

Forest cover and level of protection influence the island-wide distribution of an apex carnivore and umbrella species, the Sri Lankan leopard (*Panthera pardus kotiya*)

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Abstract Apex predators fulfil potentially vital ecological roles. Typically wide-ranging and charismatic, they can also be useful surrogates for biodiversity preservation, making their targeted conservation imperative. The Sri Lankan leopard (*Panthera pardus kotiya*), an endangered, endemic sub-species, is the island's apex predator. Of potential keystone importance, this carnivore also fulfills “umbrella” and “flagship” criterion and is of high ecological and existence value. Apex predator conservation requires identifying factors underlying distribution, so we used multi-scale maximum entropy modelling with sampling bias correction to investigate a broad suite of relevant ecological, climatic and anthropogenic factors in order to identify potentially suitable leopard habitat. Presence locations were determined from 15 years of surveys, observations and verified reports. The best bias correction procedure and scale were uncertain, so we employed a novel method of using information from all models across analyses to determine top models and identify influential variables. Leopard presence was most strongly linked to the landscape proportion encompassed by Protected Areas strictly limiting human presence, with more porous Protected Areas less influential. All three forest composition and configuration metrics investigated (area weighted mean patch size, patch density and forest connectivity) were influential, with increased patch size and higher connectivity predicting better habitat suitability for leopards. Habitat suitability was also better where cropland extent and urban

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patch size were small. In summary, ground-level protection and natural forest extent and connectivity are of profound importance to Sri Lankan leopard distribution and are key factors in ensuring the ecological integrity of the island's faunal assemblages.

Keywords Biodiversity conservation · Habitat suitability · Maximum entropy · Sampling bias

Introduction

The disappearance of large, carnivorous mammals from the landscape is often the precursor of an unravelling ecosystem, with greater biodiversity loss likely to follow (Redford 2005). As such, targeting the conservation of these “surrogate” species is a potentially useful shortcut to minimize this impending loss (Sergio et al. 2006; Rodrigues and Brooks 2007; Caro 2010). For example, conserving wide-ranging terrestrial carnivores is theoretically linked to the default preservation of the wide array of species falling under their ecological “umbrella” (Estes 2005). This approach is not without controversy, with some selected surrogate species providing wider biodiversity preservation no more effective than that provided by randomly selected species (Andelman and Fagan 2000) and some resulting in reserve design ineffective at capturing localized rare species (Carroll et al. 2003). However in systems where biodiversity is not fully quantified and species assessments and distributional data are imperfect, it remains a valuable, cost-effective option with proven success (Caro 2003; Arponen 2012). Furthermore, apex predators—those few species whose abundance is not controlled by another predator (Steneck 2005)—typically represent a low proportion of community biomass but have profound systematic effects and are therefore likely to be “keystone” species (*sensu* Paine 1966; Power et al. 1996). Therefore, conserving an ecosystem's apex predator has the potential to both maintain that ecosystem's structure and function and reduce biodiversity loss (Ripple et al. 2014). Finally, apex carnivores are often large, charismatic species that can garner significant public interest and act as “flagships” for conservation, whereby support for their long-term preservation, more easily won than for less iconic species, can be utilized to benefit a broader range of biodiversity (Sergio et al. 2008).

Wild felids, particularly big cats, are apex carnivores in many systems across the globe, (Macdonald et al. 2010). Leopards (*Panthera pardus*) are the most adaptable of the “big cats” as defined as members of the *Panthera* genus, occurring across a range of habitats from dense tropical rainforest to arid semi-deserts (Macdonald et al. 2010), including areas in close proximity to human settlement (Athreya et al. 2013; Kuhn 2014). This adaptability is underlain by an exceptional diet breadth (Hayward et al. 2006) as leopards exploit varied prey types where necessary (Stander et al. 1997; Kittle et al. 2014; Shehzad et al. 2015). A detailed prioritization for felid conservation, which included the umbrella role of individual species, indicated that leopards are among the six highest priority felid species globally (Dickman et al. 2014).

Despite this adaptability, global leopard range, like that for most large carnivores, is rapidly diminishing due to habitat loss, landscape fragmentation and persecution (Ripple et al. 2014). With range extent now estimated at 25–37% of its historic size (Jacobsen et al. 2016), the leopard's status is now Vulnerable (Stein et al. 2016). Furthermore, of the nine recognized sub-species (Miththapala et al. 1996; Uphyrikina et al. 2001), six are threatened by isolation and habitat fragmentation including the Sri Lankan leopard (*Panthera pardus kotiya*) (Jacobsen et al. 2016). Eliminated from ~63% of its historical range (Jacobsen

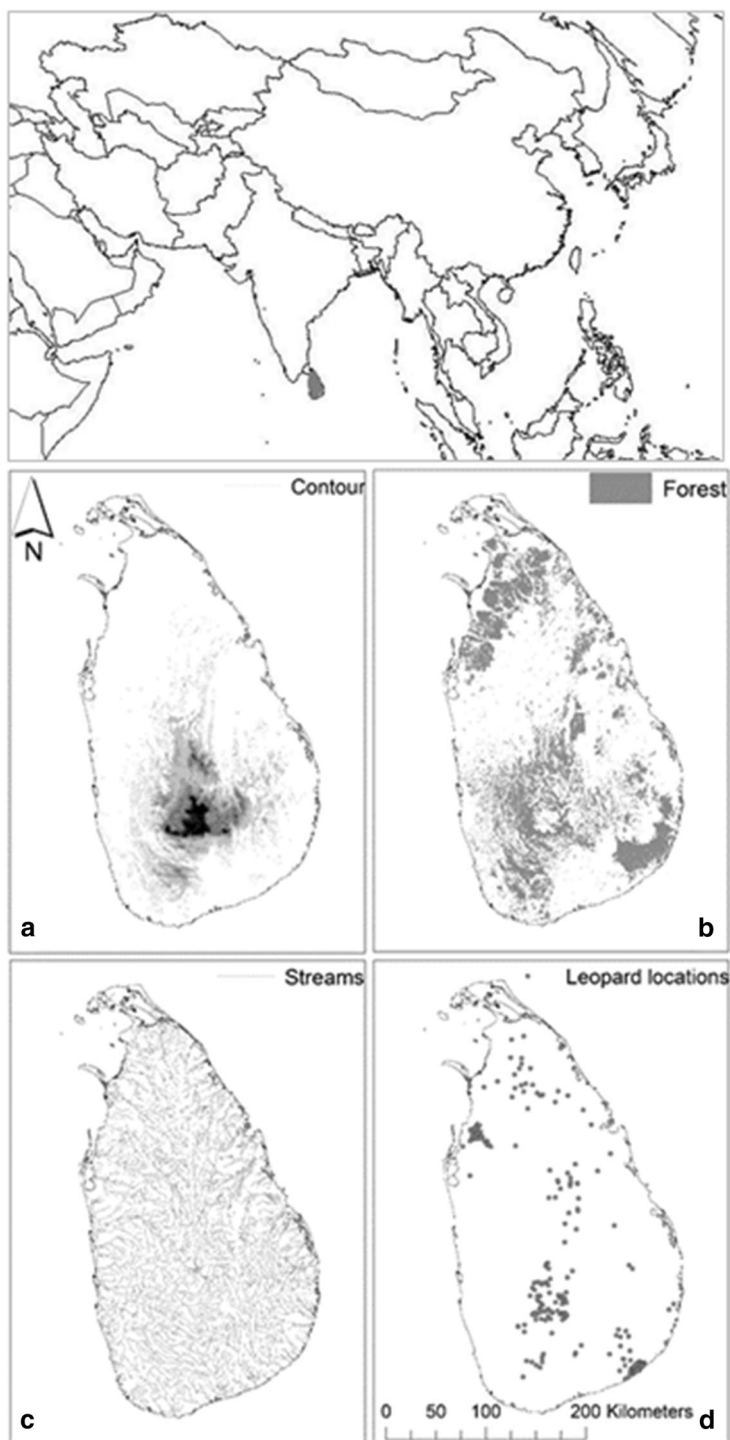
et al. 2016), and with an estimated population of 700–950 adult individuals, this sub-species is Endangered (Kittle and Watson 2008). The leopard has been Sri Lanka's apex predator since the island split from mainland India ~5000–10,000 ybp (Deraniyagala 1992; Yokoyama et al. 2000), with this extended period without dominant intra-guild competition unique amongst leopard populations (Guggisberg 1975; Miththapala et al. 1996; Turner 1997). A potential “keystone” species in Sri Lanka (Paine 1966), the leopard's local extirpation might allow for profound ecological effects to cascade across trophic levels, altering the composition and structure of the island's varied ecosystems (Terborgh et al. 2001; Ripple et al. 2014). Wide-ranging and extant across habitat types, the leopard is also a potentially useful “umbrella” species such that leopard-based policy planning may be a valuable way to ensure future protection for other, more spatially restricted wildlife (Caro 2003) such as the endemic and endangered shrew species *Crocidura miya*, *Solisorex pearsoni* and *Suncus zeylanicus*, all of which are found in pockets of the island's central highlands and lowland wet zone (de A Goonatilake et al. 2008a, b; de A Goonatilake and Molur 2008). Finally, the leopard is a large, charismatic species and strongly identified as a central component of Sri Lanka's proud natural history heritage (DWC 2014). As such leopard-focused conservation efforts have the potential to draw substantial public support, a factor that can benefit a broader array of threatened but less charismatic species such as the above-mentioned shrews, lizards (e.g. Tennents leaf-nosed lizard *Ceratophora tennentii*) and freshwater fish (e.g. Mountain labeo *Labeo fisheri*).

