Genetics, Genomics, and Social Perceptions: A Multidisciplinary Approach to Guenon Conservation in the Bijagós Archipelago

By

Ivo António Colmonero Marques Costeira

Thesis submitted to Cardiff University for the degree of Doctor of Philosophy

Supervisor: Dr Isa-Rita Russo

External Co-supervisors: Dr Maria Joana Ferreira da Silva & Dr Susana Gonçalves Costa

November 2024

School of Biosciences
Cardiff University

Genetics, Genomics, and Social Perceptions: A Multidisciplinary Approach to Guenon Conservation in the Bijagós Archipelago

By

Ivo António Colmonero Marques Costeira

Supervision: Prof. Michael W. Bruford
Organisms and Environment Division
Cardiff School of Biosciences, Cardiff University, U.K.

Dr. Isa-Rita Russo (40%)
Organisms and Environment Division
Cardiff School of Biosciences, Cardiff University, U.K.

Dr. Maria Joana Ferreira da Silva (40%)
Organisms and Environment Division
Cardiff School of Biosciences, Cardiff University, U.K.
Centro de Investigação em Biodiversidade e Recursos Genéticos (CIBIO) | Program in Genomics, Biodiversity and Land Planning (BIOPOLIS)
Universidade do Porto, Campus de Vairão, Portugal.

Dr. Susana Gonçalves Costa (20%)
Research Centre for Anthropology and Health (CIAS)
Department of Life Sciences, Universidade de Coimbra, Portugal.

Summary

In biodiversity-rich areas people are often heavily dependent on agriculture and natural resources, potentiating negative interactions with non-human primates. In the Bijagós Archipelago, Guinea-Bissau (West Africa) local populations of the *Bijagó* ethnic group co-occur with three species of guenons (tribe Cercopithecini): the spot-nosed monkey, (*Cercopithecus petaurista* Schreber, 1774), Campbell's monkey (*Cercopithecus campbelli* Waterhouse, 1838), and the green monkey (*Chlorocebus sabaeus* Linnaeus, 1766). The conservation of the insular spot-nosed monkey populations should be considered a national priority, as this guenon may have been recently extirpated from mainland. To support guenon conservation, this thesis set out to generate baseline data on main conservation threats, genetic diversity, population structure, demographic history, and adaptive variation which are essential to assess the species' local conservation status. Guenon populations showed genetic patterns typical of insular populations – strong population differentiation, reduced genetic diversity, increased inbreeding, and small effective population sizes. However, in the absence of accumulated deleterious mutations, they do not seem to be at immediate risk of extirpation due to genetic factors. Nonetheless, the effects of increased inbreeding and genetic drift, combined with high extraction rates may have unpredictable effects on population fitness, and conservation measures to avoid excess mortality should be implemented. However, the success of conservation efforts in shared landscapes depend heavily on the local communities' views. In this thesis the potential of a guenon-focused conservation program was assessed by examining *Bijagó* perceptions and attitudes. The *Bijagó* were found to have mostly negative perceptions and attitudes towards guenons due to their crop-raiding behaviours. However, if compensatory programmes or if socio-economic benefits (e.g., eco-tourism revenues) are introduced, engagement with conservation may be improved. The evidence produced in this thesis regarding genetic parameters of conservation importance, coupled with inferences on local perceptions and attitudes towards wildlife can be incorporated in the design of effective conservation strategies aligned with populations' needs and values.

Acknowledgements

This has been a more intense and bumpier journey than I expected. More than the knowledge I have acquired, I have gained something that is by far immeasurable: “family” across the multiple places I had the pleasure to live in. It was with the support and help of this scattered around “family” that I managed to accomplish this thesis. So, this is dedicated to you.

I would like to thank my supervision team. To Mike, I wish you could be here and have accompanied the developments of this project. During my brief time as your student, I always tried not to bother you do to your condition. But I remember the excellent advice you gave on our occasional discussions. I can only imagine the fruitful discussions we could have had. I hope that you would have been proud with the outcomes of this thesis. Joana, thank you for introducing me to Primatology. Your help throughout these more than six years of collaboration has been important for my development as a researcher. To Susana, thank you for your guidance, for always having words of encouragement and availability. Isa-Rita, thank you for taking me under your supervision after Mike’s untimely passing. You made an enormous commitment to support me in every way possible from scientific advice to motivational support. To Dr Hefin Jones, thank you for providing me a safe space to share my thoughts and concerns throughout this journey. To Katja, although you were not part of my supervision team, you welcomed me to your group with open arms. We started working together during a particularly hard time of my PhD and you helped bring back my confidence in the quality of my work. I can’t thank you enough! To Axel, thank you for your warm welcome in Uppsala and for always having some time to discuss the work and provide me with guidance. I have learnt so, so much from you.

I would like to acknowledge Guinea-Bissau’s governmental agencies Direção Geral de Florestas e Fauna and Instituto da Biodiversidade e das Áreas Protegidas (IBAP), Doctors Aissa Regalla, Alfredo Simões da Silva and Justino Biai for authorising the collection of the samples at the Bijagós and for allowing their exportation to Portugal. To the Instituto da Conservação da Natureza e Florestas (ICNF), Portugal, for the importation permits. To the local NGO Tiniguena for support in UROK. To the person of Helena Foito dos Santos and Vitor dos Santos for the logistic support in Bissau and Saído and João for support in Bubaque and Canhabaque islands. I acknowledge Dr R. Godinho and the CTM (Centre for Molecular Analysis, CIBIO-InBIO) staff for all the help with the molecular analysis of the tissue samples collected in 2015-2017. L. Palma for providing samples and photographs.

In Guinea-Bissau, a heartfelt thank you to the local communities and chieftains of the Bijagós Archipelago for authorising, facilitating the field work and sharing their immense knowledge with me. To Jaime *Bijagó* and Isabella Espinosa, thank you for opening your house to me. You made it feel like home! To the research assistants Baba Djaló, Nelson Fernandes, Núria Cunha, Jessica Cunha and Babazinho. This thesis would not be possible without your hard work and support. I miss our post-fieldwork *djumbai*. A special thanks to Conselheiro and Papa, I hope I can visit you in Canhabaque soon!

In Cardiff, I am thankful to everyone at Molecular Ecology lab. A huge thanks to Isa, Neil, Sarah du Plessis, and Dan for their friendship and support. To Marina, my Catalan “sister”, I am so happy I met you. You made life in Cardiff enjoyable, from our drama sessions to our old couple discussions… thank you for your unconditional support and love. You are the one of the best things I gained from this journey.

In Uppsala, a great thanks to everyone at Animal Ecology. Thank you, Charlotte, Leo, Maddie and Axel, for your friendship and constant laughs. A special thanks to my two boys, Josh and Alex, for pestering me constantly about all things random and making me feel like I belonged. These were the best 6 months of my PhD!

Back home, thank you Filipa for your friendship and continuous support since the time when we started our journey in primatology together. A special word of gratitude goes to Mariana/Dark Chansey, Jão/Joca, Bea, Ni and Soraia. Thank you for the infinite amounts of patience whenever I came back to Portugal. I am glad I kept on sharing some of the most meaningful moments of my life with you all. Alfredo, you did not witness most of this journey but on this final stretch you offered me a lot of support and kindness, thank you. To my family, Eduarda, father, sister and Sofia for your unconditional love and support.

My work was supported by the Fundação para a Ciência e Tecnologia (FCT), Portugal: SFRH/BD/146509/2019, https://doi.org/10.54499/SFRH/BD/146509/2019.

This project was funded by the FCT, Portugal, through the project PRIMATOMICS (PTDC/IVC-ANT/3058/2014), by AGRIGEN – NORTE-01-0145-FEDER-000007 supported by Norte Portugal Regional Operational Programme (NORTE2020), under the PORTUGAL 2020 Partnership Agreement, through the European Regional Development Fund (ERDF). Primate Conservation Incorporated, The Genetics Society, The Born Free Foundation, Chester Zoo Conservation Fund, Mohamed Bin Zayed (Project 232533027), CAROSI, Cápsulas do Norte, Camarc, JA-Rolhas e Cápsulas. TROPBIO research group, coordinated by Fernando Jorge Guimarães Sequeira.

Bioinformatic computations were performed on (i) Cardiff School of Biosciences' Biocomputing Hub HPC/Cloud infrastructure, resources funded by the Cardiff School of Biosciences; (ii) National Academic Infrastructure for Supercomputing in Sweden (NAISS), partially funded by the Swedish Research Council through grant agreement no. 2022-06725 (projects NAISS 2023/6-340 and NAISS 2023/5-506); (iii) Instituto Gulbenkian de Ciências' biocomputing hub.

Statement of Contributions

The work presented in this thesis is primarily my own. The specific contributions of other authors are presented below.

Chapter 2: ethnobiological observations were collected by Saidil Lamine Djaló, Núria Cunha, Jessica Cunha and Rui Sá. Manuscript published in *Primates*. doi:10.1007/s10329-023-01090-9.

Chapter 3: faecal samples of ranging primate groups were collected by Saidil Lamine Djaló and Nelson Fernandes. Furthermore, the molecular methods used to obtain microsatellite panel, and the mitochondrial d-loop fragment were optimised during my MSc thesis at the University of Minho, Braga, Portugal. A preliminary dataset of 50 genotypes and mitochondrial sequences was included in the final dataset presented here.

Chapter 5: MSVAR runs to estimate past changes to effective population size were conducted by Filipa Borges at the Population and Conservation Genetics group, at Instituto Gulbenkian de Ciência, Oeiras, Portugal.

Chapter 5: biological samples were collected by Saidil Lamine Djaló and Nelson Fernandes, and Tomás Camará. Samples were processed for whole genome sequencing under the Primate Conservation Sequencing Consortium (PCSC), represented by Prof. Tomàs Marques-Bonet (Universitat Pompeu Fabra, Barcelona, Spain). Genomic analyses were conducted at Animal Ecology, Department of Ecology and Genetics, Uppsala University, Uppsala, Sweden. The work was supervised by Axel Jensen and Dr Katerina Guschanski who contributed with bioinformatic guidance and feedback. Axel Jensen has the full authorship for the alignment of raw whole-genome sequencing reads to the reference genome as detailed in the methods section. Preprint available at doi.org/10.1101/2024.12.13.628324.

Chapters 6 and 7: ethnobiological data from female participants was collected by Núria and Jessica Cunha.

Publications

Chapter 2: Colmonero-Costeira, I., Sá, R.M., Djaló, M.L., Cunha, N., Cunha, J., Minhós, T. Russo, I.-R.M., Bruford, M.W., Costa, S. and Ferreira da Silva, M.J. 2023. Notes on the conservation threats to the western lesser spot-nosed monkey (*Cercopithecus petaurista buettikoferi*) in the Bijagós Archipelago (Guinea-Bissau, West Africa). *Primates*. doi:10.1007/s10329-023-01090-9.

Chapter 5: Colmonero-Costeira, I., Guschanski, K., Djaló, M.L., Fernandes, N., Camará, T., Farh, K.K.-H., Kuderna, L., Rogers, J., Marques-Bonet, T., Bruford, M.W., Russo I.-R.M., Jensen, A. * and Ferreira da Silva, M.J. Genomic signatures of island colonization in highly diverse primates. *In review with Molecular Ecology*. *bioRxiv preprint*. doi: doi.org/10.1101/2024.12.13.628324.

Other publications:

Colmonero-Costeira, I., Djaló, S.L., Fernandes, N., Borges, F., Aleixo-Pais, I., Gerini, F., Costa, M., Minhós, T. and Ferreira da Silva, M.J. 2024. Improving baseline information on over-looked generalists: occurrence and mitochondrial DNA diversity of Campbell's (*Cercopithecus campbelli*) and green monkeys (*Chlorocebus sabaeus*) in Guinea-Bissau, West Africa. *Research Square preprint*. doi: doi.org/10.21203/rs.3.rs-5372533/v1.

Almeida, L., Colmonero-Costeira, I., Ferreira da Silva, M.J., Veracini, C., Vasconcelos, R. 2024. Insights into the Geographical Origins of the Cabo Verde Green Monkey. *Genes.* doi:10.3390/genes15040504.

Data Accessibility

Supplementary spreadsheets and bioinformatic code have been deposited in a Public GitHub repository (https://github.com/Colmonero-CI/ICC_thesis). Raw data will be made available upon the publication of the manuscripts resulting from this thesis.

Ethics Statement

All the faecal samples were obtained non-invasively from unidentified individuals without manipulation. All collected tissue samples used in this work were provided voluntarily and free of charge by local hunters and/traders. Informed consent to participate was obtained before beginning research. The providers of tissue samples remained anonymous to local agencies and law enforcers. All sampling was carried out with the approval of the National Institute for Biodiversity and Protected Areas (IBAP). Direção Geral das Florestas e Fauna (DGFF) authorized transportation and issued CITES export permits for tissue samples. Instituto da Conservação da Natureza e Florestas (ICNF, Portugal) issued the CITES importation permits to Portugal (*Cercopithecus petaurista* – No 18PTLX00592I, *Cercopithecus campbelli* – No 18PTLX00590I, *Chlorocebus sabaeus* – No 18PTLX00586I). Samples and DNA extracts remained in Portugal for the whole duration of the project. The Nagoya protocol was not in place in Guinea-Bissau at the time of sampling. However, I aim to acknowledge the work of local researchers by including them in as co-authors of this manuscript. The main findings of this thesis will be shared with the local governmental agencies through meetings and a final progress report and disseminated to the local communities through meetings and communications in local media.

The ethnographic methodologies applied throughout this thesis followed ethical guidelines proposed by the American Anthropological Association (AAA) and the International Primatological Society (IPS). Local communities were informed of the study's aims and that they could cease my observations at any stage of the research. The consent form was read out-loud and oral informed consent to conduct and publish this research was obtained. Confidentiality and anonymity were guaranteed to everyone that interacted with the researchers. Original records of field notes, questionnaires, interviews and group discussions were coded for anonymity purposes and securely stored. Photographs were only collected after oral informed consent from the participants was obtained. I ensured the anonymity of participants in every photograph taken. Data collected was saved in electronic documents, which were stored, and password protected. This research received ethical approval from

Cardiff University's BIOSI SREC (ref: BIOSI SREC 22 11-01). In Guinea-Bissau, the timeline and the activities and methods used were approved by IBAP and local chieftains.

All documentation can be found in Annex I.

Table of Contents

List of Figures

Chapter 1

Chapter 2

Chapter 3

Chapter 4

Chapter 5

Chapter 6

Chapter 7

List of Tables

Chapter 1

Chapter 3

Chapter 4

Chapter 5

Chapter 7

Chapter 8

CHAPTER 1

General Introduction

Non-human primate conservation

The current worldwide human-induced loss of biodiversity, the sixth mass extinction, is one of the most acute environmental problems of the current geological era – the Anthropocene (Barnosky et al. 2011; Dirzo et al. 2014; Ceballos and Ehrlich 2023). For instance, mammal species are disappearing at an estimated rate 67 times higher than background rates (Ceballos and Ehrlich 2023). At the intraspecific level, the severity of the Earth's sixth mass extinction is even higher. Populations of vertebrates are being locally extirpated as a direct result of human action, such as overexploitation, loss or degradation of habitats and global climate change (Ceballos et al. 2017; Ceballos and Ehrlich 2023).

The order Primates is one of the most diverse taxonomic groups of mammals, only superseded by rodents (order Rodentia), bats (order Chiroptera), moles, shrews and hedgehogs (order Eulipotyphla). Improving the effectiveness of primate conservation is required at a global scale (Estrada et al. 2017; Estrada and Garber 2022). According to the latest updates to the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (November 2024), approximately two-thirds of living non-human primate species (523 recognized taxa; primates hereinafter) are currently threatened with extinction to some degree: 17 % have been classified as Critically Endangered; 28 % as Endangered, and 22 % as Vulnerable; the remaining taxa fall onto the Near Threatened (8 %), Least Concern (22 %) and Data Deficient (3 %) categories. Moreover, an estimated 85 % of primates are undergoing demographic contractions worldwide (IUCN 2024).

The growth and expansion of human communities and infrastructure are driving primates to extinction. The main direct threats faced by primate populations are extensive habitat loss and fragmentation due to agricultural expansion, exploitation of tropical resources, mining, fossil fuel extraction, and unsustainable hunting (Estrada et al. 2017; Estrada and Garber 2022). Impacts of climate change and disease transmission by humans also play an important synergistic role in local extinctions and range declines (Estrada et al. 2017; Estrada and Garber 2022). Additionally, primates tend to have long generation times (e.g., 25 years in chimpanzee, *Pan troglodytes* Blumenbach 1775; Langergraber et al. 2012), that may lead to intrinsic low effective population sizes and slow demographic recovery rates (Waples et al. 2013). Anthropogenic pressures threaten primate populations by reducing their abundance through direct mortality, by altering availability and distribution of food resources and, by promoting population fragmentation and isolation. In some cases, population isolation in patches of suitable habitat may cause a decrease in genetic diversity and consequent reduction of adaptive potential (Minhós et al. 2016; Wang et al. 2017; Baas et al. 2018; Minhós et al. 2023).

Promoting primate conservation may promote the maintenance and restoration of forest ecosystems. Primates' tendency to move frequently, to have large home ranges, and to feed on a large variety of fruits makes this group one of the most effective seed dispersers in tropical ecosystems (Chaves et al. 2011; Albert et al. 2013; Heleno et al. 2021). In the scenario of ever-increasing disturbance of tropical regions, primates become particularly important for habitat regeneration following the local extirpation of larger seed dispersing species such as ungulates (Albert et al. 2013; Heleno et al. 2021).

Ethnoprimatology and primate conservation

Human-wildlife interactions are thought to be an essential facet of ecosystem dynamics. While some societies draw a sharp distinction between culture and nature, others present a more fluid association between the natural world and socio-cultural traditions (Seline 2003). Primates are an integrative part of human cultures around the world and have often been integrated into traditional and religious practices. They are commonly present in paintings, inscriptions, pottery and other forms of art throughout human history (Fuentes 2012; Alves et al. 2016).

Humans often interact with primates in areas of co-existence (e.g., Costa et al. 2013; Costa et al. 2017; Hockings et al. 2020). In tropical areas, with the increase of human populations and infrastructure, the ecological overlap between humans and primates is increasing, which frequently has a negative impact on the quantity and quality of suitable primate habitat (Minhós et al., 2023). Furthermore, in these shared landscapes, where local populations are highly dependent on farming and harvesting of local resources, crop-raiding by primates may lead to significant economic losses, furthering negative attitudes and perceptions towards them (Chapman et al. 2012; Hill and Wallace 2012; Findlay and Hill 2020; Haile et al. 2024).

Ethnobiology applied to the field of primatology (hereinafter ethnoprimatology, Fuentes and Wolfe 2002) focuses on bridging traditional primatology and socio-cultural anthropology to scrutinise the multiple facets of the human attitudes towards primates and their behavioural and ecological consequences (Fuentes and Wolfe 2002; Fuentes and Hockings 2010; McKinney and Dore 2018). For instance, depending on local traditions, beliefs and behaviour of hunters, individuals targeted in bushmeat hunting may vary from i) males and/or larger-bodied species to maximise profit in commercial hunting practices (Minhós et al. 2013; Ferreira da Silva et al. 2021a); ii) hunting a particular species for ritualistic practices (Cormier 2006); iii) limited or even prohibited hunting of specific species due to cultural and religious taboos (Cormier 2006; Baker 2013). Directed hunting towards primates can lead to the overexploitation of a species, changes in demography, dispersal patterns and consequently change gene flow patterns, which can impact their long-term survival (Ferreira da Silva et al. 2018; Minhós et al. 2023). Consequently, depending on local cultural beliefs and behaviours, the long-term conservation of primates may be differentially impacted.

By integrating local knowledge and attitudes into assessments of the main conservation threats faced by primates, ethnoprimatology aims to improve effectiveness and ethical considerations of conservation measures and reduce the impact of inter-species conflicts. Ethnoprimatology has the potential to offer alternative solutions to unregulated exploitation and at the same time improve welfare, preserve socio-cultural identities, and introduce alternative sources of income for local populations (Mombeshora and le Bel 2009; van Vliet 2018; Akenji et al. 2019).

Genetic dynamics of insular populations

The study of insular populations and their demographic dynamics is a long-established field within biogeography. MacArthur and Wilson (1963) proposed the equilibrium theory of island biogeography (ETIB) to explain the relationship between an island's geographical features (i.e., distance to mainland and total area) and patterns of species richness. This theory postulates that species richness in islands tends toward a dynamic equilibrium determined by biological processes such as immigration, extinction and speciation, whose rates are in turn influenced by island area and degree of isolation (MacArthur and Wilson 1963).

Similarly to how MacArthur and Wilson (1963) depicted species richness as a balance between immigration and extinction rates, Wright's Island Model describes genetic differentiation between populations as an equilibrium between genetic drift and gene flow (Wright 1931). Combining the two models, islands more distant from the main source of colonisation are less prone to receive migrants at any given point in time, leading to decreased rates of gene flow when compared to less isolated islands (Vellend 2003). Thus, populations inhabiting more isolated islands tend to show a reduction in genetic diversity due to the effect of genetic drift and increased population differentiation. On the other hand, higher levels of genetic diversity are associated with larger islands, as the associated higher carrying capacity reduces population extinction rates, allowing for greater species abundances (Vellend 2003).

The colonisation process of novel geographical regions, such as archipelagos is often carried out by a small number of individuals. As a result, it is expected that i) island populations are generally characterised by lower genetic diversity and effective population sizes (N_e) when compared to their mainland counterparts since only a portion of the genetic variation of the original population is represented in founding individuals (Allendorf et al. 2013; Martin et al. 2023); ii) island populations often display a demographic bottleneck signal as a result of the founding effect (Martin et al. 2023); iii) the extent of the founding effect and the resulting levels of genetic diversity of the newly-formed population is correlated with the number of founding individuals as well as the number of founder events and the genetic diversity of the original population (Astanei et al. 2005; Gillis et al. 2009).

Genetic drift is stronger in populations with small N_e (Allendorf et al. 2013). Although genetic drift is a neutral evolutionary process, it can also incur fitness costs by increasing the allele frequencies of loci with deleterious variation (Bertorelle et al. 2022; Dussex et al. 2023). Strong genetic drift, in particular, can reduce the efficiency of selection in small populations, potentiating the gradual accumulation of mildly deleterious mutations (Dussex et al. 2023). Such accumulation can generate a decline in fitness and exacerbate the extinction risk of small, isolated populations (Bataillon and Kirkpatrick 2000; Khan et al. 2021).

Compared to their mainland counterparts, insular populations often diverge genetically and phenotypically (i.e., character displacement). This phenomenon, collectively known as the “island syndrome”, often includes changes in morphology, behaviour and life-history traits (Adler and Levins 1994). Because genetic drift alone cannot account for the total observed variation (Diniz-Filho and Raia 2017; Gleditsch and Sperry 2019), the process of character displacement is often thought to be driven by adaptive processes. These may arise in response to the new habitats where different traits, more advantageous to the insular environment, are selected for (Welles and Dlugosch 2019; Sendell-Price et al. 2020; Cui et al. 2021; Martin et al. 2021; Payseur and Jing 2021; Wang et al. 2023). On the other hand, non-synonymous variants can drift towards fixation in the insular populations if loci under strong selection on the mainland become effectively neutral on the islands due to the relaxation of natural selection (Cui et al., 2021; Wang et al., 2023).

Guenons of the Bijagós Archipelago, Guinea-Bissau

The Bijagós Archipelago is part of the territory of the Republic of Guinea-Bissau, a coastal West African country (Figure 1.1). The archipelago spans approximately 10,000 km^2 and is comprised of 88 islands of continental origin (Alves 2007). The island nearest to mainland Guinea-Bissau is Bolama (located approximately 1.5 km from the mainland), and the farthest away is Unhocomo (approximately 118 km from the mainland). The archipelago is thought to have been connected to mainland Africa during glacial periods when water levels decreased (Alves 2007). The climate is similar to continental Guinea-Bissau: the annual average temperature varies between 25.9 and 27.1 °C, humidity may be as high as 79 %, and the average annual rainfall fluctuates between 1,500 and 2,000 mm (Catarino et al., 2008). A quarter of the islands are permanently inhabited by rural communities of an increasing population of 32,500 inhabitants (INE 2015), and another quarter are seasonally cultivated and lack permanent settlements (Madeira 2016). The Bijagós Archipelago is one of the poorest regions in the country, however, the incidence of poverty has been decreasing, contrary to the country-wide trend (World Bank 2024).

In 1996, UNESCO recognised the bio-cultural diversity of the archipelago, establishing the Biosphere Reserve of Archipelago Bolama-Bijagós (ABBBR; Figure 1), which currently comprises two national parks (Orango National Park – ONP – and João Vieira e Poilão Marine National Park – JVPMNP) and a marine protected area (Urok Communitarian Marine Protected Area – UCMPA; (IBAP 2019)). The Bijagós Archipelago sustain a considerable variety of ecosystems including mangrove forest, savannah woodland mosaics and patches of sub-humid and dry-tropical forest (Catarino et al. 2008).

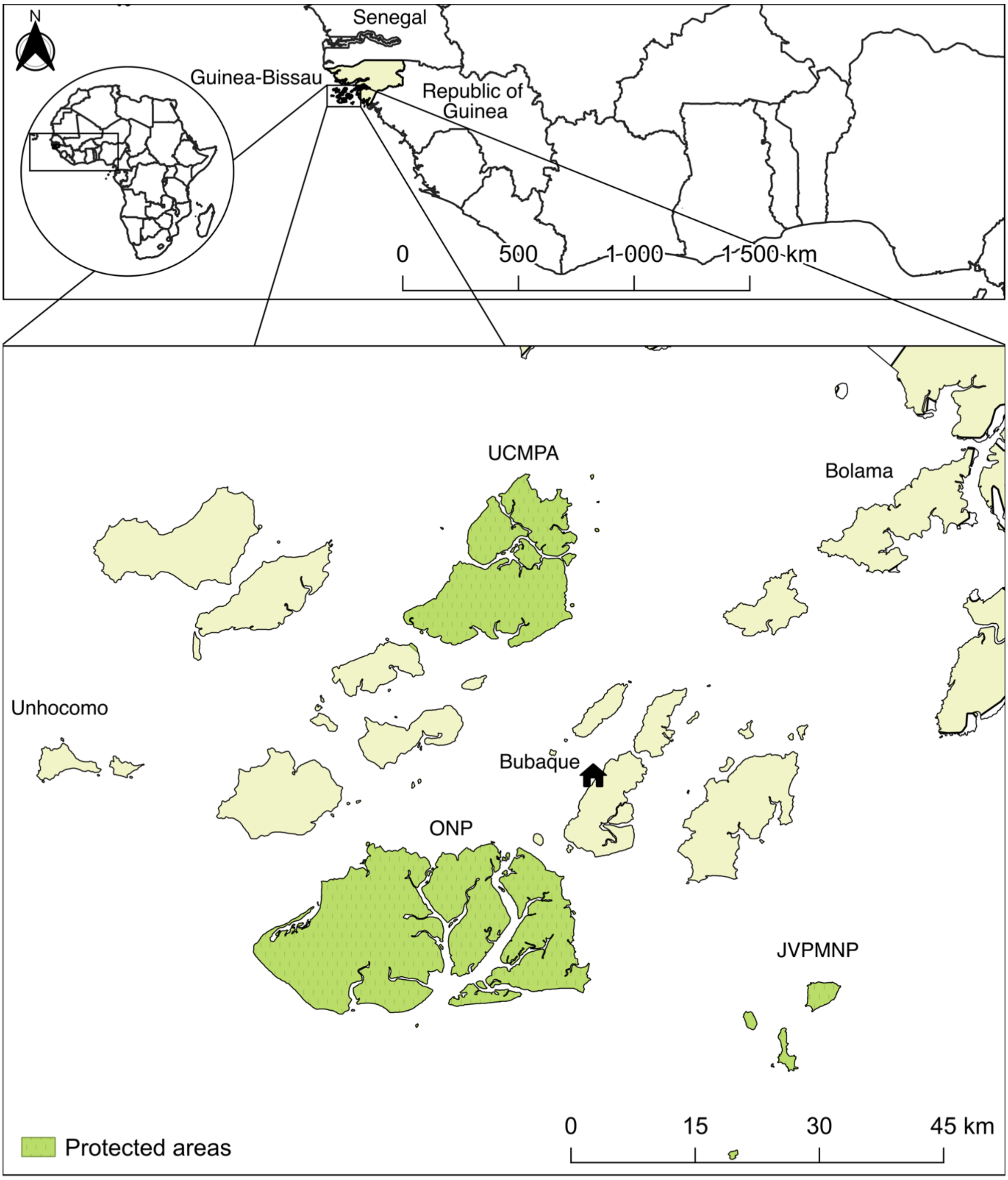


Figure 1.1. The Bijagós Archipelago in Guinea-Bissau, West Africa. Protected areas are represented in green: ONP – Orango National Park; JVPMNP –João Vieira e Poilão Marine National Park; UCMPA – Urok Communitarian Marine Protected Area. The main urban hub and seat of administration is also represented (Bubaque Island).

The archipelago is considered one of West-Africa's most important locations for many emblematic marine species such as the Vulnerable West-African manatee (*Trichechus senegalensis* Link, 1975; Silva and Araujo. 2001; Keith 2015) and the

Endangered green turtle (*Chelonia mydas* Linnaeus, 1758; Catry et al. 2002; Seminoff 2004). For the latter, the Bijagós Archipelago is considered one of the most important nesting sites on the West-African coast. The archipelago is also considered one of the most important wintering sites in Western Africa for migrating shorebirds (order Charadriiformes), after the Banc d'Arguin in Mauritania (Salvig et al. 1994). A minimum of twenty-two species of mammals have been registered for the archipelago (Rainho and Palmeirim 2018), including three primate species of the guenon group (tribe Cercopithecini; Colmonero-Costeira et al. 2019). Despite the recognised diversity of the terrestrial mammals, species occurrence, ecology and colonisation history remain unstudied for most species.

The *Bijagó* ethnic group

The *Bijagó* are the most predominant ethnic group in the Bijagós Archipelago, accounting for approximately 90 % of the total inhabitants. The *Bijagó* have shared ancestry with populations from the surrounding countries of Guinea-Bissau (Senegal, Gambia and Mali; Rosa et al. 2007; Spínola et al. 2008) and their arrival at the archipelago is likely a consequence of the expansion of the Mali Empire across West Africa (Rodney 1970). This expansion, initiated around the XIth century, likely induced the displacement of coastal populations from mainland Guinea-Bissau and neighbouring countries into the archipelago (Rodney 1970). The first descriptions of the *Bijagó* from the XVth century describe the group as fierce belligerent people recognised for their naval expertise and raiding capacity (d'Almada 1984). This aggressive reputation successfully challenged European colonisers, namely the Portuguese. Despite the Portuguese having arrived at Guinea-Bissau in 1450, the loss of *Bijagó* sovereignty over the Bijagós Archipelago occurred only in 1936 and was re-established in 1946 (Bowman 1997).

Conditioned by a life of insularity, the *Bijagó* demonstrate cultural adaptations to explore their natural resources efficiently, namely, in traditional canoe making and subsistence fishing techniques (Madeira 2009). For instance, the *Bijagó* use a variety of tools for fishing (e.g., nets, harpoons and fishhooks) and developed management techniques applied in intertidal areas, including the employment of dams to retain fish stocks during low tides (Madeira 2009). The animistic belief system of the *Bijagó* is thought to contribute for the preservation of the islands' natural ecosystems (Madeira 2009; Cardoso 2010; Madeira 2016). Several locations in the archipelago are regarded as sacred and used exclusively for religious, cultural ceremonies, and as a result, economic and subsistence activities are limited or even prohibited in such areas (Madeira 2009; Cardoso 2010; Madeira 2016).

Internal and external threats to bio-cultural diversity

In the archipelago, most threats to the marine ecosystems are usually perpetrated by foreigners, and these include unsustainable harvesting of marine resources and clearing of mangrove trees (Rebelo and Catry 2011). The threats to the terrestrial ecosystems include habitat loss and fragmentation and bushmeat hunting (Karibuhoye 2004; Rebelo and Catry 2011). The livelihoods of local communities at the archipelago are dependent on subsistence agriculture of rice and secondary crops (e.g., cowpea and groundnut; Madeira 2016). However, annual cereal production is usually insufficient and, consequently, rice is imported to the islands (Madeira 2016). To afford the acquisition of rice, farmers have been increasing local cashew nut production, which likely intensifies deforestation on the archipelago (Madeira 2016). Organised industries with commercial purposes are also a growing threat for the archipelago's biodiversity as is demonstrated by the private concession of the Anagaru Islet for resource exploration, which has been approved by the Guinea-Bissau's Council of Ministers in September 2020. Additionally, importation of non-traditional methods of hunting and fishing is allowing for increased extraction of forest and marine resources (Karibuhoye 2004), which are naturally limited in insular ecosystems.

Recent socio-cultural changes to the *Bijagó* societies could also endanger the bio-cultural diversity of the archipelago. Exposure to external western influences, including religious missions, may have contributed to changes on the adherence to the local socio-cultural traditions (Bordonaro 2006; Madeira 2009; Cardoso 2010). Consequently, the protection of the insular ecosystems intrinsically promoted by the *Bijagó*'s animistic beliefs may be at risk, which in turn may have a negative influence on the local biodiversity.

Guenons (tribe Cercopithecini)

Guenons (order Primates, family Cercopithecidae, sub-family Cercopithecinae, tribe Cercopithecini) are the most species-rich group of African primates with 35 recognised species (IUCN 2024). With a complex evolutionary history characterised by high gene flow and hybridisation between lineages (Jensen et al. 2023) it is not surprising that the guenons are also the most genetically diverse African primate group (Kuderna et al. 2023).

Guenons are distributed throughout Sub-Saharan Africa and inhabit a variety of ecosystems, such as tropical forests, mangrove forests and woodland savannahs (Butynski 2002; Glenn and Cords 2002). Feeding preferences are also very variable in the group. In general, guenons feed mostly on fruits but may include in their diet invertebrates and small vertebrates (Butynski 2002). The species belonging to the tribe exhibit variable body sizes (0.8 – 13 kg) and skeletal features that are not specifically adapted to neither arboreal nor terrestrial habits (Elton et al. 2016). However, exceptions have been found (e.g., skeletal adaptations to running in the patas monkey, *Erythrocebus patas* Schreber, 1774; Zihlman and Underwood 2013).

The lesser spot-nosed monkey, Campbell’s monkey and the green monkey

The three focal species of guenons of this dissertation are the spot-nosed monkey, (*Cercopithecus petaurista* Schreber, 1774), Campbell’s monkey (*Cercopithecus campbelli* Waterhouse, 1838), and the green monkey (*Chlorocebus sabaeus* Linnaeus, 1766). The spot-nosed monkey and Campbell’s monkey occur in coastal West-African countries, and the green monkey has a broader continental distribution while also occurring in coastal countries (Figure 1.2; Gonedelé Bi et al. 2020; Matsuda Goodwin et al. 2020a; Matsuda Goodwin et al. 2020b).

The three species are considered habitat generalists, occupying primary and secondary forest, gallery forest, woodland savannah, and mangrove forest (Rowe and Myers 2016; Matsuda Goodwin et al. 2020a; Matsuda Goodwin et al. 2020b). Spot-nosed and Campbell’s monkeys share very similar socio-biological traits, such as forest strata and feeding preferences, social group composition and sex-biased dispersal behaviour, while green monkeys are socio-ecologically differentiated from the other two (Table 1.1).

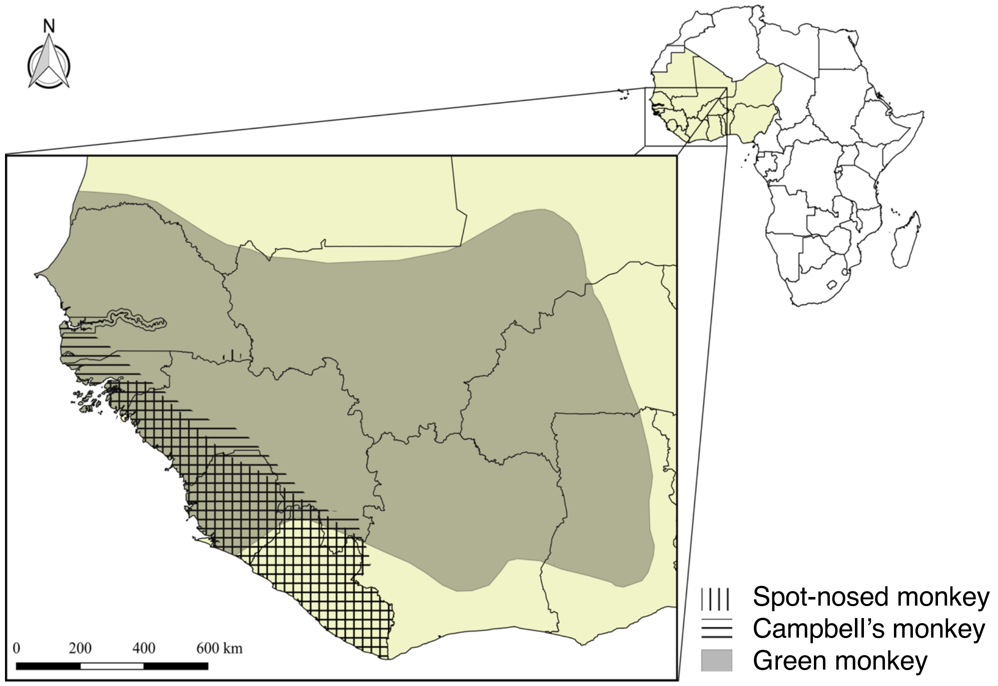


Figure 1.2 Global distributions of the spot-nosed monkey (*Cercopithecus petaurista*), the Campbell's monkey (*Cercopithecus campbelli*) and the green monkey (*Chlorocebus sabaeus*). Geographic range shapefiles extracted from IUCN (2024).

The IUCN Red List of threatened species has classified the three species as Least Concern over the past two decades. However, in the latest assessment (2020), the spot-nosed monkey and Campbell's monkey were considered as having higher conservation concern and were upgraded to Near Threatened (Matsuda Goodwin et al. 2020a; Matsuda Goodwin et al. 2020b). The rationale behind the elevation of their conservation status was the decreasing population trends as a result of the ever-increasing impact of bushmeat hunting and habitat loss throughout their range (Matsuda Goodwin et al. 2020a; Matsuda Goodwin et al. 2020b). Despite the acknowledged population declines, the demographic declines of green monkey populations do not exceed 30 % over the past three generations (Gonedelé Bi et al. 2020). Thus, the species maintained the previous conservation status of Least Concern (Gonedelé Bi et al. 2020).

Table 1.1 Socio-ecological traits of guenon species under study.

Species	Forest Strata	Feeding preferences	Social group composition	Dispersing sex
Spot-nosed monkey (*Cercopithecus petaurista*)	Arboreal, low-medium strata	Omnivore: Mainly fruits (77.2 %), leaves (5.5 %) and animal matter to a lesser extent (7.3 %)	Groups of 2-30 individuals; One male and multiple females	Males
Campbell's monkey (*Cercopithecus campbelli*)	Arboreal, low-medium strata	Omnivore: fruits (46 %), leaves (8 %), and animal matter (33 %)	Groups of 5-33 individuals; One male and multiple females	Males
Green monkey (*Chlorocebus sabaeus*)	Terrestrial	Omnivore: fruits (26.6 %), leaves (37 %), and animal matter (13.2 %)	Fission-fusion groups up to 174 individuals; multiple males/females;	Males and females

Based on (Rowe and Myers 2016; Gonedelé Bi et al. 2020; Matsuda Goodwin et al. 2020a; Matsuda Goodwin et al. 2020b).

In Guinea-Bissau, the spot-nosed monkey (*santchu nariz-branku*/*santchu-bidjugu* in Creole) is possibly restricted to the Bijagós Archipelago (Gippoliti and Dell'Omo 2003; Karibuhoye 2004). Historically, the species was present in mainland Guinea-Bissau (Cufada Lagoons Natural Park and Dulombi National Park; Reiner and Simões 1999; Gippoliti and Dell'Omo 2003), but recent studies have failed to detect the species in the reported areas (Bersacola et al. 2018; Colmonero-Costeira 2023). Despite the recognised need for conservation, the species in not under any formal protection due to errors relating to the species taxonomic identity within Guinea-Bissau (Annex II).

Campbell's monkey (*santchu mona* in Creole) and the green monkey (*santchu-di-tarrafi*, in Creole), are widespread throughout the mainland region of the country with the exception of the North-east (Figure 1.3; Reiner and Simões 1999; Gippoliti and Dell'Omo 2003). Both species have been suggested by several authors as the most abundant non-human primates in the country (Monard 1938; Karibuhoye 2004; Bersacola et al. 2018).

The three guenon species under study have only received particular attention in the past six years. These studies focused on confirming the occurrence of the three species on the Bijagós Archipelago using molecular methods (Colmonero-Costeira et al. 2019), mitochondrial diversity and phylogenetic structure of Campbell's and green monkeys (Colmonero-Costeira et al. 2024), a preliminary study on the population structure (Colmonero-Costeira 2019) and the mitochondrial diversity (Thomas 2011) of the spot-nosed monkey. Not much is known about the specific threats to their conservation. Nonetheless, populations of these species are thought to be increasingly threatened by bushmeat hunting. Campbell's and green monkeys are the most hunted primates for bushmeat consumption in urban markets in mainland Guinea-Bissau, with an estimated volume of trade of around 500 specimens of each species over the course of the dry season (Minhós et al. 2013). Other threats include the pet trade (Gippoliti and Dell'Omo 2003; Karibuhoye 2004), but this is often a subproduct of bushmeat hunting (Ferreira da Silva et al. 2021a). While subsistence hunting of guenons has also been confirmed (Karibuhoye 2004) at the Bijagós Archipelago, commercial hunting has never been reported in the literature. Furthermore, the increasing habitat conversion to monocultures of cashew nut (*Anacardium occidentale*) and oil palm (*Elais* sp.) in the country may have severely reduced the area and number of suitable habitat fragments for many species across Guinea-Bissau (Monteiro et al. 2017), primates included (Casanova and Sousa 2007).

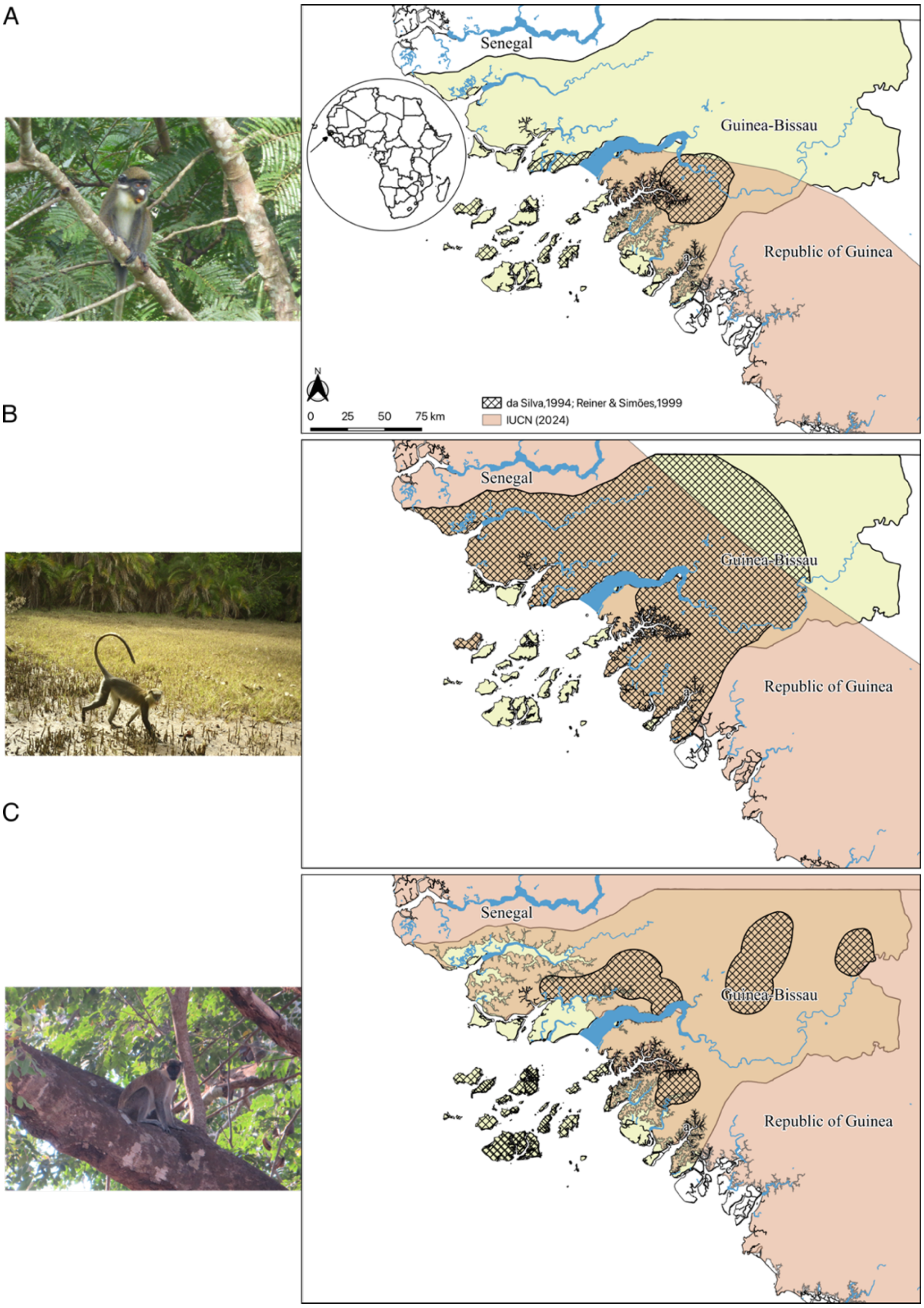


Figure 1.3 Distributions of the spot-nosed monkey (A), the Campbell's monkey (B) and the green monkey (C) in Guinea-Bissau. Based on IUCN (2020), and regional surveys from Campredon et al. (2001) and Reiner & Simões (1999). Photo credits to Isa Aleixo-Pais and Luís Palma.

Thesis aims and outline

The three guenons of the Bijagós Archipelago are thought to be intrinsically threatened by the demographic and genetic processes incurrent from the colonisation of this insular system. Furthermore, they are likely to be threatened by anthropogenic factors. The long-term conservation of the spot-nosed monkey, in particular, is of utmost national importance. The species has thought to have been extirpated from mainland Guinea-Bissau during the last three decades. For these reasons, it is fundamental to gather baseline knowledge on genetic diversity, population structuring, demographic history, and adaptive variation of these populations to access their local conservation status. Effective conservation management of local guenon populations does not only require genetics-informed measures but also requires an understanding of the knowledge and attitudes of human populations that co-exist with the primates.

The overall objective of this thesis is to use genetic, genomic and ethnographic tools to explore the different dimensions of guenon conservation at the Bijagós Archipelago. The thesis is composed of a general introduction, **Chapter 1,** six data chapters, **Chapters 2 – 7**, and synthesis chapter of the key findings, **Chapter 8.**

Chapter 2 initiates these efforts by focusing on the description of anthropogenic activities that are possibly threatening the long-term conservation of the spot-nosed monkey. Furthermore, it provides an evaluation of the primate’s perceived demographic trend, based on non-systematic ethnographic assessments collected during fieldwork in two islands of the archipelago.

Chapter 3 focuses on assessing the genetic diversity and population structure of the spot-nosed monkey across five islands of the archipelago using a panel of microsatellite loci and a fragment of the mitochondrial d-loop. This was particularly important, not only to establish a baseline on the conservation status of these populations based on genetic parameters, but also for the establishment of competing hypotheses of the colonisation history of the primate.

Following on the results of the previous chapter, in **Chapter four I** aimed to employ Approximate Bayesian Computation (ABC) model testing to reconstruct the colonisation scenario that better explains the current genetic parameters of the insular spot-nosed monkeys. As an additional output of the ABC framework, I estimated the contemporary effective population size (N_e), a widely accepted genetic parameter that reflects the populations' capacity to retain genetic diversity on the long-term.

In **Chapter five**, I aimed to explore the genome-wide effects of insularity on the guenons of the Bijagós Archipelago. The inclusion of novel genomic tools, allowed to investigate these effects on both neutral and adaptive variation which can be particularly informative in conservation. This chapter is taxonomically broader than the previous chapters as it includes the two additional guenon species that occur at the archipelago, the Campbell's monkey and the green monkey.

Afterwards, the thesis' focus moves away from conservation genetics/genomics to explore the human dimension of guenon conservation at the Bijagós Archipelago, using ethnobiological tools. This part of the thesis started with a description of the employed methods and of socio-cultural context of the *Bijagó* sample (**Chapter six**) which was needed for the interpretation of local perceptions and attitudes assessed on the following chapter.

Chapter seven builds on the previous chapter and focuses on the perceptions and attitudes of the *Bijagó* towards wild mammals. I aimed to reconstruct the local sociozoological scale (i.e., hierarchical ranking of local wildlife according to their perceived moral status – "good" or "bad" animals). There is a particular focus on how the guenons compare to other wildlife and how to integrate this knowledge to promote their conservation.

To finish, **Chapter eight** summarises the main findings of all data chapters and discusses the conservation implications for the guenons of the Bijagós Archipelago

CHAPTER 2

Notes on the conservation threats to the spot-nosed monkey of the Bijagós Archipelago

The lesser spot-nosed monkey (*Cercopithecus petaurista*) is a widely distributed West African guenon, generally considered less vulnerable to local extinctions, than other sympatric primate species. Guinea-Bissau harbours the westernmost populations of the species. Here, the species is thought to be very rare or even extinct from the mainland with putative populations in some islands of the Bijagós Archipelago. However, due to a lack of regional studies, baseline information on these insular populations is missing. Here, I collected baseline data on the anthropogenic activities possibly threatening the long-term conservation of this primate using non-systematic ethnographic methodologies. The species was reported to be decreasing or rare by local inhabitants of two islands. I identified two main conservation threats: generalised habitat loss/degradation and bushmeat hunting. While subsistence hunting has been recorded before, the semi-organised commercial bushmeat trade was reported for the first time. The carcasses of spot-nosed monkeys were observed being stored and shipped from the seaports to be sold in urban hubs (Bissau and Bubaque Island). The effect of commercial trade on the species could be severe considering the small carrying capacities typical of insular ecosystems. This study highlights the importance of understanding the leading social drivers of bushmeat hunting and of conducting a baseline genetic characterisation of the insular populations, for which further qualitative and quantitative research should be implemented.

Introduction

According to the latest reports of the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (2024), more than half of the living African primate species are currently threatened with extinction to some degree. Moreover, most African primate species are undergoing demographic contractions throughout their ranges due to habitat loss and exploitation (Estrada et al. 2017; Estrada and Garber 2022).

The spot-nosed monkey (*Cercopithecus petaurista*, Schreber, 1774) is the smallest West African guenon (Cercopithecidae, tribe Cercopithecini). The primate is distributed from Guinea-Bissau and east Senegal to the western part of Togo (Rowe and Myers 2016). Two subs-species have been described – the western spot-nosed monkey (*C. p. buettikoferi* Jentink, 1886) and the eastern spot-nosed monkey (*C. p. petaurista* Jentink, 1886). Their ranges are separated by the Cavally River, located on the border between the Republic of Liberia and the Republic of Côte d'Ivoire (Rowe and Myers 2016). Until recently, the species was considered less vulnerable to local extinctions than other West African primates due to its small size and flexible socio-ecological features, which in theory should divert commercial hunting towards stockier primates and allow the spot-nosed monkey populations to remain in viable sizes (Matsuda Goodwin et al. 2020). However, as of 2020, the conservation status of the species was elevated to Near Threatened due to reported increased habitat loss and targeted hunting throughout its range (Matsuda Goodwin et al. 2020). Nevertheless, specific extant populations of this species could be even more threatened than previously considered.

Guinea-Bissau is a small West African state (36,125 km^2) bordered by Senegal to the north and Guinea to the southeast. The country is comprised of the mainland and the Bijagós Archipelago. In the country, the spot-nosed monkey (*santchu nariz-branku/bidjugu*, in Creole) is nowadays likely restricted to the Bijagós Archipelago (Gippoliti and Dell'Omo 2003; Karibuhoye 2004). Historically, the species was present in mainland Guinea-Bissau, Cufada Lagoons Natural Park, and Dulombi National Park (Figure 2.1; Reiner and Simões 1999; Gippoliti and Dell'Omo 2003). At Cufada Lagoons Natural Park, where the species was reported as hunted for meat consumption (Amador et al. 2015), ex-hunters and guides state that the spot-nosed monkey is currently very rare or even extinct (Colmonero-Costeira et al., 2023). At Dulombi National Park, the species has not been detected in recent surveys (Bersacola et al. 2018). The last viable populations of the primate in Guinea-Bissau are thought to occur in five to seven of the largest islands of the Bijagós Archipelago (Colmonero-Costeira et al. 2019), none of which are included in currently established protected areas (Figure 2.1). Here, the species is known to live near human communities and subsistence hunting of the species has been reported (Karibuhoye 2004).

Despite the acknowledged rarity of the species in Guinea-Bissau, conservation actions targeting the species have been non-existent, and baseline information for these populations (e.g., conservation threats, population densities, and genetic diversity) is missing. In this chapter, I aimed to initiate this effort by conducting a non-systematic ethnographic assessment on:

1. Anthropogenic activities that are possibly threatening the long-term conservation of the spot-nosed monkey in the Bijagós Archipelago.
2. The primate's perceived demographic trend based on non-systematic collection of local testimonies.

Methods

The study area included two islands in the Bijagós Archipelago, Guinea-Bissau (Figure 2.1). The precise islands where the study was conducted have been anonymised to protect the identity of the local communities and the location of primate populations. The archipelago spans approximately 10,000 km^2 and comprises 88 islands and islets of continental origin (Alves 2007). Individually, the islands are relatively small, the largest not surpassing a total area of 130 km^2. In 1996, UNESCO recognised the bio-cultural diversity of the archipelago, establishing the Bolama Bijagós Biosphere Reserve (BBBR; Figure 2.1). This reserve currently comprises two national parks (Orango National Park – ONP – and João Vieira and Poilão Marine National Park – JVPMNP) and a marine community protected area

(Urok Communitarian Marine Protected Area – UCMPA), none of which encompasses the described range of the spot-nosed monkey.

A quarter of the islands are permanently inhabited by rural communities, and another quarter are seasonally cultivated (Madeira 2016). The estimated human population size was 32,500 in 2015 (INE 2015). The livelihoods of local communities are dependent on subsistence agriculture of rice crops and other secondary crops (e.g., cowpea, *Vigna unguiculata* and groundnut, *Arachis hypogaea*) and cash crops (e.g., cashew nuts, *Anacardium occidentale*; Madeira 2016).

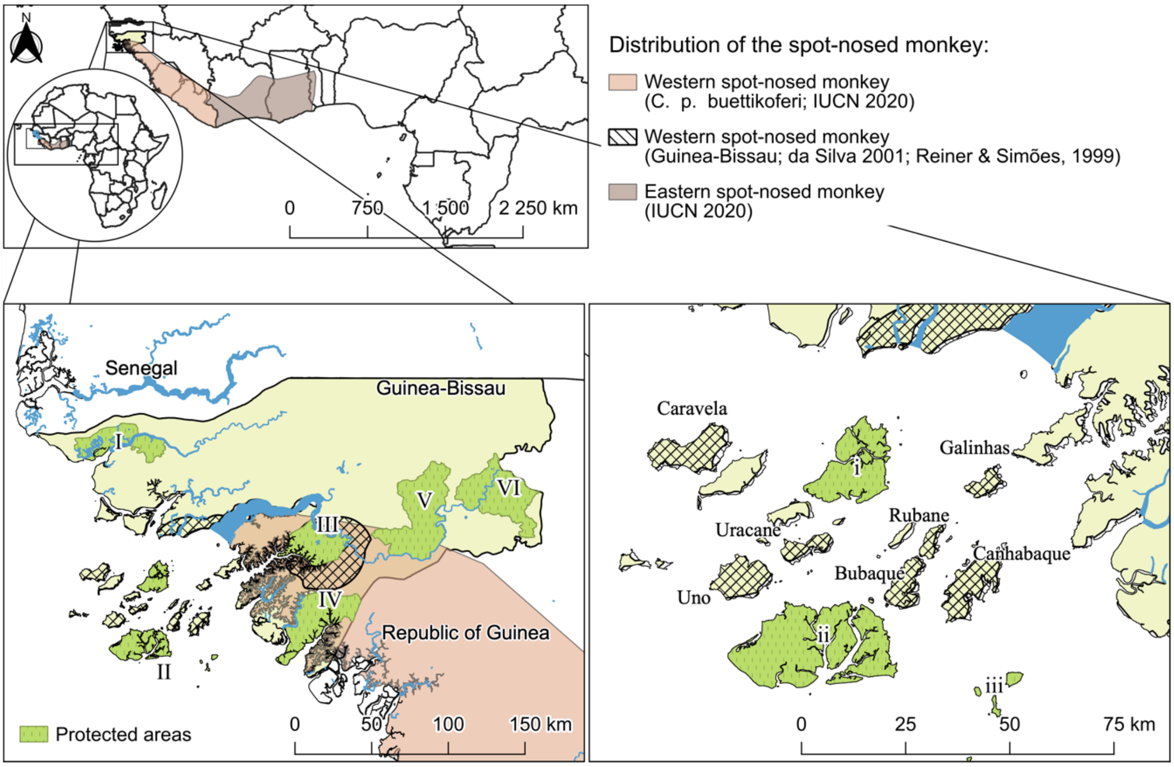


Figure 2.1 Distribution of the spot-nosed monkey (*Cercopithecus petaurista*) in Guinea-Bissau. The species distribution area was drawn based on IUCN polygon (accessed in 2023). The distribution of the eastern subspecies (*C. p. petaurista*) was included. Distributions based on regional surveys conducted in Guinea-Bissau (da Silva, 2001; Reiner and Simões, 1999) are represented as hatched areas. The maps depict protected areas established in Guinea-Bissau: I) CRMNP, Cacheu River Mangroves Natural Park; II) BBBR, Bolama Bijagós Biosphere Reserve; III) CLNP, Cufada Lagoons Natural Park; IV) CFNP, Cantanhez Forests National Park; V) DNP, Dulombi National Park; VI) BNP, Boe National Park; i) UCMPA, Urok Communitarian Marine Protected Area; ii) ONP, Orango National Park; iii) JVPMNP, João Vieira and Poilão Marine National Park.

Data Collection

I conducted a non-systematic ethnographic assessment on activities with a potential for human-wildlife interactions with the spot-nosed monkeys during field expeditions to two islands. These expeditions were also aimed at collecting faecal samples for non-invasive genetic studies on locally ranging primate groups. While in the area, I routinely questioned local communities to provide impressions on the demographic trends of the local primate populations and threats. I took field notes regarding the observations while contacting the local communities. When relevant and authorised by the participants, I took photographic records of the activities. A thematic analysis on the collected fieldwork notes was conducted. This analysis included reading the data thoroughly and reorganising it according to themes as they appeared throughout the notes (e.g., bushmeat hunting, perceptions on population size) to draw insights on the observations (Newing et al. 2010).

Results

I interacted with the local *Bijagó* communities for approximately ten days on each island (20 days in total). The length of stay at the different villages varied between eight hours and two days.

On the first island, I visited seven villages. When addressing the perceived population demographic trends, local inhabitants consistently reported that spot-nosed monkeys were commonly observed, but population size was decreasing. Two putative main conservation threats to these populations were found – habitat loss and/or degradation, and semi-organised hunting.

Recently cleared patches of forest were common. In addition, cashew orchards of various ages were observed in the vicinity of villages. These extensive monocultures were usually planted in areas where dry or sub-humid forest patches were present in the past (Figure 2.2). Hunting of spot-nosed monkeys was conspicuous and widespread. I found recently hunted carcasses in half of the sampling days in distinct locations – three different villages, the main road between villages, and the main seaport. The number of carcasses found per event varied between one and seven.

Hunters were young adult men (19–35 years). The carcasses were smoked and disembowelled shortly after hunting and stored whole.

Figure 2.2 Habitat conversion at the Bijagós Archipelago. a) recently cleared forest patch with grazing cows; b – d) cashew orchards with increasing ages.

The commercial bushmeat trade was observed and described by local inhabitants as a semi-organised practice. Descriptions of the trade included the transportation of carcasses by canoes to the country's urban hubs (Bubaque Island and Bissau, the capital city). These boats would arrive from Bissau carrying ice that was deposited in unplugged freezers at the local seaports. The primate carcasses (whole, smoked, and disembowelled) were stored in the ice-filled freezers until transportation (Figure 2.3, a). Other local terrestrial mammals, namely the giant pouched rat (*Cricetomys gambianus*) and maxwell's duiker (*Philantomba maxwellii*), were also observed to be traded. Although I only observed trade at the main seaport, testimonies by local participants suggested it occurred in at least three seaports of the island.

Additionally, I observed a captive infant monkey that had been caught during a hunting event (Figure 2.3, b).

In the five villages I visited on the second island, local inhabitants reported the presence of two distinct primate species, the spot-nosed monkey and the green monkey (*Chlorocebus sabaeus* Linnaeus, 1766). The spot-nosed monkey was reported to be less common than the green monkey. However, the population of spot-nosed monkeys was mentioned to be increasing by some participants after hunting regulations were enforced. I observed generalised habitat degradation, with expanding cashew orchards in several locations on the island. I did not see direct evidence of primate bushmeat hunting although local inhabitants acknowledged that it occurs. I found two infants and one juvenile green monkey as captives.

Figure 2.3 Wild-meat hunting of spot-nosed monkeys in the Bijagós Archipelago. a) storage of carcasses for commercial trade; b) pet infant monkey caught during a hunting event.

Discussion

Here I present data regarding anthropogenic activities that possibly threaten the spot-nosed monkey. To the best of my knowledge, this is the first study to describe the conservation threats faced by the last remaining populations of the spot-nosed monkey in Guinea-Bissau. Past studies focused on species occurrence (Gippoliti and Dell'Omo 2003; Colmonero-Costeira et al. 2019) and mitochondrial DNA diversity (Thomas 2011), but a knowledge gap on the local demographic trends and putative threats to the species remained.

During my stay on the islands, I observed several recently cultivated orchards of cashew trees (*Anacardium occidentale*), which could indicate a generalised expansion of cash crop monocultures in the archipelago replacing natural primate habitat. Cashew nuts were introduced to Guinea-Bissau in the 19th Century, and at present, it represents the country's most important agricultural export item (Catarino et al. 2015; Monteiro et al. 2017). Cashew orchards are typically located in the vicinity of rural villages. Despite being considered a low-input, low-investment, and assured revenue crop (Temudo and Abrantes 2014), cashew production in Guinea-Bissau is considered unsustainable (Monteiro et al. 2017). Cashew orchards are single-crop agroecosystems where plant species richness is insignificant underneath and around the trees (Monteiro et al. 2017). Furthermore, due to little agricultural management, cashew orchards are typically characterised by low yields per hectare, possibly leading to an ever-increasing expansion of cultivated areas (Catarino et al. 2015; Monteiro et al. 2017). Past studies have never specifically addressed the expansion of cashew crops in the Bijagós Archipelago. However, my observations suggest a systematic investigation of its impacts on the insular ecosystems should be conducted.

Subsistence hunting targeting the spot-nosed monkeys had been previously observed in several islands of the archipelago (Karibuhoye 2004) and commercial trade has been mentioned by tourists and inhabitants of the islands (RS, MJFS personal observations). Here, I report observations of commercial bushmeat trade occurring on the archipelago. I also observed a few captive infant/juvenile primates. However, no evidence of trading of captive individuals was observed. Apart from the Western chimpanzee (*Pan troglodytes verus* Schwarz, 1934), which are explicitly targeted to supply the exotic pet trade, other Cercopithecoidea kept captive were probably harvested during hunting events on lactating females (Ferreira da Silva et al. 2021a). Hunting for bushmeat consumption in mainland Guinea-Bissau has been interpreted as the result of low food security and structurally deficient supply chains of fresh livestock and fish (Costa 2010). Moreover, a recent increase in bushmeat hunting may have been motivated by unstable sources of income, which may encourage young men to engage in this immediate return activity (Ferreira da Silva et al. 2021a). For example, in some mainland rural areas, primate carcasses were reported to be worth between USD 1.27-3.69 (Ferreira da Silva et al. 2021a), which is a significant revenue considering that a significant portion of the country's population lives under USD 2.15 per day (World Bank, 2022). Similar motivations may be behind the commercial primate meat trade on the Bijagós Archipelago. A societal dichotomy between young and elder generations has been suggested to be arising within *Bijagó* communities due to new aspirations of younger generations to abandon traditional socio-cultural systems, in favour of western views of modernity, personal and regional development (Bordonaro 2006), which potentially favour fast revenue activities.

