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Levels of ecological conservatism in African Guenons: a comparative study using MaxEnt modelling and ENMTools.

Thesis by A.E. Thom Masters by Research in Biological sciences Bangor University Supervised by Dr I. Winder and Dr V. Shaw February 2023 I hereby declare that this thesis is the results of my own investigations, except where otherwise stated. All other sources are acknowledged by bibliographic references. This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree unless, as agreed by the University, for approved dual awards.

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Abstract

Guenons, or genus Cercopithecus, have been studied for over a hundred years, but new insights into speciation as well as the introduction of genetic methods into primatology have created difficulties with the taxonomic definition of different species. Scientists now recognise more guenon species than ever before, but it is unclear whether these are truly distinct from one another anatomically, genetically or ecologically. There is also a bias in knowledge: diet has been explored quite extensively, and polyspecific associations are well-known, but we remain uncertain about fundamental ecological and behavioural features of all guenon species. There are also currently no investigations into their present ecological needs using MaxEnt modelling as a research tool, this research addresses this gap. It aims to create the first species distribution models for all the guenon species listed by the IUCN Red List, and explore zones of overlap to characterise their ecological distinctiveness. To make these models, I took locality data points from GBIF and iNaturalist and historical environmental data from various sources. I used this data to create MaxEnt models which were then converted to presence absence maps in ArcGIS. Using ENMTools to quantify the species overlap. These show the predicted suitable habitat of the guenons and genus Allochrocebus, used as an outgroup. Guenons are known to have conservative anatomy and genetics that show very limited divergence between species, despite having high variation in chromosome numbers. My results show that guenons also have conservative ecological needs, however the MaxENT models still demonstrate some areas of distinct habitat for each species. There is therefore enough ecological difference to provide distinct geographical outlines for each species, though most species could coexist across much of their ranges. Using ENMTools also shows that Guenons are ecologically conservative. As a genus, guenons have high levels of ecological flexibility, this likely contributes to the species also having a great amount of predicted suitable habitat overlap, allowing them to have so much ecologically in common. This leads to the situation where many guenon ranges are predicted as suitable habitat for more than one species. I have thus demonstrated that the guenons

are ecologically conservative and capable, according to my models, of potentially extending the ranges that they occupy beyond their current boundaries. Some are also extant in areas that are not predicted suitable. There must therefore be some other driving force than just their ecology that makes it advantageous to live in these areas, perhaps through methods like polyspecific association as it is seen in some known associations that species associate more when they are less similar than others in their area; or perhaps some geographic barriers (not all of them currently visible) that prevent certain species from occupying all their suitable habitat. The ENMTools results also show that in the case of some polyspecific associations where similarity is high that strategies are used to reduce competition. This research suggest that there is still much to be learned about guenon ecology and how the genus *Cercopithecus* partitions ecological space.

Introduction

Guenons have been known to science since 1773, where the species *Cercopithecus diana* and *Cercopithecus cephus* were described in a paper by Buffon, Daubenton and Engelen (1773). Their skeletal morphology, dietary ecology and genetics have been investigated extensively (see for example Arenson et al., 2020; Butynski, 1990; Gilbert et al., 2014; Glenn & Cords, 2002; lo Bianco et al., 2017; Manaster, 1979). However, their ecology has not been investigated through MaxEnt modelling or ENMTools raster.overlap to understand the ecological conditions preferred by the different species of the Guenon. This piece of research addresses that gap.

What is a guenon?

Guenons, referring to the whole of tribe Cercopithecini, are considered to be the most diverse primate group in Africa (Cardini & Elton, 2008a; Glenn & Cords, 2002; lo Bianco et al., 2017), with genus *Cercopithecus* the most diverse genus within Cercopithecini (lo Bianco, Masters and Sineo, 2017). They are monkeys endemic to Sub-saharan Africa (Glenn and Cords, 2002). 'Guenon' can refer to either the whole tribe Cercopithecini or to only the genus *Cercopithecus* (which exists within tribe Cercopithecini). For the purpose of this investigation, 'guenon' is used only in reference to Genus *Cercopithecus*.

Glenn and Cords (2004) state that the Cercopithecini are spread from Mauritania to the Cape of Good Hope. The habitats of Cercopithecini range from mangrove swamp (sea level) to alpine moorland (4,500m above sea level) and they live on the edges of the Sahara and Kalahari deserts as well as in woodland, bamboo forests and rainforest (Glenn and Cords, 2002). It is important to note that guenons are widely sympatric. Different species have similar diet and morphology ence between the guenons and their outgroup.

Lo Bianco, Masters and Sineo (2017, p 337) describes the Cercopithecuini as having 'slender mediumsized bodies, tails that are longer than the head and body combined'. The Cercopithecus also show very little divergence in their skeletal structure, both cranial (Cardini and Elton, 2008c, 2008b) and post cranial (Nakatsukasa, 1994; lo Bianco, Masters and Sineo, 2017). However, despite their conserved skeletal structure guenons have diverse soft tissue morphology and pelage (Cardini and Elton, 2008b; Moulin *et al.*, 2008). For example, many species have features such as stand out moustaches, eyebrows and nose spots.

Ecological investigations of guenons in the literature have tended to focus on diet. The flexibility of a guenon's diet is affected by their biogeography (Coleman and Hill, 2014), seasonal changes, sex great diversity in, for example the karyotype (lo Bianco, Masters and Sineo, 2017). There have also been multiple comparisons of diets between species that are in polyspecific association with others (Paul J. Buzzard, 2006b; Bryer, Chapman and Rothman, 2013) and ecology papers where the diet is a

major part of the research (Wahome, Rowell and Tsingalia, 1993; Peignot, Fontaine and Wickings, 1999; Kaplin and Moermond, 2000; Hutchinson, 2015). Exploring diet is a practical method for evaluating ecological differences between species. It tells us about trophic relationships, interactions within their food webs or population dynamics and how the structure and function of an ecosystem works (Wagner *et al.*, 2013).

Cercopithecus monkeys eat various amounts of fruit, leaves, flowers, animal matter (such as insects), fungi, seeds and gum (Glenn and Cords, 2002). Diet has been investigated either by looking at the percentage of different types of food found in the stomachs of cadavers (Gautier-Hion, 1980; Coleman and Hill, 2014), or through behavioural studies observing the frequency of what the monkeys eat in the field. In this instance scientists are only able to record what they see, which creates a constraint as the monkeys may be at stratum in the forest that is difficult to observe (Wahome, Rowell and Tsingalia, 1993; Twinomugisha, Basuta and Chapman, 2003; Paul J. Buzzard, 2006b; Bryer, Chapman and Rothman, 2013; Coleman and Hill, 2014; Hutchinson, 2015).

In terms of Guenons and genetics it follows the theme of anatomy and ecology, the monkeys show great diversity in, for example the karyotype (lo Bianco, Masters and Sineo, 2017). They also show a wide range of diploid chromosome numbers between 58 for *Cercopithecus diana* and *Cercopithecus roloway* and 72 for *Cercopithecus mitis, Cercopithecus petaurista* and *Cercopithecus pogonias* (Moulin *et al.*, 2008) it is noted however by lo Bianco, Masters and Sineo (2017) that the Cercopithcini genetics do not have as high sequencing divergence as would be expected, describing it as 'remarkably low' despite there being 'evidence of extensive genetic reshuffling'.

What species are included in the guenons?

Genus *Cercopithecus* includes 20 species recognised by the International Union for Conservation of Nature's Red List of Threatened Species (*IUCN Red List of Threatened Species*, 2021). The Red List is a tool that is used by organisations and governments to understand biodiversity and inform conservation efforts. Because of this the IUCN is regularly updated with new information found in literature. For guenons, this is particularly important because their taxonomy has experienced a lot of change over the last few decades and has fluctuated since the genus was first described by Buffon, Daubenton and Engelen in 1773. The original methods for naming of species have developed over the intervening decades particularly because of advances in the use of genetics. The taxonomy of various species has therefore been updated, and some species formerly considered to be within genus *Cercopithecus* have come to belong to other genera (Zinner and Roos, 2014).

These taxonomic changes seem to have mostly been caused by arguments about the importance of different species concepts and their relative validity (de Queiroz, 2007; Carstens *et al.*, 2013). There are many different species concepts such as the genetic species concept, the morphological species concept, the ecological species concept, pluralistic species concept and phenetic species concept (Groves, 2012; Zinner and Roos, 2014; Park and Allaby, 2017; Aldhebiani, 2018). However, this seems to have mostly been solved by an agreement to view concepts as 'alternative descriptions of the general lineage concepts'. In other words, the definitions mean the same things but with different emphasis , describing it as 'remarkably low' despite there being 'evidence of extensive genetic reshuffling'.

I use the IUCN Red List through my thesis as the core taxonomic paradigm around which inconsistencies can be demonstrated. Table 1 provides a summary of each species listed by the IUCN and the uncertainties still visible in other sources.



Fig 1. Shows research grade images of the investigated monkeys outlined in the same colour and pointing at the IUCN predicter extant habitat. Photos and ranges for seven species of genus *Cercopithecus*, including (1) *C. ascanius* (photograph © Gregoire Dubois 2014, some rights reserved under a CC-BY-NC license); (2) *C. campbelli* (photograph © iNaturalist user G0mette 2021 under a CC-BY license); (3) *C. cephus* (photography © Mathias D'haen 2019, some rights reserved under a CC-BY-NC license; (4) *C. denti* (photography © Mathias D'haen 2019, some rights reserved under a CC-BY-NC licence); (5) *C.diana* (photograph © iNaturalist user mlanguy 2022, some rights reserved under a CC-BY-NC licence); (6) *C.dryas* (photograph © iNaturalist user dalempijevic1 2016, some rights reserved under a CC-BY-NC licence); (7) *C.erythrogaster* (photograph © iNaturalist user wouyou 2018, some rights reserved under a CC-BY-NC licence).



Fig 2. Shows research grade images of the investigated monkeys outlined in the same colour and pointing at the IUCN predicter extant habitat. Photos and ranges for seven species of genus *Cercopithecus*, including (1) *C.erythrotis* (photograph © iNaturalist user arakso 2014 some rights reserved CC-BY-NC licence); (2) *C.hamlyni* had no research grade imaged in iNaturalist or in the IUCN red list; (3) *C. lomamiensis* had no research grade images in iNaturalist or in the IUCN red list; (4) *C. lowei* (photography © Cesar Maria Aguilar Gomez 2017 some rights reserved CC-BY-NC); (5) *C. mitis* (photography © Yvonne A. de Jong 2016 some rights reserved CC-BY-NC); (7) *C. neglectus* (photography © Mike G. Rutherford 2017 some rights reserved CC-BY-NC); (7) *C. neglectus* (photography © Mathaias D'haen 2019 some rights reserved CC-BY-NC)



Fig 3. Shows research grade images of the investigated monkeys outlined in the same colour and pointing at the IUCN predicter extant habitat. Photos and ranges for seven species of genus *Cercopithecus*, including (1) *C. nictitans* (photography © Xavier Rufray 2020 some rights reserved CC-BY-NC licence); (2) *C. petaurista* (photography © Niall Perrins 2021 some rights reserved CC-BY-NC licence); (3) *C. pogonias* (photography © Derozier Violette 2020 some rights reserved CC-BY-NC licence); (4) *C. sclateri* (photography © Lynne R. Baker 2019 IUCN red list) ; (5) *C. wolfi* (photography © Derozier Violette 2018 some rights reserved CC-BY-NC licence); (6) *A. lhoesti* (photography © Susanne Spindler 2016 some rights reserved CC-BY-NC-NC licence); (7) *A.preussi* (photography © Lennart Hudel some rights reserved CC-BY licence).

Table 1. This table shows the taxonomy of the genera *Cercopithecus* and *Allochrocebus* according to their Red List classification. For context, other taxonomies for these species has been included with some examples of literature where this alternative taxonomy is used.

Species name as currently listed by the	IUCN classification (reference)	Taxonomy that is not in agreement with the IUCN (including examples of
		by these alternative names)
Allochrocebus Ihoesti Fig 3	Vulnerable (Ukizintambara, Olupot and Hart, 2019)	<i>Cercopithecus Ihoesti</i> (Gebo and Sargis, 1994; Kaplin and Moermond, 2000; Glenn and Cords, 2002; Tosi <i>et al.</i> , 2003; Tosi, Melnick and Disotell, 2004; Tosi, Detwiler and Disotell, 2005; Grubb, 2006; Cardini and Elton, 2008b, 2008a, 2008c; Moulin <i>et al.</i> , 2008; Chatterjee <i>et al.</i> , 2009; Kamilar, Martin and Tosi, 2009; Motsch <i>et al.</i> , 2015; lo Bianco, Masters and Sineo, 2017)
Allochrocebus preussi Fig 3	Endangered (Cronin <i>et al.,</i> 2019)	<i>Cercopithecus preussi/lhoesti preussi</i> (Gebo and Sargis, 1994; Glenn and Cords, 2002; Tosi, Melnick and Disotell, 2004; Grubb, 2006; Cardini and Elton, 2008b, 2008a, 2008c; Moulin <i>et al.</i> , 2008; Chatterjee <i>et al.</i> , 2009; Kamilar, Martin and Tosi, 2009; Motsch <i>et al.</i> , 2015)
Allochrocebus solatus	Near Threatened (Abernathy, Maisels and Coad, 2019)	<i>Cercopitheucs solatus /lhoesti solatus</i> (Peignot, Fontaine and Wickings, 1999; Glenn and Cords, 2002; Tosi, Melnick and Disotell, 2004; Tosi, Detwiler and Disotell, 2005; Grubb, 2006; Cardini and Elton, 2008b, 2008a, 2008c; Moulin <i>et</i> <i>al.</i> , 2008; Chatterjee <i>et al.</i> , 2009; Kamilar, Martin and Tosi, 2009; Motsch <i>et al.</i> , 2015)
<i>Cercopithecus ascanius</i> Fig 1	Least Concern (de Jong and Buynski, 2019)	
<i>Cercopithecus campbelli</i> Fig 1	Near threatened (Matsuda Goodwin, Gondele Bi and Kone, 2020)	
<i>Cercopithecus cephus</i> Fig 1	Least Concern (Abernathy and Maisels, 2020)	
<i>Cercopithecus denti</i> Fig 1	Least Concern (Detwiler, Hart and Hicks, 2020)	Cercopithecus pogonias denti (Glenn and Cords, 2002)
<i>Cercopithecus diana</i> Fig 1	Endangered (Kone, McGraw, et al., 2019)	

Cercopithecus dryas	Endangered	
Fig 1	(Hart, Detwiler and	
	Alempijevic, 2021)	
Cercopithecus	Endangered	
erythrogaster	(Matsuda Goodwin,	
Fig 1	Oates, et al., 2020)	
Cercopithecus erythrotis	Vulnerable	
Fig 2	(Hofner <i>et al.,</i> 2020)	
Cerocpithecus hamlyni	Vulnerable	
Fig 2	(Hart and Maisels, 2019)	
Cercopithecus	Vulnerable	
Iomamiensis	(Detwiler and Hart, 2020)	
Fig 2		
Cercopithecus lowei	Vulnerable	Cercopithecus campbelli
Fig 2	(Wiafe <i>et al.,</i> 2019)	(Glenn and Cords, 2002)
Cercopithecus mitis	Least Concern	Cercopithecus albogularis, as a species
Fig 2	(Butynski and de Jong,	separated from C. mitis.
	2019)	(Sineo, 1990; Tosi, Detwiler and Disotell,
		2005; Moulin <i>et al.,</i> 2008; Kamilar,
		Martin and Tosi, 2009; lo Bianco,
		Masters and Sineo, 2017)
Cercopithecus mona	Near Threatened	
Fig 2	(Matsuda Goodwin,	
	Segniagbeto, Nobime, et	
	al., 2020)	
Cercopithecus neglectus	Least Concern	
Fig 2	(Mwenja, Maisels and	
	Hart, 2019)	
Cercoithecus nictitans	Near Threatened	
Fig 3	(Cronin <i>et al.,</i> 2020)	
Cercopithecus petaurista	Near Threatened	
Fig 3	(Matsuda Goodwin,	
	Segniagbeto, Wiafe, et	
	al., 2020)	
Cercopithecus pogonias	Near Threatened	
Fig 3	(Maisels <i>et al.,</i> 2020)	
Cercoptihecus roloway	Critically Endangered	Cercopithecus diana
Fig 3	(Kone, Oates, <i>et al.</i> , 2019)	(Glenn and Cords, 2002)
Cercopithecus sclateri	Endangered	
Fig 3	(Baker <i>et al.,</i> 2019)	
Cercopithecus wolfi	Near Threatened	Cercopithecus pogonias wolfi
Fig 3	(Hart, Detwiler and	(Glenn and Cords, 2002)
_	Maisels, 2020)	

Chlorocebus albogularis has been excluded from the table and my thesis as this species is no longer considered to be a member of the *Cercopithecus* genus ((Moulin *et al.*, 2008; Hart *et al.*, 2012; lo Bianco, Masters and Sineo, 2017).

Initial literature research

Before starting on ecological modelling, I did literature research on the guenons, investigating their ecology. Due to the breadth of research on the genus *Cercopithecus* and guenons I chose to focus on specific key words, initially I searched for 'guenon', then more specifically 'Cercopithecus' and 'ecology'. I excluded any species names that weren't included in the IUCN list for genus *Cercopithecus* as well as papers that referred to genera other than *Cercopithecus* within the guenons.

Ecology papers where species within the guenons were compared usually focused on polyspecific associations (Bryer et al., 2013; Buzzard, 2006b, 2010) or in one case skull morphology and how the ecology (diet, locomotion and habitat type) can affect this (Cardini & Elton, 2008). Others focused on one species and how biogeography or ecological differences between troops affect the members (T. M. Butynski, 1990; Coleman & Hill, 2014; Gautier-Hion, 1980) or various other investigations into single species ecology (Bitty & McGraw, 2007; J. Hart et al., 2012; Kaplin & Moermond, 2000; Peignot et al., 1999; Sinsin et al., 2002; Twinomugisha et al., 2003; Wahome et al., 1993).