To ensure future persistence of the Sri Lankan leopard and the diverse array of species falling under its wide ecological “umbrella”, describing leopard distribution and characterizing the factors that underlie this distribution, are important (Elith and Leathwick 2009). We used 15 years of leopard presence data to investigate island-wide habitat suitability for the species and identify the environmental and anthropogenic factors that most influence observed distribution. We used multi-scale maximum entropy models to link presence locations to relevant independent variables, and employed two bias correction methods at four spatial scales to accommodate sampling bias. Multiple-scale optimization is critical to obtain reliable estimates of habitat associations (e.g., Thompson and McGarigal 2002; Shirk et al. 2014), and has recently been strenuously recommended for all habitat suitability modelling studies (McGarigal et al. 2016). A secondary goal was to understand whether the modeling stage at which bias correction methods were introduced affects model interpretation and inference.

Materials and methods

Study area

Sri Lanka is an island nation of 65,610 km² situated between 5°55'–9°50'N and 79°42'–81°53'E, which, together with India's Western Ghats, comprises one of the world's 25 global biodiversity hotspots (Brooks et al. 2002). Topography is dominated by a south-central highland massif (maximum elevation 2524 m) surrounded by a broad, flat peneplain (Fig. 1a). The climate is tropical monsoonal, characterized by two distinct wind regimes bringing rainfall to the island—the south-west (May–July) and north-east (October–January) monsoons—which ranges from <1000 mm/year in the south-eastern and north-western coastal regions to >5000 mm/year along the western slopes of the central highlands (de Silva 1997). Temperature follows the elevational gradient,



◀ **Fig. 1** Top panel shows location of Sri Lanka (shaded grey; 5°55′–9°50′N and 79°42′–81°53′E) within Asia. Below four maps of Sri Lanka show **a** elevation as a combination of contour lines (150 m) and a digital elevation model with 300 m gradations from light grey (300–600 m) to black (>2400 m), **b** forest cover (>15%) from the European Space Agency's Climate Change Initiative's Land Cover project 2014–2017 global land cover map (ESA CCI LC 2016), **c** streams, rivers, lake and reservoir boundaries derived from Sri Lanka Survey Department DSR250_shapefiles, and **d** presence only (PO) leopard locations from 15 years of observations

averaging >27.5 °C in the northern and eastern lowlands and <17.5 °C in the central highlands (de Silva 1997).

Remaining forest cover is lowland rainforest in the south-west with sub-montane rainforest along the southern portion of the central hills. Northern and eastern forests are monsoonal dry-zone evergreen with patches of scrub. Approximately 31.5% of the island is forested, of which ~8.1% is primary growth, ~10.4% plantations and the remainder (81.5%) secondary or regenerating (FAO 2015). Annual reduction is ~0.4% from 1990 to 2015 representing a cumulative 10% loss over this period (FAO 2015; Fig. 1b). Sri Lanka supports extensive plantation sectors with coconut (*Cocos nucifera*) in the lowlands (~442,000 ha), rubber (*Hevea brasiliensis*) in the narrow intermediate zone (~161,000 ha) and tea (*Camilla sinensis*) in the higher elevation slopes (~193,000 ha) accounting for ~12% of the island's land cover (Somasekaram 1997). Rice paddy cultivation is extensive (~732,000 ha) with smaller *Pinus* and *Eucalyptus* plantations in the central highlands (Somasekaram 1997). The island has 103 river basins, with most rivers originating in the central highlands (Fig. 1c; Perera 1997a).

Leopard presence data

We used 492 verified leopard presence locations from 2001 to 2016, determined from direct sightings, photographs/video, remote camera images, confirmed reports/newspaper articles, extensive sign surveys and supported by interviews with Department of Wildlife Conservation (DWC) personnel. Where locations were obtained from second-hand sources, all attempts were made to visit locations and determine as accurately as possible exact coordinates. Data were collected as part of ongoing research to map island-wide leopard distribution (Watson and Kittle 2004, 2008), and as such intensive efforts have been made to access all parts of the country, especially areas where little information previously existed. As such, the data represents an un-systematic but comprehensive set of locations, each marked with GPS coordinates. A 100 × 100 m² (1 hectare) grid was then imposed over the distribution map, and each quadrat with ≥1 leopard location was considered a single presence only (PO) location. This reduced the number of PO locations to 403 and was an initial step towards reducing potential sampling bias arising from multiple re-locations in frequently visited areas (Fig. 1d). Since 91.2% (n = 448) of original locations had exact coordinates identified, there should be minimal bias resulting from the imposition of this relatively fine-scale grid, especially given the scale optimization which follows.

Due to the extended time period of location records and the potential for land cover changes to have altered occupancy, we investigated whether these locations were still useful as presence indicators in 2016. Three hundred and eighty-three of these locations were from a total of 38 Protected Areas. These areas have maintained their essential ecological integrity and all were known to still be occupied by leopards in 2016 based on personal knowledge and discussions with on-site Department of Wildlife Conservation

field officers. Of the 109 locations outside of Protected Areas, 79.8% ($n = 87$) were from the post-war period (post-2009) and were considered recent enough to be relevant. Of the remaining 22 pre-2010, unprotected area locations, 18 were in areas where leopards were still present in 2016 based on their proximity to more recent verified locations, with the remaining four in areas where continued leopard presence was unknown. Since we had no information to indicate that leopards were no longer present in these locations, and they represented 0.8% of total locations and were therefore unlikely to unduly influence results, we elected to keep these records within the data set.

Initial variable selection

As leopards are remarkably adaptable we investigated a broad range of variables with potential to influence distribution (Table S1). Variables were divided into four categories: anthropogenic, environmental/topographical, landscape-level land cover composition/configuration and class-level land cover composition/configuration. Variables were kept at their original finest scale (range 30 m–1 km²) and using the same 1 ha (100 × 100 m²) grid as for the PO dataset, for each cell mean variable values were calculated at six different spatial scales using circular windows with radii 1, 2, 4, 8, 16 and 32 km. This spatial range encompasses the species' full complement of ecological responses to perceived environmental gradients, with the exception of very fine scale responses (Kittle et al. 2012). Leopard home range size varies by habitat and prey availability (Carbone and Gittleman 2002; Marker and Dickman 2005) and the spatial scales considered here cover the full global spectrum from 8 (Grassman 1999) to 451 km² (Stander et al. 1997).

Mean elevation was determined from World Climate Data layers (www.worldclim.org) in meters above sea level, originally derived from NASA's SRTM—Shuttle Radar Topography Mission—at an initial grain of 30 m (LP DAAC 2016). Mean annual temperature and rainfall was derived from World Climate Data's Bioclimatic variables, with original grain at 30 s arc (~1 km). Data was from tile 28 which covers the whole of Sri Lanka. Temperature was calculated as °C * 10 and rainfall in mm, so we divided each by 10 to get °C and cm. Human density (#/km²) was determined by combining a divisional secretariat-level administrative area shapefile from the Sri Lanka Survey Department (DSL250 2015) with divisional secretariat-level human population density values (Department of Census and Statistics 2012) and creating a raster of 1 ha cells. Primary/secondary/tertiary road densities (km/unit area) were determined from DSL250_Shp files, which are 1:250,000 digital data extracted from 4 map sections (DSL250 2015). Primary roads were major, paved roads, defined as “Main road A Grade” or “Expressway” in the original shape files. Secondary roads (“Minor road B Grade”) were also paved but smaller, whereas tertiary roads were unpaved and defined as “Jeep Tracks” in the original shape files. We converted road lengths from meters to km by dividing by 1000. Island-wide road lengths totaled 13,394 km (Primary = 3735 km, Secondary = 5320 km, Tertiary = 4339 km). Stream density (km/unit area) was also determined from DSL250_Shp files and similarly converted from m to km. Streams included all linear waterways as well as lake and reservoir boundaries. Total stream length island-wide was 23,258 km.

