Global Ecology and Conservation 62 (2025) e03820

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: www.elsevier.com/locate/gecco

Original research article

Identifying suitable forested areas and protected forests for the conservation of white-thighed (*Colobus vellerosus*) and king (*C. polykomos*) colobus monkeys under climate change in West Africa

F. Darius Accrombessi [a,b,c,*], S.S. Mireille Toyi [a,b], Inza Kone [a,d,1], Dietmar Zinner [c,e,1]

[a] West African Science Service Centre on Climate Change and Adapted Land Use, Climate Change and Biodiversity Research Program, University Félix Houphouët-Boigny, Côte d'Ivoire
[b] Laboratory of Applied Ecology, Faculty of Agronomic Sciences, University of Abomey-Calavi, Benin
[c] Cognitive Ethology Laboratory, German Primate Center, Leibniz Institute for Primate Research, Göttingen, Germany
[d] Centre Suisse de Recherches Scientifiques en Côte d'Ivoire, Côte d'Ivoire
[e] Department of Primate Cognition, Georg-August-Universität Göttingen, Göttingen 37077, Germany

ARTICLE INFO

Keywords:
Habitat suitability
Climatic refugia
Colobines
Ensemble modelling
Reintroduction

ABSTRACT

Colobus vellerosus and *Colobus polykomos* are closely related, parapatric species endemic to West Africa. Both species face severe threats from illegal hunting and habitat destruction, with population declines exceeding 80 % for *C. vellerosus* and 50 % for *C. polykomos* over the past 30 years. Particularly, the critically endangered *C. vellerosus* necessitates urgent conservation initiatives, including potential reintroductions into suitable habitats where the species has been extirpated in the last decades. We used ensemble modelling to assess habitat suitability for both species under current and future climate conditions, and identified suitable habitats within and outside of protected areas for reintroduction. We found that, under current climate conditions, the size of climatically suitable area for *C. vellerosus* and *C. polykomos* is 520,193 km^2 and 240,398 km^2, respectively. However, within our area of interest of 1,624,800 km^2, encompassing 370,000 km^2 of forest cover, only 7.3 % of these forests are suitable for *C. vellerosus*, compared to 43.3 % for *C. polykomos*. Of these suitable forested areas, 47.9 % and 82.9 % are located outside protected areas, respectively. Under a low greenhouse gas emission scenario for 2050, these potential habitats may decline by 58.7 % and 71.8 %, respectively. Key recommendations from our study include protecting suitable habitats, assessing the genetic population structure of *C. vellerosus* and *C. polykomos*, developing reintroduction programs for *C. vellerosus*, and establishing ecological corridors.

* Corresponding author at: West African Science Service Centre on Climate Change and Adapted Land Use, Climate Change and Biodiversity Research Program, University Félix Houphouët-Boigny, Côte d'Ivoire.
E-mail address: fdaccrombessi@gmail.com (F.D. Accrombessi).
[1] shared senior authorship

https://doi.org/10.1016/j.gecco.2025.e03820
Received 14 April 2025; Received in revised form 23 August 2025; Accepted 25 August 2025
Available online 25 August 2025
2351-9894/© 2025 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/).

1. Introduction

The white-thighed colobus (*Colobus vellerosus*) and the king colobus (*Colobus polykomos*) are closely related species endemic to West Africa (Fashing, 2022). Molecular studies indicate that both species are the most recently diverged members of the colobus clade (Roos and Zinner, 2022; Ting, 2008). The distribution range of *C. vellerosus* spans from southwestern Nigeria through Benin, Togo, and Ghana, reaching the interfluvial region between the Sassandra and Bandama Rivers in Ivory Coast (Djègo-Djossou, 2013; Matsuda Goodwin et al., 2020a, 2020b; Saj and Sicotte, 2013). *Colobus polykomos* is found from the Ivory Coast, through Liberia, Sierra-Leone, Guinea, to Guinea-Bissau (Alonso et al., 2019; Korstjens and Galat-luong, 2013). Hybridization might occur in the interfluvial zone, where the ranges of both species might overlap. A taxon described from the interfluvial zone, "*C. polykomos dollmani*" might be a hybrid form (Groves et al., 1993; Oates and McGraw, 2009). This form, however, is also highly threatened by extinction (Gonedelé Bi et al., 2006).

Both colobus species are highly threatened by hunting, habitat destruction and fragmentation, and human encroachment throughout their geographical range (Gonedelé Bi et al., 2020; Matsuda Goodwin et al., 2020a, 2020b). These threats have led to an inferred population decline of more than 80 % and 50 %, respectively, for *C. vellerosus* and *C. polykomos*, over their entire range during their last 30 years (Gonedelé Bi et al., 2020; Matsuda Goodwin et al., 2020a, 2020b). Both species are currently the most vulnerable of the five black-and-white colobus species (Fashing, 2022). *Colobus polykomos* is listed as endangered. While fragmentation is largely ongoing over its range, it does not persist in degraded areas and requires at least some mature forests (Gonedelé Bi et al., 2020). The situation of *C. vellerosus* is even worse. It is classified as critically endangered (Matsuda Goodwin et al., 2020a, 2020b) and is one of the 25 most endangered primate species in the world (Mittermeier et al., 2022). Although it inhabits a variety of forest habitats such as lowland rain, dry, gallery, and swamp forests (Fashing, 2022), it is essentially found in a few sacred or community forests with small population densities (Schwitzer et al., 2019).

In particular, the situation of *C. vellerosus* necessitates urgent effective conservation measures. Potential conservation methods to redeem *C. vellerosus* populations from extinction include their reintroduction into still-existing suitable forests or reforestation in climatically suitable areas with subsequent reintroduction. To that end, it is important to determine the spatial extent of the species' climate niches (current climatically suitable areas) and identify still-forested, but colobus-empty, areas within the climatically suitable areas. In addition, there is a need to understand how climate change might affect suitable habitats (future suitable habitats - areas of potential reforestation). Korstjens (2019) predicted an overall shrinkage in the distribution range of the *Colobus* genus due to climate change, emphasizing that even minor shifts in their suitable habitats could lead to the extinction of *Colobus* species. This is particularly alarming for *C. vellerosus*, given its critical conservation status.

In this study, we modelled the climatically suitable areas of *C. vellerosus* and *C. polykomos* under current and future climate conditions by 2050. Within these ranges, we assessed the amount of forest cover that remains as suitable habitats for each species. Additionally, we evaluated the extent to which these suitable forested habitats overlap with existing protected areas of adequate size, which could function as refugia or support long-term reintroduction and in-situ conservation efforts.

2. Methods

2.1. Study area

For our study area, we established an area of interest (AOI) that extends approximately 150 km beyond the terrestrial boundaries of

