Predicting suitable habitat for the Critically Endangered African wild ass *Equus africanus* in the Danakil Desert of Eritrea

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Abstract The Critically Endangered African wild ass *Equus africanus* is one of the most threatened equids, with fewer than 400 individuals persisting in the Danakil Desert (Eritrea), and fewer than 600 globally. To effectively conserve the species, it is essential to determine the extent of available suitable habitats and understand the environmental factors that most influence its current distribution. During 2016–2019 we observed African wild asses, recorded their locations during both the wet and dry seasons and analysed the bioclimatic data and topography using the maximum entropy species distribution model. Distance from water sources and precipitation of the driest month were the top predictors of suitable habitat for the dry season, whereas seasonal temperature variability and precipitation during the warmest quarter were the top predictors for the wet season. Model performances were high, with area under the curve values of 0.97 and 0.98 for the dry and wet seasons, respectively. In the Danakil Desert of Eritrea, the extent of optimal habitat for African wild asses is estimated to be 130 km² in the dry season and 739 km² in the wet season, with a potential range of 11,000 km² for both seasons. Our model results also indicate that in the dry season 89 km² of the Messir Plateau is optimal habitat, and the entire plateau area of 124 km² provides optimal habitat during the wet season. These findings provide wildlife management authorities with substantive information and rationale for the establishment of a protected area on the Messir Plateau for African wild asses in Eritrea.

Keywords African wild ass, Danakil Desert, *Equus africanus*, habitat suitability, *Maxent*, Messir Plateau, water source

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Introduction

The African wild ass *Equus africanus* is one of the most threatened wild equids and is categorized as Critically Endangered on the IUCN Red List (Moehlman et al., 2015, 2016). Historically, this species occurred in Egypt, Sudan, Eritrea, Ethiopia, Djibouti and Somalia (Moehlman, 2002). However, the global population has been significantly reduced both in numbers and in range, with fewer than an estimated 600 individuals remaining in the wild (Moehlman et al., 2015). Currently, the African wild ass is only known to persist in the wild in the Danakil Desert of Eritrea and Ethiopia (Moehlman, 2002; Tesfai et al., 2019). Hunting, habitat loss because of land-use change and competition with livestock are the main reasons suggested for its decline (Moehlman, 2002; Moehlman et al., 2016; Tesfai et al., 2021b).

In Eritrea, the African wild ass is protected by the local community as part of their cultural practice (Moehlman, 2002; Tesfai et al., 2019), although the species' range is not formally protected (Tesfai et al., 2021b). The villages in the Danakil Desert in Eritrea are mostly permanent settlements, with some temporary settlements being established during the wet season. During rainfall months, herders and their livestock, particularly cattle, migrate from the highlands to the Danakil Desert (Tesfai et al., 2021b), which may displace African wild asses and reduce their access to quality forage and water. In Ethiopia, African wild asses are hunted illegally by local people for food and traditional medicine (Moehlman, 2002; Kebede et al., 2014), and are often found in remote areas away from permanent and temporary settlements and close to permanent water sources (Kebede et al., 2014).

Within the potential range of African wild asses in Eritrea, the Messir Plateau is an important area for females with young foals (Moehlman, 2002; Tesfai et al., 2019). Females with young foals and males are observed in higher densities on the Messir Plateau compared to other areas of the species' potential range in Eritrea. Based on studies that identified individual asses, the area supports a population of c. 44 individuals, including 24 adult females, five adult males and their offspring (Tesfai et al., 2021a). However, the Messir Plateau covers only 124 km² of the potential range of the species (11,000 km²) in Eritrea (Tesfai, 2006). The potential range of African wild asses in

Eritrea is estimated based on observational field studies. Determining the extent of suitable habitat for African wild asses is necessary to identify conservation priorities, designate protected areas and monitor environmental conditions that could affect available habitats and population viability.