Ecology

The literature on the ecology of guenons as was discussed earlier is broad, covering many subjects. These mainly pertain to different aspects of diet; how diet varies by season and sex (Gautier-Hion, 1980), how diet changes because of polyspecific association (Gautier-Hion, 1980; Lawes, 1990; Sineo, 1990; Kaplin and Moermond, 2000; Paul J. Buzzard, 2006b; Buzzard, 2010; Bryer, Chapman and Rothman, 2013; Coleman and Hill, 2014; lo Bianco, Masters and Sineo, 2017; Detwiler, 2019) and how their diets are flexible (Chapman *et al.*, 2005; Paul J. Buzzard, 2006b; Buzzard, 2010; Coleman and Hill, 2014).

However there has been no systematic comparative ecological study made between the members of *Cercopithecus* as it is currently considered by the IUCN. This investigation explores the ecological needs of the guenons, in order to provide valuable insight into their distribution as a whole genus and help toward understanding their needs for conservation. As seen in Table 1 the *Cercopithecus* range between Least Concern and Critically Endangered with Near Threatened being the most common designation. This suggests that establishing the environmental requirements of each species, and how they can co-exist so extensively, will be important to conserving guenons in the next few decades and centuries.

Polyspecific Association

Species that are in polyspecific association are species that occupy the same area, and thus must share resources and space. Because the monkeys have to divide the resources in this shared space it affects their diet. It has been seen in Buzzard (2006b, 2010) and Bryer, Chapman and Rothman (2013) guenons are able to be flexible with the proportions of different foods in their diet to facilitate this overlap and still allow the association to benefit the species (Gautier-Hion, 1980; Paul J. Buzzard, 2006b; Buzzard, 2010; Bryer, Chapman and Rothman, 2013).

Species that associate	Literature studying this association	
polyspecifically		
C.cephus, C.nictitans and	(Gautier-Hion, 1980; Gautier-Hion, Quris and Gautier, 1983;	
C.pogonias	Mitani, 1991; Hutchinson, 2015)	
C.nictitans and C.cephus	(Mori, 1988a)	

Table 2. shows the species that have had their polyspecific association investigated.

C.ascanius and C.mitis	(Butynski, 1990; Chapman and Chapman, 2000; Houle, Chapman and Vickery, 2010; Bryer, Chapman and Rothman,
	2013; Hutchinson, 2015; lo Bianco, Masters and Sineo, 2017;
	Detwiler, 2019)
C.wolfi, C.ascanius and	(McGraw, 1994)
C.neglectus	
C.diana and C.nictitans	(Eckardt and Zuberbühler, 2004)
C.diana and C.campbelli	(Wolters and Zuberbühler, 2003)
C.nictitnas and C.cephus	(Mori, 1988b)
C.campbelli and C.petaurista	(le Floch <i>et al.,</i> 2021)
C.campbelli, C.petaurista and	(Paul J. Buzzard, 2006a; Buzzard, 2010; Hutchinson, 2015)
C.diana	
C.mitis and A.lhoesti	(Hutchinson, 2015)

A focus point for this research is the ecological niche overlap of all the *Cercopithecus* with *Allochrocebus* as the outgroup, this may bring more to the discussion on how polyspecific association is related to ecology.

Background and Significance

Literature research of the guenons has shown that they are consistently conservative. Exploring this conservatism for general background a few apparent key points are:

The differences in the skeletal structure for the post cranial anatomy appears to be based more on differences such as positional behaviour. For example, *Cercopithecus mona* and *Cercopithecus* mitis show more arboreal adaptations, such as a wider intertuberosity angle of the humerus in the shoulder joint in comparison to more terrestrial Cercopitheini monkey (*Chlorocebus aethiops*). There are also differences between *Cercopithecus mitis and Cercopithecus mona*, where Cercopithecus mitis is noted to have a longer and less robust neck than *Cercopithecus mona* (Nakatsukasa, 1994), and between *Cercopithecus mitis* and *Chlorocebus aethiops* where *Cercopithecus mitis* has a longer and heavier body than *Chlorocebus aethtiops* for ground running (Anapol *et al.*, 2005). Arenson et al., (2020) have postulated a generalised skeletal plan based on the guenons having a semiterrestrial ancestor, and this hypothesis ties in with the skeletal differences described above.

The scapular morphology of the cercopithecoids appears to be related to the foraging method the species employs most, as well as how terrestrial or arboreal they are (Dunham, Kane and Mcgraw, 2015; Dunham, Kane and McGraw, 2017), or how they locomote (Bitty and McGraw, 2007) and even how they sit or rest (Dunham, Kane and McGraw, 2017). The *Cercopithecus* also possess a generalist forelimb, to compensate for the ability to use a variety of locomotor strategies for the dynamic arboreal environment (Elton *et al.*, 2016).

The anatomical difference in skulls is linked to size. Cardini and Elton (2008a, 2008b) also showed there was no correlation between ecological or behavioural differences and skull morphology. The strongest correlation for skull shape change was allometry (allometry is the relationship between size and shape (Nijhout and McKenna, 2019)) where the pattern is that skulls become more differentiated the bigger the average skull size was. Only modest differences were found for genus *Cercopithecus*, with relatively poor separation of most species although there are still small quantitative differences, large enough for discriminate analysis to identify (Cardini and Elton, 2008a, 2008b).

Though according to the above paragraphs, ecology doesn't have significant effect on the morphology diet does effect ecology (Wagner *et al.*, 2013). The *Cercopithecus* all have a very similar diet (Glenn and Cords, 2002), they are however flexible with the proportions of food. Dietary flexibility can be linked to the sex of the animal or abundance of food, for example Gautier-Hion (1980) observed the polyspecific association of *Cercopithecus cephus, Cercopithecus nictitans* and *Cercopithecus pogonias*, and noted that their diet was shown to overlap less when food was either scarce or at its most abundant but when the diet does overlap more the monkeys changed the proportions of their fruit, insects and leaves in their diet, thereby reducing the competition for resources. *Cercopithecus nictitans* increased the proportion of leaves they ate and *Cercopithecus nictitans*. It was also noted that for all these species the females ate more leaves and insects as the diet provided more protein that is required by pregnant and lactating females, and the males ate more fruit (Gautier-Hion, 1980).

Inter-specific competitions appear to not affect their interaction too heavily even to the point that the *Cercopithecus* are also known to hybridise, and long-term hybridisation between *Cercopithecus mitis doggetti* and *Cercopithecus ascanius schmidti* has been observed at Gombe National Park. At this point, the population *Cercopithecus mitis doggetti* is genetically distinct from conspecifics as they have been hybridising so long that they have *Cercopithecus ascanius schmidti* mitochondrial DNA (Detwiler, 2019). They are still counted as a sub species of *Cercopithecus mitis* according to the latest Red List assessment by Butynski & de Jong (2021).

Another factor that affects ecology and diet is the density of the population, which can be different between groups of the same species within one forest. Competition for food is obviously higher at the higher population density, with the lower density population eating more fruit and less foliage as the lower density population was below carrying capacity and therefore had greater fruit availability (Butynski, 1990).

It can be understood therefore why there is such difficulty using species concepts with the Guenons. Going forward there is less emphasis on one concept vs another and more agreement that a difference is the only necessary factor for delimitation (de Queiroz, 2007), but that all avenues of differentiation should be investigated (Padial *et al.*, 2010).

Aims and Hypotheses

My research aims to investigate what the ecological overlap of genus *Cercopithecus* and genus *Allochrocebus* (as the outgroup) is (say that this is the overarching aimand using r as a tool to do this comparison). The aim will be to compare the known polyspecific associating species to see how much their ecology overlaps., using the MaxEnt modelling programme. As well as comparing the overlaps of these species using ENMTools in R. The outgroup is an important part of the process as they show the differences between genera by providing another group for comparison. I am to produce high-quality MaxEnt models for each species of genus *Cercopithecus* and genus *Allochrocebus*, and explore the degree of ecological overlap between them using R.

To meet my aim, I will use IUCN, Global Biodiversity Information Facility (GBIF) and iNaturalist to map locality points for Genus *Cercopithecus* and *Allochrocebus* in ArcGIS. Looking at the locality points on a map doesn't give a quantitative understanding of ecology in that area. I therefore will use MaxEnt modelling to build understanding of the most important ecological needs of each species, in terms of biome requirements and climatic tolerances. For example this will allow me to demonstrate preferences such as rainfall and temperature variables for each species. In order to

understand the degree of ecological overlap, I have used the MaxEnt model asc files and inputted them into R. In order to compare between two specific species, I used the ENMTools raster overlap function to compare how similar their requirements for ecological variables and also how similar their reactions are to ecological variables (Schoener, 1968; Warren, Glor and Turelli, 2008; Warren *et al.*, 2010).

I hypothesise that different members of the genus *Cercopithecus* will have similar ecological needs due to them being so capable of adaptation as seen in their diet and ability to adapt to polyspecific association and ecological partitioning (Paul J. Buzzard, 2006b). This would be reflected in high degrees of overlap in the distributions of suitable habitat for different guenon species, and in the environmental requirements identified by each species' model. Genus *Allochrocebus* I anticipate will have slightly different ecological needs, due to them being more terrestrial.

Therefore, in this thesis, I will be filling the gap in comparing the ecology of the genera *Cercopithecus* and *Allochrocebus* using species distribution models built using ArcGIS and MaxEnt software.

This project aims to explore whether members of genus *Cercopithecus* are also conservative with their ecological needs, and how their ecology differs between species that overlap geographically. Using their sister genus of Allochrocebus as a small outgroup, to investigate whether the conservative ecological needs of *Cercopithecus* extends to closely related taxa.

Materials and Methods

In terms of ecological niche modelling, there has been little work on guenons and none of what has been done compares different species to one another systematically. There is one unpublished report from USAID and USFWS Plumptre, Ayebare and Kujirakinja (2015) that includes *Cerocpitheucs hamlyni* and Allochrocebus l'hoesti as some of several species modelled, the other species were included as a survey of the area, this did include several other primates such as chimpanzees, gorillas, red colobus and grey-cheeked mangabey. Primates were not the main focus of this report however, other mammals, birds, reptiles, amphibians and plants were investigated as the reports main focus was to determine where conservation efforts were most needed (Plumptre, Ayebare and Kujirakwinja, 2015).

There have also been some single-species studies of guenons' ecological niches, e.g. by Butynski (1990) who investigates *Cercopithecus mitis* and its differing ecological niches in different regions by assessing the availability of food and counting the trees and monkey species it encounters. Buzzard (2006b) looked at the species *Cercopithecus campbelli, Cercopithecus cephus* and *Cercopithecus petaurista*, again using observations of habituated groups of monkeys and their area to characterise dietary niches. There is one investigation using species distribution modelling, however this is not using MaxEnt but general linear models and climatic data which was used to investigate the genera *Cercopithecus* and *Colobus*, with a focus on future distribution models using projected future climatic conditions (Korstjens, 2019).

There are a few other papers investigating conservation that use ecological niche modelling to look at the broader diversity, but without focusing on the species individually. Ayebare et al (2018), for example, use MaxEnt to investigate a large area and a variety of species again including mammals, birds, reptiles, ampibians and plants as in Plumptre et al (2015) to identify areas for conservation. Cronin et al (2017) also looked at multiple species, including *Cercopithecus erythrotis*, *Cercopithecus pogonias* and *Cercopithecus nicticans*, while trying to figure out how to combat the primate

bushmeat trade on Bioko Island (Cronin et al., 2017). They used their niche models to identify biodiversity hotspots and did not report individual species' niches or environmental requirements.

This means there is a gap in our understanding of the ecology of the guenons, specifically in the comparison of the ecology of members of the genus *Cercopithecus* using niche modelling and specifically Maxent. There is a limited understanding of how environments affect the guenons and what guenons' environmental needs are, or how different species' niches compare.

Ecology through R

Ecological niches can be compared to each other in R specifically giving values to how similar the niches of the species being compared and also show how the species compare to one another in terms of their reactions to their environments (Warren *et al.*, 2010).

It has been known to show how comparison so that how conservative or separate species are in terms of their environmental needs, this can both be used to distinguish where there are similarities (Bett, Blair and Sterling, 2012; Hending, 2021).

Data Collection and Processing

Building a Species Distribution Model (SDM) requires locality data and environmental layers. The sources of information I used were the IUCN range map data (*IUCN Red List of Threatened Species*, 2021), the iNaturalist (A Community for Naturalists · INaturalist, 2021) and GBIF (*GBIF*, 2021) locality points which are presence only data, and the climate and ecological information from WorldClim 2.1 (Fick and Hijmans, 2017), EarthExplorer (*EarthExplorer*, 2021), and the WWF report by Olson et at (2001) that describes terrestrial ecoregions. Table 2 lists the environmental variables used and their sources.

There is a difference between the three most often occurring environmental variables and three most often occurring variables in the top three percentage contribution. Though terrestrial ecoregion and temperature seasonality remain within the top three percentage contributions, the environmental variable of precipitation is instead precipitation of coldest quarter (this quarter refers to season). It does still show however that the guenons require a high amount of rainfall.

The results of the environmental variable terrestrial ecoregion (Olson *et al.*, 2001) are Tropical and Sub Tropical Moist Broadleaf Forest, Mangrove or Tropical and Subtropical Grasslands and Shrublands, however mangrove occurs only in four of the investigated species and Tropical and subtropical grasslands and shrublands five times with Tropical and subtropical moist broadleaf forest occurring for thirteen species. Allochrocebus Ihoesti is an anomaly for its preferred ecoregions as it has equal importance for Tropical and Subtropical Moist Broadleaf Forest, Subtropical Dry Broadleaf Forest, Temperate Broadleaf and Mixed Forest, Temperate Conifer Forest, Tropical and Subtropical Grasslands Savanna and Shrubland, Temperate Grasslands Savannas and Shrublands, Flooded Grassland and Savanna, Mediterranean Forest Woodland and Shrubland, Desert and Xeric Shrubland, Mangrove and Central Zambezian Woodland.

Table 3. The environmental layers used to build models in this project. Most came from WorldClim, which describes itself as the highest resolution source for global weather and climate data. I used version 2.1 (Fick and Hijmans, 2017) historical climate data . This was supplemented with a map from EarthExplorer for the altitude (*EarthExplorer*, 2021), and data from Olson et at (2001) that describes terrestrial ecoregions. The data set was originally curated by Sarah Hill for her paper investigating the biogeography of genus *Papio* (Hill and Winder, 2019), and made available via the DataDryad repository.

Variable	Designation	Citation
Annual Mean Temperature	BIO1	(Fick and Hijmans, 2017)
Mean Diurnal Range (Mean of Monthly (Max	BIO2	(Fick and Hijmans, 2017)
temperature – Min temperature)		
Isothermality (BIO2/BIO7)(x100)	BIO3	(Fick and Hijmans, 2017)
Temperature Seasonality (Standard Deviation x 100)	BIO4	(Fick and Hijmans, 2017)
Max Temperature of Warmest Month	Bio5	(Fick and Hijmans, 2017)
Max Temperature of Coldest Month	Bio6	(Fick and Hijmans, 2017)
Temperature Annual Range (BIO5 - BIO6)	Bio7	(Fick and Hijmans, 2017)
Mean Temperature of Wettest Quarter	Bio8	(Fick and Hijmans, 2017)
Mean Temperature of Driest Quater	Bio9	(Fick and Hijmans, 2017)
Mean Temperature of Warmest Quarter	Bio10	(Fick and Hijmans, 2017)
Mean Temperature of Coldest Quarter	Bio11	(Fick and Hijmans, 2017)
Annual Precipitation	BIO12	(Fick and Hijmans, 2017)
Precipitation of Wettest Month	BIO13	(Fick and Hijmans, 2017)
Precipitation of Driest Month	BIO14	(Fick and Hijmans, 2017)
Precipitation Seasonality (Coefficient of Variation)	BIO15	(Fick and Hijmans, 2017)
Precipitation of Wettest Quarter	BIO16	(Fick and Hijmans, 2017)
Precipitation of Driest Quarter	BIO17	(Fick and Hijmans, 2017)
Precipitation of Warmest Quarter	BIO18	(Fick and Hijmans, 2017)
Precipitation of Coldest Quarter	BIO19	(Fick and Hijmans, 2017)
Altitude	Altitude	(EarthExplorer, 2021)
Ecoregions	Terrestrial	(Olson et al., 2001)
	Biome	

I used ArcGIS 10.7.1 (ESRI, 2011), an interactive mapping software that can analyse locality points and extrapolate relationships. ArcGIS is a software commonly used in biogeography papers that want to create Species Distribution Models (SDMs) (Hill and Winder, 2019) to cut down maps and set up data for modelling. MaxEnt 3.4.1 (Phillips, Dudík and Schapire, 2004) was used to create the models themselves. MaxEnt uses presence only data in conjuncture with environmental data to produce SDMs, and creates understandable outputs (Elith et al., 2011; Hill and Winder, 2019; Zeng et al., 2021).

The IUCN Red List has range maps for each species that can be imported to ArcGis, the range maps provide a reference for the validity of locality points from the Global Biodiversity Information Facility (GBIF) and iNaturalist. The Data from GBIF and iNaturalist was cleaned initially to dismiss any captive or blank latitude longitude points in Excel.

Locality points were then imported into ArcGIS along with the IUCN Red List range map and the points were again cleaned using the Clip tool in the Analysis toolbox to only include points that were within the species' known IUCN range or within 10km of its borders. This was done by species, and each species' locality dataset was then rarefied using the SDM toolbox 2.0 and the Spatially Rarefy Occurrence Data tool, to help prevent sampling bias that can make the MaxEnt maps unreliable (Elith *et al.*, 2011; Brown, Bennett and French, 2017). The rarification distance was set to .027 km as this represents the square root of the average home range size for all *Cercopithecus* species (Buzzard, 2006a; Campbell et al., 2012; see Table 3). Final point sample sizes are shown in Table 4.

I used R with ENMTools (how do I cite this?) to investigate the neich overlap specifically using the tool raster.overlap, to measure the overlap between two Neich Models giving the metric data of I D and Spearmans.

Table 4. The species home range sizes for *Cercopithecus* species from Campbell et al (2012) and Buzzard et al. (2006a) that were used to find the average of 70.3 Ha (0.703km²) that was square rooted for rarefication distance, such that points closer than this linear distance were thinned out. Using the square root of the average home range ensures no two points left after rarefication are close enough to represent repeat samples of the same troop of monkeys.