The landscape proportion classified as protected was determined using the World Database on Protected Areas (IUCN and UNEP-WCMC 2015). Landscape was categorized as un-protected, Level 1 Protected Area (PA) or Level 2 PA. Un-protected areas had no formal protection. Level 1 PAs, which includes all National Parks (18), Strict Natural Reserves (3) and the Sinharaja Man and Biosphere Reserve (1), are afforded the country's

highest level of protection, with human activity prohibited except via permit (e.g. tourism, research). Department of Wildlife Conservation (DWC) officers, and in Sinharaja, Forest Department (FD) officers, patrol Level 1 PA boundaries. Although well-patrolled, Sinharaja does allow surrounding villagers' limited access to procure forest products. Level 2 PAs include Sanctuaries (39), Forest Reserves (94), Reserved Forests (160), Conservation Forests (19) and other State forest/nature reserves (27). These largely un-patrolled PAs allow for limited human activity and are more frequently encroached and illegally exploited.

Land cover data were derived from the European Space Agency's Climate Change Initiative's Land Cover project 2014–2017 300 m resolution global land cover map (ESA CCI LC 2016). The original map was clipped using a Sri Lanka boundary shapefile (DSL250 2015) and the sixteen remaining land cover categories amalgamated to create eight new ones, six of which were considered potentially influential and used for the analysis (Table S2). We then used FRAGSTATS version 4.2.1 (McGarigal et al. 2012) to calculate several metrics quantifying landscape patterns at class (land cover proportion, area-weighted mean, cohesion, and patch density) and landscape (contagion, patch density, edge density, contrast-weighted edge density, aggregation index and shannon diversity index) levels (Table S1).

Data extraction for variable determination was conducted using ArcGIS 10.3.1 (ESRI 2015) and Geospatial Modelling Environment (Beyer 2012) platforms.

Bivariate scaling and final variable selection

Organisms respond to their surroundings at a variety of spatial scales (Johnson 1980; Wiens 1989; Boyce 2006; Kittle et al. 2008; McGarigal et al. 2016). To determine the scale at which independent variables were most strongly related to leopard distribution we used Maxent (Phillips et al. 2006), a maximum entropy algorithm using PO data, to predict relative habitat suitability based on each individual variable at each of the six spatial scales sampled (Elith et al. 2006). Selecting the appropriate scale for independent variables improves the ability of models to discriminate between areas of species occurrence and background areas (Vergara et al. 2016; Timm et al. 2016) with scale-dependent habitat-selection behaviour now widely supported in mammalian research (Wasserman et al. 2012; Mateo-Sánchez et al. 2013; Bellamy et al. 2013; Shirk et al. 2014; Rostro-Garcia et al. 2016). Maxent is the most widely used habitat suitability modelling software (HSM) for predicting species distributions using PO data (Fourcade et al. 2014), typically outperforming other methods based on predictive accuracy (Merow et al. 2013). It uses known focal species locations and randomly selected background points to estimate a focal distribution, maximizing entropy but subject to constraints imposed by the presence locations, and employs a penalized maximum likelihood function, the gain function, to most accurately differentiate presences from background locations (Merow et al. 2013). We used 10,000 background data points from across Sri Lanka so as to adequately reflect the possible environmental conditions against which the presence locations were contrasted (Saupe et al. 2012). We used a maximum of 500 iterations, a convergence threshold of 0.00001 and the default regularization setting, which is based on tested performance across a range of taxonomic groups (Phillips and Dudik 2008). A key element of tuning this setting is to produce simpler models given that the default regularization setting typically retains many potentially correlated features (Merow et al. 2013); however in this analysis we were not concerned with model variable reduction as we were testing models with the same number of input variables, so elected to utilize the default. We used only linear and

quadratic features, as they represent more straightforward ecological associations and are more easily interpreted (Syfert et al. 2013; Vergara et al. 2016). We withheld a randomly selected 25% of the data for testing, with the remaining 75% used for model training (Elith et al. 2006; Mateo Sánchez et al. 2013; Vergara et al. 2016). Output was logistic. We used the Area Under the receiver operating characteristic Curve (AUC; Fielding and Bell 1997) to compare univariate model performance, selecting the spatial scale with the highest AUCtest value for each variable (Wasserman et al. 2012; Mateo Sánchez et al. 2013; Vergara et al. 2016). Although Maxent accommodates correlated variables more effectively than other algorithms (Elith et al. 2011), we discarded highly inter-correlated explanatory variables using a Pearson correlation matrix incorporating all variables at their selected spatial scale and pruning variables with the lowest AUCtest from each variable pair with correlation coefficients ≥ 0.7 (Dorman et al. 2013). This resulted in a final set of 31 independent variables (Table 1).

A limitation of Maxent is that it does not include a measure of detection probability (Elith et al. 2011). It is likely that detection probability varies across our study area, however there is no way to know which variables influence the probability of detection across the region and in what manner they influence this probability. In addition, given that multiple methods were used to determine leopard locations (i.e. opportunistic observations, dedicated sign surveys, remote camera captures) assigning definitive detection probabilities is not possible. As such, it is important to emphasize that model outputs here represent a predicted index of habitat suitability and not a prediction of probability of occurrence.

Multivariate modelling

We developed 200 HSMs, each containing a different set of five randomly selected variables from the final optimized-scale variable set (Table 1). Models were restricted to five variables to allow valid comparisons between them and avoid overfitting (Mateo Sánchez et al. 2013; Vergara et al. 2016). Multivariate models were run in Maxent using the same structural parameters as for the univariate models, and were ranked based on AUCtest values.

Sampling bias correction

A problem with PO data that relies heavily on opportunistic observations is the potential for sampling bias given unequal sampling of the landscape under scrutiny (Phillips et al. 2009). Failure to accommodate sampling bias in the modelling procedure can lead to spurious results, for example when ignoring potentially viable areas of the landscape or oversampling sub-optimal habitat due to ease of access (e.g., Vergara et al. 2016). Recommendations based on biased results can lead to misdirected management action (Fourcade et al. 2014).

To address potential sampling bias we implemented two established bias correction methods—spatial rarefaction of species occurrence records (SR) and the development of sampling probability maps using Gaussian kernel methods (GK) (Fourcade et al. 2014; Vergara et al. 2016)—using the SDM toolbox v.1.1 (Brown 2014) in ArcMap (ESRI 2015). Bias correction methods were each applied at four spatial scales (1, 2, 4 and 8 km radii). To implement SR we used the *spatially rarefy occurrence data* tool, which reduces clustered leopard presence locations to a single point within a specified Euclidian distance. Datasets of filtered locations were then used as leopard presence records at each scale. We then re-ran the original 200 multivariate models at each spatial scale using the spatially

Table 1 Final list of independent variables (N = 31) indicating the most appropriate spatial scale determined from univariate Maxent models

Variable type	Factor	Abbreviation and scale	Description
Environmental/topographical	Stream density	strm_16 km	Total length of streams, rivers, lake and reservoir edges (km)
	Mean altitude	alt_1 km	Average altitude above sea level (m)
	Mean rainfall	rain_1 km	Average annual rainfall (cm)
Anthropogenic	Primary road density	Rd_P_32 km	Total length of primary (major, tarred) roads (km)
	Secondary road density	Rd_s_8 km	Total length of secondary (minor, tarred) roads (km)
	Tertiary road density	Rd_t_16 km	Total length of tertiary (untarred) roads (km)
Class-level land cover composition	Proportion PA Level 1	PA1_32 km	Proportion of landscape under Level 1 ^a Protection
	Proportion PA Level 2	PA2_32 km	Proportion of landscape under Level 2 ^b Protection
	Area weighted mean	AREA_AM_For_32 km	Area weighted mean size of forest patches (≥ 0)
		AREA_AM_Moscrop_32 km	Area weighted mean size of mosaic patches with cropland > forest (≥ 0)
		AREA_AM_Mosfor_16 km	Area weighted mean size of mosaic patches with forest > cropland (≥ 0)
		AREA_AM_Shrib_4 km	Area weighted mean size of shrubland patches (≥ 0)
		AREA_AM_Urban_32 km	Area weighted mean size of urban patches (≥ 0)
	Patch density	PD_Crop_16 km	Number of patches of cropland (#/100 ha)
		PD_For_16 km	Number of patches of forest (#/100 ha)
		PD_Moscrop_8 km	Number of mosaic patches consisting of cropland > forest (#/100 ha) (#/100 ha)
		PD_Mosfor_8 km	Number of mosaic patches consisting of forest > cropland (#/100 ha)
		PD_Shrib_32 km	Number of patches of shrub land (#/100 ha)
		PD_Urban_16 km	Number of urban patches (#/100 ha)
	Land cover proportion	PLAND_Crop_32 km	Proportion of landscape composed of cropland (%)
		PLAND_Shrib_32 km	Proportion of landscape composed of shrubland (%)
		PLAND_Urban_4 km	Proportion of landscape composed of urbanland (%)