The extent to which hunting impacts populations of the spot-nosed monkey in Guinea-Bissau is currently unknown. Nevertheless, demographic changes related to anthropogenic activities have been reported for other primate species in the country. These include decreased effective population size (Minhós et al. 2023), increased dispersal distance and preferential gene flow towards areas with lower density due to hunting-related mortality coupled with secondary contact between divergent lineages (Ferreira da Silva et al. 2014) and possible disruption of the sex-biased dispersal pattern (Ferreira da Silva et al. 2018). Moreover, insular populations may be intrinsically threatened by genetic factors, such as reduced genetic diversity and increased inbreeding between conspecifics (Allendorf et al. 2013; Bérénos et al. 2016; Stoffel et al. 2021), which could be exacerbated by an artificial inflation of the mortality rates due to commercial hunting, and should be further investigated. I also highlight that the sustainability and implications of hunting will be better evaluated after conducting comprehensive baseline research on these populations. Specifically, I suggest that assessing the species distribution and abundance, as well as estimating population structure and demographic history based on genetic data should be a priority.

This work highlights that non-systematic ethnographic assessments that integrate local inhabitants as knowledgeable partners can provide baseline knowledge on the conservation threats faced by primate populations. Relatively fast assessments such as this could be particularly important in understudied, over-looked primate species. However, the reports presented here have associated caveats resulting from a relatively unsystematic sampling approach (Newing et al. 2010) and low collection times, which limits the explanatory power of my observations. I stress the need to conduct further qualitative and quantitative ethnobiological research to better understand the main social drivers of the conservation threats affecting these populations.

CHAPTER 3

Genetic diversity and population structure of the spot-nosed monkey of the Bijagós Archipelago

Anthropogenic activities in West Africa are increasing at an alarming rate, threatening its biodiversity-rich ecosystems. The westernmost populations of the spot-nosed monkey (*Ceropithecus petaurista*) can be found in the Bijagós Archipelago, Guinea-Bissau. The primate, which is globally considered wide-spread and of little conservation importance, is thought to have been recently extirpated from mainland Guinea-Bissau and the insular populations on the archipelago are likely the last remaining in the country. Despite their acknowledged rarity in the country, the conservation status of these populations is not well understood. Insular populations can be of conservation concern, as they are often characterised by intrinsically low levels of genetic diversity and subjected to high genetic drift. Here, I conducted a non-invasive genetic study in five islands where the spot-nosed monkey is known to occur. I aimed to estimate genetic diversity, population structure and gene flow using eleven autosomal microsatellite loci and a fragment of the mitochondrial d-loop. Contrary to the expectation, insular populations were not depauperated of genetic diversity when compared to other primate species in Guinea-Bissau. Populations were structured by island and no evidence of contemporary gene flow within the archipelago was found. Furthermore, I found that populations across the archipelago did not differentiate strictly according to the colonisation model typical of natural colonisations – the stepwise colonisation model. Instead, human-facilitated translocations of primates could be an alternative explanatory hypothesis for the observed pattern.

Introduction

The world-wide human-induced loss of biodiversity is one of the most acute environmental problems of the current geological era - the Anthropocene (Barnosky et al. 2011; Dirzo et al. 2014; Ceballos and Ehrlich 2023). Mammal species are perishing at an estimated rate of two species extinctions per 10,000 species every 100 years as result of anthropogenic actions (Ceballos et al. 2017). Human-induced deforestation is particularly severe in the West African biodiversity hotspots (Myers 1993; Myers et al. 2000) where only 10% of the primary vegetation remains (Myers et al. 2000).

Guinea-Bissau is a coastal West African country, neighboured by Senegal and Guinea Conakry and consists of the mainland region and the Bijagós archipelago. The Bijagós Archipelago (total area ca. 10,000 km2) is formed by 88 islands of continental origin (Alves 2007). The archipelago is thought to have been formed during the lower Flandrian transgressions (15 – 6 KYA) as a consequence of the rapidly increasing sea levels associated with the melting of polar ice caps (Alves 2007). Currently, extensive intertidal mudflats connect some of the islands during low tides (Alves 2007).

The spot-nosed monkey (*Cercopithecus petaurista* Schreber, 1774) is a small-bodied primate endemic to West Africa (Rowe and Myers 2016). The conservation status of the species by the International Union for Conservation of Nature (IUCN) has been recently upgraded to Near Threatened (Matsuda Goodwin et al. 2020). Populations are decreasing globally, mainly as a result of deforestation and the bushmeat trade (Rowe and Myers 2016; Matsuda Goodwin et al. 2020). The spot-nosed monkey occurs on some of the largest islands of the Bijagós Archipelago, such as Bubaque, Rubane, Canhabaque, Caravela, Galinhas, Uno and Uracane (Campredon et al. 2001; Gippoliti and Dell'Omo 2003; Colmonero-Costeira et al. 2019). The primate was also thought to occur on mainland Guinea-Bissau (Gippoliti and Dell'Omo 2003) but have not been recorded in more than 30 years (Bersacola et al., 2018, 2022; Colmonero-Costeira 2023). At the archipelago, the species is reported to have decreased during the last decades, most likely due to subsistence and commercial bushmeat hunting and degradation of natural habitats (Chapter 2, Karibuhoye, 2004).

In addition, insular populations of the primate may be threatened by intrinsic genetic factors associated with insularity. Typically, islands are colonised by few individuals of a species that carry only a small proportion of the genetic diversity present in the source populations (Allendorf et al. 2013; Martin et al. 2023). Consequently, insular populations usually display low levels of genetic diversity and potentially, reduced long-term viability (Allendorf et al. 2013; Martin et al. 2023). Additionally, these primate populations are expected to show low levels of gene flow between islands, which further exacerbates the loss of genetic diversity (Allendorf et al. 2013).

Due to their intrinsic genetic factors, an assessment of the genetic diversity, population structure and gene flow dynamics of the insular populations of spot-nosed monkeys is a crucial stepping stone for the assessment of its local conservation status. Using a panel of microsatellite loci and a fragment of the mitochondrial d-loop I aimed to:

1. Estimate the genetic diversity of different insular populations.
2. Estimate population structure within the archipelago.
3. Characterise the gene flow dynamics and the main axes of genetic differentiation.

Methods

Sampling

Faecal samples (N = 390) were collected between January and June 2016, on the five islands of the Bijagós Archipelago (Caravela, Uracane, Uno, Canhabaque, Galinha; Figure 3.1 a) where spot-nosed monkeys were reported to occur (Campredon et al. 2001; Gippoliti and Dell'Omo 2003).

Areas frequently used by primates were identified by the local communities and the pinpointed locations were subsequently visited. Faecal samples were collected, non-invasively, whenever a social group was detected. All the collected faecal samples were georeferenced. The preservation of the faecal samples was achieved following the two-step ethanol-silica gel protocol (Roeder et al. 2004) and were stored at room temperature until DNA extraction. Additionally, tissue and blood samples were collected from carcasses found opportunistically in local villages. These were preserved in 99 % ethanol and stored at -20 ºC.

DNA extraction and microsatellite genotyping

DNA from 145 faecal samples was extracted using the QIAamp DNA Stool Mini Kit (Qiagen, Germany) with few modifications (following the method in Ferreira da Silva et al. 2014). Extractions were conducted in the facilities at Centro de Testagem Molecular (CTM, CIBIO-InBIO, Vairão, Portugal). DNA from nine tissues and one blood sample was extracted using the DNeasy Blood & Tissue Kit (Qiagen, Germany) according to the manufacturer's protocol.

Samples were genotyped using a panel of 11 autosomal microsatellite (STR) loci (Supplementary Table 3.1). The microsatellite loci were human-derived but known to cross-amplify across in other Cercopithecidae species [e.g., Guinea baboon (*Papio papio* Desmarest, 1820; Ferreira da Silva et al. 2014; Kopp et al. 2014), king colobus (*Colobus polykomos* Zimmermann, 1780), and the western red colobus (*Piliocolobus badius temminckii* Kuhl, 1820; Minhós et al. 2013b; Minhós et al. 2016; Minhós et al. 2023)]. All primers except D7s503 were fluorescent-labelled. To amplify locus D7s503, I used a combination of non-fluorescent D7s503 primers, and fluorescent primer tails (Schuelke 2000). The microsatellite loci were amplified in three multiplex PCRs with the exception of locus D7s503. Each PCR reaction contained 1X MyTaq™ Mix (Bioline, UK), 0.6 μL of primer mix, 2 μL of DNA extract and molecular grade water for a final volume of 6 μL. The final concentration for each primer pair varied across the microsatellite panel (Supplementary Table 3.1). PCR reactions were performed in a T100™ 96 Well Thermal Cycler (Bio-Rad, USA). Cycling conditions started with a Taq activation step at 95 ºC for 15 minutes, followed by 40 cycles of denaturing step at 94 ºC for 30 seconds, annealing at 57 – 59 ºC for between 40 and 90 seconds and extension at 72 ºC for between 40 and 90 seconds

(Supplementary Table 3.1). The PCR cycles ended with a final extension of 30 minutes at 72 ºC. The PCR products were analysed on a 3130xl automated sequencer (Applied Biosystems™, USA) using GeneScan™ 500 LIZ™ size standard (Thermo Fisher Scientific, USA) at CTM. Alleles were scored using GeneMapper v4.0 (Applied Biosystems™, USA).

Data quality control

When conducted on non-invasive DNA, the PCR amplification of microsatellite loci is prone to systematic and stochastic errors such as null alleles (NA), false alleles (FA) and allelic dropout (ADO; Valière and Berthier 2002; Bonin et al. 2004; Pompanon et al. 2005). To circumvent this limitation, the number of PCR repeats and the number of times an allele needs to be scored to obtain 95% confidence in genotypes was estimated using the simulation software GEMINI v1.3.0 (Valière and Berthier 2002). Initially, a maximum likelihood approach implemented in Pedant v1.0 (Johnson and Haydon 2007) was used to estimate a preliminary ADO and FA rates per locus using a subset of samples. Considering that the model is based on the assumption of a population in Hardy-Weinberg Equilibrium (HWE) and that population substructure between islands is plausible, only samples from a single island (Uno Island, N = 18) were used to estimate the error rates.

It was estimated that for the faecal samples, the consensus genotype obtained from four independent PCR repeats across loci would produce 95% confidence genotypes. Genotypes at any loci were considered as heterozygous after each allele was scored in at least two independent PCR repeats. In the particular case where three homozygotic amplifications and a fourth heterozygotic amplification were observed, a fifth PCR repeat was conducted. Considering the higher quality of the DNA obtainable from tissue and blood samples, the samples were only amplified twice for each multiplex and for the D7s503 locus. The final genotypes were reviewed by a second independent scorer (MJFS) to reduce the subjectivity associated with allele calling.

The Quality Index (QI; Miquel et al. 2006) was used to assess the reliability of consensus genotypes; only the samples with a QI above 0.55 were included in the final dataset. The threshold of missing data across loci for a genotyped individual to be included in the final database was defined based on the minimum combinations of loci that minimises the probability of identity between siblings (PI_{sib}) estimated using GenAlEx v6.5 (Peakall and Smouse 2006; Peakall and Smouse 2012). Duplicate genotype profiles were detected by identity analysis in Cervus v3.0.7 (Kalinowski et al. 2007). Profiles differing by a single heterozygous locus were considered duplicates and were removed from the final database. The existence of null alleles and scoring errors due to stuttering or considerable ADO was checked using Micro-Checker v2.2.3 (Van Oosterhout et al. 2004). Departures from HWE per locus and pairwise linkage disequilibrium (LD) were calculated using GENEPOP v4.7.5 (Raymond and Rousset 1995; Rousset 2008). Deviations from HWE and LD can be caused by underlying population sub-structure (Selkoe and Toonen 2006). Therefore, deviations from HWE and LD between all pairs of loci were calculated for the pooled dataset and by island.

Genetic diversity

Genetic diversity was estimated based on the number of alleles per locus (n_A), the effective number of alleles (n_E), unbiased expected heterozygosity (uH_E), the observed heterozygosity (H_O), and the inbreeding coefficient (G_{IS}; Nei 1987) using GenoDive v3.06 (Meirmans and Van Tienderen 2004; Meirmans 2020). Additionally, the rarefied allelic richness (AR) across loci was estimated using the hierfstat R package v0.5-11 (Goudet and Jombart 2022). Significant differences in genetic diversity between islands were tested by Analysis of Variance (ANOVA). When statistical significance was found, the Tukey's HSD multiple comparison procedure was employed.

Population structure

Estimates of pairwise fixation index (F_{ST}) between islands were obtained using hierfstat v0.5-11 R package. Genetic variation between samples was visualised by Principal components analysis (PCA) using adegenet v2.1.10 (Jombart 2008) and vegan v2.6.4 R packages (Oksanen et al. 2022). Missing genotyped loci across individual profiles were replaced by the mean allelic frequencies. Allelic frequencies were left unscaled. Additionally, population structure was assessed using STRUCTURE v2.3.4 (Pritchard et al. 2000). STRUCTURE was run using the admixture model with correlated allele frequencies (Falush et al. 2003). Ten independent runs were conducted with inferred genetic clusters (*K*) varying between one to eight, a burn-in period of 100,000 steps followed by 1,000,000 MCMC iterations. The most likely number of *K* was estimated using the log likelihood of the data (Pritchard et al. 2000), and the degree of change of log likelihood between successive clusters (Δ*K*; Evanno et al. 2005). The individual probability of assignment to each genetic cluster (Q) across multiple *K* were aligned across runs using the CLUMPP greedy algorithm (Jakobsson and Rosenberg 2007). All post-processing procedures of the STRUCTURE results were performed using pophelperShiny R package (Francis 2017).

Two potential sources of bias were signalled a priori in this dataset, unbalanced sampling between putative sub-populations (Wang 2017), and the inclusion of highly related individuals typical of non-invasive datasets from arboreal primate species (e.g., Minhós et al. 2013b; Minhós et al. 2023). To test the effect of an unbalanced sample size between sampling locations in STRUCTURE, an alternative set of ancestry prior setting suggested by Wang (2017) was employed. This alternative set of priors included estimating the individual values of alpha for each genetic cluster with initial alpha set to 1/*K* (expected), and uncorrelated allele frequencies between clusters (Wang 2017). To inspect whether population sub-structure was being detected due to the presence of highly related individuals, STRUCTURE was re-run with a reduced dataset where one individual from each significantly related dyad was removed. Pairwise relatedness was estimated using the Queller and Goodnight's estimator (1989; Konovalov et al. 2004) within islands using Kingroup v2_101202 (Konovalov et al. 2004).

Spatial trends of genetic differentiation

The contribution of geographic locations on genetic differentiation was estimated by combining redundancy analysis (RDA) and trend-surface analysis using vegan v2.6.4 R package. Redundancy analysis combines an ordination method (PCA) with multiple regressions of independent predictors, here a polynomial trend-surface of the geographic locations (Legendre and Legendre 2012). For the matrices of geographic variables, I generated a third-degree orthogonal polynomial trend-surface of the geographic coordinates ($long, lat, long * lat, long^2, lat^2, long^2 * lat, long * lat^2, long^3, lat^3$). Third-degree orthogonal polynomials allow modelling of linear gradients and other more complex patterns over the trend-surface (Legendre and Legendre 2012). A forward selection procedure was applied to prevent a possible over-fitting of the multiple regression. I selected a stringent significance level of 0.01 and the adjusted determination coefficient (R^2_{adj}) as stopping criteria (Blanchet et al. 2008) to account for the increased type-I error rates due to multiple testing. Subsequently, the variance inflation factor (VIF) of the variables was estimated, and highly collinear variables (VIF > 5) were removed in a stepwise manner. After conducting the selection procedure, the geographic variables $long, lat, long * lat, long^2$, were included as explanatory variables. Statistical significance of the multiple regression models and each of the resulting canonical axes was obtained by ANOVA-like permutation tests (9,999 permutations).

To explore the existence of areas within the archipelago with higher or lower gene flow than expected under a strictly isolation-by-distance (IBD) model, I estimated effective migration surfaces using EEMS (Petkova et al. 2015). EEMS is expected to be insensitive to some degree of location uncertainty (Petkova et al. 2015). Thus, genotype profiles from tissue samples whose exact origin within the sampled island was unknown were included. For these genotype profiles I estimated their sampling locations by jittering around the centroid of the islands. Initially, I explored EEMS models for increasing deme sizes (200, 400 and 800 demes) and optimised the variances for the proposal distributions. Optimisation runs consisted of three independent MCMC chains of 1,000,000 iterations, burn-in of 200,000, and thinning of 2,000. The optimal number of demes was selected based on the determination coefficient (r^2) between the observed and fitted pairwise genetic dissimilarities between and within demes. The final EEMS analysis was run for eight independent chains of 5,000,000 MCMC iterations, burn-in of 1,000,000, and thinning of 10,000. Plotting of the effective migration surfaces and visual inspection of the convergence of the MCMC chains was conducted using reemsplots2 v0.1.0 (Petkova 2023) and maptools v1.1-8 (Bivand and Lewin-Koh 2023) R packages.

Mitochondrial diversity

A fragment of the hypervariable region I (HVRI) of the mitochondrial d-loop with a predicted size of 388 bp was amplified by PCR using primers LCERCOHVRI (5’ CGTGCATTACTGCTAGCCAAC 3’) and HCERCOHVRI (5’ GGGATATTGATTTCACGGAGGA 3’; Colmonero-Costeira et al. 2019). Only samples from unique genotype profiles were used. The PCR reactions were conducted in 10 μL of total volume, containing 1X MyTaq™ Mix (Bioline, UK), 0.2 μM of forward and reverse primer, 2 μL of DNA extract and 2 μL molecular grade water for a final volume of 10 μL. The PCR reactions were performed in a T100™ 96 Well Thermal Cycler (Bio-Rad, USA). The cycling conditions started with a Taq activation step at 95ºC for 15 minutes, followed by 40 cycles of denaturing step at 94ºC for 30 seconds, annealing at 58ºC for 30 seconds and extension at 72ºC for 30 seconds. The final cycling step corresponded to a final extension at 72ºC for 15 minutes. The amplified products were purified by enzymatic hydrolyzation of nucleotides using 1 μL (1/4 ratio) of Exonuclease I (20 UμL-1) and FastAP (1 UμL-1) (Thermo Fisher Scientific™, USA). Fragments were sequenced on a 3130XL automated sequencer (Applied Biosystems™, USA) at CTM. Sequences were manually corrected using Geneious v4.8.5 (Kearse et al. 2012). A consensus for each sequence was obtained by aligning the forward and reverse sequence. Sequences containing double electrophoretic peaks were removed from the final database. Additionally, all polymorphic positions (i.e., substitutions, insertions, and deletions) were re-checked by eye. All sequences were aligned using Geneious’ in-built algorithm. The final alignment was corrected by eye and trimmed to the length of the shortest sequence.

The number of haplotypes, haplotype diversity (Hd, Nei 1987), and nucleotide diversity (π, Nei 1987) and Tajima’s D (Tajima 1989) was estimated using DNAsp v6.12.03 (Rozas et al. 2017). To assess relationships between haplotypes, haplotype networks were constructed based on statistical parsimony using TCS v1.21 (Templeton et al. 1992) coupled with tcsBU visualiser (Múrias Dos Santos et al. 2016) and complemented with multidimensional scaling analysis (MDS) on pairwise genetic distances between haplotypes. Genetic distances were calculated based on the best-fit model of molecular evolution which was identified using ModelFinder (Kalyaanamoorthy et al. 2017) restricted to the models available in ape 5.7.1 R package (Paradis and Schliep 2019). The model TN93 was selected based on the Bayesian Information Criteria (BIC). The MDS analysis was conducted using vegan v2.6.4 R package. R packages and statistical analysis were run under R v4.2.2 (R CoreTeam 2022; Posit team 2023) coupled with RStudio v2023.06.2+561 (Posit team 2023).

Results

Genotyping and data quality control

The final dataset included a total of 64 spot-nosed monkey individual profiles genotyped at 8-11 microsatellite loci. The dataset had an average QI of 0.88 and 5% missing data across loci. The micro-checker analysis did not detect the presence of null alleles and scoring errors due to stuttering or considerable ADO. Significant departure from HWE was found for all the loci when samples were pooled. When subsetted by island, only locus D12s372 in Canhabaque island was found to have a significant departure from HWE. Calculating LD by island reduced the total number of loci in LD from 35 in the pooled dataset to none. Individuals could be effectively distinguished using a minimum combination of eight loci ($PI_{sib} < 0.001$; Waits et al. 2001) and PI_{sib} using the full set of 11 loci was of 1.0x10-12.

Genetic diversity

Overall, I did not find low levels of genetic diversity (Table 3.1). With the exception of H_O and H_E, other genetic diversity measures were heterogeneous across islands (n_A: $F_{(4, 50)} = 5.82$, $p < 0.001$; n_E: $F_{(4, 50)} = 3.49$, $p < 0.01$; AR: $F_{(4, 50)} = 2.97$, $p < 0.05$). Post-hoc comparisons on these genetic diversity measures revealed that Caravela and Galinha generally yielded lower genetic diversity than the remaining islands. Canhabaque showed the highest AR. Overall the inbreeding coefficient was 0.04 ± 0.03 and significant differences were found between islands (G_{IS}: $F_{(4, 48)} = 3.72$, p <

0.05) with Caravela showing significantly higher inbreeding coefficient than Uracane (Tukey HSD, $p < 0.05$).

Population structure

Mean pairwise F_{ST} between islands was 0.32 ± 0.09. The lowest estimated pairwise F_{ST} value was found between the populations of Uno and Canhabaque islands ($F_{ST} = 0.17$), and the largest value was obtained between Caravela and Galinha islands ($F_{ST} = 0.46$; Figure 3.1 b). In the PCA, the first and second PCs explained 34.80% of the total variance and revealed four main groups: Galinha, Uracane, Uno and a fourth group formed by genotype profiles from Caravela, Canhabaque and a few from Uno islands (Figure 3.1 c). After the removal of the samples from Galinha, which dominated the original PC1, genotype profiles from Canhabaque and Uno islands become more segregated, while the same cannot be observed between those from Caravela and Canhabaque islands which still overlap across the two PCs (not shown).

Table 3.1 Genetic diversity of the spot-nosed monkey across eleven microsatellite loci.

Island (N)	n_A	n_E	AR	H_O	H_E	G_{IS}
Caravela (4)	2.45±0.31	1.96±0.23	2.30±0.86	0.39±0.08	0.49±0.09	0.19±0.10
Uracane (15)	4.09±0.44	2.75±0.23	2.70±0.89	0.59±0.09	0.55±0.09	-0.08±0.04
Uno (18)	4.36±0.43	2.65±0.23	2.75±0.51	0.64±0.05	0.61±0.03	-0.05±0.05
Canhabaque (12)	5.00±0.41	3.37±0.28	3.24±0.69	0.60±0.06	0.69±0.06	0.13±0.04
Galinha (15)	3.55±0.39	2.10±0.29	2.24±0.72	0.45±0.08	0.45±0.08	0.00±0.06
Overall (64)	8.27±0.57 ***	2.28±0.20 **	8.11±1.80 *	0.54±0.04 NS	0.56±0.05 NS	0.04±0.03 *

N – number of genotype profiles; n_A – alleles per locus; n_E – effective number of alleles; AR – allelic richness; H_O – observed heterozygosity; H_E – expected heterozygosity; G_{IS} – inbreeding coefficient. Asterisks represent significant ANOVA tests between means (NS $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

In the STRUCTURE analysis, the starting point of the log-likelihood plateau and the first ΔK peak was obtained at $K = 4$ (Supplementary Figure 3.1), followed by a maximum log-likelihood and a second ΔK peak at $K = 5$. The STRUCTURE results for increasing values of K ($K = 1$ to $K = 5$) suggest the existence of hierarchical population structure and a strong correspondence between geography and genetic clusters (Supplementary Figure 3.2). Similar to the PCA, at $K = 4$, populations within each island were considered independent genetic clusters except for the Caravela and Canhabaque populations which were clustered together but segregated at $K = 5$. Negligible levels of admixture between clusters were found, suggesting that individuals from different islands have very little or no shared ancestry (Figure 3.1 d). STRUCTURE runs were shown to be insensitive to the unbalanced sampling and the inclusion of significantly related individuals (Supplementary Figure 3.3).

The RDA analyses detected significant spatially-induced genetic differentiation. The polynomial trend-surface of the geographic coordinates explained 43.58% of the total variance ($r^2 = 0.39$, ANOVA-like $F_{(4, 52)} = 10.04$, $p < 0.001$). The EEMS model across 400 demes displayed the highest r^2 between the observed and estimated pairwise genetic dissimilarities between and within demes ($r^2_{\text{between demes}} = 0.78$ and $r^2_{\text{within demes}} = 0.72$; Supplementary Table 3.2). The obtained effective migration surface suggested genetic differentiation across the archipelago violates a strict IBD model (Figure 3.1 e). Areas of low gene flow relative to the expected under strict IBD were found between the island pairs of Uracane – Uno, and Canhabaque – Galinha, which overlapped with open sea barriers, but also potential dispersal corridors (e.g., sand banks). On the other hand, higher gene flow than expected was found between Uno and Canhabaque islands.

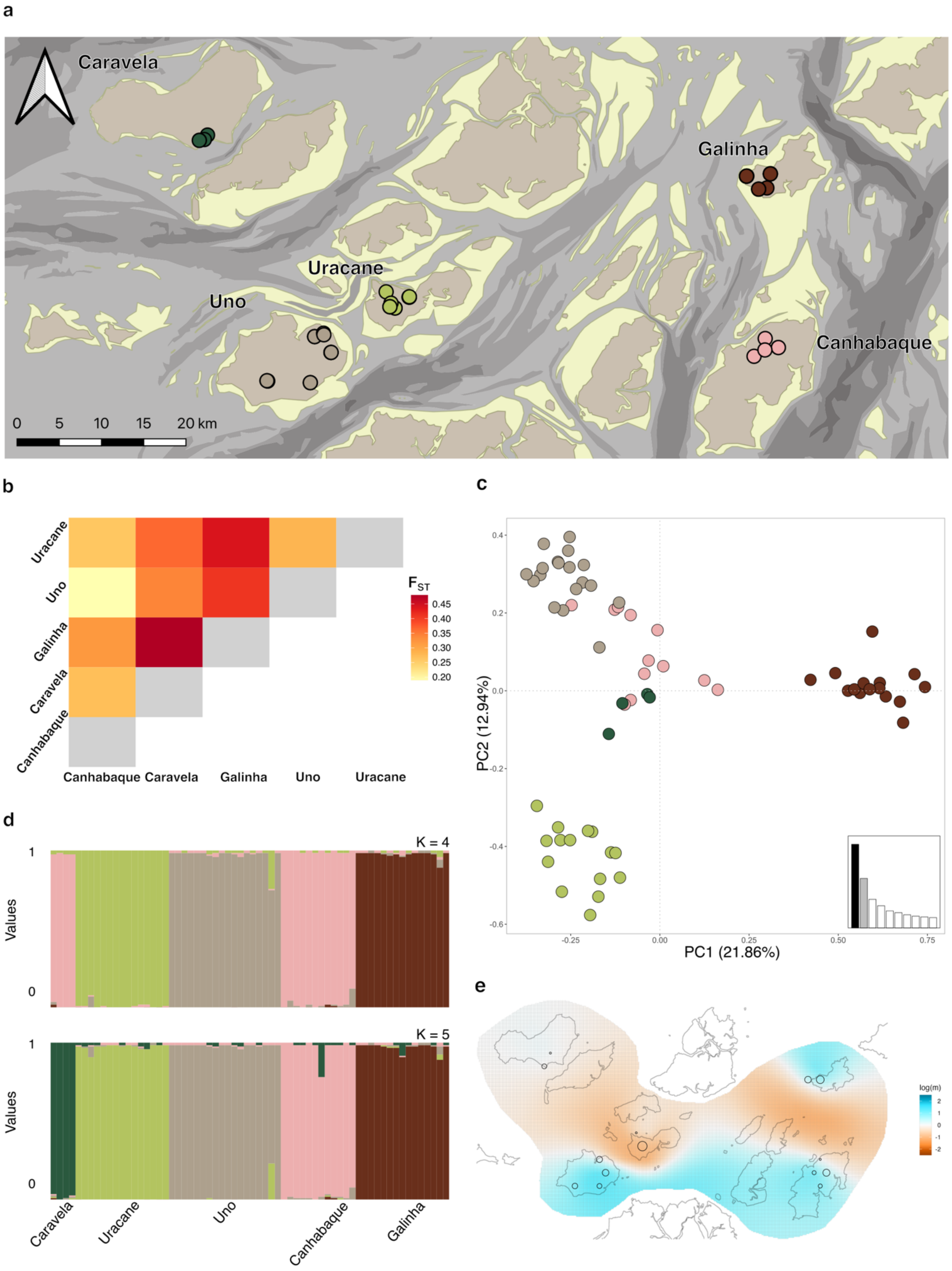

a
Caravela
Galinha
Uracane
Uno
Canhabaque
0 5 10 15 20 km
b
Uracane
Uno
Galinha
Caravela
Canhabaque
Canhabaque Caravela Galinha Uno Uracane
F_{ST}
0.45
0.40
0.35
0.30
0.25
0.20
c
PC2 (12.94%)
PC1 (21.86%)
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.25
0.00
0.25
0.50
0.75
d
K = 4
K = 5
Values
1
0
Caravela
Uracane
Uno
Canhabaque
Galinha
e
log(m)
2
1
0
-1
-2

Figure 3.1. Population structure of the spot-nosed monkey in the Bijagós Archipelago based on eleven microsatellite loci. **a** Location of sampled individuals and landscape features of the archipelago. Sandbanks are represented in yellow. The bathymetry is represented as a grey-scale gradient towards increasing water depth (dark grey). **b** Pairwise F_{ST} between islands. **c** Individual-based principal components analysis. Genotype profiles were coloured according to the island where sampled. The eigenvalues for each PC are plotted in the bottom left corner. **d** STRUCTURE plots depicting the average individual cluster assignment probabilities across 10 independent runs for K = 4 and K = 5. **e** effective migration surface estimated by 8 independent EEMS runs. Colour gradient represents log migration rates and is a proxy of gene flow. Blue tones represent increased effective migration from the expected under IBD, which decreases towards lower effective migrations in red.

Mitochondrial diversity

I obtained 56 HVRI sequences with a final length of 290 bp after trimming to the shortest sequence. A total of 22 haplotypes over a total of 41 polymorphic sites were sampled and overall estimated mitochondrial diversity was high (Table 3.2). In agreement with the genetic diversity estimated using microsatellite loci, the population of Canhabaque Island was the most diverse (Hd = 0.92 ± 0.06; $\pi = 1.58 \pm 0.20 \times 10^{-2}$), the population of Galinha Island the least diverse (Hd = 0.40 ± 0.16; $\pi = 0.40 \pm 0.22 \times 10^{-2}$), and the remaining populations showed mitochondrial diversity levels intermediate to these. The population of Galinha Island showed a mitochondrial diversity pattern that significantly deviated from a neutral pattern of evolution (Tajima's D = -2.05, $p < 0.05$), revealing an excess of low frequency polymorphisms (Table 3.2).

Table 3.2. Mitochondrial genetic diversity of the spot-nosed monkey (290 bp fragment of the hypervariable region I).

Island (N)	S	H	Hd	π	D
Caravela (4)	8	2	0.50±0.27	$1.38 \pm 0.73 \times 10^{-2}$	-0.82 NS
Uracane (11)	7	4	0.67±0.12	$0.58 \pm 0.22 \times 10^{-2}$	-1.22 NS
Uno (15)	13	4	0.62±0.12	$1.14 \pm 0.35 \times 10^{-2}$	-0.05 NS
Canhabaque (12)	15	8	0.92±0.06	$1.58 \pm 0.20 \times 10^{-2}$	-0.35 NS
Galinha (14)	8	4	0.40±0.16	$0.40 \pm 0.25 \times 10^{-2}$	-2.06 *
Overall (56)	22	22	0.92±0.02	$2.33 \pm 0.11 \times 10^{-2}$	-0.93 NS

N – number of sequences; S – number of polymorphic positions; H – number of haplotypes; Hd – Haplotype diversity; π – nucleotide diversity; D – Tajima's D. Asterisks represent significant deviations from neutrality (NS $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

The haplotype network lacked a central highly frequent haplotype and instead displayed high levels of reticulation (Figure 3.2). The sampled haplotypes were private to each of the islands, and sightly differentiated groups of closely related haplotypes were found in Uno and Galinha Islands (Figure 3.2). These haplotypes dominated the variation along the first two MDS dimensions. Most of the haplotypes sampled at Caravela, Uracane and Canhabaque clustered together.

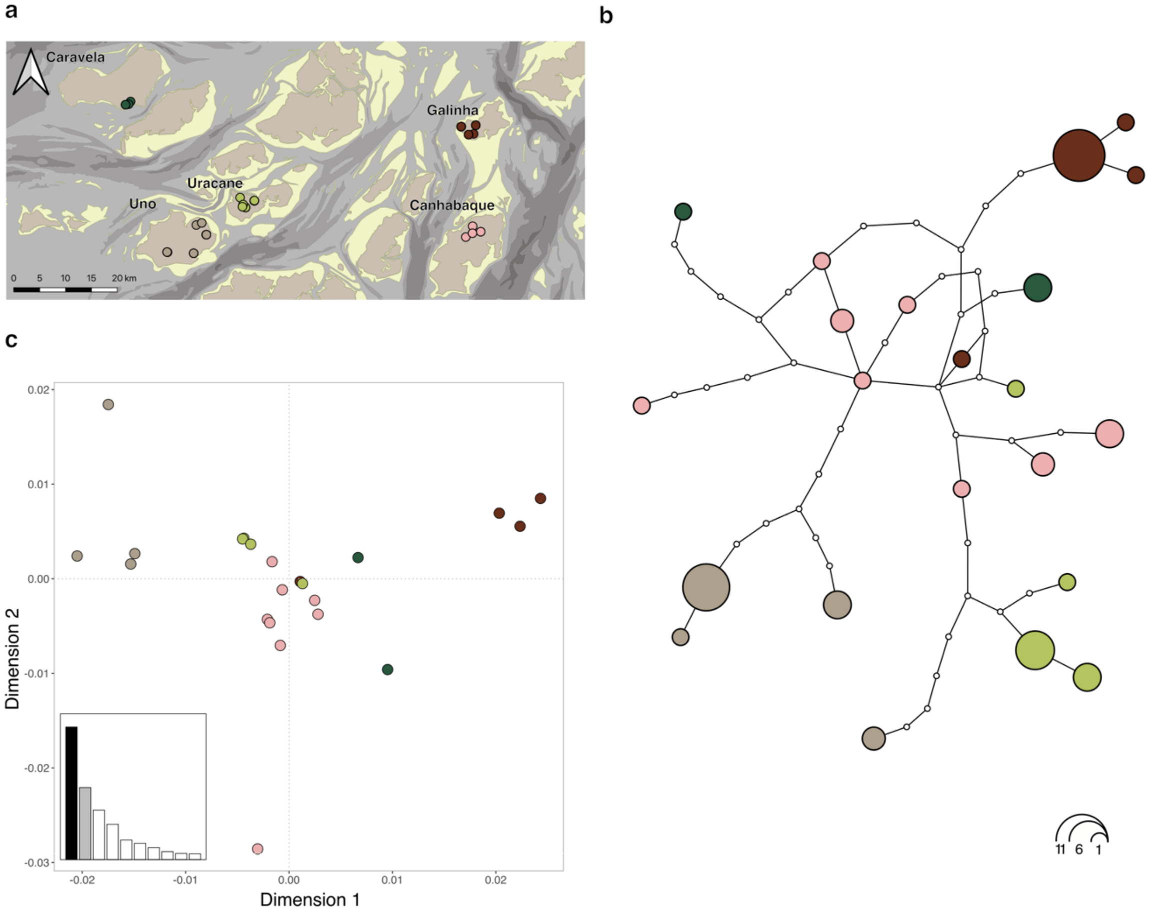


Figure 3.2. Patterns of mitochondrial diversity of the spot-nosed monkey in the Bijagós Archipelago using a 290 bp fragment of the HVRI. **a** Location of sampled individuals and landscape features of the archipelago. Sandbanks are represented in yellow. The bathymetry is represented as a grey-scale gradient towards increasing water depth. **b** TCS haplotype network. **c** Individual-based multidimensional scaling analysis. The eigenvalues for each MDS dimension are plotted in the bottom right corner. Haplotypes and individuals are coloured according to the sampling location.

Discussion

The putative last viable populations of the spot-nosed monkey in Guinea-Bissau can be found at the Bijagós Archipelago (Gippoliti and Dell'Omo 2003; Colmonero-Costeira et al., 2019). Not much is known on the local conservation status of these populations, but they are likely of conservation concern. Insular populations typically carry only a portion of the genetic diversity of the mainland source populations and are more susceptible to further genetic erosion due to increased genetic drift (Allendorf et al. 2013; Martin et al. 2023). As such, a baseline assessment of the genetic dynamics (i.e., genetic diversity and genetic differentiation) of these populations is needed for the assessment of its local conservation status. Here, this was achieved using a panel of 11 microsatellite loci and a HVRI fragment of the mtDNA.

Genetic diversity

Contrary to the expectations for insular populations, the spot-nosed monkey of the Bijagós Archipelago does not appear to be depauperated of genetic diversity. Although differences in the employed genetic markers can make direct comparisons genetic diversity between taxa unprecise, spot-nosed monkey genetic diversity was within the range of other primates in mainland Guinea-Bissau [e.g., Guinea baboon: $0.68 \leq Hd \leq 0.91$, $1.04\% \leq \pi \leq 2.10\%$, $0.55 \leq H_E \leq 0.64$ (Ferreira da Silva et al. 2014; Gerini 2018); Western chimpanzee, *Pan troglodytes verus* Schwarz, 1934: $0.90 \leq Hd \leq 0.95$, $3.40\% \leq \pi \leq 3.70\%$, $0.63 \leq H_E \leq 0.75$ (Borges 2017; Gerini 2018); black-and-white colobus: $Hd = 0.16$, $\pi = 0.04\%$, $H_E = 0.42$ (Minhós et al., 2013a); and, red colobus: $Hd = 0.83$, $\pi = 3.80\%$, $H_E = 0.51$ (Minhós et al., 2013a)]. However, in the absence of mainland samples, it cannot be assumed that insularity did not promote a decrease in genetic diversity.

Genetic diversity was heterogenous across the sampled islands suggesting that the colonisation of each individual island may have been characterised by different factors, such as the size of the founding population. The proximity between Canhabaque Island and the mainland, associated with the high genetic diversity of its spot-nosed monkey population, makes it good candidate for the first island being colonised (Costanzi and Steifetten 2019). Additionally, in the ordination analysis, individual genotypes and mitochondrial haplotypes sampled at this island were positioned central to the populations from the remaining islands, a pattern common to source populations (Grossen et al. 2018).

Population structure and gene flow dynamics

Spot-nosed monkey populations were clearly structured by island and contemporary gene flow within the different populations of the archipelago seems low or inexistent. While there was evidence for IBD-driven differentiation, the EEMS analysis clearly refutes the existence of a strict pattern of IBD. Lower estimates of effective migration than the expected were found between closely located islands (Uno and Uracane only distanced by approximately 6 km). Other observed patterns that clearly violated the theoretical expectations for an insular system: i) the clustering of genotypes from Caravela and Canhabaque islands in the PCA and late segregation in STRUCTURE at $K = 5$, and ii) low values of pairwise FST between Uno and Canhabaque, and a corridor of high effective migration between the two islands. These results suggest these two pairs of islands likely have a more recent shared ancestry compared to the remaining islands, despite being located at opposite edges of the archipelago.

Humans have been suggested as the vector for the introduction of mammals in the Bijagós Archipelago (Rebelo and Catry 2011). Two potential time periods can be proposed, 1) when the *Bijagó* ethnic group established on the archipelago and 2) during the Trans-Atlantic trafficking of enslaved people (Hawthorne 2003). A similar Trans-Altantic colonisation history has been observed in other guenon species across several Atlantic archipelagos (van Der Kuyl et al. 1996; Horsburgh et al. 2003; Hazevoet and Masseti 2011; Glenn and Bensen 2013; Almeida et al. 2024). Translocated populations can readily become differentiated from their source populations over the course of a few generations when isolated, including the Bojer's skink, *Gongylomorphus bojerii* Desjardins, 1831 (du Plessis et al. 2018), the bare-nosed wombat, *Vombatus ursinus* Shaw, 1800 (Martin et al. 2019), and European ibex, *Capra ibex* Linnaeus, 1758 (Grossen et al. 2018). Under this alternative hypothesis, the patterns of population differentiation between islands would be related to the human movements in the area rather than distance.

The occurrence of highly divergent mitochondrial haplotypes within islands is at odds with the human-mediated colonisation hypothesis. Considering the significantly lower mutation rate of the mitochondrial d-loop (humans, 2.4 x 10-7 substitutions/site/year; Santos et al. 2005) the existence of divergent haplotypes within each island would not be expected in the short span of 200–900 years. It can be argued, however, that the mitochondrial diversity currently present at the islands are representative of the genetic diversity of a bigger, highly diverse source population(s) whose fixation within each individual island was a random product of genetic drift which acts faster on haplotypic DNA (Allendorf et al. 2013).

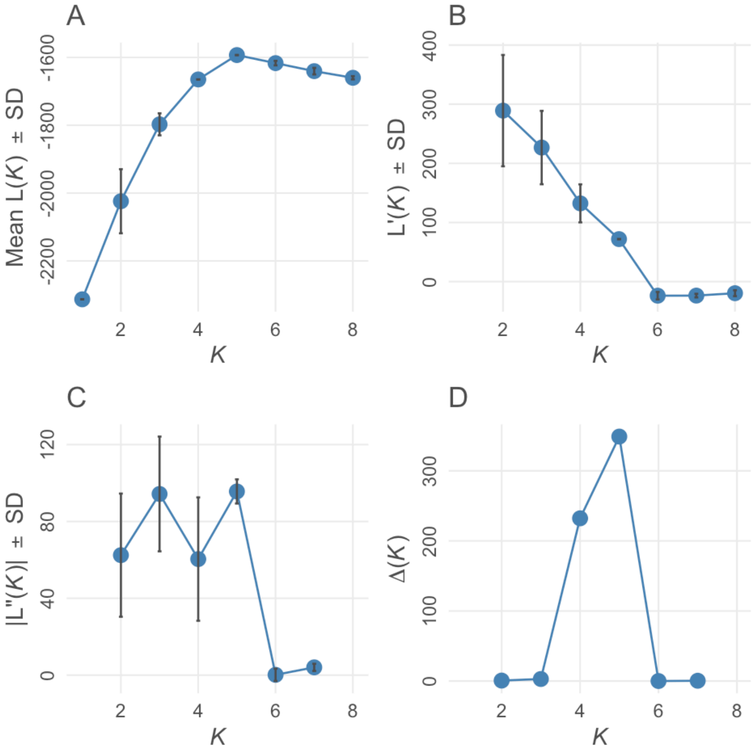
In light of these results, I propose that demographic scenario testing by Approximate Bayesian Computation (ABC) analyses would likely elucidate on the colonisation process of the Bijagós Archipelago by the spot-nosed monkey (e.g., Sharma et al. 2018), namely by giving support to either naturally occurring or human-mediated colonisation hypotheses.

Supplementary Materials

Supplementary Table 3.1 Details of the three Multiplex Polymerase Chain Reactions employed.

Multiplex	**ATemp (°C)**	**AT (s)**	**ET (s)**	**Locus**	**Forward Primer** **Reverse Primer (5' – 3')**	**Repeat Motif**	**Concentration (μM)**
D7s503	57	50	40	D7s503	ATGACTTGGAGTAATGGG AACCTTTAATCAGGATACAGAC	CA	0.30
M1	57	40	60	D2s1326	AGACAGTCAAGAATAACTGCCC CTGTGGCTCAAAAGCTGAAT	TCTA	0.50
				D14s306	AAAGCTACATCCAAATTAGGTAGG TGACAAAGAAACTAAAATGTCCC	GATA	0.13
				D1s548	GAACTCATTGGCAAAAGGAA GCCTCTTTGTTGCAGTGATT	TCTA	0.20
M2	57	50	40	D5s1457	TAGGTTCTGGGCATGTCTGT TGCTTGGCACACTTCAGG	GATA	0.10
				D7s2204	TCATGACAAAACAGAAATTAAGTG AGTAAATGGAATTGCTTGTTACC	GATA	0.40
				D3s1768	GGTTGCTGCCAAAGATTAGA CACTGTGATTTGCTGTTGGA	GATA	0.075
M3	59	90	90	D2s442	AAGGGAAGGAGCATAGCAAC GATTTGGTAGATAGACAGATGTGA	TCTA	0.10
				D11s2002	CATGGCCCTTCTTTTCATAG AATGAGGTCTTACTTTGTTGCC	GATA	0.12
				D12s372	TGGACCACAGGGTATCATCT TCCAATGGAAAGAAATGGAG	GATA	0.05
				FESFPS	GGAAGATGGAGTGGCTGTTA CTCCAGCCTGGCGAAAGAAT	ATTT	0.08

ATemp – annealing temperature; AT – annealing time; ET – extension time

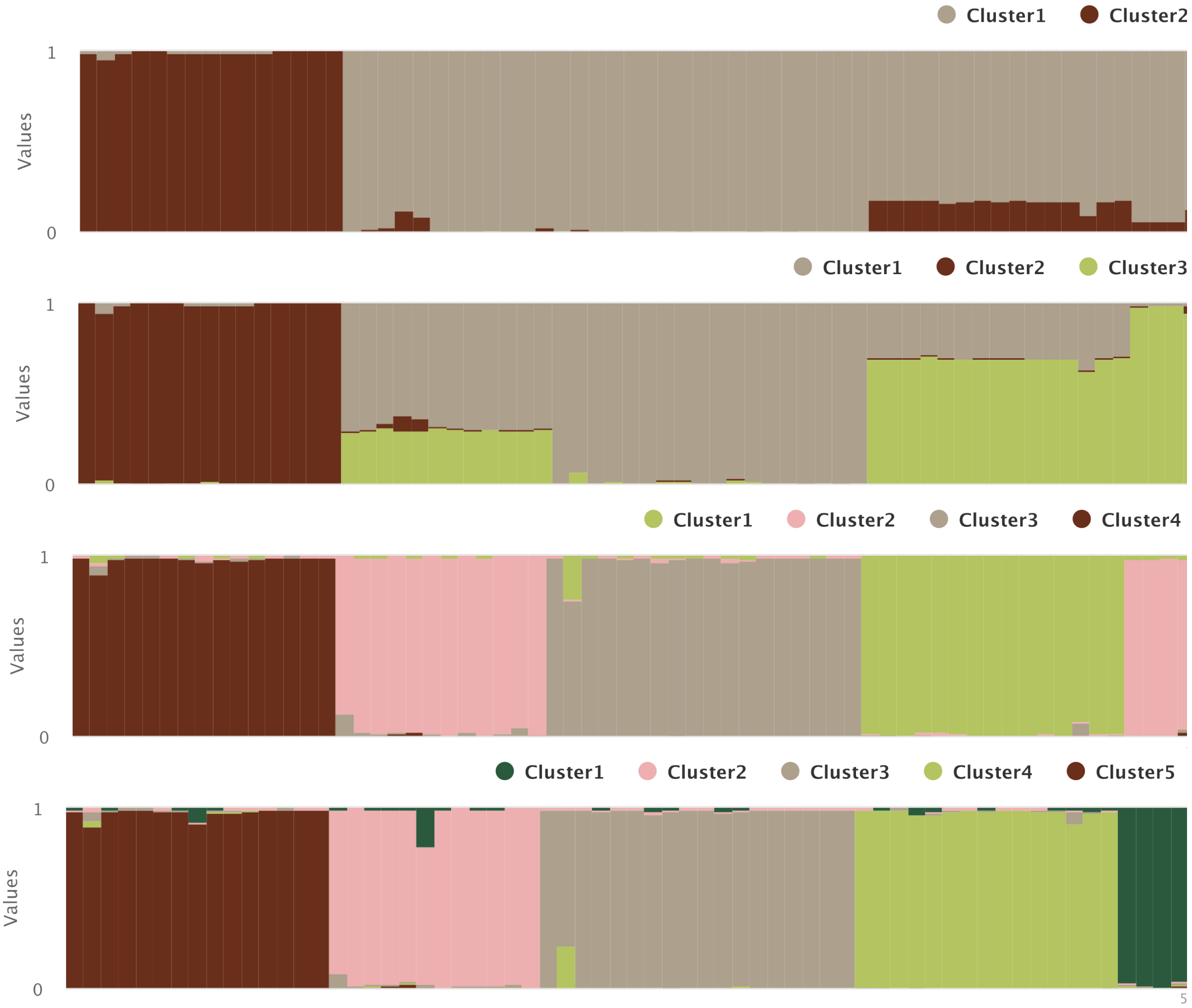


Supplementary Figure 3.1 Diagnostic plots for STRUCTURE best number of genetic clusters (*K*). Based on mean L(*K*) and *ΔK*, the most likely number of *K* is *K* = 5. There is some support for *K* = 4.

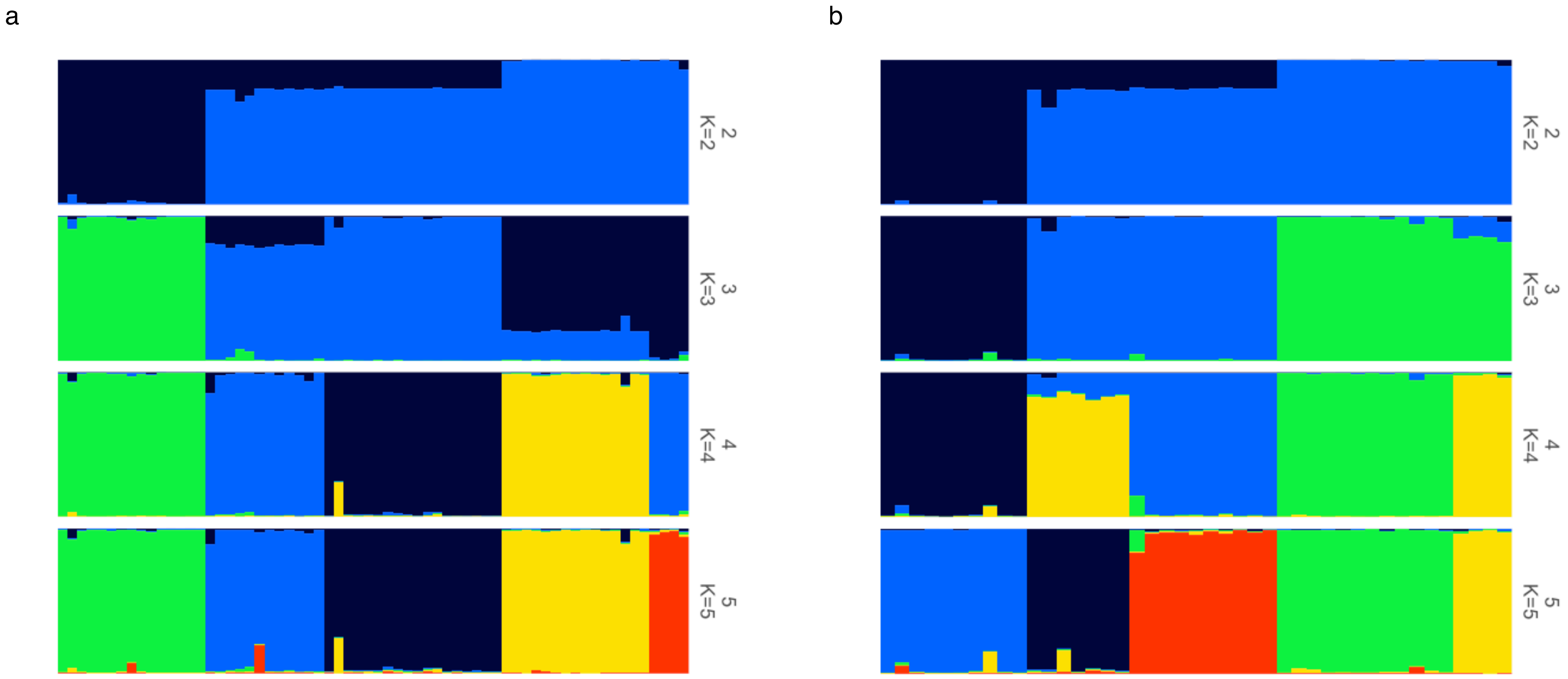
Supplementary Table 3.2 Optimisation of EEMS deme size

Number of demes	**r^2 between demes**	**r^2within demes**
200	0.80	0.58
400	0.79	0.72
800	0.41	0.28

r^2 – coefficient of determination



Supplementary Figure 3.2 STRUCTURE results for increasing numbers of *K*. Bars depict the average individual cluster assignment probabilities across 10 independent runs.



Supplementary Figure 3.3 STRUCTURE results to test for the effect of unbalanced sampling (A) and the inclusion of related individuals (B). Bars depict the average individual cluster assignment probabilities across 10 independent runs. Results suggest STRUCTURE runs were shown to be insensitive to these potential sources of bias.

CHAPTER 4

Colonisation history of the spot-nosed monkey of the Bijagós Archipelago

The spot-nosed monkey (*Ceropithecus petaurista*) is one of three guenon species occurring on the Bijagós Archipelago in Guinea-Bissau (West Africa). This species is thought to have been recently extirpated from the mainland, and the putative last populations are isolated on the archipelago. Not much is known about the colonisation history of these insular primate populations, however, in Chapter 3 I found that populations across the archipelago did not differentiate according to a strict stepwise colonisation model which is unexpected for natural sequential colonisations of insular systems. Human-facilitated translocations have been suggested as an alternative hypothesis and two relevant timings have been proposed: the arrival of the first human (*Bijagó*) communities to the archipelago; or during the Trans-Atlantic enslaved trafficking. Using a total of 60 unique genotypes for 11 microsatellite loci, I aimed to characterise the colonisation history of four populations of spot-nosed monkey. I used Approximate Bayesian Computation (ABC) to compare three competing hypotheses: (i) gradual isolation; (ii) natural colonisation; and (iii) human-mediated colonisation. Additionally, I estimated the contemporary effective population size (N_e) to inform the local conservation status of the species. Under the employed ABC framework, I obtained high support for the occurrence of human-mediated founding events across all sampled populations, suggesting a likely influence of the local *Bijagó* communities on the colonisation history of the primate. The estimated contemporary N_e of these populations were below the recommended for long-term maintenance of genetic diversity (< 500),

suggesting that the current anthropogenic pressures could hamper the long-term survival of these relatively small and isolated primate populations.

Introduction

The Bijagós Archipelago is small archipelago of the coast of Guinea-Bissau (West Africa). The archipelago is of continental origin and was once fully connected to the mainland (Alves 2007). It became gradually isolated as sea-level rose after the LGM (Last Glacial Maximum), particularly during the late Flandrian transgression (ca. 12,000 years ago (YA); (Alves 2007). Despite being recognised as a biodiversity hotspot withing Guinea-Bissau (Rebelo and Catry 2011), not much is known about its terrestrial faunistic communities.

The spot-nosed monkey (*Cercopithecus petaurista* Scheber, 1774) is one of the three guenon species occurring on the Bijagós Archipelago,The species occurs on some of the largest and inhabited islands of the Bijagós Archipelago, such as Bubaque, Canhabaque, Caravela, Galinhas, Uno and Uracane (Campredon et al. 2001; Gippoliti and Dell’Omo 2003; Colmonero-Costeira et al. 2019). Despite being classified as Near Threatened by the International Union for Conservation of Nature (Matsuda Goodwin et al. 2020), it is arguably one of the most threatened primate species in the country. At the Bijagós Archipelago, the species is thought to be increasingly threatened by commercial bushmeat hunting and degradation of natural habitats (Chapter 2, Karibuhoye, 2004).

The colonisation history of the Bijagós Archipelago by the spot-nosed monkey remains unstudied but it is crucial to understand current levels of genetic diversity and other genetic parameters of conservation interest such as effective population size (N_e). Potential hypotheses for the origins of the primate include naturally occurring phenomenon, vicariance hypothesis (i), range expansion (ii), or human-mediated colonisation hypothesis (iii) (Figure 4.1). The vicariance hypothesis (i) was formulated based on the geological nature of the archipelago and assumes a gradual isolation of existing populations during the flooding of continental platform where the archipelago is inserted. Unlike other archipelagos on the African Atlantic coast, the Bijagós Archipelago is of continental origin and was once fully connected to the mainland (Alves 2007). The archipelago became gradually isolated as sea-level rose after the LGM (Last Glacial Maximum), particularly during the late Flandrian transgression (ca. 12,000 years ago (YA); (Alves 2007). This hypothesis implies a gradual N_e reduction as populations became increasingly disconnected from mainland populations. Alternatively, the range expansion hypothesis (ii) assumes that coastal primate populations have colonised the islands after the isolation of the archipelago.

Archipelago-wide population structure and gene flow dynamics of the spot-nosed monkey of the Bijagós Archipelago suggested the absence of genetic differentiation strictly promoted by isolation-by-distance (IBD; Chapter 3). An overlap between IBD is expected in naturally occurring colonisations where islands are colonised in a stepwise manner from the mainland towards the outer edge of the archipelagos (Orsini et al. 2013). In the absence of the expected pattern, the human-mediated hypothesis was proposed. This hypothesis assumes that the colonisation timing of the spot-nosed monkey is related to the human movements in the area.

To understand putative scenarios of human-mediated colonisation one must look into the history of the local ethnic group, the *Bijagó.* The *Bijagó* have shared ancestry with populations from the surrounding countries of Guinea-Bissau (Senegal, Gambia and Mali; Rosa et al. 2007; Spínola et al. 2008). The colonisation of the islands by the ethnic group is not documented. However, their arrival at the archipelago is likely a consequence of the expansion of the Mali Empire across West Africa (Rodney 1970). This expansion, initiated around the 11th century, likely induced the displacement of coastal populations from mainland Guinea-Bissau and neighbouring countries into the archipelago (Rodney 1970). Particularly, the *Bijagó* are thought to have been displaced from Quínara region in mainland Guinea-Bissau due to territorial disputes with the *Beafada* ethnic group, after the latter lost territory to the expanding Mali Empire (Rodney 1970; Madeira 2009; Lundy 2015).

Despite the lack of historical documentation, oral traditions passed on by *Bijagó* elders suggest that mammals with subsistence or socio-cultural importance, such as domestic and bushmeat species (e.g., primates, gazelles and duikers) may have arrived at the archipelago with the first *Bijagó* colonies. In their own words: *“Our* *elders and religious authorities say that the animals came from the south* [mainland]*. They brought them here. For example, the gazelles, whoever brought them, brought them from the south. They* [the founding *Bijagó*] *brought them and released them so they could reproduce. So that there would be animals to hunt and feed their children."* – Interview CEND102022, son of local chieftain (Colmonero-Costeira 2022).

Alternatively, the primates may have arrived at the archipelago as a consequence of the Trans-Atlantic enslaved people-trade, which was at its highest in West Africa during the 16th–17th Centuries (Hawthorne 2003; Rawley and Behrendt 2005). During contact periods with European countries, the *Bijagó* established economic treaties based mainly on the trade of enslaved people (Hawthorne 2003). This activity was recorded as particularly lucrative due to their raiding proficiency on the settlements in coastal mainland Guinea-Bissau, the high demand for enslaved people and the existence of dedicated ports on many of the islands (Hawthorne 2003). Transatlantic enslaved-trading ships passing through the archipelago may have transported live primates together with a variety of luxury goods bounded for the American and European markets (Rawley and Behrendt 2005). European societies considered guenons, such as *Chlorocebus* spp. (Veracini 2017) or *Cercopithecus* spp. (Horsburgh et al. 2003) as valuable exotic pets (Veracini 2017). The trans-Atlantic ships transporting live animals docking in the local harbours may have provided opportunities for the introduction of some species to the archipelago, including primates. The recorded geographic origin of goods traded in important enslaved trafficking markets in Guinea-Bissau (e.g., Bissau and Guinala; Madeira 2009; Campos 2012) were the regions surrounding the Geba Channel, namely Quínara region (Campos 2007). Indeed, recent research on the mitochondrial phylogenetic structure of Campbell's monkey (*Cercopithecus campbelli* Waterhouse, 1838), and the green monkey in southern Guinea-Bissau, have revealed a close relationship between the insular populations of these primates at the Bijagós Archipelago and the mainland populations from Quinara, suggesting that this region may be the source of the insular primate populations (Colmonero-Costeira et al. 2024). A similar Trans-Atlantic colonisation history has been suggested for other guenon species, namely the mona monkey (*Cercopithecus mona* Schreber, 1774) on the islands of Grenada and São Tomé and Príncipe (Horsburgh et al. 2003; Glenn and Bensen 2013); and the green monkeys (*Chlorocebus* sp. Gray, 1870), in the Caribbean and Cape Verde (Van Der Kuyl et al. 1996; Hazevoet and Masseti 2011; Almeida et al. 2024).

In the absence of historical and fossil records for the Bijagós Archipelago and its terrestrial mammalian biodiversity, population genetic tools could provide clues to resolve the competing hypotheses for the colonisation dynamics of the spot-nosed monkey (Moodley et al. 2018; Sharma et al. 2018). In this chapter I used the genetic dataset from chapter 3 to characterise the colonisation history of the spot-nosed monkey of the Bijagós Archipelago and estimating genetic parameters of conservation importance (e.g., current N_e). Specifically, my aims were:

1. Evaluate changes in N_e throughout time.
2. Reconstruct the most appropriate colonisation scenario of the insular populations using Approximate Bayesian Computation (ABC) based on the three competing hypotheses.
3. Elucidate the long-term conservation status of these insular populations based on estimates of current N_e.

This chapter has contributions from Filipa Borges, PhD student at Centre for Research in Anthropology (CRIA – NOVA FCSH), Universidade Nova de Lisboa, Lisbon, Portugal (detailed below).

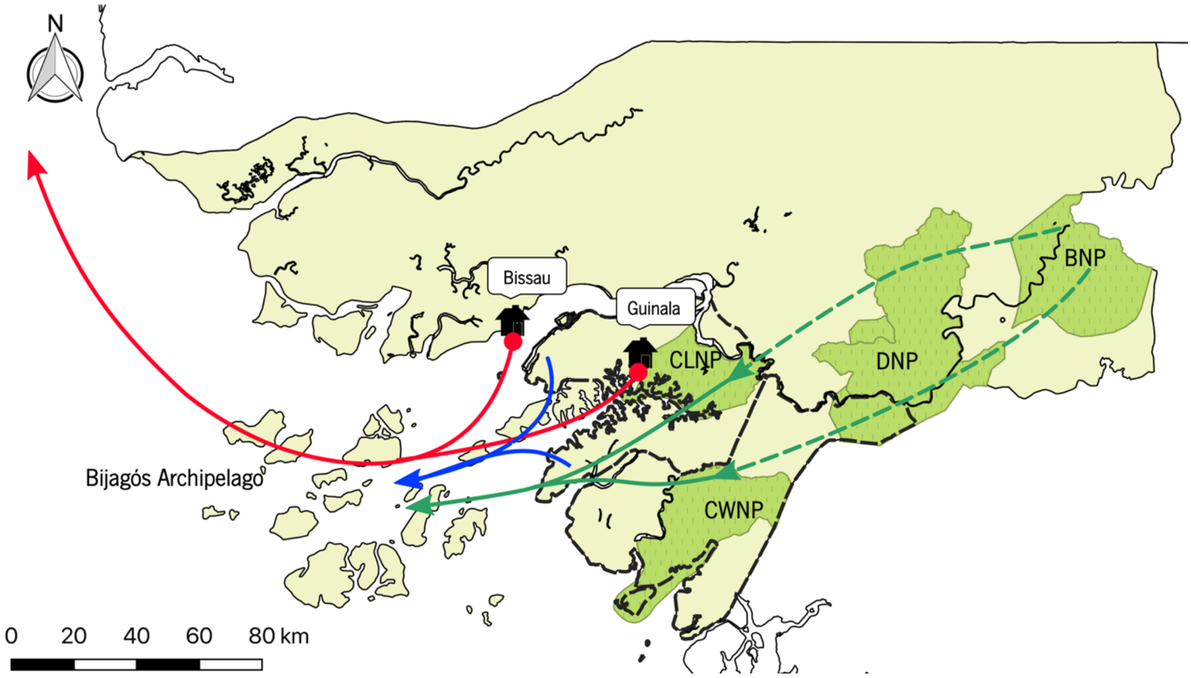


Figure 4.1 Proposed hypotheses for the colonisation of the Bijagós Archipelago (Guinea-Bissau, West Africa) by the spot-nosed monkey. All protected areas in Southern mainland GB (CLNP – Cufada Lagoons Natural Park, CWNP – Cantanhez Woodlands National Park, DNP – Dulombi National Park and BNP – Boe National Park) are represented. Green arrows represent the range expansion hypothesis (ii) from coastal Guinea-Bissau (Quinara and Tombali regions (dashed areas). Dashed green arrows represent possible historical dispersal between inner regions of Guinea-Bissau (DNP and BNP) towards the coast. Blue and red arrows represent the hypothesis (iii) of colonisation mediated by the displacement of the *Bijagós* ethnic group from the Quinara region (dashed area comprising CLNP) or mediated by Trans-Atlantic enslaved trafficking, respectively. The house marker on the map represents one of the most prominent slave-trading markets in the southern coast of Guinea-Bissau during Portuguese occupancy (16 – 19th centuries). Please note that the direction of the arrows is a hypothetical graphical representation as the colonisation routes within the archipelago are currently unknown.