Species	Home range in Buzzard et al	Home range in Campbell et al
	(2006a),Ha	(2012), Ha
C. ascanius	60 and 24	28, 68, 60
C. campbelli	59.5	-
C. cephus	86	18 and 45
C. diana	58.9	41 and 29
C. mitis	51 and 88	50, 335, 44, 38, 26
C. neglectus	-	50, 4, 10
C. nictitans	168	148, 119
C. pogonias	168	148, 119
C. petaurista	68.8	-
A. Lhoesti	117	-

The environmental data from Table 2 was imported into ArcGIS and converted into ASCII files with a consistent 30 arc second cell size by a colleague, Sarah Hill (working on Hill & Winder, 2019) and provided to me on an external hard drive. Only one file, the ecoregions map, was originally a vector map. Sarah converted this to raster data comparable to all the other files using the Feature to Raster conversion tool in ArcGIS 10.7.

Table 4: Occurrence data points by species for the investigated taxa after clipping and rarefication, and the reference for the IUCN Red List range map used to clip them (*IUCN Red List of Threatened Species*, 2021). For the species *Cercopithecus roloway* and *Allochrocebus solatus* there were not enough data points in iNaturalist (*iNaturalist*, 2021) or GBIF (*GBIF*, 2021) to run in MaxEnt (Phillips, Dudík and Schapire, 2004).

Species name	Number of locality points obtained (from both iNaturalist (<i>iNaturalist</i> , 2021)and GBIF(GBIF, 2021))	IUCN Red List reference
Cercopithecus ascanius	205	(de Jong and Buynski, 2019)
Cercopithecus campbelli	63	(Matsuda Goodwin, Gondele
		Bi and Kone, 2020)
Cercopithecus cephus	45	(Abernathy and Maisels,
		2020)
Cercopithecus denti	8	(Detwiler, Hart and Hicks,
		2020)
Cercopithecus diana	101	(Kone, McGraw, et al., 2019)
Cercopithecus dryas	3	(Hart, Detwiler and
		Alempijevic, 2021)
Cercopithecus	48	(Matsuda Goodwin, Oates,
erythrogaster		et al., 2020)

Cercopithecus erythrotis	15	(Hofner <i>et al.,</i> 2020)
Cercopithecus hamlyni	7	(Hart and Maisels, 2019)
Cercopithecus	10	(Detwiler and Hart, 2020)
lomamiensis		
Cercopithecus lowei	14	(Wiafe <i>et al.,</i> 2019)
Cercopithecus mitis	630	(Butynski and de Jong, 2019)
Cercopithecus mona	144	(Matsuda Goodwin,
		Segniagbeto, Nobime, et al.,
		2020)
Cercopithecus neglectus	47	(Mwenja, Maisels and Hart,
		2019)
Cercopithecus nictitans	92	(Cronin <i>et al.,</i> 2020)
Cercopithecus petaurista	77	(Matsuda Goodwin,
		Segniagbeto, Wiafe, et al.,
		2020)
Cercopithecus pogonias	25	(Maisels <i>et al.,</i> 2020)
Cercopithecus sclateri	13	(Baker <i>et al.,</i> 2019)
Cercopithecus wolfi	14	(Hart, Detwiler and Maisels,
		2020)
Allochrocebus lhoesti	99	(Ukizintambara, Olupot and
		Hart, 2019)

The environmental variables that occur most often in the percentage contributions of the model are, in this case, three variables that occur in some capacity for all of the investigated species. These are terrestrial ecoregion, which is based in the paper Olson et al (2001) that split the globe into 867 'distinct units'. Temperature seasonality which is the standard deviation of the temperature through the year times 100 and precipitation seasonality which is measured as the coefficient of variation.

Model Building

MaxEnt version 3.4.1 (Phillips, Dudík and Schapire, 2004) was then used to build models for each species using the datasets described in table 4 and table 2. I built crossvalidated ecological niche models for each species studied. The crossvalidation is an automatic setting in MaxEnt that splits locality points of the model into equal shares and uses each share as both training and testing data in different combinations. This creates multiple models that can be averaged, and provides more accurate predictions with less uncertainty (Young, Carter and Evangelista, 2011; Wenger and Olden, 2012). The setting of four replicates means that this runs crosvalidation four times with different 'outgroups' (Young, Carter and Evangelista, 2011).

As the *Cercopithecus* genus is widespread over most of sub-Saharan Africa, the evolution of the guenons is currently understood to have been caused by the breaking up and re-joining of forests (lo Bianco, Masters and Sineo, 2017). Leaving the background sample settings as default allows the model to use all the different habitats currently in Africa to find the any potential suitable habitats outside of the species actual range (Young, Carter and Evangelista, 2011; Hill and Winder, 2019).

Total number of iterations was lowered from 5000 to 1500 because it is a compromise between generating the most accurate models possible and having enough memory on the laptop to accommodate the maps (Young, Carter and Evangelista, 2011). 1500 iterations should allow each

model to run to completion, and I will check the model outputs to identify any areas where uncertainty is still significant (i.e. where the standard deviation of the averaged models is high).

Using the maxent models comparing each species with all the other species by inputting them to R. Where using the ENMTools and the raster.overlap function produce 3 results that show how similar the ecology and reactions to variables are (Schoener, 1968; Phillips, Dudík and Schapire, 2004; Warren, Glor and Turelli, 2008; Spearman, 2010; Hending, 2021; Warren *et al.*, 2021).

Data Analysis and Interpretation

The extrapolated maps of suitable habitat for each species were compared to the ranges to see if my models could predict the species' IUCN ranges well. I then created presence-absence maps in ArcGIS using the 10th percentage logistic presence threshold (the habitat suitability score above which 90% of known localities fall) as a cut off between potentially suitable habitats which were given a score of 1/present and unsuitable habitats which were converted to a score of 0 or absent. These were also compared to the IUCN range maps for the species, to see whether mismatches between the original output and the IUCN map might result from a species having large areas of very marginal habitat showing beyond where they currently live.

To further analyse the data from MaxEnt I looked at AUC values as well as percentage contribution and permutation importance scores for each variable. The AUC (Area Under the Curve) values are the measuring how fitted the maps are i.e. 1. Is considered over fitted these are not reliable (Philips, Dudik and Silander, 2013) while an AUC score below 1 but over 0.75 is considered accurate in terms of prediction (Cho *et al.*, 2021). An AUC score of 0.5 would indicate a model performing no better than chance. Percentage contribution shows how important a specific environmental variable was for aspecies during modelling. Permutation importance is similar, but measures of how important small permutations of the ecological factor were the models' predictions of suitable habitat. I also noted the response curves of each of the environmental variables with the 3 highest percentage contribution scores and the highest permutation importance score for each species.

The area of suitable habitat for each species was calculated using the number of cells marked as 1 (suitable/present) in my presence-absence map for that species. Each cell was 30 arc-seconds in height and width, and a distance converter (*OpenDEM*, 2022)was used to calculate the size of the side of a cell in kilometres at roughly zero degrees latitude, in the middle of the maps generated. Squaring this and multiplying by the number of cells the species occupied gave an area of suitable habitat in km² for that species.

Analysis involved exploring how much species' niches and suitable habitats overlapped. First, I used the IUCN Red List outlines maps to identify pairs or sets of of species that overlap or border each other today. Then I created new ArcGIS project files and imported the presence-absence maps for the overlapping species. These were then added together using Raster Calculator to create biodiversity maps and allow for the measurement of areas of suitable habitat each pair shared. The area of this shared suitable habitat in km² was calculated using the same method as described above for single species. Lastly using ENMTools to show the ecological overlap of all species to compare metrically the ecological needs as well as the overlap of species.

Results

Using MaxEnt and ArcGIS software I was able to make models for all but two species, *Cercopithecus roloway* and *Allochrocebus solatus*. The Maxent models I did create have AUC (Cho *et al.*, 2021) values between 0.955 (*Cercopithecus mitis*) and 0.999 (*Cercopithecus sclatteri*). These are very high AUC values, AUC values being a measure of the predictive ability of the model. This means that the models should be able to accurately predict the ecology and suitable habitat distribution of these species.

Important environmental variables

For each species' model temperature and precipitation variables are always important, with precipitation in the top three contributors to models of 20 out of 21 of the species and temperature in the top three of 18. Where they are not a part of the top three most important variables, they get reduced to as low as 1.1% contribution (temperature) and 2.8% contribution (precipitation). The other variables explored through maxent are altitude and the terrestrial ecoregion. Terrestrial ecoregion is important to every species and appears as one of the most important (top three) variables in models of 14 species. It also contributes to every species' model when including variables lower than the top three. Other than terrestrial ecoregion, temperature seasonality and precipitation seasonality also contribute to all the species' models. Mean temperature of the driest quarter is the least common variable in my models. It does not appear in any of the top three percentage contributions but does occur 10 times otherwise.

If I'm doing a results matrix would that mean starting with these below and putting them in a table instead??

For percentage contributions for precipitation the most common variable is precipitation of the coldest quarter, which is among the top three percentage contributions for *C. campbelli, C. diana, C. erythrogaster, C. erythrotis, C. mona, C. neglectus, C. petaurista, C. sclateri* and *A. preussi* with percentage contributions between 9.0 (*C. neglectus*) and 40.1 (*C. diana*) (see Table 5).

The next most common precipitation variable to appear in the top three is tied between annual precipitation, which is important to *C. campbelli, C. cephus, C. diana, C. erythrotis, C. mitis, C. nictitans* and *C. pogonias* with a perentage contribution value between 11.2 (*C. erythrotis*) and 67.1 (*C. campbelli*), and precipitation of driest month, which is important to *C. ascanius, C. lomamiensis, C. mitis, C. mona, C. neglectus, C. petaurista, C. wolfi* and *A. lhoesti* with percentage contribution values between 10.9 (*C. mona*) and 75.1 (*C. neglectus*).

The least common precipitation variable appearing in the top three is precipitation seasonality, with *C. denti, C. dryas* and *C.hamlyni* having it in their top three most important variables with percentage contribution values between 7.4 (*C. dryas*) and 19.4 (*C. denti*).

For temperature variables the most commonly in the top three as well as the most commonly important of all the variables is temperature seasonality. This is important to *C. ascanius, C. denti, C. dryas, C. hamlyni, C. lomamiensis, C. lowei, C. mitis, C. neglectus, C. nictitans, C. petaurista, C. pogonias, C. wolfi* and *A. lhoesti*, with percentage contributions between 6.9 (*C. pogonias*) and 42.6 (*C. dryas*).

Then is mean diurnal range which is important to *C. cephus, C. erythrogaster, C. lowei, C. mona* and *C. sclateri*, with a percentage contribution between 15.5 (*C. sclateri*) and 36.0 (*C. erythrogaster*).

The last two temperature variables that appear in the top three percentage contributions for some models are annual mean temperature for *C. erythrogaster* at 13.6 percentage contribution and max temperature of warmest month for *A .preussi* with a percentage contribution of 10.0.

Ecoregions is the most common variable appearing in the top three percentage contributions for my models. It is important in models for *C. campbelli, C. cephus, C. denti, C. diana, C. erythrotis, C. hamlyni, C. lomamiensis, C. lowei, C. nictitans, C. pogonias, C. sclateri, C. wolfi and A. preussi.* Percentage contributions to these models from terrestrial ecoregions are between 1.9 (*C. campbelli*) and 61.4 (*C. hamlyni*).

The final variable that appears in the top three percentage contributions to any model is altitude, which appears in the top three only for *C. ascanius* at 8.9 percentage contribution.

Table 6. Percentage contributions of each of the ecological variables to Maxent models for each species in genus *Cercopithecus* (top) and *Allochrocebus* (bottom). This is not including the species *Cercopithecus roloway* and *Allochrocebus solatus* as neither of these species had enough locality points to run the models. The bold text highlights the three variables making the highest percentage contributions to each species' model.

Species	Important variables, in order of percentage contribution to the model (with		
modelled (AUC	contributions in percent)		
score)			
Cercopithecus	Precipitation of Driest Month (58.0), Temperature Seasonality (19.0), Altitude		
ascanius (0.972)	(8.9), Annual mean temp (4.9), Annual precipitation (3.1), Terrestrial Ecoregion		
	(2.5), Precipitation Seasonality (2.2), Max Temperature of Warmest month		
	(0.7), Mean Diurnal Range (0.6)		
Cercopithecus	Annual Precipitation (67.1), Precipitation of Coldest Quarter (27.3),		
Campbelli	Terrestrial Ecoregion (1.9), Mean Diurnal Range (1.1), Temperature seasonality		
(0.991)	(0.7), Precipitation of driest month (0.7), Max Temperature of Warmest month		
	(0.4), Precipitation seasonality (0.3), Annual mean temperature (0.3)		
Cercopithecus	Annual Precipitation (36.5), Terrestrial Ecoregion (30.0), Mean Diurnal Range		
cephus (0.986)	(16.3), Temperature Seasonality (6.9), Precipitation of Driest Month (2.9),		
	Precipitation of Coldest Quarter (2.5), Mean Temperature of Driest Quarter		
	(1.8), Precipitation seasonality (1.2), altitude (0.8), Max Temperature of		
	Warmest Month (0.6), Annual Mean Temperature (0.4)		
Cercopithecus	Terrestrial Ecoregion (46.5), precipitation seasonality (24.0), Temperature		
denti (0.993)	Seasonality (19.4), Mean diurnal Range (7.1), Precipitation of Driest Month		
	(1.3), Annual Precipitation (0.6), Annual Mean Temperature (0.5), Max		
	Temperature of Warmest Month (0.5)		
Cercopitheus	Precipitation of Coldest Quarter (40.1), Terrestrial Ecoregion (34.0), Annual		
<i>diana</i> (0.994	Precipitation (18.0), Precipitation of Driest Month (4.2), Mean Diurnal Range		
	(2.0), Precipitation Seasonality (1.0), Temperature Seasonality (0.7)		
Cercopithecus	Temperature Seasonality (42.6), Terrestrial Ecoregion (40.2), Precipitation		
dryas (0.977)	Seasonality (7.4), Annual Precipitation (3.3), altitude (2.6), Mean Diurnal Range		
	(2.4), Max Temperature of Warmest Month (0.7), Annual Mean Temperature		
	(0.5), Precipitation of Driest Month (0.2), Mean Temperature of Driest Quarter		
	(0.1), Precipitation of Coldest Quarter (0.1)		
Cercopithecus	Mean Diurnal Range (36.0), Precipitation of Coldest Quarter (27.9), Annual		
erythrogaster	Mean Temperature (13.6), Precipitation of Driest Month (9.2), Terrestrial		
(0.997)	Ecoregion (5.7), altitude (4.9), Precipitation Seasonality (1.3), Temperature		
	seasonality (0.6), Annual Precipitation (0.5), Mean Temperature of Driest		
	Quarter (0.3)		

Cerconithecus	Terrestrial Ecoregion (50.7). Precipitation of Coldest Quarter (31.4). Annual
ervthrotis	Precipitation (11.2) Mean Diurnal Range (3.3) Max Temperature of Warmest
(0.995)	Month (2.1). Temperature seasonality (0.7). Precipitation seasonality (0.6)
Cerconithecus	Terrestrial Ecoregion (61.4). Temperature seasonality (22.3). Precipitation
hamlvni (0.983)	seasonality (11.2) Precipitation of Driest Month (5.0), altitude (0.1)
Cerconithecus	Terrestrial Ecoregion (32.8). Precipitation of Driest Month (31.3).
lomamiensis	Temperature seasonality (12.1) Precipitation of Coldest Quarter (9.2).
(0.999)	Precipitation Seasonality (7.3), altitude (6.1), Mean Diurnal Bange (0.7), Mean
(0.000)	Temperature of Driest Quarter (0.3). Annual Mean Temperature (0.3)
Cerconithecus	Mean Diurnal Range (27.9). Terrestrial Ecoregion (26.8). Temperature
lowei (0.984)	Seasonality (15.7), altitude (11.2). Mean Temperature of Driest Month (6.7).
	Precipitation of Driest Month (2.8). Precipitation Seasonality (2.5). Precipitation
	of Coldest Quarter (2.4). Annual Mean Temperature (2.0). Max Temperature of
	Warmest Month (2.0)
Cercopithecus	Precipitation of Driest Month (36.6), Annual Precipitation (18.0),
, mitis (0.955)	Temperature Seasonality (12.6) , Max Temperature of Warmest Month (10.6),
	Annual Mean Temperature (7), altitude (5.1), Mean Diurnal Range (3.5),
	Precipitation of Coldest Quarter (3.2), Terrestrial Ecoregion (2.3), Precipitation
	Seasonality (0.7), Mean Temperature of Driest Quarter (0.4)
Cercopithecus	Precipitation of Coldest Quarter (42.8), Mean Diurnal Range (16.6),
, mona (0.987)	Precipitation of Driest Month (10.9), Annual Mean Temperature (8.2),
	Terrestrial Ecoregion (5.8), Temperature Seasonality (5.7), Annual Precipitation
	(4.6), altitude (4.2), Mean Temperature of Driest Quarter (0.6), Precipitation
	Seasonality (0.4), Max Temperature of Warmest Month (0.1)
Cercopithecus	Precipitation of Driest Month (75.1), Precipitation of Coldest Quarter (9.0),
neglectus	Temperature seasonality (8.2), altitude (2.3), Annual Precipitation (2.1),
(0.963)	Terrestrial Ecoregion (1.6), Mean Diurnal Range (1.0), Precipitation Seasonality
	(0.7)
Cercopithecus	Terrestrial Ecoregion (47.6), Annual Precipitation (29.5), Temperature
nictitans (0.982)	Seasonality (8.1), Precipitation of Coldest Quarter (4.6), Precipitation
	Seasonality (3.9), Mean Diurnal Range (3.2), Precipitation of Driest Month (1.9),
	altitude (0.9), Annual Mean Temperature (0.2)
Cercopithecus	Precipitation of Coldest Quarter (29.8), Precipitation of Driest Month (24.3),
petaurista	Temperature Seasonality (15.0), Annual Precipitation (11.5), altitude (9.0),
(0.984)	Terrestrial Ecoregion (8.8), Max Temperature of warmest Month (0.7), Annual
	Mean Temperature (0.5), Mean Temperature of Driest Quarter (0.2), Mean
	Diurnal Range (0.2), Precipitation Seasonality (0.1)
Cercopithecus	Terrestrial Ecoregion (49.5), Annual Precipitation (35.6), Temperature
pogonias	Seasonality (6.9), Mean Diurnal Range (3.5), Precipitation Seasonality (1.5),
(0.971)	Precipitation of Coldest Quarter (0.8), Precipitation of Driest Month (0.7),
	Annual Mean Temperature (0.7), altitude (0.6)
Cercopithecus	Terrestrial Ecoregion (39.4), Precipitation of Coldest Quarter (15.7), Mean
sclateri (0.999)	Diurnal Range (15.5), Annual Precipitation (13.8), Annual Mean Temperature
	(11.5), Temperature Seasonality (1.2), Precipitation Seasonality (1.2), Mean
	temperature of Driest Quarter (1.1), Max Temperature of Warmest Month
Constant in the second	(0.4), altitude (0.2), Precipitation of Driest Month (0.1)
	rerrestrial Ecoregion (37.5), remperature Seasonality (21.6), Precipitation of
WUJI (U.989)	Temperature Secondlity (E2 C). Precipitation of Drivet Marsh (24 2) while the
Allochrocebus	remperature Seasonality (52.6), Precipitation of Driest Month (21.3), altitude (14.2) Precipitation of Coldect Quarter (0.0). Annual Mean Temperature (0.0)
moesti (0.994)	(14.2), Frecipitation of Coldest Quarter (9.0), Annual Mean Temperature (0.8),
L	renestinal Ecolegion (0.0), Annual Precipitation (0.4), Max Temperature of