Table 1 continued

Variable type	Factor	Abbreviation and scale	Description
Class-level land cover configuration	Cohesion	COH_For_32 km	Connectivity of forest patches (0–100)
		COH_Moscrop_16 km	Connectivity of mosaic patches consisting of cropland > forest (0–100)
		COH_Mosfor_32 km	Connectivity of mosaic patches consisting of forest > cropland (0–100)
		COH_Shruh_2 km	Connectivity of shrub land patches (0–100)
		COH_Urban_32 km	Connectivity of urban patches (0–100)
Landscape-level land cover composition	Shannon Diversity Index	SHDI_8 km	Diversity of patch types within the landscape (≥ 0)
Landscape-level land cover configuration	Aggregation Index	AI_32 km	Ratio of adjacent patches of the same type to all available adjacent patches (%)
	Contagion	CONT_32 km	Landscape clumpiness based on similarity of adjacent patch types (%)
	Patch Density	PD_32 km	Number of patches (all classes) per unit area (#/100 ha)

^a National Parks, Strict Natural Reserves, Sinharaja Rainforest Reserve

^b Forest Reserves, Reserved Forest, Other State Forest, Sanctuary, Nature Reserve, Jungle Corridor and/or Conservation Forest

rarefied locations, resulting in 800 new models. To implement GK we created bias grids using the *Gaussian Kernel Density of sampling localities* tool, which weights PO data points according to the number of neighbours in the geographic landscape (Vergara et al. 2016). Bias grids at each scale were implemented in Maxent using the bias file option and the same suite of 200 multivariate models again run, resulting in 800 additional models. We re-ran the entire suite of HSMs for each bias correction method at each scale instead of a sub-set based on the independent variables in the best raw HSMs (sensu Vergara et al. 2016) to ensure that any variables determined influential in the absence of bias correction but not influential when bias correction methods were employed from the beginning, were not mistakenly included. For each bias correction method, models were ranked at each spatial scale according to AUCtest values as previously.

Determining best models and variable influence

To evaluate which procedure resulted in the best models we investigated the top 10 models for each of our nine analyses (one uncorrected, four SR and four GK) using two threshold-independent metrics—AUCtest and AUCdiff (Vergara et al. 2016). AUCtest is a measure of general model fit appropriate for comparison of models created with different settings representing the same species and study area (Anderson and Gonzalez 2011). AUCdiff measures the difference between AUCtrain and AUCtest values and is used to quantify overfitting, with the lowest value indicative of the best fit (Warren and Seifert 2011). Theoretically, the analysis method and spatial scale with the highest AUCtest values and lowest AUCdiff values is considered the most appropriate for the data and results from that analysis used for inference.

In the event that no single method and/or spatial scale was clearly superior we elected to investigate the relative influence of individual independent variables by employing three methods in a manner theoretically aligned to Burnham and Anderson's (2002) model averaging, whereby we used information from all models from all analyses at all scales to detect the most influential variables. This is considered less biased than utilizing only the information from the best models (Burnham and Anderson 2002). First, we calculated the proportion of top 10 models for each analysis ($n = 9$) in which each variable was included. This provides a crude measure of variable importance. However, because variables were randomly selected for inclusion in the model suite, each was represented in a different number of total models ($n = 29\text{--}41$) out of the 200. To standardize variable comparison we divided the proportion of top models ($n = 90$) in which each variable was represented (e.g. if variable X was in 2 of the 10 top models for each analysis, the proportion was $(2 \times 9) = 18/90 = 0.2$) by the proportion of all models ($n = 1800$) in which each variable was represented (e.g. if variable X was in 32 of the 200 multivariate models, the proportion was $(32 \times 9) = 288/1800 = 0.16$) to get a ratio (e.g. $0.2/0.16 = 1.25$). A ratio > 1 indicates that a given variable is represented in top models more than would be expected based only on its proportional representation within the full model set (i.e. chance). The variable showing the highest ratio was considered most influential in that it showed the highest representation in the top model sets relative to its total representation within model suites. Third, we calculated the average AUCtest values for each variable across all 200 models for each analysis. The rationale here was that any variable with strong influence would elevate the AUCtest value of any model it was in, regardless of the effect of other variables, especially since we employed random model building in which each variable would theoretically be included in models with other independent variables that were equally proportioned between strong and weak. The nine resulting average values were

themselves averaged to determine an overall AUCtest value for each variable across all analyses, allowing us to utilize the results from all 1800 individual multivariate models to understand the influence of independent variables. Finally, we used response curves to analyze the direction and strength of relationship between the most influential independent variables and leopard habitat suitability (Vergara et al. 2016).

Results

Bivariate scaling

Leopard occurrence was sensitive to the scale of analysis (Table 1). Temperature was related to leopard occurrence at a broad scale but both rainfall and elevation influenced leopard distribution at a much finer scale (1 km). Anthropogenic variables were related to leopard distribution at broad scales (16–32 km) except secondary road density, which was most influential at an intermediate scale (8 km). Similarly, all of the landscape-level habitat composition and configuration variables were most influential at the broadest scale (32 km) except the Shannon Diversity Index (8 km). Class-level habitat composition and configuration variables were also most influential at broad scales (16–32 km). Exceptions were area weighted mean patch size and cohesion of shrub land, both linked to leopard distribution at considerably finer scales (4 and 2 km respectively). The proportion of the landscape composed of a single land cover class influenced leopard occurrence at the broadest scale for all classes except urban which was most strongly associated with leopard occurrence at an intermediate scale (4 km). Patch densities of the forest-crop and crop-forest mosaics were also most influential at intermediate scales. Overall, leopard distribution reflected broad-scale (16–32 km) responses for 77.5% of potential variables ($n = 40$).

Uncorrected multivariate models

The 200 HSMs exhibited good overall model performance with AUCtest values ranging from 0.739 to 0.932. The top ranked model, in order of variable contribution, was PA1_32 km > alt_1 km > PD_For_16 km > AREA_AM_Urban_32 km > CONT_32 km (Table 2). Overall, 9 of the top 10 models included PA1_32 km, the only variable occurring in >3 top models (Tables 2, 3). PA1_32 km, which positively affected leopard habitat suitability, was also the most influential variable based on average AUCtest (0.904) across all models (Table 4). The three forest composition and configuration variables were in the top 8 using this metric (AREA_AM_For_32 km = 0.871, #4; COH_For_32 km = 0.869, #6; PD_For_16 km = 0.866, #8; Table 4), and all exerted a positive influence on habitat suitability. Primary road density (Rd_P_32 km; 0.874) which negatively impacted leopard habitat suitability and tertiary road density (Rd_t_16 km; 0.869), which exerted a positive effect, were ranked #2 and #7 respectively (Table 4). The crop measures PLAND_Crop_32 km (0.871) and PD_Crop_16 km (0.864) were ranked #3 and #9 respectively and PD_Shruh_32 km (0.871) ranked #5 (Table 4). Both crop measures negatively impacted leopard habitat suitability, which was improved at intermediate shrub patch density. The top ranked landscape-level land cover variable was AI_32 km (0.862), ranked #11, whereas the top ranked environmental/topographical variable was strm_16 km

Table 2 The top ten models from the uncorrected analysis (without spatial bias correction) with variables listed in order of model contribution

