Volume 31 (July 2021), 132-141

Herpetological Journal

FULL PAPER

https://doi.org/10.33256/31.3.132141

Published by the British Herpetological Society

Potential distribution of the endemic Short-tailed ground agama *Calotes minor* (Hardwicke & Gray, 1827) in drylands of the Indian sub-continent

Ashish Kumar Jangid[1], Gandla Chethan Kumar[1, 2], Chandra Prakash Singh[3] & Monika Böhm[4]

[1]Wildlife Institute of India, Dehradun, Uttarakhand- 248001, India

[2]Centre for Biodiversity and Conservation Studies (CBCS), #F6, Central Facilities for Research and Development (CFRD), Osmania University, Hyderabad, Telangana State-500007, India

[3]Space Applications Centre, Indian Space Research Organisation, Ahmedabad, Gujarat, India

[4]Institute of Zoology, Zoological Society of London, London, UK

The Short-tailed ground agama or Hardwicke's bloodsucker *Calotes minor* (Hardwicke & Gray, 1827) is known to occur in the Indian subcontinent and is largely confined to arid to semiarid environments, such as hard barren desert and abandoned fields. The precise distribution of this species is largely unknown to date, with few locality records spread biogeographically across Eastern Pakistan, Central and Western India. To improve on the existing spatial knowledge on this species and assess the ability to predict species distributions for taxa with few locality records, we studied the distribution of *C. minor* using a species distribution modelling framework. Our study allowed us to predict the distribution range of *C. minor* and help define a niche for this habitat-specific species. Highly probable habitats for *C. minor* were arid and semi-arid dryland habitats, characterised by plains or less rugged terrain with moderately narrow temperature range, lower aridity index, moderate to low vegetation index, and wide precipitation range. Furthermore, we report four additional occurrence records of *C. minor* from central Rajasthan.

Keywords: Agamidae; small sample size; environmental niche modelling; distribution range; arid environment

INTRODUCTION

The genus *Calotes* Cuvier, 1817 comprises 25 species, with the Indian subcontinent harbouring 11 of them (Uetz et al., 2020). The genus can be identified by its laterally compressed body, naked tympanum, presence of dorsal crest, equal-sized scales on back and sides of the body, well-developed gular sac, absence of femoral or preanal pores and round swollen tail-base in males (Günther, 1864; Smith, 1935). Xeric grasslands of the Indian subcontinent are home to two species of *Calotes*: the Short-tailed ground agama *Calotes minor* (Hardwicke & Gray, 1827) (Fig. 1) and the Oriental garden lizard *Calotes versicolor* (Daudin, 1802) (Patel & Vyas, 2019). Previously, *C. minor* had an unclear taxonomic position, which was disputed among the genera *Agama* (Hardwicke & Gray, 1827; Smith et al., 1935), *Brachysaura* (Blyth, 1856; Günther, 1864; Stoliczka, 1872; Moody, 1980; Manthey & Schuster, 1999; Das, 2003; Khan, 2006; Khan & Kumar, 2010; Ingle et al., 2012), *Calotes* (Blyth, 1856), *Charasia* (Boulenger, 1885), *Laudakia* (Das, 1994; Murthy, 2010), and *Acanthosaura* (Boulenger, 1885). The resolution of its taxonomic status was achieved by Deepak et al. (2015), who studied the morphology of *C. minor* including osteology and hemipenis preparations supported with molecular data to place the species in

Figure 1. *Calotes minor:* new records from central Rajasthan. **1A & 1B)** *C. minor* (individual 2 from Nasirabad, Ajmer, Rajasthan) in an agricultural field. **1C)** *C. minor* (individual 3 from Khamor, Bhilwara, Rajasthan) in an agricultural field.

Correspondence: Ashish Kumar Jangid (ashishjangid22@gmail.com)

the genus *Calotes* (subfamily *Draconinae*; Deepak et al., 2015). They also ascertained the short tail length and relatively shorter fifth toe when compared to other *Calotes* as key identification features for the species (Deepak et al., 2015). Assessed as Data Deficient on the IUCN Red List of Threatened Species in 2009 (Böhm et al., 2013; Khan & Papenfuss, 2016), the species is currently undergoing reassessment (M. Böhm pers. comm.). Given the previously uncertain taxonomy and lack of records of *C. minor*, there is a notable gap in the understanding of its distribution and niche ecology. It is thus vital to determine the distribution and niche of this species to improve our knowledge of its conservation status.

It is known that several biotic and abiotic factors define a species' niche, and can thus be applied in the predictive distribution of species using an ensemble of techniques called Environmental Niche Modelling (Hirzel & Le Lay, 2008; Warren & Seifert, 2010). Also known as species distribution models (SDMs), niche models can predict the probability of species occurrence based on the life history and ecological needs of the species, expressed through the relevant environmental variables in the localities where the species have been recorded (Guisan & Thuiller, 2005; Elith et al., 2006; Elith et al., 2010; Singh et al., 2015). However, presence records and distributional information for secretive, cryptic, fossorial and difficult to observe species are often scarce (Pearson et al., 2007). For these species, species distribution modelling is challenging, given the dearth of presence records and general lack of reliable absence records which prevents the application of established methods to partition the data into testing and training sets and derive commonly-used test statistics of model performance (Pearson et al., 2007). Jackknifing (leave-one-out method) has been successfully used to model species distribution with a small sample size; here, each locality record in turn is removed once from the distribution model and model performance is assessed by the model's ability to predict the excluded locality (Pearson et al., 2007). In addition, test statistics based on jackknifing have been developed to evaluate model testing, thus allowing SDM evaluation under low sample sizes (Pearson et al., 2007).

Here, we use niche-based distribution models and jackknifing techniques to establish the potential distribution of *Calotes minor*, despite a limited numbers of presence records. Establishing the potential distribution of this species is important since following recent taxonomic work on the species (Khan & Kumar, 2010; Ingle et al., 2012; Deepak et al., 2015), the species' distribution remains poorly understood. Current information tells us that *C. minor* occupies a wide range of habitats, i.e., stony, sandy, and dark lava soil with grass, scrub, and thorny vegetation, in Pakistan, western and central India in subtropical regions (Khan & Kumar, 2010; Deepak et al., 2015). We developed a niche-based species distribution map for *C. minor* within the arid and semiarid regions of India and Pakistan, in the Indomalayan realm. We also discuss how this map can aid future survey effort for this species (and thus refinement of the distribution map) and inform current and future conservation assessment processes within the region.