	Warmest Month (0.3), Precipitation Seasonality (0.3), Mean Temperature of Driest Quarter (0.1), Mean Diurnal Range (0.1)
Allochrocebus preussi (0.997)	Terrestrial Ecoregion (51.4), Precipitation of Coldest Quarter (28.7), Max Temperature of Warmest Month (10.0), Annual Precipitation (7.8), Mean Diurnal Range (1.2), Precipitation Seasonality (0.4), Temperature seasonality (0.3)

MaxENT Model predictions of suitable habitat

My models were able to predict the distribution of suitable habitats for each guenon species reasonably well (see Figure 2 and the subsequent species-by-species section comparing each species IUCN Red List range map to the predicted suitable habitat, Figure 3-23). The species are always predicted to have other suitable habitat outside of the IUCN Red List range map, but the amount and suitability of these areas varies. For some species, the IUCN range is uniformly predicted to be suitable. These include *Cercopithecus erythrotis, Cercopthecus hamlyni, Cercopithecus lowei, Cercopithecus mona, Cercopithecus neglectus, Cercopithecus nictitans, Cercopithecus petaurista, Cercopithecus pogonias, Cercopithecus wolfi* and *Allochrocebus preussi.*

For others, e.g. Cercopithecus ascanius, Cercopithecus cephus, Cercopithecus denti, Cercopithecus diana, Cercopithecus erythrogaster, Cercopithecus lomamiensis, Cercopithecus mitis, Cercopithecus neglectus, Cercopithecus nictitans, Cercopithecus sclateri, Allochrocebus lhoesti and Allochrocebus preussi, the IUCN range also contains some areas that are not predicted to be suitable by my models



Fig 4. Shows the MaxEnt models for each species a) *Cercopithecus ascanius* b) *Cercopithecus campbelli* c) *Cercopithecus cephus* d) *Cercopitheucs denti* e) *Cercopithecus diana* f) *Cercopithecus dryas* g) *Cercopithecus erythrogaster* h) *Cercopithecus erythrotis* i) *Cercopithecus hamlyni* j) *Cercopithecus lomamiensis* k) *Cercopithecus lowei* l) *Cercopithecus mitis* m) *Cercopithecus mona* n) *Cercopithecus neglectus* o) *Cercopithecus nictitans* p) *Cercopithecus petaurista* q) *Cercopithecus sclateri* s) *Cercopithecus wolfi* t) *Allochrocebus lhoesti* u) *Allochrocebus preussi*. Habitat suitability from 0 to 1 with white indicating zero and black 1. (pages 21 – 26)



Fig 3. Shows the MaxEnt models for each species a) *Cercopithecus ascanius* b) *Cercopithecus campbelli* c) *Cercopithecus cephus* d) *Cercopitheucs denti* e) *Cercopithecus diana* f) *Cercopithecus dryas* g) *Cercopithecus erythrogaster* h) *Cercopithecus erythrotis* i) *Cercopithecus hamlyni* j) *Cercopithecus lomamiensis* k) *Cercopithecus lowei* l) *Cercopithecus mitis* m) *Cercopithecus mona* n) *Cercopithecus neglectus* o) *Cercopithecus nictitans* p) *Cercopithecus petaurista* q) *Cercopithecus sclateri* s) *Cercopithecus wolfi* t) *Allochrocebus lhoesti* u) *Allochrocebus preussi*. Habitat suitability from 0 to 1 with white indicating zero and black 1. (Pages 21 – 26)



Fig 3. Shows the MaxEnt models for each species a) *Cercopithecus ascanius* b) *Cercopithecus campbelli* c) *Cercopithecus cephus* d) *Cercopitheucs denti* e) *Cercopithecus diana* f) *Cercopithecus dryas* g) *Cercopithecus erythrogaster* h) *Cercopithecus erythrotis* i) *Cercopithecus hamlyni* j) *Cercopithecus lomamiensis* k) *Cercopithecus lowei* l) *Cercopithecus mitis* m) *Cercopithecus mona* n) *Cercopithecus neglectus* o) *Cercopithecus nictitans* p) *Cercopithecus petaurista* q) *Cercopithecus sclateri* s) *Cercopithecus wolfi* t) *Allochrocebus lhoesti* u) *Allochrocebus preussi*. Habitat suitability from 0 to 1 with white indicating zero and black 1. (pages 21 – 26)



Fig 3. Shows the MaxEnt models for each species a) *Cercopithecus ascanius* b) *Cercopithecus campbelli* c) *Cercopithecus cephus* d) *Cercopitheucs denti* e) *Cercopithecus diana* f) *Cercopithecus dryas* g) *Cercopithecus erythrogaster* h) *Cercopithecus erythrotis* i) *Cercopithecus hamlyni* j) *Cercopithecus lomamiensis* k) *Cercopithecus lowei* l) *Cercopithecus mitis* m) *Cercopithecus mona* n) *Cercopithecus neglectus* o) *Cercopithecus nictitans* p) *Cercopithecus petaurista* q) *Cercopithecus sclateri* s) *Cercopithecus wolfi* t) *Allochrocebus lhoesti* u) *Allochrocebus preussi.* Habitat suitability from 0 to 1 with white indicating zero and black 1. (pages 21 – 26)



Fig 3. Shows the MaxEnt models for each species a) *Cercopithecus ascanius* b) *Cercopithecus campbelli* c) *Cercopithecus cephus* d) *Cercopitheucs denti* e) *Cercopithecus diana* f) *Cercopithecus dryas* g) *Cercopithecus erythrogaster* h) *Cercopithecus erythrotis* i) *Cercopithecus hamlyni* j) *Cercopithecus lomamiensis* k) *Cercopithecus lowei* l) *Cercopithecus mitis* m) *Cercopithecus mona* n) *Cercopithecus o*) *Cercopithecus nictitans* p) *Cercopithecus petaurista* q) *Cercopithecus*

pogonias r) Cercopithecus sclateri s) Cercopithecus wolfi t) Allochrocebus lhoesti u) Allochrocebus preussi. Habitat suitability from 0 to 1 with white indicating zero and black 1. (pages 21 – 26)



Fig 3. Shows the MaxEnt models for each species a) *Cercopithecus ascanius* b) *Cercopithecus campbelli* c) *Cercopithecus cephus* d) *Cercopitheucs denti* e) *Cercopithecus diana* f) *Cercopithecus dryas* g) *Cercopithecus erythrogaster* h) *Cercopithecus erythrotis* i) *Cercopithecus hamlyni* j) *Cercopithecus lomamiensis* k) *Cercopithecus lowei* l) *Cercopithecus mitis* m) *Cercopithecus mona* n) *Cercopithecus neglectus* o) *Cercopithecus nictitans* p) *Cercopithecus petaurista* q) *Cercopithecus sclateri* s) *Cercopithecus wolfi* t) *Allochrocebus lhoesti* u) *Allochrocebus preussi*. Habitat suitability from 0 to 1 with white indicating zero and black 1. (pages 21– 26)

Species by species results

For all the species the models AUC gives a value that shows how well the model is predicting (Cho *et al.*, 2021), overfitting being when it is too close of a match of the inputted data. Having an AUC score of 1 indicates that the model has been overfitted (Phillips and Dudík, 2008). An AUC values can say different things, an AUC score of 0.5 is the same as random chance, Cho et al (2021) says that 0.75 and above is considered a good fit. Therefore a AUC between 0.75 and 1 is a good model.

species	AUC score
Cercopithecus ascanius	0.972
Cercopithecus campbelli	0.991
Cercopithecus cephus	0.986
Cercopithecus denti	0.993
Cercopithecus diana	0.994
Cercopithecus dryas	0.977
Cercopithecus erythrogaster	0.977
Cercopithecus erythrotis	0.995
Cercopithecus hamlyni	0.983
Cercopithecus lomamiensis	0.999
Cercopithecus lowei	0.984
Cercopithecus mitis	0.955
Cercopithecus mona	0.987
Cercopithecus neglectus	0.963
Cercopithecus nictitans	0.963
Cercopithecus petaurista	0.984
Cercopithecus pogonias	0.971
Cercopithecus sclateri	0.999
Cercopithecus wolfi	0.989
Allochrocebus lhoesti	0.994
Allochrocebus preussi	0.997

Table 7. Shows the AUC score by species for each of the maxent models by species.

Table 8. The table uses the maxent model results showing the percentage contribution of the ecological variables. It shoes in order the first three most important variables to the species shaded in in grey, the rest of the variables with significance to the model (in order of importance) are also shown. Isothermality is mean annual temp/temp annual range x 100, temp annual range is max temp of warmest month- min temp of warmest month, precipitation seasonality is coefficient of variation.

										Bior	ne co	odes									
Species																					
	Altitude	Terrestrial Ecoregion	Annual men Temperature	Mean Diurnal range	lsothermality	Temperature seasonality	Max Temp of warmest month	Min Temp of warmest month	Temp annual range	Mean temp of wettest month	Mean temp of driest month	Mean temp of warmest quarter	Mean temp of coldest quarter	Annual precipitation	Precipitation of wettest month	Precipitation of driest month	Precipitation seasonality	Precipitation of wettest quarter	Precipitation of driest quarter	Precipitation of warmest Quarter	Precipitation of coldest quarter
C.asc	3	7	6	9		2	8							4		1	5				10
C.cam	10	3	9	4		6	7							1		5	8				2
C.cep	9	2	11	3		4	10				7			1		5	8				6
C.den		1	7	4		3	8							6		5	2				
C.dia		2		5		7								3		4	6				1
C.dry	5	2	8	6		1	7				10			4		9	3				11
C.egas	6	5	3	1		8					10			9		4	7				2
C.etis		1		4		6	5							3			7				2
C.ham	5	1				2										4	3				
C.lom	6	1	9	7		3					8					2	5				4
C.low	4	2	9	1		3					5			10		6	7				8
C.mit	6	9	5	7		3	4				11			2		1	10				8
C.mon	8	5	4	2		6	11				9			7		3	10				1
C.neg	4	6		7		3								5		1	8				2
C.nic	8	1	9	6		3								2		7	5				4
C.pet	5	6	8	10		3	7				9			4		2	10				1
C.pog	9	1	8	4		3								2		7	5				6
C.scl	10	1	5	3		6	9				8			4		11	7				2
C.wol	5	1	1	7		2	8							9		3	4				6
A.lho	3	6	5	10		1	8				9			7		2	7				4
A.pre		1		5		7	3							4			6				2

Cercopithecus ascanius

Suitable habitat for *Cercopithecus ascanius* was dependent on precipitation of the driest month (58% of the power of the model), temperature seasonality (21.1%) and altitude (10.6%) (See Table). The most suitable habitats had moderate (50-115mm) rainfall in the driest month, very limited



temperature seasonality and low altitudes. Temperature seasonality also had the highest permutation importance (82.7%), which is a measure of how much permuting the variable changes the resulting model output as opposed to the percentage of model development it contributes (Phillips and Dudík, 2008).

The model's map of potential suitable habitat is similar to the IUCN map (Fig 3(left)) however the model predicts that *Cercopithecus ascanius'* suitable habitat could extend further north east to Cameroon as well as into a separated area that is suitable to them in Ethiopia which is not present in the IUCN outline, while the IUCN outline shows that *Cercopithecus ascanius* is spread over a wider area in the north of Angola and the Democratic Republic of Congo and two isolated area in the Central African Republic and South Sudan that shows as not being that suitable in the MaxEntmap. (de Jong and Buynski, 2019).

Figure 4. Shows the IUCN Red List range map for *Cercopithecus ascanius* as a red outline and the presence-absence version of MaxEnt's suitable habitat map (created by taking the suitability maps in figure 3 and cutting off suitability scores below the species' 10th percentile Cloglog threshold value, which is a measure of the suitability value above which 90% of known localities fall) shown in blue. Blue areas are those the Maxent model predicts to be suitable.

Cercopithecus campbelli

Suitable habitat for *Cercopithecus campbelli* was dependent on annual precipitation (53.2% of the power of the model), precipitation of coldest quater (38.8%) and terrestrial ecoregion (4.2%) (see table..). The most suitable habitats had annual rainfall for 4000mm of rainfall or more and also are



more suite to areas with more than 750mm rainfall in the coldest month. The most suitable terrestrial ecoregion is mangroves. Precipitation of the coldest quarter also has the highest permutation importance (46.9%).

The model's map of potential suitable habitat is similar to the IUCN map (Figure 4 (left)) however the model predicts *C. campbelli* suitable habitat Follow the coast of Guinnea-Bissau and Guinea as well as most of Sierra Leone and Liberia. Also suitable habitat could extend to a separate area suitable to them from the South West costal area of Nigeria, Cameroon and Equatorial New Guinnea and onto the coast of Gabon. While the IUCN outline shows the extant population of *Cercopithecus campbelli* extending further North West to The Gambia and the South East of Senegal as well as larger areas inland in Guinea as well as into the East of Cote D'Ivoire that shows as not being suitable in the MaxEnt map (Matsuda Goodwin, Gondele Bi and Kone, 2020).

Figure 5. Shows the IUCN Red List range map for *Cercopithecus campbelli* as a red outline and the presence-absence version of MaxEnt's suitable habitat map (created by taking the suitability maps in figure 3 and cutting off suitability scores below the species' 10th percentile Cloglog threshold value, which is a measure of the suitability value above which 90% of known localities fall) shown in blue. Blue areas are those the Maxent model predicts to be suitable.

Cercopithecus cephus

Suitable habitat for *Cercopithecus cephus* was dependent on annual precipitation (36.5% of the model), terrestrial ecoregion (30%) and mean diurnal range (16.3%) (see table). The most suitable



habitats have more than 2400mm of annual precipitation and Tropical and subtropical moist broadleaf forest ecoregion, with any lower than 8° difference in temperature in a month. Temperature seasonality has the highest permutation importance (59.8%).

The model's map of potential suitable habitat is The IUCN map Figure 5 (left)) however the model predicts that *Cercopithecus cephus* suitable habitat extends further east showing suitability into the Democratic Republic of Congo as well as an isolated group to the West along the coast of Cote D'Ivoire and Ghana. While the IUCN outlines show that *Cercopithecus cephus* the extant population extends further north in Cameroon and North East in Central African Republic, also extending further in the Congo both East and areas at the border of Congo Gabon and Cameroon. There are large areas of Central and South West Gabon that shows as not being suitable in the MaxEnt map (Abernathy and Maisels, 2020).

Figure 6. Shows the IUCN Red List range map for *Cercopithecus cephus* as a red outline and the presence-absence version of MaxEnt's suitable habitat map (created by taking the suitability maps in figure 3 and cutting off suitability scores below the species' 10th percentile Cloglog threshold value, which is a measure of the suitability value above which 90% of known localities fall) shown in blue. Blue areas are those the Maxent model predicts to be suitable.

Cercopithecus denti



Suitable habitat for *Cercopithecus denti* was dependent on terrestrial ecoregion (46% of the power of the model), precipitation seasonality (24%) and temperature seasonality (19.4%) (see table). The most suitable habitats are Tropical and Subtropical moist broadleaf forest with as little precipitation and temperature seasonality as possible. Precipitation seasonality also has the highest permutation importance (63.3%).

The model's map of potential suitable habitats is similar to the IUCN map (Figure 6 (left)) however the model predicts that *Cercopithecus denti* suitable habitat extends further to central Kenya. While the IUCN outline shows that *Cercopithecus denti* is spread further North, West and South than the model predicts all within the North East of the Democratic Republic of Congo (Detwiler, Hart and Hicks, 2020).

Figure 7. Shows the IUCN Red List range map for *Cercopithecus denti* as a red outline and the presence-absence version of MaxEnt's suitable habitat map (created by taking the suitability maps in figure 3 and cutting off suitability scores below the species' 10th percentile Cloglog threshold value, which is a measure of the suitability value above which 90% of known localities fall) shown in blue. Blue areas are those the Maxent model predicts to be suitable.

Cercopithecus diana



Suitable habitat for *Cercopithecus diana* was dependent on precipitation of coldest quarter (40.1%), Terrestrial ecoregion (34%) and annual precipitation (18%) (see table). The most suitable habitats have rainfall in the coldest quarter around 600mm, an ecoregion of tropical and subtropical moist broadleaf forest and annual precipitation of 3500mm and above. Annual precipitation also had the highest permutation importance (55.6%)

The model's map of potential suitable habitat is similar to the IUCN map (Figure 7 (left)) however the model predicts that that *Cercopithecus diana* suitable habitat could extend to a separate area on South boarder of Nigeria and Cameroon. While the IUCN outline shows that *Cercopithecus diana* is found in larger areas of Sierra Leone, Inland Liberia, South Guinea and East Cote D'Ivoir that shows as not being suitable in the MaxEnt map (Kone, McGraw, *et al.*, 2019).

Figure 8. Shows the IUCN Red List range map for *Cercopithecus diana* as a red outline and the presence-absence version of MaxEnt's suitable habitat map (created by taking the suitability maps in figure 3 and cutting off suitability scores below the species' 10th percentile Cloglog threshold value, which is a measure of the suitability value above which 90% of known localities fall) shown in blue. Blue areas are those the Maxent model predicts to be suitable.
Cercopithecus dryas



Suitable habitat for *Cercopithecus dryas* was dependent on temperature seasonality (42.6% of the power of the model), terrestrial ecoregions (40.2%) and precipitation seasonality (7.4%). The most suitable habitats have little to no temperature seasonality, a Tropical and subtropical moist broadleaf forest ecoregion and little to no precipitation seasonality. The highest permutation importance is temperature seasonality (61.8%) (see table).