Model ID	Variables (In order of contribution)	Uncorrected	Spatial Rarefaction (SR)				Gaussian Kernel (GK)			
		1 km	2 km	4 km	8 km	1 km	2 km	4 km	8 km	
20	PA1_32 km > alt_1 km > PD_For_16 km > AREA_AM_Urban_32 km > CONT_32 km	0.932 (1)	0.892 (2)	0.889 (1)	0.873 (1)	0.860 (16)	0.923 (1)	0.912 (2)	0.885 (3)	0.837 (2)
51	PA1_32 km > PLAND_Shrub_32 km > AREA_AM_Moscrop_32 km > PD_Shrub_32 km > COH_Mosfor_32 km	0.927 (2)	0.884 (5)	0.836 (11)	0.836 (26)	0.881 (2)	0.903 (15)	0.894 (12)	0.845 (25)	0.741 (30)
160	PA1_32 km > PD_For_16 km > PLAND_Crop_32 km > PD_Moscrop_8 km > Rd_P_32 km	0.923 (3)	0.848 (45)	0.859 (3)	0.830 (39)	0.864 (14)	0.913 (5)	0.897 (9)	0.825 (48)	0.710 (60)
162	PA1_32 km > AREA_AM_Moscrop_32 km > PLAND_Crop_32 km > Crop_32 km > > Rd_t_16 km > AREA_AM_Mosfor_16 km	0.923 (3)	0.876 (9)	0.849 (6)	0.829 (43)	0.847 (25)	0.910 (8)	0.897 (9)	0.849 (20)	0.767 (14)
52	PA1_32 km > PD_Urban_16 km > COH_For_32 km > AL_32 km > COH_Mosfor_32 km	0.921 (5)	0.86 (27)	0.824 (27)	0.802 (94)	0.816 (63)	0.923 (1)	0.915 (1)	0.890 (2)	0.729 (41)
79	PA1_32 km > PD_32 km > Rd_t_16 km > PD_Shrub_32 km > COH_Mosfor_32 km	0.918 (6)	0.884 (5)	0.836 (11)	0.844 (20)	0.866 (12)	0.897 (26)	0.882 (32)	0.826 (47)	0.732 (39)
116	Rd_P_32 km > AREA_AM_For_32 km > PD_Urban_16 km > alt_1 km > strm_16 km	0.914 (7)	0.893 (1)	0.831 (19)	0.868 (2)	0.815 (64)	0.907 (11)	0.893 (13)	0.844 (26)	0.739 (33)
3	PA1_32 km > PD_Crop_16 km > Rd_t_16 km > PD_Shrub_32 km > CONT_32 km	0.913 (8)	0.867 (18)	0.823 (29)	0.833 (32)	0.857 (18)	0.910 (8)	0.901 (6)	0.853 (14)	0.758 (19)
87	PA1_32 km > PD_Crop_16 km > COH_For_32 km > PD_Mosfor_8 km > CONT_32 km	0.913 (8)	0.854 (37)	0.815 (38)	0.818 (61)	0.853 (20)	0.915 (4)	0.911 (3)	0.880 (4)	0.749 (24)
104	PA1_32 km > PD_Crop_16 km > PLAND_Shrub_32 km > Rd_P_32 km > COH_Moscrop_16 km	0.912 (9)	0.869 (16)	0.831 (19)	0.823 (52)	0.877 (4)	0.903 (15)	0.891 (17)	0.818 (55)	0.690 (79)

The AUCtest score of each model as well as the rank (out of 200 models) for each of the nine analyses are also shown

Table 3 Ranking of all independent variables (N = 31) based on the total number of Top 10 models in each analysis (1 ha = uncorrected) in which the relevant variable is included (Total rank) as well as the proportion of Top 10 models in which the relevant variable is represented divided by the proportion of all models in which the relevant variable is found (Proportional rank)

Variable	# Times in top 10										Proportion					
	Spatial rarefaction (SR)					Gaussian kernel (GK)					Total	# models				
	UC	1 km	2 km	4 km	8 km	1 km	2 km	4 km	8 km	Total	Rank	(N = 200)	All	Top 10	Ratio	Proportional
													Models	Models	Top 10/all	Rank
PA1_32 km	9	6	8	2	5	10	10	9	2	61	1	30	0.150	0.678	4.519	1
PD_For_16 km	2	1	5	4	5	3	2	1	2	25	3	30	0.150	0.278	1.852	2
PD_Shrub_32 km	3	4	0	2	4	1	2	1	5	22	6	30	0.150	0.244	1.630	3
PLAND_Crop_32 km	2	5	7	0	2	5	2	2	1	26	2	38	0.190	0.289	1.520	4
AREA_AM_For_32 km	1	2	1	8	4	1	1	0	7	25	3	40	0.200	0.278	1.389	5
CONT_32 km	3	2	2	2	0	3	5	4	4	25	3	40	0.200	0.278	1.389	5
Rd_P_32 km	3	3	3	3	3	2	1	0	0	18	7	32	0.160	0.200	1.250	7
PLAND_Shrub_32 km	2	2	1	2	5	1	1	2	0	16	9	30	0.150	0.178	1.185	8
AI_32 km	1	2	2	2	1	3	2	2	2	17	8	32	0.160	0.189	1.181	9
AREA_AM_Urban_32 km	1	1	1	2	1	1	2	4	2	15	11	29	0.145	0.167	1.149	10
alt_1 km	2	3	1	5	0	1	1	1	2	16	9	31	0.155	0.178	1.147	11
PD_Crop_16 km	3	0	0	2	4	2	2	1	1	15	11	30	0.150	0.167	1.111	12
AREA_AM_Mosfor_16 km	1	3	2	2	0	1	2	1	1	13	13	30	0.150	0.144	0.963	13
Rd_t_16 km	3	2	1	1	1	2	2	0	1	13	13	30	0.150	0.144	0.963	13
COH_Moscrop_16 km	1	0	0	1	3	0	2	3	2	12	17	29	0.145	0.133	0.920	15
AREA_AM_Moscrop_32 km	2	2	4	0	1	1	1	0	1	12	17	30	0.150	0.133	0.889	16
PD_Urban_16 km	2	1	1	2	0	1	1	2	2	12	17	30	0.150	0.133	0.889	16
PA2_32 km	0	1	4	1	3	3	1	0	0	13	13	33	0.165	0.144	0.875	18
strm_16 km	1	2	2	3	2	1	1	0	0	12	17	33	0.165	0.133	0.808	19
COH_For_32 km	2	0	1	1	1	2	2	3	1	13	13	36	0.180	0.144	0.802	20
PD_32 km	1	2	1	1	3	0	0	0	2	10	22	31	0.155	0.111	0.717	21

Table 3 continued

Variable	# Times in top 10										Proportion																
	Spatial rarefication (SR)										Gaussian kernel (GK)					Total		# models		All		Top 10		Ratio		Proportional	
	UC	1 km	2 km	4 km	8 km	1 km	2 km	4 km	8 km	Total	Rank	(N = 200)	Models	Top 10/all	Rank	Rank											
COH_Mosfor_32 km	3	2	0	1	2	1	1	1	0	11	21	41	0.205	0.122	0.596	22											
COH_Shrub_2 km	0	1	0	0	0	1	1	3	4	10	22	39	0.195	0.111	0.570	23											
PLAND_Urban_4 km	0	1	1	0	1	0	1	3	1	8	24	32	0.160	0.089	0.556	24											
PPD_Mosfor_8 km	1	0	0	1	0	1	1	1	2	7	25	31	0.155	0.078	0.502	25											
AREA_AM_Shrub_4 km	0	1	1	0	0	1	0	1	2	6	26	30	0.150	0.067	0.444	26											
PPD_Moscrop_8 km	1	0	1	1	0	1	1	0	1	6	26	30	0.150	0.067	0.444	26											
SHDI_8 km	0	1	0	2	0	0	0	1	2	6	26	31	0.155	0.067	0.430	28											
COH_Urban_32 km	0	0	1	0	1	1	1	2	0	6	26	32	0.160	0.067	0.417	29											
Rd_s_8 km	0	0	0	0	0	0	1	1	0	2	30	30	0.150	0.022	0.148	30											
rain_1 km	0	0	1	0	0	0	0	0	0	1	31	30	0.150	0.011	0.074	31											

Table 4 Ranking of all independent variables ($N = 31$) for each analysis (UC uncorrected) based on the average area under the curve score for the test set (AUCtest) from all models in which the relevant variable is found