Methods

In this chapter I used the microsatellite dataset analysed in Chapter 3. This dataset contains 60 spot-nosed monkeys genotyped for 11 microsatellite loci (Galinhas, N = 15; Canhabaque, N = 12; Uno, N = 18, Uracane, N = 12). Here, I have excluded the population of Caravela Island due to low sample size (N = 4 unique genotype profiles).

Assessing changes in effective population size (N_e)

To detect past N_e changes in the spot-nosed monkeys from the Bijagós Archipelago, F.B. used MSVAR 1.3 (Storz and Beaumont 2002). This method uses the allelic frequencies to estimate the posterior probability distribution of current population size (N_0), past population size (N_1), and time from the changes (T), under a simple model of exponential population size change based on a Bayesian coalescent MCMC approach. The model allows for a single event of demographic change – the population either remained constant ($N_0 = N_1$), increased at time T ($N_0 > N_1$) or decreased at time T ($N_0 < N_1$). The insular populations of the spot-nosed monkey are highly structured by island (Chapter 3). To take into account the spurious bottleneck effects induced by population structure in demographic reconstruction methods based on the Wright–Fisher model (i.e., assuming panmixia, etc.), such as MSVAR (Chikhi et al. 2010; Salmona et al. 2017), N_e changes were explored for each island individually. We chose to not remove highly related individuals from the dataset as these likely represent a true biological phenomenon (i.e., insular populations are expected to be more related than non-insular populations due to increased inbreeding; Allendorf et al. 2013) and was shown to not influence estimates of population structure based on allelic frequencies under HWE (STRUCTURE results, Chapter 3). To test the influence of the prior on the posterior distributions, F.B. performed five independent runs with different starting points and different sets of priors and hyperpriors for each dataset (Galinha, Canhabaque, Uno, and Uracane; Supplementary Table 4.1). F.B. varied prior distributions such that they would assume (a priori) constant, moderately or severely decreasing, moderately or severely increasing population demographic models. Broad priors and hyperpriors that span the expected N_e values for these populations, and the estimated time of the colonisation of the Bijagós Archipelago were selected. Across the different runs, the means of the lognormal N_0 and N_1 distributions were set between 3.0 and 5.0 (1,000 – 100,000 individuals) and T between 4.0 and 5.0 (10,000 – 100,000 Years Ago (YA); Supplementary Table 4.1). The standard deviation was kept at 1.0 for all prior distributions. The mean log mutation rate (μ) to −3.5, supporting mutation rates of 10^{-4} to 10^{-3} as widely assumed in demographic analyses (Storz and Beaumont 2002) and assumed a generation time of 11 years (Matsuda Goodwin et al. 2020). Each run was performed with 300,000 thinning update steps and 30,000 thinning intervals, that is, 9×10^9 steps. For burn-in, the first 10% of each independent run were discarded to avoid the influence of the starting conditions on the parameter estimations. Convergence was assessed visually and with the Brooks, Gelman, and Rubin convergence diagnostic test (Gelman and Rubin 1992; Brooks and Gelman 1998), using the package BOA v1.1.7 (Smith 2007) in *R* v4.2.2 coupled with RStudio v2023.06.2+561 (*R* CoreTeam 2022; Posit team 2023).

Approximate Bayesian Computation (ABC) analysis

To estimate a more detailed reconstruction of the demographic history of the spot-nosed monkey, I tested different demographic scenarios using an approximate Bayesian computation framework as implemented in ABCTOOLBOX v1.1 (Wegmann et al. 2010). This method compares simulated data under several alternative demographic scenarios to the real data using summary statistics. One of the advantages of ABC is that it can often be used to compare more complex scenarios other than the simple model of exponential population size change employed in MSVAR. The different scenarios can be compared, and demographic parameters of interest such as ancient N_e (N_e ANC), current N_e (N_e CUR) and the time of demographic event (T) can be estimated from the best supported scenarios (Wegmann et al. 2010). Using the coalescent simulation program *fastsimcoal28* (Excoffier et al. 2021), I generated diploid microsatellite loci data matching the empiric dataset (i.e., 11 microsatellite loci and maintaining the sample sizes for the different islands).

I tested a number of hypothesised demographic histories for the spot-nosed monkey: i) vicarance, ii) range expansion or iii) human-mediated colonisation following a hierarchical framework of increasing scenario complexity. For the first hierarchical level, I was interested in establishing the most supported overall demographic trajectory of the populations (stable, decreasing or expanding populations), rather than testing the competing colonisation hypotheses. As a starting point, I tested three simple scenarios which differed only by the type of demographic event they simulated (Figure 4.2). The first scenario (STN_NULL) assumed constant population size and acted as the null model for the first hierarchical level. The second (EXP) and third (BOT) scenarios assumed a demographic expansion and a decline, respectively. These scenarios shared similarities with the MSVAR models as they allowed for a single population size change. I used the same broad prior ranges across the initial three scenarios (see below, Supplementary Table 4.2). This allowed to minimise the influence of the choice of prior distributions on the estimated parameters.

For the second hierarchical level, I tested the competing colonisation hypotheses (Figure 4.2). The fourth scenario (ISL-NULL) can be considered as the null colonisation scenario as it modelled an exponentially decreasing population size. This scenario represented the vicariance hypothesis (i), in which existing populations on continental platform where the archipelago is inserted became gradually isolated by raising sea levels. The fifth (CLN_ACT) and sixth (CLN_ RCT) scenarios modelled an ancient and recent founding event, respectively, that were characterised by exponential population growth after the initial colonisation event by a small founding population. These scenarios aimed to represent the colonisation by range expansion (ii) or human-mediated colonisation (iii). For the third hierarchical level, I tested a combination of the colonisation scenarios from the previous hierarchical level (Figure 4.2). The seventh scenario (ISL_CLN) combined the exponentially decreasing population size of scenario ISL-NULL, followed by a recent founding event as modelled in scenario CLN_RCT. The last scenario (2CLN) combined both colonisation scenarios (CLN_ACT and CLN_ RCT) which corresponded to a scenario of an initial ancient natural colonisation of the archipelago, followed by human-mediated founding events within the archipelago.

The scenarios of this last hierarchical level were only tested if multiple scenarios of the previous hierarchical level (hierarchical level 2) were supported. The full set of scenarios was tested for each of the islands individually and a total of 300,000 simulations were generated for each scenario.

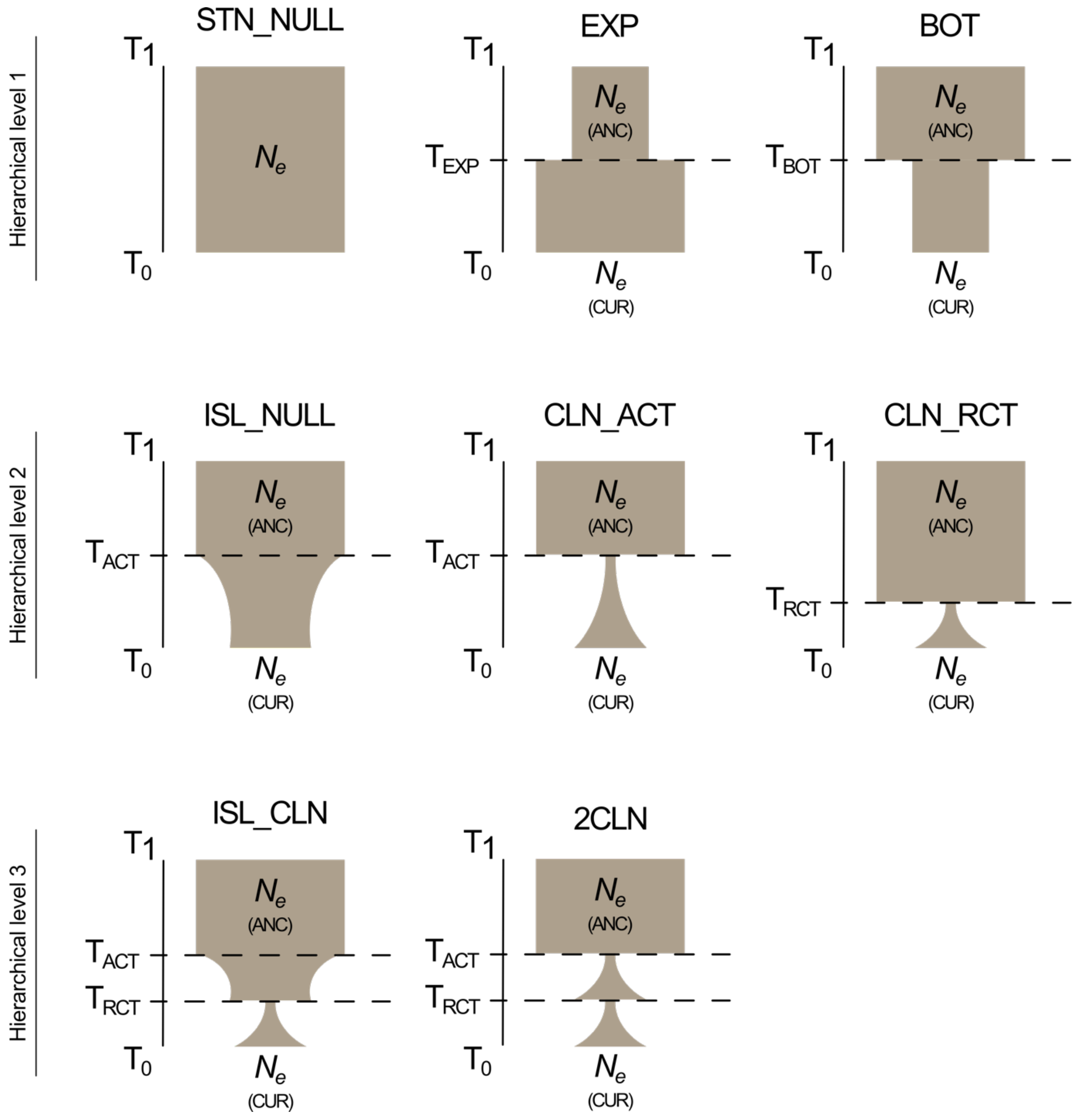


Figure 4.2. Schematic representation of the main demographic scenarios compared within the ABC framework. Models of the first hierarchical level (top) test the overall demographic trajectory of the populations (stable, decreasing or expanding populations). On the second hierarchical level (middle) I tested the main colonisation hypotheses, range expansion hypothesis (CLN_ACT), human-mediated colonisation hypothesis (CLN_RCT) and the vicariance hypothesis (ISL_NULL). The third hierarchical level (bottom) was used to test for

more complex scenarios resulting from a combination of the scenarios of the previous level. For details on the prior settings of each model see Table 4.1.

I employed historically and biologically informed priors in the tested scenarios (Supplementary Table 4.2). For the timing of the ancient demographic event (*T* ACT) employed in scenarios ISL_NULL, CLN_ACT, ISL_CLN and 2CLN, a prior window that reflected the isolation of the Bijagós Archipelago from the mainland was chosen. The current geological layout of the archipelago is thought to have been formed during the Holocene, following the Flandrian transgression (ca. 12,000 YA; Alves 2007). To accommodate the uncertainty on the exact timing of the formation of the archipelago, the *T* ACT prior was broadened to include the full period of sea-level rise after the Last Glaciation Maximum (LGM; ca. 20,000 YA), up until the establishment of the current sea level (ca. 6,000 YA). Assuming a generation time of 11 years, *T* ACT was set to 545 – 1,820 generations in the past. For the timing of human-mediated colonisation events (*T* RCT) in scenarios CLN_RCT, ISL_CLN and 2CLN, I chose a prior window that encompassed the arrival of the first humans to the archipelago and the peak Trans-Atlantic enslaved trafficking in West Africa (ca. 500 – 400 YA; Rawley and Behrendt 2005). Scant information is available on the initial arrival of the *Bijagós* ethnic group to the Bijagós Archipelago, however, it has been suggested to have occurred during the expansion of the Mali Empire in West Africa (ca. 1,000 YA; Rodney 1970). The *T* RCT prior was broadened to include the expansion of preceding West African empires (e.g., the Ghana Empire, ca. 1, 200 YA) up until the end of the Trans-Atlantic trafficking of enslaved people (ca. 100 YA; Rawley and Behrendt 2005). Hence, *T* RCT was set to 10 – 110 generations ago.

I set a wide prior for the ancestral population size (N_e ANC) between 10,000 and 300,000 (haploid log uniform 4.30 – 5.78), which encompassed the most recent estimation of the species historical N_e (≈ 180,000; Kuderna et al. 2023). The N_e ANC prior was kept the same across the different islands and scenarios. I chose different N_e CUR priors between islands as these were based on the minimum and maximum number of individuals potentially found within each island. This was estimated based on the lowest and highest spot-nosed density reported across the species range ($Dp_{min} \approx 9.6$ individuals/km^2, Karibuhoye 2004; and $Dp_{max} \approx 59$ individuals/km^2; Oates et al. 1990), and the area of each island (A_{island}). For simplicity, I assumed that the whole island was ecologically suitable for primate groups. The N_e of spot-nosed populations is likely to be much smaller than the census size (N_c) due to, for example, their social-organisation (1 adult male, multiple adult females). Thus, the minimum and maximum N_c were weighted by the expected N_e/N_c ratios.

$$N_e\ CUR_{min/max} = Dp_{min/max} \times A_{island} \times\ N_e/N_c$$

N_e/N_c ratios of 0.10 and 0.50 were assumed when estimating the critical values for the N_e CUR$_{min}$ and N_e CUR$_{max}$ priors, respectively). This resulted in relatively broad priors for all populations – N_e CUR priors ranged from 35 to 3,570 (haploid log uniform 1.89 – 3.85; Supplementary Table 4.3).

For the scenarios CLN_ACT, CLN_RCT, ISL_CLN and 2CLN, which simulated founding events, I defined a narrow prior for the N_e of the founding population (N_e FND) between 2 and 100 (haploid log uniform 0.60 – 2.00). For scenario ISL_CLN, N_e following the first historical event (T ACT) decreased exponentially before the second historical event (T RCT). The prior for N_e at T RCT (N_e RCT) was the same as N_e CUR. For scenario 2CLN, N_e following the first founding event (T ACT) increased exponentially before the second historical event (T RCT). The prior for N_e RCT was also equal to the N_e CUR prior range. Details of prior ranges of the different scenarios across the four spot-nosed population can be found in the Supplementary Table 4.2.

For all simulations, a generalised stepwise microsatellite mutation model, with a uniform mutation rate prior between 10^{-4} and 10^{-3} (similar range as the MSVAR runs) and a geometric parameter equal to 0.05 (i.e., 5 % of mutations will change the allele size by more than one step) was assumed.

Model selection between scenarios for all hierarchical levels and parameter estimation procedures started with an initial filtering step of the simulations. Specifically, 1 % of the total simulations closest to the observed summary statistics were retained. I estimated the model fit and compared competing scenarios within each hierarchical level using two complementary methods. Firstly, I estimated the marginal densities of the models and the retained simulations using ABC-GLM and calculated the posterior probability as the fraction of retained simulations with a marginal density lower than the model. Low posterior probability values indicated that most retained simulations have higher marginal densities, suggesting an inefficiency of the model to produce the observed summary statistics (see below). Additionally, I compared pairs of competing scenarios using the Bayes Factor (BF). Finally, the most supported scenarios within each hierarchical level were re-ran for a total of 1,000,000 simulations to increase the accuracy of the estimated model parameters.

I summarised the simulated and observed datasets using a set of summary statistics calculated using ARLSUMSTAT v3.5.2 (Excoffier and Lischer 2010). The aim was to choose a sufficient number of statistics that effectively summarises the data, while allowing for an effective comparison between scenarios and the estimation of the demographic parameters of interest (Wegmann et al. 2009). Here, I proposed a simple and reproducible selection procedure that aimed to decrease the subjectivity associated with the choice of summary statistics which considered the following theoretical principles: i) each summary statistic contributes a different amount of information to the various model parameters (Wegmann et al. 2009); and, ii) the variability in BF and posterior probabilities of the models under comparison reflects the ability of a set of summary statistics to distinguish between the different models (Wegmann et al. 2009). Here, I estimated the marginal densities and ABC-GLM posterior probability values for all the competing scenarios within each hierarchical level using all the possible combinations of the summary statistics.

The initial set of summary statistics included the mean and standard deviation (SD) of the number of alleles (k), expected heterozygosity (H_E) and the allelic range (R) across loci. The inbreeding coefficient (Fis) was also included for a total of seven initial summary statistics. From the initial seven summary statistics I produced a total of 28 different combinations of summary statistics (Supplementary Table 4.4). In general, the standard deviations (SDs) of summary statistics are expected to be more sensitive than the mean values to variations between individual loci or genotyping artefacts in the original dataset. Therefore, I either removed the means and SDs of the calculated statistics or only the SDs of the statistics. I did not remove correlated summary statistics as the inclusion of correlated statistics is not expected to change the predictive power of the ABC-GLM model (i.e., posterior distributions of parameters, marginal densities and posterior probabilities) after dimensionality is addressed. For each hierarchical level (*x*) the relative model selection power (MSP) of each combination of summary statistics (*s*) was estimated based the average rank of the variance of all computable log transformed BF based on ABC-GLM marginal densities ($\sigma^2_{BF_{ix}}$) and posterior probabilities ($\sigma^2_{P_{ix}}$) between scenarios. MSP values were penalised if the ranks of $\sigma^2_{BF_{ix}}$and $\sigma^2_{p_{ix}}$ differed significantly. This penalisation increased linearly with the difference between the ranks, reflecting inconsistency between them. I assumed a penalising factor (*w*) of 0.10. Finally, MSP values were normalised by the total number of combinations of summary statistics (*n*):

$$MSP_{i\,x} = 1 - \frac{average\ rank - penalty}{n}$$

In detail:

$$MSP_{ix} = 1 - \frac{\frac{rank\left(\sigma^2_{\log\,(BF_{ix}+1)}\right) + rank\left(\sigma^2_{p_{sx}}\right)}{2} - w\left(\left|rank\left(\sigma^2_{\log\,(BF_{ix}+1)}\right) - rank\left(\sigma^2_{p_{sx}}\right)\right|\right)}{n}$$

Results

Changes in effective population size (N_e)

Overall, the MSVAR analysis based on allelic frequencies showed a signal consistent with N_e decline for all the spot-nosed monkey populations (Figure 4.3). The median value of N_0/N_1 ratio across the different populations varied between 0.017 and 0.161, corresponding to a ~59 to 6 fold decrease in N_e (Figure 4.3 A). However, the support for the demographic decline differed between populations.

Particularly at Canhabaque and Uracane islands, estimates of N_0 and N_1 showed a higher overlap suggesting a less evident N_e decrease or even a stationary population. Posterior distributions of time since the demographic change, *T*, of the different populations varied between ~35,000 – 2,680 YA (median *T*, Supplementary Table 4.5-4.8).

Additionally, MSVAR-like scenarios tested in the ABC framework also found strong support for a reduction in population size for all populations (BOT, $P \geq 0.71$; BOT vs. STN_NULL, BF ≥ $2.33\text{x}10^{148}$; Figure 2B). The BOT model consistently produced posterior estimates of current N_e (N_e CUR) two orders of magnitude smaller than those of past *Ne* (N_e ANC; Figure 4.3 B). The EXP model was not supported in any of the populations ($P = 0$; not shown).

ABC modelling of complex demographic scenarios

To disentangle the colonisation history of the Bijagós Archipelago by the spot-nosed monkey, I adopted an ABC framework to compare the main colonisation hypotheses (hierarchical level 2): i) vicariance hypothesis (ISL_NULL) characterised by gradually decreasing N_e; ii) range expansion hypothesis (CLN_ANC) characterised by a founding event after the isolation of the archipelago from mainland; and, iii) human-mediated colonisation (CLN_RCT) characterised by a recent founding event.

The highest posterior probabilities were obtained for the model emulating a founding event after the estimated time of arrival of humans to the Bijagós Archipelago (CLN_RCT, $P \geq 0.77$ across populations; Figure 4.4). Regardless of the population, the support of the CLN_RCT model against the vicariance model (ISL_NULL) was always higher but only significantly higher for Uracane Island (CLN_RCT $P = 0.77$, ISL_NULL $P = 0.43$; CLN_RCT vs. ISL_NULL BF = 3.65). As such, I tested a more complex demographic model combining both ISL_NULL and CLN_RCT models (ISL_CLN; Figure 1). Albeit not significant, the ISL_CLN model was estimated to have higher support than the gradual isolation model, but lower support than the model of a recent, human-mediated, founding event ($P > 0.90$, $BF < 3$; not shown).

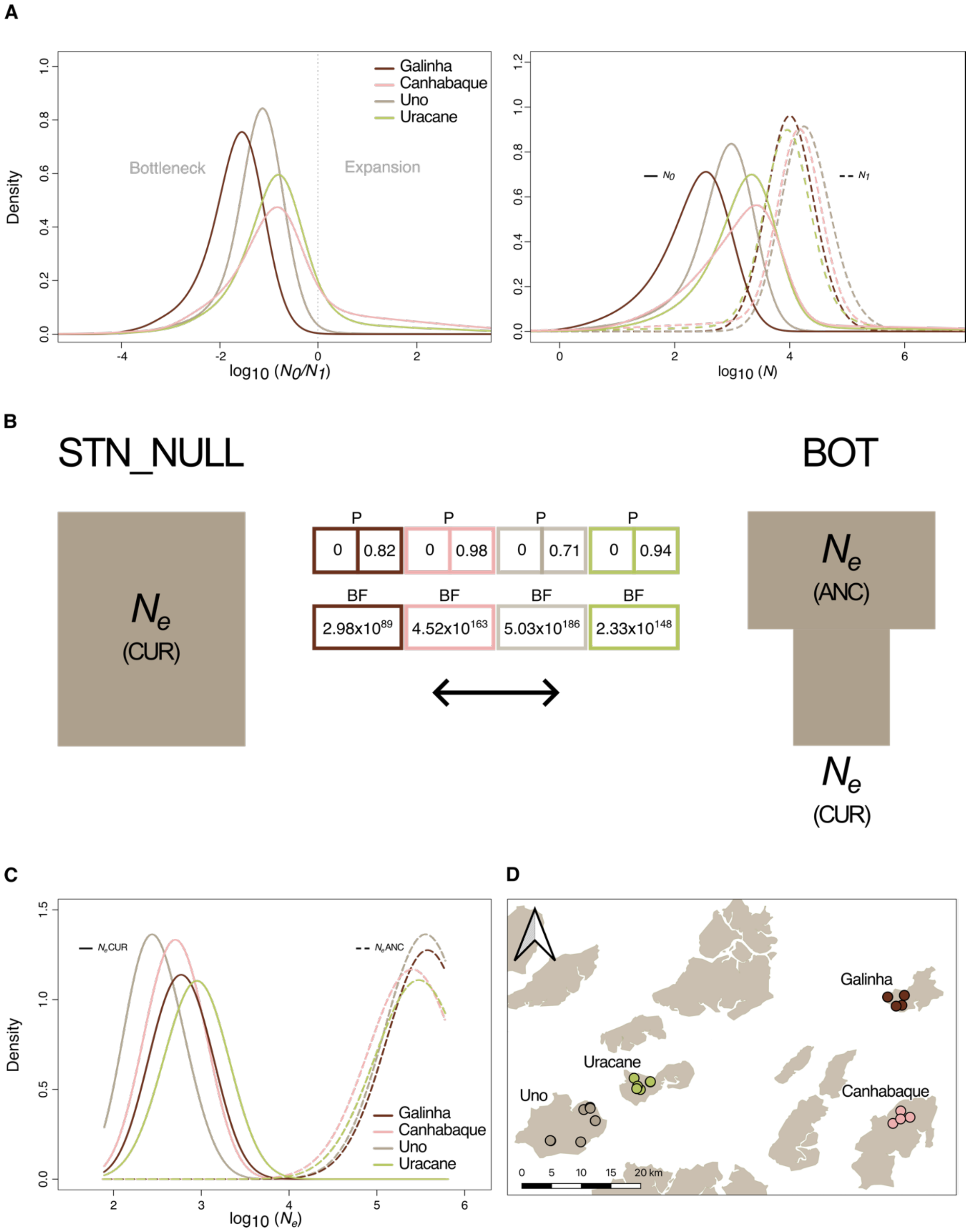


Figure 4.3 Demographic trend of the insular populations of the spot-nosed monkey. A) MSVAR analysis based on allelic frequencies, (left) the $\log_{10}$ ratios for current and past population size (N_0/N_1) where a value equal to zero (vertical dotted line) corresponds to a stationary population; and (right) the posterior distributions of population sizes (N_0 solid lines, N_1 dashed lines). Note that for illustrative purposes, only a single run per population is shown (population level results are represented in Supplementary Table 4.5-4.8). B) ABC

model comparisons for MSVAR-like models (hierarchical level 1). Note that model comparison based on ABC-GLM assumed different combinations of summary statistics for each population: Galinha, combination 13; Canhabaque, combination 25; Uno, combination 1; Uracane, combination 25. Model identifiers correspond to those used in Figure 4.1. Boxes between the schematic representation of the demographic models show the models' posterior probabilities (P) and Bayes Factor (BF) of the comparison. Only results for STN_NULL and BOT are shown as the EXP model was not supported in any of the populations (P = 0; not shown). C) Posterior distributions of population size parameters (current N_e, N_e CUR; past N_e, N_e ANC) based on the BOT model. D) Locations of the sampled individuals. Note that population size numbers are in haploid number of individuals. All posterior distributions (A and C) and boxes (B) are coloured by population.

The CLN_ANC model was characterized by extremely low marginal densities and posterior probabilities, clearly rejecting the hypothesis of ancient colonisation for all populations ($P \leq 0.01$; CLN_ANC vs. ISL_NULL BF << 0; CLN_RCT vs. CLN_ANC BF >> 3; Figure 4.4). Consequently, none of the populations were tested for two consecutive founding events.

ABC parameter estimation

While these results suggest that humans are likely one of the most important actors of the colonisation history of the archipelago, both ISL_NULL and CLN_RCT models were kept when estimating parameters for the Galinha, Canhabaque and Uno populations (Table 4.1; Supplementary Figure 4.1-4.6). For Uracane Island, I only retained the CLN_RCT model (Table 4.1; Supplementary Figure 4.7). It was inferred that the spot-nosed monkey populations have been founded by a small number of individuals (N_e RCT ~14 – 20) from a large stationary or potentially gradually declining source population of ~70,270 – 125,800 effective individuals (N_e ANC). Populations have then likely been gradually expanding to its current size of ~240 – 470, which remains more than two orders of magnitude smaller than the source population size (N_e CUR). As for the timing of the demographic events, I estimated a founding event overlapping with human presence at the Bijagós Archipelago approximately 480 – 690 YA (T RCT, CLN_RCT model; Table 4.1), and a putative reduction of the past N_e starting during the isolation of the archipelago from mainland Guinea-Bissau approximately 9,815 – 9,940 YA (T ISL, ISL_NULL model; Table 4.1). Estimates of T by model ISL_NULL were skewed towards lower values of the prior distribution, suggesting increased parameter uncertainty compared to the CLN_RCT model (Supplementary Figure 4.1-4.7).

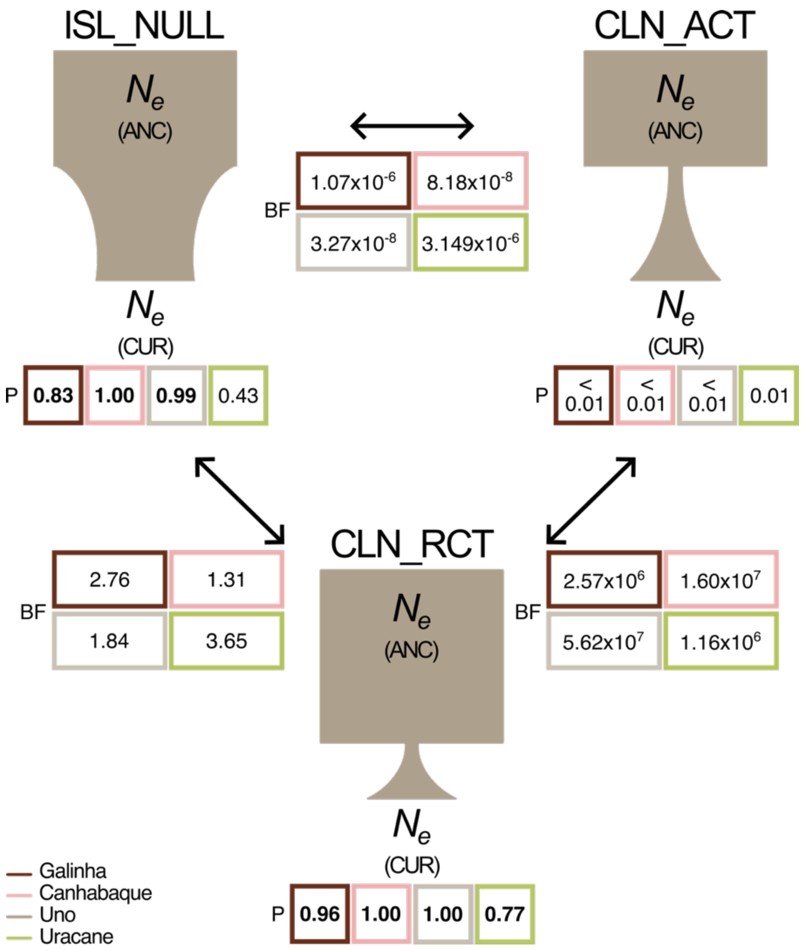


Figure 4.4. ABC model comparisons for colonisation models (hierarchical level 2) across populations of the spot-nosed monkey. Model identifiers correspond to those used in Figure 4.1. Boxes below the schematic representation of the demographic models show the models' posterior probabilities (P); values in bold represent the best ABC models for each population. Boxes in between arrows show the Bayes Factor of the comparison. All boxes are coloured by population. Note that model comparison based on ABC-GLM assumed different combinations of summary statistics for each population: Galinha, combination 14; Canhabaque, combination 26; Uno, combination 6; Uracane, combination 23.

Discussion

Insular populations are often of conservation concern as they are typically more susceptible to loss of genetic diversity due to demographic processes associated with colonisation of the insular systems, aggravated by the disruption of gene flow with the source populations (Allendorf et al. 2010; Martin et al. 2023).

Table 4.1 Posterior distributions of estimated parameters of the best ABC colonisation scenarios (hierarchical level 2).

		ISL_NULL			**CLN_RCT**			
		N_e ANC	**N_e CUR**	**T ACT**	**N_e ANC**	**N_e RCT**	**N_e CUR**	**T RCT**
Galinha	**prior[a]**	4.30 5.78	1.89 3.34	545 1,820	4.30 5.78	0.60 2.00	1.89 3.34	10 110
	mode	94,022	240	8,814	70,276	18	275	480
	median	89,546	268	11,652	72,570	13	251	598
	HPD-5	33,082	148	5,995	24,726	4	62	154
	HPD-95	271,831	512	17,482	245,301	46	1,003	1,049
Canhabaque	**prior**	4.30 5.78	2.36 3.85	545 1,820	4.30 5.78	0.60 2.00	2.36 3.85	10 110
	mode	123,663	345	9,941	104,198	20	447	607
	median	112,901	365	12,533	99,517	15	544	640
	HPD-5	49,899	198	6,558	40,629	5	138	192
	HPD-95	301,259	688	18,469	281,313	50	2,110	1,088
Uno	**prior**	4.30 5.78	2.28 3.77	545 1,820	4.30 5.78	0.60 2.00	2.28 3.77	10 110
	mode	125,796	297	9,941	102,430	14	341	635
	median	111,557	295	12,703	973,71	11	450	636
	HPD-5	46,594	159	6,699	38,596	3	109	176
	HPD-95	301,265	543	18,540	281,313	39	1,816	1,082
Uracane	**prior**	–	–	–	4.30 5.78	0.60 2.00	1.94 3.43	10 110
	mode	–	–	–	63,414	18	470	695
	median	–	–	–	67,541	13	337	679
	HPD-5	–	–	–	22,697	4	96	237
	HPD-95	–	–	–	225,174	44	1,322	1,138

[a] Effective population size (N_e) prior ranges are represented in haplotype $\log_{10}$ values; and, time since the demographic event (T) in generations. The estimated N_e parameters were converted from haploid $\log_{10}$ into linear scale of diploid N_e, and T parameters into years ago, assuming a generation time of 11 years. Posterior distributions were obtained based on ABC-GLM using different combinations of summary statistics for each population: Galinha, combination 14; Canhabaque, combination 26; Uno, combination 6; Uracane, combination 23.

The reconstruction of a species' demographic history and current effective population size remains a key aspect of predicting the long-term viability of populations and maintenance of a species' adaptive potential (Moodley et al. 2018; Sharma et al. 2018). Using a previously generated microsatellite dataset (60 individual genotypes across 11 loci, Chapter 3), I explored the demographic history of four populations of the spot-nosed monkey from the Bijagós Archipelago, with particular interest in testing different colonisation hypotheses. Additionally, I aimed at estimating genetic parameters of interest, such as the current N_e to inform future conservation management.

Changes to N_e and colonisation history

A decrease in N_e throughout time was inferred for all the spot-nosed populations under study. Previous studies have shown that bottleneck-like signals can be detected in coalescent-based approaches and ABC frameworks alike as a result of true demographic changes, reduction in the connectivity among sub-populations in a metapopulation dynamics or both (Chikhi et al. 2010; Salmona et al. 2017; Sharma et al. 2018). In the particular case of insular populations, the evident N_e decline likely results from a combination of demographic and population isolation, associated with the colonisation process of the islands.

Unlike mona monkey and the green monkey populations form other Atlantic archipelagos, whose introduction was recorded during the Trans-Atlantic enslaved trafficking, the timing of the founding events pre-dates the establishment of Portuguese colonialism in the region (~late 15th Century, Rawley and Behrendt 2005), suggesting that the primates could have been translocated by the local ethnic group, which arrived to the archipelago before the Europeans. However, the relatively broad T HPD intervals do not allow for a clear distinction of these two relevant human historical events.

The conclusions could be hindered by methodological and non-methodological caveats. Firstly, the ABC framework showed only a moderate ability to distinguish the vicariance (ISL_NULL) and the human-mediated colonisation (CLN_RCT) hypotheses. This can probably be a limitation associated with i) the relatively low resolution of summary statistics derived from few microsatellite loci, ii) the confounding effects of deeper (more ancient) population structure or iii) more complex demographic scenarios not accounted for in the chosen ABC framework (Salmona et al. 2017). Particularly, the gradual N_e decline could be associated with a significant demographic event occurring in the source populations prior to the human-mediated colonisation of the sampled islands. This can include other unsampled source populations that pre-existed in the area during the isolation of the archipelago from mainland (ca. 12,000 – 6,000 YA) and may already be extinct.

While it seems tentative to assume that the spot-nosed monkeys were introduced to the Bijagós Archipelago, akin to the other guenons inhabiting other Atlantic archipelagos, this cannot be concluded based on these results alone. Particularly, in the complete absence of fossil evidence and historical records of primates and other mammals currently found at the islands. Instead, I propose that they should retain their native status and be protected, regardless of the likely involvement of humans in their colonisation history. In fact, since the history of the spot-nosed monkey of the Bijagós Archipelago could be deeply intertwined with the history of the *Bjagó* ethnic group, the species ought to be considered an important part of the region's bio-cultural diversity. This recognition is particularly important as insular guenons are being prosecuted and remain understudied regarding genetic parameters of conservation interests (Guedes et al. 2021).

Conservation implications of N_e estimates

While it is true that some discrepancies between the current N_e estimates were found between the two complementary methods employed here, these are likely associated with the different assumptions of coalescent analysis of historic N_e changes (MSVAR) and parameter estimation under an ABC framework (Sharma et al. 2018). Particularly, MSVAR assumes a single demographic event and likely retrieved the most prominent pattern of demographic change in the genetic data, which would be the population bottleneck associated with the founding event. Since the ABC framework allowed to estimate the current N_e based on a more complex demographic scenario that more closely resembles the true demographic trajectory of the sampled populations, downstream interspecific comparisons and inferences on the overall risk of genetic erosion of the sampled populations will be based on these.

Based on contemporary genetic data, informative posterior distributions for N_e estimates were obtained. The spot-nosed monkey populations of the Bijagós Archipelago are characterised by a contemporary (or current) N_e below 500 individuals, despite demographic recovery from the initial founding events, thus remaining below the recommended for long-term maintenance of genetic diversity (Frankham et al. 2014). While this could potentially be circumvented if the current populations keep their estimated demographic trajectory (post founding event demographic expansion), exploitation of the primates is thought to be increasing in the last few decades (Chapter 2) and could potentially exacerbate the loss of genetic diversity, hampering the long-term survival of these populations. As such, conservation strategies should focus on promoting alternative sources of revenue other than primate bushmeat, limiting the number of extracted individuals and safeguarding these populations from additional loss of diversity.

Supplementary Materials

Supplementary Table 4.1 MSVAR prior and hyperprior parameters used for each of the five demographic models considered in the MSVAR 1.3 analyses.

		Model 1	**Model 2**	**Model 3**	**Model 4**	**Model 5**
		Stable population	Severe bottleneck	Severe expansion	Moderate expansion	Moderate bottleneck
Priors	$\log_{10}(N_0)$	4 1	3 1	5 1	5 1	4 1
	$\log_{10}(N_1)$	4 1	5 1	3 1	4 1	5 1
	$\log_{10}(\Theta)$	-3.5 1	-3.5 1	-3.5 1	-3.5 1	-3.5 1
	$\log_{10}(T)$	5 1	5 1	4 1	4 1	5 1
Hyperpriors	$\log_{10}(N_0)$	6 2 0 0.5	4 2 0 0.5	4 2 0 0.5	3 2 0 0.5	5 2 0 0.5
	$\log_{10}(N_1)$	5 2 0 0.5	4 2 0 0.5	5 2 0 0.5	5 2 0 0.5	3 2 0 0.5
	$\log_{10}(\Theta)$	-3.5 0.25 0 0.5	-3.5 0.25 0 0.5	-3.5 0.25 0 0.5	-3.5 0.25 0 0.5	-3.5 0.25 0 0.5
	$\log_{10}(T)$	5 2 0 0.5	5 2 0 0.5	5 2 0 0.5	5 2 0 0.5	5 2 0 0.5

N_0: current population size; N_1: past population size; θ: $2N_0\mu$, where μ is the per locus mutation rate; T: time of demographic change

Supplementary Table 4.2 Details on ABC prior ranges for the competing scenarios of each hierarchical level.

Prior[a]		**Hierarchical level 1**			**Hierarchical level 2**			**Hierarchical level 3**	
		STN_NULL	**EXP**	**BOT**	**ISL_NULL**	**CLN_ACT**	**CLN_RCT**	**ISL_CLN**	**2CLN**
Non Island Specific	N_e ANC	-	2.36 – 5.78	2.36 – 5.78	4.30 – 5.78	4.30 – 5.78	4.30 – 5.78	4.30 – 5.78	4.30 – 5.78
	N_e FND	-	-	-	-	0.60 – 2.00	0.60 – 2.00	0.60 – 2.00	0.60 – 2.00
	T EXP	-	10 – 1820	-	-	-	-	-	-
	T BOT	-	-	10 – 1820	-	-	-	-	-
	T ACT	-	-	-	545 – 1820	545 – 1820	-	545 – 1820	545 – 1820
	T RCT	-	-	-	-	-	10 – 110	10 – 110	10 – 110
Galinha	N_e CUR	1.89 – 3.34	1.89 – 3.34	1.89 – 3.34	1.89 – 3.34	1.89 – 3.34	1.89 – 3.34	1.89 – 3.34	1.89 – 3.34
	N_e RCT	-	-	-	-	1.89 – 3.34	1.89 – 3.34	1.89 – 3.34	1.89 – 3.34
Canhabaque	N_e CUR	2.36 – 5.78	2.36 – 5.78	2.36 – 5.78	2.36 – 3.85	2.36 – 3.85	2.36 – 3.85	2.36 – 3.85	2.36 – 3.85
	N_e RCT	-	-	-	-	2.36 – 3.85	2.36 – 3.85	2.36 – 3.85	2.36 – 3.85
Uno	N_e CUR	2.28 – 3.77	2.28 – 3.77	2.28 – 3.77	2.28 – 3.77	2.28 – 3.77	2.28 – 3.77	2.28 – 3.77	2.28 – 3.77
	N_e RCT	-	-	-	-	2.28 – 3.77	2.28 – 3.77	2.28 – 3.77	2.28 – 3.77
Uracane	N_e CUR	1.94 – 3.43	1.94 – 3.43	1.94 – 3.43	1.94 – 3.43	1.94 – 3.43	1.94 – 3.43	1.94 – 3.43	1.94 – 3.43
	N_e RCT	-	-	-	-	1.94 – 3.43	1.94 – 3.43	1.94 – 3.43	1.94 – 3.43

[a] Effective population size (N_e) prior ranges are represented in haplotype $\log_{10}$ values; and, time since the demographic event (T) in generations. The same mutation rate prior was assumed for all the tested scenarios across islands (10^{-4} and 10^{-3}).

Supplementary Table 4.3 Details on the estimation of the critical values of N_e CUR prior for each island.

Island	**Area (km^2)**	[a] $N_e\ CUR_{min}$	[b] $N_e\ CUR_{max}$
Galinha	37	35	1092
Canhabaque	121	115	3570
Uno	99	96	2920
Uracane	46	44	1357

[a] $N_e\ CUR_{min} = Dp_{min} \times A_{island} \times N_e/N_c$; assuming Dp_{min} = 9.6 individuals/km^2, Karibuhoye, 2004; and N_e/N_c = 0.1.

[b] $N_e\ CUR_{max} = Dp_{max} \times A_{island} \times N_e/N_c$; assuming Dp_{min} = 59 individuals/km^2, Oates et al., 1990; and N_e/N_c = 0.5.

Supplementary Table 4.4 Details on the combinations of summary statistics used during model selection and parameter estimation

Combination	Summary statistics						
1	k	k_SD	H_E	H_E _SD	R	R_SD	Fis
2	k	k_SD	H_E	H_E _SD	R	Fis	
3	k	k_SD	H_E	R	R_SD	Fis	
4	k	H_E	H_E _SD	R	R_SD	Fis	
5	k	k_SD	H_E	R	Fis		
6	k	H_E	R	R_SD	Fis		
7	k	H_E	H_E _SD	R	Fis		
8	k	H_E	R	Fis			
9	k	k_SD	H_E	H_E _SD	Fis		
10	k	k_SD	H_E	Fis			
11	k	H_E	H_E _SD	Fis			
12	k	k_SD	R	R_SD	Fis		
13	k	k_SD	R	Fis			
14	k	R	R_SD	Fis			
15	H_E	H_E _SD	R	R_SD	Fis		
16	H_E	H_E _SD	R	Fis			
17	H_E	R	R_SD	Fis			
18	k	H_E	Fis				
19	k	R	Fis				
20	H_E	R	Fis				
21	k	k_SD	H_E	H_E _SD	R	R_SD	
22	k	k_SD	H_E	H_E _SD	R		
23	k	k_SD	H_E	R	R_SD		
24	k	H_E	H_E _SD	R	R_SD		
25	k	k_SD	H_E	R			
26	k	H_E	R	R_SD			
27	k	H_E	H_E_SD	R			
28	k	H_E	R				

number of alleles (k), expected heterozygosity (H_E) and the allelic range (R) across loci. The inbreeding coefficient (Fis)

Supplementary Table 4.5 MSVAR results of Galinha Island on five independent runs assuming (a priori) constant, moderately or severely decreasing, moderately or severely increasing population demographic models.

Galinha		**Run 1 - stable**	**Run 2 - bottleneck**	**Run 3 – severe expansion**	**Run 4 – moderate expansion**	**Run 5 – moderate bottleneck**
N0	Mean	263	158	149	128	201
	Median	331	211	215	194	257
	HPD 90 %	13 - 2,955	5 - 2,123	3 - 2,427	1 - 2,535	9 - 2,239
N1	Mean	12,805	10,505	11,151	10,836	10,456
	Median	12,388	10,307	10,882	10,579	10,262
	HPD 90 %	2,293 - 74,273	2,006 - 54,951	2,179 - 60,273	2,086 - 59,154	1,979 - 57,861
N0/N1	Mean	0.04	0.51	0.03	0.03	5.63
	Median	0.03	0.02	0.02	0.02	0.02
	HPD 90 %	1.25e-07 - 0.12	4.09e-06 - 0.11	2.80e-07 - 0.10	8.04e-07 - 0.10	2.83e-05 - 0.12
T	Mean	11,202.78	6,309.20	6,080.40	5,302.93	8,172.58
	Median	12,842.37	7,599.80	7,739.63	7,057.34	9,528.95
	HPD 90 %	399.83 - 226,616.23	180.15 - 141,110.39	118.99 - 169,635.60	62.99 - 172,655.33	275.34 - 155,596.92

Supplementary Table 4.6 MSVAR results of Canhabaque Island on five independent runs assuming (a priori) constant, moderately or severely decreasing, moderately or severely increasing population demographic models.

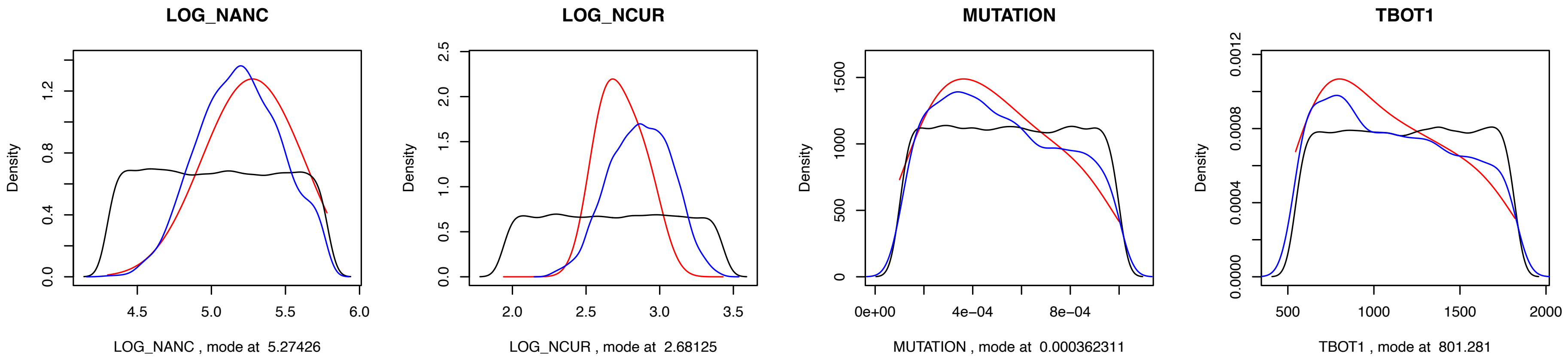
Canhabaque		**Run 1 - stable**	**Run 2 - bottleneck**	**Run 3 – severe expansion**	**Run 4 – moderate expansion**	**Run 5 – moderate bottleneck**
N0	Mean	4,087	735	810	470	1,741
	Median	2,589	955	1,065	640	1,702
	HPD 90 %	14 - 27,668,014	3 - 21,767	4 - 20,932	3 - 14,945	6 - 508,753
N1	Mean	13,595	8,812	12,442	11,382	5,855
	Median	9,571	8,575	9,604	9,373	7,528
	HPD 90 %	397 - 7,718,768	299 - 479,050	573 - 2,228,963	803 - 543,458	21 - 173,141
N0/ N1	Mean	515,405.50	30,677.44	681.91	79.20	32,246.02
	Median	0.16	0.08	0.07	0.05	0.16
	HPD 90 %	2.65e-10 - 1,971.40	2.86e-09- 12.06	6.37e-11 - 5.52	8.49e-09 - 1.55	2.43e-08 - 451.84
T	Mean	18,528.11	7,553.72	10,249.48	5,550.97	13,538.64
	Median	7,141.49	3,437.98	4,078.85	2,684.57	5,204.99
	HPD 90 %	6.28 - 440,578,195.68	9.02 - 121,969,993.31	13.25 - 178,487,168.50	8.14 - 92,458,533.34	9.90 - 348,025,447.04

Supplementary Table 4.7 MSVAR results of Uno Island on five independent runs assuming (a priori) constant, moderately or severely decreasing, moderately or severely increasing population demographic models.

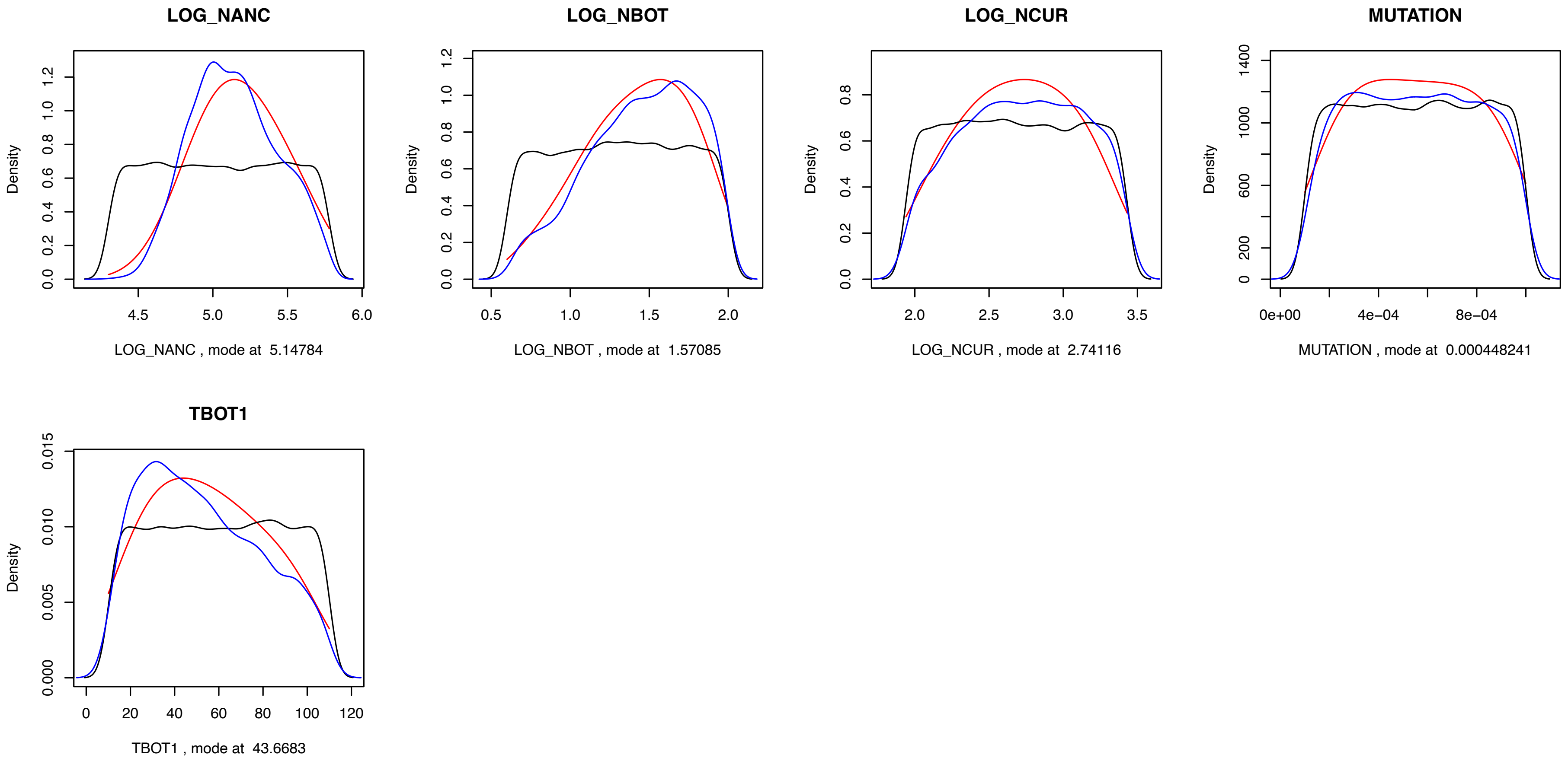
Uno		**Run 1 - stable**	**Run 2 - bottleneck**	**Run 3 – severe expansion**	**Run 4 – moderate expansion**	**Run 5 – moderate bottleneck**
N0	Mean	900	543	592	466	620
	Median	1,039	762	804	684	792
	HPD 90 %	75 - 7,046	16 - 5,975	23 - 6,079	11 - 5,292	30 - 5,829
N1	Mean	14,639	11,270	12,439	11,477	10,723
	Median	13,572	10,673	11,585	10,753	10,237
	HPD 90 %	2,158 - 111,957	1,857 - 75,855	1,989 - 88,422	1,947 - 76,545	1,767 - 72,581
N0/N1	Mean	18,321.00	9.55	0.47	0.17	276.05
	Median	0.07	0.06	0.06	0.05	0.07
	HPD 90 %	$1.28e^{-07}$ - 0.304	$6.28e^{-08}$ - 0.28	$1.18e^{-08}$ - 0.27	$2.33e^{-09}$ - 0.25	$2.78e^{-05}$ - 0.32
T	Mean	28,926.77	15,102.23	17,102.75	12,880.72	16,490.66
	Median	35,048.71	21,111.79	22,924.61	17,987.43	21,105.03
	HPD 90 %	582.75 - 809,144.34	129.73 - 594,385.22	181.13 - 595,011.01	112.81 - 449,644.20	247.10 - 515,582.30

Supplementary Table 4.8 MSVAR results of Uracane Island on five independent runs assuming (a priori) constant, moderately or severely decreasing, moderately or severely increasing population demographic models.

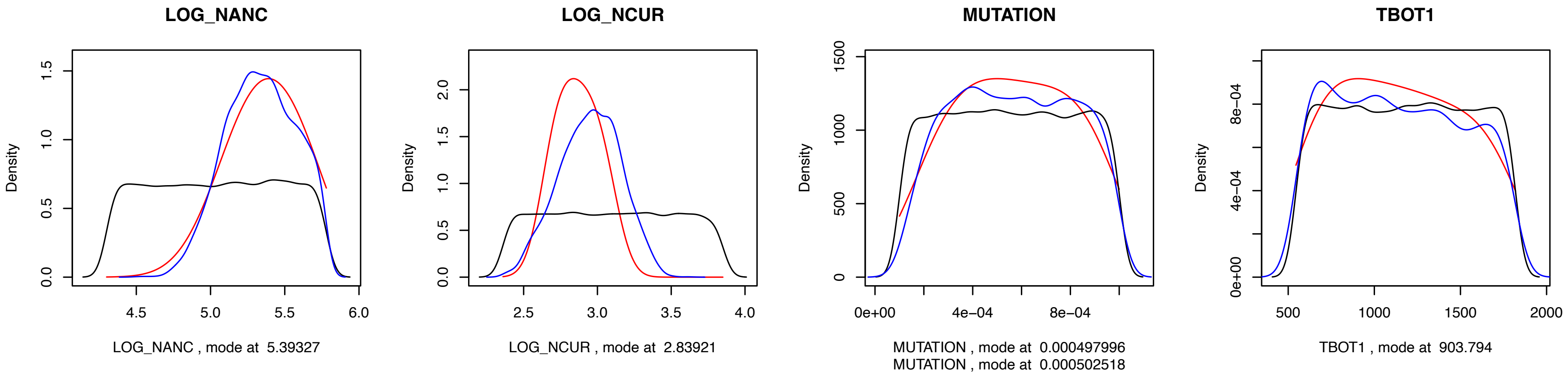
Uracane		Run 1 - stable	Run 2 - bottleneck	Run 3 – severe expansion	Run 4 – moderate expansion	Run 5 – moderate bottleneck
N0	Mean	1,584	598	565	439	955
	Median	1,259	775	780	633	967
	HPD 90 %	8 - 449,937	9 - 8,900	6 - 9,737	6 - 7,352	7 - 19,626
N1	Mean	9,274	6,155	8,028	7,800	4,732
	Median	6,509	5,521	6,116	5,950	4,968
	HPD 90 %	511 - 1,336,481	506 - 187,671	545 - 397,575	594 - 306,843	243 - 153,154
N0/ N1	Mean	285,755.90	1,239.87	1,290.00	43.89	18,412.40
	Median	0.13	0.11	0.09	0.08	0.15
	HPD 90 %	5.46e-11 - 122.37	3.43e-09 - 2.15	1.57e-10 - 1.39	2.27e-10 - 0.99	3.15e-08 - 39.80
T	Mean	22,701.00	12,005.22	12,549.00	10,040.33	13,560.48
	Median	16,566.43	8,963.32	9,198.88	7,326.79	10,275.67
	HPD 90 %	20.69 - 86,645,298.05	19.69 - 23,899,124.96	16.21 - 27,038,961.04	13.71 - 19,141,016.60	20.77 - 44,101,666.42



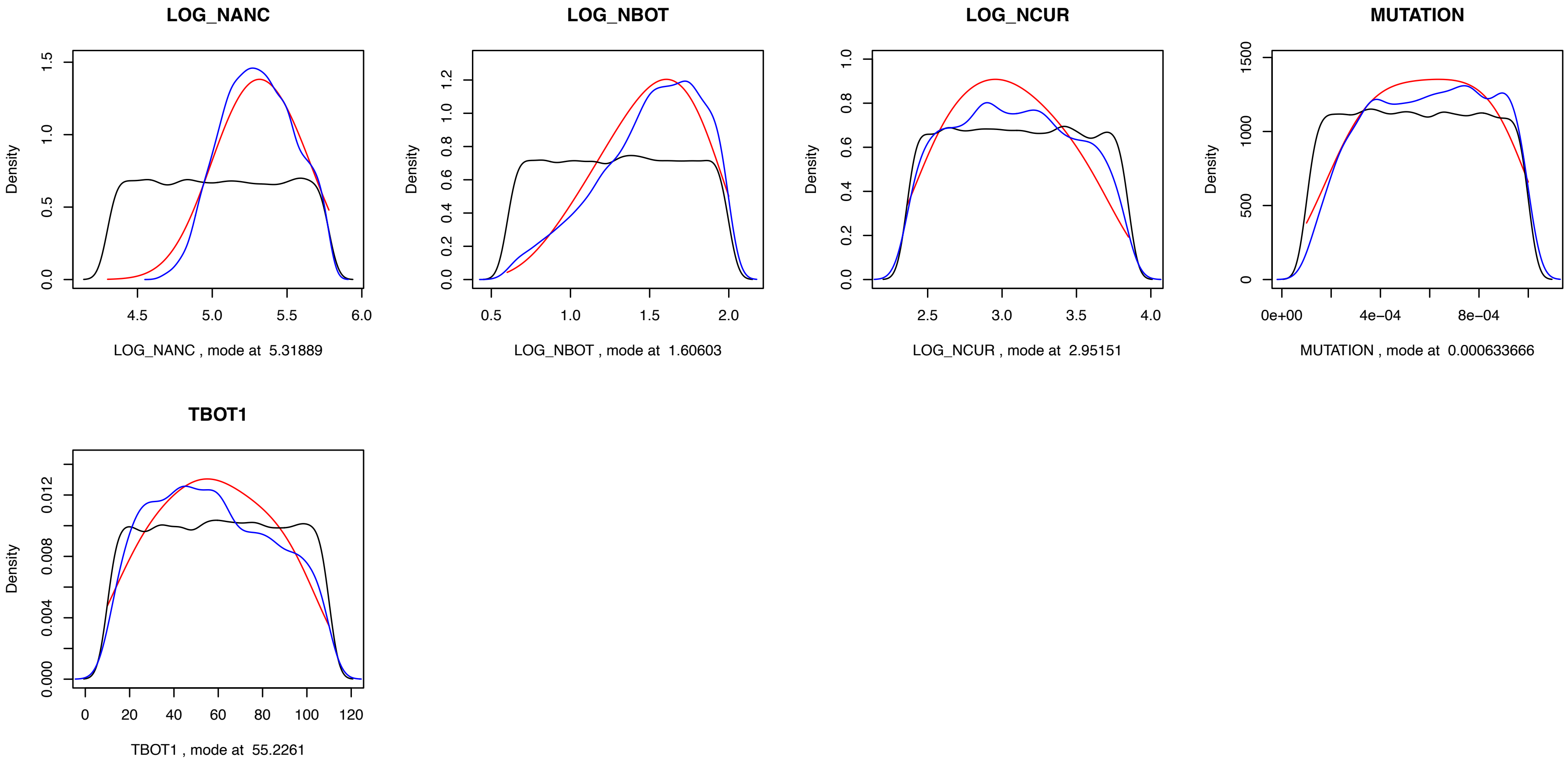
Supplementary Figure 4.1 Posterior distributions of ISL_NULL scenario for Galinha Island (red). Distributions of prior sample and retained simulations are represented in blue and black, respectively.



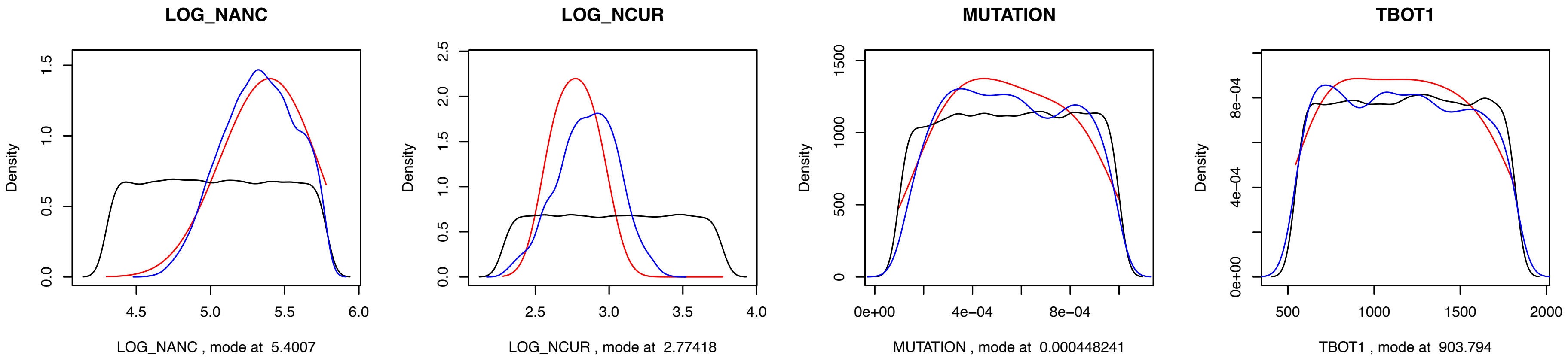
Supplementary Figure 4.2 Posterior distributions of CLN_RCT scenario for Galinha Island (red). Distributions of prior sample and retained simulations are represented in blue and black, respectively.