The model map of potential suitable habitat is similar to the IUCN map (Figure 8 (left)). The model predicts that *Cercopithcus dryas* suitable habitat in Democratic Republic of Congo that extends across the Center of the country. While the IUCN outline shows that Cercopithecus dryas extant population is contained in two small areas also in the Democratic Republic of Congo, the Northmost area is not considered suitable by the MaxEnt map (Hart, Detwiler and Alempijevic, 2021).

Figure 9. Shows the IUCN Red List range map for *Cercopithecus dryas* as a red outline and the presence-absence version of MaxEnt's suitable habitat map (created by taking the suitability maps in figure 3 and cutting off suitability scores below the species' 10th percentile Cloglog threshold value, which is a measure of the suitability value above which 90% of known localities fall) shown in blue. Blue areas are those the Maxent model predicts to be suitable.

Cercopithecus erythrogaster



Suitable habitat for *Cercopithecus erythrogaster* was dependent on mean diurnal range (36% of the power of the model), precipitation of the coldest quarter (27.9%) and annual mean temp (13.6%) (see table). The most suitable habitats had little to no diurnal range, around 1200mm of rainfall in the coldest quarter and a mean annual temperature of 30° or higher. The mean diurnal range had the highest permutation importance (31.9%).

The model's map of potential suitable habitat is similar to the IUCN map (Figure 9 (left)) however the model predicts that *Cercopithecus erythrogaster* suitable habitat could extend further West to Cote D'ivoire and Ghana and Furter East in Nigeria as well as to Cameroon. While the IUCN outline shows that *Cercopithecus erythrogaster* is spread over a wider area of Nigeria that shows as not being suitable in the MaxEnt map (Matsuda Goodwin, Oates, *et al.*, 2020).

Figure 10. Shows the IUCN Red List range map for *Cercopithecus erythrogaster* as a red outline and the presence-absence version of MaxEnt's suitable habitat map (created by taking the suitability maps in figure 3 and cutting off suitability scores below the species' 10th percentile Cloglog threshold value, which is a measure of the suitability value above which 90% of known localities fall) shown in blue. Blue areas are those the Maxent model predicts to be suitable.

Cercopithecus erythrotis

Suitable habitat for *Cercopithecus erythrotis* was dependent on terrestrial ecoregion (50.7% of the



power of the model), precipitation of the coldest quarter (31.4%) and annual precipitation (11.2%). The most suitable habitats had an ecoregion of tropical and subtropical moist broad leaf forest, precipitation with 1700mm or more of rain in the coldest quarter and annual precipitation of 3700mm and over. Precipitation of the coldest quarter has the highest permutation importance (28.8%)

The model's map of potential suitable habitat is similar to the IUCN map (Figure 10 (left)) however the model predicts that *Cercopithecus erythrotis* suitable habitat can extend across the South of Nigeria as well as a separated are that extends from the south border of Cote D'Ivoire and Libreia and then along the coast of Liberia, Sierra Leone, Guinea and Guinea Bissau. The IUCN only shows a small area in Nigeria where the population is extant as being unsuitable in the MaxEnt map (Hofner *et al.*, 2020).

Figure 11. Shows the IUCN Red List range map for *Cercopithecus erythrotis* as a red outline and the presence-absence version of MaxEnt's suitable habitat map (created by taking the suitability maps in figure 3 and cutting off suitability scores below the species' 10th percentile Cloglog threshold value, which is a measure of the suitability value above which 90% of known localities fall) shown in blue. Blue areas are those the Maxent model predicts to be suitable.

Cercopithecus hamlyni



Suitable habitat for *Cercopithecus hamlyni* was dependent on terrestrial ecoregions (61.4% of the power of the model), temperature seasonality (22.3%) and precipitation seasonality (11.2%) (see table). The most suitable habitats had a terrestrial ecoregion of tropical and subtropical moist broad leaf forest, little to no temperature and precipitation seasonality. Temperature seasonality has the highest permutation importance (70.8%)

The model's map of potential suitable habitat is similar to the IUCN map (Figure 11 (left)) however the model predicts that *Cercopithecus hamlyni* suitable habitat could extend further East and West in the Democratic Republic of Congo. While the IUCN outline shows *Cercopithecus hamlyni* has areas in the North and South that as shown as not suitable in the MaxEnt map (Hart and Maisels, 2019).

Figure 12. Shows the IUCN Red List range map for *Cercopithecus hamlyni* as a red outline and the presence-absence version of MaxEnt's suitable habitat map (created by taking the suitability maps in figure 3 and cutting off suitability scores below the species' 10th percentile Cloglog threshold value, which is a measure of the suitability value above which 90% of known localities fall) shown in blue. Blue areas are those the Maxent model predicts to be suitable.

Cercopithecus Iomamiensis



Suitable habitat for *Cercopithecus lomamieneis* was dependent on terrestrial ecoregion (32.8%), precipitation of driest month (31.3%) and temperature seasonality (12.1%). The most suitable habitats are in a ecoregion of tropical and subtropical moist broadleaf forest, that get more than 140mm of rainfall in the driest month and little to no temperature seasonality. Temperature seasonality has the highest permutation importance (43.3%).

The model's map of potential suitable habitats is not similar to the IUCN map (Figure 12 (left)) the model and the IUCN both predict that *Cercopitheucs lomamiensis* exisits in the Democratic Republic of Congo. However the model predicts suitable habitat for *Cercopithecus lomamiensis* mostly to the west and a small amount to the east of the IUCN outline. The area inside the IUCN outline is shown as not suitable in the MaxEnt map (Detwiler and Hart, 2020).

Figure 13. Shows the IUCN Red List range map for *Cercopithecus lomamiensis* as a red outline and the presence-absence version of MaxEnt's suitable habitat map (created by taking the suitability maps in figure 3 and cutting off suitability scores below the species' 10th percentile Cloglog threshold value, which is a measure of the suitability value above which 90% of known localities fall) shown in blue. Blue areas are those the Maxent model predicts to be suitable.

Cercopithecus lowei

Suitable habitat for *Cercopithecus lowei* was dependent on mean diurnal range (27.9% of the power



of the model), terrestrial ecoregion (26.8%) and temperature seasonality (15.7%). The most suitable habitats had little to no diurnal range, a terrestrial ecoregion of tropical and subtropical moist broadleaf forest and little to no temperature seasonality. Temperature seasonality also had the highest permutation importance (72.4%).

The model's map of potential suitable habitat is similar to the IUCN map (Figure 13 (left)) however the model predicts that Cercopithecus lowei suitable habitat extends to Togo Benin and Nigeria with a separated area in Cameroon, Equatorial Guinea and Gabon, a separate area within Congo and along the East Coast of Africa from the South of Somalia through Kenya and Tanzania. While the IUCN outlines shows extant populations exist in areas that the MaxEnt model predicts as not being suitable in the North and North East of the IUCN map (Wiafe *et al.*, 2019).

Figure 14. Shows the IUCN Red List range map for *Cercopithecus lowei* as a red outline and the presence-absence version of MaxEnt's suitable habitat map (created by taking the suitability maps in figure 3 and cutting off suitability scores below the species' 10th percentile Cloglog threshold value, which is a measure of the suitability value above which 90% of known localities fall) shown in blue. Blue areas are those the Maxent model predicts to be suitable.

Cercopithecus mitis

Suitable habitat for *Cercopithecus mitis* was dependent on the precipitation of the driest month



(36.6% of the power of the model), annual precipitation (18%) and temperature seasonality (12.6%). The most suitable habitat had rainfall between 50mm and 120mm in the driest month, around 600mm of annual rainfall and little to no temperature seasonality. Temperature seasonality has the highest permutation importance (29.9%).

The model's map of potential suitable habitat is similar to the IUCN map (Figure 14 (left)) however the model predicts that *Cercopithecus mitis* suitable habitat could extend to larger areas of Tanzania and Uganda as well as larger areas North and East of the IUCN map in Ethiopia, also coastal areas in West Africa of Ghana, Togo and Benin. While the IUCN outline shows that *Cercopithecus mitis* is spread over the north of Zambia and the South of Democratic Republic of Congo as well as inland Mozambique and South East Malawi that are shown as not being suitable in the MaxEnt map (Butynski and de Jong, 2019).

Figure 15. Shows the IUCN Red List range map for *Cercopithecus mitis* as a red outline and the presence-absence version of MaxEnt's suitable habitat map (created by taking the suitability maps in figure 3 and cutting off suitability scores below the species' 10th percentile Cloglog threshold value, which is a measure of the suitability value above which 90% of known localities fall) shown in blue. Blue areas are those the Maxent model predicts to be suitable.

Cercopithecus mona

Suitable habitat for *Cercopithecus mona* was dependent on precipitation of coldest quarter (42.8% of the power of the model), mean diurnal range (16.6%) and precipitation of the driest month



(10.9%). The most suitable habitat had around 250mm of rainfall in the coldest quarter with between 4° -5.5° diurnal range and little to no rainfall in the driest month. Precipitation of the coldest quarter has the highest permutation importance (23.2%).

The model's map of potential suitable habitat is similar to the IUCN map (Figure 15 (left)) however the model predicts that *Cercopithecus mona* suitable habitat could extend further West further across Ghana and Cote D'Ivoire as well as two isolated areas one on the border of Guinea and Sierra Leone and the other beginning on the south coast of Somalia through kenya and the North of Tanzania. While the IUCN outline shows that Cercopithecus mona is spread further North in Cameroon, Nigeria, Benin,Togo and Ghana that shows as not being suitable by the MaxEnt map (Matsuda Goodwin, Segniagbeto, Nobime, *et al.*, 2020).

Figure 16. Shows the IUCN Red List range map for *Cercopithecus mona* as a red outline and the presence-absence version of MaxEnt's suitable habitat map (created by taking the suitability maps in figure 3 and cutting off suitability scores below the species' 10th percentile Cloglog threshold value, which is a measure of the suitability value above which 90% of known localities fall) shown in blue. Blue areas are those the Maxent model predicts to be suitable.

Cercopithecus neglectus



Suitable habitat for *Cercopithecus neglectus* was dependent on precipitation of driest month (75.1% of the power of the model), precipitation of coldest quarter (19.9%) and temperature seasonality (8.2%). The most suitable habitat has around 60mm rainfall in the driest month, and around 500mm rainfall in the coldest quarter, moderate temperature seasonality (500 units). Temperature seasonality has the highest permutation importance (80.8%).

The model's map of the potential suitable habitat is similar to the IUCN map (Figure 16 (left)) however the model predicts that *Cercopithecus neglectus* suitable habitat could extend further into Uganda, Tanzania and more area in Kenya also extending further East in Ethiopia. While the IUCN outline shows *that Cercopithecus neglectus* is spread over a wider area if Cameroon, Gabon, Central African Republic, Congo and the Democratic Republic of Congo that shows as not being suitable in the MaxEnt map (Mwenja, Maisels and Hart, 2019).

Figure 17. Shows the IUCN Red List range map for *Cercopithecus neglectus* a red outline and the presence-absence version of MaxEnt's suitable habitat map (created by taking the suitability maps in figure 3 and cutting off suitability scores below the species' 10th percentile Cloglog threshold value, which is a measure of the suitability value above which 90% of known localities fall) shown in blue. Blue areas are those the Maxent model predicts to be suitable.

Cercopithecus nictitans

Suitable habitat for *Cercopithecus nictitans* was dependent on terrestrial ecoregion (47.6% of the power of the model), annual precipitation (29.5%) and temperature seasonality (8.1%). The most suitable habitat had an ecoregions of tropical and subtropical moist broad leaf forest or mangrove,



between 2200mm and 2500mm of annual rainfall and a small amount of temperature seasonality (around 900 units). Temperature seasonality had the highest permutation importance (59.8%).

The model's map of potential suitable habitat is similar to the IUCN map (Figure 17 (left)) however the model predicts that *Cercopithecus nictitans* suitable habitat could extend further into the Central African Republic and Further East into the Democratic Republic of Congo. To the East as well the predicted suitable habitat extends into Guineas Sierra Leone and more of Liberia as well as some East coastal areas of Cote D'Ivoire and West Ghana. While the IUCN outline shows that *Cercopithecus nictitans* is spread over a wider area of Democratic Republic of Congo, Congo, South Gabon, Central Cameroon and South East Nigeria. Also a small area in Cote D'Ivoire that shows as not being suitable in the MaxEnt map (Cronin *et al.*, 2020).

Figure 18. Shows the IUCN Red List range map for *Cercopithecus nictitans* as a red outline and the presence-absence version of MaxEnt's suitable habitat map (created by taking the suitability maps in figure 3 and cutting off suitability scores below the species' 10th percentile Cloglog threshold value, which is a measure of the suitability value above which 90% of known localities fall) shown in blue. Blue areas are those the Maxent model predicts to be suitable.

Cercopithecus petaurista

Suitable habitat for *Cercopithecus petaurista* was dependent on precipitation of the coldest quarter (29.8% of the power of the model), precipitation of the driest month (24.3%) and temperature



seasonality (15%). The most suitable habitat had around 250mm of rainfall in the coldest quarter, around 19mm of rainfall in the driest month and a small amount of temperature seasonality (between 800 and 1200 units). Temperature seasonality also has the highest permutation importance (82.2%).

The model's map of predicted suitable habitat is similar to the IUCN map (Figure 18 (left)) however the model predicts that *Cercopithecus petaurista* suitable habitat could extend to a separate area in South Nigeria, Cameroon and Equatorial Guinea as well as an area in the Central African Republic and Coastal Tanzania. While within the IUCN outline shows that *Cercopithecus petaurista* is spread over more North areas of Togo, Ghana and Cote' D'Ivoire as well as Ginea-Bissau and Guinea that show as not being suitable in the MaxEnt map (Matsuda Goodwin, Segniagbeto, Wiafe, *et al.*, 2020).

Figure 19. Shows the IUCN Red List range map for *Cercopithecus petaurista* as a red outline and the presence-absence version of MaxEnt's suitable habitat map (created by taking the suitability maps in figure 3 and cutting off suitability scores below the species' 10th percentile Cloglog threshold value, which is a measure of the suitability value above which 90% of known localities fall) shown in blue. Blue areas are those the Maxent model predicts to be suitable.

Cercopithecus pogonias

Suitable habitat for *Cercopithecus pogonias* was dependent on terrestrial ecoregion (49.5% of the power of the model), annual precipitation (35.6%) and temperature seasonality (6.9%). The most



suitable habitats had an ecoregion of tropical and subtropical moist broadleaf forest, more than 1700mm of annual rainfall and a small amount of temperature seasonality (800 units). Temperature seasonality had the highest permutation importance (80.4%).

The model's map of potential suitable habitat is similar to the IUCN map (Figure 19 (left)) however the model predicts that *Cercopithecus pogonias* suitable habitat could extend further into the Democratic Republic of Congo as well as South Nigeria and South Cote D'Ivoire, Liberia, Sierra Leone, and Guinea. While the IUCN outline shows that *Cercopithecus pogonias* is extant in North East Angola and East Democratic Republic of Congo as well as in the North of the Democratic Republic of Congo and the South East of the Central African Republic that shows as not being suitable in the MaxEnt map (Maisels *et al.*, 2020).

Figure 20. Shows the IUCN Red List range map for *Cercopithecus pogonias* as a red outline and the presence-absence version of MaxEnt's suitable habitat map (created by taking the suitability maps in figure 3 and cutting off suitability scores below the species' 10th percentile Cloglog threshold value, which is a measure of the suitability value above which 90% of known localities fall) shown in blue. Blue areas are those the Maxent model predicts to be suitable.

Cercopithecus sclateri



Suitable habitat for *Cercopithecus sclateri* was dependent on terrestrial ecoregion (39.4% of the power of the model), precipitation of the coldest quarter (15.7%) and mean diurnal range (15.5%). The most suitable habitat had an ecoregion of tropical and subtropical moist broadleaf forest, around 1200mm of rainfall in the coldest quarter and little to no mean diurnal range. Annual mean temperature has the highest permutation importance (64.2%).

The models map of potential suitable habitat is similar to the IUCN map (Figure 20 (left)) however the model predict that *Cercopithecus sclateri* suitable habitat could extend further into Cameroon as well as the South and East coast of Nigeria and small area of Coastal Sierra Leone. While the IUCN outline shows that *Cercopithecus sclateri* is spread further North within the red list outline than is shown as being suitable in the MaxEnt map (Baker *et al.*, 2019).

Figure 21. Shows the IUCN Red List range map for *Cercopithecus sclateri* as a red outline and the presence-absence version of MaxEnt's suitable habitat map (created by taking the suitability maps in figure 3 and cutting off suitability scores below the species' 10th percentile Cloglog threshold value, which is a measure of the suitability value above which 90% of known localities fall) shown in blue. Blue areas are those the Maxent model predicts to be suitable.

Cercopithecus wolfi



Suitable habitat for *Cercopithecus wolfi* was dependent on terrestrial ecoregion (37.5% of the power of the model), temperature seasonality (21.6%) and precipitation of the driest month (18.9%). The most suitable habitat had an ecoregion of tropical and subtropical grasslands savannas and shrubland with little to no temperature seasonality and any precipitation of the driest month. Precipitation seasonality had the highest permutation importance (51.3%).

The model's map of potentially suitable habitat is similar to the IUCN map (Figure 21 (left)) howevert he model predicts that Cercopithecus wolfi suitable habitat could extend further into Congo as well as further West in the Democratic Republic of Congo. While within the IUCN outline according to the MaxEnt map Cercopitehcus wolfi finds large areas to the South and a small area in the North of its extant population as not suitable (Hart, Detwiler and Maisels, 2020).

Figure 22. Shows the IUCN Red List range map for *Cercopithecus wolfi* as a red outline and the presence-absence version of MaxEnt's suitable habitat map (created by taking the suitability maps in figure 3 and cutting off suitability scores below the species' 10th percentile Cloglog threshold value, which is a measure of the suitability value above which 90% of known localities fall) shown in blue. Blue areas are those the Maxent model predicts to be suitable.