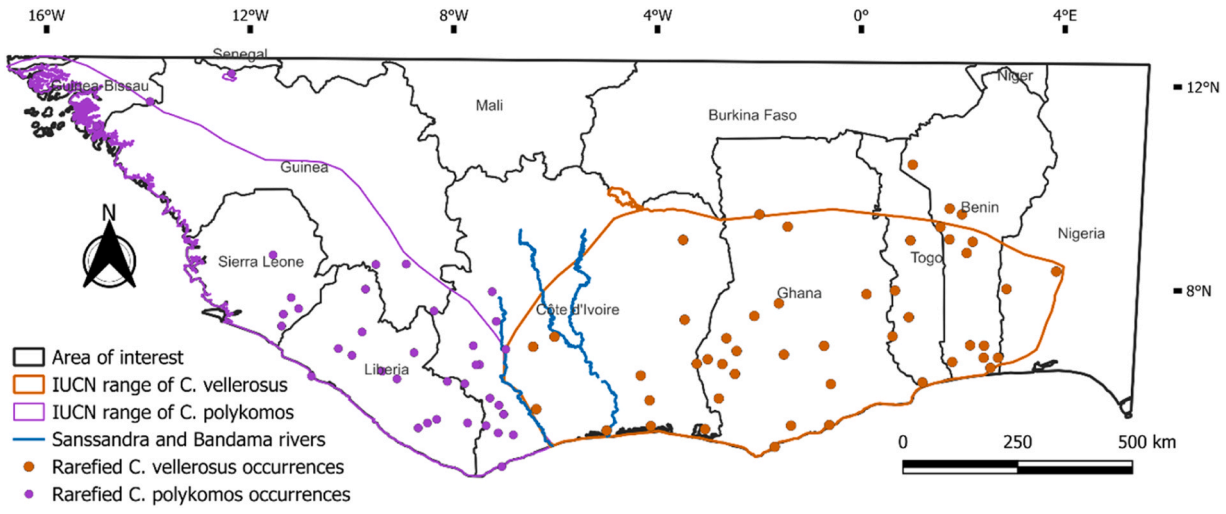


Fig. 1. Area of interest, IUCN distribution ranges, and rarefied occurrences of *Colobus vellerosus* and *Colobus polykomos*.

the IUCN-defined geographic distribution ranges for *C. vellerosus* and *C. polykomos*. Thus, our AOI encompasses the IUCN distribution ranges of both species (Fig. 1). This region features a diverse array of habitats, including both intact forests and areas significantly affected by degradation. It predominantly experiences an equatorial climate and is characterized by lowland rainforests, swamp forests, semi-deciduous forests, savannah-woodlands, and gallery forests.

2.2. Occurrence records

We collected the presence records of both species from the Global Biodiversity Information Facility (GBIF), with 157 occurrences for *C. vellerosus* and 700 occurrences for *C. polykomos* (https://www.gbif.org/, 2024). In addition, we screened the literature (Alonso et al., 2019; Djègo-Djossou, 2013; Gonedelé Bi et al., 2014; Matsuda Goodwin et al., 2020a; Guilherme, 2014; Kazeem, 2017; Schwitzer et al., 2019; Segniagbeto et al., 2017; Wiafe, 2021; Wiafe et al., 2023) and consulted the museum catalogues from the Natural History Museums in London and Paris. We also took occurrence points using the SMART Conservation version 7.5.6 (Meadows, 2022) and the Global Positioning System (GPS, Garmin 78) during our fieldwork from November 2022 to June 2023 and from March to April 2024 in central and southern Benin. To improve the accuracy of our dataset, we plotted the occurrences in Google Earth Pro and excluded records that fell outside forested areas. We matched occurrence points with the IUCN ranges of both species and ensured that any records falling outside these ranges originated from scientific research or "colobine experts". Occurrences recorded before 1970 were excluded to reduce temporal biases and ensure occurrence data align with current climate datasets.

We removed duplicates, and to account for spatial autocorrelation, we accepted only occurrence records with a mean Euclidean distance of more than 20 km using SDM Toolbox v2.6 in ArcMap (Brown, 2014). From 711 occurrences for *C. polykomos* and 350 occurrences for *C. vellerosus*, we retained only 39 rarefied occurrences for *C. polykomos* and 48 for *C. vellerosus* for our modelling.

2.3. Bioclimatic variables selection

We downloaded the 19 bioclimatic variables at 30 arc-seconds (~1 km^2) resolution from WorldClim v2.1 (Fick and Hijmans, 2017). We clipped the area of interest from these variables' rasters using QGIS 3.34.11. We used a Pearson correlation running with the "cor" function in R v4.3.1 to select a subset of 10 less correlated bioclimatic variables. The correlation coefficient of the retained variables is smaller than $|r| \leq 0.78$ (Figs. S1 and S2). The selected variables are: annual mean temperature (bio01), mean diurnal temperature range (bio02), maximum temperature during the warmest month (bio05), mean temperature during the wettest quarter (bio08), mean temperature during the driest quarter (bio09), precipitation during the wettest month (bio13), precipitation during the driest month (bio14), precipitation seasonality (bio15), precipitation during the warmest quarter (bio18), and precipitation during the coldest quarter (bio19).

We selected these climatic variables due to their importance in shaping primate distribution patterns. Korstjens (2019) has shown that most of these climatic variables affect the distribution of the genus *Colobus*. In particular, folivorous primates, such as *Colobus* should inherently counteract the increased cost of leaf digestion for their adaptations to climate change in scenarios of increased temperature and decreased rainfall (Korstjens and Hillyer, 2016). Furthermore, previous studies have highlighted the effects of the climatic predictors on the behavioural and feeding ecology, physiological processes, and biogeographical distribution of folivorous primates (Korstjens et al., 2010; Lehmann et al., 2010; van Schaik and Pfannes, 2005; Zhang et al., 2021).

We utilized the IPSL-CM6A-LR Global Climate Model (GCM) from the CMIP6 model to project future climate conditions for the period 2041–2060. This model has been identified in several studies as performing well in West Africa (Ajibola et al., 2022; Nkrumah et al., 2022). Our projections are based on the low greenhouse gas emission scenario for 2050, corresponding to the Shared Socio-economic Pathways (SSPs) SSP1-2.6.

2.4. Multivariate environmental similarity surface analysis and MaxEnt optimal parameters selection

The "raster", "sp", and "dismo" packages were used in R to analyse the multivariate environmental similarity surface (MESS) following the method described by Elith et al. (2010). This analysis investigates the presence of anomalies within both current and future climatic conditions across the area of interest. The selected bioclimatic variables serve as a reference for this analysis. The MESS analysis reveals negative values, prompting us to enable clamping in the MaxEnt modelling process. These negative values indicate new climate conditions distinct from the species niche within the area of interest.

The key tuning parameters for MaxEnt, including the regularization beta-multipliers and feature class combinations, were identified using the ENMeval package (Muscarella et al., 2014). We evaluated six feature class combinations: L, LQ, H, LQH, LQHP, and LQHPT, where L represents linear, Q represents quadratic, P stands for product, T for threshold, and H for hinge. For this analysis, the adjusted regularization multipliers ranged from 0.5 to 2 in increments of 0.5. Based on the lowest delta Akaike information criterion (delta AICc = 0) (Muscarella et al., 2014), we selected the optimal MaxEnt model, which comprises the linear (L) and quadratic (Q) feature classes with a beta-multiplier of 2.

2.5. Climatic niche ensemble modelling and evaluation

We built an ensemble ecological niche model using the Biomod2 package (Thuiller et al., 2023) and MaxEnt (Phillips et al., 2017) in R version 4.3.1. To apply the modelling approach to both species, we developed a wrapper that considered the species' name as the argument and stored the single niche modelling procedure. We randomly generated two sets of pseudo-absence points, each containing

the same number of rarefied occurrence records. Our ensemble model comprises a presence-background algorithm (MaxEnt), and three widely used presence-pseudo-absence algorithms, namely Generalized Boosting Model (GBM/BRT) (Ridgeway and Developers, 2003), Generalized Linear Model (GLM) (McCullagh and Nelder, 2019), and Random Forest (RF) (Breiman, 2001). We used the ENMeval-defined optimal settings for the MaxEnt model and the default settings for the other individual algorithms.

We randomly split 80 % of our dataset for calibrating and training the models and used the 20 % remainder for testing them. We made five cross-validations for each of the four modelling algorithms. Presences and pseudo-absences were equally weighted in the model computing process. Each modelling algorithm was evaluated based on the True Skill Statistic (TSS) and the Area Under the Curve (AUC) of a Receiver Operating Characteristics (ROC) plot. To build the EM, we excluded models with TSS and AUC, respectively, lower than 0.5 and 0.8 (Allouche et al., 2006; Fielding and Bell, 1997; Swets, 1988).