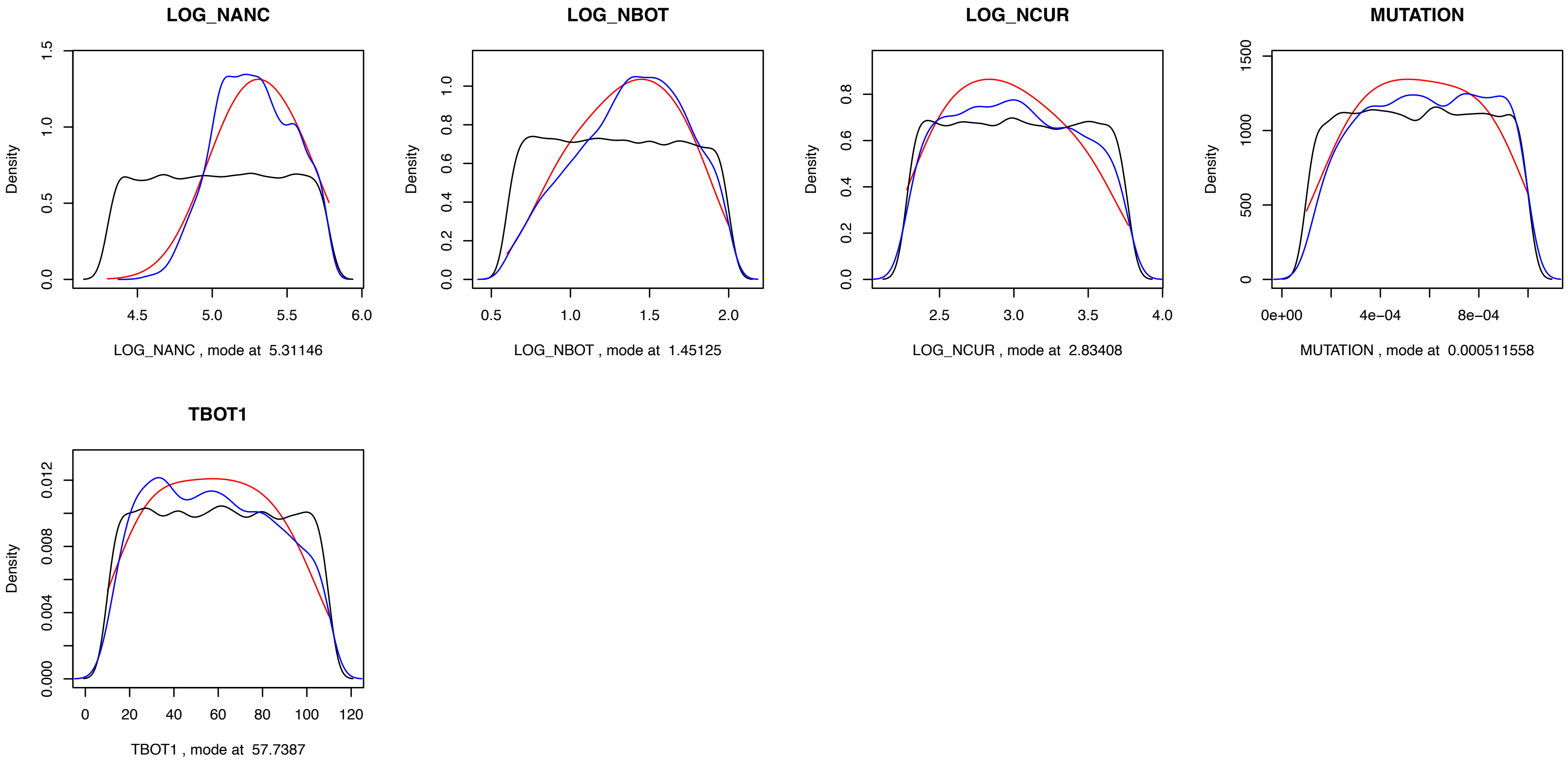
Supplementary Figure 4.3 Posterior distributions of ISL_NULL scenario for Canhabaque Island (red). Distributions of prior sample and retained simulations are represented in blue and black, respectively.



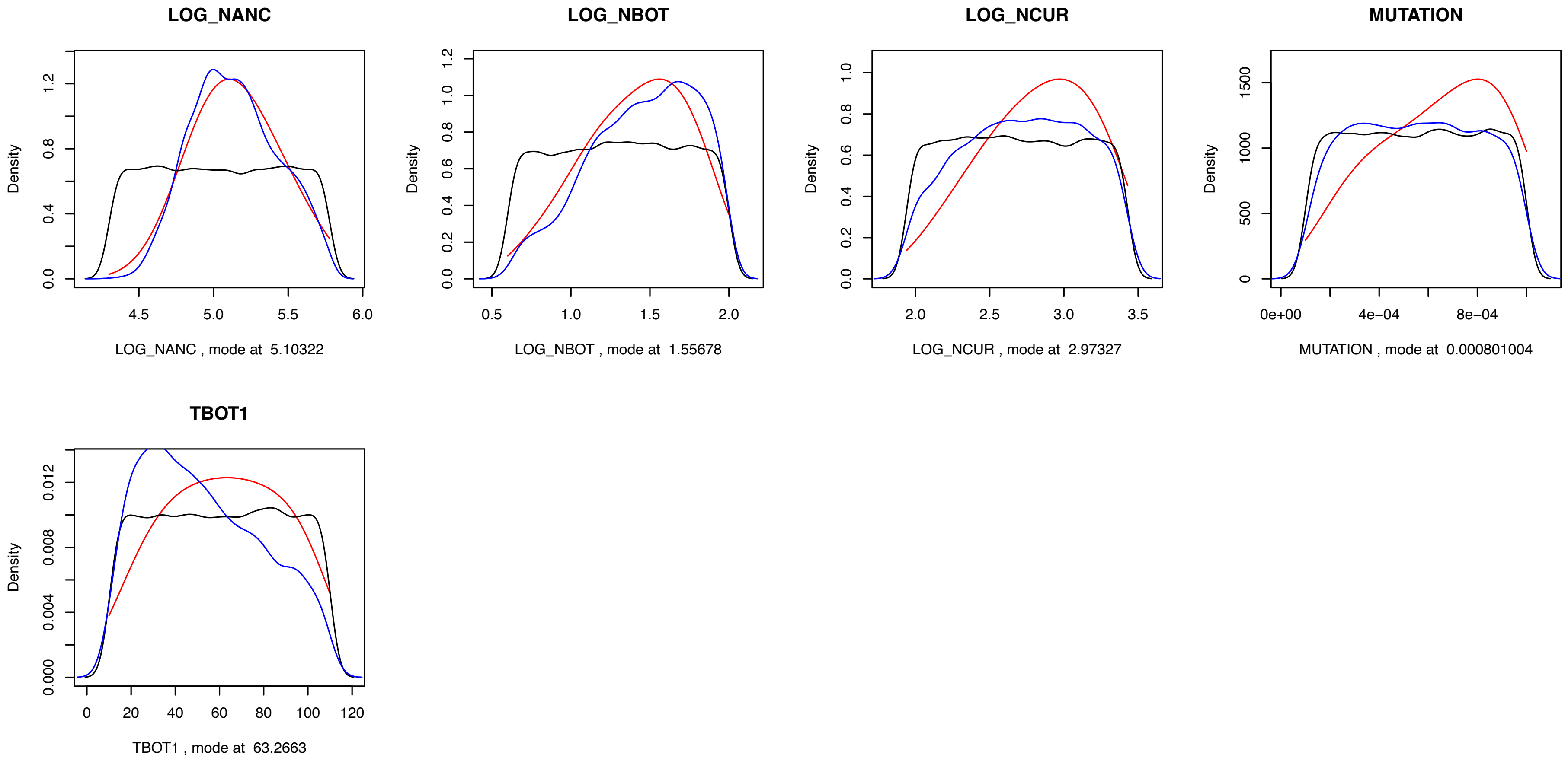
Supplementary Figure 4.4 Posterior distributions of CLN_RCT scenario for Canhabaque Island (red). Distributions of prior sample and retained simulations are represented in blue and black, respectively.



Supplementary Figure 4.5 Posterior distributions of ISL_NULL scenario for Uno Island (red). Distributions of prior sample and retained simulations are represented in blue and black, respectively.



Supplementary Figure 4.6 Posterior distributions of CLN_RCT scenario for Uno Island (red). Distributions of prior sample and retained simulations are represented in blue and black, respectively.



Supplementary Figure 4.7 Posterior distributions of CLN_RCT scenario for Uracane Island (red). Distributions of prior sample and retained simulations are represented in blue and black, respectively.

CHAPTER 5

Genomic signatures of island colonisation in the guenons of the Bijagós Archipelago

Understanding how small populations cope with loss of genetic diversity and deleterious variation is crucial to address the current biodiversity crisis. Insular populations are particularly interesting as they have often persisted at low population sizes and higher inbreeding than their mainland counterparts. While the genome-wide consequences of inbreeding in threatened insular species have received some attention, comparative genomics between insular and mainland populations of wide-spread and genetically diverse species have rarely been performed. Yet, they are particularly well suited to inform on the consequences of drastic population declines from initially large populations – a phenomenon that is becoming increasingly common. The spot-nosed monkey (*Cercopithecus petaurista*), the Campbell's monkey (*Cercopithecus campbelli*) and the green monkey (*Chlorocebus sabaeus*) are common and genetically diverse West African primates. Insular populations can be found at the Bijagós Archipelago, Guinea-Bissau. In this chapter, I assessed the genome-wide diversity, inbreeding, genetic load and adaptive variation using whole genome sequencing data from insular and mainland populations. In the three species, island populations showed lower genome-wide diversity and higher inbreeding. Genetic drift has likely promoted the conversion of masked genetic load into realized load without increased purging of deleterious variation. Additionally, no evidence for accumulation of deleterious variation was found, suggesting that these populations are not yet at risk of extinction by genetic factors and may act as reservoirs of mainland genetic diversity. I highlight, however, that other anthropogenic factors are threatening these insular primates and therefore conservation management should target their immediate threats to safeguard against additional loss of diversity.

Introduction

In a time when anthropogenic activities increasingly impact ecosystems, conservation of biodiversity has become a global challenge. Intraspecific genetic diversity has recently received wider recognition by governmental bodies (CBD 2020; Hoban et al. 2021; Mastretta-Yanes et al. 2024). Since its inclusion in the Convention on Biological Diversity's (CBD) Kunming-Montreal Global Biodiversity Framework, greater accessibility to genomic data for non-model species has improved our capacity to disentangle neutral and adaptive components of genetic diversity, opening the door to better understand species demographic and adaptive responses to environmental or anthropogenic changes (Allendorf et al. 2010).

Insular populations can be particularly vulnerable to extinction due to genetic factors resulting from the demographic processes inherent to the colonization dynamics. Island colonization typically involves a small number of founding individuals, which carry only a fraction of the total genetic diversity of the source populations (Allendorf et al. 2013; Martin et al. 2023). The intrinsic low levels of genetic diversity in insular populations tend to be aggravated by restricted or no gene flow with the source populations and increased inbreeding among founding individuals and their descendants. Genetic drift is stronger in populations with small effective population size (N_e), as often is the case in insular systems (Allendorf et al. 2013). Although genetic drift is a neutral evolutionary process, it can also incur fitness costs by increasing the allele frequencies of loci with deleterious variation (Bertorelle et al. 2022; Dussex et al. 2023). As masked genetic load (i.e., recessive deleterious mutations present in their heterozygous state) is converted into realized load (i.e., homozygous deleterious mutations with expressed fitness effects (Bertorelle et al. 2022), individual genetic load may increase, reducing the individual fitness and increasing the risk of inbreeding depression (Bertorelle et al. 2022; Dussex et al. 2023; Smeds and Ellegren 2023). However, the increased frequency of strongly deleterious mutations in their homozygous states makes them visible to selection, allowing for their removal through purging (Xue et al. 2015; Grossen et al. 2020; Dussex et al. 2021; Khan et al. 2021; von Seth et al. 2022; van der Valk et al. 2024). Although purifying selection is expected to purge mutations with large fitness effects, strong genetic drift can reduce the efficiency of selection in small populations, potentiating the gradual accumulation of mildly deleterious mutations during prolonged bottlenecks (Dussex et al. 2023). Such accumulation can generate a decline in fitness and exacerbate the extinction risk of small, isolated populations (Bataillon and Kirkpatrick 2000; Khan et al. 2021).

Insular populations frequently exhibit genetic and phenotypic differences compared to mainland populations in response to novel ecosystems. This phenomenon, collectively known as the “island syndrome”, often includes changes in morphology, behaviour and life-history traits (Adler and Levins 1994). It has been attributed to adaptive processes in response to the new habitats where different traits, more advantageous to the insular environment, are selected for (Welles and Dlugosch 2019; Sendell-Price et al. 2020; Martin et al. 2021; Payseur and Jing 2021). Another hypothesis is that loci under strong selection on the mainland become effectively neutral on the islands due to the relaxation of natural selection (Cui et al. 2021; Wang et al. 2023). Consequently, non-synonymous variants can drift towards fixation in the insular populations.

Due to their vulnerability coupled with high potential for neutral and adaptive differentiation, insular populations are of great conservation concern. Except for the Soay sheep, a breed of the domestic sheep (*Ovis aries* Linnaeus, 1758, Stoffel et al., 2021), previous studies have focused mainly on highly threatened insular populations from already genetically depauperate species (e.g., kākāpō, *Strigops habroptilus* Gray, 1845*,* Dussex et al. 2021; Chatham Island black robin, *Petroica traversi* Buller, 1872, von Seth et al. 2022). However, little attention has been given to widespread and genetically diverse species. Such species, many of which are classified as non-threatened on the International Union for Conservation of Nature (IUCN) Red List, are becoming increasingly threatened due to anthropogenic activities in their ranges (Finn et al. 2023). As the genomic consequences of inbreeding and decreasing population sizes of widespread populations may differ from those of more threatened taxa (Robinson et al. 2016; Taylor et al. 2024), it is increasingly important to consider non-flagship species in the field of conservation genomics in order to pre-emptively promote their conservation (but see Smeds and Ellegren (2023) for genomic analysis of recently extirpated populations of the grey wolf, *Canis lupus* Linnaeus, 1758, an otherwise widespread species).

Here, I investigated the effects of insularity and low population size in three guenon species, tribe Cercopithecini, the most genetically diverse African primate group (Jensen et al. 2023; Kuderna et al. 2023). I used sequencing data of insular and mainland populations of the spot-nosed monkey (*Cercopithecus petaurista*, Scheber, 1774), the Campbell's monkey (*Cercopithecus campbelli*, Waterhouse, 1838), and the green monkey (*Chlorocebus sabaeus*, Linnaeus, 1766) in Guinea-Bissau, West Africa. My specific aims were:

1. Estimate genome-wide diversity and inbreeding.
2. Estimate changes to adaptive variation including genetic load and differential variation in protein-coding genes between insular and mainland populations.
3. Discuss the importance of insular populations for the conservation of genetically diverse species.

This chapter has contributions from Axel Jensen, PhD student at Department of Ecology and Genetics, Uppsala University, Uppsala, Sweden (detailed below)

Methods

Study area and focal species

The Bijagós Archipelago is a continental archipelago of 88 islands and islets located off the coast of Guinea-Bissau, West-Africa. It has been proposed that the separation of the archipelago from mainland started as early as ca. 19,000 years ago (YA) but is thought to have become fully isolated during the Holocene, particularly during the lower Flandrian transgression, ca. 6,000 – 12,000 YA (Alves 2007). Both climate and vegetation are similar to southern areas of the mainland (Catarino et al. 2008), which is characterized as a mosaic of forest of Guinean affinity and woodland savannah. Primates coexist with local communities whose arrival on the archipelago has been associated with the expansion of West African trading empires, including the peak expansion of the Ghana and Mali Empires, c.a. 800 – 1,200 YA (Rodney 1970).

The spot-nosed monkey and the Campbell's monkey are classified by the IUCN as Near Threatened (Matsuda Goodwin et al. 2020a; Matsuda Goodwin et al. 2020b), whereas the green monkey is listed as Least Concern (Gonedelé Bi et al. 2020). These guenon species are the only non-human primates occurring on the Bijagós Archipelago (Gippoliti and Dell'Omo 2003; Colmonero-Costeira et al. 2019). Across the archipelago, the distribution of the three species does not overlap except on Caravela Island, where both the spot-nosed monkey and the Campbell's monkey can be found in sympatry (Gippoliti and Dell'Omo 2003; Colmonero-Costeira et al. 2019). The three species are widespread and considered habitat generalists, exhibiting high behavioural and dietary flexibility (Rowe and Myers 2016; Bersacola et al. 2022).

In Guinea-Bissau, the spot-nosed monkey (*santchu nariz-branku/santchu bidjugu* in Creole) is possibly restricted to the Bijagós Archipelago (Gippoliti and Dell'Omo 2003). Historically, the species is thought to have been present on the mainland (Gippoliti and Dell'Omo 2003) but has been absent/not reported from the mainland for the last 30 years (Bersacola et al. 2018; Bersacola et al. 2022; Colmonero-Costeira 2023). The Campbell's monkey (*kankulma* or *santchu mona* in Creole) and the green monkey (*santchu-di-tarrafi* in Creole) are considered the most abundant non-human primate species in the country (Karibuhoye 2004; Bersacola et al. 2018). However, past studies suggest that their populations are threatened by illegal commercial hunting and habitat destruction (Gippoliti and Dell'Omo 2003). Campbell's and green monkeys are the most traded primates for meat consumption in the urban bushmeat markets in the capital city and the most commonly available species in bushmeat dedicated restaurants/bars in the south of the country (Minhós et al. 2013; Ferreira da Silva et al. 2021b). On the Bijagós Archipelago, the commercial trade of spot-nosed monkey meat has been recently described

(Colmonero-Costeira et al. 2023) and subsistence hunting is reported for the remaining two species (see below).

Sample collection

Tissue samples of spot-nosed monkeys, Campbell's monkeys, and green monkeys were obtained as part of previous research that focused on primate meat hunting and consumption in Guinea-Bissau between 2010 and 2017. Samples from the Bijagós Archipelago were collected directly from local hunters or villagers preparing the carcasses for consumption (2002 – 2016). Samples from mainland Guinea-Bissau were collected at meat markets in the capital city, Bissau (March – June 2010; Minhós et al. 2013a), or from drinking establishments located in the vicinity of protected areas in southern mainland (2015 – 2017; Ferreira da Silva et al. 2021b). The DNA extractions of samples collected in Bissau is described in Minhós et al. (2013). DNA of the samples collected between 2015 and 2017 was using a salting out procedure (Miller et al. 1988) at the CIBIO-InBIO research centre. Negative controls were included throughout the entire process to test for DNA contamination. Samples with low DNA concentrations were re-extracted using the Qiagen DNeasy Blood & Tissue kit (QIAGEN® Hilden, Germany) following the manufacturer's protocol. To minimize the inclusion of highly related individuals in the dataset, only samples collected in different weeks or different commercial establishments or in different hunting events were selected. A total of 50 samples were sequenced on Illumina NovaSeq6000 (150bp PE), aiming for 30x coverage per sample. High quality whole-genome sequences from the three guenon species present on the Bijagós Archipelago (eight spot-nosed, one Campbell's and three green monkeys), and the mainland counterparts of Campbell's (n = 25) and green monkey (n = 10) were generated (Supplementary Table 5.1). Since no spot-nosed monkeys are present on the mainland Guinea Bissau, a publicly available spot-nosed monkey genome of unknown geographic origin from mainland Africa was included in the analyses (Kuderna et al. 2023).

Mapping and variant calling

A.J. used Picard v2.23.4 (http://broadinstitute.github.io/picard/) to add read group information and mark adapter content in the sequencing reads and aligned them to the rhesus macaque (*Macaca mulatta* Zimmermann, 1780) reference genome (Mmul_10, GCF_003339765.1) with the Burrows-Wheeler Aligner (BWA) v0.7.17 (Li & Durbin, 2009). Picard was used to sort and deduplicate the mapped bam-files. Next, A.J. used GATK v4.3.0.0 to call genotypes per sample with HaplotypeCaller, which were subsequently combined with CombineGVCFs and jointly genotyped with GenotypeGVCFs. Insertions and deletions were excluded, VariantFiltration was used to filter variants based on the following exclusion criteria: QD < 2.0, QUAL < 30.0, SOR > 3.0, FS > 60.0, MQ < 40.0, MQRankSum < -12.5, ReadPosRankSum < -8.0. Repetitive regions were excluded following the SNPable regions pipeline (https://lh3lh3.users.sourceforge.net/snpable.shtml). Heterozygous genotypes with skewed allelic balance (minor allele support < 0.25), as well as genotypes with less than half or more than double the genome-wide average read depth per sample were masked.

Mitochondrial genome assembly and haplotype networks

The mitochondrial genomes were assembled using the MitoFinder pipeline (Allio et al. 2020). The assembly was started by trimming adapter sequences using Trimmomatic (Bolger et al. 2014) and running MitoFinder with the metaspades assembler. The assembled contigs were corrected for circularization and rotated to the same starting position using a custom Python script (https://github.com/axeljen/guenon_phylogenomics) and annotated using the green monkey (NC_008066.1) reference mitochondrial genome. Annotated assemblies were aligned for each species separately using MAFFT aligner (Katoh et al. 2002). I inspected the species-specific alignments visually and trimmed the non-coding hypervariable region 1 (positions 16,010 – 16,361), and hypervariable region 2 (positions 56 – 364) of the green monkey reference genome and misassembles/misalignments. For the spot-nosed monkey I included publicly available mitochondrial genomes (JQ256931.1, JQ256932.1, JQ256982.1 and JQ256983.1) in the final alignment (Guschanski et al. 2013). The relationships between the assembled mitochondrial genomes were visualised by reconstructing median joining haplotype networks using PopART (Leigh and Bryant 2015).

Population structure and historical population size

To assess population structure between the insular and mainland populations, I conducted a principal component analysis (PCA) in PLINK v1.9 (Purcell et al. 2007), removing positions with missing genotypes within each species (--geno 0) and thinning the total autosomal SNPs to 100,000 SNPs. I inferred the long-term changes in N_e of all the populations using the pairwise sequentially Markovian coalescent model implemented in beta-PSMC (Liu et al. 2022) with default parameters and five sub-atomic time intervals. The variance of the estimated N_e trajectories was assessed by 20 randomized resampling runs across the genome. The output was scaled assuming a generation time of 11 years for the spot-nosed monkey, 12 years for both Campbell's and green monkeys, and a mutation rate of 4.65×10^{-9} per site per generation (average mutation rate across guenons; Kuderna et al. 2023).

Genome-wide diversity and inbreeding

I identified autosomal runs of homozygosity (ROH) using PLINK v1.9 and estimated autosomal heterozygosity for each individual genome using VCFtools (Danecek et al. 2011). To minimize the detection of false positive ROH, the number of SNPs that constituted a ROH (--*homozyg-snp* setting) was scaled by the within species average heterozygosity (Purfield et al. 2012):

$$L = \frac{log_e \frac{a}{n_s n_i}}{log_e(1 - het)}$$

where n_s is the number of genotyped SNPs, n_i the number of genotyped individuals, α the false positive ROH threshold (set at 0.05), and *het* the mean heterozygosity. Based on L, the minimum number of SNPs that constituted a ROH was set to 77, 88, and 80 for spot-nosed monkey, the Campbell's monkey, and the green monkey, respectively. I selected a scanning window length equal to L as suggested by (Meyermans et al. 2020). For the remaining ROH search parameters I used the default values. The fraction of the genome contained in ROH (F_{ROH}) for each individual was estimated as:

$$F_{ROH} = \frac{L_{ROH}}{L_{ROH,\ HOM}}$$

where L_{ROH} is the sum of the length of all detected ROHs, and $L_{ROH,\ HOM}$ is the maximal detectable ROH length of a synthetic homozygous genome of each individual, under the same ROH searching parameters (Meyermans et al. 2020). The synthetic homozygous genome for each of the individuals was obtained by changing all heterozygous genotypes to homozygous using a custom Python script. This minimized the impact of stochastic genome-specific sequencing artefacts that potentially prevent the correct detection of ROH in window-based methods (Meyermans et al. 2020).

I estimated the distribution of ROHs arising from inbreeding after the isolation of the Bjagós Archipelago or during human coexistence using the expected ROH coalescent time in generations (g):

$$g = \frac{100}{2rl}$$

equivalent to:

$$l = \frac{50}{rg}$$

where r is recombination rate and l the ROH length (Thompson 2013). I used the rhesus macaque average genome-wide recombination rate of 0.448 cM/Mb (Xue et al. 2020). As such, I established ROH ≥ 1 Mb as human-contemporary (up to 110 guenon generations, ≈ 1,200 YA) and ROH <1 Mb as historical (older than 110 guenon generations ago). The chosen time windows reflect the earliest time of the arrival of humans to the Bijagós Archipelago and the isolation of the archipelago, respectively.

Genetic load

To investigate if isolation on the islands may have led to the purging of deleterious mutations, and a reduction of individual genetic load, I characterised the positions in coding regions that derived from their ancestral state in both insular and mainland guenon genomes. An individual's genetic load can be defined as the potential fitness burden of mutations in the individual's genome, affecting its fitness and the fitness of its offspring and generally measured as the sum of selection coefficients across all loci that are homozygous for the mutant allele, plus half the selection coefficients of all heterozygous (Bertorelle et al., 2022). In the absence of selection coefficients, genetic load was simplified to the number of loci containing derived positions that have a putative deleterious effect on the individual and/or population fitness. Strongly deleterious mutations are often purged from the populations by means of purifying selection (Dussex et al., 2023). When small populations are characterised by lower numbers (or frequencies) of highly deleterious mutations compared to their large-population counterparts it is often a signal of increased purging of deleterious mutations (Dussex et al., 2023).

Derived positions in protein coding regions were characterised using Ensembl's variant effect predictor (VEP; McLaren et al. 2016). Prior to the VEP annotation, the ancestral alleles were polarized using the Guinea baboon (*Papio papio* Desmarest, 1820; GCA_028645565.1), the Angolan colobus monkey (*Colobus angolensis* Sclater, 1860; GCF_000951035.1), and rhesus macaque (Mmul_10) as outgroups. The additional outgroups were aligned to the Mmul_10 reference genome using Minimap2's cross-species full-genome alignment (Li 2018), assuming a species divergence below 20 % (asm20). I called the genotypes on the outgroups using BCFtools mpileup (Danecek et al. 2021), multiallelic-caller (-m). Alleles present in the three outgroup species in the homozygous state were defined as ancestral. These positions were identified using a custom Python script. Invariable sites in the guenons were removed for downstream analysis.

The effects of the retained variants were predicted based on the rhesus macaque (Mmul_10) annotations. For sites on overlapping transcripts, a single prediction per variant was selected based on VEP's standard ordered set of criteria (--pick), including the canonical status of a transcript, APPRIS functional isoform notation (most functionally important transcripts), transcript support level, biotype (protein coding preferred), consequence rank (most severe). The annotated variants were classified as loss-of-function (LoF: transcript ablation, stop gained, stop lost, start lost, frameshift variant, splice region variant, splice donor variant, splice acceptor variant), missense, and synonymous. Missense variants were further classified into two classes: 1. likely deleterious or 2. tolerated, using the Experimental exchangeability score of amino acids (EX; Yampolsky and Stoltzfus, 2005). The EX of missense variants was calculated using a custom Python script adapted from Smeds and Ellegren (2023) (https://github.com/linneas/wolf-deleterious). Sites were classified as likely deleterious if the Experimental exchangeability score was ≤ 0.256 (Williamson et al. 2005).

A decrease in the number of deleterious variants across the genome can potentially arise as a combination of purifying selection and stochastic loss due to genetic drift. Considering that without selection, genetic drift does not change allele counts of the derived mutations (Dussex et al. 2023), I estimated the individual genetic load as the relative abundance (RA) of the derived alleles ($A^{x}{}_{A}$) for each individual (i) of population x and standardized it by the number of derived alleles within species across the different mutational categories:

$$RA_{A\,ix} = \frac{n_{R/A\,i} + 2n_{A/A\,i}}{2n_p}$$

where $n_{R/A\,i}$ is the number of derived heterozygous positions (R, reference allele; A, alternative allele), $n_{A/A\,I}$ is the number of derived homozygous positions and n_p is the total number of derived positions across all the genomes for a particular species (insular and mainland).

Furthermore, based on the VEP output, I performed a functional analysis of the LoF variants that have become fixed in the homozygous state in insular populations. Gene ontology (GO) enrichment analysis was conducted using g:Profiler (https://biit.cs.ut.ee/gprofiler/gost) and the g:SCS multiple testing correction algorithm on these sets of genes (Kolberg et al. 2023).

Differential variation in protein-coding genes

I identified variants in protein-coding regions that were fixed for alternative alleles between insular and mainland populations of the same species using a custom

Python script (Jensen et al. 2023). Differentially fixed positions were annotated using VEP. To filter out variants that accumulate through drift in potential pseudogenes, all genes that contained a LoF variant were removed. Next, I looked for sets of genes that contained differentially fixed variants in at least two of the studied guenon species and conducted a GO enrichment analysis using g:Profiler.

All statistical analysis and plots were conducted in R v4.2.2 (R CoreTeam 2022) coupled with RStudio v2023.06.2+561 (Posit team 2023).

Results

Sequencing and genotyping

Across the 48 genomes, average autosomal mapping coverage of the dataset varied between 25.95x and 35.00x (median = 30.35x; Supplementary Table 5.1). After calling the genotypes against the rhesus macaque Mmul_10 reference genome, 18,415,827 autosomal biallelic SNPs were identified in the spot-nosed monkey, 22,007,478 SNPs in the Campbell's monkey, and 15,760,456 SNPs in the green monkey. Additionally, I assembled and annotated the mitochondrial genomes for all the samples.

Population structure and changes to N_e

The PCAs suggested the existence of population structure in all three guenon species, with PC1 differentiating insular and mainland populations within each species and explaining 33.3 %, 7.19 % and 15.7 % of the variance for the spot-nosed, Campbell's, and green monkeys, respectively (Figure 5.1). Further differentiation was observed between the spot-nosed monkey individuals from Canhabaque and Caravela Islands. In contrast, the green monkeys from Ganogo and Orango Islands (separated by a ~500 m water channel) were almost indistinguishable from each other in the PC space. In the absence of clear population structure, individuals from these two neighbouring islands were treated as one population in downstream analyses, designated as the Orango Islands Group (OIG). Mainland samples were generally more spread along the PC2 axis indicating more variation.

None of the mtDNA haplotypes sampled from the islands were shared with the mainland in any of the three species (Supplementary Figures 5.1–5.4). In the Campbell's monkey and the green monkey, the pairwise number of substitutions between insular and mainland haplotypes were within the range of the pairwise comparisons among the mainland haplotypes. In contrast, the spot-nosed monkey showed insular haplotypes that differed from each other by only a few substitutions, but these haplotypes were separated from the mainland haplotype by more than 400 substitutions. Since the geographic origin of the mainland spot-nosed individual is not known, this separation could be the result of deep population structure within the species, such as genetic differentiation at the sub-species level. After the inclusion of the historical mtDNA genomes (Guschanski et al. 2013), the mtDNA haplotype from the mainland spot-nosed monkey included in the dataset was more closely related to mtDNA haplotypes sampled in Togo, Liberia and Ivory Coast. This result suggests the mainland individual used in this study could be from the eastern *C. petaurista* subspecies (*Cercopithecus petaurista petaurista* Jentink, 1886), whereas the archipelago individuals likely belong to the western subspecies (*C. p. buettikoferi* Jentink, 1886), which would explain the deep genomic divergence.

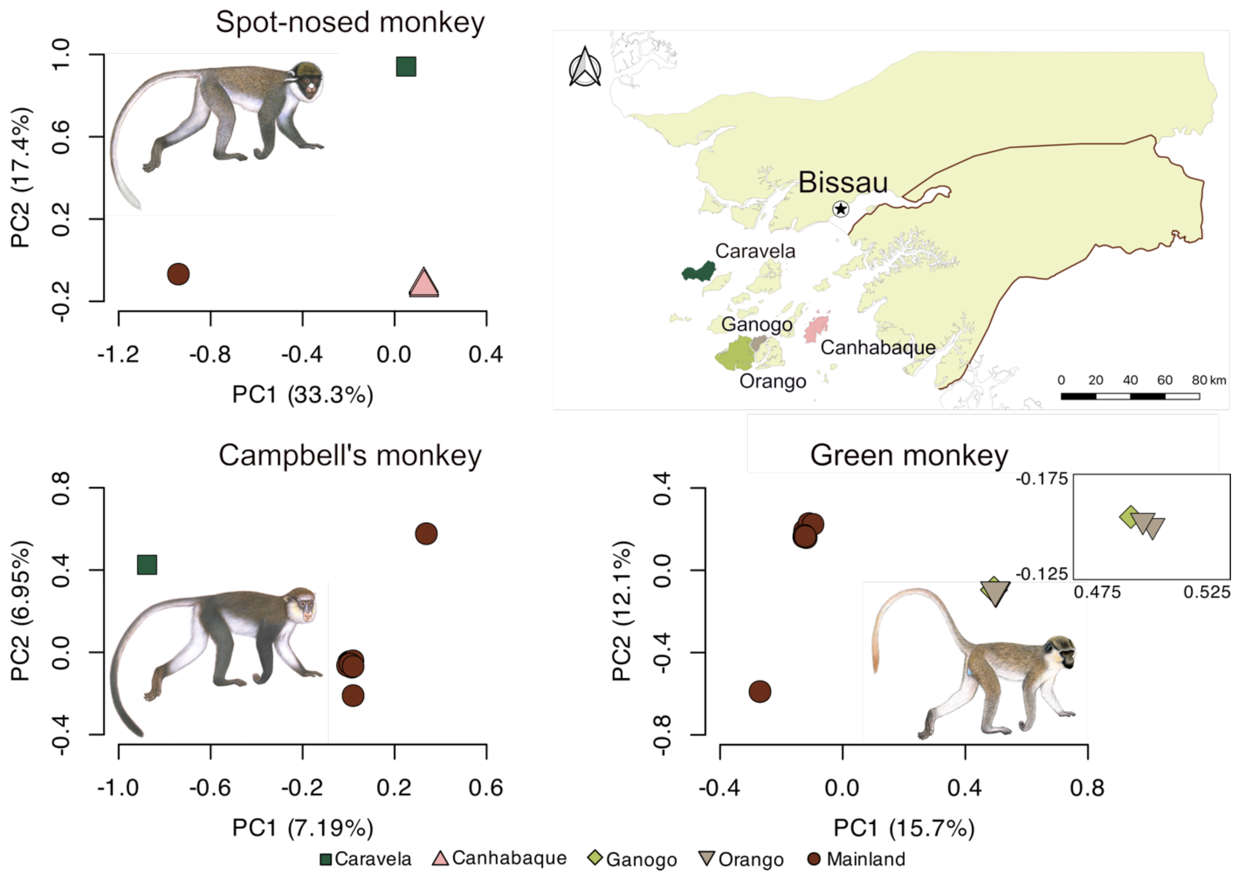


Figure 5.1 Principal Component Analysis (PCA) based on autosomal biallelic single nucleotide polymorphisms. An inset focusing on the insular green monkeys is shown on the right of the green monkey PCA plot. Each individual sample is coloured according to their sampling area, as illustrated on the map of Guinea-Bissau, West Africa. The exact provenance of the mainland samples of Campbell's and green monkeys is not known but they likely originate from Southern Guinea-Bissau (represented by the brown contour in the map in the upper right side) (Minhós et al., 2013; Ferreira da Silva et al., 2021). The geographic origin of the mainland spot-nosed sample is unknown, but it likely belongs to the eastern subspecies based on mtDNA analyses (Supplementary Figure 5.2). Illustrations copyright 2022 Stephen D. Nash / IUCN SSC Primate Specialist Group. Used with permission.

Changes in N_e over time were estimated using beta-PSMC analyses. Overall, the three species showed different demographic histories roughly before the onset of the Penultimate Glacial Period (PGP, > 200,000 YA; Figure 5.2 A). The maximum N_e of the three species was observed close to the end of the PGP (slight timing variation between species), after which they all underwent a severe decline in N_e that extends until the end of the Last Glacial Period (LGP, ~12,000 YA). The insular populations showed more rapid and severe declines than the mainland populations since the

PGP, with population trajectories diverging between 100,000 – 40,000 YA in the three species.

Genome-wide diversity and inbreeding

The insular individuals of the three species showed ~73 – 90 % higher proportion of the genome in ROH than mainland populations (Figure 5.2 B). The differences between insular and mainland populations were driven by both an increase in short (< 1Mb) and long ROHs (≥ 1Mb). The largest differences in the proportion of the genome in long ROHs was found in the spot-nosed monkey and Campbell's monkey from Caravela Island, which displayed a ~90 % and 98 % increase in ROH compared to the mainland individuals of the same species, respectively. Moreover, all insular individuals displayed lower heterozygosity (~15 – 53 % fewer autosomal heterozygous positions, Figure 5.2 C).

Genetic load

To understand if small effective population sizes and increased inbreeding associated with insularity led to changes in the frequency of deleterious mutations, I estimated the individual genetic load for each genome. After identifying the ancestral states of the segregating SNPs in the guenon species using three outgroup species, a total of 181,372 derived SNPs in the spot-nosed monkey, 217,297 in the Campbell's monkeys, and 189,118 in green monkeys, were annotated (Supplementary Table 5.2). In all three species, I found that the proportion of homozygous derived variants is higher in island individuals than in mainland individuals regardless of variant category (Figure 5.3). This is a pattern consistent with conversion of masked into realized genetic load in the insular populations by inbreeding and genetic drift. There was a general trend of lower numbers of LoF and other deleterious variants among insular individuals compared to their mainland conspecifics (Supplementary Table 5.2). However, after standardizing for the relative abundance of segregating alleles within species, there were no apparent differences between islands and mainland individuals (Figure 5.3). Additionally, I highlight that the patterns between the genetic load of insular and mainland individuals across different categories of deleterious variants were similar to those of synonymous variants, which are expected to behave neutrally (Figure 5.3).

In the insular spot-nosed monkeys a total of 17 genes containing LoF variants that have become fixed in homozygous states were identified, 32 genes in the insular Campbell's monkey, and eight genes in the insular green monkeys (Supplementary Table 5.4). These sets of genes were species-specific, with some being associated with immune response (spot-nosed monkey: APOL5; Campbell's monkey: ACP5, ADGRG5, TRBV7-3, REG3G; green monkey: IFI16) and fecundity (Campbell's monkey: PADI6). Gene ontology (GO) enrichment analysis revealed no overrepresented GO terms.

Differential variation in protein-coding genes between island and mainland populations

To explore the hypothesis that insularity can lead to specific, potentially adaptive, genetic and phenotypic changes between insular populations and their mainland counterparts, all differentially fixed positions between the island and mainland populations were identified in each species. I found differentially fixed variants in 2,794 protein-coding genes on the spot-nosed monkey, 491 on the Campbell's monkey, and 125 on the green monkey. Within these gene sets, 203 genes were found in at least two species (Supplementary Figure 5.6). The GO enrichment analysis of this overlapped gene set revealed several overrepresented terms, mostly related to various metabolic functions and organism developmental processes (Supplementary Table 5.4). Specifically, several of the genes with differential variation between insular and mainland populations are involved in cellular division and organogenesis (PDGFRA, TGFB2, E2F8, NIN), neuronal and muscular development (SYNE2, BRINP1, TNC, ARNT2, TENM4, ACTN3, FMN1), skeletal development (CHST11, COL2A1) and, thyroid development and functioning (PAX8).

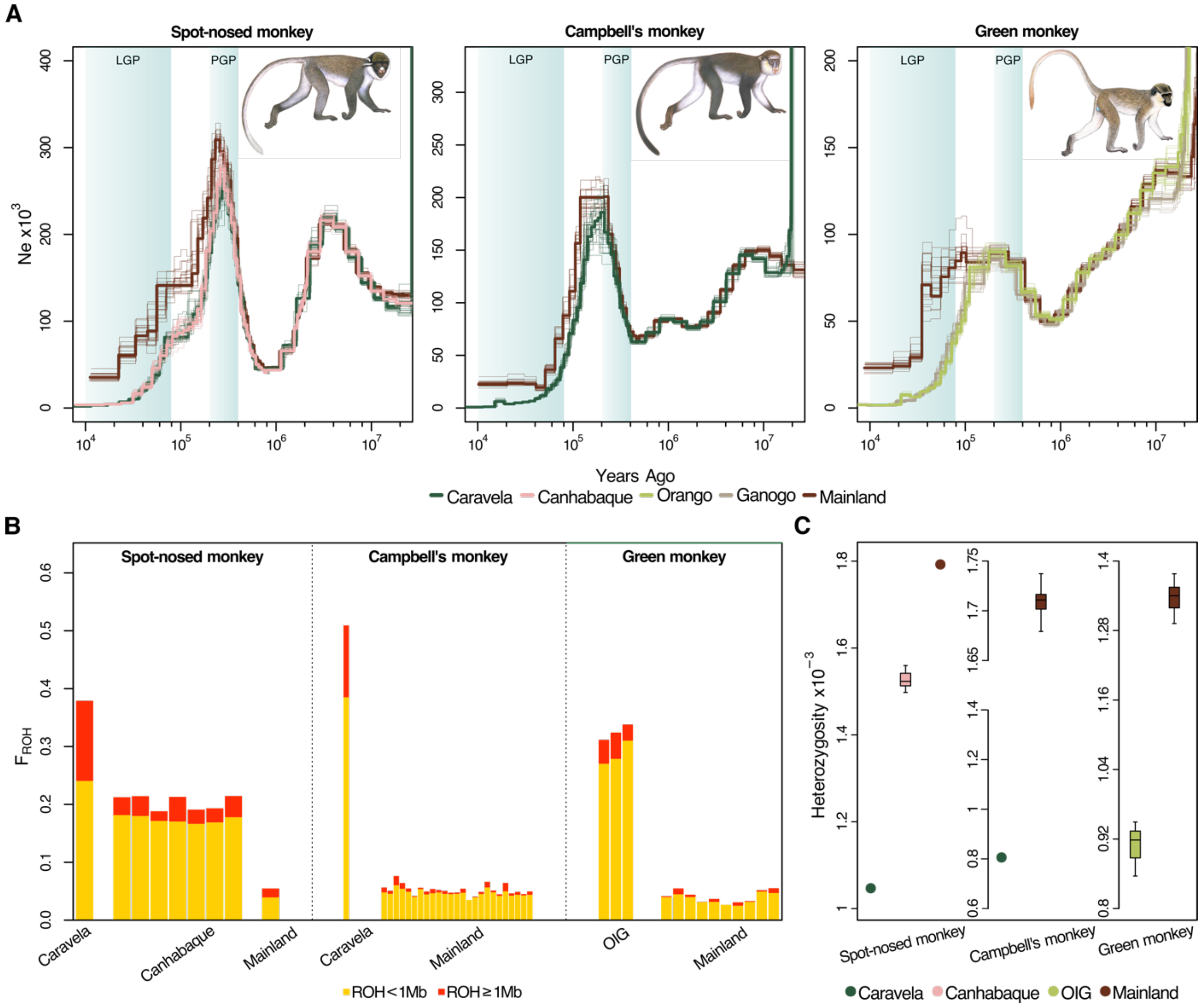


Figure 5.2 Genome-wide consequences of insularity in spot-nosed (left), Campbell's (center), and green monkey populations (right). A) Estimation of long-term changes in N_e of populations using the pairwise sequentially Markovian coalescent model of insular (Caravela, Canhabaque, Orango and Ganogo) and mainland populations as inferred using beta-PSMC (Liu et al. 2022). Colors correspond to the sampling locations. Bootstrap runs are represented as pale lines. Light blue backgrounds correspond to the Last Glacial Period (LGP) and the Penultimate Glacial Period (PGP). For illustrative purposes, only a single genome per population is represented as the variation within populations is negligible (Supplementary Figure 5.5). B) Faction of the genome in ROH (F_{ROH}). FROH for each sampled individual is represented in the stacked bars. The proportion of short ROHs (< 1 Mb, 111 – 1,450 guenon generations, ≈ 1,211 – 16,000 YA) and long ROHs (≥ 1 Mb, 110 generations ago, ≈ 1,200) are represented in yellow and red, respectively. C) Heterozygosity based on bi-allelic autosomal SNP positions. The circles or boxplots (when N > 3 genomes) were coloured according to the sampling location. Differences in autosomal heterozygosity between insular and mainland green monkeys were significant [(Welch's two sample t-test, p<0.001; statistical significance could not be tested for the other species (N < 3 genomes in one of the groups)]. Green monkey individuals from Ganogo and Orango islands were clustered together into the Orango Islands Group (OIG). Note differences on the y-axis for each species. Illustrations copyright 2022 Stephen D. Nash / IUCN SSC Primate Specialist Group. Used with permission.

Discussion

Insular populations are often of conservation concern as they are typically more susceptible to loss of genetic diversity due to demographic processes associated with island colonization. In this Chapter, I explored the genomic signatures of insularity and reduced population size in guenons, a primate group known for their overall high genetic diversity (Jensen et al. 2023; Kuderna et al. 2023). By comparing island and mainland populations in three guenon species from the Bijagós Archipelago, Guinea-Bissau (in West Africa), I explored their common genetic patterns which likely represent the broad effects of insularity. Finally, the results were used to inform future conservation management actions for the three guenon species of the Bijagós Archipelago in Guinea-Bissau. These results are potentially applicable to other wide-spread and genetically diverse taxa, now under increasing threats from anthropogenic activities.

Genome-wide effects of insularity

In all three guenon species considered here, island populations were genetically differentiated from the mainland populations. The timing of the divergence between insular and mainland populations varied between species but has generally happened between the PGP and the start of the LGP (250,000 – 100,000 YA), according to bPSMC analyses. Since this time period, the island populations have experienced a steadier decline in the estimated N_e than their mainland counterparts. The observed lower genome-wide heterozygosity and higher F_{ROH} in the insular populations of all three species compared to mainland populations support long-term reduction of the N_e as suggested by the bPSMC. The genome-wide effects of population bottlenecks associated with island colonization could be further exacerbated in archipelagos, where sequential colonization events from the initial founding populations are likely (Allendorf et al. 2013; Martin et al. 2023). In the study species, this effect can potentially be observed in the spot-nosed monkey individual from Caravela Island, the outermost island of the Bijagós Archipelago. This individual has lower genome-wide diversity and higher F_{ROH} compared to the Canhabaque population.

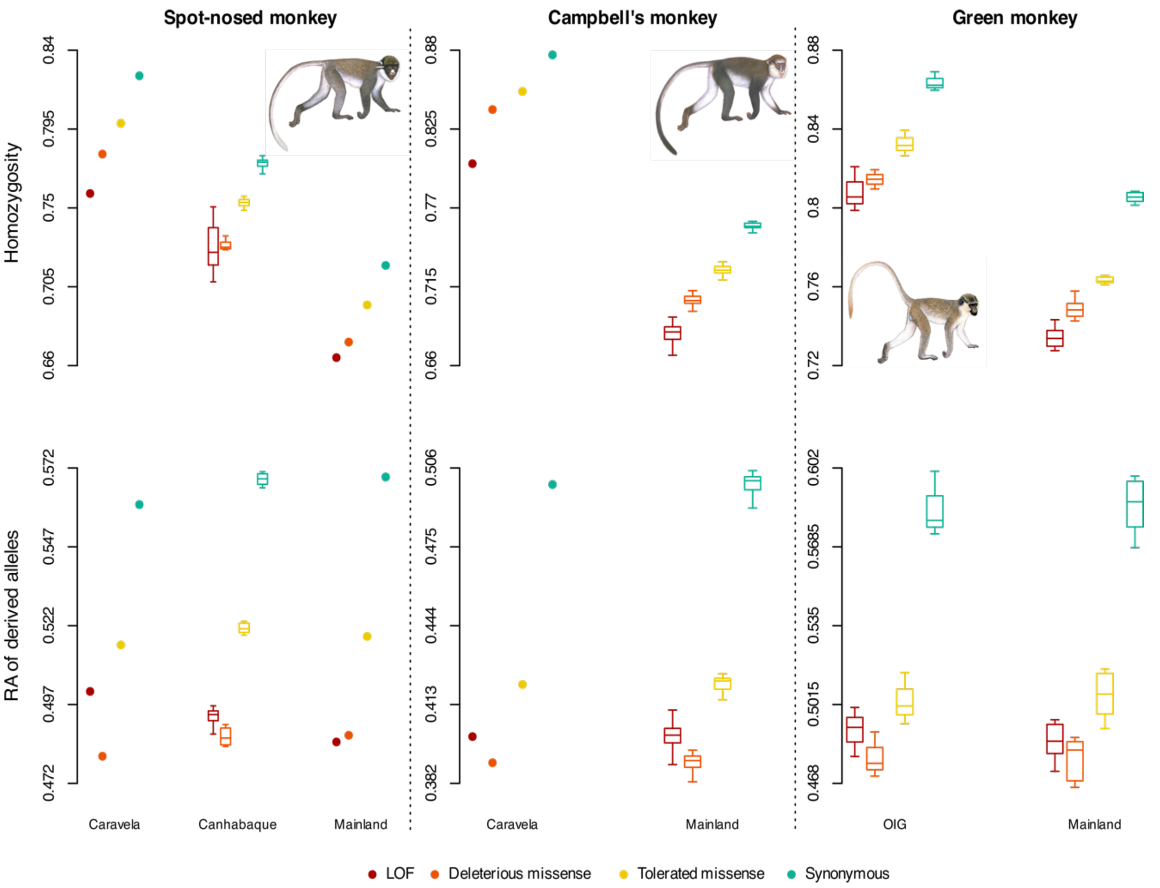


Figure 5.3 Individual mutational load in insular spot-nosed, Campbell's, and green monkey populations. Upper panels: Homozygosity of variants across different categories of mutational effects of the annotated derived SNPs. Lower panels: Relative abundance of derived alleles. Boxplots are presented when N > 3 individuals. The statistical comparisons for both the homozygosity and the relative abundance of derived alleles was performed within each variant category (i.e., LoF insular vs. LoF mainland) for the green monkey [Welch's two sample t-test: homozygosity $p < 0.01$ across all categories; relative abundance of derived alleles, $0.32 < p < 0.90$ across all categories; statistical significance could not be tested for the other species ($N < 3$ genomes in one of the groups)]. Missense mutations were classified as potentially deleterious or tolerated based on the experimental exchangeability score (Yampolsky and Stoltzfus 2005).

The timing of divergence between the insular and mainland populations as estimated by the bPSMC analyses is unexpectedly old considering the proposed timing of isolation of the Bijagós Archipelago during the Holocene (ca 12,000 – 6,000 YA; Alves 2007). Previous works have shown that fluctuations in stair-case plots from coalescent-based methods can reflect true changes in N_e, cessation of panmixia, or both (Mazet et al. 2016). Indeed, the timing of the divergence of the N_e trajectories coincides with cycles of dryer and wetter climate and, consequently repeated retraction and expansion of forests across sub-Saharan Africa (Hoag and Svenning 2017) – a known promoter of changes in connectivity in forest dwelling species such as primates (van der Valk et al. 2024). Thus, it is plausible that the reported divergence of the N_e trajectories reflects a scenario of the disruption of panmixia/population structure arising prior to the colonization of the archipelago. Moreover, the mainland populations included here may not represent the most closely related source populations, particularly for the spot-nosed monkey, whose presence has not been reported from mainland Guinea-Bissau for over 30 years.

A recurring question in conservation genomics regarding the fate of small and inbred populations, such as those inhabiting insular systems, is whether genetic load is accumulating after a demographic bottleneck or if genetic purging is effective in decreasing the genetic load of highly deleterious mutations, thus preventing mutational meltdown. The decrease in the frequency of LoF variants following the conversion of masked load (i.e., heterozygous, partially recessive deleterious mutations) into realized load (i.e., homozygous states) is often the main diagnostic features of purging in bottlenecked populations (Xue et al. 2015; Grossen et al. 2020; Dussex et al. 2021; Khan et al. 2021; von Seth et al. 2022; van der Valk et al. 2024). Although a higher proportion of homozygous LoF variants was found in the insular guenon populations studied here, similar patterns were present in missense and neutral variants. Furthermore, after standardizing the genetic load to the number of segregating sites (i.e., relative abundance of derived alleles), I observed that insular and mainland individuals have similar numbers of deleterious alleles across all variant categories, which is expected under genetic drift alone (Dussex et al. 2023; Smeds and Ellegren 2023).

Another commonly reported genomic consequence of prolonged periods of small N_e is the accumulation of mildly deleterious (e.g., missense) mutations (Dussex et al. 2023). Since drift diminishes the effectiveness of purifying selection, *de novo* mildly deleterious mutations are more likely to drift to higher frequencies in small populations (Dussex et al. 2023). I did not observe such a pattern in the insular guenon populations, suggesting that the effectiveness of purifying selection against deleterious derived alleles has been retained overall (Dussex et al. 2023). I argue that the insular guenon populations of the Bijagós Archipelago lack the typical genomic features of small, inbred populations. These results suggest that the increased inbreeding and loss of genetic diversity in the insular populations have, so far, not led to increased purging of highly deleterious variants nor accumulation of genetic load (Robinson et al. 2016; Dussex et al. 2023; Taylor et al. 2024).

Several guenon species have been successful in establishing insular populations following human-assisted introduction (e.g., green monkeys in Cape Verde Hazevoet and Masseti 2011; Almeida et al. 2024; and multiple Caribbean Islands Denham and Denham 1981, mona monkeys, *Cercopithecus mona* Schreber, 1774*,* in São Tomé and Príncipe and Grenada Horsburgh et al. 2003; Glenn and Bensen 2013). Based on historical records, these populations are thought to have been founded by relatively small numbers of individuals and the populations have increased to thousands of individuals within 300 – 500 years. While most of these populations remain poorly studied, there are no reports suggesting the presence of deleterious inbreeding effects on the islands when compared to mainland Africa (e.g., Grenada mona monkeys; Glenn and Bensen, 2013). The success of guenon colonization and potential avoidance of inbreeding effects could be attributed to a high ecological and behavioural flexibility, and the relatively beneficial island ecosystems (e.g., decreased interspecific competition; Glenn and Bensen, 2013) and overall high genetic diversity (Jensen et al. 2023; Kuderna et al. 2023).

Finally, some differentially fixed variation between insular and mainland populations was observed. Some of the affected genes were present in two or three species and encoded for metabolic and developmental processes, which included cellular proliferation and organ size. While the specific phenotypic expression of these genes is unknown, these functional categories are amongst those commonly associated with the “island syndrome” in vertebrate species (Nolte et al. 2020; Sendell-Price et al. 2020; Payseur and Jing 2021). As populations are exposed to novel ecological challenges in insular ecosystems, which include changes in inter-specific competition and predation dynamics, and access to novel food items, selection pressures acting in insular and source populations are likely to differ in several aspects (Welles and Dlugosch 2019). Common adaptations to the same insular ecosystem are a possible mechanism behind the overlapping gene sets across the three species (Welles and Dlugosch 2019; Payseur and Jing 2021). However, since this work suggest that genetic drift is likely the predominant evolutionary mechanism differentiating insular and mainland populations, an alternative explanation is that these genes are under relaxed selection on the islands. The relaxation of selection in genes linked to increased fitness in the mainland populations would allow drift to fix non-synonymous variants that may be otherwise deleterious on the mainland (Cui et al. 2021; Wang et al. 2023). I stress however, that these results should be interpreted with caution as differences in phenotypic traits between the guenon populations of the Bijagós Archipelago and the mainland populations have never been studied, the current mapping to a distant reference genome (rhesus macaque) and unbalanced sample sizes prevents the unbiased assessment of differentially fixed non-synonymous variation, as neutrally evolving variation could be wrongly annotated as protein coding variation (e.g., pseudogenes).

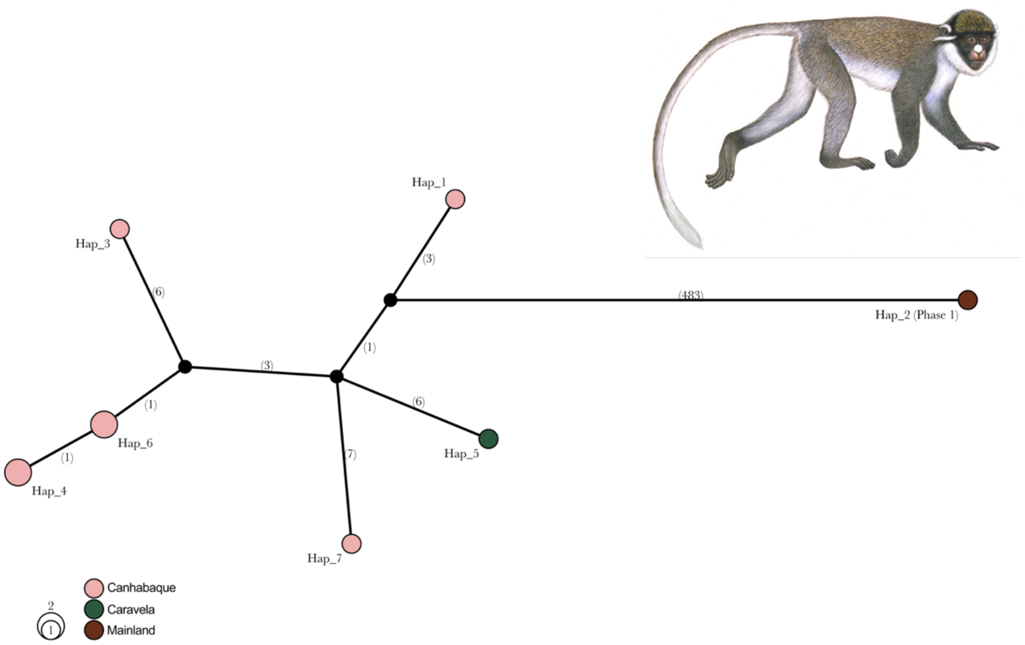
Importance of insular populations for the conservation of genetically diverse species

Even though guenon populations of the Bijagós Archipelago are thought to be more threatened than their mainland counterparts - due to the overall loss of genetic diversity and inbreeding associated with insularity - this study did not find increased accumulation of deleterious variation on the islands. However, the increased inbreeding and genetic drift on the islands resulted in higher levels of realized load which may affect population fitness negatively. I found fixed LoF variants in genes involved in immune and reproductive functions in the insular populations of the three guenon species, although their fitness effects are unknown.

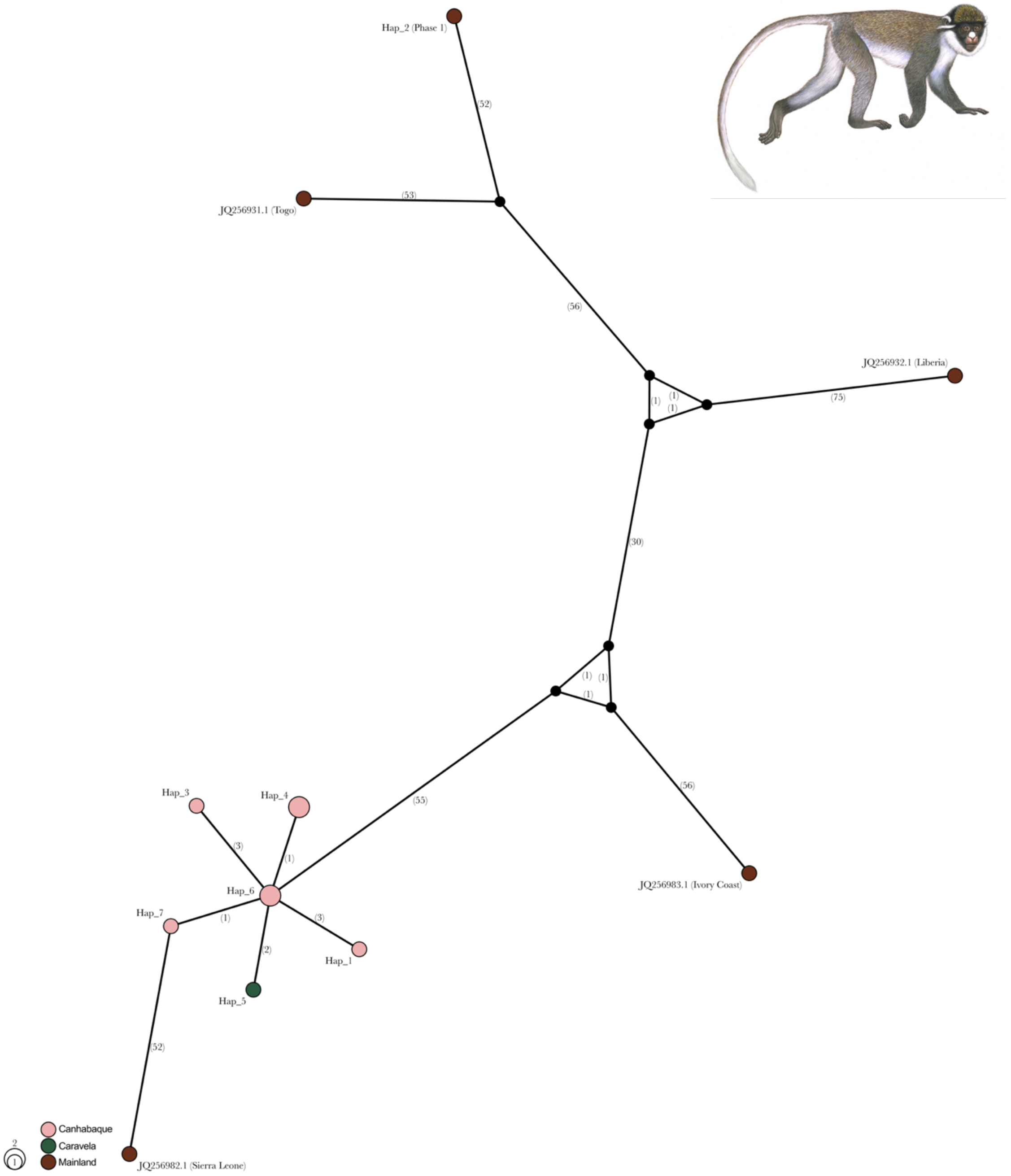
It is important to highlight that natural processes are not the only factor determining individual survival of these primates. Habitat degradation and harvesting of individuals for meat consumption are current conservation threats, which may increase their risk of extinction (Colmonero-Costeira et al. 2023). Indeed, the insular populations of the three species show significantly higher fraction of their genome in long runs of homozygosity, which likely arose due to mating of closely related individuals in the last 1,200 years after the arrival of humans on the archipelago. In particular, the illegal harvesting for the commercial meat trade has been described recently and is thought to be an increasing practice on the islands (Colmonero-Costeira et al. 2023). In the absence of immediate threats from genetic factors, long-term conservation of these insular populations should be promoted mainly by reducing their immediate threats and safeguarding from additional loss of diversity by anthropogenic factors. For Guinea-Bissau in particular, the insular guenon populations are of high conservation interest, particularly the spot-nosed monkeys. Here it was shown that these relict populations are not genetically depauperate and could potentially act as reservoirs for the recently extinct (or very rare) mainland populations, creating the opportunity for future re-introduction of the species in mainland Guinea-Bissau.

Recent studies have proposed that small and threatened populations that underwent extensive purging are expected to be less sensitive to the effects of additional bottlenecks and can tolerate smaller N_e and still avoid severe inbreeding depression and extinction due to genetic factors (Caballero et al. 2016). However, not much is known about the response of genetically diverse species to demographic bottlenecks, such as the insular guenons studied here. Akin to this system, high realized genetic load in the absence of purging following population bottlenecks has been reported in other widespread and diverse species, such as the North American caribou (*Rangifer tarandus* Linnaeus, 1758; Taylor et al. 2024) and the Channel Island fox (*Urocyon littoralis* Baird, 1857; Robinson et al. 2016). In these populations the interplay between the increasing anthropogenic threats and the dynamics of deleterious variation following demographic declines remains poorly studied and ought to be further investigated in order to pre-emptively promote their conservation.