Allochrocebus Ihoesti



Suitable habitat for *Allochrocebus lhoesti* was dependent on temperature seasonality (52.6% of the power of the model), precipitation of the driest month (21.3%) and altitude (14.2%). The most suitable habitat had little to no temperature seasonality, 110mm or more of rainfall in the driest month and high altitude between 3000 and 3500m. Temperature seasonality has the highest permutation importance (80.7%).

The model's map of potential suitable habitats not similar to the IUCN map (Figure 22 (left)) the model predicts that *Allochrocebus lhoesti* suitable habitat occurs in Rwanda and a small area of the border of Democratic Republic of Congo and Uganda. While the IUCN outline for *Allochrocebus lhoesti* shows area that is not suitable according to the MaxEnt model which is East Democratic Republic of Congo (Ukizintambara, Olupot and Hart, 2019).

Figure 23. Shows the IUCN Red List range map for *Allochrocebus lhoesti* as a red outline and the presence-absence version of MaxEnt's suitable habitat map (created by taking the suitability maps in figure 3 and cutting off suitability scores below the species' 10th percentile Cloglog threshold value, which is a measure of the suitability value above which 90% of known localities fall) shown in blue. Blue areas are those the Maxent model predicts to be suitable.

Allochrocebus preussi

Suitable habitat for *Allochrocebus preussi* was dependent on terrestrial ecoregion (51.4% of the power of the model), precipitation of the coldest quarter (28.7%) and max temp of warmest month



(10%). The most suitable habitat had a terrestrial ecoregion of tropical and subtropical moist broadleaf forest, 1500mm or more rainfall in the coldest quarter and a max temperature between 10°C and 25°C. Precipitation of the coldest quarter has the highest permutation importance (32.3%).

The model's map of potential suitable habitat is similar to the IUCN map (Figure 23 (left)) however the model predicts that *Allochrocebus preussi* suitable habitat could extend more through South East of Cameroon and South West Nigeria, with separate areas along the West coast of Africa through Guinea, Sierra Leone and Liberia well as further East with suitable areas in the East of Democratic Republic of Congo, Rwanda, Burundi and Kenya. While the IUCN outline shows that *Allochrocebus preussi* North most extant population which crosses the Cameroon Nigeria border that shows as not being suitable in the MaxEnt map (Cronin *et al.*, 2019).

Figure 24. Shows the IUCN Red List range map for *Allochrocebus preussi* as a red outline and the presence-absence version of MaxEnt's suitable habitat map (created by taking the suitability maps in figure 3 and cutting off suitability scores below the species' 10th percentile Cloglog threshold value, which is a measure of the suitability value above which 90% of known localities fall) shown in blue. Blue areas are those the Maxent model predicts to be suitable.

Zones of overlap and the ecological distinctiveness of guenon species

The zones of suitable habitat predicted for each guenon species vary in extent (see Table 6). The species with the largest area of predicted habitat is *Cercopithecus mitis* with 2,144,965km² of habitat that is scored as potentially suitable. Here and in Table 6, suitable habitat is defined as any habitat with a suitability score above the species' calculated 10th percentile Cloglog threshold, which is the value above which 90% of known localities fall according to MaxEnt. The species with the smallest area of suitable habitat, as predicted by my models, is *Allochrocebus lhoesti* with 54,351.12km².

To find out whether individual guenon species are ecologically distinct, I overlaid their suitable habitat maps to see what proportion of habitat they shared. Table 6 lists the number of other guenon species each focal species was predicted to share suitable habitat with, while Table 7 gives the percentage of each species' suitable habitat that is shared with each of these potentially coexisting species. In a few cases, where predicted zones of overlap are small, these may occur in places where one or both species do not presently live, but overall, the map of guenon biodiversity created using my Maxent model outputs (Figure 24b) lines up well with the same map of diversity created by overlaying species' IUCN Range maps (Figure 24a). My findings suggest that guenon habitat suitability is often controlled by the same handful of environmental variables (Table 5) and thus what is suitable for one guenon species is also potentially suitable for others. There are enough differences in environmental needs however that the each species does have distinct biogeography (Fig 3-23) even with the minimal ecological distinctions between taxa. This is backed up by the fact

that many cells are potentially suitable to be shared not just by two guenon species but by five, six or even eight all the way up to potentially twelve for a very small area (Table 8 and Figure 24b).

Guenons are most suited to areas with low seasonality for both temperature and rainfall with both being continuously relatively high and mostly preferring a terrestrial ecoregion with Tropical and Subtropical Moist Broadleaf Forest, Tropical and Subtropical Grasslands Savannas and Shrublands and Mangrove (Olson *et al.*, 2001).

Species	Area of suitable	Number of species predicted to share
	habitat (km²)	part of this suitable habitat
Cercopithecus ascanius	1,872,360	11
Cercopithecus campbelli	288,538.1	4
Cercopithecus cephus	542,593.7	7
Cercopithecus denti	87,565.45	7
Cercopithecus diana	1,1748	4
Cercopithecus dryas	229,805.3	7
Cercopithecus erythrogaster	102,748	4
Cercopithecus erythrotis	237,648.5	6
Cercopithecus hamlyni	657,058.1	7
Cercopithecus lomamiensis	71,738.16	5
Cercopithecus lowei	684,481.9	5
Cercopithecus mitis	2,144,965	10
Cercopithecus mona	776,433.4	10
Cercopithecus neglectus	1,431,313	14
Cercopithecus nictitans	900,627.6	15
Cercopithecus petaurista	690,996.2	5
Cercopithecus pogonias	1,837,207	10
Cercopithecus sclateri	121,129.6	5
Cercopithecus wolfi	664,328.7	10
Allochrocebus lhoesti	54,351.12	5
Allochrocebus preussi	211,288.9	5

Table 9. Shows the area of predicted suitable habitat from the niche model of suitable predicted habitat.

	C. ascanius	C.campbelli	C.cephus	C.denti	C.diana	C.dryas	erythrogaster	C.erythrotis	C.hamlyni	. lomamiensis	C.lowei	C.mitis	C.mona	C.neglectus	C.nictitans	C.petaurista	C.pogonias	C.sclateri	C.wolfi	A.lhoesti	A.preussi
species							Ū			0											
C.asc			I																		
C.cam	0.825																				
C.ceph	0.912	0.901																			
C.denti	0.862	0.784	0.803																		
C.diana	0.845	0.957	0.916	0.741			1														
C.dryas	0.930	0.885	0.959	0.845	0.915																
C.egas	0.634	0.581	0.695	0.472	0.662	0.711															
C.etis	0.879	0.816	0.954	0.791	0.877	0.914	0.588														
C.ham	0.921	0.877	0.920	0.965	0.838	0.946	0.598	0.883													
C.lom	0.797	0.801	0.797	0.910	0.730	0.821	0.688	0.688	0.909			_									
C.low	0.687	0.639	0.757	0.511	0.718	0.796	0.964	0.650	0.656	0.397											
C.mitis	0.840	0.824	0.882	0.720	0.820	0.873	0.472	0.889	0.829	0.699	0.555										
C.mona	0.578	0.546	0.662	0.465	0.630	0.633	0.818	0.654	0.552	0.455	0.787	0.836									
C.neg	0.907	0.938	0.927	0.903	0.935	0.947	0.577	0.898	0.969	0.867	0.642	0.888	0.552								
C.nic	0.895	0.950	0.962	0.777	0.973	0.954	0.662	0.912	0.583	0.755	0.732	0.902	0.598	0.945							
C.pet	0.847	0.946	0.929	0.775	0.956	0.945	0.709	0.836	0.893	0.800	0.787	0.836	0.635	0.937	0.957						
C.pog	0.914	0.933	0.972	0.795	0.953	0.971	0.684	0.911	0.917	0.784	0.757	0.894	0.589	0.945	0.992	0.953					
C.scl	0.688	0.794	0.810	0.601	0.811	0.813	0.848	0.655	0.744	0.700	0.865	0.649	0.612	0.759	0.825	0.874	0.838				
C.wol	0.891	0.757	0.863	0.913	0.746	0.889	0.707	0.802	0.929	0.852	0.729	0.701	0.647	0.859	0.792	0.803	0.826	0.710			
A.lho	0.714	0.650	0.726	0.625	0.736	0.719	0.345	0.868	0.688	0.471	0.408	0.801	0.437	0.755	0.746	0.643	0.714	0.410	0.575		
A.pre	0.824	0.703	0.848	0.760	0.761	0.830	0.431	0.963	0.817	0.616	0.499	0.834	0.558	0.816	0.812	0.707	0.810	0.475	0.748	0.890	

Fig 25. This table shows the rank correlation coefficient *rho*, this is the measure of overlap of the neiches. This is then meant to show the responses of these species to the variable that are used to create the maxent model. It shows comparatively how the species react the their environmental (Warren *et al.*, 2021). The

	C. ascanius	C.campbelli	C.cephus	C.denti	C.diana	C.dryas	erythrogaster	C.erythrotis	C.hamlyni	C.lomamiensis	C.lowei	C.mitis	C.mona	C.neglectus	C .nictitans	C.petaurista	C.pogonias	C.sclateri	C.wolfi	A.lhoesti	A.preussi
species							0														
C.asc	0 242																				
C.conh	0.545	0.500																			
C.cepii	0.396	0.300	0.264																		
C diana	0.745	0.314	0.545	0 345																	
C dryas	0.300	0.531	0.763	0.343	0 5 5 0																
Clegas	0.146	0.409	0.364	0.058	0.378	0.322															
Cetis	0.701	0.749	0.749	0.609	0.771	0.832	0.420														
C.ham	0.854	0.451	0.622	0.884	0.496	0.927	0.175	0.796													
C.lom	0.510	0.237	0.349	0.676	0.226	0.731	0.489	0.489	0.742												
C.low	0.510	0.460	0.731	0.348	0.482	0.719	0.609	0.704	0.567	0.397											
C.mitis	0.713	0.261	0.497	0.424	0.289	0.545	0.208	0.632	0.535	0.274	0.535										
C.mona	0.274	0.501	0.472	0.087	0.490	0.388	0.755	0.523	0.243	0.068	0.725	0.426									
C.neg	0.894	0.493	0.689	0.779	0.539	0.858	0.220	0.785	0.907	0.574	0.590	0.614	0.344								
C.nic	0.518	0.785	0.873	0.348	0.786	0.692	0.431	0.832	0.583	0.265	0.632	0.422	0.553	0.682							
C.pet	0.440	0.712	0.647	0.271	0.745	0.581	0.656	0.716	0.452	0.210	0.765	0.426	0.775	0.591	0.761						
C.pog	0.707	0.685	0.911	0.514	0.713	0.845	0.367	0.898	0.757	0.454	0.722	0.572	0.484	0.794	0.925	0.717					
C.scl	0.207	0.572	0.411	0.204	0.541	0.468	0.811	0.575	0.342	0.234	0.537	0.198	0.565	0.317	0.526	0.599	0.483				
C.wol	0.658	0.391	0.635	0.721	0.425	0.916	0.210	0.697	0.894	0.851	0.616	0.881	0.234	0.772	0.523	0.423	0.700	0.384			
A.lho	0.769	0.203	0.330	0.741	0.238	0.599	0.071	0.538	0.742	0.400	0.287	0.514	0.121	0.709	0.367	0.230	0.417	0.141	0.477		
A.pre	0.691	0.718	0.734	0.607	0.755	0.817	0.391	0.994	0.788	0.482	0.662	0.640	0.484	0.770	0.814	0.680	0.879	0.556	0.681	0.555	

Fig 26. This table shows the I measure which measures similarity of the 'geographic spaces' that the species inhabit (Warren *et al.*, 2021). I is different a measure of 1 - Hellinger Distance, it is a similarity measure that compares habit suitability by grid cell and is based in probability theory (Warren *et al.*, 2010).

	C. ascanius	C.campbelli	C.cephus	C.denti	C.diana	C.dryas	erythrogaster	C.erythrotis	C.hamlyni	C.lomamiensis	C.lowei	C.mitis	C.mona	C.neglectus	C.nictitans	C.petaurista	C.pogonias	C.sclateri	C.wolfi	A.lhoesti	A.preussi
species							ن.			0											
C.asc																					
C.cam	0.159																				
C.ceph	0.341	0.228																			
C.denti	0.471	0.128	0.190																		
C.diana	0.180	0.623	0.271	0.155																	
C.dryas	0.528	0.242	0.455	0.455	0.264																
C.egas	0.037	0.217	0.141	0.010	0.170	0.099	0.405														
C.etis	0.461	0.452	0.459	0.388	0.472	0.593	0.185			l											
C.ham	0.591	0.176	0.335	0.647	0.215	0.713	0.036	0.517													
C.lom	0.249	0.082	0.157	0.389	0.079	0.464	0.245	0.245	0.467												
C.low	0.283	0.207	0.453	0.167	0.238	0.407	0.315	0.403	0.291	0.187			I								
C.mitis	0.402	0.118	0.222	0.196	0.151	0.407	0.067	0.333	0.269	0.096	0.277			l							
C.mona	0.094	0.275	0.207	0.023	0.253	0.259	0.472	0.282	0.071	0.014	0.446	0.195									
C.neg	0.671	0.222	0.426	0.501	0.260	0.149	0.060	0.548	0.658	0.305	0.311	0.336	0.124								
C.nic	0.279	0.447	0.665	0.164	0.480	0.618	0.207	0.563	0.285	0.102	0.355	0.181	0.322	0.399			1				
C.pet	0.194	0.426	0.459	0.095	0.447	0.382	0.382	0.418	0.163	0.067	0.485	0.195	0.491	0.266	0.482			I			
C.pog	0.458	0.366	0.688	0.296	0.399	0.259	0.141	0.659	0.450	0.215	0.436	0.269	0.239	0.550	0.707	0.284			l		
C.scl	0.087	0.323	0.182	0.081	0.263	0.562	0.537	0.289	0.133	0.095	0.261	0.088	0.286	0.129	0.260	0.315	0.221				
C.wol	0.388	0.150	0.327	0.498	0.181	0.196	0.050	0.426	0.712	0.597	0.313	0.154	0.069	0.510	0.245	0.150	0.394	0.153			
A.lho	0.480	0.087	0.156	0.444	0.109	0.714	0.013	0.280	0.407	0.175	0.149	0.251	0.034	0.388	0.134	0.087	0.266	0.066	0.230		
A.pre	0.691	0.087	0.445	0.384	0.462	0.577	0.171	0.925	0.507	0.240	0.374	0.342	0.258	0.531	0.540	0.388	0.633	0.279	0.412	0.294	
	Fig 27.	this is th	e D fact	or which	n measu	res the s	imilarity	of the h	nabitats	betweer	n the tw	o specie	s (Warro	en <i>et al.,</i>	2021)	This is do	one by o	verlap c	omparin	g	
	'freque	ency by v	olume a	ind then	plotted	against	overlap	in struct	ural hat	oitat' D s	tops ske	ews from	n happei	ning beca	ause of s	small nu	mbers o	f observ	ations		

(Schoener, 1968). Mathematically D is "1 – total variation distance" total D also has an ecological interpretation (Warren et al., 2010)



Fig 28. The IUCN Red List range maps for all species (a). Maxent maps used in (b) were converted to presence-absence maps using the 10% Cloglog threshold value and added together in ArcGIS to show biodiversity (number of species present in each cell). IUCN Red List range maps were layered in ArcGIS by setting transparency to 15% such that shade indicates number of species coexisting and (a) Guenon biodiversity maps as created using my Maxent models. (c) is map (a) superimposed over environmental from the ArcGIS website (Esri., 2014) that shows the major rivers of Africa as well as

basic Environmental data and (d) is similarly map (b) superimposed over environmental data from (Esri., 2014) that shows the major rivers of Africa as well as basic environmental data.

Discussion

Tribe Cercopithecini are the most speciose clade of African monkeys (Cardini and Elton, 2008b, 2008c) and the guenons (genus *Cercopithecus*) are considered the most diverse within Tribe Cercopithecini (lo Bianco, Masters and Sineo, 2017). The guenons have very diverse pelage and are considered to have the most diverse soft tissue morphology of African monkeys (Cardini and Elton, 2008b). In terms of facial features, they sport distinct eyebrows and nose spots which they use to identify conspecifics (Winters, Allen and Higham, 2020). However, their skeletal structure is highly conservative(lo Bianco, Masters and Sineo, 2017), specimens of *Cercopithecus* are mistaken for other species, in Cardini and Elton (2008) 88.4% of their specimens had been correctly labelled according to the discriminant analysis, more than 10% of the samples incorrectly labelled is a high degree of error for taxonomy.

The differences in guenon biogeography are most likely a result of allopatric speciation, where evolution occurs due to the population of a species getting separated (Kamilar, Martin and Tosi, 2009). In the case of the Guenons, it is hypothesised that their populations were split as the forests retreated and expanded due to ice ages and global warming (Kamilar, Martin and Tosi, 2009; Arenson *et al.*, 2020). This is likely related to what can be seen in Figure 25 the spearman's rank values that show how similar the reactions to the changes in the environment are.

The guenons have broad biogeography and flexible diet, perhaps their flexibility is due to the broad geographical areas that they inhabit, and therefore the difference in available food forces them to become flexible (Coleman and Hill, 2014). *Cercopithecus mitis* is the guenon with the largest predicted suitable habitat, and is known to have a highly flexible diet. However, dietary flexibility is true of primates in general, it is simply the degree of flexibility that changes (Chapman *et al.*, 2005). Otherwise, for our investigated species, there is also a distinct difference in the diet of *Allochrocebus* and *Cercopithecus*. The three largest proportions of the diet on average for the *Cercopithecus* are leaves, fruit and insects. The Allochrocebus has one major difference; although they too eat fruit and insects, they eat grasses instead of leaves which is liked to them being semiterrestrial (Gautier-Hion, 1980; Wahome, Rowell and Tsingalia, 1993; Peignot, Fontaine and Wickings, 1999; Kaplin and Moermond, 2000; Twinomugisha, Basuta and Chapman, 2003; Paul J. Buzzard, 2006b; Bryer, Chapman and Rothman, 2013; Coleman and Hill, 2014; Hutchinson, 2015; Arenson *et al.*, 2020).

Species distribution models (SDM's) are the areas that have been predicted to be suitable to each species based on the ecological variables that correlate with the locality points that were inputted into ArcGIS, and the environmental factors are correlated with those positions. The ecological variables mentioned above are the environmental layers from Table 3.