The range of a species is dynamic and often responsive to its basic niche requirements (Pearson, 2007; Barnard & Thuiller, 2008). Spatial and temporal variations in available resources such as food and water influence species distribution (Linder et al., 2012). The area of the Danakil Desert where we conducted this study is in the eastern lowland region of Eritrea. Although no studies have been conducted in Eritrea to investigate the effects of climate variability on species distribution, prolonged droughts and erratic rainfall are common climatic characteristics of the eastern lowland of Eritrea (Ghebrezgabher et al., 2016). Any precipitation that may occur in both the wet and dry seasons could stimulate forage production and thus influence the potential distribution of herbivore species (O'Donnell & Ignizio, 2012). The Danakil Desert, one of the hottest places in the world, has greater temperature variability than the highlands of Eritrea (Measho et al., 2019). The topographical variation of this region affects precipitation and temperature regimes (Measho et al., 2019), which in turn may influence both resource availability and the distribution of African wild asses (Evangelista et al., 2008).

Understanding the drivers of habitat suitability and the seasonal distribution of a species is important for establishing successful management, conservation and restoration strategies (Boitani et al., 2008; Kebede et al., 2014). The availability of and access to suitable habitat are essential for the persistence of a species, providing wildlife managers with a scientific rationale for targeting areas for formal protection and species conservation (Kebede et al., 2012; Morrison, 2013). However, information on the ranges of many threatened wildlife species is limited. Species distribution models use occurrence records with spatial layers representing environmental conditions to map suitable habitat across an area of interest (Elith & Leathwick, 2009). They have been widely used in the conservation and management of rare and cryptic wildlife (Evangelista et al., 2008; Freeman et al., 2019), including the African wild ass in other areas (Kebede et al., 2014; Evangelista et al., 2018).

The goal of this study was to identify the seasonal range of African wild asses in the Danakil Desert of Eritrea, to support effective management and long-term conservation of the species. Specifically, our objectives were to use maximum entropy modelling to estimate the potential range of the African wild ass, determine the environmental and anthropogenic conditions that affect its distribution, and distinguish habitat characteristics between the dry and wet seasons.

Study area

The study area lies within the Danakil Desert of Eritrea and is considered part of the larger Danakil Depression that extends into Ethiopia (Fig. 1). Characterized as a semi-desert agro-ecological zone, the Danakil Desert of Eritrea covers c. 11,000 km². Elevation ranges from 126 m below sea level in the Danakil Depression to c. 1,600 m above sea level on Wongebo Peak. The study area is characterized by a dissected volcanic desert of lava ridges and a rocky landscape (Moehlman, 2002; Tesfai et al., 2021b).

The potential range of the African wild ass in the Danakil Desert of Eritrea is estimated to be c. 11,000 km² (Tesfai, 2006), which we used to define the extent of our study area. We delineated this area based on locations of observed African wild asses and their movements to permanent water sites. The Danakil Desert has low primary productivity and limited and localized surface water in the dry season (Tesfai et al., 2021a). African wild asses have been observed foraging close to permanent water sources, but they dispersed within a radius of 10–25 km from water when livestock, particularly cattle, were present (Kebede et al., 2014; Tesfai et al., 2021b).

The Northern Red Sea Region of Eritrea, where the study area is located, is vulnerable to recurrent droughts (Measho et al., 2019), experiencing extremely hot summers (mean daily maximum temperature of 35 °C; Tesfai et al., 2019). The mean annual rainfall recorded at Massawa Rainfall Station located in the northern region of our study site is c. 160 mm over a 50-year period, with high annual variability (coefficient of variation = 73%; Department of Land, 1998). Most of the rain usually occurs during December–February, with less rain falling during March–April. The dry season begins in May or June and lasts until October or November (Government of Eritrea, 1995). Although no reliable rainfall data are available for the study area, the 2000–2021 data from the Climate Hazards Group InfraRed Precipitation with Station (USAID, 2019) indicate that during the dry season (May–October) areas near the Red Sea, such as the Messir Plateau, received more rain (annual mean 133.4 mm) than those farther inland (annual mean 72.5 mm). Cooler temperatures during the night could result in less transpiration and correlate with higher primary productivity (Raich et al., 1991).

Within the study area, there are at least 11 permanent water sources that are potentially utilized by African wild asses throughout the year (Figs 1 & 2). Temporary water sources occur during the rainfall season but persist for only a few months after the rains end. Most of the known range of the African wild ass in the Danakil Desert has low herbaceous cover (ESA CCI, 2017; R.T. Tesfai, pers. obs., 2016–2019). The vegetation in these areas consists of sparse grasses and forbs with scattered trees and shrubs that include *Vachellia tortilis*, *Senegalia mellifera*,

Fig. 1 Topographical map of the study area in the Danakil Desert of Eritrea, with locations of permanent water sources and settlements.