MATERIALS AND METHODS

Study species and distribution records

Calotes minor is known to occur in grassland, agricultural land, and scrub-dominated landscapes in hot xeric (arid) and semiarid regions, with preferences for dry forest, barren and desolate land (Khan, 2006; Khan & Kumar, 2010; Deepak et al., 2015). The species is identified as both diurnal and crepuscular in habit, resides in burrows under the roots of bushes, and feeds on insects, leaves, and flowers (Khan, 2006). The species provides an important case study to examine the efficacy of jackknifing in niche-based species distribution modelling in the context of the tropical subcontinental and South Asian regions, as the species requires a specific range of temperatures, precipitations, and aridity (Deepak et al., 2015). *Calotes minor* has been documented from several Indian states, such as Gujarat, Rajasthan, Madhya Pradesh and Uttar Pradesh in India (Blyth, 1856; Günther, 1864; Stoliczka, 1872; Cockburn, 1882; Boulenger 1885; Smith, 1935; Vyas & Singh, 1998; Vyas, 2000; Vyas, 2002; GEER, 2014; Deepak et al., 2015; Ardesana, 2018); while substantial records were available from Sindh, Punjab and Balochistan in Pakistan (Khan 1999, Khan, 2002; Khan & Kumar, 2010; Deepak et al., 2015).

We collected species presence records along with their geographical coordinates from various sources, i.e., verified published records (n=17) by Khan & Kumar (2010), Ingle et al. (2012), Deepak et al. (2015), and Patel & Vyas (2019), personal observations (n=6), and personal communications with subject experts (n=1) (Table 1; Phillips et al., 2006; Pearson et al., 2007; Hosseinian Yousefkhani et al., 2016). Records from Banda and Allahabad, Uttar Pradesh, were not considered in the study, since there were no subsequent records after 1856 from these regions. We excluded the type locality of *C. minor* from the analyses since it is suggested to be erroneous (Khan & Kumar, 2010; Deepak et al., 2015). We also incorporated four recent locality records of *C. minor* from central Rajasthan, India (Fig. 2), recorded by the lead author. All reported individuals were sighted in agricultural fields dominated by green gram *Vigna radiata*, with an average crop height of around 15 cm (height range 3 – 20 cm). The sites were surrounded by landscapes dominated by the invasive shrub *Prosopis juliflora*. The species identity was confirmed using the key characters of sighted individuals, also suggested by Deepak et al. (2015), i.e., tail length less than snout-vent length; shorter fifth toe; two tufts of spines near tympanum. All observed characters of these new records are listed in Table 1. By merging all scrutinised records, we obtained a total of 24 locality records (from the years 1856-2019; Table 2).

Species distribution modelling

Addressing cluster bias

To avoid cluster biases and spatial correlation, a 100 km^2 (10 km × 10 km) grid framework was used to eliminate double records from each grid cell, so that we included only one presence record per grid cell for further analysis

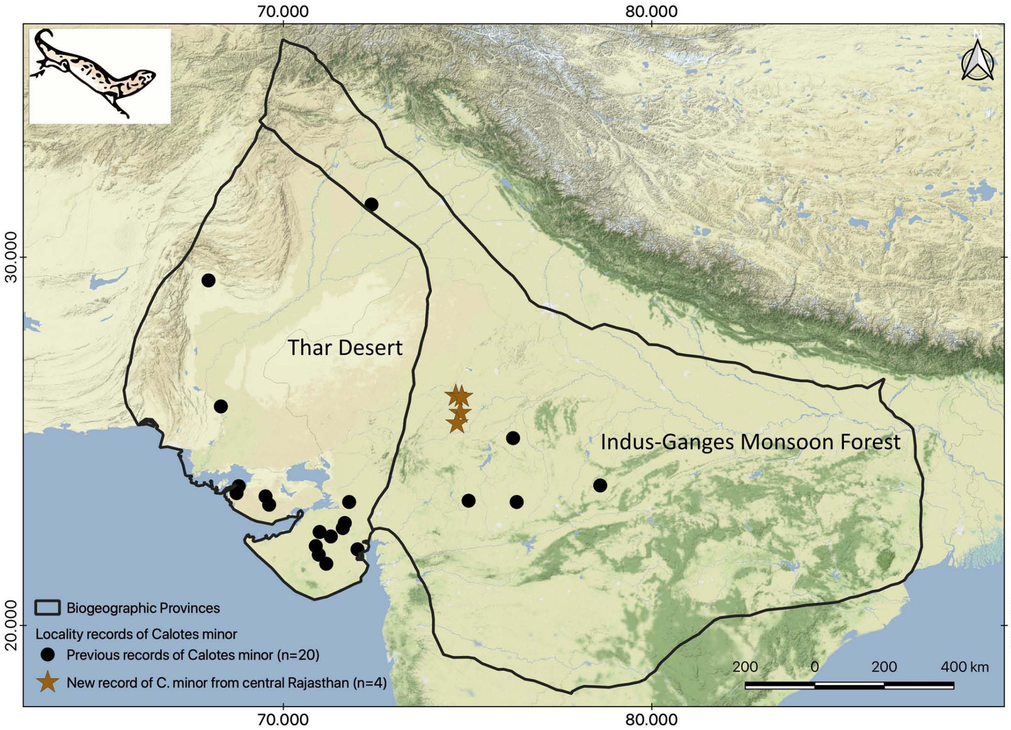

Figure 2. Map showing the previous records (n=20) and newly added records (n=4) of *Calotes minor*, scrutinised for predicting the distribution of *C. minor* (presented in current study).