The reactions and similarity of ecological suitability from the ENMTools then showed their conservatism. Specifically the *Cercopithecus* and *Allochrocebus* conserve much of their ecological reactions as shown in Fig 25. This is possibly a result of allopatric speciation, the species still react similarly to each other with only a few species in comparison to one another having relatively low similarity their reaction, such as *C.erythrogaster* and *C.denti* or *C.mitis* and *C.erythrogaster* that have lower than 0.5 similarity.

This investigation shows that guenons have similar ecological needs, in much the same way as their anatomy is simultaneously conservative yet distinct. The SDMs are painting a picture of rainforest conditions, although mangrove and grassland and shrubland are also included in the suitable terrestrial biome. They do have enough differences in the importance of environmental variables to still have distinct predicted suitable biogeographic ranges. They have a great similarity in reaction to environmental changes as seen by Fig 25. However according to Fig 26 and Fig 27

Predicted suitable habitats do not always occur where the extant population is according to the Red List. Though most of the species show that predicted suitable habitat occurs within the area of their extant population, there are always areas outside of that according to the model that could be suitable for them to live in currently, there must therefore be barriers that are preventing the species from living in those areas at this time. This could be natural barriers such as mountains and rivers (Aliaga-Samanez *et al.*, 2020), and as it is not climate that is a barrier the possibilities could also be currently anthropogenic (Sales *et al.*, 2019).

The differences between the *Allochrocebus* and *Cercopithecus* in terms of their percentage contributions as can be seen in table 8. Is that *Allochrocebus preussi* has an environmental variable in its top three that doesn't occur in the top three for any other investigated species. This is the max temperature of warmest month. This variable does occur lower than the top three percentage contribution for other species however as can be seen in table 8 and the relationships differ for this variable, *Allochrocebus preussi* and 6 others show a negative relationship, three show no relationship and two have a positive relationship. The difference is therefore a small one as the variable does occur for other species its simply that it is not as high a contribution for the others as it is for *Allochrocebus preussi*. However even when consolidating these differences as is shown in Figures 25, 26 and 27 that the as a whole the species have similar relationships to the environmental variables (Fig 25) and also occur in similar habitats (Fig 26) though it can be seen then that there are some species that are ecologically more similar to each other than others (Fig 27).

In other words, the environmental needs of these genus' are similar to each other, in that the top three percentage contributions for *Allochrocebus* other than max temp of warmest month all occur within the top three percentage contribution of *Cercopithecus*. The other variables that do occur within the top three percentage contributions of *Allochrocebus* are; Temperature seasonality which is also found in twelve *Cercopithecus* top three percentage contributions, precipitation of the driest month which is in six *Cercopithecus* top three percentage contributions. All rarification distance was set to .027 km as this represents the square root of the average home range size for all *Cercopithecus* species (Paul J Buzzard, 2006), to. However, their ecology has not been investigated through MaxEnt modelling to understand the ecological conditions preferred by the different species of the Guenon. This piece of research addresses that gap.

Environmental variables

Looking at environmental factors in table 8, we can again see this distinct, yet generalist trend already seen in their anatomy and genetics. They are effected by the same environmental variables which links to the similarity they show in Fig 25 and 26

The Guenons all require an environment that has stable high temperature and rainfall, with as little seasonal changes to both temperature and rainfall as possible.

The apparent importance for the environmental variables, Terrestrial Ecoregion and Temperature Seasonality. Literature on temperature seasonality has linked small amounts of temperature seasonality and how this creates seasonality in terms of vegetation growth more so than other climate variables (Kitayama, Ushio and Aiba, 2021). However there is another school of thought that the most important factor for the forest growth is soil type (Han, Huang and Zang, 2022).

A major difference in habitat use to consider is that genus *Allochrocebus* are all semi terrestrial whereas *Cercopithecus* are arboreal, with the exceptions of *Cercopithecus lomamiensis* (terrestrial to semiterrestrial), *Cercopithecus hamlyni* (terrestrial) and *Cercopithecus neglectus* (semiterrestrial) (Arenson *et al.*, 2020).

Presence Absence models

The Red List last assessed the monkeys of Genus *Cercopithecus* and *Allochrocebus* between 2016 and 2020, and the information is therefore still relatively recent. In sites that collate species locality points, iNaturalist and GBIF, the datapoint locations are historical as well as current. GBIF has data points as old as 1886 (Cercopithecus mitis) whereas the oldest iNaturalist data points are from 2012. The points shouldn't be unreliable as though the points are historic, they were clipped within 5Km of the IUCN extant range outline, the historical points that were too far outside the extant area have therefore not been included.

The presence absence model, which is the predicted suitable habitat of the species, shows biogeography that could be suitable for each of the species to live in. This type of model is used to study the ecological niche and even to predict their distribution into the future (Hill and Winder, 2019). Figures 4 to 24 shows that, even with the predicted suitable habitat being created from locality points that had been clipped to the IUCN extant range outline. The IUCN extant range doesn't fully match up with the predicted suitable habitat. There are areas within the IUCN range for all the species that is considered not suitable by the model and equally for all species there are areas outside IUCN range that are considered suitable by the model.

Figure 24c uses the IUCN extant range, and shows that there is a geographical barrier in the form of rivers. Figure 28d however shows that the boundaries that are present for their extant ranges do not appear to apply to the predicted suitable habitat. The model therefore doesn't take geographical barriers into account. Comparing Figure 28a and 28b you can see that there are more visible and higher amounts of overlap for the predicted suitable habitat (fig28b).

For example, in Hart et al (2012) investigating *Cercopithecus lomamiensis* states that the limits of its biogeography is contained by rivers to the East and West (the Lomami and the Tsuapa river respectively). The southern border of *Cercopithecus* lomamiensis is constrained because it comes to the end of the forest, and not much is known about the northern limit of their habitat.

Ecological niche overlap

Table 8 shows that the investigated species are conservative with which biome effect the suitability of the habitat. They are conservative both in this and their reactions to the changes in the environmental variables, there are indeed only a small amount of species that are dissimilar in this when compared to other species such as *C.mona* and *C.denti* or *C.mitis* and *C.erythrogaster* in fig 25.

From Figures 28b and 28d it can be seen that there is a lot of overlap in predicted suitable habitat as well as well as them having similar reactions but figure 26 and 27 also show that some species are more similar than others for similarity of the ecology. *Cercopithecus mitis* is surprisingly low in its similarity (fig 26) when considering the size of the predicted suitable habitat and extant habitat they occupy.

The habitat similarity (fig 26) show that some species are mire conservative than others, *Cercopithecus erythrotis* for example is greater than 0.5 similar to 16 of the *Cercopithecus* species as well as both of the *Allochrocebus* species whereas *Cercopithecus lomamiensis* is the lowest where it is greater than 0.5 similar to 5 *Cercopithecus* species and 2 *Allochrocebus*. *Cercopithecus mitis* is also only similar to 7 other species however these are all *Cercopithecus*. Perhaps this is because as seen in Figure 28b the predicted suitable habitat shows as 1 species finding it suitable in the areas shown by fig 15 to be *Cercopithecus* mitis predicted suitable habitat. Again showing dissimilarity to the extant habitats in 28 allude to *Cercopithecus* species not extending as much in these areas that are mountainous or being separated geographically by rivers.

There is also a trend within the two-way overlaps (appendix table b), that most of the overlapping species share one or two of their top three percentage contribution variables. Sharing one or two variables is much more common than sharing all three top percentage contributions, and it is less common again to share none of the top three percentage contributions. Their similarity is perhaps because of their ecological flexibility, allowing them to find a great amount of areas suitable (Coleman and Hill, 2014). This is again a trend of having only small amounts of divergence, the least likely possibility of sharing none of the top three percentage contributions is more extreme when pairing off species that are less similar though there are still some like the crossover between Cercopithecus mona and Cercopithecus petaurista that share 46.3% and 52.0% respectively with each other so there can be a lot of shared suitable habitat without much overlap in the importance of percentage contributions. On the other hand, this does not always hold true, for example having all three highest percentage contributions be the same and it can be as with Cercopithecus denti and Cercopithecus dryas that share 1.1% and 0.1% of their predicted suitable habitat so there is very little predicted crossover but they still share their top three percentage contributions. The figures 25 to 27 show that for Cercopithecus denti and Cercopithecus dryas have more similarity in their reaction to environmental variables but show lower similarity in habitat than Cercopithecus mona and Cercopithecus petaurista. Negating the idea that you can predict which monkeys will share habitat based on their percentage contribution. Another example would be Cercopithecus ascanius and Allochrocebus lhoesti that share 2.9% and 100% area respectively with each other, with this where one species total predicted suitable area exists within another species predicted suitable area. This means that Allochrocebus lhoesti always has predicted suitable habitat found cohabiting with Cercopithecus ascanius, but less than 3% of Cercopithecus ascanius have predictable suitable habitat with Allochrocebus lhoesti, the other 97% predicted suitable habitat is elsewhere(table b in appendix) in Figures 25 to 27 they are appear to be similar in their reactions to ecological variables and require similar habitats.

Figure 28b also shoes that there is a great amount of area in terms of biogeography that overlaps the highest visible proportions of this being the 'red' areas of 9 species overlapping. Again when using Fig 26 to compare this on average the *Cercopithecus* species are < 0.5 similar to 10.7 other *Cercopithecus* species. Also similar to the above paragraph Figure 27 shows that there are some species that have more similar habitats than others.

Polyspecific association and ecological flexibility

Polyspecific association is a common theme for primates though appears to have drawbacks in the forms of resource sharing and competition for preferred strata however there are a variety of ways that this is overcome(Buzzard, 2010). For example sex and species related partitioning of food types or strata (Gautier-Hion, 1980; Houle, Chapman and Vickery, 2010). A great advantage of this appears to be related to predator avoidance (Gautier-Hion, Quris and Gautier, 1983; Bryer, Chapman and Rothman, 2013).

Polyspecific association in *Cercopithecus ascanius* who associate polyspecifically with several species put themselves at a disadvantage in terms of food resources, however the predator avoidance benefits again outweigh the cost. For example *Cercopithecus ascanius* associating with grey-cheeked mangaby (*Lophocebus albigena*) has a similar diet and *Cercopithecus ascanius* is submissive if they are feeding from the same fruit tree. They do provide aerial predator protection, as mangabys are known to attack aerial predators. The crowned hawk eagle is *Cercopithecus ascanius* primary predator, so the protection afforded them by the mangabys is very valuable (Bryer, Chapman and Rothman, 2013).

Ecological flexibility can be seen in various forms and for various reasons, as above with their penchant for polyspecific association, and otherwise because they are widespread geographically and also change their diet according to the seasonal variation or how dense the population of conspecifics are. The effect of biogeography has been investigated in Cercopitheucs mitis as it has the most widespread biogeography of the guenons, though its range it is shown to have great dietary flexibility (Coleman and Hill, 2014). The seasonal effect on the species is that diets overlap less when food iseither less available or directly when food is in abundance. The effect of seasonal variation is different to each species as well as by sex within the species (Gautier-Hion, 1980). (Gautier-Hion, 1980). *Cercopithecus mitis* show ecological differences depending on the density of the population, they are able to change their diet as there is lower food availability at the high density areas (Butynski, 1990).

Specifically using these known polyspecific associations and comparing them to the results shown in Figures 25 to 27 we can understand better how these species ecology are interacting with each other.

Cercopithecus campbelli, Cercopithecus petaurista and Cercopithecus diana

Buzzard (2010) studied a three-way crossover on the polyspecific association between *Cercopithecus diana, Cercopithecus petaurista* and *Cercopithecus campbelli* to establish what the costs and benefits are of this association. The area that these species find suitable together is 96,799.61km2 (appendix table a). The guenons in this study provide a good example of why so much of the habitat that is suitable to the guenons is shared. That they associate so often with each other that the benefits must outweigh the competitive cost. Different species usually live in different strata depending on their antipredator strategies and depending on their preferred food resources, in this case *Cercopithecus petaurista* and *Cercopithecus campbelli* adapt to less preferable strata when in polyspecific association with *Cercopithecus diana*. Lower than if they associate with species other than diana, that is still higher strata than they use alone when associating with *Cercopithecus diana* (Buzzard, 2010).

Cercopithecus campbelli seems to prefer the association of *Cercopithecus diana* to their own antipredator strategy when alone which consists of using lower denser foliage and remaining inconspicuous, Cercopithecus diana is vigilant and detect potential predators as well as giving a warning first. For *Cercopithecus petaurista* however they associate with *Cercopithecus diana* less than *Cercopithecus campbelli* does because they rely less on *Cercopithecus diana* for antipredator strategy. *Cercopithecus diana's* strategy is very different to their own cryptic antipredator strategy which is dependent on using dense lina tangles and food items. There also appears to be a link between Chimpanzee presence and when the species associate with *Cercopithecus diana*, lower association with *Cercopithecus diana* correlates with higher chimpanzee presence (Paul J. Buzzard, 2006b; Buzzard, 2010) however when polyspecific association with red colobus ant the behaviour changes during chimpanzee hunting season were investigated in Kane and McGraw (2018b) there was no reason suggested as to why *Cercopithecus diana* would be effected by chimpanzee presence.

The ability to polyspecifically associate is linked to the ecological partitioning, in terms of diet. This can be either that the guenons eat different amounts of their overlapping foods of their main diet, or through strata partitioning (Paul J. Buzzard, 2006b; Kane and McGraw, 2018a). *Cercopithecus diana* also is known for its predator alarm (Stephan and Zuberbühler, 2014) calls which is a benefit to any association species.

There are few costs to *Cercopithecus diana* for associating with red colobus (*Procolobus rufomitratus*) even during the chimpanzee hunting season. *Cercopithecus diana* do not appear to be affected by the increased risk of chimpanzee predation, more frequently coming to the forest floor to forage for a fruit that they favour that is in season around this time. They may benefit as the red colobus live at higher strata and therefore may be an antipredator benefit to them. Either by calling to warn of the predator or by physically being higher than *Cercopithecus diana*, thus easier to grab reducing *Cercopithecus diana*'s chances of being predated upon by raptors (Kane and McGraw, 2018b).

The relationships between all species for their reactions to environmental change are very similar between 0.957 for *Cercopithecus campbelli* and *Cercopithecus Diana* and 0.946 between *Cercopithecus campbelli* and *Cercopithecus petaurista*. Similarly their habitat and ecological similarity appear high for each table, between 0.851 and 0.712 for Figure 26 and 0.623 and 0.426 for Figure 27. Consistently it is *Cercopithecus campbelli* and *Cercopithecus petaurista* that have the higher similarities and *Cercopithecus campbelli* and *Cercopithecus petaurista* that have the lowest similarity. This may be an echo of how Cercopithecus diana is the species that both *C.petaurista* and *C.campbelli* are appearing to associate with or an indication that it is more a ecological preference that *C.petaurista* appears to polyspecificically associate less than the others.

Cercopithecus diana, Cercopithecus nictitans

Also observed for *Cercopithecus diana* is behavioural flexibility depending on population density and whether their habitat is primary forest or old secondary forest (Decellieres, Zuberbühler and León, 2021). The ecological flexibility is shown by the ranging patterns for *Cercopithecus diana*, *C. campbelli* and *C. petaurista* because they are not affected by food availability, they are able to switch their diet or resource monitor (Paul J Buzzard, 2006).

Cercopithecus nictitans, Cercopithecus cephus and Cercopithecus pogonias

Another three-way polyspecific association found in the literature is *Cercopithecus nictitans*, *Cercopithecus cephus* and *Cercopithecus pogonias*. These monkeys share the second largest area of predicted suitable habitat with an area of 380,776.8km² (appendix table a).

The polyspecific association of these three species has shown that they partition their diet to rely more heavily on different sources of food to reduce their competition (Gautier-Hion, 1980). There is a notable change in habitat use and with the change in diet, specifically the diversity of fruit. There was also notably an anti predatory benefit to their association, *C.cephus* occurring in lower strata gave advantage to the others through alarms for terrestrial predators. In exchange *C.pogonias* alarms for areal, this did appear to benefit *C.cephus* by decreasing their predation by monkey-eagles (Gautier-Hion, Quris and Gautier, 1983).

Environmental variable changes were very high for all three overlaps of this species all greater than 0.9. They also show that there are also very high for habitat similarity as well. This high similarity may contribute to the quantifiable differences seen in the dietary changes and strata use.

Cercopithecus wolfi, Cercopithecus ascanius and Cercopithecus neglectus

The observations of McGraw (1994) looked at the polyspecific association and habitat use of *Cercopithecus wolfi, Cercopithecus ascanius* and *Cercopithecus nictitans*. They found that C.wolfi and *C.ascanius* commonly associate together however *C.nictitans* was not seen to associate with either though they occurred in the same area. *C.nictitans* was also found not to leave a specific habitat type within the investigated area (swamp) (McGraw, 1994). It was noted that C.wolfi would polyspecifically associate more often when in primary forest and this was proposed to be because of increased emphasis on sentinel activity in reaction to a predator (specifically the crowned hawk eagle)(McGraw, 1994).

The reactions to changes in the ecological variables and habitat similarity show that the species that are seen to associate the most appear to have lower similarity *C.wolfi* and *C.ascanius* have a less similar reaction than *C.ascanisu* and *C.neglectus* and the least similarity in comparison to the other pairings in terms of habitat and geography. The highest similarities for all overlap results was *C.ascanius* and *C.neglectus*.

The lack of ecological similarity for *C.ascanius* and *C.wolfi* could be what allows their more frequent polyspecific association in comparison to the higher similarity but not seen to associate *C.neglectus*. Perhaps in this case beyond *C.neglectus* being confined to swamp areas, their more similar habitat and ecology is a competitive exclusion. Where as the *C.ascanius* and *C.wolfi* are known to separate themselves vertically to avoid competition (McGraw, 1994).

Cercopithecus ascanis and Cercopithecus mitis

Cercopithecus ascanius and *Cercopithecus mitis* diet overlaps considerably (ascanius associate closer to conspecifics when eating fruit than when eating leaves and insects) (Bryer, Chapman and Rothman, 2013). *Cercopithecus mitis* and *Cercopithecus ascanius* are also known to hybridize (Detwiler, 2019).

For overcoming the competition for food for these two species that there is a dominant vs submissive interaction here, *C.mitis* being dominant over *C.ascanius*. This results in the competitive exclusion of *C.ascanius* from the higher preferred feeding strata when in association with *C.mitis* (Houle, Chapman and Vickery, 2010).