2.6. Range change analysis

We analysed the range size change (RSC) using the "BIOMOD_RangeSize" function of the Biomod2 package. This function requires a binary dataset and is a one-to-one comparison method that allows the calculation of habitat change differences between projections of SDMs. This approach is used to quantify the predicted range changes in terms of the number of pixels (Thuiller et al., 2023).

Given that *C. vellerosus* has a low dispersal capacity, which may be exacerbated by habitat fragmentation and tree species richness (Kankam and Sicotte, 2013), we propose that the zero-migration assumption represents the most realistic hypothesis. Nevertheless, we also project the change in range size based on the unlimited migration assumption to estimate potential range size changes in an optimal scenario, where conservation efforts implement corridors to facilitate species dispersal.

2.7. Identification of the suitable forests for re-introduction

We downloaded the protected areas and other effective area-based conservation measures of Africa from Protected Planet (UNEP-WCMC and IUCN, 2024) (Fig. S3-S5). Additionally, we obtained the land cover raster of Africa with a resolution of 20 m from the Climate Change Initiative project of the European Space Agency (https://2016africalandcover20m.esrin.esa.int/).

We polygonised the binary rasters generated from our modelling and extracted suitable areas for each taxon. Afterward, we clipped the land cover raster according to our AOI and extracted the layer representing forested areas. Utilizing the modelled suitable areas examined against the current and future climate change scenarios, we clipped, polygonised, extracted, and calculated the forested areas for each taxon. We then intersected these forested areas with protected areas to determine and calculate the protected forested areas that are suitable for each taxon. Considering that the home range of *C. vellerosus* is about 11 ha (Fashing, 2022) and the necessity to establish ten groups for sustainable population conservation, we specifically focused on identifying suitably protected forests that encompass at least 1 km^2. We conducted this analysis for both species, identifying forests that could potentially be used for their reintroductions. All spatial analyses and area calculations were performed using QGIS v3.34.11, and the attribute tables were exported to CSV files for subsequent calculations in R v4.3.1. Additionally, we uploaded our area of interest (AOI) to Global Forest Watch (GFW) (https://www.globalforestwatch.org/dashboards/aoi/67225c0ecb8e690020602a58/) for follow-up and analysis of forest cover change.

3. Results

3.1. Model accuracy and contribution of the climatic variables

The ensemble model demonstrated high accuracy, with AUC and TSS values of 0.96 and 0.81 for *C. vellerosus*, and 0.99 and 0.95 for *C. polykomos*, respectively (Table S1). The selected climatic variables contributed an average of 71.8 % (TSS) to the habitat suitability of *C. vellerosus* and 42.1 % (TSS) to that of *C. polykomos*. The mean diurnal temperature range, precipitation during the coldest quarter, precipitation seasonality, precipitation during the wettest month, and precipitation during the warmest quarter accounted for 82.7 % of the climatic suitability for *C. vellerosus*. For *C. polykomos*, the maximum temperature during the warmest month, mean diurnal temperature range, precipitation during the driest month, precipitation during the wettest month, precipitation during the warmest quarter, and annual mean temperature accounted for 83.8 % of its climatic suitability (Tables S2 and S3).

Table 1
Computation of range size changes for the ensemble forecasting of *C. vellerosus* and *C. polykomos*. CCSA: current climatically suitable areas; Loss: currently suitable areas predicted to be lost, Stable: occupied stable areas; Gain: areas predicted to become suitable; %SRC: percentage of species range change; FRS0D: future range size assuming zero dispersal; FRSFD: future range size assuming full dispersal. Projections are based on the low greenhouse gas emission scenario for the years 2040–2060. All dimensions are in km^2.

Taxon	CCSA km^2	Loss km^2	Stable km^2	Gain km^2	Loss %	Gain %	SRC %	FRS0D km^2	FRSFD km^2
C. vellerosus	520,193	113,000	407,193	18,886	21.7	3.6	−18.1	407,193	426,079
C. polykomos	240,398	181,971	58,427	2857	75.7	1.2	−74.5	58,427	61,284

3.2. Current climatically suitable areas

The climatically suitable area for *C. vellerosus* spans 520,193 km² (Table 1; Fig. 2), exceeding its IUCN-defined distribution range of 478,687 km². The predicted suitable area overlaps with the IUCN range by 71 %, amounting to 366,822 km² of the total 520,193 km². The 29 % of the predicted suitable area that lies outside the IUCN distribution range encompasses the Tai National Park to the southwest, significantly surrounds the region where the species is probably extinct in Burkina Faso to the northwest, and extends southeast to include Okomu National Park and Ologbo Game Reserve in Nigeria. Suitable areas for *C. vellerosus* have also been identified in the Fouta Djallon Highlands of Guinea.

For *C. polykomos*, the estimated climatically suitable area is 240,398 km², which is smaller than the IUCN-defined distribution range of 343,041 km². This predicted suitable area overlaps with the IUCN-defined distribution range of *C. polykomos* by 78 %, representing 186,728 km² of the total predicted area of 240,398 km². The remaining 22 % of the predicted suitable habitat, which does not overlap with the known range, extends into the Bandama and Sassandra interfluvial zone, encompassing the vicinity of the Yikpa waterfall in Togo and covering the western portions of Okomu National Park and Ologbo Game Reserve in Nigeria (Table 2 and Fig. 2).

3.3. Future climatically suitable areas

Based on the low greenhouse gas emission scenario and projections for the years 2040–2060, climatically suitable areas for *C. vellerosus* are expected to decrease by approximately 21.7 % (113,000 km²), while those for *C. polykomos* are projected to decline by 75.7 % (181,971 km²) under the zero-migration assumption (Fig. 3). In the case of the unlimited migration assumption, *C. vellerosus* will gain 3.6 % (18,886 km²), and *C. polykomos* 1.2 % (2857 km²). Therefore, for *C. vellerosus* we anticipate a reduction in suitable area of 18.1 %, while for *C. polykomos* a decrease of around 74.6 % is expected (Table 1 and Fig. 3).

3.4. Current and future overlapping suitable areas

Under present climatic conditions, the total climatically suitable area for the two species amounted to 740,923 km² (Fig. 2), with 500,525 km² for *C. vellerosus* and 220,730 km² for *C. polykomos*. The spatial overlap of both species encompassed an area of 19,668 km², which represents 2.7 % of the total suitable are for both taxa.

Under the low greenhouse gas emission scenario, the projected climatically suitable area for both taxa was 485,313 km² (Fig. 3), 424,029 km² for *C. vellerosus*, and only 59,234 km² for *C. polykomos*. Most currently overlapping areas are predicted to become unsuitable for *C. polykomos*, reducing the overlapping area to just 2,050 km² (0.4 % of the total projected suitable area for both species).

3.5. Forested and protected forested areas within the suitable range for long-term conservation

Covering an area of approximately 1624,800 km², representing our study's focus, there was about 370,000 km² of tree cover (Fig. S3). From 2001–2023, this area has lost 127,000 km² of its tree cover, amounting to a 26 % reduction since the 2000s. Only 7.3 % (27,066 km²) and 43.3 % (160,189 km²) of this tree cover were suitable forested areas for *C. vellerosus* and *C. polykomos*, respectively. Furthermore, we found that 52.1 % (14,102 km²) and 17.1 % (27,385 km²) of these suitable forested areas were located within protected zones of at least 1 km² for *C. vellerosus* and *C. polykomos*, respectively (Table 2, Fig. 4, Fig. 5). Our modelling predicted that by 2050, 41.3 % (11,188 km²) of the current suitable forested areas will remain viable for *C. vellerosus*, while only 28.1 % (45,019 km2) will remain suitable for *C. polykomos*. Almost all current overlapping areas were expected to become unsuitable for *C. polykomos*.