Variable	UC	Rank	Spatial Rarefaction (SR)						Gaussian Kernel (GK)						Overall				
			1 km		2 km		4 km		8 km		1 km		2 km				4 km		8 km
			Rank	Value	Rank	Value	Rank	Value	Rank	Value	Rank	Value	Rank	Value	Rank	Value	Rank	Value	Rank
PA1_32 km	0.904	1	0.856	1	0.825	1	0.807	6	0.836	1	0.903	1	0.892	1	0.841	1	0.722	1	1
AREA_AM_For_32 km	0.871	4	0.846	2	0.800	3	0.830	1	0.820	3	0.872	4	0.852	6	0.802	2	0.719	2	2
COH_For_32 km	0.869	6	0.834	3	0.793	4	0.811	4	0.810	6	0.868	5	0.857	4	0.796	4	0.676	5	3
PD_Shrub_32 km	0.871	5	0.833	4	0.772	16	0.805	7	0.804	7	0.867	6	0.854	5	0.800	3	0.682	4	4
PD_For_16 km	0.866	8	0.796	27	0.803	2	0.819	2	0.822	2	0.863	9	0.847	10	0.786	10	0.673	7	5
AI_32 km	0.862	11	0.825	7	0.779	12	0.800	9	0.787	11	0.865	7	0.850	8	0.791	9	0.670	8	6
PD_32 km	0.861	12	0.831	6	0.788	6	0.819	3	0.817	4	0.856	15	0.839	16	0.781	14	0.676	6	6
PD_Crop_16 km	0.864	9	0.820	11	0.774	15	0.803	8	0.815	5	0.864	8	0.850	7	0.786	11	0.666	9	8
PLAND_Crop_32 km	0.871	3	0.832	5	0.792	5	0.793	11	0.799	8	0.862	10	0.846	13	0.778	16	0.656	12	8
Rd_t_16 km	0.869	7	0.816	12	0.782	11	0.791	12	0.769	16	0.873	2	0.860	2	0.792	8	0.643	16	10
Rd_P_32 km	0.874	2	0.824	9	0.782	10	0.774	21	0.768	17	0.872	3	0.857	3	0.774	17	0.577	29	11
alt_1 km	0.854	20	0.824	8	0.787	7	0.810	5	0.764	20	0.846	23	0.836	20	0.792	7	0.695	3	12
CONT_32 km	0.856	17	0.814	14	0.776	13	0.797	10	0.797	9	0.856	16	0.844	14	0.781	13	0.659	10	13
AREA_AM_Urban_32 km	0.858	14	0.812	15	0.770	18	0.775	19	0.763	21	0.858	12	0.849	9	0.795	5	0.652	13	14
AREA_AM_Moscrop_32 km	0.860	13	0.810	17	0.786	8	0.771	24	0.774	14	0.859	11	0.847	12	0.770	20	0.628	20	15
COH_Moscrop_16 km	0.855	19	0.811	16	0.767	21	0.787	15	0.789	10	0.854	17	0.842	15	0.782	12	0.651	14	15
PLAND_Shrub_32 km	0.855	18	0.810	18	0.784	9	0.791	13	0.786	12	0.847	21	0.832	22	0.763	24	0.657	11	17
AREA_AM_Mosfor_16 km	0.856	16	0.816	13	0.775	14	0.788	14	0.781	13	0.849	19	0.833	21	0.755	27	0.623	22	18
PD_Urban_16 km	0.857	15	0.800	24	0.749	28	0.774	20	0.752	26	0.857	13	0.847	11	0.793	6	0.636	19	19
strm_16 km	0.863	10	0.821	10	0.768	20	0.773	22	0.767	19	0.856	14	0.839	17	0.742	30	0.573	30	20
SHDI_8 km	0.851	21	0.807	19	0.764	22	0.786	16	0.739	30	0.848	20	0.838	18	0.781	15	0.641	17	21
AREA_AM_Shrub_4 km	0.850	23	0.806	20	0.769	19	0.778	18	0.758	24	0.845	24	0.830	26	0.766	22	0.640	18	22

Table 4 continued

Variable	UC	Rank	Spatial Rarefication (SR)						Gaussian Kernel (GK)						Overall				
			1 km		2 km		4 km		8 km		1 km		2 km				4 km		8 km
			Rank	Rank	Rank	Rank	Rank	Rank	Rank	Rank	Rank	Rank	Rank	Rank	Rank	Rank	Rank	Rank	Rank
PA2_32 km	0.848	26	0.803	22	0.771	17	0.779	17	0.773	15	0.854	18	0.831	23	0.736	31	0.589	27	23
COH_Urban_32 km	0.847	27	0.800	25	0.744	30	0.762	28	0.756	25	0.847	22	0.837	19	0.772	19	0.603	23	24
PLAND_Urban_4 km	0.841	29	0.805	21	0.762	23	0.772	23	0.767	18	0.837	29	0.824	30	0.759	26	0.623	21	25
COH_Mosfor_32 km	0.849	25	0.796	28	0.752	25	0.771	25	0.759	23	0.841	26	0.831	25	0.765	23	0.601	25	26
COH_Shruh_2 km	0.840	30	0.795	29	0.750	27	0.759	29	0.760	22	0.837	28	0.828	28	0.772	18	0.645	15	27
Rd_s_8 km	0.850	24	0.801	23	0.751	26	0.763	27	0.745	28	0.840	27	0.829	27	0.759	25	0.588	28	28
PD_Moscrop_8 km	0.841	28	0.798	26	0.754	24	0.768	26	0.749	27	0.834	31	0.822	31	0.751	28	0.603	24	29
rain_1 km	0.850	22	0.789	30	0.747	29	0.752	31	0.741	29	0.843	25	0.831	24	0.749	29	0.561	31	30
PD_Mosfor_8 km	0.837	31	0.775	31	0.730	31	0.755	30	0.731	31	0.835	30	0.825	29	0.768	21	0.591	26	31

The Overall Rank is based on the combined ranks of each variable across all analyses (N = 9)

Table 5 Summary table showing the analysis (SR Spatial rarefaction, GK Guassian kernel), the number of presence only (PO) locations, the average area under the curve score for the test subset (AUCtest), and the average difference between the area under the curve score for the test set and the training set (AUCdiff)

Analysis	PO locations	Avg. AUCtest	Avg. AUCdiff
Uncorrected	403	0.920	0.026
1 km_SR	254	0.883	0.026
2 km_SR	214	0.855	0.009
4 km_SR	162	0.859	0.034
8 km_SR	116	0.876	0.059
1 km_GK	403	0.914	0.022
2 km_GK	403	0.904	0.026
4 km_GK	403	0.874	0.025
8 km_GK	403	0.814	0.013

(0.863) ranked #10 (Table 4). No AREA_AM or COH variables, except those of the forest class, were ranked among the top 15 variables (Table 4).

Bias corrected models and variable importance

Based on AUCtest and AUCdiff scores from the top 10 models from all analyses, it was unclear which bias correction method (SR or GK) or spatial scale (1, 2, 4 or 8 km radii) was most appropriate for this data set (Table 5). The highest average AUCtest score was for the uncorrected analysis (0.920) closely followed by 1km_GK (0.914). The best (lowest) AUCdiff score was for 2 km_SR (0.009) followed by 8km_GK (0.013) which also had the lowest average AUCtest score (0.814). The worst (highest) AUCdiff score was for 8km_SR (0.059). Due to these uncertainties, we elected to utilize the information contained in all models from all analyses (as detailed above in the methods) to further investigate the factors influencing leopard habitat suitability.

Based on variable representation within top 10 models across analyses, PA1_32km was clearly most influential, included in 67.8% of top models ($n = 90$) despite inclusion in only 15% of total models (Table 3). In total, 12 variables (38.7%) were overrepresented in top models relative to their representation across all models, with PD_For_16 km, PD_Shruh_32 km and PLAND_Crop_32 km all in top models with a frequency at least 50% greater than expected by chance alone (Table 3). AREA_AM_For_32 km and CONT_32 km were also considerably overrepresented (Table 3). In analyses where PA1_32 km was in only 2 of the top 10 models (4 km_SR and 8 km_GK), AREA_AM_For_32 km was the most consistently influential variable, represented in 8 and 7 of the top 10 models respectively.

Based on average AUCtest values, PA1_32 km was again the most influential variable, top ranked in 8/9 analyses (Table 4) with AREA_AM_For_32 km top ranked once (4 km_SR) and the 2nd ranked variable overall. The other two forest metrics (COH_For_32 km and PD_For_16 km) were also amongst the top 5 variables, together with PD_Shruh_32 km (Table 4).

Four explanatory variables appeared in the top 5 under both variable importance metrics (PA1_32 km, AREA_AM_For_32 km, PD_For_16 km and PD_Shruh_32 km),

influencing leopard habitat suitability in various ways. Habitat suitability for leopards increased with increasing Level 1 protection of the landscape as well as increasing forest patch size (as weighted by area), although this latter variable showed a humped response, particularly at smaller scales (Fig. S1 A, B). Conversely, leopard habitat suitability was highest at intermediate patch densities of both forest and scrub, with the former typically maximized with ~ 0.06 patches/100 ha and the latter ~ 0.08 patches/100 ha (Fig. S1 C, D). For other top 5 variables, farmland (PLAND_Crop_32 km) offered low habitat suitability to leopards as did areas with low connectivity between forest patches (COH_For_32 km; Fig. S1 E, F).

Top overall model

The top model from the uncorrected analysis (PA1_32 km, alt_1 km, PD_For_16 km, AREA_AM_Urban_32 km and CONT_32 km) was also the top model overall as it was top ranked in the 2 km_SR, 4 km_SR and 1 km_GK analyses, #2 in the 1 km_SR, 2 km_GK and 8 km_GK analyses, and #3 in the 4 km_GK analysis. Only in the 8 km_SR analysis did this model not feature in the top 10. PA1_32 km contributed most to the model under all analyses except 4 km_GK and 8 km_GK, where alt_1 km contributed more.

The response curves for the variables in this model suggest that leopard habitat suitability is maximized in well-protected, homogenous areas of higher elevation forest with little urban infrastructure and an intermediate density of forest patches (Fig. 2).