The similarity between these two species in terms of their reaction to environmental variable is high as is their similarity of habitat types. This supports the apparent need for this more aggressive competition/exclusion relationship that is seen between these species.

Conclusion

In conclusion there has been a broad investigation into the conservatism of the guenons that appears to show that the *Cercopithecus* have great ecological conservatism between their constituent species. In terms of polyspecific association it shows that they all have relative similarity in their habitat types and that there are several different strategies by which they overcome these similarities. Only one instance shows a relatively lower similarity, with a species known to polyspecifically associate more than the others in this grouping. This may show that sometimes differences in niche preference are overcome for the benefit of polyspecific association. It appears to be more common, that the species develop strategies to overcome their great ecological similarity. Further research is needed into polyspecific association of Cercopithecus to truly understand if these types of relationships are repeated.

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Appendix

Table a. Table to shows the overlaps that occur for predicted suitable habitat for three way crossovers that could possibly occur according to the IUCN red list range outline. The area that is

predicted suitable to be occupied by the three species in km2 and the names of the variables top three percentage contributions that are shared by all the species included in the overlap.

Three way overlap	km ²	Shared top three percentage contribution
C.ascanius-C.neglectus-	606,007.4	Temperature seasonality
C.pogonias		
C.cephus-C.nictitans-	380,776.8	Terrestrial biome, Annual precipitation
C.pogonias		
C.ascanius-C.hamlyni-	363,160.8	Temperature seasonality
C.neglectus		
C.ascanius-C.mitis-	335,513.2	Temperature seasonality, precipitation of
C.neglectus		driest month
C.ascanius-C.hamlyni-	311,371	Temperature seasonality, precipitation of
C.wolfi	201.010.0	driest month
C.hamlyni-C.neglectus-	281,949.3	lemperature seasonality
C.WOIfi	264.272.6	
C.ascanius-C.negiectus-	264,373.6	Temperature seasonality, precipitation of
C.WOIJI		dhest month
C.IOWEI-C.MONA-	217,544.2	
C.petdulistu	205 501	Tomporaturo coaconality
Cinegiectus-Cinictituris-	205,501	
C.poyonius C.mona-C.nictitans-	196 8/6 5	Annual precipitation
Cinona-cinicitaris-	150,840.5	
C nealectus-C noaonias-	190 460 9	Temperature seasonality
C.wolfi	190,100.9	
C.ervthrotis-C.nictitans-	177.023.3	Terrestrial biome. Annual precipitation
C.poqonias	,	· · · · · · · · · · · · · · · · · · ·
C.campbelli-C.nictitans-	176,336.5	
C.petaurista	,	
C.ascanius-C.pogonias-	168,952.8	Temperature seasonality
C.wolfi		
C.ascanius-C.nictitans-	161,892.3	Temperature seasonality
C.pogonias		
C.ascanius-C.nictitans-	157,560.4	Temperature seasonality
C.neglectus		
C.erythrotis-C.pogonias-	156,870.9	Terrestrial biome
A.preussi		
C.erythrotis-C.nictitans-	149,038.8	Terrestrial biome
A.preussi		
C.nictitans-C.pogonias-	142,672.9	Terrestrial biome
A.preussi		
C.cephus-C.neglectus-	134,373.3	
C.pogonias	400 770 0	A 1
C.erythrotis-C.mona-	128,779.2	Annual precipitation
C.nictitans	124 102 5	
C.erythrotis-C.mona-	124,102.5	Annual precipitation
Cascanius Chambuni	110 099 2	Tomporaturo coaconality
C.uscumus-C.numnym-	113,300.3	
Cinnus	1	

C.ascanius-C.cephus-	113,703	
C.pogonias		
C.ascanius-C.dryas-	112,691.2	Temperature seasonality
C.wolfi		
C.ascanius-C.cephus-	112,163	
C.neglectus		
C.dryas-C.hamlyni-C.wolfi	109,726.1	Terrestrial biome, Temperature seasonality
C.cephus-C.nictitans-	100,572.5	
C.neglectus	,	
C.mona-C.nictitans-	98.974.17	
A.preussi	/ -	
C.ervthrotis-C.mona-	98.882.42	
Apreussi	00,00111	
C campbelli-C diana-	96,799,61	
Cpetaurista	50,755101	
C mong-C pogonias-	96 622 97	
A nreussi	50,022.57	
C mona-C nictitans-	95 178 98	
C sclateri	55,170.50	
C nictitans-C pogonias-	94 744 24	Terrestrial hiome
C sclateri	54,744.24	
Clowei-Cnictitans-	89 910 65	Temperature seasonality
C. not aurista	85,510.05	
C.mong_C.nogonias_	88 705 80	
C.mona-C.pogomas-	88,705.85	
C. diana_C nictitans_	88 680 17	
C. addina-C. metricitaris-	88,080.17	
Cascanius C danti	91 704 6	Tomporaturo coasonality
C.uscumus-C.uenti-	01,704.0	
Cascanius C conhus	90 00E 42	
C.uscumus-C.cephus-	80,903.43	
Caruthrotis-Chictitans-	78 082 11	Terrestrial hiome
C.erytinotis-C.nictituns-	70,902.11	
C.scuteri	72 / 97 / 1	Terrestrial hiome
C.erytinotis-C.poyonius-	73,487.41	
Cascanius_C denti-	72 704 57	Temperature seasonality
C.uscumus-c.uenti-	12,194.37	
Chamboni-C mitis-	71 866 78	Temperature seasonality
Cinamyn-Cinntis-	/1,000.70	
Cascanius-C denti-C mitic	60 852 12	Temperature seasonality
C.donti C.hambuni	67,736,02	
C.aenti-C.namiyni-	67,726.03	Temperature seasonality
C.neglectus	67 700 00	
C.erythrotis-C.mona-	88.801,10	
	64 770 00	
C.aenti-C.mitis-	64,778.02	remperature seasonality
C.negiectus	F7 667 02	
C.erythrogaster-C.mona-	57,667.83	Iviean diurnal range (monthly (max temp-
		min temp))
C.erythrogaster-	55,/61.66	Terrestrial biome
C.nictitans-C.sclateri		

C.denti-C.hamlyni-C.mitis	55,476.98	Temperature seasonality
C.erythrogaster-C.mona-	55,301.2	
C.nictitans		
C.ascanius-	50,098.89	Temperature seasonality
C.lomamiensis-C.wolfi		
C.cephus-C.mona-	46,771.89	Annual precipitation
C.pogonias		
C.dryas-C.lomamiensis-	44,825.42	Terrestrial biome, Temperature seasonality
C.wolfi		
C.hamlyni-C.mitis-	36,747.99	Temperature seasonality
A.lhoesti		
C.ascanius-C.mitis-	34,516.84	Temperature seasonality
C.pogonias		
C.ascanius-C.dryas-	34,303.33	Temperature seasonality
C.lomamiensis		
C.mitis-C.neglectus-	32,826.75	Temperature seasonality
C.pogonias		
C.cephus-C.mona-	32,789.02	Annual precipitation
C.nictitans		
C.dryas-C.neglectus-	32,579.8	Temperature seasonality
C.wolfi		
C.dryas-C.hamlyni-	32,347.42	Temperature seasonality
C.neglectus		
C.ascanius-	32,320.84	Temperature seasonality, precipitation of
C.lomamiensis-		driest month
C.neglectus		
C.lomamiensis-	31,409.35	Temperature seasonality, precipitation of
C.neglectus-C.wolfi		driest month
C.mitis-C.neglectus-	29,977.36	Temperature seasonality, Annual
A.lhoesti		precipitation
C.ascanius-C.dryas-	27,459.81	Temperature seasonality
C.neglectus		
C.hamlyni-C.neglectus-	21,652.13	temperature seasonality
A.lhoesti		
C.dryas-C.lomamiensis-	20,782.65	Temperature seasonality
C.neglectus		
C.mitis-C.neglectus-	14,737.44	Temperature seasonality
C.nictitans		
C.mitis-C.nictitans-	13,845.66	Temperature seasonality, Annual
C.pogonias		precipitation
C.ascanius-C.mitis-	13,791.64	Temperature seasonality
C.nictitans		
C.denti-C.mitis-A.lhoesti	12,851.85	Temperature seasonality
C.denti-C.hamlyni-	12,758.39	Temperature seasonality
A.lhoesti		
C.cephus-C.pogonias-	11,754.28	Terrestrial biome
C.wolfi		
C.denti-C.neglectus-	9,850.684	Temperature seasonality
A.lhoesti		

C.cephus-C.neglectus- C.wolfi	9,097.82	
C.ascanius-C.cephus- C.wolfi	7,342.567	
C.dryas-C.hamlyni-C.mitis	5,147.428	
C.ascanius-C.mitis-C.wolfi	4,037.854	Temperature seasonality, precipitation of
		driest month
C.hamlyni-C.mitis-C.wolfi	3,472.778	Temperature seasonality
C.campbeli-C.lowei-	3,348.444	Terrestrial biome
C.nictitans		
C.ascanius-	2,760.215	Temperature seasonality, Precipitation of
C.lomamiensis-C.mitis		driest month
C.ascanius-C.dryas- C.mitis	2,577.573	Temperature seasonality
C.cephus-C.nictitans- C.wolfi	2,344.339	Terrestrial biome
C.dryas-C.mitis-C.wolfi	2,148.835	Temperature seasonality
C.lomamiensis-C.mitis- C.neglectus	2,047.653	Temperature seasonality, precipitation of driest month
C.ascanius-C.denti-C.wolfi	1,979.912	Temperature seasonality
C.denti-C.hamlyni-C.wolfi	1,886.447	Terrestrial biome, Temperature seasonality
C.denti-C.neglectus-	1,774.118	Temperature seasonality
C.wolfi		, , ,
C.erythrotis-C.neglectus- C.nictitans	1,772.403	
C.lomamiensis-C.mitis- C.wolfi	1,597.478	Temperature seasonality, Precipitation of driest month
C.mitis-C.neglectus- C.wolfi	1,493.723	Temperature seasonality
C.denti-C.mitis-C.wolfi	1,206.469	Temperature seasonality
C.neglectus-C.nictitans- C.wolfi	1,155.878	Temperature seasonality
C.denti-C.dryas-C.hamlyni	949.2259	Terrestrial biome, Temperature
		seasonality, precipitation seasonality
C.denti-C.dryas-	940.6512	Temperature seasonality
C.neglectus		
C.denti-C.dryas-C.wolfi	913.2119	Terrestrial biome, Temperature seasonality
C.campbelli-C.lowei-	907.2096	
C.petaurista		
C.dryas-C.mitis-	690.2682	Temperature seasonality
C.neglectus		
C.aryas-C.lomamiensis-	563.361/	i emperature seasonality
C.MITIS C.donti C.drugo C.mitic	F01 622F	Tomporaturo cooconality
C.uenili-C.uryus-C.millis	301.0235	
C.uscanius-C.nictitans-	438.1702	remperature seasonality
C.WUIJI	110 2217	
C sclateri	110.331/	
C.mitis-C.nictitans-C wolfi	116.6167	Temperature seasonality

C.diana-C.lowei-	106.327	Terrestrial biome
C.nictitans		
C.diana-C.lowei-	106.327	
C.petaurista		
C.erythrotis-C.neglectus-	64.3107	
C.pogonias		
C.erythrotis-C.mona-	45.44623	
C.neglectus		

Table b. showing the two way crossovers as seen in table 7 (forward showing the percentage of total predicted suitable habitat the first mentions species in the pair shares with the second. Backward showing the percentage of total predicted suitable habitat the second species shares with the first. Showing which of the environmental variables of the top three percentage contributions are shared by the pair.

Species cross	Forward	Backward	Shared top three percent contribution
C.ascanius-C.cephus	6.1	21.2	
C.ascanius-C.denti	4.7	99.6	Temperature seasonality
C.ascanius-C.dryas	6.4	52.4	Temperature seasonality
C.ascanius-C.hamlyni	27.0	76.9	Temperature seasonality
C.ascanius- C.lomamiensis	2.8	72.2	Temperature seasonality, precipitation of driest month
C.ascanius-C.mitis	28.7	25.0	Temperature seasonality, precipitation of driest month
C.ascanius-C.neglectus	64.4	84.3	Temperature seasonality, precipitation of driest month
C.ascanius-C.nictitans	8.8	18.3	Temperature seasonality
C.ascanius-C.pogonias	36.0	36.7	Temperature seasonality
C.ascanius-C.wolfi	18.5	52.2	Temperature seasonality, precipitation of driest month
C.ascanius-A.lhoesti	2.9	100	Temperature seasonality, precipitation of driest month, Altitude
C.campbelli-C.diana	37.2	96.0	Terrestrial biome, Precipitation of coldest quarter, Annual precipitation
C.campbelli-C.lowei	1.2	0.5	Terrestrial biome
C.campbelli-C.nictitans	67.0	22.4	Terrestrial biome, Annual precipitation
C.campbelli- C.petaurista	76.3	31.9	Precipitation of coldest quater
C.cephus- C.erythrogaster	1.2	6.2	Terrestrial biome, Annual precipitation
C.cephus-C.mona	8.9	6.2	Mean diurnal range
C.cephus-C.neglectus	25.3	6.9	
C.cephus-C.nictitans	70.5	42.5	Terrestrial biome, Annual precipitation
C.cephus-C.pogonias	97.8	28.9	Terrestrial biome, Annual precipitation
C.cephus-C.wolfi	2.2	1.8	Terrestrial biome
C.denti-C.dryas	1.1	0.4	Terrestrial biome, Temperature seasonality, Precipitation seasoality
C.denti-C.hamlyni	83.1	11.1	Temperature seasonality, precipitation seasonality
C.denti-C.mitis	80.2	3.3	Temperature seasonality
C.denti-C.neglectus	93.7	5.7	Temperature seasonality

C.denti-C.wolfi	2.3	0.3	Terrestrial biome, Temperature seasonality
C.denti-A.lhoesti	14.7	23.6	Temperature seasonality
C.diana-C.lowei	0.1	0.0	Terrestrial biome
C.diana-C.nictitans	87.5	10.9	Terrestrial biome, Annual precipitation
C.diana-C.petaurista	90.2	14.6	Precipitation of coldest quarter
C.dryas-C.hamlyni	50.2	17.6	Terrestrial biome, precipitation seasonality
C.dryas-C.lomamiensis	19.5	62.5	Terrestrial biome
C.dryas-C.mitis	2.3	0.2	Temperature seasonality
C.dryas-C.neglectus	14.2	2.3	Temperature seasonality
C.dryas-C.wolfi	91.3	31.6	Terrestrial biome
C.erythrogaster- C.mona	94.3	12.5	Mean diurnal range
C.erythrogaster- C.nictitans	58.9	6.7	Terrestrial biome
C.erythrogaster- C.sclateri	59.3	50.2	Terrestrial biome, Precipitation of coldest quarter, mean diurnal range
C.erythrotis-C.mona	54.2	16.6	Annual precipitation
C.erythrotis- C.neglectus	3.2	0.5	Precipitation of coldest quarter
C.erythrotis-C.nictitans	79.4	20.9	Terrestrial biome, Annual precipitation
C.erythrotis- C.pogonias	81.8	10.6	Terrestrial biome, Annual precipitation
C.erythrotis-C.sclateri	35.0	68.7	Terrestrial biome, Precipitation of coldest Quater, Annual Precipitation
C.erythrotis-A.preussi	80.8	90.8	Terrestrial biome, precipitation of coldest quarter
C.hamlyni-C.mitis	18.3	5.6	Temperature Seasonality
C.hamlyni-C.neglectus	64.8	29.8	Temperature Seasonality
C.hamlyni-C.wolfi	70.4	69.6	Terrestrial biome, Temperature Seasonality
C.hamlyni-A.lhoesti	5.6	67.6	Temperature seasonality
C.lomamiensis-C.mitis	3.9	0.1	Temperature Seasonality, Precipitation of driest month
C.lomamiensis- C.neglectus	45.7	2.3	Temperature seasonality, Precipitation of Driest Month

C.lomamiensis-C.wolfi	97.1	10.5	Terrestrial Biome, Temperature seasonality, Precipitation of Driest Month
C.lowei-C.mona	52.5	46.3	Mean Diurnal Range
C.lowei-C.nictitans	18.8	14.3	Terrestrial Biome, Temperature seasonality
C.lowei-C.petaurista	46.0	45.6	Temperature Seasonality
C.mitis-C.neglectus	17.0	25.4	Temperature seasonality, Precipitation of Driest Month
C.mitis-C.nictitans	0.9	2.2	Temperature Seasonality
C.mitis—C.pogonias	2.2	2.6	Temperature Seasonality, Annual Precipitation
C.mitis-C.wolfi	0.2	0.6	Temperature Seasonality, Precipitation of Driest Month
C.mitis-A.lhoesti	2.5	100	Temperature Seasonality, Precipitation of Driest month
C.mona-C.neglectus	0.0	0.0	Precipitation of Driest Month
C.mona-C.nictitans	26.9	23.2	Annual Precipitation
C.mona-C.petaurista	46.3	52.0	
C.mona-C.pogonias	31.1	13.1	Annual Precipitation
C.mona-C.sclateri	13.1	83.8	Mean Diurnal Range
C.mona-A.preussi	12.8	46.9	
C.neglectus-C.nictitans	14.7	23.4	Temperature Seasonality
C.neglectus- C.pogonias	50.4	39.2	Temperature Seasonality
C.neglectus-C.wolfi	22.9	49.4	Temperature Seasonality, Precipitation of Driest Month
C.neglectus-A.lhoesti	2.1	55.2	Temperature Seasonality, Precipitation of Driest Month
C.neglectus-A.preussi	1.2	8.3	Precipitation of Coldest Quater
C.nictitans- C.petaurista	39.4	51.3	Temperature Seasonality
C.nictitans-C.pogonias	96.6	47.3	Temperature Seasonality, Terrestrial Biome, Annual Precipitation
C.nictitans-C.sclateri	11.9	88.2	Terrestrial Biome
C.nictitans-C.wolfi	0.3	0.4	Terrestrial Biome, Temperature Seasonality
C.nictitans-A.preussi	16.9	71.9	Terrestrial Biome
C.pogonias-C.sclateri	5.3	80.4	Terrestrial Biome
C.pogonias-C.wolfi	16.6	46.0	Terrestrial Biome, Temperature Seasonality

C.pogonias-A.preussi	8.7	75.5	Terrestrial Biome
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