Table 1. Recorded characteristics of four individuals of *Calotes minor*, recorded from central Rajasthan

	Individual 1	Individual 2	Individual 3	Individual 4
Place	Shokaliya, District Ajmer, State Rajasthan	Nasirabad, District Ajmer, State Rajasthan	Khamor, District Bhilwara, State Rajasthan	Shahpura, District Bhilwara, State Rajasthan
Location	26.21˚N 74.84˚E	26.24˚N 74.68˚E	25.77˚N 74.80˚E	25.49˚N 74.71˚E
Altitude	400m	448m	502m	393m
Period	July 2015	July 2017	August 2017	August 2017
Gender	♀	♂	♂	♂
Total length (Snout to Tail tip)	152 mm	163 mm	173 mm	171 mm
SVL length	81 mm	86 mm	91 mm	89 mm
Scales around midbody	49	54	58	57
Supralabials	13	14	14	14
Infralabials	11	13	13	12

Table 2. Information of predictor variables, used for modelling the species distribution for *Calotes minor*

Variable	Mean ± SD	Original spatial resolution	Resampled spatial resolution	Source
Aridity Index (AI)	0.18 ± 0.03	1000m	1000m	Global Aridity and PET Database (CGIAR-CSI)
Normalised Vegetation Difference Value (NDVI)	0.3 ± 0.18	1000m	1000m	Copernicus Global Land Service
Precipitation Seasonality (bio15)	127.62 ± 25.47	1000m	1000m	Worlclim version 2
Temperature Seasonality (bio4)	596.16 ± 148.4	1000m	1000m	Worlclim version 2
Terrain Ruggedness Index (TRI)	0.44 ± 0.11	30m	1000m	SRTM-USGS

(Pearson et al., 2007; Boria et al., 2014; Krishna Muliya et al., 2020). Since no multiple points were found in a single grid cell, we retained all 24 non-spatially correlated records for further analysis.

Variables selection

Selection of predictor variables was based on the known ecology of *C. minor*. We selected Aridity Index (AI), Normalised Difference Vegetation Index (NDVI), Precipitation Seasonality (bio15), Temperature Seasonality (bio4), and Terrain Ruggedness Index (TRI) (Table 3) as predictor variables. The AI is the degree of dryness, which is represented by the ratio of mean annual precipitation and mean annual evapotranspiration per year between 1970-2000 (Trabucco & Zomer, 2009). We computed mean NDVI across the months of July to October of each year over the time frame of 1999-2017 (Table 2), since grasslands and scrublands flourish in monsoon season in the tropical regions (Muratkar et al., 2015). Precipitation Seasonality and Temperature Seasonality for the timeframe of 1970 to 2000 were obtained from Worldclim version 2 (Fick & Hijmans, 2017). The Terrain Ruggedness Index (TRI) was derived from a digital elevation model (DEM) using the "Terrain Ruggedness Index" tool in QGIS version 2.14.3, which produces the mean difference in elevation between a pixel in the DEM and the surrounding eight neighbouring cells (Riley et al., 1999). We cropped all five variables to the layer extent of Thar and Indo-Gangetic biogeographic provinces (proposed by Udvardy, 1975) and the spatial resolution of the TRI data layer was resampled to 1,000 m using a bilinear resampling approach to match the resolution of the other variables. All data were transformed into the Asia Lambert Conformal Conic projection to perform spatial analyses. We extracted raster values of species presence locations for each predictor variable using the "Extract values to point" tool in ArcMap version 10.6. To avoid multi-collinearity, we computed Pearson's correlation coefficient (r) among our predictor variables using the "stats" package version 3.5.2 in R studio version 1.2.1335. Since no variable pair showed a strong correlation of > |0.7|, we retained all variables in further analyses (Chu et al., 2018).

Estimation of species occurence probability

We carried out the niche modelling for *C. minor* using a maximum entropy algorithm and presence-only framework in Maxent version 3.4.1 (Phillips et al., 2006; Norris, 2014). We implemented the jackknife evaluation approach proposed by Pearson et al. (2007) to assess model accuracy, given the small sample size of locality records for *C. minor* (n=24).

In total, we built 24 models, by leaving out one presence location at a time, so that each location is left out only once (Supplementary Figs. 5A-X; Pearson et al., 2007). We confirmed the settings of the modelling software as default, as follows: regularisation multiplier = 1; convergence threshold = 10^{e-6}; prevalence value = 0.5; and 500 maximum iterations. Regularisation values for linear, quadratic, threshold and hinge responses of variable features were computed using the default settings (Pearson et al., 2007, Baldwin, 2009). Background points were configured to 200,000 since the raster has around 2 million pixels. The models' predictions of relative suitability were configured into presence probabilities (ranges between 0 – 1), wherein the value of a given grid cell is the probability of the presence of the species (Phillips et al., 2006). The 10 percentile logistic presence threshold values (LPT) were considered as the decision thresholds to classify the species occurrence probability into a binomial framework, in which pixel values higher than the 10 percentile logistic presence threshold were considered as "1" (high probability) and pixel values lower than the 10 percentile logistic presence threshold (10 percentile LPT) were designated as "0" (low probability) (Pearson et al., 2007). This is because other commonly used threshold-independent validation statistics (such as AUC) are considered unsuitable for presence-only SDMs (Boyce et al., 2002). This differs from the approach by Pearson et al. (2007) which utilised the lowest presence threshold and a second threshold which rejected the lowest 10 % of possible predicted values. This is because, after testing of different thresholds, the 10 percentile LPT produced a good balance between overprediction of suitable areas and conservative prediction of potential species range (Escalante et al., 2013). Using these classes (1/0), we further tested whether the particular i^{th} model successfully predicted the higher species presence probability (higher than 10 percentile LPT) at the eliminated presence points (*i*) or not. If the model successfully predicted species presence, we recorded the prediction as "1" (success), if not, we coded it as "0" (failure). Using the program "*pvalue*" (Pearson et al., 2007), we calculated p-value to test the predictive ability of our jackknifed models.

Also, to give a sense of relative probability of occurrence per grid cell, we classified the pixel values of species occurrence probability into five equal categories, i.e., 0 – 0.2, 0.2 – 0.4, 0.4 – 0.6, 0.6 – 0.8 and 0.8 – 1. The pixel values >0.6 were considered as highly probable sites, in which priority surveys should be carried out for the species to elucidate its full distribution. These sites may also be focus areas for conservation actions for the species. Pixel values between 0.4 and 0.6 were considered as moderately probable sites.

To illustrate the size of the area where *C. minor* is potentially present, we calculated the area coded with "1" (higher presence probability than the 10 percentile logistic presence threshold) using ArcGIS version 10.6. We then plotted the relationship between predictor variables and probability of species occurrence for *C. minor* to describe climatic and topographical characteristics of the suitable species distribution.

RESULTS

Presence data

The locality points used in the environmental niche modelling are shown in Fig. 2 & Table 3. The first occurrence records for central Rajasthan (n=4), obtained by the lead author, were added to the 20 previously available and scrutinised records of *C. minor*, resulting in 24 locality records in total.