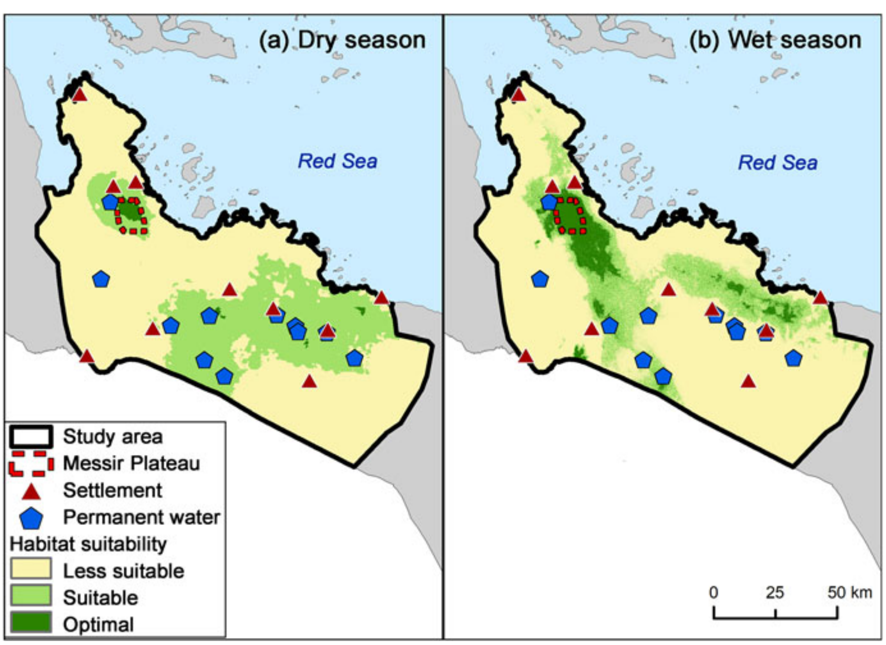

Fig. 2 Habitat suitability models for the African wild ass *Equus africanus* in the Danakil Desert of Eritrea (Fig. 1) during the (a) dry and (b) wet seasons. We generated the models using *Maxent* software and field survey data collected during 2002–2006 and 2016–2019.

Senegalia laeta, *Vachellia seyal*, *Salvadora persica*, *Ziziphus spina-christi*, *Hyphaene thebaica*, *Suaeda monoica*, *Artiplex* spp, *Salsola* spp, *Euphorbia* spp and *Tamarix aphylla* (Tesfai, 2006). Because of the scarcity of water and forage, human and livestock densities are low. The residents in the area are predominantly Afar pastoralists who raise goats, sheep, camels and domestic donkeys. Approximately 22 villages and two small towns (Ghelao and Tio) are situated within and on the periphery of the study area (Fig. 1), with an estimated 30,000 people living within the study area.

Methods

Data collection

Locating African wild asses in the Danakil Desert presents many physical and logistical challenges. The African wild ass is physiologically dependent on water sources and has frequently been observed up to 20 km from the main water sources used by the population during the dry season (R.T. Tesfai, pers. obs., 2016–2019). Based on this knowledge, we surveyed an area with a radius of 20–30 km around the 11 known permanent water source sites in the potential range of the Danakil Desert in Eritrea (Fig. 1).

We surveyed c. 80% of the potential range of the species twice per year during August 2016–March 2019 with local guides. We conducted the surveys throughout the day, performing more intensive observations in the morning from 06.00 to 11.00 and in the afternoon from 15.00 to 18.00 when African wild asses are most active. As the terrain is undulating and covered with lava rubble, some areas were inaccessible by vehicles, and in such cases we performed surveys on foot and with camels. In the more rugged terrain, we had to walk to high points and survey all of the valleys using binoculars or a spotting scope. We recorded the locations of places where the observed African wild asses had been (after they had moved away, so as to not disturb them) using a GPS device. If we observed fresh tracks and faecal piles around permanent water sources, we set up camera traps on the narrow paths leading to each water point to document the presence of African wild asses. We collected 116 African wild ass sightings and faecal samples (51 during the dry seasons and 65 during the wet seasons).