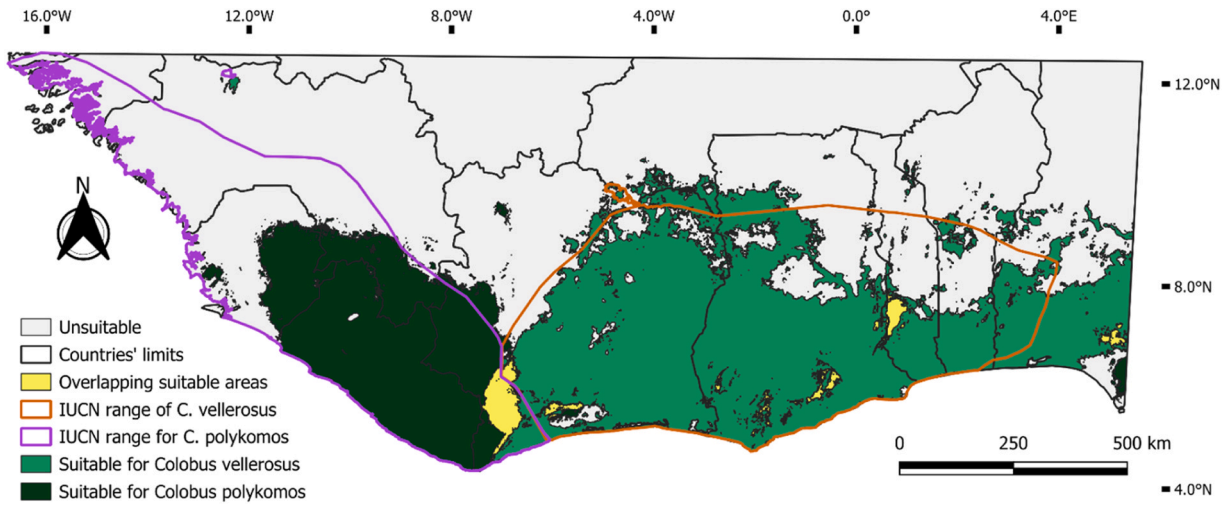


Fig. 2. Current climatically suitable and overlapping areas for *Colobus vellerosus* and *C. polykomos*.

Table 2
Sizes of the IUCN defined-ranges, climatically suitable areas, suitable forested areas, and suitable forested areas within protected areas for *Colobus vellerosus* and *C. polykomos*.

Taxa	IUCN range size	climatically suitable area	suitable forested area	suitable forested area within PAs
C. vellerosus	478,687	520,193	27,066	14,102
C. polykomos	343,041	240,398	160,189	27,385

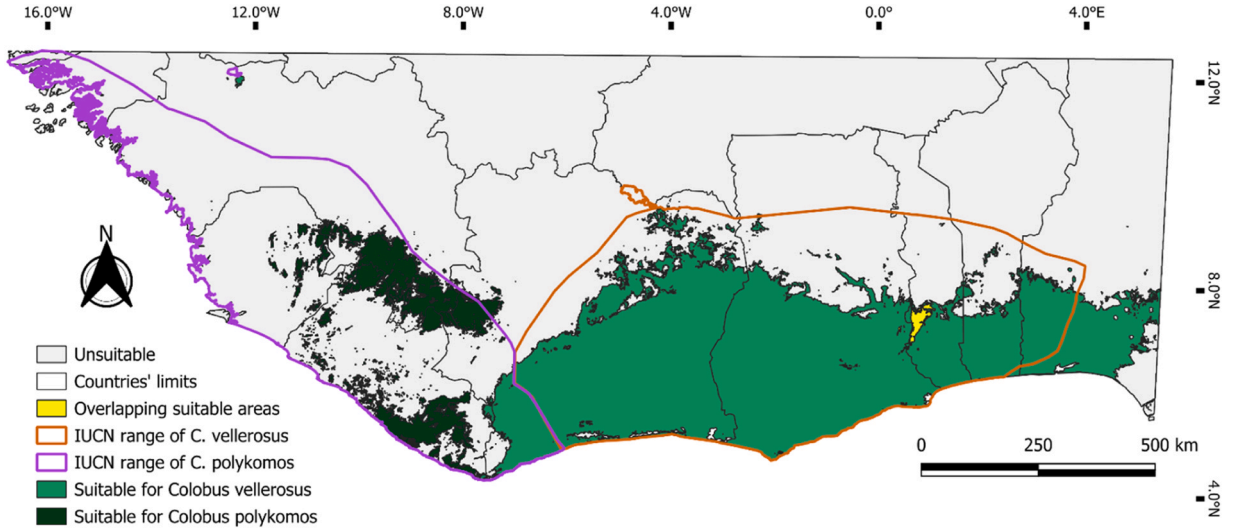


Fig. 3. Climatically suitable areas and overlapping areas for *Colobus vellerosus* and *C. polykomos* based on the low greenhouse gas emission scenario by 2050.

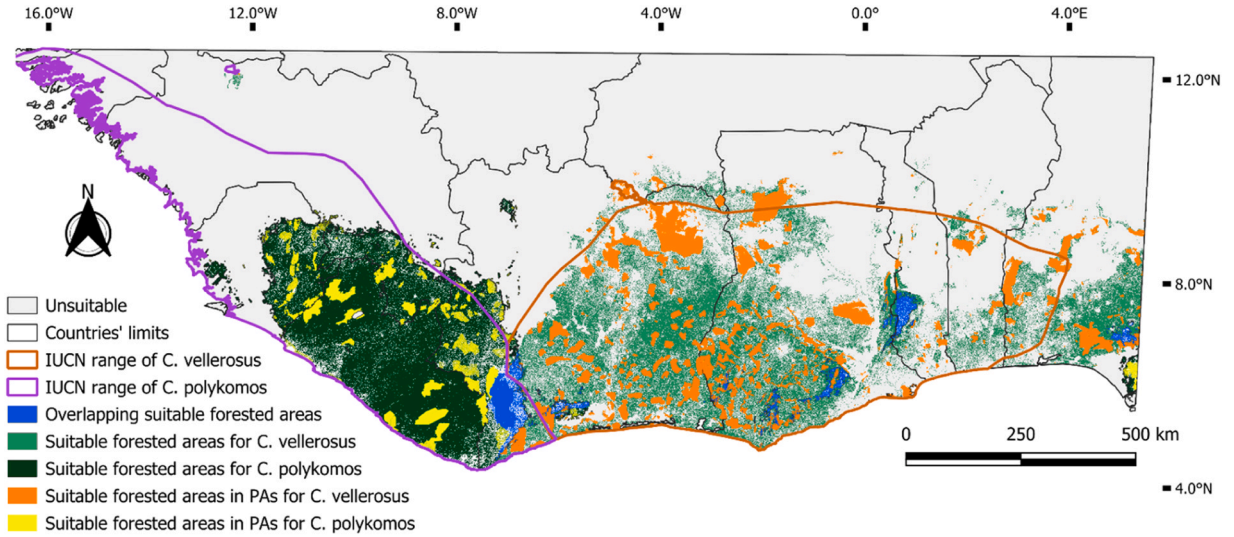


Fig. 4. Suitable forested areas for *Colobus vellerosus* and *C. polykomos* based on current climate conditions.