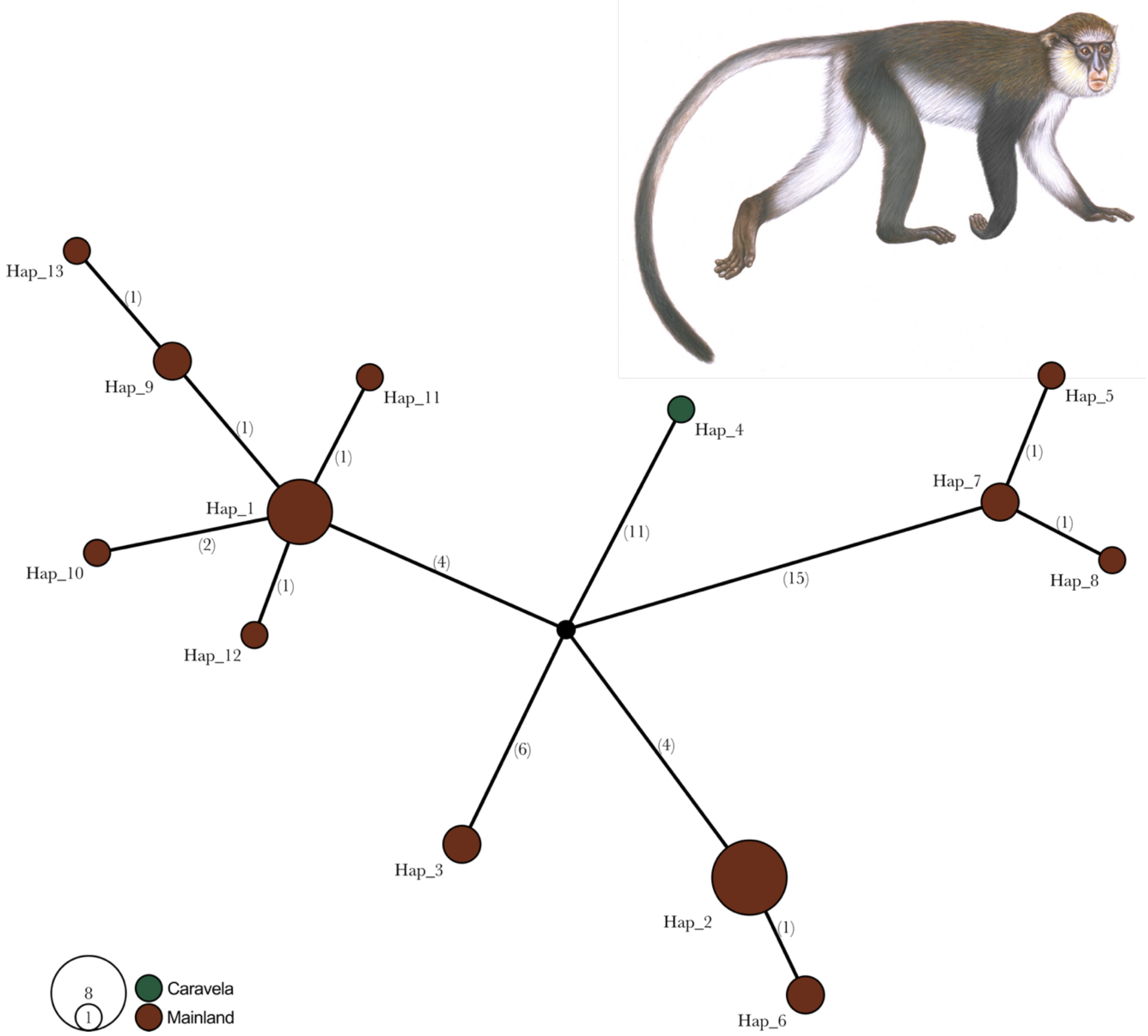
Supplementary Materials



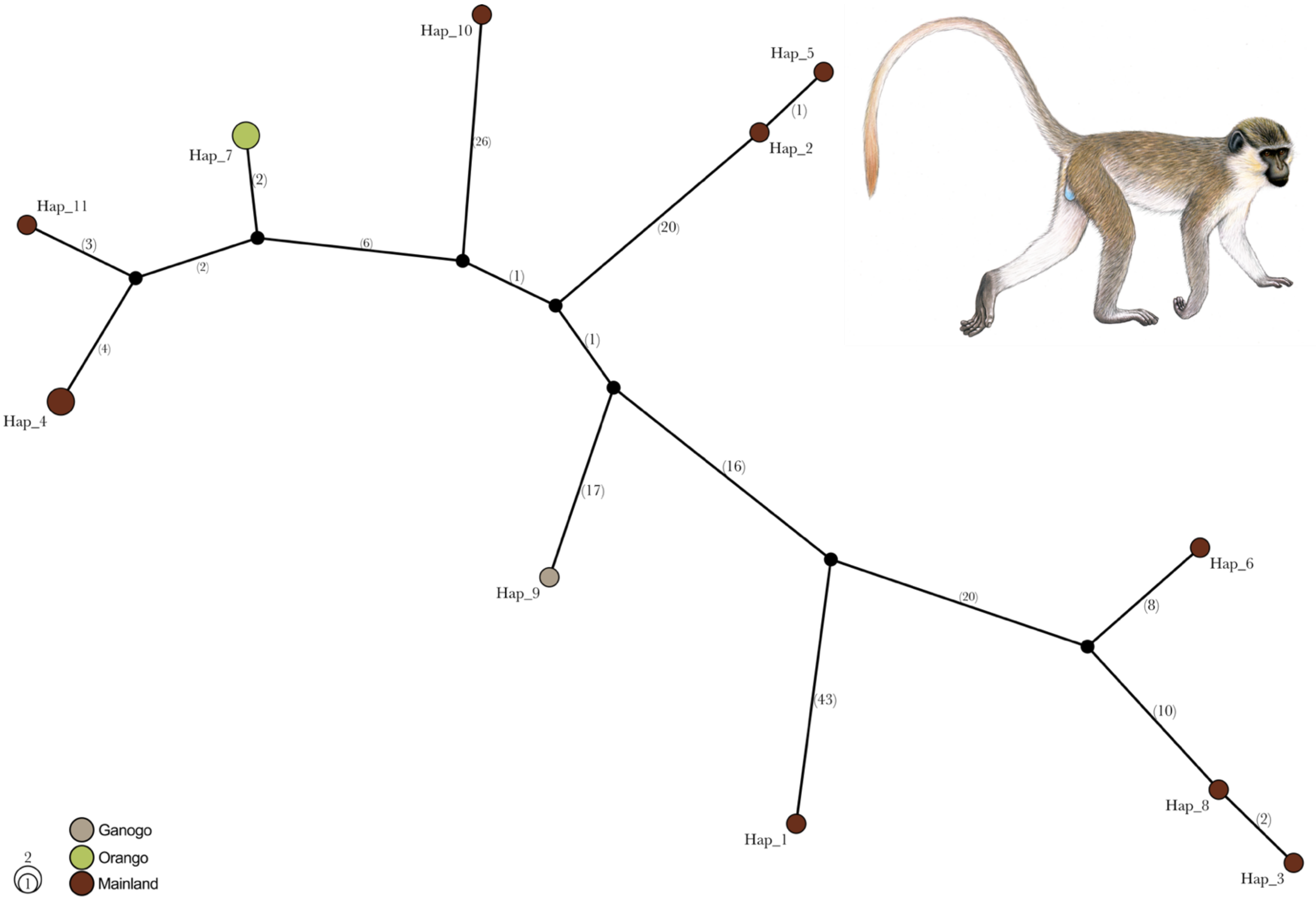
Supplementary Figure 5.1 Spot-nosed monkey (*Cercopithecus petaurista*) haplotype network based on whole mitochondrial sequences. Haplotype size is proportional to the number of samples and are coloured according to their sampling location in Guinea-Bissau. There are no shared haplotypes between sampling locations. Note that the spot-nosed monkey Phase_1 mainland sample is of unknow origin (Kuderna et al. 2023) but likely belongs to the Eastern spot-nosed monkey subspecies (*Cercopithecus petaurista petaurista*). The number of mutational steps between haplotypes is annotated on the branches. Illustrations copyright 2022 Stephen D. Nash / IUCN SSC Primate Specialist Group. Used with permission.



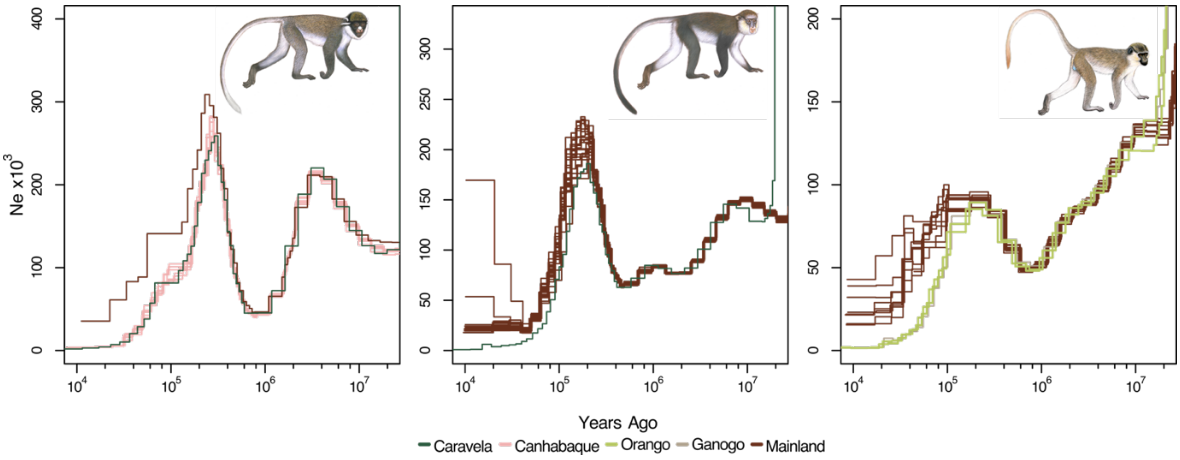
Supplementary Figure 5.2 Spot-nosed monkey (*Cercopithecus petaurista*) haplotype network based on whole mitochondrial sequences with mitochondrial genomes publicly available in GenBank. Sampling locations were extracted from Guschanski et al., 2013. Haplotype size is proportional to the number of samples and are coloured according to their sampling location in Guinea-Bissau. There are no shared haplotypes between sampling locations. Note that the spot-nosed monkey Phase_1 mainland sample is of unknow origin (Kuderna et al., 2023) but likely belongs to the Eastern spot-nosed monkey subspecies (*Cercopithecus petaurista petaurista*). The number of mutational steps between haplotypes is annotated on the branches. Illustrations copyright 2022 Stephen D. Nash / IUCN SSC Primate Specialist Group. Used with permission.



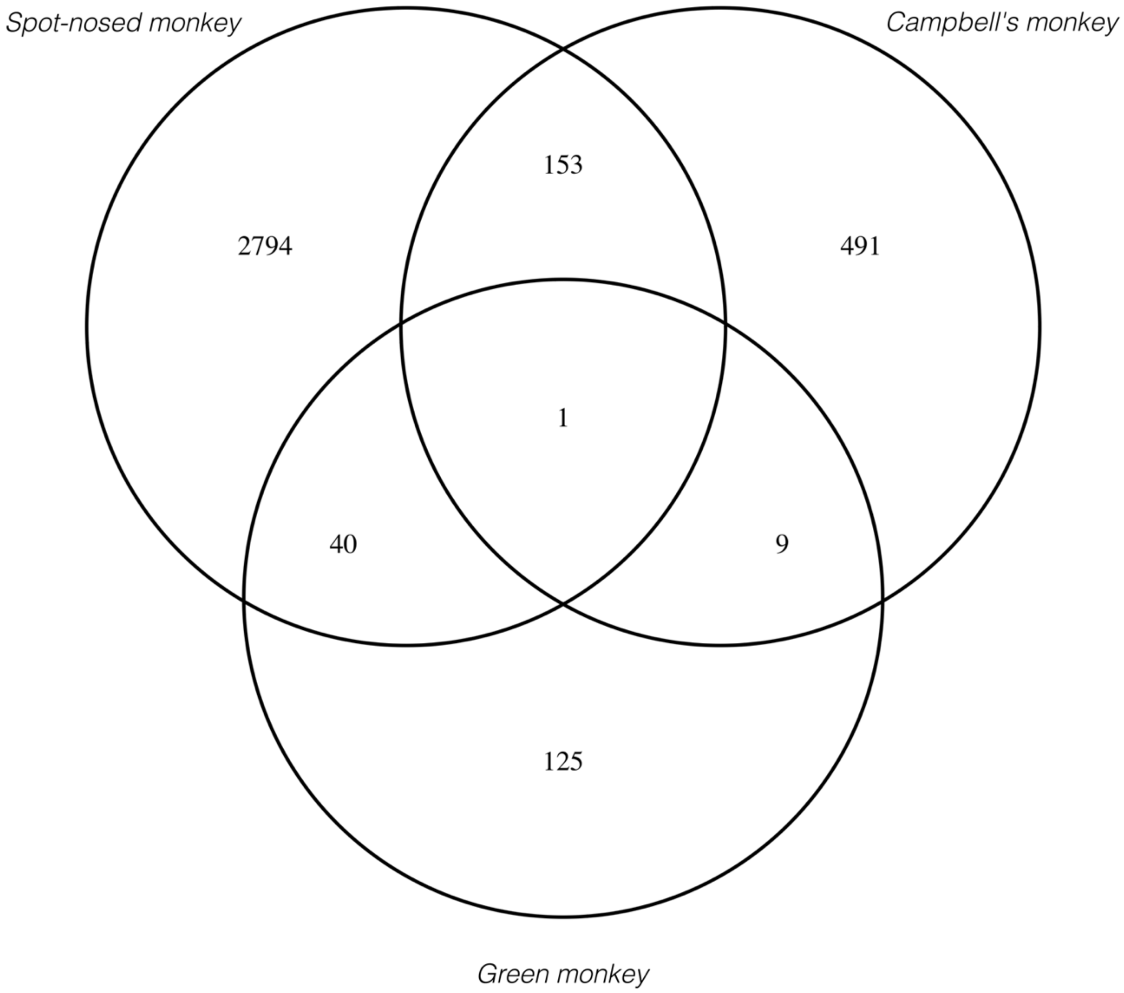
Supplementary Figure 5.3 Campbell's monkey (*Cercopithecus campbelli*) haplotype network based on whole mitochondrial sequences. Haplotype size is proportional to the number of samples and are coloured according to their sampling location in Guinea-Bissau. There are no shared haplotypes between sampling locations. The number of mutational steps between haplotypes is annotated on the branches. Illustrations copyright 2022 Stephen D. Nash / IUCN SSC Primate Specialist Group. Used with permission.



Supplementary Figure 5.4 Green monkey (*Chlorocebus sabaeus*) haplotype network based on whole mitochondrial sequences. Haplotype size is proportional to the number of samples and are coloured according to their sampling location in Guinea-Bissau. There are no shared haplotypes between sampling locations. The number of mutational steps between haplotypes is annotated on the branches. Illustrations copyright 2022 Stephen D. Nash / IUCN SSC Primate Specialist Group. Used with permission.



Supplementary Figure 5.5 Beta-PSMC analysis for all the spot-nosed monkey (*Cercopithecus petaurista*; left), Campbell's monkey (*Cercopithecus campbelli*; middle), and green monkey (*Chlorocebus sabaeus*; right) genomes. Each line represents a distinct genome and are coloured according to the sampling location. Illustrations copyright 2022 Stephen D. Nash / IUCN SSC Primate Specialist Group. Used with permission.



Supplementary Figure 5.6 Venn diagram of illustrating the number of protein-coding genes containing differentially fixed variants overlapping in the spot-nosed monkey (*Cercopithecus petaurista*: top left), the Campbell's monkey (*Cercopithecus campbelli*; top right) and the green monkey (*Chlorocebus sabaeus*; bottom). Each line represents a distinct genome and are coloured according to the sampling location. Illustrations copyright 2022 Stephen D. Nash / IUCN SSC Primate Specialist Group. Used with permission.

Supplementary Table 5.1 Sample information and autosome mapping coverage.

Sample ID	Species	Sampling location	Other info	Autosome mapping coverage
PD_0984_Cercopithecus_campbelli	*Cercopithecus campbelli*	Mainland	southern Guinea-Bissau (Ferreira da Silva et al., 2017)	30.70
PD_0985_Cercopithecus_campbelli	*Cercopithecus campbelli*	Mainland	southern Guinea-Bissau (Ferreira da Silva et al., 2017)	30.58
PD_0990_Cercopithecus_campbelli	*Cercopithecus campbelli*	Bijagós Archipelago (Caravela)		31.63
PD_0998_Cercopithecus_campbelli	*Cercopithecus campbelli*	Mainland	southern Guinea-Bissau (Ferreira da Silva et al., 2017)	30.95
PD_1001_Cercopithecus_campbelli	*Cercopithecus campbelli*	Mainland	Bissau (Minhós et al., 2013)	33.27
PD_1006_Cercopithecus_campbelli	*Cercopithecus campbelli*	Mainland	southern Guinea-Bissau (Ferreira da Silva et al., 2017)	31.62
PD_1007_Cercopithecus_campbelli	*Cercopithecus campbelli*	Mainland	southern Guinea-Bissau (Ferreira da Silva et al., 2017)	32.72
PD_1008_Cercopithecus_campbelli	*Cercopithecus campbelli*	Mainland	southern Guinea-Bissau (Ferreira da Silva et al., 2017)	31.76
PD_1009_Cercopithecus_campbelli	*Cercopithecus campbelli*	Mainland	southern Guinea-Bissau (Ferreira da Silva et al., 2017)	31.42
PD_1010_Cercopithecus_campbelli	*Cercopithecus campbelli*	Mainland	southern Guinea-Bissau (Ferreira da Silva et al., 2017)	32.01
PD_1011_Cercopithecus_campbelli	*Cercopithecus campbelli*	Mainland	southern Guinea-Bissau (Ferreira da Silva et al., 2017)	31.23
PD_1012_Cercopithecus_campbelli	*Cercopithecus campbelli*	Mainland	southern Guinea-Bissau (Ferreira da Silva et al., 2017)	30.50
PD_1014_Cercopithecus_campbelli	*Cercopithecus campbelli*	Mainland	southern Guinea-Bissau (Ferreira da Silva et al., 2017)	29.88
PD_1015_Cercopithecus_campbelli	*Cercopithecus campbelli*	Mainland	southern Guinea-Bissau (Ferreira da Silva et al., 2017)	31.47

PD_1016_Cercopithecus_campbelli	*Cercopithecus campbelli*	Mainland	southern Guinea-Bissau (Ferreira da Silva et al., 2017)	33.82
PD_1017_Cercopithecus_campbelli	*Cercopithecus campbelli*	Mainland	southern Guinea-Bissau (Ferreira da Silva et al., 2017)	30.80
PD_1018_Cercopithecus_campbelli	*Cercopithecus campbelli*	Mainland	southern Guinea-Bissau (Ferreira da Silva et al., 2017)	30.52
PD_1019_Cercopithecus_campbelli	*Cercopithecus campbelli*	Mainland	southern Guinea-Bissau (Ferreira da Silva et al., 2017)	30.31
PD_1020_Cercopithecus_campbelli	*Cercopithecus campbelli*	Mainland	southern Guinea-Bissau (Ferreira da Silva et al., 2017)	30.82
PD_1021_Cercopithecus_campbelli	*Cercopithecus campbelli*	Mainland	southern Guinea-Bissau (Ferreira da Silva et al., 2017)	31.14
PD_1023_Cercopithecus_campbelli	*Cercopithecus campbelli*	Mainland	southern Guinea-Bissau (Ferreira da Silva et al., 2017)	30.03
PD_1024_Cercopithecus_campbelli	*Cercopithecus campbelli*	Mainland	southern Guinea-Bissau (Ferreira da Silva et al., 2017)	30.97
PD_1173_Cercopithecus_campbelli	*Cercopithecus campbelli*	Mainland	southern Guinea-Bissau (Ferreira da Silva et al., 2017)	32.38
PD_1175_Cercopithecus_campbelli	*Cercopithecus campbelli*	Mainland	southern Guinea-Bissau (Ferreira da Silva et al., 2017)	35.00
PD_1177_Cercopithecus_campbelli	*Cercopithecus campbelli*	Mainland	southern Guinea-Bissau (Ferreira da Silva et al., 2017)	32.07
PD_1178_Cercopithecus_campbelli	*Cercopithecus campbelli*	Mainland	southern Guinea-Bissau (Ferreira da Silva et al., 2017)	31.72
PD_0091_Cercopithecus_petaurista	*Cercopithecus petaurista*	Mainland	published in Kuderna et al., 2023	32.91
PD_0991_Cercopithecus_petaurista_buettikoferi	*Cercopithecus petaurista*	Bijagós Archipelago (Caravela)		30.54
PD_0992_Cercopithecus_petaurista_buettikoferi	*Cercopithecus petaurista*	Bijagós Archipelago (Canhabaque)		27.06

PD_0995_Cercopithecus_petaurista_buettikoferi	*Cercopithecus petaurista*	Bijagós Archipelago (Canhabaque)		27.13
PD_0996_Cercopithecus_petaurista_buettikoferi	*Cercopithecus petaurista*	Bijagós Archipelago (Canhabaque)		27.25
PD_0997_Cercopithecus_petaurista_buettikoferi	*Cercopithecus petaurista*	Bijagós Archipelago (Canhabaque)		29.06
PD_1170_Cercopithecus_petaurista_buettikoferi	*Cercopithecus petaurista*	Bijagós Archipelago (Canhabaque)		26.85
PD_1171_Cercopithecus_petaurista_buettikoferi	*Cercopithecus petaurista*	Bijagós Archipelago (Canhabaque)		27.43
PD_1172_Cercopithecus_petaurista_buettikoferi	*Cercopithecus petaurista*	Bijagós Archipelago (Canhabaque)		28.75
PD_0983_Chlorocebus_sabaeus	*Chlrocebus sabaeus*	Mainland	southern Guinea-Bissau (Ferreira da Silva et al., 2017)	25.95
PD_0986_Chlorocebus_sabaeus	*Chlrocebus sabaeus*	Mainland	southern Guinea-Bissau (Ferreira da Silva et al., 2017)	29.50
PD_0987_Chlorocebus_sabaeus	*Chlrocebus sabaeus*	Mainland	southern Guinea-Bissau (Ferreira da Silva et al., 2017)	28.35
PD_0988_Chlorocebus_sabaeus	*Chlrocebus sabaeus*	Mainland	southern Guinea-Bissau (Ferreira da Silva et al., 2017)	28.24
PD_0989_Chlorocebus_sabaeus	*Chlrocebus sabaeus*	Bijagós Archipelago (Ganogo)		31.63
PD_0993_Chlorocebus_sabaeus	*Chlrocebus sabaeus*	Bijagós Archipelago (Orango)		28.50
PD_0994_Chlorocebus_sabaeus	*Chlrocebus sabaeus*	Bijagós Archipelago (Orango)		28.57
PD_0999_Chlorocebus_sabaeus	*Chlrocebus sabaeus*	Mainland	Bissau (Minhós et al., 2013)	31.56
PD_1000_Chlorocebus_sabaeus	*Chlrocebus sabaeus*	Mainland	Bissau (Minhós et al., 2013)	29.55

PD_1002_Chlorocebus_sabaeus	*Chlrocebus sabaeus*	Mainland	Bissau (Minhós et al., 2013)	26.24
PD_1022_Chlorocebus_sabaeus	*Chlrocebus sabaeus*	Mainland	southern Guinea-Bissau (Ferreira da Silva et al., 2017)	29.49
PD_1174_Chlorocebus_sabaeus	*Chlrocebus sabaeus*	Mainland	southern Guinea-Bissau (Ferreira da Silva et al., 2017)	30.07
PD_1176_Chlorocebus_sabaeus	*Chlrocebus sabaeus*	Mainland	southern Guinea-Bissau (Ferreira da Silva et al., 2017)	29.01

Supplementary Table 5.2. Number of segregating sites per category of mutational effects on protein-coding genes for the three guenon species.

Spot-nosed monkey				
	Caravela	Canhabaque [†]	Mainland	Total[‡]
Synonymous	66,289	68,926±803	71,565	10,7964
Tolerated missense (Ex)	29,216	30,181±347	31,165	50,921
Deleterious missense (Ex)	10,959	11,409±144	11,823	20,303
LoF	1,245	1,247±11	1,273	2,184
Campbell's monkey				
	Caravela		Mainland[†]	Total
Synonymous	66,531		71,783±658	12,6305
Tolerated missense (Ex)	28,164		30,444±272	62,452
Deleterious missense (Ex)	10,857		11,846±130	25,905
LoF	1,195		1,255±17	2,635
Green monkey				
	OIG		Mainland[†]	Total
Synonymous	69,048±1807		71,426±1421	11,0026
Tolerated missense (Ex)	30,027±757		31,341±602	54,681
Deleterious missense (Ex)	11,728±268		12,142±231	22,206
LoF	1,250±29		1,292±23	2,305

† for sampling locations with N > 3, values represent the mean ± SD
‡ total number of derived variants within species
EX missense mutations were classified as potentially deleterious or tolerated based on the experimental exchangeability score (Yampolsky and Stoltzfus 2005).

Supplementary Table 5.3. List of genes containing LoF variants that have become fixed in the homozygous state in insular populations.

Species	**Genes/Transcripts (*Macaca mulatta*)**
Spot-nosed monkey	ENSMMUG00000051680
	ENSMMUG00000021448
	DACT2 - Dishevelled Binding Antagonist Of Beta Catenin 2
	PPIL6 - Peptidylprolyl Isomerase Like 6
	FAM162B - Family With Sequence Similarity 162 Member B
	SOX4 - SRY-Box Transcription Factor 4
	SLC25A4 - Solute Carrier Family 25 Member 4
	ENSMMUG00000050756
	APOL5 - Apolipoprotein L5
	ENSMMUG00000055526
	ENSMMUG00000052168
	ENSMMUG00000059839
	ENSMMUG00000050594
	ENSMMUG00000050747
	ENSMMUG00000054137
	ENSMMUG00000065197
	ENSMMUG00000052116
Campbell's monkey	ENSMMUG00000050830
	ARHGAP12 - Rho GTPase Activating Protein 12
	ENSMMUG00000051718
	ACP5 - Acid Phosphatase 5, Tartrate Resistant
	ZNF835 - Zinc Finger Protein 835
	C1H1orf167 - chromosome unknown C1orf167 homolog
	ENSMMUG00000062652
	ENSMMUG00000055109
	ENSMMUG00000050178
	ADGRG5 - Adhesion G Protein-Coupled Receptor G5
	PADI6 - Peptidyl Arginine Deiminase 6
	TRBV7-3 - T Cell Receptor Beta Variable 7-3
	ENSMMUG00000063097
	CKMT2 - Creatine Kinase, Mitochondrial 2
	ENSMMUG00000060509
	REG3G - Regenerating Family Member 3 Gamma
	PIGH - Phosphatidylinositol Glycan Anchor Biosynthesis Class H
	LRRC27 - Leucine Rich Repeat Containing 27
	GPR35 - G Protein-Coupled Receptor 35
	ENSMMUG00000056921
	ENSMMUG00000057135
	OR51F1 - Olfactory Receptor Family 51 Subfamily F Member 1

	ENSMMUG00000055884
	STXBP5L - Syntaxin Binding Protein 5L
	ENSMMUG00000058449
	ENSMMUG00000020261
	ENSMMUG00000058606
	ENSMMUG00000056939
	MAP6D1 - MAP6 Domain Containing 1
	TMPRSS6 - transmembrane serine protease 6
	MICOS13 - Mitochondrial Contact Site And Cristae Organizing System Subunit 13
	ENSMMUG00000058177
Green monkey	ENSMMUG00000050435
	IFI16 - Interferon Gamma Inducible Protein 16
	TEX261 - Testis Expressed 261
	ENSMMUG00000058409
	SGSH - N-sulfoglucosamine sulfohydrolase
	ZNF667 - Zinc Finger Protein 667
	ENSMMUG00000064724
	ENSMMUG00000055933

Supplementary Table 5.4 GO enrichment analysis of genes that contained differentially fixed variants in at least two of the studied guenon species

GO category	GO term id	GO term name	Adjusted p-value	GO gene intersections
GO:MF	GO:0032559	Adenyl ribonucleotide binding	8.29E-06	ABCA1,ABCA3,ABCA4,ABCB4,ABCC10,ATP4A,BLM,BRSK2,CAMK2A,CSF1R,DHX37,DNAH6,DYNC1H1,EIF2AK3,ENSMMUG00000013436,GRK5,KIF12,KIF16B,MDN1,MYH11,MYO18A,NLRP1,PDGFRA,PFAS,PFKL,PNPLA3,RFFL,SGK2,STK39,TNK2,TTN,UBE2U,VWA8,WNK4,ZNF805
	GO:0005524	ATP binding	1.29E-05	ABCA1,ABCA3,ABCA4,ABCB4,ABCC10,ATP4A,BLM,BRSK2,CAMK2A,CSF1R,DHX37,DNAH6,DYNC1H1,EIF2AK3,ENSMMUG00000013436,GRK5,KIF12,KIF16B,MDN1,MYH11,MYO18A,NLRP1,PDGFRA,PFAS,PFKL,RFFL,SGK2,STK39,TNK2,TTN,UBE2U,VWA8,WNK4,ZNF805
	GO:0030554	Adenyl nucleotide binding	4.36E-05	ABCA1,ABCA3,ABCA4,ABCB4,ABCC10,ATP4A,BLM,BRSK2,CAMK2A,CSF1R,DHX37,DNAH6,DYNC1H1,EIF2AK3,ENSMMUG00000013436,GRK5,KIF12,KIF16B,MDN1,MYH11,MYO18A,NLRP1,PDGFRA,PFAS,PFKL,PNPLA3,RFFL,SGK2,STK39,TNK2,TTN,UBE2U,VWA8,WNK4,ZNF805
	GO:0043167	Ion binding	1.94E-04	ABCA1,ABCA3,ABCA4,ABCB4,ABCC10,ACTN3,ARL6,ATP4A,BLM,BRSK2,CAMK2A,CHDH,CPA4,CSF1R,DCHS2,DHX37,DIDO1,DNAH6,DST,DYNC1H1,EFCAB5,EIF2AK3,ENSMMUG00000013436,F13A1,GRK5,HELZ2,HMCN2,HSPG2,KIF12,KIF16B,MACF1,MDN1,MGAT5B,MYH11,MYO18A,NIN,NLRP1,PDE10A,PDE6A,PDGFRA,PFAS,PFKL,PKD2L1,PNPLA3,POLE,RAG1,RFFL,RNF213,RPTN,RYR3,SGK2,SMYD4,SPTLC2,STK39,TATDN3,TNK2,TRIM67,TRPM2,TTN,TXNRD1,UBE2U,UMODL1,VWA8,WNK4,ZCCHC3,ZFHX3,ZFPM1,ZFR2,ZNF226,ZNF528,ZNF667,ZNF805

GO:1901363	Heterocyclic compound binding	4.12E-04	ABCA1,ABCA3,ABCA4,ABCB4,ABCC10,ARL6,ATP4A,BLM,BRSK2,CAMK2A,CHDH,CSF1R,DHX37,DNAH6,DYNC1H1,EIF2AK3,ENSMMUG00000013436,GRK5,KIF12,KIF16B,MDN1,MYH11,MYO18A,NLRP1,PDGFRA,PFAS,PFKL,PNPLA3,POLE,RFFL,SGK2,SPTLC2,STK39,TNK2,TRPM2,TTN,TXNRD1,UBE2U,VWA8,WNK4,ZNF805
GO:0140657	ATP-dependent activity	4.42E-04	ABCA1,ABCA3,ABCA4,ABCB4,ABCC10,ATP4A,BLM,DHX37,DNAH6,DYNC1H1,HELZ2,KIF12,KIF16B,MDN1,MYO18A,NLRP1,RFFL,RNF213,VWA8
GO:0032555	Purine ribonucleotide binding	6.87E-04	ABCA1,ABCA3,ABCA4,ABCB4,ABCC10,ARL6,ATP4A,BLM,BRSK2,CAMK2A,CSF1R,DHX37,DNAH6,DYNC1H1,EIF2AK3,ENSMMUG00000013436,GRK5,KIF12,KIF16B,MDN1,MYH11,MYO18A,NLRP1,PDGFRA,PFAS,PFKL,PNPLA3,RFFL,SGK2,STK39,TNK2,TTN,UBE2U,VWA8,WNK4,ZNF805
GO:1901265	Nucleoside phosphate binding	7.32E-04	ABCA1,ABCA3,ABCA4,ABCB4,ABCC10,ARL6,ATP4A,BLM,BRSK2,CAMK2A,CHDH,CSF1R,DHX37,DNAH6,DYNC1H1,EIF2AK3,ENSMMUG00000013436,GRK5,KIF12,KIF16B,MDN1,MYH11,MYO18A,NLRP1,PDGFRA,PFAS,PFKL,PNPLA3,POLE,RFFL,SGK2,STK39,TNK2,TTN,TXNRD1,UBE2U,VWA8,WNK4,ZNF805
GO:0000166	Nucleotide binding	7.32E-04	ABCA1,ABCA3,ABCA4,ABCB4,ABCC10,ARL6,ATP4A,BLM,BRSK2,CAMK2A,CHDH,CSF1R,DHX37,DNAH6,DYNC1H1,EIF2AK3,ENSMMUG00000013436,GRK5,KIF12,KIF16B,MDN1,MYH11,MYO18A,NLRP1,PDGFRA,PFAS,PFKL,PNPLA3,POLE,RFFL,SGK2,STK39,TNK2,TTN,TXNRD1,UBE2U,VWA8,WNK4,ZNF805
GO:0032553	Ribonucleotide binding	8.45E-04	ABCA1,ABCA3,ABCA4,ABCB4,ABCC10,ARL6,ATP4A,BLM,BRSK2,CAMK2A,CSF1R,DHX37,DNAH6,DYNC1H1,EIF2AK3,ENSMMUG00000013436,GRK5,KIF12,KIF16B,MDN1,MYH11,MYO18A,NLRP1,PDGFRA,PFAS,PFKL,PNPLA3,RFFL,SGK2,STK39,TNK2,TTN,UBE2U,VWA8,WNK4,ZNF805

GO:0035639	Purine ribonucleoside triphosphate binding	9.43E-04	ABCA1,ABCA3,ABCA4,ABCB4,ABCC10,ARL6,ATP4A,BLM,BRSK2,CAMK2A,CSF1R,DHX37,DNAH6,DYNC1H1,EIF2AK3,ENSMMUG00000013436,GRK5,KIF12,KIF16B,MDN1,MYH11,MYO18A,NLRP1,PDGFRA,PFAS,PFKL,RFFL,SGK2,STK39,TNK2,TTN,UBE2U,VWA8,WNK4,ZNF805
GO:0036094	Small molecule binding	1.00E-03	ABCA1,ABCA3,ABCA4,ABCB4,ABCC10,ACTN3,ARL6,ATP4A,BLM,BRSK2,CAMK2A,CHDH,CPA4,CSF1R,DCHS2,DHX37,DIDO1,DNAH6,DST,DYNC1H1,EFCAB5,EIF2AK3,ENSMMUG00000013436,F13A1,GRK5,HELZ2,HMCN2,HSPG2,KIF12,KIF16B,MACF1,MDN1,MGAT5B,MYH11,MYO18A,NIN,NLRP1,PDE10A,PDE6A,PDGFRA,PFAS,PFKL,PKD2L1,PNPLA3,POLE,RAG1,RFFL,RNF213,RPTN,RYR3,SGK2,SMYD4,SPTLC2,STK39,TATDN3,TNK2,TRIM67,TRPM2,TTN,TXNRD1,UBE2U,UMODL1,VWA8,WNK4,ZCCHC3,ZFHX3,ZFPM1,ZFR2,ZNF226,ZNF528,ZNF667,ZNF805
GO:0097367	Carbohydrate derivative binding	1.15E-03	ABCA1,ABCA3,ABCA4,ABCB4,ABCC10,ARL6,ATP4A,BLM,BRSK2,CAMK2A,COL2A1,CSF1R,DHX37,DNAH6,DYNC1H1,EIF2AK3,ENSMMUG00000013436,GRK5,KIF12,KIF16B,MDN1,MYH11,MYO18A,NLRP1,PDGFRA,PFAS,PFKL,PNPLA3,RFFL,SGK2,STK39,TNC,TNK2,TRPM2,TTN,UBE2U,VWA8,WNK4,ZNF805
GO:0016887	ATP hydrolysis activity	1.32E-03	ABCA1,ABCA3,ABCA4,ABCB4,ABCC10,ATP4A,DNAH6,DYNC1H1,MDN1,NLRP1,RFFL,RNF213,VWA8
GO:0017076	Purine nucleotide binding	2.53E-03	ABCA1,ABCA3,ABCA4,ABCB4,ABCC10,ARL6,ATP4A,BLM,BRSK2,CAMK2A,CSF1R,DHX37,DNAH6,DYNC1H1,EIF2AK3,ENSMMUG00000013436,GRK5,KIF12,KIF16B,MDN1,MYH11,MYO18A,NLRP1,PDGFRA,PFAS,PFKL,PNPLA3,RFFL,SGK2,STK39,TNK2,TTN,UBE2U,VWA8,WNK4,ZNF805

GO:0043168	Anion binding	2.95E-03	ABCA1,ABCA3,ABCA4,ABCB4,ABCC10,ARL6,ATP4A,BLM,BRSK2,CAMK2A,CHDH,CSF1R,DHX37,DNAH6,DYNC1H1,EIF2AK3,ENSMMUG00000013436,GRK5,KIF12,KIF16B,MDN1,MYH11,MYO18A,NLRP1,PDGFRA,PFAS,PFKL,PNPLA3,RFFL,SGK2,SPTLC2,STK39,TNK2,TRPM2,TTN,TXNRD1,UBE2U,VWA8,WNK4,ZNF805
GO:0005515	Protein binding	1.21E-02	ABCA1,ACTN3,AKAP6,ANKRD13A,ARHGEF17,ARL6,ARNT2,ARNTL2,ASB2,BLM,BRSK2,CAMK2A,CAMSAP1,CASP9,CBARP,CDC25C,CEP164,CLASP1,CLCN1,CLTCL1,CNTRL,COL2A1,COL6A3,CSF1R,CTDP1,DGCR2,DNAH6,DNAJB13,DST,DYNC1H1,E2F8,E4F1,EIF2AK3,EIF3C,ENSMMUG00000013436,ENSMMUG00000054038,FAM161A,FBXL16,FMN1,GNB1L,HMCN2,HSPG2,IGSF9,IL16,KIF12,KIF16B,LAMA3,LRRCC1,MACF1,MYH11,MYO18A,MYRIP,NCAPD2,NECTIN2,NIN,NLRP1,NLRP13,NLRP8,NRDE2,NWD1,OPLAH,OSBP,PDE10A,PDE6A,PDGFRA,PEAR1,PFKL,PKD1,PKD2L1,POMGNT2,PTPRJ,PZP,RAG1,RFFL
GO:0003774	Cytoskeletal motor activity	2.29E-02	DNAH6,DYNC1H1,ENSMMUG00000013436,KIF12,KIF16B,MYH11,MYO18A
GO:0140359	ABC-type transporter activity	3.54E-02	ABCA1,ABCA3,ABCA4,ABCB4,ABCC10
GO:0140326	Atpase-coupled intramembrane lipid transporter activity	4.23E-02	ABCA1,ABCA3,ABCA4,ABCB4

GO:BP	GO:0032501	Multicellular organismal process	1.36E-04	ABCA1,ABCA3,ABCA4,ACTN3,ADGRG3,ARNT2,ASB2,BFSP1,BRINP1,BRSK2,CAMK2A,CAMSAP1,CHST11,CLCN1,CNTRL,COL2A1,CSF1R,CSMD1,CSMD3,DCHS2,DGCR2,DHX37,DYNC1H1,E2F8,E4F1,EIF2AK3,ENSMMUG00000055992,F13A1,FCHO1,FMN1,FSIP2,HMCN2,HSPG2,IGSF9,IL16,LAMA3,LAMC3,MYH11,MYO18A,NECTIN2,NIN,NLRP1,NUP155,OMP,OR8B8,PAX8,PDE6A,PDGFRA,PEAR1,PKD1,PKD2L1,POMGNT2,PTPRJ,RAG1,RP1L1,SDK1,SEMA6B,SMYD4,STK39,SYNE2,SYNM,TCP11,TENM4,TGFB2,THEMIS,TNC,TRIM67,TTN,TXNRD1,VWF,WNK4,ZCCHC3,ZDHHC8,ZFPM1
	GO:0007010	Cytoskeleton organization	1.41E-03	ACTN3,ARHGEF17,ASB2,BFSP1,BRSK2,CAMSAP1,CLASP1,CSF1R,DNAJB13,DST,DYNC1H1,EVPL,FAM171A1,FMN1,FSIP2,MACF1,MYO18A,NECTIN2,NIN,PDGFRA,PKD1,RP1L1,SYNE2,SYNM,TRPM2,TTN
	GO:0048731	System development	3.87E-03	ABCA3,ACTN3,ARNT2,ASB2,BFSP1,BRINP1,BRSK2,CAMK2A,CAMSAP1,CHST11,CNTRL,COL2A1,CSF1R,CSMD1,CSMD3,DCHS2,DHX37,E2F8,EIF2AK3,FMN1,HMCN2,HSPG2,IGSF9,LAMC3,MYH11,NIN,OMP,PAX8,PDE6A,PDGFRA,PKD1,POMGNT2,RAG1,RP1L1,SDK1,SEMA6B,SMYD4,SYNE2,TENM4,TGFB2,TNC,TRIM67,TTN,WNK4,ZFPM1
	GO:0048513	Animal organ development	1.09E-02	ABCA3,ACTN3,ARNT2,ASB2,BFSP1,BRINP1,CHST11,CNTRL,COL2A1,CSF1R,CSMD1,DCHS2,DHX37,E2F8,EIF2AK3,EVPL,FMN1,HSPG2,LAMC3,MYH11,NIN,PAX8,PDE6A,PDGFRA,PKD1,RAG1,RP1L1,SEMA6B,SMYD4,SPTLC2,SYNE2,TENM4,TGFB2,TNC,TTN,WNK4,ZFPM1
	GO:0048856	Anatomical structure development	1.78E-02	ABCA3,ACTN3,ADGRG3,ARNT2,ASB2,BFSP1,BRINP1,BRSK2,CAMK2A,CAMSAP1,CHST11,CNTRL,COL2A1,CSF1R,CSMD1,CSMD3,DCHS2,DHX37,E2F8,E4F1,EIF2AK3,EVPL,FAM171A1,FMN1,FSIP2,HMCN2,HSPG2,IGSF9,LAMA3,LAMC3,MYH11,NECTIN2,NIN,OMP,PAX8,PDE6A,PDGFRA,PFAS,PKD1,POMGNT2,RAG1,RP1L1,SDK1,SEMA6B,S

			MYD4,SPTLC2,SYNE1,SYNE2,TCP11,TENM4,TGFB2,THEMIS,TNC,TRIM67,TTN,TXNRD1,WNK4,ZFPM1
GO:0065007	Biological regulation	3.21E-02	ABCA1,ABCA3,ABCA4,ABCB4,ACTN3,ADGRD1,ADGRG3,AKAP6,ANKRD13A,ARFGEF3,ARNT2,ARNTL2,ASB2,ATP4A,BLM,BRINP1,BRSK2,CAMK2A,CAMSAP1,CASP9,CBARP,CDC25C,CHAT,CHST11,CLASP1,CLCN1,CLTCL1,COL2A1,CSF1R,CSMD3,CTDP1,DHX37,DIDO1,DLGAP2,DYNC1H1,E2F8,E4F1,EIF2AK3,ENSMMUG00000054038,ENSMMUG00000055992,EVPL,F13A1,FAM161A,FAM171A1,FCHO1,FMN1,FRMD4A,GNB1L,GRIN3B,GRK5,GRM3,HELZ2,IGSF9,IL16,LAMA3,LARP4B,MACF1,MYO18A,NCAPD2,NECTIN2,NIN,NLRP1,NLRP13,NUP155,NUP98,NWD1,OMP,OR8B8,PAPPA,PAX8,PDE10A,PDE6A,PDGFRA,PEAR1,PFKL,PKD1,PKD2L1,PTPRJ,RAG1,RFFL,RP1L1,SDK1,SLC12A6,SPTLC2,STK39,SYNE2,TCP11,TENM4,TGFB2,THEMIS,TNC,TNFRSF10A,TNK2,TRIM67,TRPM2,VWF,WNK4,YRDC,ZCCHC3,ZDHHC8,ZFHX3,ZFPM1,ZNF226,ZNF528,ZNF667,ZNF805,
GO:0007275	Multicellular organism development	4.00E-02	ABCA3,ACTN3,ARNT2,ASB2,BFSP1,BRINP1,BRSK2,CAMK2A,CAMSAP1,CHST11,CNTRL,COL2A1,CSF1R,CSMD1,CSMD3,DCHS2,DHX37,E2F8,E4F1,EIF2AK3,FMN1,HMCN2,HSPG2,IGSF9,LAMA3,LAMC3,MYH11,NIN,OMP,PAX8,PDE6A,PDGFRA,PKD1,POMGNT2,RAG1,RP1L1,SDK1,SEMA6B,SMYD4,SYNE2,TENM4,TGFB2,TNC,TRIM67,TTN,TXNRD1,WNK4,ZFPM1

GO:CC	GO:0071944	Cell periphery	7.33E-07	ABCA1,ABCA3,ABCA4,ABCB4,ABCC10,ACIN1,ACTN3,ADGRD1,ADGRG3,ANKRD13A,ATP4A,BFSP1,C9H10orf90,CBARP,CLASP1,CLCN1,CLTCL1,COL15A1,COL2A1,COL6A3,CSF1R,CSMD3,DCHS2,ENSMMUG00000054038,ENSMMUG00000055992,EVPL,FAM171A1,FCHO1,GRIN3B,GRK5,GRM3,HMCN2,HSPG2,IGSF9,IL16,LAMA3,LAMC3,MYRIP,NECTIN2,NIN,OR8B8,PDE6A,PDGFRA,PEAR1,PKD1,PKD2L1,POLE,PTPRJ,RFFL,SLC12A6,SLC28A1,SLC6A20,STK39,SYNE1,SYNE2,SYNM,TENM4,TGFB2,TMC5,TNC,TNFRSF10A,TNK2,TRPM2,UMODL1,VWF
	GO:0042995	Cell projection	2.52E-04	ABCA4,ACTN3,CAMK2A,CBARP,CEP164,CHAT,CNTRL,DNAH6,DNAJB13,DST,DYNC1H1,FAM161A,FSIP2,GRM3,IGSF9,MACF1,MYRIP,NIN,OMP,PDE6A,PDGFRA,PEAR1,PKD1,PKD2L1,RP1L1,SLC12A6,SLC28A1,SYNE2,TCP11,TENM4
	GO:0005856	Cytoskeleton	3.24E-04	ACTN3,BFSP1,BRSK2,CAMSAP1,CEP164,CLASP1,CLTCL1,CNTRL,CTDP1,DNAH6,DNAJB13,DST,DYNC1H1,E4F1,ENSMMUG00000013436,EVPL,FAM161A,FAM184A,FMN1,FRMD4A,KIF16B,LRRCC1,MACF1,MDN1,MYH11,MYO18A,MYRIP,NIN,PKD2L1,RP1L1,SYNE2,SYNM,TRIM67,ZNF805
	GO:0005604	Basement membrane	3.35E-04	COL15A1,COL2A1,HMCN2,HSPG2,LAMA3,LAMC3,TNC

GO:0005737	Cytoplasm	5.67E-04	ABCA1,ABCA3,ABCA4,ABCB4,ABHD12B,ACIN1,ACTN3,ADGRD1,AKAP6,ANKRD13A,ARFGEF3,ARNT2,ARNTL2,BFSP1,BLM,BRINP1,BRSK2,C9H10orf90,CAMK2A,CAMSAP1,CASP9,CBARP,CDC25C,CHAT,CHGB,CHST11,CLASP1,CLTCL1,CNTRL,COL15A1,COL2A1,DHX37,DNAH6,DNAJB13,DST,DYNC1H1,E2F8,EIF2AK3,EIF3C,ENSMMUG00000013436,ENSMMUG00000030822,ENSMMUG00000054038,EVPL,FAM161A,FAM184A,FCHO1,FMN1,FRMD4A,GNB1L,GRK5,HELZ2,HMCN2,IL16,KIF16B,LAMA3,LARP4B,LY6K,MACF1,MDN1,MGAT5B,MYO18A,MYRIP,NCAPD2,NIN,NLRP1,NLRP13,NOL6,NWD1,OMP,OSBP,PDGFRA,PFAS,PFKL,PKD1,PKD2L1,PNPLA6,POMGNT2,PWWP3A,RFFL,RNF213,RP1L1,SLC28A1,SMYD4,SPAG1,SPTLC2,STK39,SYNE1,SYNE2,SYNM,TCP11,TENM4,THEMIS,TNFRSF10A,TNK2,TRIM67,TRPM2,TTN,TXNRD1,VPS35L,VWA8,VWF,WNK4,YRDC,ZCCHC3,ZDHHC8,ZFHX3,ZNF687
GO:0005886	Plasma membrane	8.08E-04	ABCA1,ABCA3,ABCA4,ABCB4,ABCC10,ACIN1,ACTN3,ADGRD1,ADGRG3,ANKRD13A,ATP4A,BFSP1,C9H10orf90,CBARP,CLCN1,CLTCL1,COL6A3,CSF1R,CSMD3,DCHS2,ENSMMUG00000054038,ENSMMUG00000055992,EVPL,FAM171A1,FCHO1,GRIN3B,GRK5,GRM3,HMCN2,IGSF9,IL16,NECTIN2,NIN,OR8B8,PDE6A,PDGFRA,PEAR1,PKD1,PKD2L1,POLE,PTPRJ,RFFL,SLC12A6,SLC28A1,SLC6A20,STK39,SYNE1,SYNE2,SYNM,TENM4,TMC5,TNFRSF10A,TNK2,TRPM2
GO:0062023	Collagen-containing extracellular matrix	2.36E-03	COL15A1,COL2A1,HMCN2,HSPG2,LAMA3,LAMC3,TGFB2,TNC,VWF
GO:0099512	Supramolecular fiber	4.15E-03	ACTN3,BFSP1,CAMSAP1,CLASP1,COL2A1,DNAH6,DST,DYNC1H1,FAM161A,FMN1,MACF1,MYO18A,NIN,SYNE1,SYNE2,SYNM,TTN

GO:0120025	Plasma membrane bounded cell projection	4.25E-03	ABCA4,CAMK2A,CBARP,CEP164,CHAT,CNTRL,DNAH6,DNAJB13,DYNC1H1,FAM161A,FSIP2,GRM3,IGSF9,MYRIP,NIN,OMP,PDE6A,PDGFRA,PEAR1,PKD1,PKD2L1,RP1L1,SLC12A6,SLC28A1,SYNE2,TCP11,TENM4
GO:0099081	Supramolecular polymer	4.80E-03	ACTN3,BFSP1,CAMSAP1,CLASP1,COL2A1,DNAH6,DST,DYNC1H1,FAM161A,FMN1,MACF1,MYO18A,NIN,SYNE1,SYNE2,SYNM,TTN
GO:0005929	Cilium	1.02E-02	ABCA4,CEP164,CNTRL,DNAH6,DNAJB13,FAM161A,FSIP2,MYRIP,NIN,PDE6A,PDGFRA,PKD1,PKD2L1,RP1L1,TCP11
GO:0099080	Supramolecular complex	1.27E-02	ACTN3,BFSP1,CAMSAP1,CLASP1,COL2A1,DNAH6,DST,DYNC1H1,FAM161A,FAM184A,FMN1,LARP4B,MACF1,MYO18A,NIN,NUP98,SYNE1,SYNE2,SYNM,TTN
GO:0031012	Extracellular matrix	2.46E-02	COL15A1,COL2A1,COL6A3,HMCN2,HSPG2,LAMA3,LAMC3,TGFB2,TNC,VWF
GO:0030312	External encapsulating structure	2.54E-02	COL15A1,COL2A1,COL6A3,HMCN2,HSPG2,LAMA3,LAMC3,TGFB2,TNC,VWF

CHAPTER 6

The *Bijagó* socio-cultural context: data collection and descriptive analysis

Effective conservation strategies in human-non-human shared landscapes require the incorporation of local knowledge and perceptions. Personal perceptions are shaped by individual factors (e.g., personality, cognitive abilities and experiences) and socio-cultural backgrounds. Exploring these socio-economic and cultural dimensions is crucial to understand local perceptions and attitudes towards wildlife. On the Bijagós Archipelago, Guinea-Bissau, the *Bijagó* are the most prominent ethnic group. The *Bijagó*'s animistic religious authorities have designated several locations on the islands as sacred, restricting anthropogenic activities in those locations, which may act as refuges for local wildlife. However, adherence to *Bijagó* socio-cultural traditions may be changing on the archipelago as exposure to western influences increases, potentially changing the *Bijagó*'s relationship with the local ecosystems. This chapter describes the methodology I used to collect ethnobiological data across three islands/island groups from the Bijagós Archipelago with unique socio-cultural contexts: Urok Island Group (protected area with rural settlements), Canhabaque Island (rural settlements, no protection) and Bubaque Island (urbanised). Additionally, I aimed to describe the socio-cultural context of the participants and their adherence to socio-cultural traditions. As expected, the islands had different socio-cultural contexts linked to their degree of urbanisation. For example, urbanisation in Bubaque was accompanied with changes to the religious affinities of the participants and consequently a decrease in the adherence to local socio-cultural traditions. This reduction in adherence could be detrimental for the conservation of biodiversity.

Introduction

Factors such as income, access to education, reliance on natural resources, community roles and adherence to local cultural and religious beliefs may shape attitudes and perceptions toward wildlife and its conservation among those living in shared landscapes (Costa et al. 2013; Baker et al. 2014; Bencin et al. 2016; Nyirenda et al. 2019). To understand local attitudes and perceptions, and how these shape relationships with nature and wildlife, it is essential to examine the socio-economic context at the level of the study area and of the individual. By exploring these socio-economic and cultural dimensions, conservation strategies can be tailored to align with the needs, values, and concerns of the community, promoting stronger and more sustainable conservation strategies (König et al. 2021).

The *Bijagó* is the most predominant ethnic group in the Bijagós Archipelago, accounting for approximately 90 % of the total inhabitants. The *Bijagó* are often one of the few ethnic groups in Guinea-Bissau with a matriarchal society. Their social organization is based on four matrilineal clans (*Ominca*, *Ogubane*, *Oraga* and *Orácuma*), each with their own rights and powers within the islands (Madeira 2009). Adult women are endowed to sexual and matrimonial freedom, and actively contribute towards societal policies as religious authorities. However, as suggested by Lima (1947b), other aspects of the *Bijagó* society are characteristic of patriarchal societies. For example, the highest non-religious social hierarchies and material inheritances are reserved to men and polygamy is common (Lima 1947b). Additionally, regardless of the family composition, women are submissive to the male "head of the family", usually their husbands (Lima 1947b).

Conditioned by a life of insularity, the *Bijagó* demonstrate cultural adaptations to explore the natural resources they depend upon efficiently (Madeira 2009). The animistic belief system of the *Bijagó* is thought to contribute for the preservation of the islands' natural ecosystems (Madeira 2016) as several locations in the archipelago are regarded as sacred and used exclusively for religious and cultural ceremonies (Madeira 2009; Cardoso 2010). Such areas may act as refuges for wildlife as subsistence and revenue activities, such as hunting, are limited or even prohibited (Madeira 2009; Cardoso 2010).

However, more recently, ethnic composition, intrinsic cultural variation within the *Bijagó* ethic group, as well as exposure to external western influences (Madeira 2009; Cardoso 2010) may have contributed to geographic variation in their relationship with nature and wildlife. (Bordonaro 2006) mentions that the exposure to mass media and tourism has created a societal dichotomy between young and elder generations in Bubaque Island. In this urbanised island of the archipelago, the younger individuals can observe and experience an alternative socio-economic system to the traditional agricultural livelihoods. On the other hand, older members of the *Bijagó* society actively resist westernising socio-cultural initiatives (Bordonaro 2006).

Currently, two decades after the study by Bordonaro (2006), a wider continuum of adherence to *Bijagó* socio-cultural traditions may be in place at the archipelago which could imply that perceptions and attitudes towards wildlife and conservation are becoming increasingly heterogenous. In this chapter I aimed to present the methodology for the collection of ethnobiological data (i.e., perceptions and attitudes towards wildlife) and describe the socio-cultural context of the Bijagós Archipelago. Specifically, I aimed to:

1. Present the methodology for the questionnaires, in-depth interviews and women-only focus groups.
2. Discuss the challenges that I have encountered during the data collection, analyses and interpretations.
3. Present a descriptive analysis of the socio-economic context of the sampled locations, including participants’ perceptions on socio-cultural adherence.

The sociozoologic scale and perceptions on wildlife for the *Bijagó* ethnic group will be presented in Chapter 7.

Methods

Data collection

The study area included three islands or island groups of the Bijagós Archipelago in Guinea-Bissau, West Africa. The Bijagós Archipelago is a small (~10,000 km^2) archipelago located in close proximity to mainland Guinea-Bissau. The Bolama-Bijagós Biosphere Reserve was established in the region and currently contains three protected areas: UCMPA – Urok Communitarian Marine Protected Area (Formosa, Tchedia and Nago Islands), ONP – Orango National Park (Orango, Ganogo, Menegue and Orangozinho Islands), JVPMNP – João Vieira and Poilão Marine National Park (João Vieira, Cavalos, Meio and Poilão Islands; Figure 6.1). Although a significant area of the archipelago is protected, conservation actions have been targeted towards intertidal and marine ecosystems (Rebelo and Catry 2011). The conservation of terrestrial ecosystems has been mainly neglected and enforcement against illegal exploitation of terrestrial fauna is virtually non-existent.

Three islands or island groups with different socio-cultural contexts were studied: Urok Island group (protected area with rural settlements and with a strong presence of the local NGO *Tiniguena*), Bubaque Island (the urban hub of the Bijagós Archipelago) and, Canhabaque Island (rural settlements and under no formal protection; Figure 6.1). I collected data between April and June 2022 (April – Urok Island Group, nine villages; May – Canhabaque Island, ten villages; June – Bubaque Island, eight villages). The choice of the villages included in the study was limited by accessibility and availability of transportation, attempting to cover a large geographical area. I conducted questionnaires, in-depth interviews and focus groups (the original questionnaire and interview scripts can be found in Supplementary Materials section).

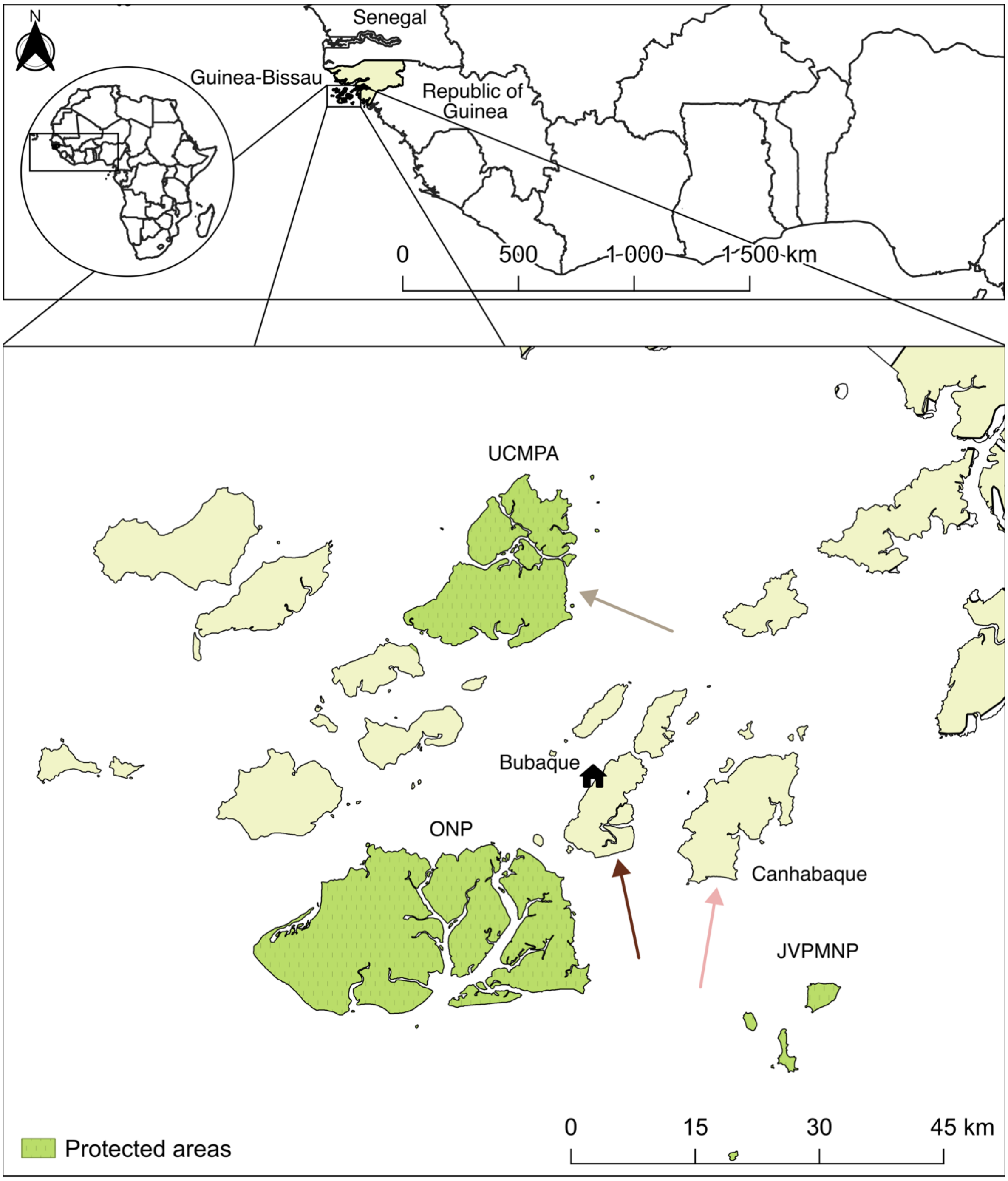


Figure 6.1 The Bijagós Archipelago in Guinea-Bissau, West Africa. Protected areas are represented in green: ONP – Orango National Park; JVPMNP –João Vieira e Poilão Marine National Park; UCMPA – Urok Communitarian Marine Protected Area. The main urban hub and seat of administration is also represented (Bubaque Island). Arrows point to the sampled islands.

The samples used to conduct the questionnaire were selected based on a snowball approach. Each respondent was asked to point out another interviewee and so on, respecting age and gender pre-defined quotas. In Guinea-Bissau, the exact demographic composition of the population is unknown (Costa 2010), making the collection of probabilistic data virtually impossible. Therefore, I decided to collect data balanced by island, gender and age (Costa 2010; Costa et al. 2013). Questionnaires were mainly composed of closed questions related to the participant's daily income activities, diet (other than rice), hunting activities, the use of meat (e.g., consumption or trade), perceptions on socio-cultural traditions and sociozoological scales (i.g., how the *Bijagó* organised animals according to their perceived societal roles; Chapter 7). Personal information including, gender, age, ethnic background, religion, education level and family background (e.g., household size) were also collected.

Secondly, I conducted in-depth interviews with adult males considered "knowledgeable" by the local community on the matters of hunting and socio-cultural traditions. Interviewees included elders, chieftains, religious representatives, but also younger individuals more likely to be active hunters at the time of data collection. Questions were open-ended covering similar topics used to conduct the questionnaires. More sensitive subject matters were approached indirectly in order to avoid discomfort in respondents. For instance, instead of asking "Do you hunt primates?", participants were asked broader questions that did not imply primate-target hunting: "Do you eat meat?", "What kind of meat?", "Is bushmeat commonly consumed in this village?". Unlike other parts of Guinea-Bissau, where hunting is perceived as an illegal activity and participants in other studies are usually reluctant to answer questions due to potential legal consequences (Costa 2010), this was not the case for this study area, which meant that information on this topic was obtainable without the need to establish extensive rapport with participants.

Finally, I conducted discussions with women-only focus-groups. The meetings were conducted by a trained local female fieldwork assistant, since women can feel uncomfortable and reluctant to answer questions when interviewed by a man (see below). The focus groups were pre-scheduled during the collection of the questionnaire data and conducted on the day after the questionnaires. The topics discussed in the focus groups were similar as those of the in-depth interviews with men in order to compare the results from the two genders that often have different perceptions on the socio-cultural traditions, ecosystems and wildlife (Costa 2013; Costa et al. 2017).

The socio-economic data and the distribution of local perceptions on insularity and socio-ecological changes were explored using descriptive statistics and cross-tabulations (Chi-squared test). The accuracy of the Chi-squared test can be reduced if the expected number of counts for a particular cell is inferior to five (Jeong and Lee 2017). In such cases, I estimated the statistical significance by Monte Carlo simulations ($1x10^6$ replicates). This number of iterations estimated p-values that varied less than 0.001 between independent runs (not shown). Some under-represented categories within the participant variables were grouped together for analysis (e.g., Catholic, Evangelical, Protestant Cristians, and Islamic were grouped into non-Animistic religions). All statistical analysis and plots were conducted in R v4.2.2 (R CoreTeam 2022) coupled with RStudio v2023.06.2+561 (Posit team 2023).

