopening and road development work, we observed that the number of road-killed felids has risen. Personal communication with J. Rathnayaka confirmed the above. This area is especially the territory of jungle cats and some fishing cats when the road runs closer to the reservoir. Additionally, we recorded road kills of golden jackals and ring-tailed civets. The authors joining together with the Wildlife Circle-USJ, Department of Wildlife Conservation and MONP officials carried out a road sign project to alert the speeding drivers in 2021 with funding from Rufford Small Grants. As an additional precaution, we suggest possible closure of the road at least partially at night.

The present study can be identified as one of the initial efforts of modeling the habitat suitability and identifying the spatiotemporal niches of small and medium-sized felids in a wild habitat of Sri Lanka. The results can be utilized to facilitate the conservation and management of focal species as well as their natural habitats. It will ultimately help conserve a wider biological community that is associated with these species.

Conclusion

MONP was identified as a protected area with suitable habitats for fishing cats, jungle cats, and rusty-spotted cats. There was a considerable spatial niche partitioning between the species of concern. However, the temporal (activity) overlap was identified to be high between all three species. The present study identified the importance of diverse habitats in MONP for the survival of small and medium-sized felids. Conservation priorities and threats were identified.

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