3.6. Identified suitable protected forests for C. vellerosus

We identified 527 protected areas (PAs) and other effective conservation measures (OECMs, Fig. S4) that were suitable for *C. vellerosus*, each containing at least 1 km^2 of forest under the current climate conditions. Within these PAs and OECMs, *C. vellerosus* has been observed in eight forests over the past two decades (from 2004 to 2024), specifically: Lama Classified Forest, Comoe National Park, Boabeng-Fiema Monkey Sanctuary, Kakum National Park, Mole National Park, Opara (Okpara) Forest/Game Reserve, Old Oyo, and Fazao-Malfakassa. However, since 2004, *C. vellerosus* has not been recorded in four of the identified forests: Ouémé Supérieur

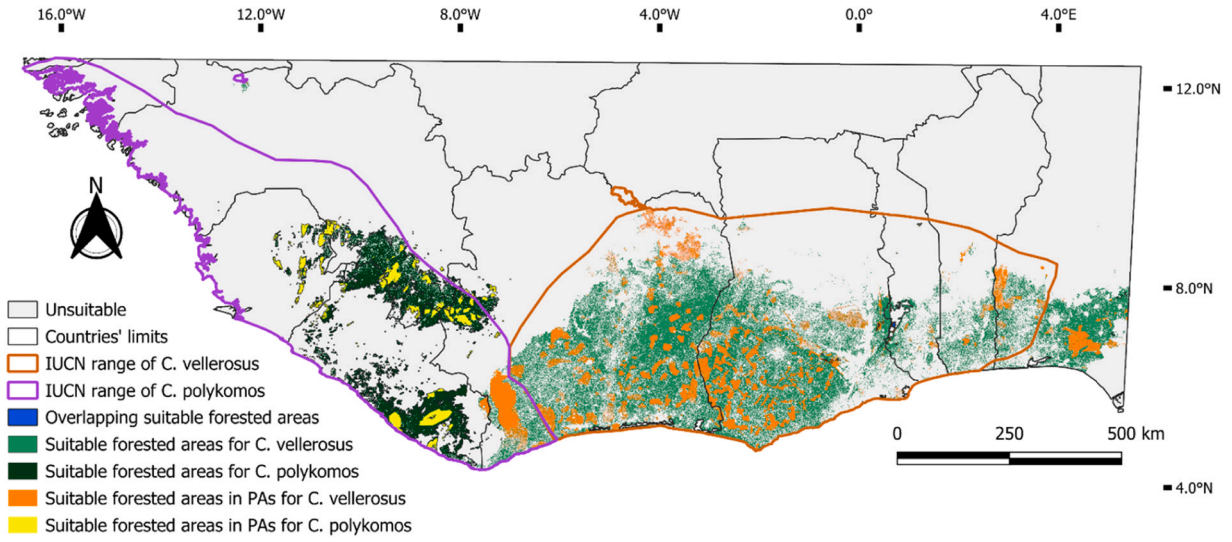


Fig. 5. Suitable forested areas for *Colobus vellerosus* and *C. polykomos* according to the low greenhouse gas emission scenario for 2050.

Classified Forest, Bosomoa Forest Reserve, Bui National Park, and Digya National Park, and it may have possibly gone extinct in four others: Mont-Kouffé Classified Forest, Wari-Maro Classified Forest, Pénéssoulou Classified Forest, and Comoé-Léraba Partial Wildlife Reserve. No sightings of *C. vellersosus* have been documented in the remaining 511 forests. Of the 527 identified PAs, 437 were expected to remain suitable for *C. vellerosus*, based on the low greenhouse gas emission scenario in 2050.

4. Discussion

Our research assessed suitable forested areas for two closely related parapatric species, *C. vellerosus* and *C. polykomos*. Given the high risk of extinction that *C. vellerosus* is facing, we identified protected suitable habitats of adequate size that could serve for its reintroduction or support its long-term conservation efforts over its next three generations. We found that *C. vellerosus* has a climatically suitable area larger than its IUCN-defined range, while *C. polykomos* has a smaller suitable area than its IUCN-defined range. Even under a low greenhouse gas emission scenario by 2050, both species may face significant habitat reductions.

Our results show a significant gap between the climatically suitable areas and the current known distributions of both taxa. Moreover, there are overlapping regions for both taxa that contrast with their reported parapatric distribution. This discrepancy suggests that both species face limitations in their natural expansion, despite the availability of suitable habitats at present. Such constraints on expansion may be attributed to a variety of factors, including ancient ecological and historical barriers, differing habitat preferences, phylogeographic and evolutionary influences, and anthropogenic pressures. Previous research has highlighted the probable geographic barrier posed by the Sassandra and Bandama rivers concerning *C. vellerosus* and *C. polykomos* (Booth, 1954), separating *C. polykomos* west of the Sassandra River and *C. vellerosus* east of the Bandama River (Groves, 2007; Groves et al., 1993). Groves et al. (1993) hypothesized that *C. polykomos* once extended as far east as the Bandama River. Whether this was the case remains currently an open question, because genetic studies on the interfluvial form "*Colobus polykomos dollmani*", which might be a hybrid, are still missing (Gonedelé Bi et al., 2006; Oates and McGraw, 2009).

Furthermore, the Dahomey Gap, which stretches across Ghana, Togo, and Benin, is believed to have served as a major natural barrier to the distribution of forest-dwelling mammals (Campbell et al., 2008), such as colobine monkeys. While both species are folivorous, the diet of *C. polykomos* contains a greater proportion of fruit (Korstjens et al., 2009) than *C. vellerosus,* which is regarded as the most folivorous species among the West African black-and-white colobus (Fashing, 2022). *Colobus polykomos* relies more on rainforest and gallery forest (Gonedelé Bi et al., 2020), whereas *C. vellerosus* inhabits lowland rainforest, swamp forests, semi-deciduous forests, and gallery forests within the savannah zone (Matsuda Goodwin et al., 2020a, 2020b). Climate-only models do not account for the above-mentioned ecological constraints (Soberón and Nakamura, 2009), which could explain the parapatric distribution of the two species, despite our climatic model showing overlapping areas.

A concerning trend has emerged from our models, revealing a southward reduction in climatically suitable areas for both species. This suggests that climatic conditions may remain favourable only in the southern regions of their geographic ranges. Thus, our modelling projected that the Mole National Park in Ghana, the Fazao-Malfakassa in Togo, and the Kikélé Sacred Forest (KSF) in central Benin, current habitats for *C. vellerosus*, will likely become unsuitable for its survival. The KSF is the only habitat in Benin where *C. vellerosus* suffers less pressure from illegal hunting, as its population has been protected by the traditional beliefs of the Kikélé villagers for several decades (Djègo-Djossou et al., 2012). This underscores the need to extend and restore the KSF to protect *C. vellerosus* and its ecosystem.

Currently, only a small amount of existing forested habitats are suitable for both species. A significant proportion of these viable

habitats are located outside protected areas. Under a best-case climate scenario to 2050, we anticipate a substantial reduction in suitable habitats for both species. In light of this, it is vital to enhance conservation efforts beyond the current boundaries of protected areas by incorporating secondary forests and community-managed forested areas deemed suitable in the medium term. Yet *C. vellerosus* is predominantly found in community forests (Matsuda Goodwin et al., 2019), and many protected areas continue to face threats from illegal hunting (Djagoun et al., 2018; Schwitzer et al., 2017, 2019). Priorities should include expanding the protected area network, implementing sustainable management practices for unprotected forests, and establishing ecological corridors. Furthermore, the case of *C. vellerosus*, which may have already vanished from eight historically occupied forests, underscores the urgent need for field monitoring programs and reassessment of the status of remaining populations.

Identifying potentially suitable forested areas for the reintroduction of *C. vellerosus* is a vital strategy for its survival. Such areas could serve not only to re-establish viable populations but also to enhance ecological connectivity between fragmented habitats, particularly among the 437 sites projected to remain suitable by 2050. This connectivity is useful for mitigating genetic isolation and preventing inbreeding (Bergl and Vigilant, 2006; Lawes, 2005). However, illegal hunting (Oates, 2011; Refisch and Koné, 2005) and habitat fragmentation (McGraw, 2005; Minhós et al., 2023) are the most significant anthropogenic pressures likely affecting the distribution of both species. Particularly, these two threats are important drivers of *C. vellerosus* declines across West Africa (Djègo-Djossou and Sinsin, 2009; Gautier-Hion et al., 1999; Ota, 2020, Oates, 2011). Therefore, any reintroduction program for *C. vellerosus* must effectively address hunting risk and establish long-term habitat protection to ensure success.