Data collection constraints

The first limitation I encountered was the language barrier. Even though Portuguese is the official language in Guinea-Bissau, the total number of fluent speakers is limited. This required me to learn Creole from Guinea-Bissau, which is widely spoken across the country, the Bijagós Archipelago included. Regardless, for the translation of more complex or particular expressions, I had to be accompanied by a Guinean interpreter in order to provide a more accurate Creole – Portuguese translation. Additionally, a *Bidjugu - Creole* interpreter was also needed for those participants that only spoke the local language. The participants that required the *Bidjugu* – Creole translator were mostly elderly individuals. The presence of a local interpreter can be another factor adding bias to the data collection process. The local interpreter, being part of the communities, may manipulate the participant's answer or even change the reported translation in order to hide the true meaning of the participant (Costa 2010). The Creole – Portuguese interpreters were trained on these matters and informed beforehand that I was expecting these types of biases and their consequences on the quality of the data to discourage any false translations. Since my knowledge of Creole was sufficient to understand most of the content of the translations between the local interviewers and the participants, I believe that the data collected did not contain significant biases introduced by the interpreters. Furthermore, the questionnaire and the interview script were back translated from *Bidjugu* – Creole – Portuguese to ensure the accuracy of the translations.

The second limitation I encountered was due to my own cultural background and gender. Being a white male meant that creating rapport with participants could often be a challenge. With male participants, this was readily solved with the inclusion of the local interpreter which aided in the creation of rapport and made the local communities more comfortable and secure in answering my questions. However, I could not establish any rapport with female participants, which remained apprehensive in my presence. This is not to be unexpected in the context of Guinea-Bissau. I found that women's livelihoods were still heavily controlled by the men of the community despite the *Bijagó* being described as a "matriarchal society" (Madeira 2009). Men were frequently interfering with the data collection from women and had to be asked to leave the area for them to feel secure and willing to participate and to collect data unbiased by men's own views and perceptions. Furthermore, the *Bijagó* have male and female specific socio-cultural traditions, which are kept secret from one another (Madeira 2009). As such, I had to include a female interpreter to collect the questionnaire and focus group data from the women. The choice of the female interpreter was more thorough than that of the male interpreter, as I would not be able to supervise the data collection. I opted for an interpreter that had experience in collecting both questionnaire and focus-group data. The female interpreter was also thoroughly trained before the data collection. Both the questionnaires and the interviews were tested *in situ* in Bissau and in Formosa Island. Data from the *in situ* test were not included in the final dataset.

The third limitation in the data collection was the wide-spread alcohol abuse by the participants. During the early stages of the data collection, I realised that both male and female participants, regardless of age, were often fully inebriated after the conclusion of their daily activities. This caused some delays in the data collection as I did not want to include any false testimonies or induce any sort of conflict between the research team and the inebriated participants. I decided to start collecting data before participants began their daily activities. However, this approach came with its own constraints which included the need to schedule with willing participants one or two days before the intended data collection activities.

Regarding the data analysis, the absence of census on the number and the demographic distribution of the local inhabitants meant that questionnaire data is non-probabilistic which unable direct extrapolations of the sample to the general population (Newing et al. 2010). Furthermore, the usage of nominal variables, non-normally distributed data means that only non-parametric statistical tests (Chi-squared test) could be employed during data exploration (Newing et al. 2010). While a balance by gender and location was relatively easy to achieve, I didn’t manage to obtain a balanced distribution for the age classes. Specifically, I collected more data from younger participants (19 – 35 years) than elders (51+ years). However, this may be a reflection of the likely demographic skew of the populations of Guinea-Bissau (INE 2015).

Results and Discussion

I obtained questionnaire data from 193 (~64 hours and 30 minutes of data) *Bijagó* participants (male n = 93, female n = 100) from the three island/island groups (Urok n = 55, Canhabaque n = 70, Bubaque n = 68). Data was obtained across three age classes (18 – 35 n = 81; 36 – 50 n = 62; 51+ n = 50). The four matrilineal *Bijagó* clans were represented in the dataset (Ogubane n = 56; Ominca n = 21; Oracuma n = 58; Oraga n = 49) but a few participants did not know which clan they belonged to (n = 9). Additionally, I conducted 16 in-depth interviews (~11 hours and 37 minutes of data) and thirteen women-only focus-groups discussions (~6 hours and 14 minutes of data). Qualitative data from interviews and focus-groups was used to triangulate the semi-quantitative data collected during questionnaires and to provide content-rich data to aid their interpretation (Costa 2010; Newing et al. 2010).

Socio-economic context

I was interested in understanding the socio-economic context of the *Bijagó* and how reliant the participants were on local forest and coastal resources. I enquired the participants on their most important source of revenues, daily activities and nutrient sources. In Guinea-Bissau, 58 % of the total population lives in rural areas (INE 2015). Similar to other rural populations in the country (Temudo and Abrantes 2014), the main revenue source and main daily activities of the *Bijagó* seems to be farming and harvesting natural resources. Participants frequently mentioned the collection and trade of both forest and coastal resources as their main source of revenue and daily activities (Figure 6.2).

Considering the urban settings of the “Praça” in Bubaque Island, which includes the most significant harbour of the archipelago, permanent markets, shops, restaurants and hotels, I was expecting that the local inhabitants would have greater access to different livelihoods than those in the more rural Canhabaque and Urok Island Group. This difference in socio-cultural context was verified in the sample with the participants from Bubaque Island having described alternative revenue and daily activities (revenue activities $X^2 = 28.82$, simulated p-value < 0.05; daily activities: $X^2 = 51.17$, df = 6, p-value < 0.001). For example, 37 % (n = 21) of participants from Bubaque Island (all females) stated that their main daily activity was cooking for restaurants and other establishments (Figure 6.2). The distribution of the main activities and revenue sources of male and female participants were significantly different (revenue activities X2 = 93.15, df = 7, p-value < 0.001; daily activities: X2 = 29.20, df = 3, p-value < 0.001). Particularly, women reported to be more engaged with the plantation and maintenance of crops, while men are typically more engaged in the clearance of the forest that precedes crop establishment and extraction of non-timber forest products (NTFP). The collection of mussels was mentioned almost exclusively by women, and fishing by men (not shown). Additionally, female participants from Urok mentioned more often the plantation of monocultures, such as cashew, as a source of revenue, suggesting that cash crops are becoming a more prevalent source of revenue on the archipelago (Figure 6.2).

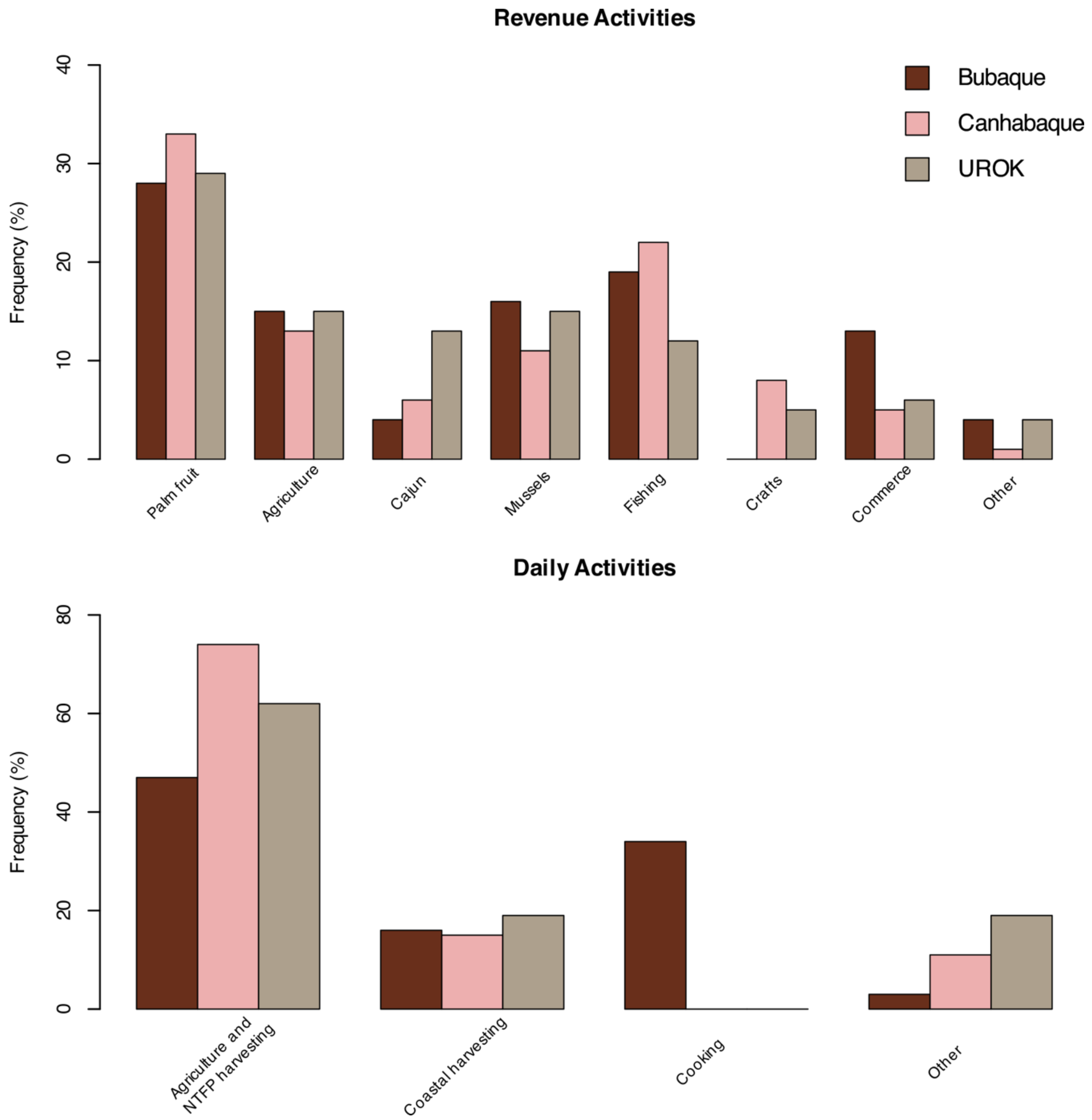


Figure 6.2. Most important revenue (top) and daily activities (bottom) for the *Bijagó* from Bubaque, Canhabaque and Urok islands, according to the participants. NTFP - non timber forest products.

With the exception of Bubaque, farming and extraction of NTFP seemed to be mostly for revenue purposes rather than personal or communal consumption (Figure 6.2). Indeed, compared to the other islands, participants from Bubaque Island appeared to have greater purchasing power, allowing for an easier acquisition of different goods under a stricter cash economy at the permanent market on the island (Bordonaro 2006). Overall, participants mentioned that they consumed mostly mussels and fish in their meals (~84 % of total participants across islands, n = 157; Figure 6.3). Approximately 16 % (n = 11) of the participants from Canhabaque Island mentioned subsistence bushmeat hunting, while the frequency of this item decreased to less than 5 % on the remaining islands (Figure 6.3). Only two participants across the study specified non-human primate meat as their most important source of protein (Urok).

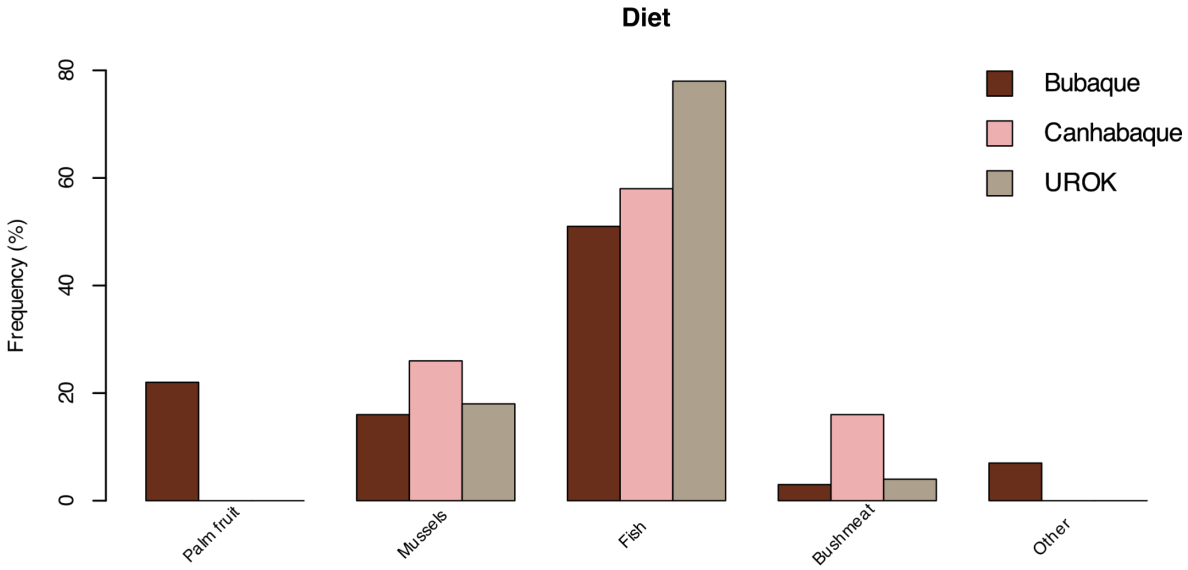


Figure 6.3 Most important dietary items other than rice for the *Bijagó* from Bubaque, Canhabaque and Urok islands, according to the participants.

When asked specifically about trade of live or dead animals, approximately 72 % (n = 138) of participants from Bubaque, Canhabaque and Urok, respectively, mentioned they had traded animals at least once. During the in-depth interviews and focus groups, this activity was reported as a means to cover any sporadic expenses that families may encounter (e.g., medical care and medicines). Bushmeat trade, in particular, was more commonly reported by participants from Bubaque Island (23 %, n = 22). On the remaining islands, this activity was reported by less than 10 % of the participants. Non-human primate meat in specific was only reported to be sold by 9 participants. The remaining participants did not want to specify which species of animals they were trading.

The level of formal education of the participants seemed to be low. Approximately 46 % (n = 89) of participants reported to have not attended or finished the lower elementary school and only about 8% (n = 15) finished secondary school (Figure 6.4). For the current sample, the level of formal education was shown to vary between Islands ($X^2 = 14.13$, simulated p-value < 0.05) and age group ($X^2 = 33.29$, simulated p-value < 0.001). Higher levels of education were found at Bubaque Island and across younger age classes (Figure 6.4). In Guinea-Bissau, higher schooling levels such as elementary and secondary schools are often restricted to urban areas. With access to higher levels of education, Bubaque Island has been recognised as an attractive site for youths homing from the remaining parts of the archipelago (Bordonaro 2006). Additionally, as the seat of the Portuguese colonial government at the Bijagós Archipelago until independence in 1974, the island has had formal state education for longer (Bordonaro 2006), which was pointed out by the participants as one of the reasons why educational levels were higher even across older age classes (35+ years old). This contrasted to the rest of the islands, where higher levels of education (Upper elementary school and above) was found mostly on younger individuals. Despite the social organisation of the *Bijagó* (matriarchal), contrasting with that of the majority of the other ethnic groups in Guinea-Bissau (patriarchal), I found that women had less access to education than men ($X^2 = 26.68$, df = 3, p-value < 0.001), which is common in patriarchal societies.

Religious context and adherence to socio-cultural traditions

Bijagó societies are described as having animistic beliefs and traditions (Lima 1947a; Madeira 2009). However, the religious composition of their societies was found to have been changing recently with the increased incursions of Catholic, Protestant and Evangelical missions to the islands. Thus, I was also interested in understanding the current religious affinities of the *Bijagó* and its consequences for the adherence to more traditional socio-cultural livelihoods. For this, I enquired participants on their religion, their perceived importance of the *Bijagó* socio-cultural traditions, their perceived changes to socio-cultural adherence and whether they would like their children to follow the same traditions.

Approximately 60 % (n = 116) of the participants mentioned that they are animists, following the *Bijagó* socio-cultural traditions (Figure 6.5). The remaining 37 % of participants were adherents/members of several branches of Christianity, including the Roman Catholic Church, Protestants and Evangelics. Muslims were a minority on the sampled islands, with only six individuals identifying themselves as such.

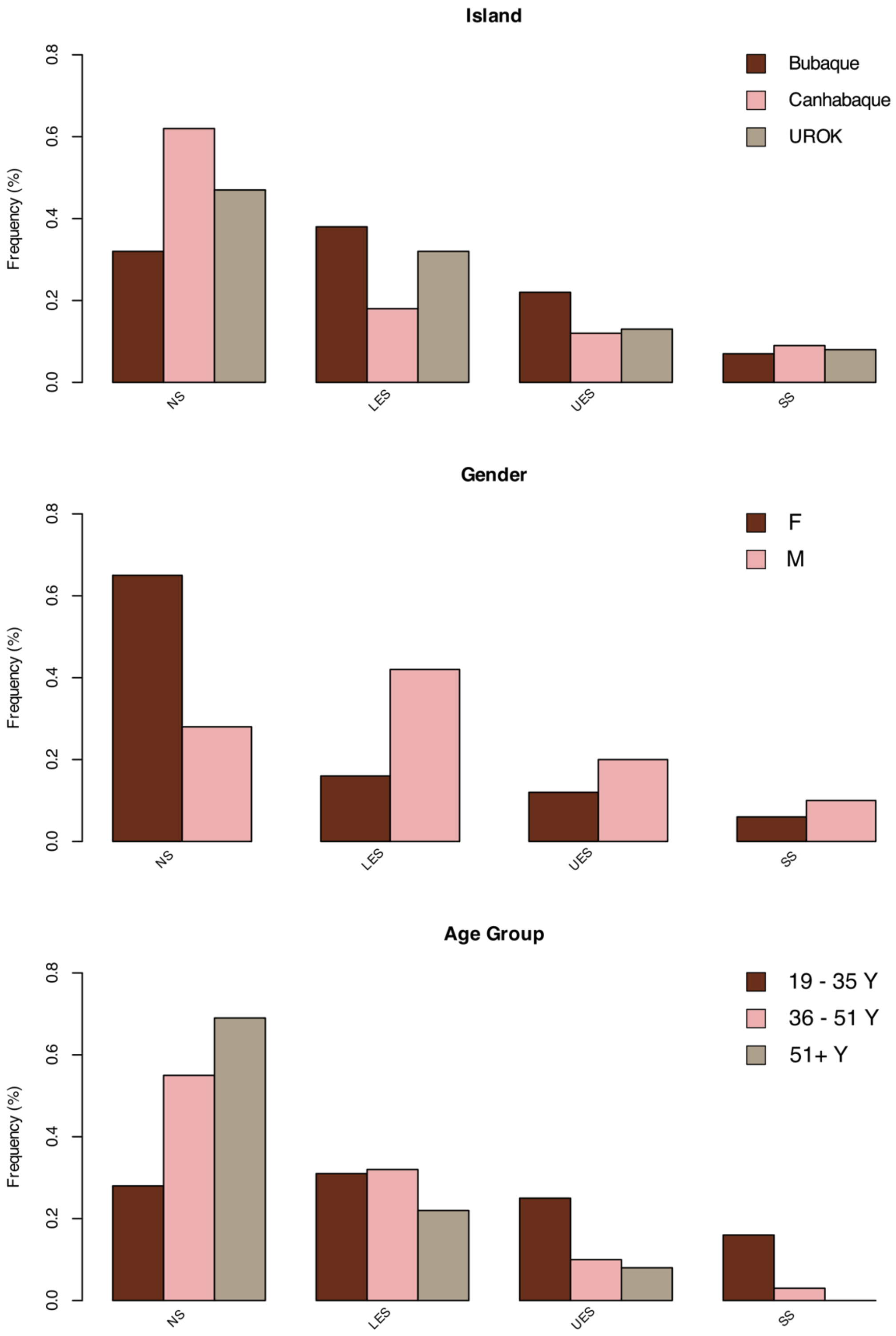


Figure 6.4 Levels of education of the *Bijagó* according to different participant variables (island, top; gender, middle; age group, bottom). Schooling levels: NS – did not attend or didn't finish elementary school; LES – finished lower elementary school; UES – finished upper elementary school; SS – finished secondary school.

I found a regional trend in which Bubaque Island had a higher composition of non-animists ($X^2 = 26.98$, df = 2, p-value < 0.001). This may be associated with the presence of Roman Catholic missions on the island since the establishment of the Portuguese control in the region (Bordonaro 2006), and the more recent incursion of other Christian missions, including the Protestant and Evangelical churches. In this sample, conversion to non-animist systems seems to be particularly attractive to younger individuals ($X^2 = 14.52$, df = 2, p-value < 0.001), particularly men ($X^2 = 9.35$, df = 1, p-value < 0.01). Bordonaro (2006), explores the "modernization" of young *Bijagó* in Bubaque Island, and their rejection of *Bijagó* traditions. To be perceived as "modern" is to behave and dress in a more western way and to be part of social activities in which going to church and school are included (Bordonaro 2006). Bordonaro (2006), explains the "modernization" of young *Bijagó* in Bubaque Island, as a rejection of kultura (*Bijagó* traditions) in such a way that their perceived dichotomy renders their coexistence impossible, particularly amongst younger men. Leaving the *Bijagó* traditions seems to be a way for younger men to reclaim their sexual and economic freedom, which are locked by extensive, often physically violent, initiation traditions imposed by their elders (Bordonaro 2006).

I hypothesised that religious identity influenced attitudes towards socio-cultural traditions of the *Bijagó.* Animists reported more frequently that local *Bijagó* traditions are important for them and their communities ($X^2 = 15.04$, simulated p-value < 0.001). A significant percentage of non-animists (25 %, n = 19) does not agree that the *Bijagó* traditions are important for them or their communities (Figure 6.6), supporting to some degree the dichotomic rejection of "modernity" vs "*kultura*" proposed by Bordonaro (2006) and highlighting that religious identity could be associated with "modernity" and the perceived importance of socio-cultural traditions in this sample. Despite the overwhelming agreement on the importance of local traditions for the animist participants, 69 % of the animists (n = 80) agreed with the questionnaire statement "I want my children to follow the *Bijagó* traditions". Among the 21 % of the animist participants that disagreed, some stated that they would prefer their children to go to formal education instead or that they did not want their children to undertake initiation because it is excessively demanding and often requires the interruption of formal studies. Regarding the participant's perceived trends of socio-cultural adherence, more than 80 % of both animists and non-animists agreed that the adherence to the local socio-cultural traditions is decreasing as younger generations choose to leave the *Bijagó* tradition system to pursue other personal objectives (Figure 6.6).

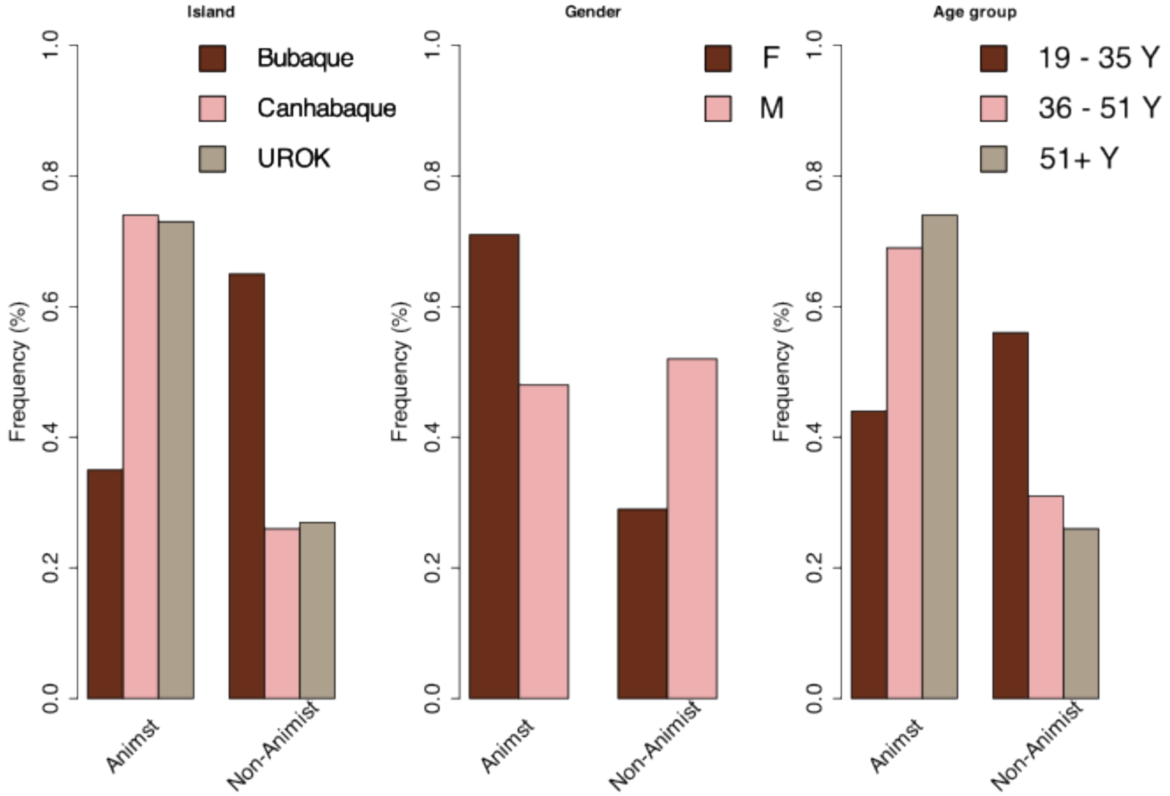


Figure 6.5 Religion of the *Bijagó* according to different participant variables (island, top; gender, middle; age group, bottom). Christians and Muslims were clustered together as non-animist.

According to this study, the socio-cultural adherence to the traditional socio-cultural traditions seems to be decreasing, and the biggest challenges that *Bijagó* traditions may be facing are their apparent contrast and incompatibility with formal schooling and other forms of "modernity" (Bordonaro 2006). While I observed Evangelical missions in both the Canhabaque Island and Urok Island Group, their presence and reach are likely hindered by the isolation of these islands and consequent decreased exposure to "modernity". However, the appearance of exploitative fast revenue activities, such as primate bushmeat trade (Chapter 2) among younger men to cover for school and other personal expenses, could be an indicative of the described chase for "modernity" occurring at a more global scale on the Bijagós Archipelago than previously described.

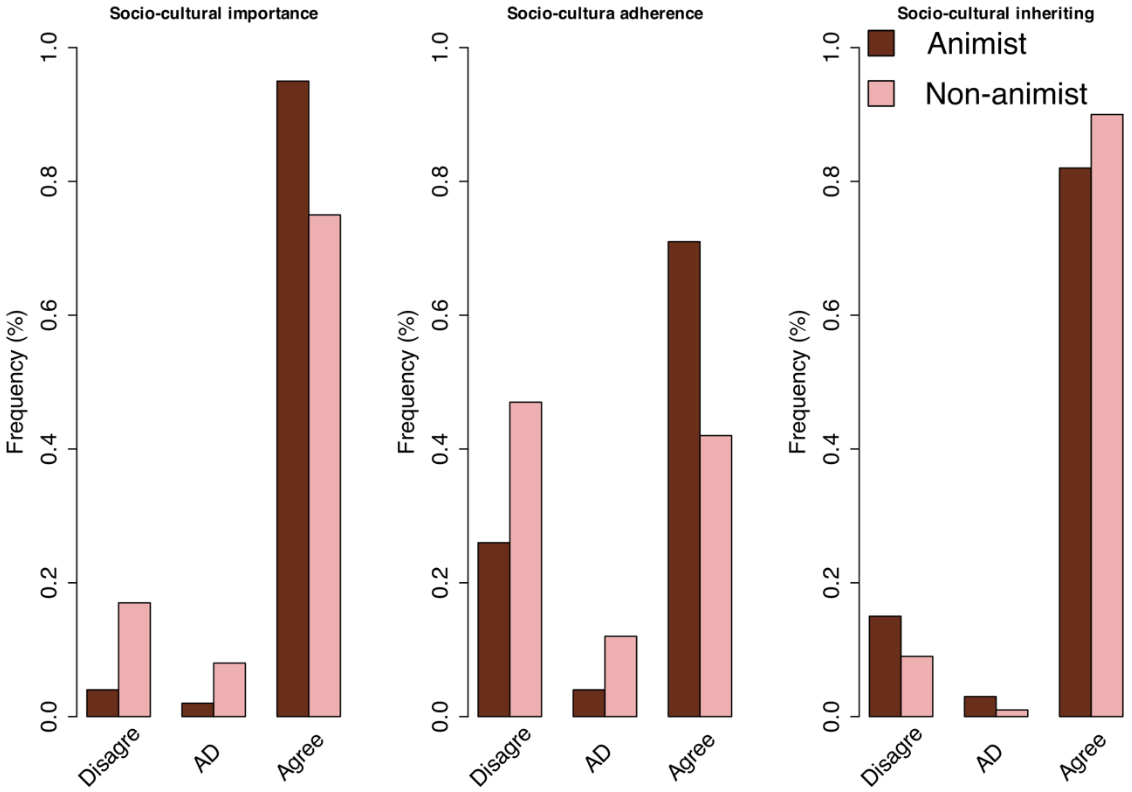


Figure 6.6 Socio-cultural adherence of the *Bijagó* according to participant testimonies. Christians and Muslims were clustered together as non-animist. Socio-cultural importance (left) reports the answers to the statement "Local *Bijagó* traditions are important"; Socio-cultural inheritance (middle) reports the answers to the statement "I want my children to follow the *Bijagó* traditions". Socio-cultural adherence (right) reports the answers to the statement "Local *Bijagó* traditions are decreasing"; AD – Do not agree nor disagree.

The link between religion, socio-cultural adherence, "modernity" and wildlife exploitation is likely complex. As in many other animist societies, *Bijagó* beliefs and traditions appear to have been protecting the unsustainable exploitation of the natural resources (Madeira 2016). As such, these recent changes to the religious composition and socio-cultural adherences of *Bijagó* societies could have unforeseeable consequences on their perceptions to the local ecosystems and be detrimental for the conservation of biodiversity. In light of these results, I highlight that wildlife conservation and cultural conservation on the Bijagós Archipelago are likely inseparable and should be considered and integrated in the local livelihood development action plans targeting younger generations in particular.

Supplementary Materials

Questionnaire

Part I. Characterization of daily-life activities:

1. State the activity that constitute your household's main income source:

   ____

2. State the activity that constitute your household's secondary income source:

   ____

3. State the activities that constitute your household's main food source:

   ____

4. State the activities that constitute your household's secondary food source:

   ____

5. Most important daily life activity:
   - a) Agriculture _____
   - b) Livestock _____ (if selected jump to 5.2)
   - c) Hunting _____ (if selected jump to 5.3)
   - d) Fishing (includes mollusk gathering) _____ (if selected jump to 5.4)
   - e) Commerce _____ (if selected jump to 5.5)
   - f) Other? _____ Specify ________________

5.1. Agricultural techniques (ask interviewee for a short description):

____

(code into traditional/modern/mixed)

5.2. Livestock rearing techniques (ask interviewee for a short description):

____

(code into traditional/modern/mixed)

5.2.1. Where did you get the domestic animals?

a. Local island _____
b. Another island _____ Which? _______________
c. Mainland _____

5.3. Hunting techniques (ask interviewee for a short description):

____

(code into traditional/modern/mixed)

5.4. Fishing techniques (ask interviewee for a short description):

____

(code into traditional/modern/mixed)

5.5. Characterization of commerce:

5.5.1. Where do you sell your goods?

a. Local tabanka _____
b. Multiple tabankas within the island _____
c. Between islands _____
d. Mainland?

5.5.2. What are your most traded items?

a. Non-animal food items _____
b. Animal food items _____ (jump to 5.5.2.1.)
c. Clothing and trinkets _____
d. Live animals _____ (jump to 5.5.2.2)
e. Other? _____ Specify _______________

5.5.2.1. From which animals do you sell meat from? (select all that apply)

a. Wild animals of the forest _____ Primates? _____
b. Wild animals of the sea _____
c. Domestic species _____

5.5.2.2. What kind of live animals do you sell? (select all that apply)

a. Wild animals of the forest _____ Primates _____ (jump to 6.)
b. Wild animals of the sea _____ (jump to 6.)
c. Domestic species _____ (jump to 6.)

5.5.3. Have you ever sold live animals?

Yes _____
No _____ (jump to 6.)

5.5.3.1. What kind of live animals have you sold? (select all that apply)

d. Wild animals of the forest _____ Primates? _____
e. Wild animals of the sea _____
f. Domestic species _____

Part II. Uses of mammal species and sociozoologic scale:

6. Of these animals select (show photos of mammals occurring in the archipelago, domestic animals included):

3 animals featured in dances	1st. ________________ 2nd. ________________ 3rd. ________________
3 animals featured in music	1st. ________________ 2nd. ________________ 3rd. ________________
3 animals used for religious practices	1st. ________________ 2nd. ________________ 3rd. ________________

3 “Good” animals	1st. ________________ 2nd. ________________ 3rd. ________________
3 “Bad” animals	1st. ________________ 2nd. ________________ 3rd. ________________
3 “Pretty” animals	1st. ________________ 2nd. ________________ 3rd. ________________
3 “Ugly” animals	1st. ________________ 2nd. ________________ 3rd. ________________
3 “Intelligent” animals	1st. ________________ 2nd. ________________ 3rd. ________________
3 “Unintelligent” animals	1st. ________________ 2nd. ________________ 3rd. ________________
3 “human-like” animals	1st. ________________ 2nd. ________________ 3rd. ________________
3 best edible animals (hide domestic animals)	1st. ________________ 2nd. ________________ 3rd. ________________

3 worst inedible animals (hide domestic animals)	1st. ________________ 2nd. ________________ 3rd. ________________
3 most common animals (hide domestic animals)	1st. ________________ 2nd. ________________ 3rd. ________________
3 most uncommon animals (hide domestic animals)	1st. ________________ 2nd. ________________ 3rd. ________________
3 animals you would like to see more (hide domestic animals)	1st. ________________ 2nd. ________________ 3rd. ________________
3 animals you would like to see less (hide domestic animals)	1st. ________________ 2nd. ________________ 3rd. ________________

Part III. Perceptions of ecosystem and socio-cultural changes:

7. From the following statements, state if you agree or not:

	Agree	Don't agree	Don't know	Don't want to answer
a) The forest provides food				

b) The forest provides materials to the community				
c) The forest is important for your socio-cultural practices				
d) The forest is important for good water				
e) The forest is important for good air				
f) The forests will last forever				
g) The animals in the forest will last forever				
h) The landscape is changing				
g) The forest is decreasing				
j) The wild animals in the forest are decreasing				
k) It is our responsibility to protect the forest				
l) Socio-cultural practices are important				

m) The importance of socio-cultural practices is decreasing				
n) It is important that the younger generation follows our traditions				

Part IV. Perceptions on the effect of insularity on mammal species

8. From the following statements, state your agreeability:

	Yes	No	Don’t know	Don’t want to answer
e) Animals in the islands are isolated (don’t move between islands)				
f) Animals in islands have birth defects				
g) Big islands have more animals than small islands				

h) Animals in big islands are healthier than in small islands				
i) Translocation of domestic animals between islands is good for their health				
j) Translocation of wild animals between islands is good for their health				

Part V. Personal and socio-economic background:

9. Gender:
   Male _____
   Female _____

10. Age (approximate): _____

11. Ethnic group: _______________ (if not *Bijagó* jump to question 11)

12. Matrilineal clan: _______________

13. Religion: _______________

    13.1. Have you always been a follower of that religion?
    Yes _____ (skip to question 12.)
    No _____

    13.2. Previous religion: _______________

14. Island: _______________

15. Have you ever travelled to other islands?

    Yes _____
    No _____ (skip to question 14.)

    15.1. What's the reason for said travel?

    ____

    15.2. Have you ever travelled to the mainland?

    Yes _____
    No _____ (skip to question 7.)

    15.3. What's the reason for said travel?

    ____

16. Village: _______________

    16.1. Is this village your place of birth?

    Yes _____ (skip to question 8.)
    No _____

    16.2. Where were you born? _______________

    16.3. When and why did you come to this village?

    ____

17. Did you attend school?

    Yes _____
    No _____ (skip to question 16)
    17.1. How many years did you attend school?

Unfinished elementary school _____
Finished elementary school _____
Unfinished high school _____
Finished high school _____
University _____

18. Household size: _____

19. What domestic animals do you have?
Chicken _____
Goat _____
Pig _____
Cow _____

20. How many domestic animals do you have?
Chicken _____
Goat _____
Pig _____
Cow _____

21. Do you own a radio?
Yes _____
No _____

22. Do you own a TV?
Yes _____
No _____

23. Do you own a bicycle?
Yes _____
No _____

24. Do you own a motorcycle or another land motorized vehicle?

Yes _____

No _____

25. Do you own a boat?

Yes _____ Motorised? _____

No _____

Interview script

(Portuguese)

Parte I. Perceções sobre a vida na aldeia e informação económica (criar reportório)**:**

1. Quais são os maiores problemas da aldeia?

   Deixar o entrevistado falar à vontade sobre o assunto depois tentar conduzir a entrevista para os subtemas seguintes:

   - Problemas no acesso à saúde
   - Problemas no acesso à comida
   - Problemas no acesso à educação

2. Qual é a tua principal atividade diária?

   - É tua principal fonte de dinheiro? Se não, qual é?

Parte II. Perceções sobre os animais domésticos:

3. Os animais domésticos são importantes para ti e para a tua família?

   Deixar o entrevistado falar à vontade sobre o assunto depois tentar conduzir a entrevista para os subtemas seguintes:

   3.1 Os animais domésticos são importantes para a tua alimentação?

   3.2 Os animais domésticos são importantes para as tuas tradições? (se o entrevistado disser que "Não" passa para a próxima pergunta)

   - Porquê?

Parte III. Perceções sobre a floresta:

4. A floresta é importante para ti e para a tua família?

   Deixar o entrevistado falar à vontade sobre o assunto depois tentar conduzir a entrevista para os subtemas seguintes:

   4.1 O que é que a floresta dá à tua família? (comida, madeira, água)

   - Qual é o recurso mais importante que obténs da floresta?
   - Porquê?

   4.2 A floresta é importante para as tuas tradições? (se o entrevistado disser que "Não" passa para a próxima pergunta)

   - Porquê?

   4.3 Achas que a floresta nunca vai desaparecer?

   - Porquê?

   4.4 Achas importante preservar a floresta?

   - Porquê?
   - A aldeia deve contribuir? De que forma?

   4.5 A floresta causa-te algum problema? (se o entrevistado disser que "Não" passa para a próxima pergunta)

Parte IV. Perceções sobre os animais da floresta:

5. Os animais da floresta são importantes para ti e para a tua família?

   Deixar o entrevistado falar à vontade sobre o assunto depois tentar conduzir a entrevista para os subtemas seguintes:

   5.1 Que animais é que há na floresta?

   - Estes animais estão a diminuir ou a aumentar?
   - Porquê?

   5.2 Achas que os animais da floresta nunca vão desaparecer?

   - Porquê?
   - De que forma é que a aldeia contribuí para isso?

5.3 Os animais da floresta são importantes para a tuas tradições? (se o entrevistado disser que "Não" passa para a próxima pergunta)

- Porquê?

5.4 Os animais da floresta causam-te algum problema? (se o entrevistado disser que "Não" passa para a próxima pergunta)

- Que tipo de problema?

Parte IV. Perceções sobre alterações à adesão das tradições socioculturais:

6. As tradições da tua aldeia são importantes para ti?
   Deixar o entrevistado falar à vontade sobre o assunto depois tentar conduzir a entrevista para os subtemas seguintes:

6.1 Achas que a importância das vossas tradições está a diminuir?

- Porquê?

6.2 Achas importante os mais novos aprenderem as tradições da aldeia?

- Porquê?

6.3 Gostarias de viver noutro local? (se o entrevistado disser que "Não" passa para a próxima pergunta)

- Qual?
- Porquê?

Parte VI. Perceções sobre insularidade:

7. Quais são as vantagens ou desvantagens de viver em ilhas para ti e para a tua família?
   Deixar o entrevistado falar à vontade sobre o assunto depois tentar conduzir a entrevista para os subtemas seguintes:

7.1 Qual o maior desafio de viver rodeado pelo mar?

- Porquê?
- De que forma é que aprendeste a resolver este problema?

8. Quais são as vantagens ou desvantagens, para os animais, de viver em ilhas?

   Deixar o entrevistado falar à vontade sobre o assunto depois tentar conduzir a entrevista para os subtemas seguintes:

8.1 Achas que os animais das ilhas são diferentes dos animais do continente? (se o entrevistado disser que “Não” passa para a próxima pergunta)

- De que forma?
- São mais ou menos saudáveis? Porquê?

8.2 Os animais domésticos movem-se de ilha em ilha?

- Como?

8.3 Os animais da floresta como os macacos movem-se de ilha em ilha?

- Como?

8.4 O que achas da ideia de mover animais domésticos e selvagens de uma ilha para a outra? (se o entrevistado disser que “Não sabe” passa para a próxima pergunta)

- Conheces algum exemplo?

Parte VII. Perceções sobre consumo de carne e caça:

9. O que é que tu e a tua família comem diariamente?

   Deixar o entrevistado falar à vontade sobre o assunto depois tentar conduzir a entrevista para os subtemas seguintes:

9.1 Comes carne?

- Qual é a tua favorita?
- Com que frequência?
- Como é que a obténs?

10. Come-se carne de mato na aldeia?

    Deixar o entrevistado falar à vontade sobre o assunto depois tentar conduzir a entrevista para os subtemas seguintes:

10.1 Como é que se caçam os animais?

- Com que frequência?

10.2 Porque é que se caçam os animais?

- Consumo da carne?
- Outros fins?
- Animais vivos?

10.3 Qual é o destino dos animais/partes de animais?

- Consumo próprio?
- Venda? Local? Noutra Tabanca? Noutra ilha? Continente?

Informação do grupo focal/ homem entrevistado

Aldeia/Tabanca: _______________

Grupo étnico(s): _______________

Clã(s): _______________

CHAPTER 7

Sociozoological scale of the *Bijagó* ethnic group and implications for guenon conservation

Human-wildlife overlap is increasing in biodiversity-rich countries. In these shared landscapes, perceptions and attitudes towards wildlife are of great importance for local livelihoods and conservation success. The Bijagós Archipelago in Guinea-Bissau is known for its bio-cultural diversity and harbours three guenon species – (*Cercopithecus petaurista*), Campbell's monkey (*Cercopithecus campbelli*), and the green monkey (*Chlorocebus sabaeus*). Although the long-term preservation of these species would benefit targeted conservation measures, these efforts may be met with resistance due to the guenons' crop-raiding success. Here, I aimed to explore the potential for a guenon-focused conservation program by examining the *Bijagó* perceptions and attitudes towards mammalian wildlife using sociozoological scales. Sociological scales reflect how societies classify and organise animals into "good" and "bad" animals according to their perceived moral status. Additionally, I investigated how the socio-cultural heterogeneity of the archipelago influenced local perceptions. I found that perceptions varied significantly between islands and genders, highlighting the need to incorporate the views of several actors in conservation actions. As predicted, guenon-focused conservation efforts are likely going to be met with low engagement or even resistance. Amongst all the assessed species, guenons ranked the lowest on the local sociozoological scale due to their high crop-raiding effectiveness. However, their high utilitarian value as food sources and socio-cultural symbols suggests that if compensatory programmes or socio-economic benefits (e.g., eco-tourism revenues) are introduced, the *Bijagó*'s tolerability towards these primates may also increase, improving conservation

engagement. These results highlight the applicability of sociozoological scales in the context of conservation.

Introduction

Deforestation and habitat fragmentation force humans and non-humans in biodiversity-rich countries to overlap in their distributions. In shared landscapes, where local populations are dependent on farming and natural resources, crop-raiding or livestock predation by local wildlife may lead to significant economic losses and increased food insecurity (Torres et al. 2018; Findlay and Hill 2020; Gulati et al. 2021; Haile et al. 2024). In such complex systems, those involved in conservation practices should also work towards the understanding and incorporation of local needs and values in order to enhance collaboration and produce positive social and conservation outcomes (König et al. 2021).

The assessment of local sociozoological scales is a useful starting point to understand the link between local livelihoods and attitudes towards wildlife (Costa et al. 2013). While taxonomy which classifies animals according to their evolutionary relationships and biological features, sociological scales reflect how societies classify and organise animals into “good” and “bad” animals according to their perceived role or moral status in the society they relate to (Arluke and Sanders 1996). The ranks of species within the sociozoological scale depend on species-specific traits relating to their perceived subordination, utilitarian and aesthetic values, and capacity to overrule the imposed societal order (Arluke and Sanders 1996). For example, “good” animals such as livestock or companion animals often have subordinate roles, and strong utilitarian and aesthetic values. They are perceived as “decent citizens” as they provide us with food and companionship (Costa et al. 2013). Contrarily, “bad” animals are viewed as uncontrollable, not owing humans any servitude (Costa et al. 2020). Wildlife such as large carnivores and snakes are associated with negative perceptions due to their ability to harm humans and other “decent” non-human citizens (Costa et al. 2020).

The Bijagós Archipelago in Guinea-Bissau, West Africa, is recognised for its biodiversity, having been declared a UNESCO Biosphere Reserve in 1996 (IBAP 2018). Although the marine and coastal ecosystems of the archipelago have received some attention from conservation agencies (Rebelo and Catry 2011; IBAP 2018; IBAP 2019), their terrestrial ecosystems remain relatively understudied. Here, the growing population of 32,000 inhabitants (INE 2015) remains highly dependent on farming and harvesting of natural resources (Chapter 6). Most inhabitants belong to the *Bijagó* ethnic group (~90 %; Madeira 2016) which are thought to promote the conservation of terrestrial ecosystems by establishing sacred groves where extraction activities, hunting included, are prohibited (Madeira 2009; Cardoso 2010).

There are three guenon species on the archipelago: the spot-nosed monkey (*Cercopithecus petaurista* Schreber, 1774), the Campbell's monkey (*Cercopithecus campbelli* Waterhouse, 1838) and the green monkey (Chlorocebus sabaeus Linnaeus, 1766). While these species are not in immediate threat of extinction (Gonedelé Bi et al. 2020; Matsuda Goodwin et al. 2020b; Matsuda Goodwin et al. 2020a), their long-term conservation would benefit from addressing the human-induced population size reductions caused by hunting (Chapters 2-5). Non-human primates' popularity make them potential flagship species for conservation projects (Williams et al. 2000; Estrada et al. 2017). However, the choice of a flagship species associated with negative perceptions and attitudes by the local inhabitants is likely to be met with resistance and undermine original conservation efforts (Douglas and Veríssimo 2013; Moyo et al. 2016; Xu et al. 2024). Such is the case for the Western chimpanzee (*Pan troglodytes* verus Schwarz, 1934) in Guinea-Bissau, whose tendency for crop-raiding and direct physical confrontations with farmers makes them likely unfit for the role of flagship species in this particular context (Costa et al. 2013). Similarly, guenons are likely to be perceived negatively due to their crop-raiding behaviours (Chapman et al. 2012; Hill and Wallace 2012; Findlay and Hill 2020; Haile et al. 2024). However, the inclusion of these species on the socio-cultural repertoire of the *Bijagó* (e.g., local legends; Paiva 1990) may increase their tolerability.

While societies often share a core set of values and beliefs, an individual's perceptions are derived from a combination of their individual factors (e.g., personality, cognitive abilities and experiences) and their socio-cultural background (Deth and Scarbrough 1995; Costa et al. 2020). Differences in perceptions and attitudes towards wildlife are expected in heterogeneous socio-cultural contexts. As seen in Chapter 6, *Bijagó* men and women use different ecosystems for their daily activities: men primarily harvest resources from forest and marine ecosystems, while women stay closer to the villages farming and harvest from intertidal resources. This likely leads to differences in wildlife encounters (rate and the types of species), impacting perceptions and attitudes. Additionally, animists and non-animist *Bijagó* people expressed different views on local socio-cultural traditions, which are predicted to shape how they perceive and interact with nature and wildlife (Chapter 6).

In this chapter, I assessed the *Bijagó*'s sociozoological scale and explored the effect of different variables related to the local socio-cultural contexts on perceptions and attitudes towards wildlife. I employed questionnaires to assess the local perceptions towards 14 wild mammal species and four domestic animals across three islands, each with distinct socio-cultural contexts. My main goal was to make an initial assessment of the potential for a guenon-focused conservation program in the region, based on the premise that non-human species are perceived differently, and those viewed more positively are more likely to succeed in conservation efforts (Costa et al. 2013).

Methods

Data collection

I conducted questionnaires (N = 193 ~64 hours and 30 minutes of data) on three islands or island groups of the Bijagós Archipelago with contrasting socio-cultural contexts: the Urok Island Group (protected area), Bubaque Island (the urban hub of the archipelago) and Canhabaque Island (rural and under no formal protection; see Chapter 6 for more information on data collection and descriptive analysis of the socio-cultural context of the sample).

To establish which mammal species were considered “good” and “bad” based on their roles and/or perceived moral status to the *Bijagó* society, I showed photos of domestic (N = 4) and wild mammal species of the Bijagós Archipelago, including primates, gazelles, duikers, rodents, small carnivores, hippopotamus and manatees (N = 14; Table 7.1). Due to limited baseline research, the ranges of most terrestrial species within the archipelago are uncertain, with the exception of three guenons species (Gippoliti and Dell’Omo 2003; Colmonero-Costeira et al. 2019).

A photo of a capuchin monkey (*Cebus capucinus* Linnaeus, 1758 a South American primate) was also included to assess the reliability of the respondents. All photos were of the same size and quality to avoid potential artefacts. Afterwards, I asked participants to rank three species in regard to certain dichotomic traits/attributes that likely modulate their perceptions (Costa et al. 2013). These were: likeability (“good” and “bad”), appearance (“beautiful” and “ugly”), intelligence (“intelligent” and “unintelligent”), similarity to humans (“human-like”), edibility (“edible” and “inedible”), and perceived encounter rate (“common” and “uncommon”). Other variables such as their usage in traditional dances and ceremonies and the willingness to interact with the animals (“want to see” and “do not want to see”), were also included. The photos of the domestic animals were removed for questions directly related to wildlife conservation such as the ones regarding edibility, perceived encounter rate, and willingness to encounter. The order of the photos was randomized between participants. I assumed that the order in which participants chose the animals reflected their quality for a specific trait (Hayes 2000). The first chosen species was given a quality score of 3, the second a score of 2 and the last chosen species a score of 1. Species that were not chosen for a specific trait were given a value of 0. Morphologically similar species that were often confused by the participants were grouped together for downstream analyses (Table 7.1).

Ordination analyses of perceptions

I employed principal component analysis (PCA) to explore and identify associations between species’ traits that likely represented different clusters of perceptions across the participants. To avoid missing-data induced artefacts (Legendre and Legendre 2012), only traits mentioned by more than 8 % (n = 15) of the participants were used.

This was the threshold chosen because it represented the lowest sample size for a single category within the explanatory variables, n = 15) for each species. The adequacy of the dataset for the analysis was assessed using the Kaiser–Meyer–Olkin test (KMO) and Bartlett’s test of sphericity. Loadings were rotated using varimax rotation and components with eigenvalues larger than one were retained (Hair et al. 2010). Only traits with loadings higher than 0.4 (or lower than -0.4) were considered meaningful (Hair et al. 2010).

Next, I employed redundancy analysis (RDA, Legendre and Anderson 1999) to understand how perceptions change according to a set of explanatory variables. RDA combines an ordination method (PCA) with multiple regressions with the explanatory variables (Legendre and Legendre 2012). I chose as explanatory variables: i) the different socio-cultural contexts within the Bijagós Archipelago (location), and ii) the participant characteristics (gender, age and education level) all of which were explored in Chapter 6. To prevent a possible over-fitting of the multiple regression models, I used a forward selection procedure. I selected a stringent significance level of 0.01 and the adjusted determination coefficient (R^2_{adj}) as stopping criteria (Blanchet et al. 2008) to account for the increased type-I error rates due to multiple testing. Subsequently, I estimated the variance inflation factor (VIF) of the model and removed highly collinear variables (VIF > 5) in a stepwise manner. Statistical significance of the multiple regression models and each of the resulting canonical axes was obtained by ANOVA-like permutation tests (using 9,999 permutations). Ordination analyses were performed using packages psych v2.4.6.26 (Revelle 2024) and vegan v2.6-4 (Oksanen et al. 2022). R packages and statistical analysis were run under R v4.2.2 (R CoreTeam 2022) coupled with RStudio v2023.06.2+561 (Posit team 2023).

Table 7.1. List of animals presented for ranking.

Groupings	Common name	Scientific name	Creole name
Guenons	Spot-nosed monkey	*Cercopithecus petaurista*	Santchu nariz-branku
	Green monkey	*Chlorocebus sabaeus*	Santchu-di-tarrafe
	Campbell's monkey	*Cercopithecus campbelli*	Santchu mona
Gazelles	Bushbuck	*Tragelaphus scriptus*	Gazela pintadu
	Kob	*Kobus kob*	Gazela di lala
	Maxwell's duiker	*Philantomba maxwellii*	Kabra matu
Squirrels	Gambian sun squirrel	*Heliosciurus gambianus*	Saninhu di pó
	Striped ground squirrel	*Xerus erythropus*	Saninhu di tchon
	Northern giant pouched rat	*Cricetomys gambianus*	Djiguindor
	Marsh mongoose	*Atilax paludinosus*	Catchur mangu
	African clawless otter	*Aonyx capensis*	Londri
	Pardine genet	*Genetta pardina*	Gato lagaria
	Hippopotamus	*Hippopotamus amphibius*	Pis-cabalu
	West African manatee	*Trichechus senegalensis*	Pis-bus
Domestic animals			
	Chicken	*Gallus gallus domesticus*	Galinha
	Goat	*Capra hircus*	Kabra
	Pig	*Sus domesticus*	Purku
	Cow	*Bos taurus*	Baka

Photos used can be found in Supplementary Table 7.1.

Results

Based on the ranks for likeability traits (“good” or “bad”) and the participant’s reporting frequency, the studied species can be organised into five groups that likely reflect their moral status for the *Bijagó* (Figure 7.1). Both (i) domestic animals (chicken, goat, cow and pig) and (ii) gazelles and duikers were considered “good species”, having a positive mean likeability score. However, duikers and gazelles were mentioned infrequently suggesting an overall lower socio-cultural importance compared to domestic species (frequency: domestic animals 0.56 – 0.86; gazelles and duikers 0.06 – 0.11). The (iii) manatees were considered neutral with likeability scores and reporting frequency close to zero. The otters, civet, squirrels, mongoose, hippopotamus and giant pouched rat or were considered as “bad animals” with negative mean likeability scores and having been chosen at varying frequencies (frequency varying between 0.08 and 0.47; Figure 7.1). In the last category (v) I found that guenons were the most mentioned and least liked species group (frequency = 0.61, average likeability score = -2.16).

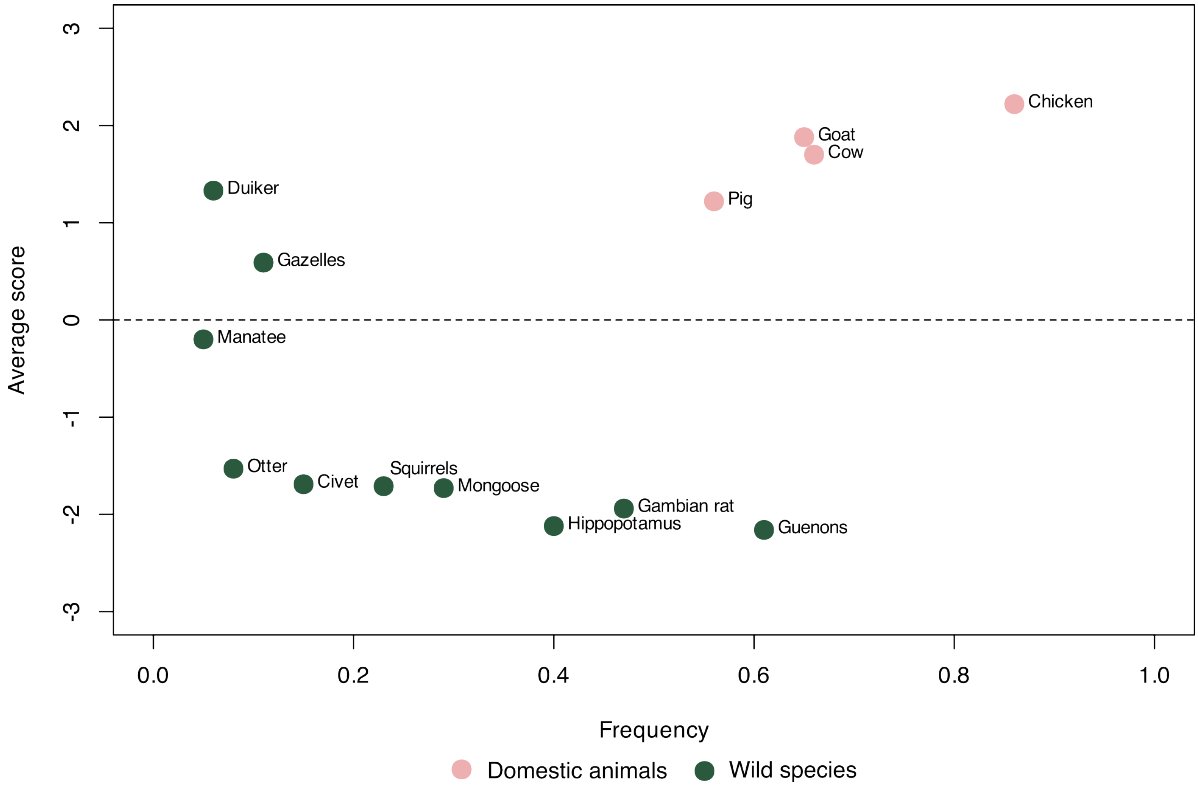


Figure 7.1 Likeability of domestic animals and wildlife mammal species for the *Bijagó*. Positive likeability scores correspond to the ranks of the likeability attribute “good” and negative scores to ranks of the likeability attribute “bad”. Average scores were estimated using a sample of 192 *Bijagó* questionnaires.

Perceptions on wild mammal species’ traits

For all the examined wild mammal species except the African clawless otter, shared variance and correlations between perceived species traits was found (KMO > 0.5; Bartlett’s test of sphericity $p < 0.001$), suggesting that ordination techniques, such as PCA and RDA, were applicable and allowed for grouping of species traits into clusters of perceptions. The explanatory variables explained a significant portion of the variance in perceptions for the guenons, gazelles, duiker, giant pouched rat, squirrels, hippopotamus and the manatee (ANOVA-like permutation p-value < 0.001).

In the guenons, varimax rotated principal component (PC) 1 represented the species' utilitarian value in which "edible", their perceived encounter rate, and the willingness of participants to encounter species more frequently all loaded highly onto this component (Supplementary Table 7.2). The second component represented the intelligence cluster, and the third negative attitudes. The fourth component represented their usage in socio-cultural ceremonies ("dance") which is associated with high loadings of their perceived encounter rate and willingness of participants to encounter the species more frequently. The last component, PC5, the "human-like" trait was the only trait to present a high loading, suggesting an absence of any clear association with other traits. Variance in perceptions was significantly explained by location and gender (constrained variance = 8.62 %, $p < 0.001$; Figure 7.2 A). Negative attitudes (PC3) were more prominent in Urok and Bubaque Island. The utilitarian status of guenons (PC1) was also more pronounced in Urok compared to the remaining islands. Gender differences in the intelligence cluster (PC2) indicated that females tended to perceive guenons as "intelligent", while males associated them "unintelligent". Other less prominent gender-based differences can be found in traits associated with aesthetic traits and encounter rates, with males associating them with "ugly" and "human-like" traits and females linking them to rarer encounters.