Predictor variables

The selection of environmental variables could influence the results of species distribution models (Austin, 2002). We therefore carefully selected and tested potential predictor variables. These included 19 bioclimatic variables (data source: *CHELSA version 2.1*; Karger et al., 2017), dominant land-cover type (ESA CCI, 2017), topography (elevation, aspect and slope; NASA Shuttle Radar Topography Mission, 2013) and vegetation greenness measured by the enhanced vegetation index (Didan, 2015). Categories of land cover included tree cover, shrub cover, grassland, cropland, aquatic or regularly flooded vegetation, lichen and mosses/sparse vegetation, bare areas, built-up areas, snow and/or ice, and open water. For model development, we compiled each land-cover type into a single layer that represented the percentage of that specific cover type in a 1-km² area. We calculated the 20-year mean (2000–2019) of the enhanced vegetation index in *Google Earth Engine* (Gorelick et al., 2017). We used the mean enhanced vegetation index over an extended time period because we aimed to identify habitat suitability that would represent long-term conditions of forage quality (Villamuelas et al., 2016), rather than specific conditions at the time of observation. We calculated distance from permanent water sources and from settlements for each season using *ArcGIS 10.7.1* (Esri, 2019). We selected major predictor variables that could potentially limit the distribution of the African wild ass in the Danakil Desert based on expert opinion and contributions to initial model iterations. We retained only variables with the greatest contribution in the modelling after running covariate correlation matrix tests for each dataset (bioclimatic, environmental variables, or both predictors, for dry vs wet season separately). We removed one of each pair of highly correlated variables (Spearman correlation coefficient $|r| > 0.7$) from model development (Dormann et al., 2013). We selected six of the 19 bioclimatic variables because of their influence on forage production and the seasonal distribution of the African wild ass during the sampling period. The final variables considered for the dry season models were distance from the nearest water source, distance from the nearest permanent settlement, precipitation of the driest month, precipitation seasonality (coefficient of variation), mean temperature of the warmest quarter and grass cover. Variables included in the wet season models were distance from the nearest settlement, elevation, aspect (eastness), precipitation of the warmest quarter (mm/quarter), temperature seasonality (standard deviation), mean temperature of the driest quarter and grass cover. We projected all predictor variables onto the WGS84 UTM zone 37N coordinate reference system, converted them to ASCII format for processing in maximum entropy modelling and clipped them to the extent of the study area (11,000 km²) with a resolution of 90 m.

Data analysis

The maximum entropy model is one of several species distribution models developed in recent years that are valuable tools for estimating a probable distribution and habitat suitability for species (Phillips et al., 2006; Pearson, 2007). We used *Maxent 3.3.3k* (Phillips et al., 2006) because it supports presence-only data and has been shown to perform well with small datasets (Elith et al., 2006; Pearson et al., 2007; Baldwin, 2009; Evangelista et al., 2016). We created background samples by generating 10,000 locations across the study area. We used the default settings in the *Maxent* software except for increasing the beta-multiplier parameter as needed for each iteration to control for overfitting, keeping the difference between the training and test area under the receiver operating characteristics curve (AUC) < 0.05, whilst allowing more generalized response curves to improve extrapolation (Elith et al., 2010) and using a 10-fold cross-validation for model evaluation. As such, the background point generation we used accurately captured the area accessible to African wild asses in this region, which is critical when developing habitat suitability models to avoid biases and inflated model results (Barve et al., 2011, Jarnevich et al., 2015). In addition, although we would have preferred to use the multiple-block cross-validation techniques as recommended, our dataset was too limited, too confined spatially and involved observations of individuals in groups that moved together, limiting our confidence that this approach would produce reliable results (Roberts et al., 2017).