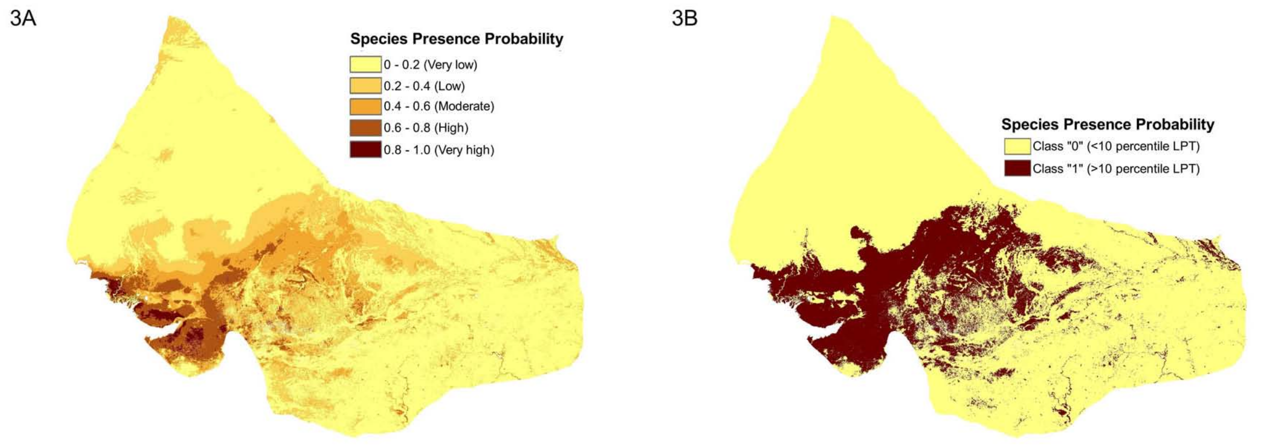

Figure 3. Species Presence Probability of *Calotes minor* in the study extent in India and Pakistan, using various thresholds. **3A)** Five categories of species distribution probability, indicating the areas of importance with higher distribution probability. **3B)** Binomially classified probability of the species distribution for *Calotes minor*, with putting 10 percentile logistic presence threshold (LPT) as classifier.

Estimation of species occurence probability

Binomial pixel classification based on the 10-percentile logistic presence threshold disclosed that, on average, 30.72 % of the study area are classified as higher than the 10 percentile LPT (Fig. 3B). Assessment of the importance of predictor variables in describing relative suitability of areas for *C. minor* found that precipitation seasonality (0.466 ± 0.007 SE) makes the largest contribution, followed by NDVI (0.323 ± 0.005 SE), temperature seasonality (0.165 ± 0.004 SE), aridity (0.041 ± 0.002 SE), and terrain ruggedness (0.005 ± 0.0002 SE). Distribution probability maps indicate that the Gujarat state has the highest probable sites to hold *C. minor*, since most of the areas, i.e., Kutch, Saurashtra, and central Gujarat have grid cells with suitability values of more than 0.6 (Fig. 3). South-western, central and eastern Rajasthan, north-western Madhya Pradesh in India, and southern Pakistan hold a moderate probability of species occurrence (0.4-0.6) (Fig. 3).

Precipitation Seasonality (bio15) has a positive relationship with predicted species distribution (Pearson correlation coefficient r=0.92, p<0.05), where in distribution probability of more than 0.6 is defined within the range of 140.53 mm to 187.81 mm precipitation seasonality (Fig. 4A). Normalised Difference Vegetation Index (NDVI) was found to be negatively related to species distribution probability with a sharp threshold in grassland and scrublands' NDVI values (r=0.74, p<0.05), and 0.05 – 0.26 units of NDVI indicate the areas where species distribution probability was more than 0.6 (Fig. 4B). There is a slightly negative relationship between temperature seasonality and predicted species distribution probability (r=-0.11, p<<0.05); areas with a temperature seasonality between 34.7 ˚C and 55.8 ˚C had a distribution probability of more than 0.6 for *C. minor* (Fig. 4C). Less arid areas, i.e., areas with high evapotranspiration and lower precipitation, are more suitable for the presence of *C. minor* (r=0.74, p<0.001); areas of predicted presence probability of more than 0.6 have Aridity Index values between -0.02 and 0.2 (Fig. 4D). TRI is negatively correlated with predicted distribution probability for *C. minor* (r=-0.74, p<0.001); areas of more than 0.6 probability of species distribution are found in areas with low TRI values between -0.05 and 1.05 (Fig. 4E).

The mean 10-percentile presence area was 0.303 (±0.006 SE), mean AUC was 0.89 (±0.001 SE), mean entropy was 11.32 (±0.01 SE) and mean prevalence was 0.02 (±0.002 SE).

The p-value estimation yielded that 83.33 % of jackknifed models successfully predicted the removed i^{th} locality records, which was supported by the p-value <0.001.

DISCUSSION

In this study, we used environmental niche modelling to define the species occurrence probability for a previously understudied species, *C. minor*. Our study showed that predicted suitable areas for *C. minor* had less rugged terrain (i.e., in Sindh in Pakistan; north-western Gujarat and south-western Rajasthan in India), in landscapes dominated by grasses or scrubs (throughout the western extent of study area; mainly covered by hot xeric parts of Pakistan; Gujarat and Rajasthan in India; avoiding higher ruggedness and forest areas of Indo-Gangetic province), with relatively moderate to low aridity (in Thar province, excluding Thar sand dunes, since areas of Thar desert have low precipitation seasonality as well; also found in Sindh, Balochistan and Punjab provinces in Pakistan; north-western Gujarat and south-western Rajasthan in India), moderate to low temperature variability (especially in mid-longitudinal areas of the study area; Sindh in Pakistan; Gujarat, Rajasthan, northern Madhya Pradesh and southern Uttar Pradesh in India) and higher precipitation variability (whole study area, except the north-western sides; Sindh region of Pakistan; Gujarat, Rajasthan, Madhya Pradesh and southern Uttar Pradesh in India).