Discussion

Scale effects

As wide-ranging, adaptable carnivores, leopards are expected to have a broad perceptual range (Fisher et al. 2013; Wegmann et al. 2014). This is reflected in that the environmental/topographical, anthropogenic and land cover variables we examined were overwhelmingly linked to habitat suitability at the largest scales analyzed. Furthermore, with

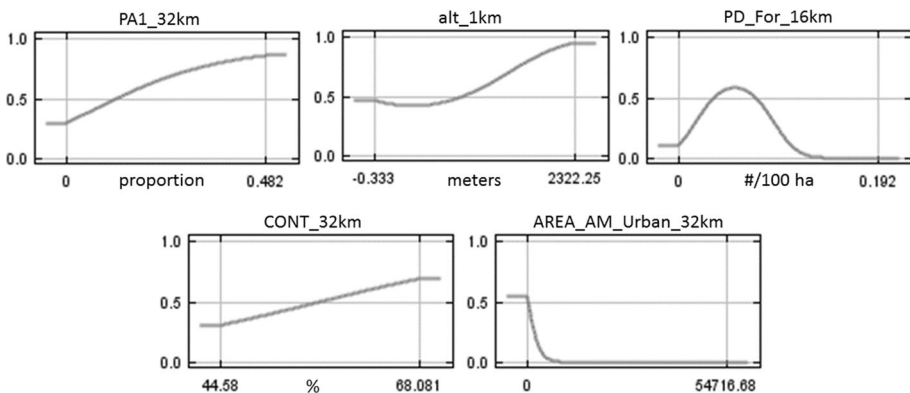


Fig. 2 Response curves for variables in top model at 1 km_GK, in order of variable contribution. The 1 km_GK analysis was selected for illustration as it was the bias correction analysis with the highest AUCtest values and a competitive AUCdiff score. Variables are plotted as univariate models to avoid influence of variable interactions

the exception of alt_1 km, none of the variables ($n = 9$) to which leopards responded at fine and intermediate scales, were strong predictors of habitat suitability. For example, rainfall was optimized at the smallest scale but was the least influential variable of the entire variable set, suggesting that leopards do not appear to respond to rainfall at any scale and that rainfall is not a strong predictor of habitat suitability. This result is supported in that leopards occur across climatic zones in Sri Lanka. However, large, wide-ranging terrestrial mammals genuinely respond to certain habitat factors at fine scales (Mateo-Sánchez et al. 2013). In this analysis leopards exhibited a fine scale response to elevation (alt_1 km), a variable included in the top overall model and consistently influential. Given the rugged, steeply varied terrain that characterizes Sri Lanka's central highlands, and numerous inselbergs protruding from the surrounding peneplain, an awareness of small-scale elevational gradients might be relevant to leopard habitat suitability, reflecting a need to identify less accessible areas for shelter and to avoid human disturbance (Bouyer et al. 2015). Similar fine scale awareness of topographical variation has been observed in various species (Wasserman et al. 2012; Timm et al. 2016).

Variable importance

The importance of Level 1 protection apparent across analyses suggests a preference of leopards for areas with minimal human disturbance. Entrance to these PAs requires a valid permit and DWC rangers are present and actively patrol to ensure compliance. These areas typically harbor increased biodiversity, including potential prey, as well as relatively high leopard densities (Kittle et al. 2017). In comparison, Level 2 PAs were less influential, typically ranking in the lower 50% of variables. These PAs have less restricted access, with nature reserves allowing for “traditional” use including access to medicinal plants and forest foods such as fruits and nuts, and sanctuaries not requiring any form of entry permit. Level 2 PAs are often used for fuelwood procurement and frequently exploited, illegally, for gem mining, hunting and timber harvesting. Government officers (DWC and FD) can be present in Level 2 PAs and act to stop detected illegal activities, but they do not routinely patrol with this purpose, effectively reducing their impact. The value of PA management to large carnivore conservation is evident in Africa where intensive management practices positively correlate with lion population stability (Bauer et al. 2015). Our results suggest that the extent of strictly protected reserves is the single most important factor governing leopard habitat suitability in Sri Lanka. The relative importance of human absence and prey presence, as well as their inter-dependencies in these PAs, is a question worth pursuing.

It is worth noting, as the response curves demonstrate, that although increasing Level 1 PA proportion increases the suitability of habitat for leopards, individuals also occur outside these PAs. This is particularly notable in northern Sri Lanka and the central highlands (Fig. 3) where Level 1 PAs are scarce and leopards range in completely unprotected areas. Leopards in these areas are already incurring elevated mortality risks due to being outside PAs (Balme et al. 2009) and are more susceptible to future habitat depletion due to this lack of formal protection. This combination of factors may be an important indication of the fragility of these populations. These areas are facing short-term threats, from rapid post-war (since 2009) development in the north and the increasing probability of land use change in the central highlands. This latter process stems from the decline of the Sri Lankan tea industry, whose vast estate lands, to which leopards appear to have adapted and through which they move (Fig. 4; Kittle et al. unpublished data), are threatened by conversion to less wildlife-friendly land use types.

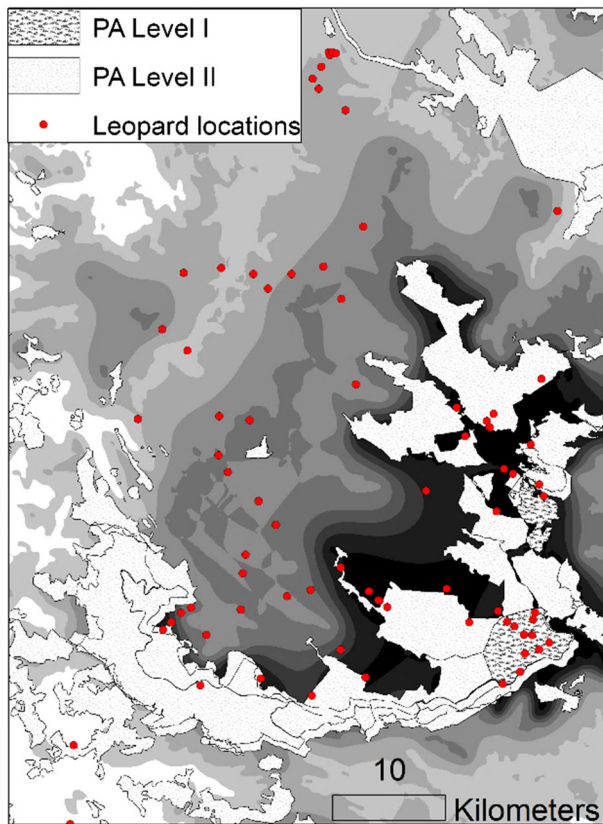


Fig. 3 Map of the Central Highlands of Sri Lanka showing elevation as a combination of contour lines (150 m) and a digital elevation model with 300 m gradations from light grey (300–600 m) to black (>2400 m), Protected Areas Level 1 and 2, and leopard presence only (PO) locations. This illustrates the many PO locations outside PAs, as well as the relative lack of Level 1 PAs in this important sub-montane and montane ecosystem

Our results also underscore the importance of forest cover and connectivity for leopard distribution in Sri Lanka. The suitability of habitat for leopards increased with forest patch size (AM_AREA_For_32 km) but was very low until forest connectivity (COH_For_32 km) reached high levels. These patterns emphasize the vulnerability of large mammalian carnivores to isolation and habitat fragmentation, processes linked to higher extinction probability and to which south Asian Felidae are considered particularly exposed (Crooks et al. 2011). The importance of corridors connecting suitable habitat patches is already acknowledged as central to range-wide conservation planning for mammalian carnivores (e.g. Rabinowitz and Zeller 2010; Cushman et al. 2015; Carvalho et al. 2016). That habitat suitability was maximized at intermediate forest patch densities suggests landscapes with too few, or alternately numerous, presumably smaller forest patches are both less than ideally suitable for leopards. Leopards do reside and reproduce in small, seemingly isolated patch forests in Sri Lanka (Kittle et al. 2012), and these patches might represent important components of larger, compromised ranges; however at the broad, island-wide scale of analysis it is unlikely that these patches represent high



Fig. 4 A remote camera image of an adult female leopard moving through an active tea estate in the middle of the afternoon. This image was captured <100 m from a secondary road and <500 m from a busy tea estate village

quality habitat. In India, in competition with tigers (*Panthera tigris*) for limited resources (Odden et al. 2010), leopards inhabit highly compromised areas with no natural forest patches and almost no available wild prey (Athreya et al. 2016). In Sri Lanka the situation differs, possibly because lack of dominant intra-guild competition allows leopards to utilize the highest quality habitat available, precluding the need to adapt to ecologically depauperate conditions. This explanation, however, appears insufficient for a territorial species like the leopard because intra-specific competition, especially if population densities are near capacity, should expose at least some individuals—particularly young males searching for vacant areas—to these poor quality habitats (Fattebert et al. 2015). Recent habitat-specific leopard density estimates in Sri Lanka (Kittle et al. 2017; Kittle and Watson 2017) are illuminating important aspects of the island’s apex predator population, but an enhanced understanding of population-level parameters such as mortality, recruitment and carrying capacity are needed to more thoroughly understand observed patterns.