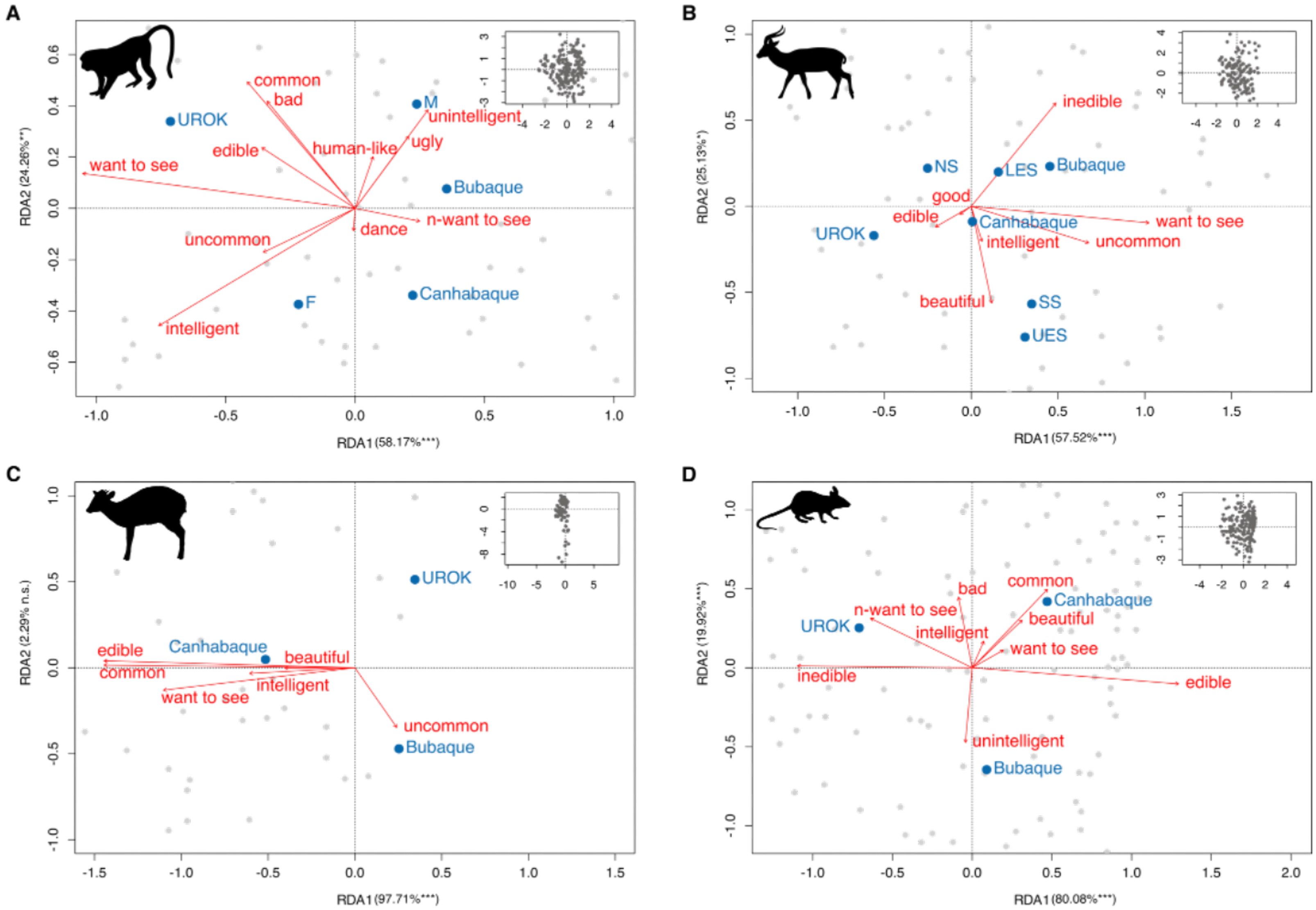
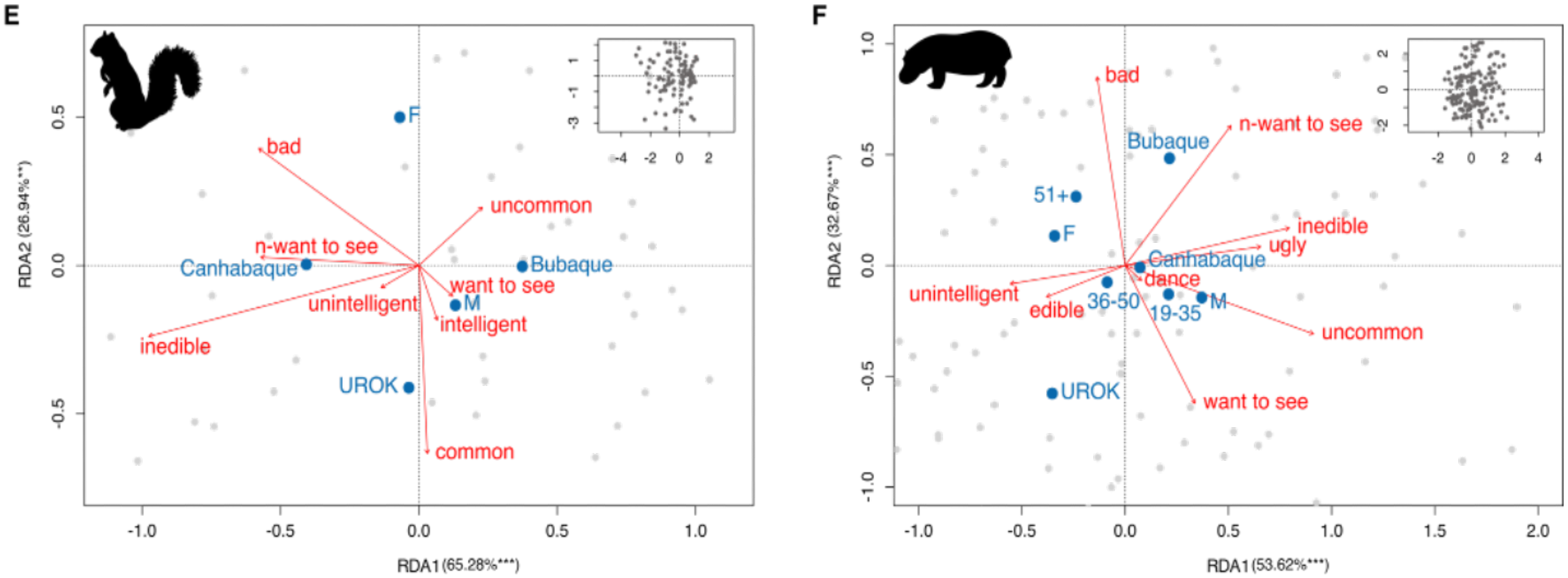


Figure 7.2. Perceptions of the *Bijagó* towards wild mammal species. (continues)



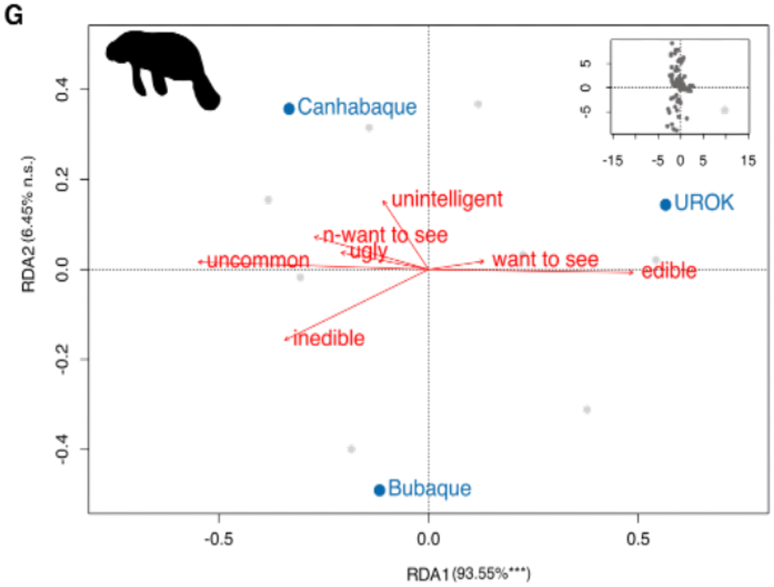


Figure 7.2. Plots represent correlation triplots of redundancy analysis (RDA) between the traits (response variables, red arrows) and the individuals' personal information (explanatory variables, blue centroids). A) guenons (R^2_{adj} = 0.072, constrained variance = 8.62 %, pseudo-F = 5.91, df = 3, p < 0.001); B) gazelles (R^2_{adj} = 0.057, constrained variance = 8.12 %, pseudo-F = 3.28, df = 5, p < 0.001); C) duikers (R^2_{adj} = 0.20, Constrained variance = 20.78 %, pseudo-F = 24.79, df = 2, p < 0.001); D) Giant pouched rat (R^2_{adj} = 0.095, constrained variance = 10.47 %, pseudo-F = 11.06, df = 2, p < 0.001); E) squirrels (R^2_{adj} = 0.073, constrained variance = 8.72 %, pseudo-F = 5.99, df = 3, p < 0.001); F) hippopotamus (R^2_{adj} = 0.091, constrained variance = 11.44 %, pseudo-F = 4.81, df = 5, p < 0.001); G) manatee (R^2_{adj} = 0.023, constrained variance = 3.28 %, pseudo-F = 3.20, df = 2, p < 0.001). Statistical significance of the constrained axes: * p < 0.05; ** p < 0.01; * p < 0.001. Credits of the guenon silhouette from Kai Caspar, attribution 3.0 (https://creativecommones.org/licenses/by/3.0/), altered. Remaining silhouettes are part of the public domain.

Gazelles and duikers were ranked similarly for their edibility and positive traits. Both species shared a pattern where the first two components (PC1 and PC2; Supplementary Table 7.2) emphasised their utilitarian and aesthetic values correlated with perceived “intelligence” and willingness to encounter them more frequently. In gazelles, PC3 reflected positive perceptions related to rarity (“uncommon”). Location and education level were found to significantly explain the variance in perceptions of gazelles (constrained variance = 8.12 %, $p < 0.001$; Figure 7.2 B, C). In this sample of participants, education level was shown to vary with location (Chapter 6). Regardless of the potential collinearity, partial RDAs were also significant ($p < 0.001$; not shown), suggesting that the significance of the location and education level model was not inflated by the potential autocorrelation between the two variables. Gazelles were ranked highly for rarity by participants from Bubaque Island, while those with higher education valued their aesthetic traits. The traits associated with the utilitarian values (PC1) have small loadings suggesting they are not major drivers of constrained variance. Contrary to gazelles, the duiker's utilitarian and aesthetic value was only recognised by those who encountered them more frequently (“common”). This trend was particularly pronounced in Canhabaque Island (constrained variance = 20.78 %, $p < 0.001$), where the duiker's utilitarian and aesthetic value was acknowledged, likely due to its higher encounter frequency.

The giant pouched rat had similar perception clusters to guenons, with PC1 reflecting utilitarian traits, PC2 for negative perceptions, and PC3 for perceived intelligence (Supplementary Table 7.2). Unlike guenons, some participants also identified the species as “inedible” (negative loadings in PC1). Some aesthetic value was illustrated in PC5, although it was not clearly associated with any other traits. Perceptions were significantly explained by location (constrained variance = 10.47 %, $p < 0.001$), with participants from Canhabaque Island emphasising its utilitarian and aesthetic value, while those from Urok highlighted negative perceptions (PC3) and inedibility (Figure 7.2 D).

Squirrels, the marsh mongoose and the civet were predominantly associated with negative attitudes and traits (Supplementary Table 7.2). Compared to other species generally deemed as “bad” species, such as guenons and the giant pouched rat, the squirrels and these small carnivores lacked the utilitarian status as “edible” species. The perceptions towards squirrels were more nuanced than those of the small carnivores. For instance, the third and fourth principal components were associated with positive traits and attitudes including an association between “common” and the willingness to encounter more frequently (PC3) and perceived intelligence (PC5). The perceptions towards squirrels varied significantly with location and gender (constrained variance = 8.72 %, $p < 0.001$). In Canhabaque Island, squirrels were mainly viewed negatively (PC1), while in Bubaque Island they were associated with positive attitudes and traits (PC3 and PC5). Gender differences emerged in perceived encounter rates, with men considering squirrels more “common”, and attitudes with women perceiving squirrels as “bad” and men perceived them more positively (PC3 and PC5). For the small carnivores, the variance in perceptions was not significantly explained by any of the explanatory variables (marsh mongoose – full model $p = 0.24$; civet – full model $p = 0.53$).

Hippopotamuses were mostly perceived negatively. Principal component one contained high loadings for visually discernible traits such as “ugly” and “inedible”, “uncommon”, and willingness to encounter less frequently, while PC3 contained subjective negative traits such as “bad” and “unintelligent” associated with lower rankings for the “inedible” trait (Supplementary Table 7.2). The second principal component was reserved for the utilitarian status of hippopotamus in socio-cultural traditions (“dance”), which was associated with higher willingness of participants to encounter the species. Perceptions varied significantly with the gender, age class of the participants and location (constrained variance = 11.44 %, $p < 0.001$). Male participants were particularly knowledgeable on the distribution ranges of the species, often mentioning that you could mostly see them at the Orango Island Group rather than any of the sampled islands. Men and younger participants were more associated with the visually discernible negative traits (PC1) and socio-cultural importance of the species, while women and older participants were more associated with the subjective negative traits (e.g., “bad”; Figure 7.2 F). Regarding location, the differentiation between participants from Bubaque Island and the remaining Islands resulted from more pronounced negative attitudes towards hippopotamuses at the island.

The manatee was not consistently ranked as neither “good” nor “bad”. However, PC1 was associated with negative attitudes and traits (Supplementary Table 7.2). Principal components two and three represented opposed perceptions of edibility (PC2 – “inedible”; PC3 – “edible”) and perceived encounter encounter rate (PC2 – “uncommon”; PC3 – “common”). Variance in perceptions were significantly explained by location, but the overall explanatory power of the constraining model was very low (constrained variance = 3.28 %, $p < 0.001$; Figure 7.2 G). Regardless, negative attitudes (PC1) were associated with Canhabaque and Bubaque islands, and Urok participants recognised the species as edible (PC3).

Discussion

Understanding how human societies, living in shared landscapes with non-humans, perceive and relate with biodiversity, and how these relationships can threaten the long-term survival of wildlife is a key challenge in conservation management and policy. Here, using sociozoological scales, I explored how the *Bijagó* perceive and organise the local wild mammal species according to their utilitarian, aesthetic and behavioural traits. Finally, I use the results to identify potential factors that may hinder guenon conservation on the Bijagós Archipelago and explore alternative approaches to promote their long-term conservation in the region. These results highlight the practicality of sociozoological scales in the context of biodiversity conservation.

Sociozoological scale of the *Bijagó*

For the *Bijagó*, domestic animals were clearly different from wild animals and ranked at the top of the sociozoologic scale. Domestic animals are often considered “good” animals due to their subordinate roles (Arluke and Sanders 1996). As these animals are dominated by humans and are compliant to their expected societal role, they are deemed to live alongside human societies (Arluke and Sanders 1996). Opposingly, the wild animals are often associated with “chaos” of the forest, unrulable by humans (Arluke and Sanders 1996). The *Bijagó* are highly dependent on the harvesting of natural resources and agriculture. Consequently, some of the mammal species are thought to be capable of threatening their societies' order either by crop-raiding (guenons, giant pouched rat, squirrels and the hippopotamus) or by killing domestic animals (mongoose and the civet). This may explain why wild mammal species tend to rank at the bottom of the sociozoological scale. The gazelles and the duiker appeared to be differentiated from the remaining species as they are considered "intelligent" in respect to not being able to subvert the social order through crop-raiding, and held both utilitarian, and aesthetic values.

The willingness to encounter an animal more frequently was expected to be linked with an animal's higher position along the local sociozoological scale and the disposition to engage with conservation. However, among "neutral" (the manatee) and "bad" animal species, this trait was tightly linked to the species' perceived edibility. Bushmeat hunting is an ever-increasing threat to biodiversity in Guinea-Bissau (Minhós et al. 2013; Ferreira da Silva et al. 2021b; Ferreira da Silva et al. 2021a). In this conservation context "edibility" should be considered as a trait with negative implications towards conservation and, by extension, the *Bijagós*' willingness to encounter an animal more frequently is not a good predictor of conservation engagement. Another note regarding edibility, none of the participants except the Muslim minority (n = 6) identified any restrictions or taboos regarding hunting and consuming any of the species under study. Another trait that was predicted to be positively associated with ranks on the sociozoological scale was the inclusion of certain species in socio-cultural traditions. However, the only species that were ranked consistently for their role in traditional *Bijagó* dances were the guenons and the hippopotamus, both of which were among the lowest ranking species.

Participant variables and their impact on attitudes towards wildlife

An individual's perceptions result from the interplay between individual factors and their socio-cultural background (Deth and Scarbrough 1995). Given the inherent complexity of these response variables, the constraining models of the individual's explanatory variables captured an overall low but statistically significant portion of the total variance in the data. Thus, the incorporation of RDA to the exploratory PCA analysis was valuable for the extraction of individual's characteristics with conservation importance, elucidating how individual factors relate to perceptions and attitudes towards wildlife.

The perceptions and attitudes towards wild mammals showed significant regional differences. Some differences were likely attributed to species' presence or absence in each of the islands. For example, the edibility of the duiker, the giant pouched rat and the manatee were strongly associated with the participants from islands where these species have confirmed occurrences (Canhabaque Island: duiker and giant pouched rat; Urok: manatee; Reiner and Simões 1999; Campredon et al. 2001; Colmonero-Costeira et al. 2019).

Participants from Bubaque Island were generally less associated with negative attitudes towards wild mammals, which could be associated with a decreased exposure to wild species, or decreased impact of human-wildlife competition for natural resources, which is likely a consequence of the more urban settings of the island. The hippopotamus is an exception for which the inhabitants of Bubaque Island have particularly negative attitudes, even though the species does not occur permanently on the island (Reiner and Simões 1999; Campredon et al. 2001). However, this could be attributed to widespread fear of the ferocity and destructive power of the hippopotamus associated with their rare incursions outside their native range (Orango Island Group, 5 km southwest of Bubaque Island) to the rice plantations on the island of Bubaque.

Differences in the societal roles of the *Bijagó* men and women were also reflected in their perceptions and attitudes towards guenons, squirrels and hippopotamus. Traditionally, the *Bijagó* men are responsible for forest-related activities and fishing, while women remain closer to the village (Chapter 6). Consequently, men are more likely to encounter wildlife more frequently than women, which is reflected in their perceived encounter rate of wild species. In the specific case of the hippopotamus, the "uncommon" trait was highly ranked by men and could reflect their knowledge on the species ecology (e.g., occurrence at Orango Island Group), rather than encounter rates per se. Additionally, because men are typically in closer contact with species in their preferential habitat, they may have had more opportunities to assess species aesthetics and behaviour (Costa et al. 2013), thus ranking these traits higher than women. Intelligence was also found to be perceived differently between men and women which could represent different gender specific attitudes towards species' intentions (e.g., intent to crop-raid) or deceptiveness (e.g., evading capture or undermining anti-crop-raiding strategies).

Other participant variables that appeared to significantly modulate perceptions and attitudes towards wildlife were formal education level (higher education level associated with higher rankings of the aesthetic value of gazelles), and age (older participants more likely to report hearsay incidents with hippopotamus). The *Bijagó* society seemed to be undergoing changes to their religious affinities with a significant portion of this sample (40 %, n = 77, Chapter 6) no longer recognising themselves as animists. Contrary to my expectation, religion as a proxy to socio-cultural adherence was not a significant driver of differences in perceptions towards any of the examined wild mammal species.

Are guenons good conservation flagship species at the Bijagós Archipelago?

Guenons were ranked as a highly edible species, particularly in areas where they are the only wild terrestrial mammal (with known occurrence) recognised as "edible" (e.g., Urok). This suggests that their meat might be preferentially targeted, stressing that bushmeat hunting likely poses one of biggest threats to the guenon populations of the Bijagós Archipelago which may need to be addressed in the future.

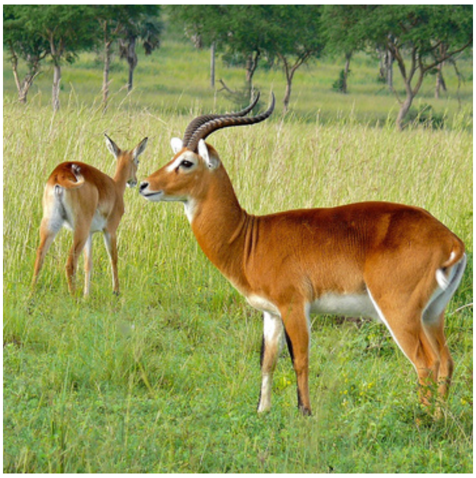
However, considering their current position in the sociozoological scale of the *Bijagó*, conservation actions directed towards guenons do not seem to align with local interests and might be met with a lack of involvement or even resistance (Costa et al. 2013; Douglas and Veríssimo 2013; Moyo et al. 2016; Xu et al. 2024). Guenons were the species most frequently mentioned as "bad" for both men and women, suggesting that negative interactions during encounters are common and an important aspect of *Bijagó* livelihoods. Similar to other shared landscapes between humans and guenons, encounters might be seen as negative due to competition behaviours with local populations (Chapman and Gogarten 2012; Hill and Wallace 2012; Findlay and Hill 2020; Haile et al. 2024). At the Bijagós Archipelago in particular, guenons were reported to compete with men for non-timber forest products (e.g., palm tree nuts) and with women in the crop-raiding of rice, cashew and other agricultural produce. In the socio-context of the Bijagós Archipelago where local communities are highly dependent on these resources, guenons could exacerbate food insecurity (Chapman and Gogarten 2012; Hill and Wallace 2012; Findlay and Hill 2020; Haile et al. 2024). The local communities' intolerant behaviours towards the guenons may in fact be the highest among all crop-raiding species on the archipelago. Other than being destructive, *Bijagó* participants often mentioned the guenons' ability to evade preventive measures against crop-raiding behaviours. This trait has been commonly attributed to non-human primates (Hill and Wallace 2012; Findlay and Hill 2020). Negative attitudes varied with location and were stronger in Urok and Bubaque islands, where the green monkey can be found, compared to Canhabaque Island, where only the spot-nosed monkey occurs (Colmonero-Costeira et al. 2019). Different species could often display crop-raiding behaviours and cognitive capacities to evade deterrents and, consequently, different perceived threat potentials to the local populations (Hill and Wallace 2012; Quirin and Dixon 2012; Findlay and Hill 2020).

Negative perceptions and attitudes towards guenons may be counterbalanced locally by compensatory programmes or if alternative socio-economic benefits from the co-existence with guenons are introduced. Tourism at the Bijagós Archipelago has been suggested as a tool to promote the conservation of its ecosystems (IBAP 2016). Eco-tourism featuring primates is mostly reserved to iconic species such as the great apes. However, in specific contexts, guenon eco-tourism could be a valuable approach to promote their long-term conservation (e.g., Golden monkey, *Cercopithecus mitis kandti* Matschie, 1905, in Uganda; Tuyisingize et al. 2023). However, the success of such actions would depend on their sustainability, and whether local communities perceive these as sources of income or development.

Supplementary Materials

Supplementary Table 7.1 Photographs of animals used for ranking.

Common name	Scientific name	Creole name	Photographs
Spot-nosed monkey	*Cercopithecus petaurista*	Santchu nariz-branku	
Green monkey	*Chlorocebus sabaeus*	Santchu-di-tarrafe	
Campbell's monkey	*Cercopithecus campbelli*	Santchu mona	

Bushbuck	*Tragelaphus scriptus*	Gazela pintadu	
Kob	*Kobus kob*	Gazela di lala	
Maxwell's duiker	*Philantomba maxwellii*	Kabra matu	

Gambian sun squirrel	*Heliosciurus gambianus*	Saninhu di pó	
Striped ground squirrel	*Xerus erythropus*	Saninhu di tchon	
Northern giant pouched rat	*Cricetomys gambianus*	Djiguindor	

Marsh mongoose	*Atilax paludinosus*	Catchur mangu	
African clawless otter	*Aonyx capensis*	Londri	
Pardine genet	*Genetta pardina*	Gato lagaria	

Hippopotamus	*Hippopotamus amphibius*	Pis-cabalu	
West African manatee	*Trichechus senegalensis*	Pis-bus	
Domestic Animals			
Chicken	*Gallus gallus domesticus*	Galinha	

Goat	*Capra hircus*	Kabra	
Pig	*Sus domesticus*	Purku	
Cow	*Bos taurus*	Baka	

Supplementary Table 7.2 Varimax rotated principal components of species attributes (continues).

Traits	**Guenons** (KMO = 0.52)					**Gazelles** (KMO = 0.54)			**Duiker** (KMO = 0.70)	
	PC1	**PC2**	**PC3**	**PC4**	**PC5**	**PC1**	**PC2**	**PC3**	**PC1**	**PC2**
Dance	-0.08	0.27	0.16	**-0.60**	-0.23					
Good						0.08	**0.71**	-0.19		
Bad	-0.06	0.04	**0.77**	0.12	0.04					
Beautiful						-0.03	**0.69**	-0.01	**0.56**	0.31
Ugly	-0.06	-0.12	**0.58**	-0.06	0.09					
Intelligent	0.08	**0.81**	0.06	0.06	0.15	**0.70**	0.10	0.22	**0.56**	0.02
Unintelligent	-0.01	**-0.76**	0.15	0.04	0.05					
Human-like	0.05	0.09	0.16	-0.01	**0.92**					
Edible	**0.62**	0.06	-0.11	0.09	0.22	**0.80**	0.01	-0.16	**0.69**	**-0.42**
Inedible						**-0.40**	-0.02	**0.58**		
Common	**0.52**	0.07	**0.41**	-0.35	-0.12				**0.56**	**-0.58**
Uncommon	0.00	0.24	0.19	**0.74**	-0.2	0.14	-0.15	**0.76**	0.14	**0.84**
Want to see	**0.67**	0.23	0.16	0.39	-0.12	0.19	**0.51**	**0.46**	**0.73**	-0.04
Don’t w. to see	**-0.66**	0.15	0.34	0.15	0.04					
Explained variance (%)	14	13	12	11	10	19	18	18	33	22

Supplementary Table 7.2 Varimax rotated principal components of species attributes (continues).

Traits	**Giant pouched rat** (KMO = 0.63)				**Squirrels** (KMO = 0.60)				**Mongoose** (KMO = 0.60)	
	PC1	**PC2**	**PC3**	**PC4**	**PC1**	**PC2**	**PC3**	**PC4**	**PC1**	**PC2**
Dance										
Good										
Bad	0.07	**0.85**	0.07	-0.06	**0.66**	0.01	-0.12	0.03	0.22	**0.58**
Beautiful	0.12	0.01	0.03	**-0.87**						
Ugly									**0.65**	-0.04
Intelligent	0.14	0.05	**0.78**	0.21	0.02	-0.09	0.00	**0.95**		
Unintelligent	0.08	0.10	**-0.76**	0.33	**0.60**	0.21	0.13	0.16	-0.19	**0.66**
Human-like										
Edible	**0.77**	-0.12	0.01	-0.21						
Inedible	**-0.68**	0.19	0.10	0.22	**0.48**	-0.37	0.11	-0.11	-0.05	**0.61**
Common	**0.61**	0.14	0.22	0.23	0.14	**-0.44**	**0.65**	-0.16	**0.77**	-0.14
Uncommon					0.14	**0.82**	0.09	-0.15	**-0.41**	-0.16
Want to see	**0.41**	-0.37	0.05	0.10	-0.17	0.25	**0.79**	0.11		
Don't w. to see	-0.33	**0.63**	-0.11	0.16	**0.75**	-0.02	-0.09	-0.11	**0.44**	**0.52**
Explained variance (%)	19	15	14	12	21	14	14	13	21	21

Supplementary Table 7.2 Varimax rotated principal components of species attributes.

Traits	**Civet** (KMO = 0.53)		**Hippopotamus** (KMO = 0.58)			**Manatee** (KMO = 0.52)		
	PC1	**PC2**	**PC1**	**PC2**	**PC3**	**PC1**	**PC2**	**PC3**
Dance			0.21	**0.51**	0.21			
Good								
Bad	**0.49**	0.2	0.25	-0.35	**0.54**			
Beautiful								
Ugly	0.13	**0.72**	**0.70**	-0.17	0.14	0.34	0.37	0.16
Intelligent								
Unintelligent	0.34	**-0.53**	-0.05	0.2	**0.73**	**0.79**	0.09	0.13
Human-like								
Edible			**-0.51**	-0.03	0.04	-0.2	-0.39	**0.60**
Inedible	0.17	**0.56**	**0.52**	-0.03	**-0.53**	0	**0.64**	-0.25
Common								
Uncommon	**0.69**	0.07	**0.59**	0.32	-0.03	-0.06	**0.69**	0.22
Want to see			0.08	**0.79**	-0.04	0.1	0.23	**0.79**
Don’t w. to see	**0.68**	-0.08	**0.42**	**-0.64**	0.04	**0.68**	-0.14	-0.28
Explained variance (%)	22	19	18	18	13	18	18	17

CHAPTER 8

General Discussion

Within the order Primates – one of the most diverse mammalian groups – more than 66% of the recognised taxa are classified as threatened with extinction by the International Union for Conservation of Nature (IUCN 2024), highlighting the global need for conservation (Estrada et al. 2017; Estrada and Garber 2022). However, non-human primate (primate hereinafter) conservation is challenging as increasing overlap between primates and humans is often associated with increased inter-species competition and conflict (Chapman et al. 2012; Hill and Wallace 2012; Findlay and Hill 2020; Haile et al. 2024). As such, effective primate conservation benefits from interdisciplinary approach, combining ecology/zoology, conservation genetics/genomics and social research on local knowledge and attitudes.

This thesis demonstrates the usefulness of a multidisciplinary approach to promote the conservation of guenons (tribe Cercopithecini) of the Bijagós Archipelago, Guinea-Bissau, West Africa. I focused particularly on the spot-nosed monkey (*Cercopithecus petaurista* Schreber, 1774) whose insular populations are likely the only that currently remain in the country (Gippoliti and Dell'Omo, 2003). I also included in some chapters the remaining two species, the Campbell's monkey (*Cercopithecus campbelli* Waterhouse, 1838), and the green monkey (*Chlorocebus sabaeus* Linnaeus, 1766) to answer wider conservation questions. I started by reporting immediate conservation threats currently faced by the spot-nosed monkey based on observations during field work and testimonies of local communities (Chapter 2). I employed genetic tools to characterise the spot-nosed monkey's present genetic diversity and gene flow dynamics (Chapter 3), to reconstruct the colonisation history and estimate the effective population size (N_e; Chapter 4) and applied the recent advances in genomic sequencing to explore the neutral and adaptive effects of insularity across the three insular guenons (Chapter 5). Additionally, I investigated the perceptions and attitudes of the local ethnic group, the *Bijagó*, towards wildlife to make an initial assessment of the potential effectiveness and community assessment for guenon-focused conservation actions (Chapter 6 and 7).

Summary of Findings

In **Chapter 2**, I found that the spot-nosed monkey at the sampled islands was perceived by the local inhabitants as being increasingly rare, likely due to the conversion of the natural habitats into agricultural areas including increasing cultivation of cash crops (e.g., cashew nuts), generalised habitat degradation and bushmeat hunting. More importantly, I reported the existence of a semi-organised commercial primate bushmeat trade on the archipelago to fuel the urban areas of the country (Bubaque Island and Bissau), which may be unsustainable.

Chapter 3 focussed on characterising the current genetic diversity and population structure across a large portion of the range of the insular spot-nosed monkey populations. I found intermediate, but heterogenous levels of genetic diversity across the archipelago and strong population structuring, where each of the sampled islands represents a unique genetic cluster with negligible gene flow in contemporary times. Additionally, population differentiation between islands did not conform to the expected stepwise colonisation pattern, typical of natural and sequential colonisations. This work provided an alternative hypothesis for the proposed colonisation history of the archipelago by the primate: the human-mediated colonisation hypothesis.

To understand how the spot-nosed monkey colonised the Bijagós Archipelago, I tested several competing colonisation hypotheses under an Approximate Bayesian Computation framework in **Chapter 4.** Notably, the results suggested a likely influence of humans on the colonisation of the primate, supporting the hypothesis derived in **Chapter 3.** The timing of the colonisation was compatible with the translocations within the archipelago facilitated by the ancestral *Bijagó* communities.

This work also provided the first estimates of the contemporary N_e of these populations which were below the recommended value for long-term maintenance of genetic diversity (< 500; Frankham et al. 2014).

In **Chapter 5**, I used whole genome sequencing data of island and mainland populations of three guenon species occurring on the Bijagos Archipelago, to explore the genomic signatures of insularity and reduced population size. In the three species, island populations showed lower genome-wide diversity and higher proportions of their genome under rows of homozygosity (ROH). Unlike many small populations, genetic drift was suggested to have increased the individual's realised load without increased purging. On the other hand, there was no evidence for accumulation of deleterious variation, suggesting that these populations are not yet at risk of extinction by genetic factors.

In **Chapter 6 and 7,** I shifted my focus from conservation genetics/genomics to investigate the perceptions and attitudes of the *Bijagó* ethnic group towards local mammalian wildlife. Socio-cultural variables (e.g., socio-economic context and gender, but not religion) conditioned local perceptions, suggesting that conservation efforts on the Bijagós Archipelago should consider the internal socio-cultural heterogeneity of the archipelago. I found that the guenons were amongst the lowest ranking species in the *Bijagó* sociozoologic scale and may not be, therefore, a good flagship species for conservation in the area.

Implications for Conservation and Future Directions

Globally, the development of conservation efforts, including the establishment of legal protection of species, are dependent on species' conservation status reports, such as the IUCN Red List of Threatened Species. However, in a time when the local extirpation of species as a direct result of human action is increasing (Ceballos et al. 2017), an accurate assessment of a species' local conservation status is of utmost importance. In Guinea-Bissau, a small West African country, the local conservation status of the spot-nosed monkey, a species otherwise considered wide-spread and of little conservation concern (Matsuda Goodwin et al. 2020), is thought to be particularly dire as the last viable populations of the primate in the country can only be found on seven of the islands of the Bijagós Archipelago. Furthermore, the long-term conservation of insular populations is expected to be naturally challenging due to lower population sizes and both neutral and adaptive genetic changes associated with colonisation dynamics (Allendorf et al. 2013; Dussex et al. 2021; Martin et al. 2023).

Indeed, the populations of the guenon three species of the Bijagós Archipelago displayed genetic signatures typical of insular populations. These included strong population differentiation (Chapter 3 and 5), demographic signals of founding events characterised by small founding populations (Chapter 4), reduced genetic diversity, increased inbreeding (Chapter 3 and 5) and low estimates of contemporary N_e. Even though these results suggest that spot-nosed monkey populations of the Bijagós Archipelago (and by extension insular populations of the Campbell's monkey and the green monkey) are thought to be more threatened than their mainland counterparts, I did not find increased accumulation of deleterious variation on the islands, suggesting that these populations are not in immediate threat of extinction due to genetic factors (Chapter 5). However, the increased inbreeding and genetic drift acting on the insular populations resulted in higher levels of realised load which may affect population fitness negatively (Chapter 5), particularly if other anthropogenic factors affect individual survival of these primates.

Across West Africa, expanding human populations in areas of low food security where local populations rely mostly on unsustainable agricultural practices and extraction of natural resources are exerting an undeniable pressure on primate-rich ecosystems. Not only do these activities directly reduce total forest area, but also promote the expansion of degraded areas (Metzger 2002). The Bijagós Archipelago is not an exception to the West African trend. Here, considering the accelerated expansion of degraded habitats and increased dependency of local population on cash crops (Chapter 5; Madeira 2016), it is likely that the suitable habitat will be severely reduced in the next few decades (Chapter 2). The *Bijagó* socio-cultural traditions likely contribute to the passive conservation of local wildlife (Madeira 2009; Cardoso 2010). However, the trend of decreasing adherence to the local socio-cultural traditions and animistic beliefs may endanger the *Bijagó*'s self-regulation of the local ecosystems (Chapter 6).

The spot-nosed monkey is also threatened by subsistence and commercial bushmeat hunting pressures. Subsistence hunting of the three species occurs on several islands of the archipelago and the illegal harvesting for the commercial meat trade has been described recently (Chapter 2). This activity is thought to be an increasing practice on the islands likely motivated by the unstable sources of income in the region, which may encourage young men to engage in this activity, as it has immediate returns (Ferreira da Silva et al. 2021a). The extent to which unsustainable hunting impacts insular populations of the spot-nosed monkey is currently unknown. Nevertheless, demographic changes related to anthropogenic activities have been reported for other species of primates in the country. Changes reported for other highly hunted species include decreased effective population size (Minhós et al. 2023), and dispersal patterns due to hunting-related mortality (Ferreira da Silva et al. 2014; Ferreira da Silva et al. 2018). Furthermore, not much is known how hunting interacts with increased realised genetic load which ought to be considered an investigation priority.

Compared to other primate species in Guinea-Bissau with conservation concern, the spot-nosed monkey of the Bijagós Archipelago exhibits one of the lowest estimated N_e (Chapter 4), together with the red colobus (*Piliocolobus badius temminckii* Kuhl, 1920: N_e ~339) and the black-and-white colobus (*Colobus polykomos* Zimmermann, 1780: N_e ~417; Minhós et al. 2016; Table 8.1). Strict comparisons between N_e should always be evaluated with caution, particularly when derived from different analyses, regardless, it seems plausible to suggest that the spot-nosed monkey is one of the most locally threatened primate species in Guinea-Bissau and should be considered as a conservation priority. In the absence of immediate threats from genetic factors, long-term conservation of these insular populations could be promoted mainly by reducing their immediate threats, safeguarding additional loss of genetic diversity. Furthermore, these results support that insular populations are not genetically depauperate and could potentially act as reservoirs for the recently extinct (or very rare) mainland populations, creating the opportunity for future re-introductions of the species to mainland Guinea-Bissau.

Table 8.1 Estimated effective population size (N_e) for primates in Guinea-Bissau.

Species	Estimated N_e	Reference
Spot-nosed monkey (*Cercopithecus petaurista* Schreber, 1774)	~240 – 470 (ABC)	Chapter 4
Red colobus (*Piliocolobus badius temminckii* Kuhl, 1920)	~339 (MSVAR)	Minhós et al. 2016
Black-and-white colobus (*Colobus polykomos* Zimmermann, 1780)	~417 (MSVAR)	Minhós et al. 2016
Guinea baboon (*Papio papio* Desmarest, 1820)	~3,000 (MSVAR)	Ferreira da Silva et al. *in press*
Western chimpanzee (*Pan troglodytes verus* Schwarz, 1934)	~500 (N_eEstimator)	Ferreira da Silva et al. 2024

However, conservation actions focusing on the primates in general are likely to be met with resistance from local communities in Guinea-Bissau (Chapter 7; Costa et al., 2013), the *Bijagó* included. On the archipelago, guenons ranked low on the sociozoologic scale: encounters with guenons are likely seen as negative due to their crop-raiding behaviours which could exacerbate food insecurity of the local communities (Chapman et al. 2012; Hill and Wallace 2012; Findlay and Hill 2020; Haile et al. 2024). However, guenons have a high utilitarian value for the local communities mostly as food sources but also as socio-cultural symbols. Indeed, guenons could be a cultural heritage of the *Bijagó* (Chapter 4) which nowadays is still maintained in their oral and performative repertoire (Paiva 1990; Chapter 4). As such, the *Bijagó* might be inclined to support guenon conservation efforts if their crop-raiding damages are counterbalanced by compensatory programmes or if alternative socio-economic benefits from the co-existence with guenons are introduced. Guenons are not typically associated with eco-tourism, however in specific contexts, guenon eco-tourism could be a valuable approach to promote their long-term conservation (e.g., Golden monkey*, Cercopithecus mitis kandti* Matschie, 1905, in Uganda and Rwanda; Tuyisingize et al. 2023). However, the success of such actions would depend on their suitability to the tourism scene of the Bijagós

Archipelago, sustainability, and whether local communities perceive these as sources of income or development.

Out of the three guenon species of the Bijagós Archipelago, this thesis focused mainly on the spot-nosed monkey. Regarding the Cambpbell’s monkey, the single whole genome from Caravela Island analysed in Chapter 5 was characterised by having the lowest genome-wide diversity and the highest proportion of the genome under ROH suggesting that this species could be locally more threatened from inbreeding than its spot-nosed monkey counterparts. Further works should contemplate the other two guenon species in order to develop a unified guenon conservation action plan for the Bijagós Archipelago.

The evidence presented in this thesis on genetic parameters of conservation importance, along with insights into local perceptions and attitudes towards wildlife, can be integrated into the design of ethical conservation strategies that reflect both the conservation and local populations’ needs. Moreover, the presented findings may be applicable to other guenon species scattered around the Atlantic archipelagos which are being prosecuted despite their potential as reservoirs for extant mainland genetic diversity.

REFERENCES

Adler, G.H. and Levins, R. 1994. The Island Syndrome in Rodent Populations. *Quarterly Review of Biology* 69(4), pp. 473–490. doi: doi.org/10.1086/418744

Akenji, L. et al. 2019. Community-Based Monitoring of Cross River Gorillas in South West Region, Cameroon. *African Primates* 13, pp. 29–38.

Albert, A., Hambuckers, A., Culot, L., Savini, T. and Huynen, M.C. 2013. Frugivory and Seed Dispersal by Northern Pigtailed Macaques (*Macaca leonina*), in Thailand. *International Journal of Primatology* 34(1), pp. 170–193.

Allendorf, F.W., Hohenlohe, P.A. and Luikart, G. 2010. Genomics and the future of conservation genetics. *Nature Reviews Genetics* 11(10), pp. 697–709. doi: http://dx.doi.org/10.1038/nrg2844.

Allio, R., Schomaker-Bastos, A., Romiguier, J., Prosdocimi, F., Nabholz, B. and Delsuc, F. 2020. MitoFinder: Efficient automated large-scale extraction of mitogenomic data in target enrichment phylogenomics. *Molecular Ecology Resources* 20(4), pp. 892–905. doi: doi/full/10.1111/1755-0998.13160.

Almeida, L., Colmonero-Costeira, I., Silva, M.J.F. da, Veracini, C. and Vasconcelos, R. 2024. Insights into the Geographical Origins of the Cabo Verde Green Monkey. *Genes* 15(4). doi: 10.3390/genes15040504.

Alves, P.H. 2007. *A Geologia Sedimentar da Guiné-Bissau da Análise Geral e Evolução do Conhecimento ao Estudo do Cenozóico*. PhD thesis, Lisbon: Universidade de Lisboa.

Amador, R., Casanova, C. and Lee, P. 2015. Ethnicity and Perceptions of Bushmeat Hunting Inside Lagoas de Cufada Natural Park (LCNP), Guinea-Bissau. *Journal of Primatology* 03(02), p. 121. doi: 10.4172/2167-6801.1000121.

Arluke, A. and Sanders, C.R. 1996. *Regarding Animals*. 1st ed. Temple University Press.

Astanei, I., Gosling, E., Wilson, J. and Powell, E. 2005. Genetic variability and phylogeography of the invasive zebra mussel, *Dreissena polymorpha* (Pallas). *Molecular Ecology* 14(6), pp. 1655–1666. doi: 10.1111/j.1365-294X.2005.02530.x.

Baas, P. et al. 2018. Population-level assessment of genetic diversity and habitat fragmentation in critically endangered Grauer's gorillas. *American Journal of Physical Anthropology* 165(3), pp. 565–575. doi: doi/full/10.1002/ajpa.23393.

Baker, L.R. 2013. Links Between Local Folklore and the Conservation of Sclater's Monkey (Cercopithecus sclateri) in Nigeria. *African Primates* 8, pp. 17–24.

Baker, L.R., Olubode, O.S., Tanimola, A.A. and Garshelis, D.L. 2014. Role of local culture, religion, and human attitudes in the conservation of sacred populations of a threatened "pest" species. *Biodiversity and Conservation* 23(8), pp. 1895–1909.

Barnosky, A.D. et al. 2011. Has the Earth's sixth mass extinction already arrived? *Nature* 471(7336), pp. 51–57. doi: dx.doi.org/10.1038/nature09678.

Bataillon, T. and Kirkpatrick, M. 2000. Inbreeding depression due to mildly deleterious mutations in finite populations: size does matter. *Genetics Research* 75(1), pp. 75–81.

Bencin, H., Kioko, J. and Kiffner, C. 2016. Local people's perceptions of wildlife species in two distinct landscapes of Northern Tanzania. *Journal for Nature Conservation* 34, pp. 82–92. doi: 10.1016/J.JNC.2016.09.004.

Bérénos, C., Ellis, P.A., Pilkington, J.G. and Pemberton, J.M. 2016. Genomic analysis reveals depression due to both individual and maternal inbreeding in a free-living mammal population. *Molecular Ecology* 25(13), pp. 3152–3168. doi: 10.1111/mec.13681.

Bersacola, E., Bessa, J., Frazão-Moreira, A., Biro, D., Sousa, C. and Hockings, K.J. 2018. Primate occurrence across a human-impacted landscape in Guinea-Bissau and neighbouring regions in West Africa: using a systematic literature review to highlight the next conservation steps. *PeerJ* 6, p. e4847.

Bersacola, E., Hill, C.M., Nijman, V. and Hockings, K.J. 2022. Examining primate community occurrence patterns in agroforest landscapes using arboreal and terrestrial camera traps. *Landscape Ecology* 37(12), pp. 3103–3121. doi: 10.1007/s10980-022-01524-7.

Bertorelle, G. et al. 2022. Genetic load: genomic estimates and applications in non-model. *Nature Reviews Genetics* 23, pp. 492-503. doi: doi.org/10.1038/s41576-022-00448-x.

Bivand, R. and Lewin-Koh, N. 2023. maptools: Tools for Handling Spatial Object.

Blanchet, F.G., Legendre, P. and Borcard, D. 2008. Forward selection of explanatory variables. *Ecology* 89(9), pp. 2623–2632. doi: 10.1890/07-0986.1.

Bolger, A.M., Lohse, M. and Usadel, B. 2014. Trimmomatic: a flexible trimmer for Illumina sequence data. *Bioinformatics* 30(15), pp. 2114–2120. doi: dx.doi.org/10.1093/bioinformatics/btu170.

Bonin, A., Bellemain, E., Eidesen, P.B., Pompanon, F., Brochmann, C. and Taberlet, P. 2004. How to track and assess genotyping errors in population genetics studies. *Molecular Ecology* 13(11), pp. 3261–3273. doi: 10.1111/j.1365-294X.2004.02346.x.

Bordonaro, L.I. 2006. *Living at the Margins: Youth and Modernity in the Bijagó Islands (Guinea-Bissau)*. PhD Thesis in Anthropology, University Institute for Social Sciences, Business Studies and Technologies.

Borges, F. 2017. *A country-level genetic survey of the IUCN critically endangered western chimpanzee (Pan troglodytes verus) in Guinea-Bissau*. MSc Thesis, University of Porto, Porto, Portugal.

Bowman, Joye. 1997. *Ominous transition: commerce and colonial expansion in the Senegambia and Guinea, 1857-1919*. Aldershot, UK: Avebury.

Brooks, S.P. and Gelman, A. 1998. General methods for monitoring convergence of iterative simulations. *Journal of Computational and Graphical Statistics* 7(4), pp. 434–455. doi: 10.1080/10618600.1998.10474787.

Butynski, T.M. 2002. The Guenons: An Overview of Diversity and Taxonomy. In: Glenn, M. E. and Cords, M. eds. *The Guenons: Diversity and Adaptation in African Monkeys*. Boston, USA: Kluwer Academic Publishers, pp. 3–13.

Caballero, A., Bravo, I. and Wang, J. 2016. Inbreeding load and purging: implications for the short-term survival and the conservation management of small populations. *Heredity 2017 118:2* 118(2), pp. 177–185.

Campos, A. 2007. *História da Cidade de Bissau (Até 1915)*.

Campos, A. 2012. *História da guiné-bissau em datas*.

Campredon, P., Cuq, F., Giraudet, E., Giraudet, J., Goulemon, F., Pennober, G. and Silva, A.S. da. 2001. *Un Système dÍnformation Géographique pour láide à la gestion intégrée de lárchipel des Bijagos (Guinée-Bissau). Notice de la carte, constitution et exploitation du SIG*. Plouzané-France : Géosystèmes-CNRS.

Cardoso, A. 2010. *Saberes e práticas tradicionais da etnia Bijagós e suas relações com a organização, a gestão e a conservação da biodiversidade na Guiné-Bissau*. Master Thesis, Universidade Federal da Bahia.

Casanova, C. and Sousa, C. 2007. *Action Plan for the Conservation of Chimpanzees, red western colobus and king colobus in Guinea-Bissau Republic*. Guinea-Bissau: IBAP.

Catarino, L., Martins, E.S., Basto, M.F.P. and Diniz, M.A. 2008. An Annotated Checklist of the Vascular Flora of Guinea-Bissau (West Africa). *Blumea - Biodiversity, Evolution and Biogeography of Plants* 53(1), pp. 1–222.

Catarino, L., Menezes, Y. and Sardinha, R. 2015. Cashew cultivation in Guinea-Bissau – risks and challenges of the success of a cash crop. *Scientia Agricola* 72(5), pp. 459–467. doi: 10.1590/0103-9016-2014-0369.

Catry, P., Barbosa, C., Indjai, B., Almeida, A., Godley, B.J. and Vié, J.C. 2002. First census of the green turtle at Poilão, Bijagós Archipelago, Guinea-Bissau: The most important nesting colony on the Atlantic coast of Africa. *ORYX* 36(4), pp. 400–403.

Convention on Biological Diversity (CBD). 2020. *Zero Draft of the post-2020 global biodiversity framework*.

Ceballos, G. and Ehrlich, P.R. 2023. Mutilation of the tree of life via mass extinction of animal genera. *Proceedings of the National Academy of Sciences of the United States of America* 120(39), p. e2306987120.

Ceballos, G., Ehrlich, P.R. and Dirzo, R. 2017. Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proceedings of the National Academy of Sciences*, p. 201704949.

Chapman, C.A. and Gogarten, J.F. 2012. Primate Conservation: Is the Cup Half Empty or Half Full? *Nature Education Knowledge* 4(2)(7).

Chapman, C.A., Baranga, D., Isabirye Basuta, G. and Teichroeb, J.A. 2012. Crop raiding patterns of solitary and social groups of red-tailed monkeys on cocoa pods in Uganda. *Tropical Conservation Science* 5(1), pp. 104–111.

Chaves, Ó.M., Stoner, K.E., Arroyo-Rodríguez, V. and Estrada, A. 2011. Effectiveness of Spider Monkeys (*Ateles geoffroyi vellerosus*) as Seed Dispersers in Continuous and Fragmented Rain Forests in Southern Mexico. *International Journal of Primatology* 32(1), pp. 177–192.

Chikhi, L., Sousa, V.C., Luisi, P., Goossens, B. and Beaumont, M.A. 2010. The Confounding Effects of Population Structure, Genetic Diversity and the Sampling Scheme on the Detection and Quantification of Population Size Changes. *Genetics* 186(3), pp. 983–995. doi: dx.doi.org/10.1534/genetics.110.118661.

Chimbo. 2017. *Annual Report*.

Colmonero-Costeira, I. 2019. *Insights into insular primates: conservation genetics of Cercopithecus petaurista buettikoferi, Cercopithecus campbelli and Chlorocebus sabaeus in the Bijagós Archipelago, Guinea- Bissau*. MSc Thesis, University of Minho, Braga, Portugal.

Colmonero-Costeira, I. 2022. Fieldwork project “The importance of *Bijagó* socio-cultural traditions for the conservation of guenons at the Bijagós Archipelago, Guinea-Bissau”, April – June.

Colmonero-Costeira, I. 2023. Fieldwork project “Assessment of the local extirpation of the spot-nosed monkey (*Cercopithecus petaurista*) from mainland Guinea-Bissau using ethnographic surveys”, April.

Colmonero-Costeira, I. et al. 2023. Notes on the conservation threats to the western lesser spot-nosed monkey (*Cercopithecus petaurista buettikoferi*) in the Bijagós Archipelago (Guinea-Bissau, West Africa). *Primates* (64), pp. 581–587. doi: doi.org/10.1007/s10329-023-01090-9.

Colmonero-Costeira, I. et al. 2024. Improving baseline information on over-looked generalists: occurrence and mitochondrial DNA diversity of Campbell’s (*Cercopithecus campbelli*) and green monkeys (*Chlorocebus sabaeus*) in Guinea-Bissau, West Africa. *Research Square*. doi: doi.org/10.21203/rs.3.rs-5372533/v1.

Colmonero-Costeira, I., Minhós, T., Djaló, B., Fernandes, N. and Ferreira da Silva, M. 2019. Confirmação da ocorrência de primatas não-humanos no Arquipélago dos Bijagós com base em técnicas de identificação molecular. *Sintidus* 2, pp. 145–179.

Cormier, L. 2006. A Preliminary Review of Neotropical Primates in the Subsistence and Symbolism of Indigenous Lowland South American Peoples. *Ecological and Environmental Anthropology* 2(1), pp. 14–32.

Costa, S. 2013. Letting People Speak: The Importance of Locals’ Attitudes for Effective Conservation Programmes. *Journal of Primatology* 02(02), pp. 1–3. doi: 10.4172/2167-6801.1000e122.

Costa, S., Casanova, C. and Lee, P. 2017. What Does Conservation Mean for Women? the Case of the Cantanhez Forest National Park. *Conservation and Society* 15(2), pp. 168–178. doi: 10.4103/cs.cs.

Costa, S., Casanova, C. and Lee, P. 2020. Sociozoological scales: Human’s perceptions on non-humans through a conservation perspective. In: Roque, A. C., Brito, C., and Veracini, C. eds. *Peoples, Nature and Environments: Learning to Live Together*. Newcastle upon Tyne, UK: Cambridge Scholars Publishing, pp. 114–128.

Costa, S., Casanova, C., Sousa, C. and Lee, P. 2013. The Good, The Bad and The Ugly: Perceptions of Wildlife In Tombali(Guinea-Bissau, West Africa). *Journal of Primatology* 02(01).

Costa, S.G. 2010. *Social Perceptions of Nonhumans in Tombali (Guinea-Bissau, West Africa): a contribution to chimpanzee (Pan troglodytes verus) conservation*. University of Stirling, UK.

Costanzi, J.M. and Steifetten, Ø. 2019. Island biogeography theory explains the genetic diversity of a fragmented rock ptarmigan (*Lagopus muta*) population. *Ecology and Evolution* 9(7), pp. 3837–3849. doi: 10.1002/ece3.5007.

Cui, R. et al. 2021. Ancestral transoceanic colonization and recent population reduction in a nonannual killifish from the Seychelles archipelago. *Molecular Ecology* 30(14), pp. 3610–3623.

d'Almada, A.A. 1984. *Brief treatise on the rivers of Guinea*. Liverpool, UK: Department of History, University of Liverpool.

Danecek, P. et al. 2011. The variant call format and VCFtools. *Bioinformatics* 27(15), pp. 2156–2158. doi: dx.doi.org/10.1093/bioinformatics/btr330.

Danecek, P. et al. 2021. Twelve years of SAMtools and BCFtools. *GigaScience* 10(2). Available at: https://dx.doi.org/10.1093/gigascience/giab008.

Denham, W. and Denham, W.W. 1981. History of green monkeys in the West Indies. Part I. Migration from Africa. *Journal of the Barbados Museum and Historical Society* 36(3), pp. 211–228.

Deth, J.W. van and Scarbrough, E. 1995. *The impact of values*. Oxford: Oxford Univ. Press.

Diniz-Filho, J.A.F. and Raia, P. 2017. Island rule, quantitative genetics and brain-body size evolution in homo floresiensis. *Proceedings of the Royal Society B: Biological Sciences* 284(1857). doi: 10.1098/rspb.2017.1065.

Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B. and Collen, B. 2014. Defaunation in the Antrhopocene. *Science* 401(6195), pp. 401–406. doi: 10.1126/science.1251817.

Douglas, L.R. and Veríssimo, D. 2013. Flagships or Battleships: Deconstructing the Relationship between Social Conflict and Conservation Flagship Species. *Environment and Society* 4(1), pp. 98–116.

du Plessis, S.J. et al. 2018. Genetic diversity and cryptic population re-establishment: management implications for the Bojer's skink (*Gongylomorphus bojerii*). *Conservation Genetics*. doi; dx.doi.org/10.1007/s10592-018-1119-y.

Dussex, N. et al. 2021. Population genomics of the critically endangered kākāpō. *Cell Genomics* 1(1). doi: 10.1016/j.xgen.2021.100002.

Dussex, N., Morales, H.E., Grossen, C., Dalén, L. and van Oosterhout, C. 2023. Purging and accumulation of genetic load in conservation. *Trends in Ecology and Evolution* 38(10), pp. 961–969. doi: 10.1016/j.tree.2023.05.008.

Elton, S., Jansson, A.U., Meloro, C., Louys, J., Plummer, T. and Bishop, L.C. 2016. Exploring morphological generality in the Old World monkey postcranium using an ecomorphological framework. *Journal of Anatomy* 228(4), pp. 534–560. doi: 10.1111/joa.12428.

Estrada, A. and Garber, P.A. 2022. Principal Drivers and Conservation Solutions to the Impending Primate Extinction Crisis: Introduction to the Special Issue. *International Journal of Primatology* 43(1), pp. 1–14.

Estrada, A. et al. 2017. Impending extinction crisis of the world's primates: why primates matter. *Science Advances* 3(1), p. e1600946.

Evanno, G., Regnaut, S. and Goudet, J. 2005. Detecting the number of clusters of individuals using the software STRUCTURE: A simulation study. *Molecular Ecology* 14(8), pp. 2611–2620. doi: 10.1111/j.1365-294X.2005.02553.x.

Excoffier, L. and Lischer, H.E.L. 2010. Arlequin suite ver 3.5: A new series of programs to perform population genetics analyses under Linux and Windows. *Molecular Ecology Resources* 10(3), pp. 564–567.

Excoffier, L., Marchi, N., Marques, D.A., Matthey-Doret, R., Gouy, A. and Sousa, V.C. 2021. fastsimcoal2: demographic inference under complex evolutionary scenarios. *Bioinformatics* 37(24), pp. 4882–4885. doi: dx.doi.org/10.1093/bioinformatics/btab468.

Falush, D., Stephens, M. and Pritchard, J.K. 2003. Inference of Population Structure Using Multilocus Genotype Data: Linked Loci and Correlated Allele Frequencies. *Genetics* 164, pp. 1567–1587.

Ferreira da Silva, M.J. et al. 2018. Disrupted dispersal and its genetic consequences: Comparing protected and threatened baboon populations (*Papio papio*) in West Africa. *PLoS ONE* 13(4), p. e0194189. doi: 10.1371/journal.pone.0194189.

Ferreira da Silva, M.J. et al. 2024. Estimating the effective population size across space and time in the Critically Endangered western chimpanzee in Guinea-Bissau: challenges and implications for conservation management. *bioRxiv*, p. 2024.10.07.616982.

Ferreira da Silva, M.J., Camará, M., Egeter, B., Minhós, T., Bruford, M.W. and Godinho, R. 2021a. Using meta-barcoding tools to monitor primate meat consumption at dedicated establishments in Guinea-Bissau, West Africa. *ARPHA Conference Abstracts 4: e65575* 4, pp. e65575.

Ferreira da Silva, M.J., Godinho, R., Casanova, C., Minhós, T., Sá, R. and Bruford, M.W. 2014. Assessing the impact of hunting pressure on population structure of Guinea baboons (*Papio papio*) in Guinea-Bissau. *Conservation Genetics* 15(6), pp. 1339–1355.

Ferreira da Silva, M.J., Minhós, T., Sá, R., Casanova, C. and Bruford, M.W. 2021. A Qualitative Assessment of Guinea-Bissau's Hunting History and Culture-and Their Implications for Primate Conservation. *African Primates* 15, pp. 1–18.

Findlay, L.J. and Hill, R.A. 2020. Baboon and Vervet Monkey Crop-Foraging Behaviors on a Commercial South African Farm: Preliminary Implications for Damage Mitigation. *Human–Wildlife Interactions* 14(3), p. 19.

Finn, C., Grattarola, F. and Pincheira-Donoso, D. 2023. More losers than winners: investigating Anthropocene defaunation through the diversity of population trends. *Biological Reviews* 98(5), pp. 1732–1748. Available at: doi: doi/full/10.1111/brv.12974.

Francis, R.M. 2017. pophelper: an R package and web app to analyse and visualize population structure. *Molecular Ecology Resources* 17(1), pp. 27–32. doi: 10.1111/1755-0998.12509.

Frankham, R., Bradshaw, C.J.A. and Brook, B.W. 2014. Genetics in conservation management: Revised recommendations for the 50/500 rules, Red List criteria and population viability analyses. *Biological Conservation* 170, pp. 56–63. doi: 10.1016/j.biocon.2013.12.036.

Fuentes, A. 2012. Ethnoprimatology and the Anthropology of the Human-Primate Interface. *Annual Review of Anthropology* 41(1), pp. 101–117.

Fuentes, A. and Hockings, K.J. 2010. The ethnoprimatological approach in primatology. *American Journal of Primatology* 72(10), pp. 841–847. doi: 10.1002/ajp.20844.

Fuentes, A. and Wolfe, L.D. 2002. *Primates Face to Face: The Conservation Implications of Human-nonhuman Primate Interconnections*. 1st ed. Fuentes, A. and Wolfe, L. D. eds. Cambridge, UK: Cambridge University Press.

Gelman, A. and Rubin, D.B. 1992. Inference from Iterative Simulation Using Multiple Sequences. *Statistical Sciences* 7(4), pp. 457–472.

Gerini, F. 2018. Structure and connectivity of sympatric primate species across a human-dominated landscape: population genetics of Western Chimpanzee (*Pan troglodytes verus*) and Guinea Baboon (*Papio papio*) in Guinea Bissau, West Africa. MSc Thesis, University of Pisa, Pisa, Italy.

Gillis, N.K., Walters, L.J., Fernandes, F.C. and Hoffman, E.A. 2009. Higher genetic diversity in introduced than in native populations of the mussel *Mytella charruana*: Evidence of population admixture at introduction sites. *Diversity and Distributions* 15(5), pp. 784–795. doi: 10.1111/j.1472-4642.2009.00591.x.

Gippoliti, S. and Dell'Omo, G. 2003. Primates of Guinea-Bissau, West Africa: distribution and conservation status. *Primate Conservation* 19(19), pp. 73–77.

Gleditsch, J.M. and Sperry, J.H. 2019. Rapid morphological change of nonnative frugivores on the Hawaiian island of O'ahu. *Evolution* 73(7), pp. 1456–1465. doi: 10.1111/evo.13744.

Glenn, M.E. and Bensen, K.J. 2013. The mona monkeys of Grenada, são tomé and príncipe: Long-term persistence of a guenon in permanent fragments and implications for the survival of forest primates in protected areas. *Primates in Fragments: Complexity and Resilience*, pp. 413–422.

Glenn, M.E. and Cords, M. 2002. *The Guenons: Diversity and Adaptation in African Monkeys*. Boston, USA: Kluwer Academic Publishers.

Gonedelé Bi, S. et al. 2020. *Chlorocebus sabaeus*. *The IUCN Red List of Threatened Species* e.T136265A.

Goudet, J. and Jombart, T. 2022. hierfstat: Estimation and Tests of Hierarchical F-Statistics.

Grossen, C., Biebach, I., Angelone-Alasaad, S., Keller, L.F. and Croll, D. 2018. Population genomics analyses of European ibex species show lower diversity and higher inbreeding in reintroduced populations. *Evolutionary Applications* 11(2), pp. 123–139. doi: doi/full/10.1111/eva.12490.

Grossen, C., Guillaume, F., Keller, L.F. and Croll, D. 2020. Purging of highly deleterious mutations through severe bottlenecks in Alpine ibex. *Nature Communications* 11(1). doi: 10.1038/s41467-020-14803-1.

Guedes, P., Santos, Y. Dos, Lima, R.F. de and Bird, T.L.F. 2021. Introduced Mona monkey is a key threat to the Critically Endangered Príncipe thrush. *Oryx* 55(6), pp. 809–809.

Gulati, S., Karanth, K.K., Le, N.A. and Noack, F. 2021. Human casualties are the dominant cost of human–wildlife conflict in India. *Proceedings of the National Academy of Sciences* 118(8), p. e1921338118. doi: /doi/abs/10.1073/pnas.1921338118.

Guschanski, K. et al. 2013. Next-generation museomics disentangles one of the largest primate radiations. *Systematic Biology* 62(4), pp. 539–554. doi: 10.1093/sysbio/syt018.

Haile, M., Gadisa, T. and Gutema, T.M. 2024. Human-De Brazza's monkey conflict in Kafa Biosphere Reserve, Kafa Zone South West, Ethiopia. *BMC Zoology* 9(1), pp. 1–11.

Hair, J.F.., Black, W.C.., Babin, B.J.. and Anderson, R.E.. 2010. *Multivariate data analysis*. 7th ed. London, UK: Pearson Education Limited.

Hawthorne, W. 2003. *Planting Rice and Harvesting Slaves: Transformations along the Guinea-Bissau Coast,1400-1900*. Portsmouth, USA: Heinemann Publishing.

Hayes, N. 2000. *Foundations of Psychology*. Thomson Learning.

Hazevoet, C.J. and Masseti, M. 2011. On the history of the green monkey *Chlorocebus sabaeus* (L., 1766) in the Cape Verde Islands, with notes on other introduced mammals. *Zoologia Caboverdiana* 2, pp. 12–24.

Heleno, R.H., Mendes, F., Coelho, A.P., Ramos, J.A., Palmeirim, J.M., Rainho, A. and de Lima, R.F. 2021. The upsizing of the São Tomé seed dispersal network by introduced animals. *Oikos* (August), pp. 1–12. doi: 10.1111/oik.08279.

Hill, C.M. and Wallace, G.E. 2012. Crop protection and conflict mitigation: reducing the costs of living alongside non-human primates. *Biodiversity and Conservation* 21(10), pp. 2569–2587.

Hoag, C. and Svenning, J.-C. 2017. African Environmental Change from the Pleistocene to the Anthropocene. *Annual Review of Environment and Resources* (42), pp. 27–54. doi: doi.org/10.1146/annurev-environ-.

Hoban, S. et al. 2021. Global commitments to conserving and monitoring genetic diversity are now necessary and feasible. *BioScience* 71(9), pp. 964–976. doi: 10.1093/biosci/biab054.

Hockings, K.J., Parathian, H., Bessa, J. and Frazão-Moreira, A. 2020. Extensive Overlap in the Selection of Wild Fruits by Chimpanzees and Humans: Implications for the Management of Complex Social-Ecological Systems. *Frontiers in Ecology and Evolution* 8(May), pp. 1–12. doi: 10.3389/fevo.2020.00123.

Horsburgh, K.A., Matisoo-Smith, E., Glenn, M.E. and Bensen, K.J. 2003. Genetic Study of Translocated Guenons: Cercopithecus mona on Grenada. In: *The Guenons: Diversity and Adaptation in African Monkeys*. Boston: Kluwer Academic Publishers, pp. 289–306.

IBAP. 2016. *As áreas protegidas da Guiné-Bissau: Guia de ecoturismo*. Bissau, Guinea-Bissau: IBAP.

IBAP. 2018. *Ficha Resumo Projeto RBABB*.

INE. 2015. *Guiné-Bissau em número 2015*. Bissau, Guinea-Bissau: Imprensa Nacional.

IUCN. 2024. The IUCN Red List of Threatened Species. *Version 2022-1.*

Jakobsson, M. and Rosenberg, N.A. 2007. CLUMPP: A cluster matching and permutation program for dealing with label switching and multimodality in analysis of population structure. *Bioinformatics* 23(14), pp. 1801–1806. doi: 10.1093/bioinformatics/btm233.

Jensen, A. et al. 2023. Complex Evolutionary History With Extensive Ancestral Gene Flow in an African Primate Radiation. *Molecular Biology and Evolution* 40(12). doi: dx.doi.org/10.1093/molbev/msad247.

Jeong, H.J. and Lee, W.C. 2017. Rethinking the assumptions of chi-squared and fisher’s exact tests. *Biometrics & Biostatistics International Journal* 6(1), pp. 300-301.

Johnson, P.C.D. and Haydon, D.T. 2007. Maximum-likelihood estimation of allelic dropout and false allele error rates from microsatellite genotypes in the absence of reference data. *Genetics* 175(2), pp. 827–842. doi: 10.1534/genetics.106.064618.

Kalinowski, S.T., Taper, M.L. and Marshall, T.C. 2007. Revising how the computer program cervus accommodates genotyping error increases success in paternity assignment. *Molecular Ecology* 16(5), pp. 1099–1106. doi: doi/full/10.1111/j.1365-294X.2007.03089.x.