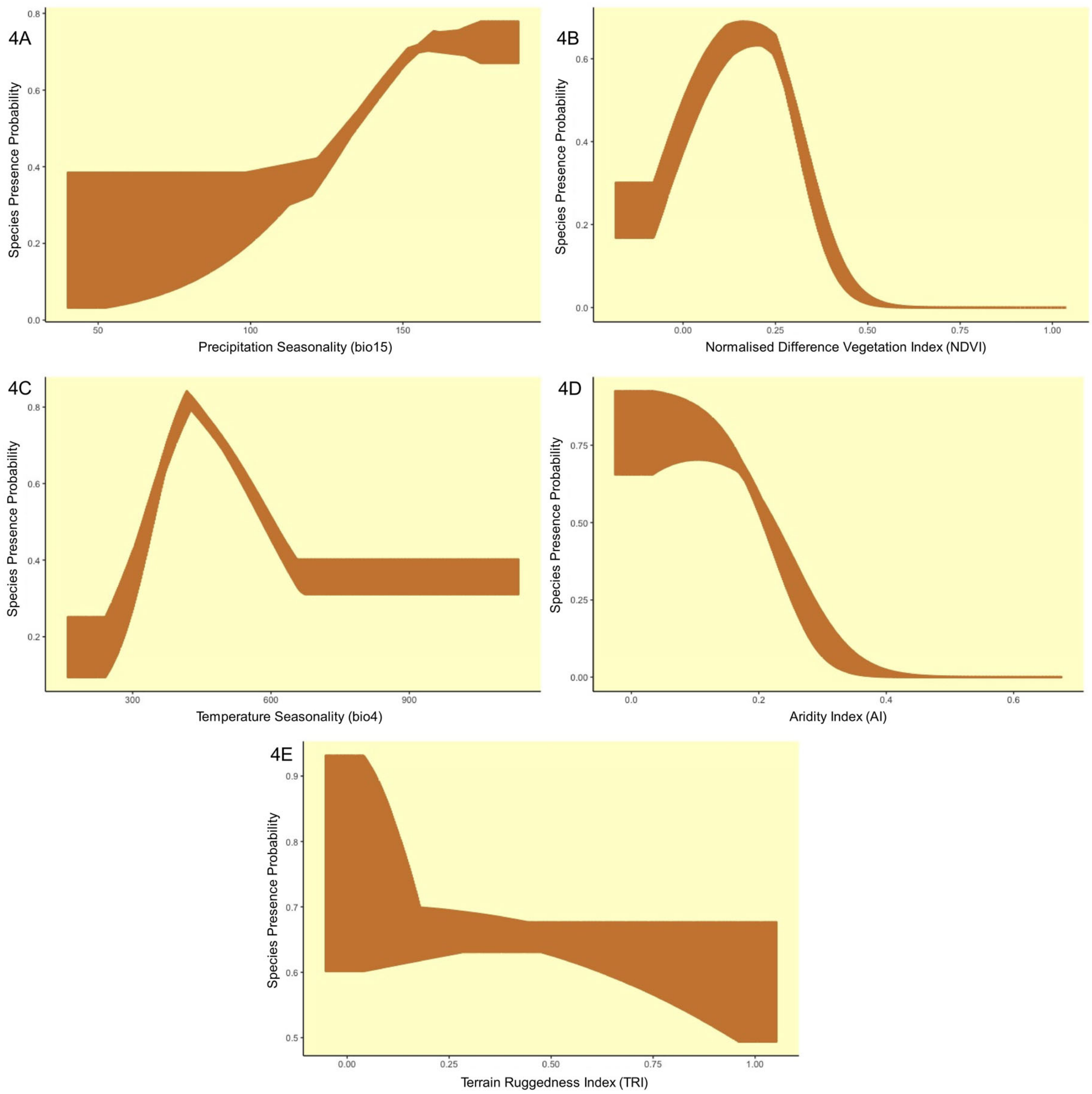

Figure 4. Response curve of predictor variables, displaying relationship with species presence probability of *Calotes minor*. **4A)** Precipitation Seasonality (bio15). **4B)** Normalised Difference Vegetation Index (NDVI). **4C)** Temperature Seasonality (bio4). **4D)** Aridity Index (AI). **4E)** Terrain Ruggedness Index (TRI)

Our models predict that the south-western extents of study area have a higher probability for the species distribution than both central and south-western biogeographic provinces combined. Politically, these high-probability areas are comprised by southern Sindh and southern Balochistan in Pakistan and Gujarat, south-western, central and eastern Rajasthan, and north-western Madhya Pradesh in India. This was found to be in accordance with the known ecology of this species (Khan, 2006; Deepak et al., 2015). Our results thus highly overlap with the known theoretical and observed ecology of *C. minor*, while allowing us to redefine its spatially explicit occurrence probability within this distributional range (Fig. 2). Responses of variables illustrate their crucial roles in defining the niche-based distribution model for *C. minor*. In addition, although the species was described in the year 1827 from the sandy plains of Chittagong (Bangladesh), its presence in the area has been regarded as questionable, especially given the habitat differences. Chittagong has a narrow temperature range (ranges from 21.7 ˚C to 30.4 ˚C), high humidity (>75 %), and heavy rainfall in monsoon (~500 mm; Khatun et al., 2016). The species has not been reported from Chittagong since 1827 (after Hardwicke & Gray, 1827). Our study further suggests that, based on the climatic niche for this species elucidated in our study, the record from Chittagong is likely erroneous (also suggested by Deepak et al., 2015; Khan & Kumar, 2010; IUCN Bangladesh, 2015).

The occurrence of the species around its distribution margins is likely sparse and sporadic. While the species may be less probable to occur there, due to difference in climate and topography, and other range-effects, there is also a need for robust ground data from those understudied margin regions. Since our leave-one-out approach accurately predicted the distribution of *C. minor* within the study extent (prediction capabilities of jackknifed models=83.33 %, p<0.001), it could be that the easternmost extents of the Indo-Gangetic plain distribution are characterised by differences in temperature and precipitation seasonality. In addition, topography also differs from the central and western parts of the distribution. Our results identify those areas for *C. minor*, where additional targeted surveys should be carried out to fill the gaps in our knowledge on the distribution of this particular species. Specifically, 10-percentile LPTs have been found favourable to uncovering potentially important distributional areas for understudied species (Pearson et al., 2007; Krishna Muliya et al., 2020). Each additional record is likely to enable better SDMs and will yield more precise distributional results.