The IUCN reintroduction guidelines explicitly require that the major threats, which caused declines, be effectively controlled at release sites (IUCN/SSC, 2013). Consistent with IUCN reintroduction standards and existing evidence-based successful reintroductions (Brando et al., 2020; Imam et al., 2002; King et al., 2012; Soorae, 2021), any conservation reintroduction program should align with national and regional conservation frameworks and recognize the roles of existing agencies and legal guidelines. It must consider the legitimate interests of local communities, addressing their socio-economic circumstances, values, expectations, and the expected costs and benefits of the translocation. In practice for *C. vellerosus*, that means prioritizing sites with demonstrably effective protection (e.g., areas with long-standing traditional taboos), co-designing no-hunting agreements with local communities backed by clear benefits (employment as guardians, tourism revenue-sharing), law-enforcement and biomonitoring capacity building, and post-release monitoring with adaptive responses to any hunting incidents.

The experience at Boabeng-Fiema Monkey Sanctuary in Ghana shows that when hunting is socially or legally suppressed, *C. vellerosus* populations can stabilize and even increase (Wiafe et al., 2023). Ensuring these safeguards are in place before reintroduction will greatly improve the likelihood that costly conservation interventions achieve lasting results.

Our research examines the climatic suitability and the presence of forests within areas deemed suitable for the species. However, selecting appropriate habitats for a species reintroduction necessitates comprehensive ecological assessments of potential sites, a thorough evaluation of anthropogenic impacts, engagement with local communities to gauge their support, and population genetic studies of the source animal populations. Importantly, the cessation of hunting activities is a prerequisite for any successful reintroduction of *C. vellerosus* or any conservation efforts for both taxa. One viable conservation strategy involves promoting ecotourism and facilitating the development of sustainable livelihoods within local communities. By generating alternative income sources and enhancing livestock production, we can help secure a stable protein supply while simultaneously fostering awareness and support for primate conservation initiatives in local communities.

5. Conclusion

In our study, we identified climatically suitable forests in and outside protected areas that can serve as refugia for *C. vellerosus* and *C. polykomos* in the face of climate change challenges. The protection of these suitable forests, combined with reintroduction efforts and sustainable habitat management, represents an essential avenue for preserving both colobus species. Successful conservation efforts will likely hinge on advancing awareness and fostering local community support to combat illegal hunting and bolster resilience to climate change impacts. Future research should investigate the population genetics of both taxa over their distribution ranges.

CRediT authorship contribution statement

Dietmar Zinner: Writing – review & editing, Visualization, Validation, Supervision, Investigation, Data curation, Conceptualization. **Inza Kone:** Writing – review & editing, Visualization, Validation, Supervision, Project administration, Investigation, Data curation. **S. S. Mireille Toyi:** Writing – review & editing, Validation, Supervision, Project administration, Investigation, Data curation. **F. Darius Accrombessi:** Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Ethical standards

Fieldwork adhered to the best practices outlined by the International Society of Primatologists for field primatology.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

The authors are grateful to the German Federal Ministry of Education and Research (BMBF) and the West African Science Service Centre on Climate Change and Adapted Land Use (WASCAL) through the Climate Change and Biodiversity Doctorate Research Program, Université Félix Houphouët-Boigny (UFHB) of Côte d'Ivoire, for funding this study. We thank our field guides Mr Ganiou ADJOFE and Mr Roger HOUNKANRIN for their help during the survey in central and southern Benin.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2025.e03820.

Data availability

Data will be made available on request.

References

Ajibola, F.O., Zhou, B., Shahid, S., Ali, M.A., 2022. Performance of CMIP6 HighResMIP simulations on west African drought. Front. Earth Sci. 10, 1–13. https://doi.org/10.3389/feart.2022.925358.

Allouche, O., Tsoar, A., Kadmon, R., 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). J. Appl. Ecol. 43 (6), 1223–1232. https://doi.org/10.1111/j.1365-2664.2006.01214.x.

Alonso, C., Hernansaiz, A.S., Fernández-Garcia, J.M., Ruiz De Azua, N., Aransay, N., Casas, S., Pacheco, L., 2019. Range extension of the king colobus *colobus polykomos* (Zimmermann, 1780) in north fouta djallon (Guinea). Afr. Primates 13, 1–8.

Bergl, R.A., Vigilant, L., 2006. Genetic analysis reveals population structure and recent migration within the highly fragmented range of the cross river gorilla (Gorilla gorilla diehli). Mol. Ecol. 16 (3), 501–516. https://doi.org/10.1111/j.1365-294X.2006.03159.x.

Booth, A.H., 1954. CV.—A note on the colobus monkeys of the gold and ivory coasts. Ann. Mag. Nat. Hist. 7 (83), 857–860. https://doi.org/10.1080/00222935408651801.

Brando, S., Atencia, R., Botting, J., Colin, C., Cunneyworth, P., Dorenmalen, A. van, Janssen, P., Mungania, N., Ortiz, S.T., Williams, S., & Tully, G. (2020). PASA study on reintroductions and releases of African primates: Understanding the impact of releases on primate conservation and determining the factors that contribute to their success (pp. 1–79). Study report, Pan African Sanctuary Alliance (PASA). ⟨https://pasa.org/wp-content/uploads/2021/09/PASA-Reintroduction-Study-Report.pdf⟩.

Breiman, L., 2001. Random forests. Mach. Learn. 45, 5–32. https://doi.org/10.1023/A:1010933404324.

Brown, J.L., 2014. SDMtoolbox: a python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. Methods Ecol. Evol. 5 (7), 694–700. https://doi.org/10.1111/2041-210X.12200.

Campbell, G., Teichroeb, J., Paterson, J.D., 2008. Distribution of diurnal primate species in Togo and Bénin. Folia Primatol. 79 (1), 15–30. https://doi.org/10.1159/000108383.

Djagoun, C.A.M.S., Sogbohossou, Etotépé A. Kassa, B., Akpona, H.A., Amahowe, I.O., Djagoun, J., & Sinsin, B. (2018). Trade in primate species for medicinal purposes. In Traffic (Vol. 30, Issue 2).

Djègo-Djossou, S., Sinsin, B., 2009. Distribution et statut de conservation du colobe de geoffroy (*colobus vellerosus*) au Bénin. Int. J. Biol. Chem. Sci. 3 (6), 1386–1397. https://doi.org/10.4314/ijbcs.v3i6.53158.

Djègo-Djossou, S.G. (2013). Aires d'occurrence et éco-éthologie du colobe de Geoffroy (Colobus vellerosus) et du colobe olive (Procolobus verus) au Bénin. PhD thesis Université d'Abomey-Calavi.

Djègo-Djossou, S.G., Huynen, M.C., Djego, J., Sinsin, B., 2012. Croyances traditionnelles et conservation du colobe de geoffroy, *Colobus vellerosus* (Geoffroy, 1834), dans la Forêt Sacrée de Kikélé, Bénin (Afrique de l'Ouest). Afr. Primates 7 (2), 193–212.

Elith, J., Kearney, M., Phillips, S., 2010. The art of modelling range-shifting species. Methods Ecol. Evol. 1 (4), 330–342. https://doi.org/10.1111/j.2041-210X.2010.00036.x.

Fashing, P.J., 2022. The natural history of black-and-White colobus monkeys. In: Matsuda, I., Grueter, C.C., Teichroeb, J.A. (Eds.), The Colobines. Cambridge University Press, Cambridge, UK, pp. 1–61. https://doi.org/10.1017/9781108347150.

Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. Int. J. Climatol. 37 (12), 4302–4315. https://doi.org/10.1002/joc.5086.

Fielding, A.H., Bell, J.F., 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environ. Conserv. 24 (1), 38–49. https://doi.org/10.1017/S0376892997000088.

Gautier-Hion, A., Colyn, M., Gautier, J.-P., Dewynter, M., Bouchain, C., 1999. Histoire naturelle des primates d'Afrique centrale. Ecofac. Gabon, Multipress.

Gonedelé Bi, S., Zinner, D., Koné, I., Bi, Z.G., Akpatou, B., Koffi Bené, J.C., Sangaré, A., Boesch, C., 2006. A west African black-and-White colobus monkey, *Colobus polykomos dollmani* schwarz, 1927, facing extinction. Primate Conserv. 21, 55–61. https://doi.org/10.1896/0898-6207.21.1.55.

Gonedelé Bi, S., Bitty, A., Ouatara, K., Scott Mcgraw, W., 2014. Primate surveys in Côte d'Ivoire's Sassandra-Bandama interfluvial region with notes on a remnant population of black-and-white colobus. Afr. J. Ecol. 52 (4), 491–498. https://doi.org/10.1111/aje.12151.

Gonedelé Bi, S., Koné, I., Matsuda Goodwin, R., Alonso, C., Hernansaiz, A., Oates, J.F., 2020. Colobus polykomos. The IUCN Red List of Threatened Species 2020, 8235(2307–8235). https://doi.org/10.2305/IUCN.UK.2020-2.RLTS.T5144A17944855.en.

Groves, C.P., 2007. The taxonomic diversity of the colobinae of Africa. J. Anthropol. Sci. 85, 7–34.

Groves, C.P., Angst, R., Westwood, C., 1993. The status of *colobus polykomos dollmani* schwarz. Int. J. Primatol. 14 (4), 573–586. https://doi.org/10.1007/BF02215448.

Guilherme, J.L., 2014. Birds of the Boé region, south-east Guinea-Bissau, including first country records of chestnut-backed sparrow lark *Eremopterix leucotis*, lesser striped swallow *Cecropis abyssinica* and Heuglin's wheatear *Oenanthe heuglini*. Bull. Afr. Bird. Club 21 (2), 155–168. https://doi.org/10.5962/p.310043.

Imam, E., Yahya, H.S.A., Malik, I., 2002. A successful mass translocation of commensal rhesus monkeys *Macaca mulatta* in Vrindaban, India. Oryx 36 (1), 87–93. https://doi.org/10.1017/S0030605302000133.

IUCN/SSC. (2013). Guidelines for Reintroductions and Other Conservation Translocations. Gland, Switzerland: IUCN Species Survival Commission. https://doi.org/10.1017/s0962728600005637.

Kankam, B.O., Sicotte, P., 2013. The effect of forest fragment characteristics on abundance of *Colobus vellerosus* in the forest-savanna transition zone of Ghana. Folia Primatol. 84 (2), 74–86. https://doi.org/10.1159/000348307.

Kazeem, A.O. (2017). *Conservation status of black and white colobus monkey* (Colobus vellerosus) *Geoffrey 1834 in upper Ogun Region, Southwest-Nigeria. MSc thesis, Federal University of Technology, Akure, Nigeria*.

King, T., Chamberlan, C., Courage, A., 2012. Assessing initial reintroduction success in long-lived primates by quantifying survival, reproduction, and dispersal parameters: western lowland gorillas (Gorilla gorilla gorilla) in Congo and Gabon. Int. J. Primatol. 33 (1), 134–149. https://doi.org/10.1007/s10764-011-9563-2.

Korstjens, A.H., 2019. The effect of climate change on the distribution of the genera *colobus* and *cercopithecus*. In: Behie, A.M., Teichroeb, J.A., Malone, N. (Eds.), Primate Research and Conservation in the Anthropocene. Cambridge University Press, Cambridge, UK, pp. 257–280. https://doi.org/10.1017/9781316662021.015.

Korstjens, A.H., Galat-luong, A., 2013. *Colobus polykomos* king colobus (Western pied colobus, Western black-and-White colobus). In: Butynski, T.M., Kingdon, J., Kalina, J. (Eds.), Mammals of Africa. Vol. II Primates. Bloomsbury, London, pp. 100–103.

Korstjens, A.H., Hillyer, A.P., 2016. Primates and climate change: a review of current knowledge. In: Wich, S., Marshall, A. (Eds.), An Introduction to Primate Conservation. Oxford University Press, Oxford, UK, pp. 175–192. https://doi.org/10.1093/acprof:oso/9780198703389.003.0011.

Korstjens, A.H., Bergmann, K., Deffernez, C., Krebs, M., Nijssen, E.C., van Oirschot, B.A.M., Paukert, C., Schippers, E.P., 2009. How small-scale differences in food competition lead to different social systems in three closely related sympatric colobines. In: McGraw, W.S., Zuberbühler, K., Noë, R. (Eds.), Monkeys of the Tai Forest: An African Primate Community. Cambridge University Press, Cambridge, UK, pp. 72–108. https://doi.org/10.1017/cbo9780511542121.004.

Korstjens, A.H., Lehmann, J., Dunbar, R.I.M., 2010. Resting time as an ecological constraint on primate biogeography. Anim. Behav. 79 (2), 361–374. https://doi.org/10.1016/j.anbehav.2009.11.012.

Lawes, M.J., 2005. Conservation of fragmented populations of *cercopithecus mitis* in South Africa: the role of reintroduction, corridors and metapopulation ecology. In: Glenn, M.E., Cords, M. (Eds.), The Guenons: Diversity and Adaptation in African Monkeys. Springer, Boston, MA, pp. 375–392. https://doi.org/10.1007/0-306-48417-X_24.

Lehmann, J., Korstjens, A.H., Dunbar, R.I.M., 2010. Apes in a changing world - the effects of global warming on the behaviour and distribution of African apes. J. Biogeogr. 37 (12), 2217–2231. https://doi.org/10.1111/j.1365-2699.2010.02373.x.

Matsuda Goodwin, R., Gonedelé Bi, S., Nobimè, G., Koné, I., Osei, D., Segniagbeto, G., Oates, J.F., 2019. Colobus vellerosus. The IUCN Red List of Threatened Species. https://doi.org/10.2305/IUCN.UK.2019-3.RLTS.T5146A17944551.en.

Matsuda Goodwin, R.M., Gonedelé Bi, S.E., Baxt, A., Bitty, E.A., Wiafe, E.D., Kone, N.A., 2020a. Surveys and canopy cameras of critically threatened monkeys in Comoé national park, Côte d'Ivoire: a preliminary report. Annu. Rep. Pro Nat. Found. Jpn. 29.

Matsuda Goodwin, R.M., Gonedelé Bi, S.E., Nobimè, G., Koné, I., Osei, D., Segniagbeto, G., Oates, J.F., 2020b. Colobus vellerosus. The IUCN Red List of Threatened Species. https://doi.org/10.2305/IUCN.UK.2020-2.RLTS.T5146A169472127.en.

McCullagh, P., Nelder, J.A., 2019. Generalized linear models. Routledge, New York. https://doi.org/10.1201/9780203753736.

McGraw, W.S., 2005. Update on the search for miss Waldron's red colobus monkey. Int. J. Primatol. 26 (3), 605–619. https://doi.org/10.1007/s10764-005-4368-9.

Meadows, M. (2022). SMART 7 Technical Training Manual. SMART Partners. ⟨https://smartconservationtools.org/en-us/Resources/SMART-Manuals⟩.