Firstly, we ran the models with selected variables for the dry and wet seasons separately. If more than one presence point fell within the area of a single pixel of 90 m^2, we removed the duplicates so that the pixel would represent a single occurrence or presence point for the model analysis. This reduced the numbers of presence points to 48 and 63 for the dry and wet seasons, respectively. For each season, we ran 10 replicate models using k-fold cross-validation, selecting 90% of the presence points for training data to build the model and using the remaining 10% for testing each model iteration. We also analysed the area under the precision recall curve (AUC-PR) for the dry and wet seasons. We averaged the final map outputs and evaluations from the 10 replicates for both dry and wet seasons. We converted the final maximum entropy output map for each model into three habitat suitability categories: less suitable, suitable and optimal. We based these categories on two threshold values: minimum training presence logistic threshold and maximum test sensitivity plus specificity logistic threshold. The minimum threshold assumes that the least suitable habitat at which the species is known to occur is the minimum suitability value for the species, whereas the maximum threshold assumes that the optimally suitable habitat at which the species is known to occur is the maximum suitability value for the species. We considered pixels with values below the minimum threshold less suitable, pixels with values between the minimum and maximum thresholds as suitable and pixels with values greater than the maximum threshold as optimal. The optimal and suitable habitat area are collectively considered as potentially suitable habitat for the African wild ass. We produced the model results for the dry and wet seasons separately to represent habitat suitability throughout the year. We evaluated the model results according to the AUC and AUC-PR. Model AUC values range from 0 to 1 (Pearce & Ferrier, 2000; Phillips et al., 2006), and using the AUC is a standard and threshold-independent method often employed to evaluate model performance. Values > 0.5 indicate progressively better model performance based on the evaluation data, whereas a value of 0.5 indicates a model that predicts no better than random chance (Elith et al., 2006; Townsend Peterson et al., 2007).

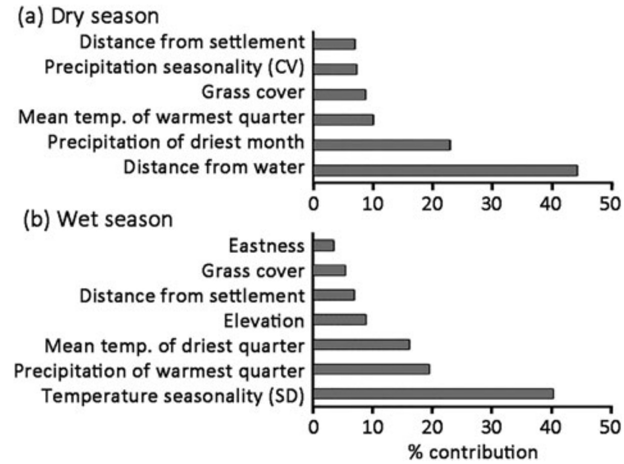

FIG. 3 The relative contribution of predictor variables to the maximum entropy model for the (a) dry and (b) wet season habitat suitability models for the African wild ass in the Danakil Desert of Eritrea.

Results

The maximum entropy models generated a mean AUC value of 0.97 and an AUC-PR (averaged across the 10 k-fold model iterations) value of 0.92 for the dry season. Model outputs indicated that the optimal habitat for the African wild ass during the dry season was 130 km^2 (1.2% of the potential range of 11,000 km^2) and suitable habitat was 3,320 km^2 (30.2% of the potential range; Fig. 2a). The mean AUC value for the wet season was 0.98 and the mean AUC-PR value was 0.92. In the wet season, the optimal and suitable habitats for the African wild ass were 739 km^2 (6.7% of the potential range) and 2,323 km^2 (21.1% of the potential range), respectively (Fig. 2b). In the dry season, the two main areas of optimal and suitable habitat were separated. In the wet season, these areas were contiguous.

Distance from water and precipitation of the driest month were the most important predictors in the dry season models (Fig. 3a), whereas temperature seasonality and precipitation of the warmest quarter had the greatest contributions to the wet season model results (Fig. 3b).