Our findings highlight several priorities for field research on *C. minor*. Specifically, given the known ecology of the species and the suggested distribution of the species in south-western parts of the study area, extensive field research is required to validate the distribution of the species from east of Aravalli to the hill, since at present, the species presence from Uttar Pradesh is based on old records by Blyth, collected in 1856. Additionally, the niche models sparsely predicted the species occurrence in the central and southern parts of the study area, and this region would benefit from further field research. The grasslands and agricultural fields of southern Uttar Pradesh, western and north-western Madhya Pradesh, and north-western Maharashtra should be surveyed as they constitute potentially suitable habitat for this species. Finally, although the species has a higher probability to be distributed in Gujarat state (probability >0.6), records from Madhya Pradesh, Rajasthan and Pakistan play critical roles as well, because these records are maintaining a wide distribution extent of the species, which can buffer against declines and higher extinction risk of this species (Böhm et al., 2016; Joppa et al., 2016). Environmental and topographical characteristics of these regions are different to those of Gujarat, which is why the distribution is predicted to be sparse and patchy in these regions. However, further field surveys in these areas are required to establish species distribution limits, vital for the calculation of extinction risk metrics (e.g. EOO; IUCN, 2012), especially because our SDM approach should not be interpreted as accurately predicting range limits of the species (Pearson et al., 2007).

The ability of our modelling approach, and other SDM approaches, to predict probable areas of occurrence is highly dependent on the underlying locality data. Here, as in many other SDM approaches, we are focussing solely on identifying climatic and topographically suitable areas. Absences at potentially suitable localities may be caused by other underlying factors which have been omitted in our model but are important in driving species distributions, such as dispersal ability and biotic interactions. However, variable selection for environmental niche modelling essentially depends on the model species in question that reflect the species' ecology (Rödder et al., 2009; Palaoro et al., 2013). Effective use of expedient environmental variables to model species distribution helps to collate ecological understanding of the species and prediction modelling, even when only few species localities are known; for example, Krishna Muliya et al. (2020) used a small sampling approach to identify new potential areas for further field surveys for another little-known species, *Lycodon flavicollis*. By adapting the habitat-based niche modelling for a small sample size (n < 25), we effectively predicted species occurrence probability for *C. minor* within its distributional range. Using jackknifing and evaluating the models with p-value analysis, we showed a high accuracy of model prediction despite small sample sizes (n=24).

However, despite high accuracy of model predictions, the probability of erroneous suitability outputs is higher under very small sample sizes, for example where omitted localities cannot be successfully predicted (e.g. a single occurrence is geographically remote from the other localities, with different environmental conditions; Pearson et al., 2007; Krishna Muliya et al., 2020). This in turn will impact the probabilities of suitability derived from the SDM approach. Thus, while probability maps may allow identification of highly suitable habitat patches, a focus on these should not come at the expense of lower probability areas which could be the result of the large influence each locality of a small sample has on model outputs (Pearson et al., 2007; Krishna Muliya et al., 2020). In this case, presence-absence maps (binomially classified using 10-percentile logistic presence threshold; Fig. 3B) can be a decision making output to inform about the conservation priority and distribution extent for the species.

Given that *C. minor* is perceived to be rare, it is important that we focus on obtaining the best possible information on the species in order to proceed to conservation assessment. The species was assessed as Data Deficient for the IUCN Red List of Threatened Species in 2009, owing to its rarity, patchy distribution, and our gap of knowledge in this ground agamid's ecology (Khan & Papenfuss, 2016). There was a need to assess the distribution of the species so that more accurate range-based metrics of extinction risk (extent of occurrence EOO and area of occupancy AOO) can be produced and appropriate conservation action can be defined. Additionally, this species is part of the random sample of reptile species which make up the sampled approach to the Red List Index (sRLI), a global biodiversity indicator which aims to track changes in extinction risk of species-rich but understudied species groups (like reptiles) over time (Baillie et al., 2008, Böhm et al., 2013). However, given its current Data Deficient status, it does at present not contribute to the index, as its extinction risk is unknown.

Environmental niche modelling can provide the first step to ensure the accurate listing of species extinction risk on the IUCN Red List and can work alongside efforts already undertaken to predict the true status of Data Deficient species (Bland & Böhm, 2016). However, it should be noted that for conservation applications, a more conservative decision threshold may be required, such as lowest presence threshold (Pearson et al., 2007), to avoid overprediction of distribution area in conservation assessments. Given that no known species-specific conservation measures are in place and that it is perceived to face human-made threats like urban development with the conversion of grasslands for agriculture and infrastructure establishments (Khan & Papenfuss, 2016), there is a dire need to conserve grassland ecosystems so that not only *C. minor* but other grassland dependent species can be protected. Further research on the habitat, threats, and population monitoring of *C. minor* is mandated.

CONCLUSION

We tested the jackknife evaluation method accompanied by the maximum entropy algorithm for predicting the species presence for the little-known ground agamid lizard *Calotes minor,* following Pearson et al. (2007). Our results show that through the inclusion of recently obtained data records from central Rajasthan, the known distribution for *C. minor* in the Indian subcontinent is extended. Our results also suggest the distribution range of *C. minor* in the dryland regions of the Indian subcontinent, mainly covered by Gujarat, south-western, central and eastern Rajasthan and north-western Madhya Pradesh in India and southern Sindh and southern Balochistan region in Pakistan. Also, our study shows that both environmental niche modelling and field study can improve our knowledge of little-known species with unexplored range limits. Specifically, environmental niche models can focus research activity to areas where a species is predicted to occur and can help to inform conservation assessments and develop targeted conservation action and research.

Funding sources
This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors. MB is supported by a research grant from the Rufford Foundation.

ACKNOWLEDGMENTS

We appreciate Dr. Varad Giri for his incredible taxonomic guidance during the study and also for reviewing the locality records. We also thank Dr. Harshil Patel, Dr. Raju Vyas, Dr. Rohit Prajapati and Mr. Anil Sarsavan for providing their records of the species from Gujarat and Madhya Pradesh. We are grateful to Nilanjan Chatterjee, Dr. Anukul Nath and Dr. Sanath Krishnamuliya for guidance during spatial analysis. We acknowledge Mr. Rishikesh Tripathi, Mr. Mohit Payal and Sibasish Sahoo for their valuable inputs to the manuscript.

REFERENCES

Ardesana, R.N. (2018). Natural history notes on the Hardwicke's bloodsucker *Calotes minor* (Hardwicke & Gray, 1827) with preliminary report on the Agamidae of Gujarat, India. *Cobra* 12(1), 1-6.