Although able to share space closely with people, including in very high density areas of human habitation (Athreya et al. 2013), it is unlikely that leopards prefer these locations, particularly where they are not competing with dominant competitors for more suitable areas (Odden et al. 2010; Harihar et al. 2011). Leopards in Sri Lanka clearly avoid dense urbanization despite, for example, their long-term presence within the municipal limits of the central highlands town of Kandy (population ~100,000; Kittle et al. 2012, 2014).

Shrub patch density and, to a lesser extent, the proportion of shrub cover, were also influential. Our shrub category included tea in the central highlands and southern wet zone hills, and seasonal slash-and-burn (“*chena*”) cultivations in the east-central part of the island, both forms of agriculture suitable for limited leopard use. Tea estates, encompassing vast fields of ~1 m high tea bushes, provide effective cover for movement between forest patches (Fig. 4). Re-growing vegetation in post-harvest *chena* cultivations provides fodder for grazing ungulates which may attract leopards (Gunasena and Pushpakumara 2015), which may then exploit this intermediate cover for hunting (Balme et al. 2007). That habitat suitability for leopards was greatest at intermediate scrub patch

densities but declined as both the number of these patches and the proportion of the overall landscape composed of scrub increased, suggests that limited scrub cover, perhaps interspersed with forest, is more suitable for leopards than homogenous expanses.

Leopard habitat suitability decreased with increasing cropland extent. Crops in this analysis include rice paddy as well as more spatially restricted vegetable crops, but not other agricultural mainstays of the Sri Lankan economy such as tea, rubber and coconut. Rice paddy landscapes are associated with low mammalian biodiversity (Edirisinghe and Bambaradeniya 2006), particularly the medium to large species that leopards preferentially prey upon (Hayward et al. 2006). These areas are typically bereft of natural forests, with large, evenly dispersed human populations and few livestock, so although human presence alone is insufficient to deter leopards, the combination of low prey availability, lack of cover and human activity likely does. This inverse relationship between leopard habitat suitability and cropland expanse is supported by field observations and reflected in the distribution map which has large holes in the central north-western segment of the island as well as along the east coast. Both areas are dominated by paddy cultivation (Perera 1997b) and lack sizeable forest patches (Fig. 1b, d).

With the clear exception of the protection level of the landscape, anthropogenic variables were not strongly influential. Leopards can live in close proximity to human infrastructure, employing temporal niche partitioning in high human disturbance areas, whereby they use the same trails nocturnally that people do diurnally (Kittle et al. 2012; Athreya et al. 2013; Carter et al. 2015). However leopards exhibit no preference for these kinds of areas, an important consideration, supported by our results showing a negative response to increasing urban area extent and consistent association with areas having the lowest human footprint (i.e. Level 1 PAs). Large carnivores often avoid areas of high road density (Whittington et al. 2005; Basille et al. 2013) and in Sri Lanka leopard habitat suitability was negatively associated with increasing primary road density but positively associated with tertiary road density. As areas with high tertiary road (jeep track) density are typically rural with low vehicular presence this suggests an apparent threshold in traffic volume to which leopards respond, a process that has been observed in other species (Gagnon et al. 2007). Alternately, leopard presence, particularly tracks, might be more easily detected on unpaved than paved roads. Additional understanding of the relationship between leopard occurrence and road networks is needed to clarify this observation.

Influence of the timing and types of bias correction methods

Unlike previous analyses which restricted bias correction implementation to the top performing raw models (e.g. Fourcade et al. 2014, Vergara et al. 2016), we implemented both bias correction methods (SR and GK) at all scales (1, 2, 4, 8 km) on the full model set. Our rationale was that bias correction, if implemented from the beginning, can potentially result in new suites of top models for each analysis given that each variable's influence is likely to depend on its vulnerability to spatial sampling bias. This expectation was clearly observed in the results with many models ranked in the top ten in the uncorrected analysis ranking much lower when bias correction was implemented (Table 3). This has implications for how individual variables are considered. For example the area weighted mean size of forest patches (AREA_AM_For_32 km) appeared in only one of the top ten uncorrected models, but was represented much more often in high ranking models with large-scale (4–8 km) bias correction methods imposed from the beginning. This had the effect of increasing the profile of this variable with respect to leopard habitat suitability using this measure. The opposite effect, also linked with the timing of bias correction methods, can

be seen with respect to the connectivity of forest-dominated forest-crop mosaics (COH_Mosfor_32 km). This variable was effectively ranked #2 in the uncorrected analysis with inclusion in 3 of the top 10 models. However, in the bias corrected models as implemented from the beginning, this variable appears in only 10% of top ten models and never in more than 2 in a single bias correction analysis. This further suggests that the timing of bias analysis influences analysis results and that applying bias correction methods only to the top models based on an uncorrected or raw analysis has the potential to overlook, or alternately, overstate, variable importance.

In terms of bias correction method results showed largely ambiguous effects. The best uncorrected model was amongst the three top models in 7 of the 8 bias correction analyses, but variation in top model sets was observed. There was also considerable variation in influence across analyses for a minority of variables, the most extreme being primary road density (Rd_P_32 km). The third most influential variable across the SR analyses, Rd_P_32 km was represented in three of the top 10 models at each scale (30%), whereas in the GK analysis, Rd_P_32 km was ranked #26 out of 31 and occurred in only 3 top models across all spatial scales (7.5%). When examining average AUCtest scores, Rd_P_32 km was #15 in the SR analysis and #13 in the GK analysis, suggesting the possibility of unexamined interaction effects.

The variation in top model suites was dependent on bias correction method and scale, with uncertainty as to which was most appropriate. This increases the challenge of drawing meaningful inferences from individual analyses and supports our method of using all models across all analyses for this purpose. Alternately, that the uncorrected model performed as well as all bias correction methods may indicate that sampling bias affecting the models in this data set was minimal.

Summary

It is estimated that only 17% of global leopard range is encompassed by PAs (Jacobsen et al. 2016). In Sri Lanka, almost 50% of leopard range is protected, however this includes both Level 1 and 2 classifications (Jacobsen et al. 2016), and it is evident from this analysis that the manner in which these classifications translate into ground-level protection is acutely relevant to leopard habitat suitability. In the northern jungles and the central highlands, where leopards are widespread but Level 1 protection is lacking (Figs. 1d, 3), increased protection appears necessary. Here it is recommended that some Level 2 PAs be up-listed or currently unprotected areas designated as Level 1 PAs. The potential importance of Level 2 PAs should not be underestimated as these include most land held under the Forest Department, which is responsible for ~55% of the island's total forest area (FAO 2015). Strengthening restrictions and the improved implementation of existing restricted use laws aimed at reducing levels of illegal logging and poaching would help to secure these areas without altering designation, and increase their suitability to use by Sri Lanka's apex carnivore.

All forest metrics investigated were shown to be influential to leopard occurrence, whereas the composition and configuration of forest-crop mosaics, which include most forest plantations, were not. This clearly indicates the importance of natural forests for leopards, and other wildlife, in Sri Lanka, supporting widespread evidence that the destruction of tropical forests represents the greatest current threat to global biodiversity (Pimm and Raven 2000; Bradshaw et al. 2009). Conserving these tropical forests is required to ensure the future ecological integrity of the island's faunal assemblages, within which the leopard fulfills a profoundly important position across habitat types.

Finally, extensive crop lands such as paddy and vegetables that require clearing of other habitats, are incompatible with leopard habitat requirements, and large urban tracts are less suitable for leopards than less anthropogenically modified habitat, despite the ability of leopards to subsist in these areas (Athreya et al. 2013). Sri Lanka is undergoing rapid post-war development (since 2009) and encouraging a scale of agriculture which would see larger plots of land farmed by fewer people, a process likely to result in both increased cropland and urban extent. We recommend that development plans be carefully crafted, ensuring that adequate wilderness remains to provide sufficient refuges for wildlife and connections between populations.

In the absence of ideal habitat, the leopard is unlikely to relocate but will instead switch to preying on domestic species where necessary (Shezhad et al. 2015; Athreya et al. 2016). This then increases the potential for human-leopard conflict (Inskip and Zimmerman 2009) leading to increased persecution of the species (Cavalcanti et al. 2010). However, Sri Lanka, with a human population density of $\sim 320/\text{km}^2$ (Department of Census and Statistics 2012), has long experience of sharing space with large terrestrial mammals, including leopards. We hope that incorporating research such as this into land-use planning enables a continuation of the adaptations that society needs to make, in order to match those being continually made by leopards, to ensure sustainable co-existence (Carter and Linnell 2016), a process necessary to maintain the structure and function of ecosystems and potentially avert widespread biodiversity loss.

Data Availability statement: The datasets during and/or analysed during the current study available from the corresponding author on reasonable request.

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