Discussion

We had expected both the optimal and suitable habitat extents to be larger in the wet season than in the dry season as available water (although temporary) would be more dispersed. Contrary to our expectation, areas of suitable habitat were greater in the dry than in the wet season. In the dry season, the few available permanent water sources are distributed far apart. During the wet season, when forage and temporary water sources are available on the Messir Plateau, African wild asses were observed within 3 km of the nearest temporary water point (Tesfai et al., 2021a). However, they were found at greater distances from temporary water sources when there were high concentrations of livestock, particularly cattle, in the area (Tesfai et al., 2021b). This suggests that high numbers of livestock and people affect the seasonal distribution of and habitat suitability for the African wild ass. Research on Grevy's zebra *Equus grevyi* habitat suitability in Ethiopia has indicated that the area of optimal habitat during the wet season was smaller than in the dry season because of displacement by people and livestock (Kebede et al., 2012). During the dry season, some African wild asses may be foraging farther from the core breeding area (the Messir Plateau) and utilizing other permanent water sources, such as Asabolo, Raineba and Shukoray. The limited forage availability could increase their dispersal area during this period. In the dry season, non-reproductive females and bachelor males are rarely observed on the Messir Plateau close to the permanent Asaila spring (Tesfai et al., 2021a). During this period, adult females with foals < 3 months of age drink daily, whereas adult males and non-reproductive females may go without water for as long as 5–10 days and thus may have larger home ranges (Tesfai et al., 2021a).

The Messir Plateau falls within the optimal habitat in both the dry and wet seasons. Previous research has suggested the importance of the permanent Asaila spring, near the Messir Plateau, for the African wild ass (Tesfai et al., 2021a). Multiple females with young foals and territorial males are regularly found in this locale. However, based on our maximum entropy model results, other potential sites such as Shukoray, Raineba and Tio could be equally important for the conservation of this species, and further surveys are needed in these regions. During the dry season, some areas closer to the Red Sea also fall within optimal habitat categories. Areas near the Red Sea may receive more precipitation in the dry season and produce relatively higher grass cover than inland areas (Figs 1 & 2).

Distance from water and precipitation of the driest month were the strongest predictors for the dry season models (Fig. 3a). This is consistent with the physiological dependence of the African wild ass on water, particularly lactating females with foals. Thus, the distribution of females with young foals in the dry season is limited by the availability of permanent water sources (Kebede et al., 2014; Tesfai et al., 2021a). A study on the spatial and dietary overlaps of African wild asses with livestock on the Messir Plateau indicated that in the dry season, African wild asses were located in the northern section towards the permanent Asaila spring that had higher vegetation greenness values compared to the central and southern sections (Tesfai et al., 2021b). This modelling result also shows a similar pattern, with the optimal habitat of the African wild ass being towards the north of the Messir Plateau during the dry season.

Temperature seasonality, precipitation of the warmest quarter and mean temperature of the driest quarter were the best predictors in the wet season (Fig. 3b). Temperature and precipitation may affect vegetation dynamics through control of the phenological development of plants (Du et al., 2019). The topographical variation affects the precipitation and temperature regimes of Eritrea, which in turn influence the spatial and temporal variability of vegetation dynamics (Measho et al., 2019). The distance from human settlements was the least important predictor in both the dry and wet seasons, which is not surprising given that African wild asses in Eritrea are protected by the local community as part of their cultural practice (Moehlman, 2002; Tesfai et al., 2019). However, African wild asses may still avoid people and are often found 10–15 km away from human settlements and closer to permanent water sources (Tesfai et al., 2021a). Previous research (Tesfai et al., 2021b) and this study in the Danakil Desert of Eritrea indicate that African wild asses were displaced from the optimal forage areas during the wet season by the immigration of people and cattle from the highlands. This is of great concern for the survival of the African wild ass as the areas close to permanent water sources are the most suitable habitats for conserving this Critically Endangered species. The optimal areas on the Messir Plateau for the dry and wet seasons, as well as areas where the dry and wet season ranges overlap, are potentially viable habitats and should be targeted for the conservation of the African wild ass in Eritrea. Although the Messir Plateau and adjacent suitable areas are at present not directly affected by the Colluli mining development, they are not formally protected (Moehlman, 2002; Tesfai et al., 2021a,b), and development projects and livestock herders are free to utilize the area. It is therefore important that the optimal habitat areas are established and demarcated as protected areas for the conservation of this Critically Endangered species in Eritrea. This study provides the scientific data that are needed for prioritizing and designating such protected areas.

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Conflicts of interest None.

Ethical standards This research abided by the *Oryx* guidelines on ethical standards.

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