Baillie, J.E.M., Collen, B., Amin, R., Akcakaya, R., Butchart, S.H.M., Brummitt, N., Meagher, T.R., Ram, M., Hilton-Taylor, C. & Mace, G.M. (2008). Toward monitoring global biodiversity. *Conservation Letters* 1(1), 18-26. DOI: 10.1111/j.1755-263X.2008.00009.x.

Baldwin, R.A. (2009). Use of maximum entropy modelling in wildlife research. *Entropy* 11, 854-866. DOI: 10.3390/e11040854.

Bland, L.M. & Böhm, M. (2016). Overcoming data deficiency in reptiles. *Biological Conservation* 204(A), 16-22.

Blyth, E. (1856). Proceedings of the Society. Report of the Curator. *Journal of Asiatic Society of Bengal* 25, 448-449.

Böhm, M., Collen, B., Baillie, J.E.M. et al. (2013). The conservation status of the world's reptiles. *Biological Conservation* 157, 372-385. DOI: 10.1016/j.biocon.2012.07.015.

Böhm, M., Williams, R., Bramhall, H., McMillan, K., Davidson, A., Garcia, A., Bland, L., Bielby, J. & Collen, B. (2016). Correlates of extinction risk in squamate reptiles: the relative importance of biology, geography, threat and range size. *Global Ecology and Biogeography* 25, 391-405. DOI: 10.1111/geb.12419.

Boria, R.A., Olson, L.E., Goodman, S.M. & Anderson, R.P. (2014). Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. *Ecological Modelling* 275, 73–77. DOI: 10.1016/j.ecolmodel.2013.12.012.

Boulenger, G.A. (1885). Catalogue of the Lizards in the British Museum (Natural History) I. Geckonidae, Eublepharidae, Uroplatidae, Pygopodidae, Agamidae. Trustees of British Museum, London, pp 450.

Boyce, M.S., Vernier, P.R., Nielsen, S.E. & Schmiegelow, F.K.A. (2002) Evaluating resource selection functions. *Ecological Modelling* 157, 281–300.

Chu, K., Liu, W., She, Y., Hua, Z., Tan, M., Liu, X., Gu, L. & Jia, Y. (2018). Modified principal component analysis for identifying key environmental indicators and application to a large-scale tidal flat reclamation. *Water* 10(1), 69. DOI: 10.3390/w10010069

Cockburn (1882). On the habits of little known lizard, *Brachysaura ornate*. *Journal of Asiatic Society of Bengal*, 50-54.

Das, I. (1994). The reptiles of South Asia: Checklist and distribution summary. *Hamadryad* 19, 15-40.

Das, I. (2003). Growth of knowledge on the reptiles of India, with an introduction to systematics, taxonomy and nomenclature. *Journal of Bombay Natural History Society* 100, 446 - 501.

Deepak, V., Vyas, R., Giri, V.B. & Karanth, P. (2015). A taxonomic mystery for more than 180 years: the identity and systematic position of *Brachysaura minor* (Hardwicke and Gray, 1827). *Vertebrate Zoology* 65(3), 371-381.

Elith, J., Graham, C.H., Anderson, R.P., Dudík, M., Ferrier, S., Guisan, A. et al. (2006). Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29,129-151. DOI: 10.1111/j.2006.0906-7590.04596.x.

Elith, J., Phillips, S.J., Hastie, T., Dudík, M., Chee, Y.E. & Yates, C.J. (2010). A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions* 17(1), 43-57. DOI: 10.1111/j.1472-4642.2010.00725.x.

Escalante, T., Rodríguez-Tapia, G., Linaje, M., Illoldi-Rangel, P. & González-López, R. (2013). Identification of areas of endemism from species distribution models: Threshold selection and Nearctic mammals. *TIP Revista Especializada en Ciencias Químico-Biológicas* 16(1), 5-17.

Fick, S.E. & Hijmans, R.J. (2017). Worldclim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* 37(12), 4302-4315. DOI: 10.1002/joc.5086

GEER (2014). Integrated Coastal Zone Management Project-Fifth Interim Progress Report for Capacity Building of GEER Foundation (Database of Marine Biodiversity and Coral Transplantation Experiment in Gulf of Kachchh). Published by Gujarat Ecological Education and Research (GEER) Foundation, Gandhinagar, pp 160.

Guisan, A. & Thuiller, W. (2005). Predicting species distribution: offering more than simple habitat models. *Ecology Letters* 8, 993-1009. DOI: 10.1111/j.1461-0248.2005.00792.x.

Günther, A.C.L. (1864). The Reptiles of British India. Published by Hardwicke, London. Pp 452+XXVII.

Hardwicke, F.R. & Gray, J.E. (1827). A synopsis of the species of Saurian reptiles, collected in India by Major-general Hardiwcke. *The Zoological Journal* 3, 213-229.

Hirzel, A.H. & Le Lay, G. (2008). Habitat suitability modelling and niche theory. *Journal of Applied Ecology* 45, 1372- 1381. DOI: 10.1111/j.1365-2664.2008.01524.x.

Hosseinian Yousefkhani, S.S., Rastegar-Pouyani, E. & Aliabadian, M. (2016). Ecological niche differentiation and taxonomic distinction between *Eremias staruchi strauchi* and *Eremias strauchi kopetdaghica* (Squamata: Lacertidae) on the Iranian plateau based on ecological niche modelling. *Italian Journal of Zoology* 83(3), 408-416. DOI: 10.1080/11250003.2016.1209581.

Ingle, M., Sarsavan, A. & Pawar, M. (2012). *Brachysaura minor* (Hardwicke & Gray, 1827) (Sauria: Agamidae: Agaminae) in Madhya Pradesh, Indien, mit Anmerkungen zu Morphologie, Verbreitung und Lebensweise. *Sauria* 34(4), 47-55.

IUCN. (2012). IUCN Red List Categories and Criteria: Version 3.1. Second edition. Gland, Switzerland and Cambridge, UK: IUCN. iv + 32pp.

IUCN Bangladesh (2015). Red List of Bangladesh Volume 4: Reptiles and Amphibians. IUCN, International Union for Conservation of Nature, Bangladesh Country Office, Dhaka, Bangladesh, pp. xvi+320.

Joppa, L.N., Butchart, S.H.M., Hoffmann, M., Bachman, S., Akçakaya, H.R., Moat, J., Böhm, M., Holland, R.A., Newton, A., Polidoro, B. & Hughes, A. (2016) Impact of alternative metrics on estimates of Extent of Occurrence for extinction risk assessments. *Conservation Biology* 30(2): 362-370.