Minhós, T., Borges, F., Parreira, B., Oliveira, R., Aleixo-Pais, I., Leendertz, F.H., Wittig, R., Fernandes, C.R., Marques Silva, G.H.L., Duarte, M., Bruford, M.W., Ferreira da Silva, M.J., Chikhi, L., 2023. The importance of well protected forests for the conservation genetics of west African colobine monkeys. Am. J. Primatol. 85 (1), e23453. https://doi.org/10.1002/ajp.23453.

Mittermeier, R.A., Reuter, K.E., Rylands, A.B., Jerusalinsky, L., Schwitzer, C., Strier, K.B., Ratsimbazafy, J., & Humle, T. (2022). *Primates in Peril: The World's 25 Most Endangered Primates 2022–2023*. IUCN SSC Primate Specialist Group, International Primatological Society, Re:wild, Washington, DC.

Muscarella, R., Galante, P.J., Soley-Guardia, M., Boria, R.A., Kass, J.M., Uriarte, M., Anderson, R.P., 2014. ENMeval: an R package for conducting spatially independent evaluations and estimating optimal model complexity for maxent ecological niche models. Methods Ecol. Evol. 5 (11), 1198–1205. https://doi.org/10.1111/2041-210X.12261.

Nkrumah, F., Quagraine, K.A., Quagraine, K.T., Wainwright, C., Quenum, G.M.L.D., Amankwah, A., Klutse, N.A.B., 2022. Performance of CMIP6 HighResMIP on the representation of onset and cessation of seasonal rainfall in Southern West Africa. Atmosphere 13 (7), 999. https://doi.org/10.3390/atmos13070999.

Oates, J.F., 2011. Primates of West Africa: a field guide and natural history. Conservation International, Arlington, VA.

Oates, J.F., McGraw, W.S., 2009. A comment on the status of '*Colobus polykomos dollmani*' in Côte d'Ivoire. Primate Conserv. 24 (1), 73–76. https://doi.org/10.1896/052.024.0104.

Ota, R.C. (2020). *Outreach and the development of primate tourism to protect the Critically Endangered white-thighed colobus* (Colobus vellerosus) *at Kikélé Sacred Forest, Benin. Final project report*, Conservation Association of Benin Fauna and Flora (CABFF), *Benin*.

Phillips, S.J., Anderson, R.P., Dudík, M., Schapire, R.E., Blair, M.E., 2017. Opening the black box: an open-source release of maxent. Ecography 40 (7), 887–893. https://doi.org/10.1111/ecog.03049.

Refisch, J., Koné, I., 2005. Market hunting in the Taï region, Côte d'Ivoire and implications for monkey populations. Int. J. Primatol. 26 (3), 621–629. https://doi.org/10.1007/s10764-005-4369-8.

Ridgeway, G., Developers, G., 2003. Gbm: generalized boosted regression models. CRAN Contrib. Packages. https://doi.org/10.32614/CRAN.package.gbm.

Roos, C., Zinner, D., 2022. Molecular phylogeny and phylogeography of colobines. In: Matsuda, I., Grueter, C.C., Teichroeb, J.A. (Eds.), The Colobines: Natural History, Behaviour and Ecological Diversity. Cambridge Studies in Biological and Evolutionary Anthropology. Cambridge University Press, Cambridge, UK, pp. 32–43. https://doi.org/10.1017/9781108347150.005.

Saj, T. l, Sicotte, P., 2013. *Colobus vellerosus* White-thighed colobus (Geoffroy's pied colobus, ursine colobus). In: Butynski, T.M., Kingdon, J., Kalina, J. (Eds.), Mammals of Africa. Vol. II Primates. Bloomsbury, London, pp. 109–111.

van Schaik, C.P., Pfannes, K.R., 2005. Tropical climates and phenology: a primate perspective. In: Brockman, D.K., van Schaik, C.P. (Eds.), Seasonality in Primates. Studies of Living and Extinct Human and Non-Human Primates. Cambridge University Press, Cambridge, UK, pp. 23–54. https://doi.org/10.1017/CBO9780511542343.003.

Schwitzer, C., Mittermeier, R.A., Rylands, A.B., Chiozza, F., Williamson, E.A., Macfie, E.J., Wallis, J., & Cotton, A. (2017). *Primates in Peril: The World's 25 Most Endangered Primates 2016–2018*. IUCN SSC Primate Specialist Group (PSG), International Primatological Society (IPS), Conservation International (CI), and Bristol Zoological Society, Arlington, VA.

Schwitzer, C., Mittermeier, R.A., Rylands, A.B., Chiozza, F., Williamson, E.A., Byler, D., Wich, S., Humle, T., Johnson, C., Mynott, H., & McCabe, G. (2019). *Primates in Peril: The World's 25 Most Endangered Primates 2018–2020*. IUCN SSC Primate Specialist Group, International Primatological Society, Global Wildlife Conservation, and Bristol Zoological Society, Washington, DC.

Segniagbeto, G.H., Assou, D., Koda, K.D., Agbessi, E.K.G., Atsri, K.H., Dendi, D., Luiselli, L., Decher, J., Mittermeier, R.A., 2017. Survey of the status and distribution of primates in Togo (West Africa). Biodiversity 18 (4), 137–150. https://doi.org/10.1080/14888386.2017.1404930.

Soberón, J., Nakamura, M., 2009. Niches and distributional areas: concepts, methods, and assumptions. Proc. Natl. Acad. Sci. 106 (supplement 2), 19644–19650. https://doi.org/10.1073/pnas.0901637106.

Soorae, P.S. (Ed.) (2021). *Global Conservation Translocation Perspectives: 2021. Case Studies from Around the Globe*. IUCN SSC Conservation Translocation Specialist Group, Environment Agency - Abu Dhabi and Calgary Zoo, Canada, Gland, Switzerland. ⟨www.iucn-ctsg.org⟩.

Swets, J.A., 1988. Measuring the accuracy of diagnostic systems. Science 240 (4857), 1285–1293. https://doi.org/10.1126/science.3287615.

Thuiller, W., Georges, D., Gueguen, M., Engler, R., Breiner, F., Lafourcade, B., & Patin, R. (2023). *Ensemble Platform for Species Distribution Modeling [R package biomod2 version 4.2-4]*. ⟨https://cran.r-project.org/package=biomod2⟩.

Ting, N., 2008. Mitochondrial relationships and divergence dates of the African colobines: evidence of miocene origins for the living colobus monkeys. J. Hum. Evol. 55 (2), 312–325. https://doi.org/10.1016/j.jhevol.2008.02.011.

UNEP-WCMC, IUCN, 2024. Protected planet: Africa; the world database on protected areas (WDPA)/Database on other effective area- based conservation measures. UNEP-WCMC and IUCN, Cambridge, UK. ⟨www.protectedplanet.net⟩.

Wiafe, E.D., 2021. Distribution and population density of endangered primate species in Ghana's forest reserves. Forestist 71 (3), 238–247. https://doi.org/10.5152/forestist.2021.20040.

Wiafe, E.D., Akuaku, K.K., Sarkodie, I., Boakye, M.K., 2023. Current populations of *Colobus vellerosus* (Geoffory, 1834) & *Cercopithecus lowei* (Thomas, 1923) and land-use, land cover changes in Boabeng-Fiema monkey sanctuary, Ghana. J. Threat. Taxa 15 (5), 23200–23209. https://doi.org/10.11609/jott.8297.15.5.23200-23209.

Zhang, K.C., Zhou, Q.H., Xu, H.L., Huang, Z.H., 2021. Diet, food availability, and climatic factors drive ranging behavior in white-headed langurs in the limestone forests of guangxi, southwest China. Zool. Res. 42 (4), 406–411. https://doi.org/10.24272/j.issn.2095-8137.2020.292.