Khan, M.S. (1999). Herpetology of habitat types of Pakistan. *Pakistan Journal of Zoology* 31(3), 275-189.

Khan, M.S. (2002). Key and checklist to the lizards of Pakistan. *Herpetozoa* 15(3/4), 99-119.

Khan, M.S. (2006). Amphibians and reptiles of Pakistan. Kreiger Publishing Company, Malabar, Florida, pp 311.

Khan, M.S. & Kumar, M. (2010). Notes on morphology, habits, ecology and distribution of Short-tailed ground agama; *Brachysaura minor* (Hardwicke and Gray 1827). *Pakistan Journal of Wildlife* 1(1), 31-35.

Khan, M.S. & Papenfuss, T. (2016). *Calotes minor.* The IUCN Red List of Threatened Species 2016: e.T170377A104646004. DOI: 10.2305/IUCN.UK.2016-3.RLTS.T170377A104646004.en.

Khatun, M.A., Rashid, M.B. & Hygen, H.O. (2016). Climate of Bangladesh: MET report. Published by Norwegian Meteorological Institute and Bangladesh Meteorological Department, pp 158.

Krishna Muliya, S., Nath, A., Kumar, G.C., Visvanathan, A., Selvan, M., Gowda, R., Santra, V. & Das, A. (2020). Addressing Wallacean shortfall using small sampling approach: a case study with endemic *Lycodon flavicollis* (Squatama: Colubridae) Mukherjee & Bhupathy, 2007. *Journal of Asia-Pacific Biodiversity*. DOI: 10.1016/j.japb.2020.12.005.

Manthey, U. & Schuster, N. (1999). Agamen, 2. Aufl. Natur und Tier Verlag (Münster), pp 120.

Moody, S.M. (1980). Phylogenetic and Historical Biogeographical Relationships of the genera in the family Agamidae (Reptilia: Lacertilia). Doctoral Dissertation, University of Michigan, Ann Arbor, pp 373.

Muratkar, G.D., Singh, R.P. & Misra, A.K. (2015). An approach to grassland management in rehabilitated areas of Satpura Tiger Resereve, Madhya Pradesh. Pp 145-151. In Rawat, G.S. and Adhikari, B.S. (Eds.) *Ecology and Management of Grassland Habitats in India*, ENVIS Bulletin: Wildlife & Protected Areas, Wildlife Institute of India, Vol 17.

Murthy, T.S.N. (2010). *The Reptile Fauna of India*. B.R. Publishing, New Delhi, pp 332.

Norris, D. (2014). Model thresholds are more important than presence location type: Understanding the distribution of lowland tapir (*Tapirus terrestris*) in a continuous Atlantic forest of southeast Brazil. *Tropical Conservation Science* 7(3), 529-547. DOI: 10.1177/194008291400700311.

Palaoro, A.V., Dalosto, M.M., Costa, G.C. & Santos, S. (2013). Niche conservatism and the potential for the crayfish *Procambarus clarkii* to invade South America. *Freshwater Biology* 58(7), 1379-1391. DOI: 10.1111/fwb.12134.

Patel, H. and Vyas, R. (2019). Reptiles of Gujarat, India: Updated checklist, distribution and conservation status. *Herpetology Notes* 12, 765-777.

Pearson, R.G., Raxworthy, C.J., Nakamura, M. & Peterson, A.T. (2007). Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *Journal of Biogeography* 34, 102-117. DOI: 10.1111/j.1365-2699.2006.01594.x.

Phillips, S.J., Anderson, R.P. & Schapire, R.E. (2006). Maximum entropy modelling of species geographic distributions. *Ecological modelling* 190, 231-259.

Riley, S.J., DeGloria, S.D. & Elliot, R. (1999). A terrain ruggedness index that quantifies topographic heterogeneity. *Intermountain Journal of Sciences* 5(1-4), 23-27.

Rödder, D., Schmidtlein, S., Veith, M. & Lötters, S. (2009). Alien invasive Slider turtle in unpredicted habitat: A matter of niche shift or of predictors studied. *PLoS ONE*, 4(11), e7843. DOI: 10.1371/journal.pone.0007843.

Singh, C.P., Chauhan, J.S., Parihar, J.S., Singh, R.P., Shukla, R. (2015). Using environmental niche modelling to find suitable habitats for the Hard-ground Barasingha in Madhya Pradesh, India. *Journal of Threatened Taxa* 7(11), 7761–7769. DOI: 10.11609/JoTT.o3899.7761-9.

Smith, M.A. (1935). The fauna of British India including Ceylon and Burma: Reptilia and Amphibia (Vol II Sauria). Published by Taylor and Francis, pp xiii + 440.

Stoliczka, F. (1872). Notes on the reptilian and amphibian fauna of Kutchh (Cutch). *Proceedings of Asiatic Society of Bengal*, 71-85.

Trabucco, A. & Zomer, R.J. (2009). Global Aridity Index (Global-Aridity) and Global Potential Evapo-transpiration (Global-PET) geospatial database. CGIAR consortium for spatial information. Link: http://www.csi.cgiar.org.

Udvardy, M.D.F. (1975). A classification of the biogeographical provinces of the world. IUCN Occasional paper number 18. Pp 48.

Uetz, P., Hallermann, J. & Jirí, H. (2020). The Reptile Database, http://www.reptile-database.org. Accessed on August 11, 2020.

Vyas, R. (2000). A review of reptile studies in Gujarat state. *Zoos' Print Journal* 15(12), 386- 390.

Vyas, R. (2002). Preliminary survey of Herpetofauna of Narayan Sarovar sanctuary, Gujarat. *Zoo Print* 17(6), 812-814.

Vyas, R. & Singh, H. (1998). Short tail agama in southeast Rajasthan. *Journal of Bombay Natural History Society* 95(2), 348-349.

Warren, D.L. & Seifert, S.N. (2010). Ecological niche modelling in Maxent: the importance of model complexity and the performance of model selection criteria. *Ecological Applications* 21(2), 335-342. DOI: 10.1890/10-1171.1.

Accepted: 10 March 2021

Please note that the Supplementary Materials are available via the Herpetological Journal website: https://thebhs.org/publications/the-herpetological-journal/volume-31-number3-july-2021