Kalyaanamoorthy, S., Minh, B.Q., Wong, T.K.F., Von Haeseler, A. and Jermiin, L.S. 2017. ModelFinder: Fast model selection for accurate phylogenetic estimates. *Nature Methods* 14(6), pp. 587–589. Available at: http://dx.doi.org/10.1038/nmeth.4285.

Karibuhoye, C. 2004. *Mammal Conservation status and Prospects for community-based wildlife management in coastal Guinea-Bissau, West Africa*. PhD Thesis, Georg-August-Universität Göttingen.

Katoh, K., Misawa, K., Kuma, K.I. and Miyata, T. 2002. MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Research* 30(14), pp. 3059–3066. doi: dx.doi.org/10.1093/nar/gkf436.

Kearse, M. et al. 2012. Geneious Basic: An integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics* 28(12), pp. 1647–1649. doi: 10.1093/bioinformatics/bts199.

Keith, D. 2015. *Trichechus senegalensis*. *The IUCN Red List of Threatened Species* e.T22104A9.

Khan, A. et al. 2021. Genomic evidence for inbreeding depression and purging of deleterious genetic variation in Indian tigers. *Proceedings of the National Academy of Sciences of the United States of America* 118(49), p. e2023018118. doi: doi/abs/10.1073/pnas.2023018118.

Kolberg, L., Raudvere, U., Kuzmin, I., Adler, P., Vilo, J. and Peterson, H. 2023. g:Profiler—interoperable web service for functional enrichment analysis and gene identifier mapping (2023 update). *Nucleic Acids Research* 51(W1), pp. W207–W212. doi: dx.doi.org/10.1093/nar/gkad347.

König, H.J., Carter, N., Ceaușu, S., Lamb, C., Ford, A.T. and Kiffner, C. 2021. Human–wildlife coexistence in science and practice. *Conservation Science and Practice* 3(3), p. e401. doi: doi/full/10.1111/csp2.401.

Konovalov, D.A., Manning, C. and Henshaw, M.T. 2004. KINGROUP: A program for pedigree relationship reconstruction and kin group assignments using genetic markers. *Molecular Ecology Notes* 4(4), pp. 779–782. doi: 10.1111/j.1471-8286.2004.00796.x.

Kopp, G.H., Ferreira da Silva, M.J., Fischer, J., Brito, J.C., Regnaut, S., Roos, C. and Zinner, D. 2014. The Influence of Social Systems on Patterns of Mitochondrial DNA Variation in Baboons. *International Journal of Primatology* 35(1), pp. 210–225.

Kuderna, L.F.K. et al. 2023. A global catalog of whole-genome diversity from 233 primate species. *Science* 380(6648), pp. 906–913. doi: doi/10.1126/science.abn7829.

Langergraber, K.E. et al. 2012. Generation times in wild chimpanzees and gorillas suggest earlier divergence times in great ape and human evolution. *Proceedings of the National Academy of Sciences* 109(39), pp. 15716–15721. doi: doi/10.1073/pnas.1211740109.

Legendre, P. and Anderson, M.J. 1999. Distance-based redundancy analysis: Testing multispecies responses in multifactorial ecological experiments. *Ecological Monographs* 69(1), pp. 1–24. doi: 10.1039/b916289e.

Legendre, P. and Legendre, L. 2012. *Numerical Ecology*. 3rd ed. Oxford, UK: Elsevier B.V.

Leigh, J.W. and Bryant, D. 2015. POPART: Full-feature software for haplotype network construction. *Methods in Ecology and Evolution* 6(9), pp. 1110–1116. doi: 10.1111/2041-210X.12410.

Li, H. 2018. Minimap2: pairwise alignment for nucleotide sequences. *Bioinformatics* 34(18), pp. 3094–3100. doi: dx.doi.org/10.1093/bioinformatics/bty191.

Lima, S. 1947a. *Organização Económica e Social dos Bijagós*. Lisbon, Portugal: Centro de Estudos da Guiné Portuguesa.

Lima, S. 1947b. Os Bijagós e o Regime do Matriarcado. *Boletim Cultural da Guiné Portuguesa* 7, pp. 593–615.

Liu, J., Ji, X. and Chen, H. 2022. Beta-PSMC: uncovering more detailed population history using beta distribution. *BMC Genomics* 23(1). doi: 10.1186/s12864-022-09021-6.

Lundy, B.D. 2015. Resistance is Fruitful: Bijagos of Guinea-Bissau. *Peace and Conflict Management Working Papers Series* 1, pp. 1–9.

MacArthur, R.H. and Wilson, E.O. 1963. An Equilibrium Theory of Insular Zoogeography. *Evolution* 17(4), pp. 373–387.

Madeira, J.P. 2009. *A Gestão do Espaço e da Propriedade Tradicional no Arquipélago dos Bijagós*. MSc Thesis in African Studies, Universidade Técnica de Lisboa.

Madeira, J.P. 2016. Bijagos Archipelago: Impacts and Challenges for Environmental Sustainability. *InterEspaço: Revista de Geografia e Interdisciplinaridade* 2(5), pp. 291–305.

Martin, A., Carver, S., Proft, K., Fraser, T.A., Polkinghorne, A., Banks, S. and Burridge, C.P. 2019. Isolation, marine transgression and translocation of the bare-nosed wombat (Vombatus ursinus). *Evolutionary Applications* 12(6), pp. 1114–1123. doi: doi/full/10.1111/eva.12785.

Martin, C.A., Armstrong, C., Illera, J.C., Emerson, B.C., Richardson, D.S. and Spurgin, L.G. 2021. Genomic variation, population history and within-archipelago adaptation between island bird populations. *Royal Society Open Science* 8(2). doi: doi/10.1098/rsos.201146.

Martin, C.A., Sheppard, E.C., Illera, J.C., Suh, A., Nadachowska-Brzyska, K., Spurgin, L.G. and Richardson, D.S. 2023. Runs of homozygosity reveal past bottlenecks and contemporary inbreeding across diverging populations of an island-colonizing bird. *Molecular Ecology* 32(8), pp. 1972–1989. doi: 10.1111/mec.16865.

Mastretta-Yanes, A. et al. 2024. Multinational evaluation of genetic diversity indicators for the Kunming-Montreal Global Biodiversity Framework. *Ecology Letters* 27(7), p. e14461. doi: doi/full/10.1111/ele.14461.

Matsuda Goodwin, R., Gonedelé Bi, S. and Koné, I. 2020a. Cercopithecus campbelli. *he IUCN Red List of Threatened Species* e.T136930A.

Matsuda Goodwin, R., Segniagbeto, G., Waife, E., Osei, D., Koné, I., Gonedeé, B. and Oates, J.F. 2020b. Cercopithecus petaurista. *The IUCN Red List of Threatened Species 2020* (eT4225A17945536).

Mazet, O., Rodríguez, W., Grusea, S., Boitard, S. and Chikhi, L. 2016. On the importance of being structured: Instantaneous coalescence rates and human evolution-lessons for ancestral population size inference? *Heredity* 116(4), pp. 362–371. doi: 10.1038/hdy.2015.104.

McKinney, T. and Dore, K.M. 2018. The State of Ethnoprimatology: Its Use and Potential in Today's Primate Research. *International Journal of Primatology* 39(5), pp. 730–748. doi: 10.1007/s10764-017-0012-8.

McLaren, W. et al. 2016. The Ensembl Variant Effect Predictor. *Genome Biology* 17(1), pp. 1–14.

Meirmans, P.G. 2020. genodive version 3.0: Easy-to-use software for the analysis of genetic data of diploids and polyploids. *Molecular Ecology Resources* 20(4), pp. 1126–1131. doi: doi/full/10.1111/1755-0998.13145.

Meirmans, P.G. and Van Tienderen, P.H. 2004. genotype and genodive: two programs for the analysis of genetic diversity of asexual organisms. *Molecular Ecology Notes* 4(4), pp. 792–794. doi: doi/full/10.1111/j.1471-8286.2004.00770.x.

Metzger, J.P. 2002. Landscape dynamics and equilibrium in areas of slash-and-burn agriculture with short and long fallow period (Bragantina region, NE Brazilian Amazon). *Landscape Ecology* 17(5), pp. 419–431.

Meyermans, R., Gorssen, W., Buys, N. and Janssens, S. 2020. How to study runs of homozygosity using plink? a guide for analyzing medium density snp data in livestock and pet species. *BMC Genomics* 21(1), pp. 1–14.

Miller, S.A., Dykes, D.D. and Polesky, H.F. 1988. A simple salting out procedure for extracting DNA from human nucleated cells. *Nucleic Acids Research* 16(3), pp. 1215–1215. doi: dx.doi.org/10.1093/nar/16.3.1215.

Minhós, T. et al. 2013a. Genetic evidence for spatio-temporal changes in the dispersal patterns of two sympatric African colobine monkeys. *American Journal of Physical Anthropology* 150(3), pp. 464–474. doi: 10.1002/ajpa.22223.

Minhós, T. et al. 2016. Genetic consequences of human forest exploitation in two colobus monkeys in Guinea Bissau. *Biological Conservation* 194, pp. 194–208. doi: dx.doi.org/10.1016/j.biocon.2015.12.019.

Minhós, T. et al. 2023. The importance of well protected forests for the conservation genetics of West African colobine monkeys. *American Journal of Primatology* 85, p. e23453. doi: 10.1002/ajp.23453.

Minhós, T., Nixon, E., Sousa, C., Vicente, L.M., Da Silva, M.F., Sá, R.M. and Bruford, M.W. 2013b. Genetic evidence for spatio-temporal changes in the dispersal patterns of two sympatric African colobine monkeys. *American Journal of Physical Anthropology* 150(3), pp. 464–474.

Miquel, C., Bellemain, E., Poillot, C., Bessière, J., Durand, A. and Taberlet, P. 2006. Quality indexes to assess the reliability of genotypes in studies using noninvasive sampling and multiple-tube approach. *Molecular Ecology Notes* 6(4), pp. 985–988. doi: 10.1111/j.1471-8286.2006.01413.x.

Mombeshora, S. and le Bel, S. 2009. Parks-people conflicts: The case of Gonarezhou National Park and the Chitsa community in south-east zimbabwe. *Biodiversity and Conservation* 18(10), pp. 2601–2623. doi: 10.1007/s10531-009-9676-5.

Monard, A. 1938. *Résultats de la Mission scientifique du Dr Monard en Guinée Portugaise*. Arquivos do Museu Bocage.

Monteiro, F., Catarino, L., Batista, D., Indjai, B., Duarte, M.C. and Romeiras, M.M. 2017. Cashew as a high agricultural commodity in West Africa: Insights towards sustainable production in Guinea-Bissau. *Sustainability* 9(9), p. 1666. doi: 10.3390/su9091666.

Moodley, Y. et al. 2018. Contrasting evolutionary history, anthropogenic declines and genetic contact in the northern and southern white rhinoceros (Ceratotherium simum). *Proceedings of the Royal Society B* 285(1890). doi: /doi/10.1098/rspb.2018.1567.

Moyo, F., Ijumba, J. and Lund, J.F. 2016. Failure by Design? Revisiting Tanzania's Flagship Wildlife Management Area Burunge. *Conservation and Society* 14(3), pp. 232–242. doi: 10.4103/0972-4923.191160.

Múrias Dos Santos, A., Cabezas, M.P., Tavares, A.I., Xavier, R. and Branco, M. 2016. tcsBU: a tool to extend TCS network layout and visualization. *Bioinformatics* 32(4), pp. 627–628. doi: dx.doi.org/10.1093/bioinformatics/btv636.

Myers, N. 1993. Tropical Forests: The Main Deforestation Fronts. *Environmental Conservation* 20(1), pp. 9–16. doi: 10.1017/S0376892900037176.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. and Kent, J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403(6772), pp. 853–858.

Nei, M. 1987. *Molecular Evolutionary Genetics*. New York, USA: Columbia University Press. doi: https://doi.org/10.7312/nei-92038.

Newing, H., Eagle, C.M., Puri, R.K. and Watson, C.W. 2010. *Conducting research in conservation: Social science methods and practice*. 1st Edition. London, UK: Routledge Taylor & Francis Group. doi: 10.4324/9780203846452.

Nolte, M.J., Jing, P., Dewey, C.N. and Payseur, B.A. 2020. Giant Island Mice Exhibit Widespread Gene Expression Changes in Key Metabolic Organs. *Genome biology and evolution* 12(8), pp. 1277–1301. doi: 10.1093/gbe/evaa118.

Nyirenda, V.R., Milimo, C. and Namukonde, N. 2019. Local people's perspectives on wildlife conservation, ecotourism and community livelihoods: A case study of Lusaka National Park, Zambia. *Natural Resources, Tourism and Community Livelihoods in Southern Africa: Challenges of Sustainable Development*, pp. 108–122.

Oates, J.F., Whitesides, G.H., Davies, A.G., Waterman, P.G., Green, S.M., Dasilva, G.L. and Mole, S. 1990. Determinants of Variation in Tropical Forest Primate Biomass: New Evidence from West Africa. *Ecology* 71(1), pp. 328–343.

Oksanen, J. et al. 2022. vegan: Community Ecology Package.

Orsini, L., Vanoverbeke, J., Swillen, I., Mergeay, J. and De Meester, L. 2013. Drivers of population genetic differentiation in the wild: Isolation by dispersal limitation, isolation by adaptation and isolation by colonization. *Molecular Ecology* 22(24), pp. 5983–5999. doi: 10.1111/mec.12561.

Paiva, M.C. 1990. *Artefactos Bijagós: O “nós” e o “outro” - das construções de alteridade nos discursos em torno de artefactos de uma população insular da África Ocidental*. MSc Thesis in Ciências Antropológicas, Universidade Técnica de Lisboa.

Paradis, E. and Schliep, K. 2019. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics* 35, pp. 526–528.

Peakall, R. and Smouse, P.E. 2006. GENALEX 6: Genetic analysis in Excel. Population genetic software for teaching and research. *Molecular Ecology Notes* 6(1), pp. 288–295. doi: 10.1111/j.1471-8286.2005.01155.x.

Peakall, R. and Smouse, P.E. 2012. GenALEx 6.5: Genetic analysis in Excel. Population genetic software for teaching and research-an update. *Bioinformatics* 28(19), pp. 2537–2539. doi: 10.1093/bioinformatics/bts460.

Petkova, D. 2023. reemsplots2: Generate plots to inspect and visualize the results of EEMS.

Petkova, D., Novembre, J. and Stephens, M. 2015. Visualizing spatial population structure with estimated effective migration surfaces. *Nature Genetics* 48(1), pp. 94–100. doi: 10.1038/ng.3464.

Pompanon, F., Bonin, A., Bellemain, E. and Taberlet, P. 2005. Genotyping errors: causes, consequences and solutions. *Nature reviews. Genetics* 6(11), pp. 847–859.

Posit team. 2023. RStudio: Integrated Development for R.

Pritchard, J.K., Stephens, M. and Donnelly, P. 2000. Inference of population structure using multilocus genotype data. *Genetics* 155(2), pp. 945–959.

Purcell, S. et al. 2007. PLINK: A tool set for whole-genome association and population-based linkage analyses. *American Journal of Human Genetics* 81(3), pp. 559–575.

Purfield, D.C., Berry, D.P., McParland, S. and Bradley, D.G. 2012. Runs of homozygosity and population history in cattle. *BMC Genetics* 13(1), pp. 1–11.

Queller, D.C. and Goodnight, K.F. 1989. Estimating Relatedness Using Genetic Markers. *Evolution* 43(2), pp. 258–275. doi: doi.wiley.com/10.1111/j.1558-5646.1989.tb04226.x.

Quirin, C. and Dixon, A. 2012. Food security, politics and perceptions of wildlife damage in Western Ethiopia. *International Journal of Pest Management* 58(2), pp. 101–114.

R CoreTeam. 2022. R: A language and environment for statistical computing. Available at: https://www.r-project.org.

Rainho, A. and Palmeirim, J. 2018. Mamíferos Terrestres. In: Catry, P. and Regalla, A. eds. *Parque Nacional Marinho de João Vieira e Poilão: Biodiversidade e Conservação*. IBAP - Instituto da Biodiversidade e das Áreas Protegidas.

Rawley, J.A. and Behrendt, S.D. 2005. *The transatlantic slave trade: a history*. Nebraska, USA: University of Nebraska Press.

Raymond, M. and Rousset, F. 1995. GENEPOP (Version 1.2): Population Genetics Software for Exact Tests and Ecumenicism. *Journal of Heredity* 86(3), pp. 248–249. doi: dx.doi.org/10.1093/oxfordjournals.jhered.a111573.

Rebelo, R. and Catry, P. 2011. O arquipélago dos Bijagós (Guiné-Bissau) - valores de biodiversidade e potencialidades para a investigação científica. *Ecologia* 2, pp. 8–15.

Reiner, F. and Simões, P. 1999. *Mamíferos Selvagens da Guiné - Bissau*. Lisbon, Portugal: Projeto Delfim - Centro Português de Estudos dos Mamíferos Marinhos.

Revelle, W. 2024. psych: Procedures for Psychological, Psychometric, and Personality Research. *Northwestern University*.

Robinson, J.A. et al. 2016. Genomic Flatlining in the Endangered Island Fox. *Current Biology* 26(9), pp. 1183–1189. doi: 10.1016/j.cub.2016.02.062.

Rodney, W. 1970. *A History of the Upper Guinea Coast, 1545 to 1800*. New York, USA: Monthly Review Press.

Roeder, A.D., Archer, F.I., Poinar, H.N. and Morin, P.A. 2004. A novel method for collection and preservation of faeces for genetic studies. *Molecular Ecology Notes* 4(4), pp. 761–764. doi: 10.1111/j.1471-8286.2004.00737.x.

Rosa, A., Ornelas, C., Jobling, M.A., Brehm, A. and Villems, R. 2007. Y-chromosomal diversity in the population of Guinea-Bissau: A multiethnic perspective. *BMC Evolutionary Biology* 7, pp. 1–11. doi: 10.1186/1471-2148-7-124.

Rousset, F. 2008. genepop'007: a complete re-implementation of the genepop software for Windows and Linux. *Molecular Ecology Resources* 8(1), pp. 103–106. doi: doi/full/10.1111/j.1471-8286.2007.01931.x.

Rowe, N. and Myers, M. 2016. *All the World's Primates*. Charlestown, Rhode Island: Pogonias Press.

Rozas, J., Ferrer-Mata, A., Sanchez-DelBarrio, J.C., Guirao-Rico, S., Librado, P., Ramos-Onsins, S.E. and Sanchez-Gracia, A. 2017. DnaSP 6: DNA sequence polymorphism analysis of large data sets. *Molecular Biology and Evolution* 34(12), pp. 3299–3302. doi: 10.1093/molbev/msx248.

Salmona, J., Heller, R., Quéméré, E. and Chikhi, L. 2017. Climate change and human colonization triggered habitat loss and fragmentation in Madagascar. *Molecular Ecology* 26(19), pp. 5203–5222. doi: /doi/full/10.1111/mec.14173.

Salvig, J.C., Asbirk, S., Kjeldsen, J.P. and Rasmussen, P.A.F. 1994. Wintering waders in the Bijagos Archipelago, Guinee-Bissau 1992-1993. *Ardea* 82, pp. 137–142.

Santini, L., Isaac, N.J.B., Maiorano, L., Ficetola, G.F., Huijbregts, M.A.J., Carbone, C. and Thuiller, W. 2018. Global drivers of population density in terrestrial vertebrates. *Global Ecology and Biogeography* 27(8), pp. 968–979. doi: 10.1111/geb.12758.

Schuelke, M. 2000. An economic method for the fluorescent labeling of PCR fragments A poor man ' s approach to genotyping for research and high-throughput diagnostics . *PRism* 18(February), pp. 1–2. doi: 10.1038/72708.

Seline, H. 2003. *Nature across cultures : views of nature and the environment in non-western cultures*. 1st ed. Seline, H. ed. Dordrecht, Netherlands: Springer Netherlands.

Selkoe, K.A. and Toonen, R.J. 2006. Microsatellites for ecologists: A practical guide to using and evaluating microsatellite markers. *Ecology Letters* 9(5), pp. 615–629. doi: doi.wiley.com/10.1111/j.1461-0248.2006.00889.x.

Seminoff, J. 2004. Chelonia mydas. *The IUCN Red List of Threatened Species* e.T4615A11.

Sendell-Price, A.T., Ruegg, K.C. and Clegg, S.M. 2020. Rapid morphological divergence following a human-mediated introduction: the role of drift and directional selection. *Heredity* 124(4), pp. 535–549. doi: dx.doi.org/10.1038/s41437-020-0298-8.

Sendell-Price, A.T., Ruegg, K.C. and Clegg, S.M. 2020. Rapid morphological divergence following a human-mediated introduction: the role of drift and directional selection. *Heredity* 124(4), pp. 535–549. doi: dx.doi.org/10.1038/s41437-020-0298-8.

Sharma, R., Goossens, B., Heller, R., Rasteiro, R., Othman, N., Bruford, M.W. and Chikhi, L. 2018. Genetic analyses favour an ancient and natural origin of elephants on Borneo. *Scientific Reports* 8(1), pp. 1–11. doi: 10.1038/s41598-017-17042-5.

Silva, M.A. and Araujo., A. 2001. Distribution and current status of the West African manatee (*Trichechus senegalensis*) in Guinea-Bissau. *MARINE MAMMAL SCIENCE 17(2):418-424. 2001. (Notes)* 17(2), p. 7. doi: doi.wiley.com/10.1111/j.1748-7692.2001.tb01285.x.

Smeds, L. and Ellegren, H. 2023. From high masked to high realized genetic load in inbred Scandinavian wolves. *Molecular Ecology* 32(7), pp. 1567–1580. doi: 10.1111/mec.16802.

Smith, B.J. 2007. *boa: An R Package for MCMC Output Convergence Assessment and Posterior Inference*.

Spínola, C., Bruges-Armas, J., Brehm, A. and Spínola, H. 2008. HLA-A polymorphisms in four ethnic groups from Guinea-Bissau (West Africa) inferred from sequence-based typing. *Tissue Antigens* 72(6), pp. 593–598. doi: 10.1111/j.1399-0039.2008.01147.x.

Stoffel, M.A., Johnston, S.E., Pilkington, J.G. and Pemberton, J.M. 2021. Genetic architecture and lifetime dynamics of inbreeding depression in a wild mammal. *Nature Communications* 12(1), pp. 1–10. doi: dx.doi.org/10.1038/s41467-021-23222-9.

Storz, J.F. and Beaumont, M.A. 2002. Testing for genetic evidence of Population expansion and contraction: An empirical analysis of microsatellite DNA variation using a hierarchical Bayesian model. *Evolution* 56(1), pp. 154–166. doi: 10.1111/j.0014-3820.2002.tb00857.x.

Tajima, F. 1989. Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. *Genetics* 123(3), pp. 585–595. doi: PMC1203831.

Taylor, R.S. et al. 2024. High genetic load without purging in caribou, a diverse species at risk. *Current Biology* 34(6), pp. 1234-1246.e7. doi: 10.1016/j.cub.2024.02.002.

Templeton, A.R., Crandall, K.A. and Sing, C.F. 1992. A cladistic analysis of phenotypic associations with haplotypes inferred from restriction endonuclease mapping and DNA sequence data. III. Cladogram estimation. *Genetics* 132(2), pp. 619–633.

Temudo, M.P. and Abrantes, M. 2014. The Cashew Frontier in Guinea-Bissau, West Africa: Changing Landscapes and Livelihoods. *Human Ecology* 42(2), pp. 217–230. doi: 10.1007/s10745-014-9641-0.

Thomas, N.E. 2011. *Mitochondrial DNA variation of the lesser spot-nosed guenon (Cercopithecus petaurista) from the Canhabaque island, Bijogo Archipelago, West Africa.* BSc Thesis, Cardiff University.

Thompson, E.A. 2013. Identity by Descent: Variation in Meiosis, Across Genomes, and in Populations. *Genetics* 194(2), pp. 301–326. doi: dx.doi.org/10.1534/genetics.112.148825.

Torres, D.F., Oliveira, E.S. and Alves, R.R.N. 2018. Chapter 22 - Understanding Human–Wildlife Conflicts and Their Implications. In: Nóbrega Alves, R. R. and Albuquerque, U. P. eds. *Ethnozoology*. Academic Press, pp. 421–445.

Tuyisingize, D. et al. 2023. *Regional golden monkey (Cercopithecus mitis kandti) conservation action plan 2023–2028.* Gland, Switzerland.

Valière, N. and Berthier, P. 2002. GEMINI: software for testing the effects of genotyping errors and multitubes approach for individual identification. *Molecular Ecology …* 2(1), pp. 83–86. doi: doi.wiley.com/10.1046/j.1471-8286.2002.00134.x.

van Der Kuyl, A.C., Dekker, J.T. and Goudsmit, J. 1996. St. Kitts green monkeys originate from West Africa: Genetic evidence from feces. *American Journal of Primatology* 40(4), pp. 361–364.

van der Valk, T., Jensen, A., Caillaud, D. and Guschanski, K. 2024. Comparative genomic analyses provide new insights into evolutionary history and conservation genomics of gorillas. *BMC Ecology and Evolution* 24(1). doi: 10.1186/s12862-023-02195-x.

van Oosterhout, C., Hutchinson, W.F., Wills, D.P.M. and Shipley, P. 2004. MICRO-CHECKER: Software for identifying and correcting genotyping errors in microsatellite data. *Molecular Ecology Notes* 4(3), pp. 535–538. doi: doi.wiley.com/10.1111/j.1471-8286.2004.00684.x.

van Vliet, N. 2018. “Bushmeat crisis” and “cultural imperialism” in wildlife management? Taking value orientations into account for a more sustainable and culturally acceptable wildmeat sector. *Frontiers in Ecology and Evolution* 6(AUG), pp. 1–6. doi: 10.3389/fevo.2018.00112.

Vellend, M. 2003. Island Biogeography of Genes and Species. *The American Naturalist* 162(3), pp. 358–362. doi: 10.1021/ja058550q.

Veracini, C. 2017. Nonhuman Primate Trade in the Age of Discoveries: European Importation and Its Consequences History in the Making. In: de Melo, C. J. and Vaz, E. eds. *Environmental History in the Making- Volume II: Acting*. Basel, Switzerland: Springer International Publishing, p. 377. doi: 10.1007/978-3-319-41139-2.

von Seth, J. et al. 2022. Genomic trajectories of a near-extinction event in the Chatham Island black robin. *BMC Genomics* 23(1). doi: 10.1186/s12864-022-08963-1.

Waits, L.P., Luikart, G. and Taberlet, P. 2001. Estimating the probability of identity among genotypes in natural populations: cautions and guidelines. *Molecular Ecology* 10(1), pp. 249–256. doi: doi/full/10.1046/j.1365-294X.2001.01185.x.

Wang, J. 2017. The computer program structure for assigning individuals to populations: easy to use but easier to misuse. *Molecular Ecology Resources* 17(5), pp. 981–990. doi: 10.1111/1755-0998.12650.

Wang, W., Qiao, Y., Li, S., Pan, W. and Yao, M. 2017. Low genetic diversity and strong population structure shaped by anthropogenic habitat fragmentation in a critically endangered primate, Trachypithecus leucocephalus. *Heredity* 118(6), pp. 542–553. doi: 10.1038/hdy.2017.2.

Wang, X., Peischl, S. and Heckel, G. 2023. Demographic history and genomic consequences of 10,000 generations of isolation in a wild mammal. *Current Biology* 33(10), pp. 2051-2062.e4. doi: 10.1016/j.cub.2023.04.042.

Waples, R.S., Luikart, G., Faulkner, J.R. and Tallmon, D.A. 2013. Simple life-history traits explain key effective population size ratios across diverse taxa. *Proceedings of the Royal Society B: Biological Sciences* 280(1768). doi: 10.1098/rspb.2013.1339.

Wegmann, D., Leuenberger, C. and Excoffier, L. 2009. *Using ABCtoolbox*.

Wegmann, D., Leuenberger, C., Neuenschwander, S. and Excoffier, L. 2010. ABCtoolbox: A versatile toolkit for approximate Bayesian computations. *BMC Bioinformatics* 11. doi: 10.1186/1471-2105-11-116.

Welles, S.R. and Dlugosch, K.M. 2019. Population Genomics of Colonization and Invasion. In: Rajora, O. P. ed. *Population Genomics*. Cham, Switzerland: Springer Nature Switzerland.

Williams, P.H., Burgess, N.D. and Rahbek, C. 2000. Flagship species, ecological complementarity and conserving the diversity of mammals and birds in sub-Saharan Africa. *Animal Conservation* 3(3), pp. 249–260.

Williamson, S.H., Hernandez, R., Fledel-Alon, A., Zhu, L., Nielsen, R. and Bustamante, C.D. 2005. Simultaneous inference of selection and population growth from patterns of variation in the human genome. *Proceedings of the National Academy of Sciences of the United States of America* 102(22), pp. 7882–7887. doi: /doi/abs/10.1073/pnas.0502300102.

World Bank. 2024. *Poverty in Guinea-Bissau – A look at pre- and post-COVID-19 trends*.

Wright, S. 1931. Evolution in Mendelian Populations. *Genetics* 16, pp. 97–159.

Xu, W. et al. 2024. Community perspectives of flagship species: can conservation motivators mitigate human-wildlife conflict? *Frontiers in Ecology and Evolution* 12. doi: 10.3389/fevo.2024.1265694.

Xue, C. et al. 2020. Reduced meiotic recombination in rhesus macaques and the origin of the human recombination landscape. *PLOS ONE* 15(8), p. e0236285.

Xue, Y. et al. 2015. Mountain gorilla genomes reveal the impact of long-term population decline and inbreeding. *Science* 348(6231), pp. 242–245. doi: doi/10.1126/science.aaa3952.

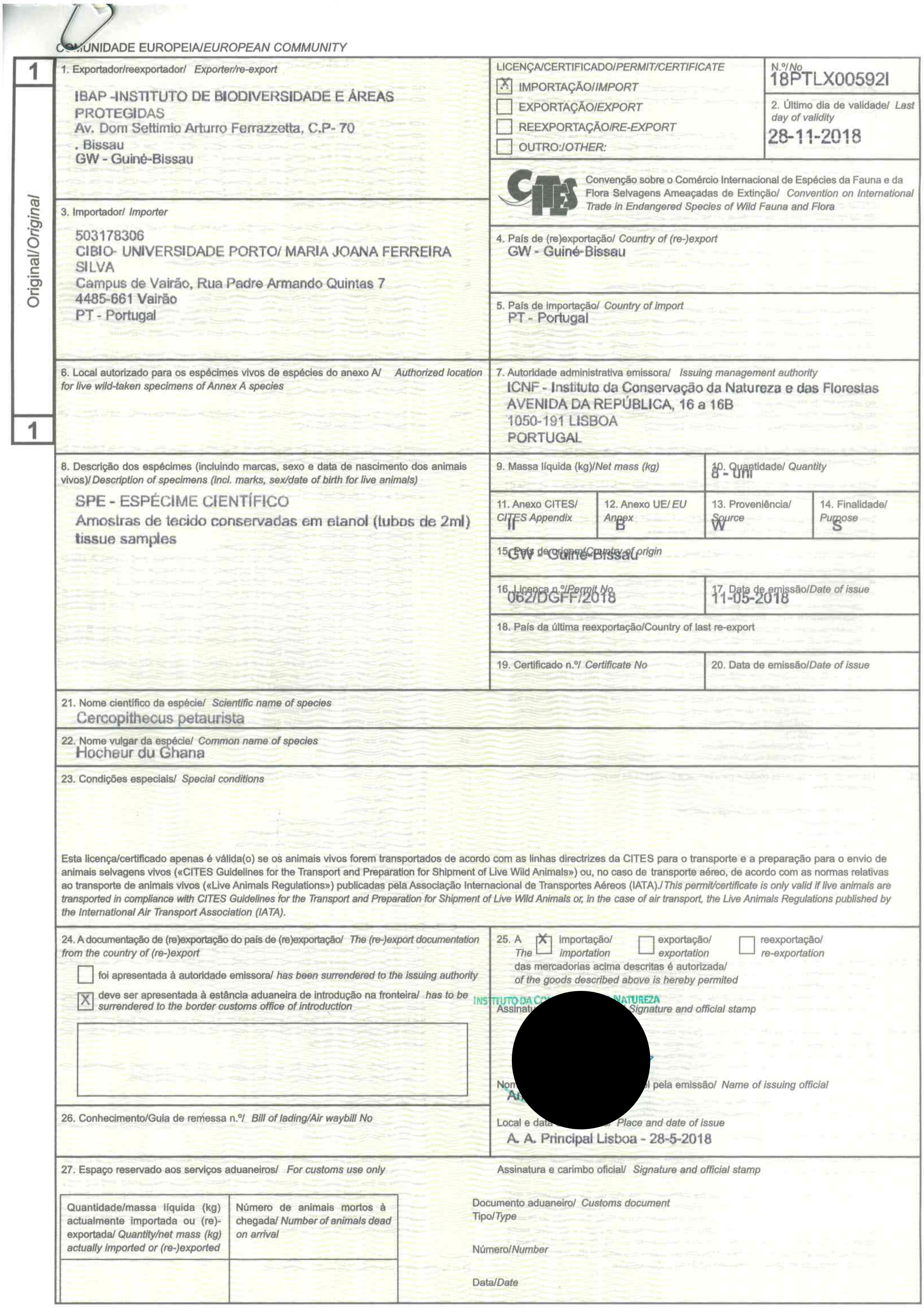
Yampolsky, L.Y. and Stoltzfus, A. 2005. The Exchangeability of Amino Acids in Proteins. *Genetics* 170(4), pp. 1459–1472. doi: dx.doi.org/10.1534/genetics.104.039107.

Zihlman, A.L. and Underwood, C.E. 2013. Locomotor Anatomy and Behavior of Patas Monkeys (*Erythrocebus patas*) with Comparison to Vervet Monkeys (*Cercopithecus aethiops*). *Anatomy Research International* 2013, pp. 1–11. doi: 10.1155/2013/409534.

ANNEX I

In this annex you may find all the documentation mentioned in the ethics section:

1. CITES importation permits to Portugal (No 18PTLX00592I, 18PTLX00590I, 18PTLX00586I).
2. Participant information sheet.
3. Participant informed consent sheet.
4. Cardiff University's BIOSI SREC ethical approval outcome letter.
5. Gatekeeping letter from the National Institute for Biodiversity and Protected Areas (IBAP) authorising the execution of the project in Guinea – Bissau.



COMUNIDADE EUROPEIA/*EUROPEAN COMMUNITY*

1 Original/*Original* 1

1. Exportador/reexportador/ *Exporter/re-export*

IBAP -INSTITUTO DE BIODIVERSIDADE E ÁREAS PROTEGIDAS
Av. Dom Settimio Arturro Ferrazzetta, C.P- 70
. Bissau
GW - Guiné-Bissau

LICENÇA/CERTIFICADO/*PERMIT/CERTIFICATE*

☒ IMPORTAÇÃO/*IMPORT*
☐ EXPORTAÇÃO/*EXPORT*
☐ REEXPORTAÇÃO/*RE-EXPORT*
☐ OUTRO:/*OTHER:*

N.º/*No*
18PTLX00592I

2. Último dia de validade/ *Last day of validity*
28-11-2018

CITES

Convenção sobre o Comércio Internacional de Espécies da Fauna e da Flora Selvagens Ameaçadas de Extinção/ *Convention on International Trade in Endangered Species of Wild Fauna and Flora*

3. Importador/ *Importer*

503178306
CIBIO- UNIVERSIDADE PORTO/ MARIA JOANA FERREIRA SILVA
Campus de Vairão, Rua Padre Armando Quintas 7
4485-661 Vairão
PT - Portugal

4. País de (re)exportação/ *Country of (re-)export*
GW - Guiné-Bissau

5. País de importação/ *Country of import*
PT - Portugal

6. Local autorizado para os espécimes vivos de espécies do anexo A/ *Authorized location for live wild-taken specimens of Annex A species*

7. Autoridade administrativa emissora/ *Issuing management authority*

ICNF - Instituto da Conservação da Natureza e das Florestas
AVENIDA DA REPÚBLICA, 16 a 16B
1050-191 LISBOA
PORTUGAL

8. Descrição dos espécimes (incluindo marcas, sexo e data de nascimento dos animais vivos)/ *Description of specimens (incl. marks, sex/date of birth for live animals)*

SPE - ESPÉCIME CIENTÍFICO
Amostras de tecido conservadas em etanol (tubos de 2ml)
tissue samples

9. Massa líquida (kg)/*Net mass (kg)*

10. Quantidade/ *Quantity*
8 - uni

11. Anexo CITES/ *CITES Appendix*
II

12. Anexo UE/ *EU Annex*
B

13. Proveniência/ *Source*
W

14. Finalidade/ *Purpose*
S

15. País de origem/*Country of origin*
GW - Guiné-Bissau

16. Licença n.º/*Permit No*
062/DGFF/2018

17. Data de emissão/*Date of issue*
11-05-2018

18. País da última reexportação/Country of last re-export

19. Certificado n.º/ *Certificate No*

20. Data de emissão/*Date of issue*

21. Nome científico da espécie/ *Scientific name of species*
Cercopithecus petaurista

22. Nome vulgar da espécie/ *Common name of species*
Hocheur du Ghana

23. Condições especiais/ *Special conditions*

Esta licença/certificado apenas é válida(o) se os animais vivos forem transportados de acordo com as linhas directrizes da CITES para o transporte e a preparação para o envio de animais selvagens vivos («CITES Guidelines for the Transport and Preparation for Shipment of Live Wild Animals») ou, no caso de transporte aéreo, de acordo com as normas relativas ao transporte de animais vivos («Live Animals Regulations») publicadas pela Associação Internacional de Transportes Aéreos (IATA)./ *This permit/certificate is only valid if live animals are transported in compliance with CITES Guidelines for the Transport and Preparation for Shipment of Live Wild Animals or, in the case of air transport, the Live Animals Regulations published by the International Air Transport Association (IATA).*

24. A documentação de (re)exportação do país de (re)exportação/ *The (re-)export documentation from the country of (re-)export*

☐ foi apresentada à autoridade emissora/ *has been surrendered to the issuing authority*
☒ deve ser apresentada à estância aduaneira de introdução na fronteira/ *has to be surrendered to the border customs office of introduction*

25. A *The* ☒ importação/ *importation* ☐ exportação/ *exportation* ☐ reexportação/ *re-exportation* das mercadorias acima descritas é autorizada/ *of the goods described above is hereby permited*

INSTITUTO DA CO[redacted] NATUREZA

Assinatu… *Signature and official stamp*

Nom… l pela emissão/ *Name of issuing official*

Local e data… *Place and date of issue*
A. A. Principal Lisboa - 28-5-2018

26. Conhecimento/Guia de remessa n.º/ *Bill of lading/Air waybill No*

27. Espaço reservado aos serviços aduaneiros/ *For customs use only*

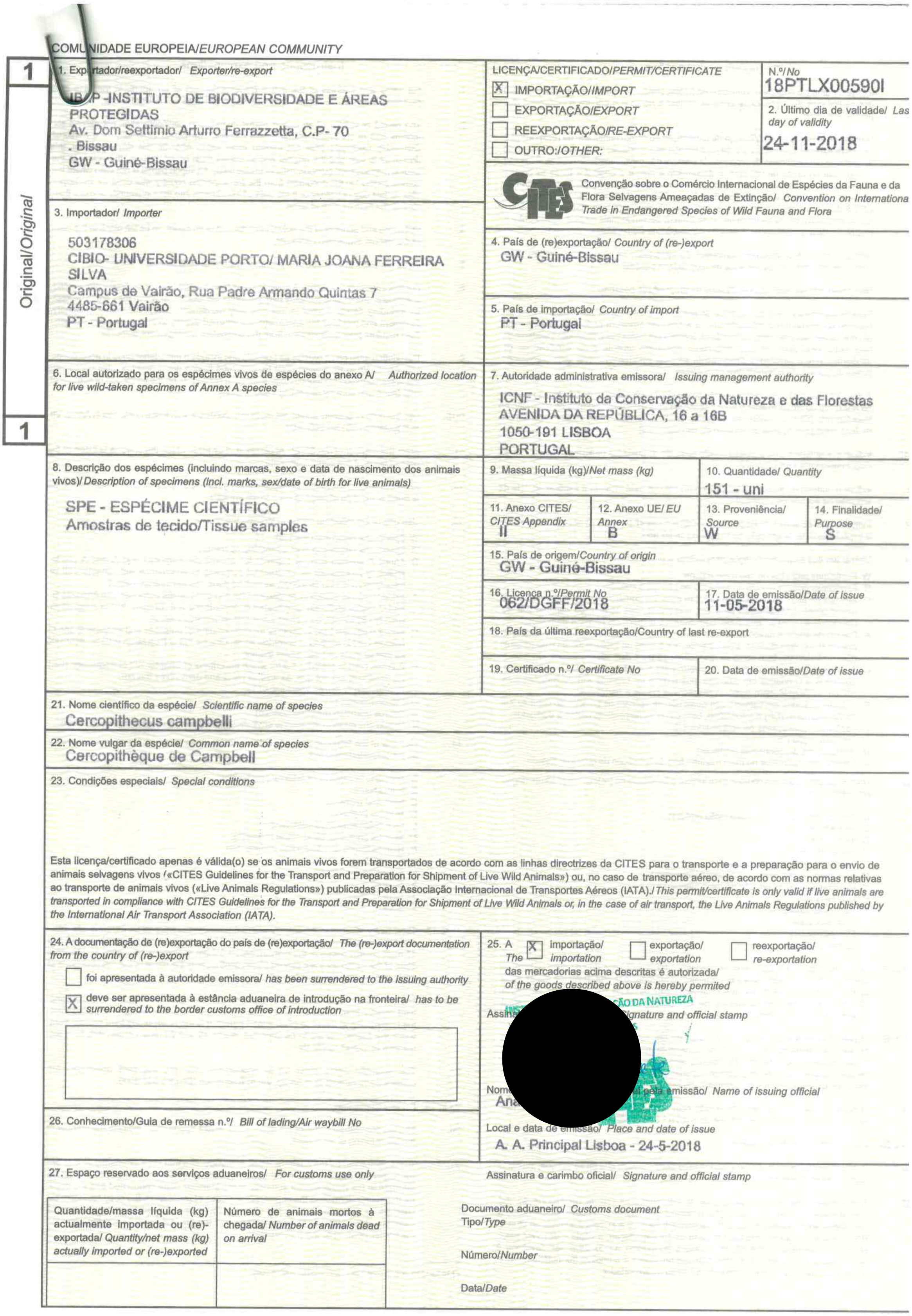
Assinatura e carimbo oficial/ *Signature and official stamp*

Quantidade/massa líquida (kg) actualmente importada ou (re)-exportada/ *Quantity/net mass (kg) actually imported or (re-)exported*	Número de animais mortos à chegada/ *Number of animals dead on arrival*

Documento aduaneiro/ *Customs document*
Tipo/*Type*

Número/*Number*

Data/*Date*



COMUNIDADE EUROPEIA/*EUROPEAN COMMUNITY*

1

1. Exportador/reexportador/ *Exporter/re-export*

IBAP -INSTITUTO DE BIODIVERSIDADE E ÁREAS PROTEGIDAS
Av. Dom Settimio Arturro Ferrazzetta, C.P- 70
. Bissau
GW - Guiné-Bissau

LICENÇA/CERTIFICADO/*PERMIT/CERTIFICATE*

☒ IMPORTAÇÃO/*IMPORT*
☐ EXPORTAÇÃO/*EXPORT*
☐ REEXPORTAÇÃO/*RE-EXPORT*
☐ OUTRO:/*OTHER:*

N.º/*No*
18PTLX00590I

2. Último dia de validade/ *Las day of validity*
24-11-2018

CITES

Convenção sobre o Comércio Internacional de Espécies da Fauna e da Flora Selvagens Ameaçadas de Extinção/ *Convention on Internationa Trade in Endangered Species of Wild Fauna and Flora*

Original/*Original*

3. Importador/ *Importer*

503178306
CIBIO- UNIVERSIDADE PORTO/ MARIA JOANA FERREIRA SILVA
Campus de Vairão, Rua Padre Armando Quintas 7
4485-661 Vairão
PT - Portugal

4. País de (re)exportação/ *Country of (re-)export*
GW - Guiné-Bissau

5. País de importação/ *Country of import*
PT - Portugal

6. Local autorizado para os espécimes vivos de espécies do anexo A/ *Authorized location for live wild-taken specimens of Annex A species*

7. Autoridade administrativa emissora/ *Issuing management authority*

ICNF - Instituto da Conservação da Natureza e das Florestas
AVENIDA DA REPÚBLICA, 16 a 16B
1050-191 LISBOA
PORTUGAL

1

8. Descrição dos espécimes (incluindo marcas, sexo e data de nascimento dos animais vivos)/ *Description of specimens (incl. marks, sex/date of birth for live animals)*

SPE - ESPÉCIME CIENTÍFICO
Amostras de tecido/Tissue samples

9. Massa líquida (kg)/*Net mass (kg)*

10. Quantidade/ *Quantity*
151 - uni

11. Anexo CITES/ *CITES Appendix*	12. Anexo UE/ *EU Annex*	13. Proveniência/ *Source*	14. Finalidade/ *Purpose*
II	B	W	S

15. País de origem/*Country of origin*
GW - Guiné-Bissau

16. Licença n.º/*Permit No*
062/DGFF/2018

17. Data de emissão/*Date of issue*
11-05-2018

18. País da última reexportação/*Country of last re-export*

19. Certificado n.º/ *Certificate No*

20. Data de emissão/*Date of issue*

21. Nome científico da espécie/ *Scientific name of species*
Cercopithecus campbelli

22. Nome vulgar da espécie/ *Common name of species*
Cercopithèque de Campbell

23. Condições especiais/ *Special conditions*

Esta licença/certificado apenas é válida(o) se os animais vivos forem transportados de acordo com as linhas directrizes da CITES para o transporte e a preparação para o envio de animais selvagens vivos («CITES Guidelines for the Transport and Preparation for Shipment of Live Wild Animals») ou, no caso de transporte aéreo, de acordo com as normas relativas ao transporte de animais vivos («Live Animals Regulations») publicadas pela Associação Internacional de Transportes Aéreos (IATA)./ *This permit/certificate is only valid if live animals are transported in compliance with CITES Guidelines for the Transport and Preparation for Shipment of Live Wild Animals or, in the case of air transport, the Live Animals Regulations published by the International Air Transport Association (IATA).*

24. A documentação de (re)exportação do país de (re)exportação/ *The (re-)export documentation from the country of (re-)export*

☐ foi apresentada à autoridade emissora/ *has been surrendered to the issuing authority*
☒ deve ser apresentada à estância aduaneira de introdução na fronteira/ *has to be surrendered to the border customs office of introduction*

25. A *The* ☒ importação/ *importation* ☐ exportação/ *exportation* ☐ reexportação/ *re-exportation*
das mercadorias acima descritas é autorizada/ *of the goods described above is hereby permited*

Assina[redacted]ignature and official stamp

...ÇÃO DA NATUREZA

Nom... pela emissão/ *Name of issuing official*
Ana

Local e data de emissão/ *Place and date of issue*
A. A. Principal Lisboa - 24-5-2018

26. Conhecimento/Guia de remessa n.º/ *Bill of lading/Air waybill No*

27. Espaço reservado aos serviços aduaneiros/ *For customs use only*

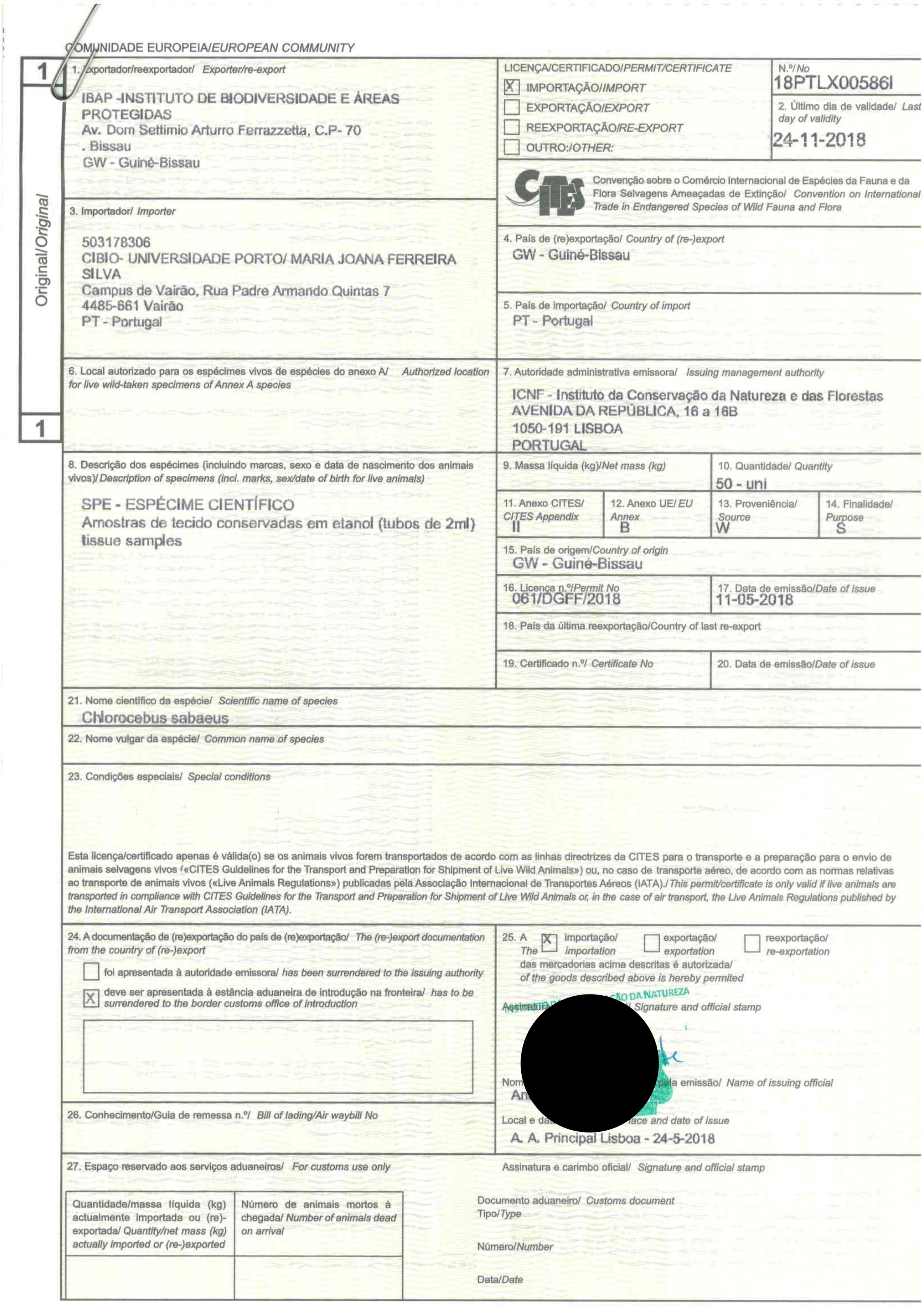
Assinatura e carimbo oficial/ *Signature and official stamp*

Quantidade/massa líquida (kg) actualmente importada ou (re)-exportada/ *Quantity/net mass (kg) actually imported or (re-)exported*	Número de animais mortos à chegada/ *Number of animals dead on arrival*

Documento aduaneiro/ *Customs document*
Tipo/*Type*

Número/*Number*

Data/*Date*



COMUNIDADE EUROPEIA/*EUROPEAN COMMUNITY*

1 Original/*Original* 1

1. Exportador/reexportador/ *Exporter/re-export*
IBAP -INSTITUTO DE BIODIVERSIDADE E ÁREAS PROTEGIDAS
Av. Dom Settimio Arturro Ferrazzetta, C.P- 70
. Bissau
GW - Guiné-Bissau

LICENÇA/CERTIFICADO/*PERMIT/CERTIFICATE*
☒ IMPORTAÇÃO/*IMPORT*
☐ EXPORTAÇÃO/*EXPORT*
☐ REEXPORTAÇÃO/*RE-EXPORT*
☐ OUTRO:/*OTHER:*

N.º/*No*
18PTLX00586I

2. Último dia de validade/ *Last day of validity*
24-11-2018

CITES Convenção sobre o Comércio Internacional de Espécies da Fauna e da Flora Selvagens Ameaçadas de Extinção/ *Convention on International Trade in Endangered Species of Wild Fauna and Flora*

3. Importador/ *Importer*
503178306
CIBIO- UNIVERSIDADE PORTO/ MARIA JOANA FERREIRA SILVA
Campus de Vairão, Rua Padre Armando Quintas 7
4485-661 Vairão
PT - Portugal

4. País de (re)exportação/ *Country of (re-)export*
GW - Guiné-Bissau

5. País de importação/ *Country of import*
PT - Portugal

6. Local autorizado para os espécimes vivos de espécies do anexo A/ *Authorized location for live wild-taken specimens of Annex A species*

7. Autoridade administrativa emissora/ *Issuing management authority*
ICNF - Instituto da Conservação da Natureza e das Florestas
AVENIDA DA REPÚBLICA, 16 a 16B
1050-191 LISBOA
PORTUGAL

8. Descrição dos espécimes (incluindo marcas, sexo e data de nascimento dos animais vivos)/ *Description of specimens (incl. marks, sex/date of birth for live animals)*
SPE - ESPÉCIME CIENTÍFICO
Amostras de tecido conservadas em etanol (tubos de 2ml)
tissue samples

9. Massa líquida (kg)/*Net mass (kg)*

10. Quantidade/ *Quantity*
50 - uni

11. Anexo CITES/ *CITES Appendix*	12. Anexo UE/ *EU Annex*	13. Proveniência/ *Source*	14. Finalidade/ *Purpose*
II	B	W	S

15. País de origem/*Country of origin*
GW - Guiné-Bissau

16. Licença n.º/*Permit No*
061/DGFF/2018

17. Data de emissão/*Date of issue*
11-05-2018

18. País da última reexportação/*Country of last re-export*

19. Certificado n.º/ *Certificate No*

20. Data de emissão/*Date of issue*

21. Nome científico da espécie/ *Scientific name of species*
Chlorocebus sabaeus

22. Nome vulgar da espécie/ *Common name of species*

23. Condições especiais/ *Special conditions*

Esta licença/certificado apenas é válida(o) se os animais vivos forem transportados de acordo com as linhas directrizes da CITES para o transporte e a preparação para o envio de animais selvagens vivos («CITES Guidelines for the Transport and Preparation for Shipment of Live Wild Animals») ou, no caso de transporte aéreo, de acordo com as normas relativas ao transporte de animais vivos («Live Animals Regulations») publicadas pela Associação Internacional de Transportes Aéreos (IATA)./ *This permit/certificate is only valid if live animals are transported in compliance with CITES Guidelines for the Transport and Preparation for Shipment of Live Wild Animals or, in the case of air transport, the Live Animals Regulations published by the International Air Transport Association (IATA).*

24. A documentação de (re)exportação do país de (re)exportação/ *The (re-)export documentation from the country of (re-)export*
☐ foi apresentada à autoridade emissora/ *has been surrendered to the issuing authority*
☒ deve ser apresentada à estância aduaneira de introdução na fronteira/ *has to be surrendered to the border customs office of introduction*

25. A/*The* ☒ importação/ *importation* ☐ exportação/ *exportation* ☐ reexportação/ *re-exportation*
das mercadorias acima descritas é autorizada/ *of the goods described above is hereby permited*

Assinatura [redacted] / *Signature and official stamp*

Nom[redacted] pela emissão/ *Name of issuing official*

Local e da[redacted] *lace and date of issue*
A. A. Principal Lisboa - 24-5-2018

26. Conhecimento/Guia de remessa n.º/ *Bill of lading/Air waybill No*

27. Espaço reservado aos serviços aduaneiros/ *For customs use only*

Quantidade/massa líquida (kg) actualmente importada ou (re)-exportada/ *Quantity/net mass (kg) actually imported or (re-)exported*	Número de animais mortos à chegada/ *Number of animals dead on arrival*

Assinatura e carimbo oficial/ *Signature and official stamp*

Documento aduaneiro/ *Customs document*
Tipo/*Type*
Número/*Number*
Data/*Date*

Appendix 3

PARTICIPANT INFORMATION SHEET

Ethnobiological insights on traditional management practices of insular mammals by the Bijagó ethnic group in Guinea-Bissau

You are being invited to take part in a research project. Before you decide whether or not to take part, it is important for you to understand why the research is being undertaken and what it will involve. Please take time to read the following information carefully and discuss it with others, if you wish.

Thank you for reading this.

1. What is the purpose of this research project?

The aim of this study is to understand how the inhabitants of the Bijagós Archipelago perceive the effects of insularity on local mammals and their traditional management strategies of the local ecosystem. We will ask you to answer a questionnaire and/or interview regarding this topic.

2. Why have I been invited to take part?

You have been invited because you are an adult member of the local community.

3. Do I have to take part?

No, your participation in this research project is entirely voluntary and it is up to you to decide whether or not to take part. If you decide to take part, we will discuss the research project with you and formerly ask for consent. If you decide not to take part, you do not have to explain your reasons and it will not affect your legal rights.
You are free to withdraw your consent to participate in the research project at any time, without giving a reason, even after signing the consent form.

4. What will taking part involve?

If you are selected to participate in the survey questionnaires, this will take approximately 30 minutes. You will be asked some personal information (*e.g.,* village, age group, cultural and religious identity) and to answer the questionnaire. Personal data collected will be as limited and as broad as possible to ensure your anonymity. No audio recording data will be produced during questionnaires.

If you are selected to participate in an interview, this will take approximately 30 minutes. We will produce audio recordings of the interviews.

All data collected will be attached to a randomised project number. Your participation will be confidential and anonymous throughout all states of the research, including publication.

5. Will I be paid for taking part?

No. You should understand that any information you give will be as a gift and you will not benefit financially in the future.

6. What are the possible benefits of taking part?

There will be no direct advantages or benefits to you from taking part, but your contribution will provide valuable information on how to preserve the ecosystem of the archipelago while avoiding conflict with local livelihoods.

7. What are the possible risks of taking part?

You may feel unease when answering certain questions. However, you are free to omit any questions or withdraw from the study without the need of an explanation.

8. Will my taking part in this research project be kept confidential?

All information collected from (or about) you during the research project will be kept confidential and any personal information you provide will be managed in accordance with data protection legislation. Please see 'What will happen to my Personal Data?' (below) for further information.

9. What will happen to my Personal Data?

Cardiff University is the Data Controller and is committed to respecting and protecting your personal data in accordance with your expectations and Data Protection legislation. Further information about Data Protection, including:

- your rights
- the legal basis under which Cardiff University processes your personal data for research
- Cardiff University's Data Protection Policy
- how to contact the Cardiff University Data Protection Officer
- how to contact the Information Commissioner's Office

may be found at https://www.cardiff.ac.uk/public-information/policies-and-procedures/data-protection; printed versions of the above-mentioned documentation will be present at all times during data collection.

After two years, the research team will anonymise all the personal data it has collected from, or about, you in connection with this research project. The records of your verbal consent will be retained for five years and may be accessed by members of the research team and, where necessary, by members of the University's governance and audit teams or by regulatory authorities. Anonymised information will be kept for a minimum of five years but may be published in support of the research project and/or retained indefinitely, where it is likely to have continuing value for research purposes.

In case of withdraw, all unpublished data will be erased and excluded from analysis.

10. What happens to the data at the end of the research project?

Access to the data will be restricted to the student and main supervisor. We do not have any intention to share the raw data collected in this study. Personal data collected during the research project will be as limited and as broad as possible to ensure anonymity.

11. What will happen to the results of the research project?

It is our intention to publish the results of this research project in academic journals and present findings at conferences and local/international stakeholders. Participants will not be identified in any report, publication, or presentation. We may use verbatim quotes from participants. However, these will not contain any personal data that can be traced to you.

12. What if there is a problem?

If you wish to complain or have grounds for concerns about any aspect of the manner in which you have been approached or treated during the course of this research, please contact Maria Joana Ferreira da Silva; mjf_silva@cibio.up.pt. If your complaint is not managed to your satisfaction, please contact the School of Biosciences Ethics Committee; BIOSI-Ethics@cardiff.ac.uk.

If you are harmed by taking part in this research project, there are no special compensation arrangements. If you are harmed due to someone's negligence, you may have grounds for legal action, but you may have to pay for it.

13. Who is organising and funding this research project?

The research is organised by Ivo Colmonero Costeira, under the supervision of Prof Mike Bruford (BIOSI), Dr Maria Joana Ferreira da Silva (BIOSI; CIBIO, Portugal) and Dr Susana Costa (CIAS, Portugal). The research is currently funded by the Portuguese Foundation for Science and Technology, Primate Incorporated and The Genetics Society.

14. Who has reviewed this research project?

This research project has been reviewed and given a favourable opinion by the Biosciences School Research Ethics Committee, Cardiff University.

15. Further information and contact details

Should you have any questions relating to this research project, you may contact us during normal working hours:

Ivo Colmonero Costeira, colmonerocosteirai@cardiff.ac.uk
Maria Joana Ferreira da Silva, mjf_silva@cibio.up.pt

Thank you for considering to take part in this research project. If you decide to participate, you will be given a copy of the Participant Information Sheet and a signed consent form to keep for your records.

Appendix 4

Participant ID no: *Do not include box for anonymised samples*

CONSENT FORM

Title of research project: Ethnobiological insights on traditional management practices of insular mammals by the Bijagó ethnic group in Guinea-Bissau

SREC reference and committee: [Insert SREC reference and committee or other relevant reference numbers]

Name of Researcher: Ivo Colmonero Costeira

	Please initial box
I confirm that I have read the information sheet provided	
I confirm that I have understood the information sheet for the above research project and that I have had the opportunity to ask questions and that these have been answered satisfactorily.	
I understand that my participation is voluntary, and I am free to withdraw at any time without giving a reason and without any adverse consequences.	
I understand that data collected during the research project may be looked at by individuals from Cardiff University or from regulatory authorities, where it is relevant to my taking part in the research project. I give permission for these individuals to have access to my data.	
I consent to the processing of my personal information (*e.g.,* village, age group, cultural and religious identity) for the purposes explained to me. I understand that such information will be held in accordance with all applicable data protection legislation and in strict confidence, unless disclosure is required by law or professional obligation.	
I understand who will have access to personal information provided, how the data will be stored and what will happen to the data at the end of the research project.	
I understand that it will not be possible to identify me from this data that is seen and used by other researchers, for ethically approved research projects, on the understanding that confidentiality will be maintained.	
I consent to being audio recorded for the purposes of the research project and I understand how it will be used in the research.	

Version 01 [February 2022]

Appendix 4

Participant ID no:
Do not include box for anonymised samples

I understand that anonymised excerpts and/or verbatim quotes from my interview may be used as part of the research publication.	
I understand how the findings and results of the research project will be written up and published.	
I agree to take part in this research project.	

Name of participant (print)	Date	
Name of person taking consent (print)	Date	Signature
Name of witness (print)	Date	Signature

THANK YOU FOR PARTICIPATING IN OUR RESEARCH

YOU WILL BE GIVEN A COPY OF THIS CONSENT FORM TO KEEP

Version 01 [February 2022]

School of Biosciences
Ysgol y Biowyddorau

Cardiff University
The Sir Martin Evans Building
Museum Avenue
Cardiff, CF10 3AX, Wales, UK
Tel +44(0)29 2087 4120
Email MurrayJA1@cardiff.ac.uk
www.cardiff.ac.uk/biosciences

Prifysgol Caerdydd
Adeiliad Syr Martin Evans
Rhodfa'r Amgueddfa
Caerdydd, CF10 3AX, Cymru, DU
Tel +44 (0)29 2087 4120
Email MurrayJA1@cardiff.ac.uk
www.caerdydd.ac.uk/biosciences

Mr I Colmonero Marques Costeira
School of Biosciences
The Sir Martin Evans Building
Museum Avenue
Cardiff
CF10 3AX

25th November 2022

Dear Mr Colmonero Marques Costeira

Research project title: Ethnobiological and genomic insights on traditional management practices of insular mammals by the Bijagó ethnic group in Guinea-Bissau and its implications to non-human primate conservation

SREC reference: 22 11-01

The School of Biosciences Research Ethics Committee ('Committee') reviewed the above application at meetings held on 10th March 2022 and 30th September 2022 and via email circulation on 13th April 2022 and 21st October 2022.

Ethical Opinion
The Committee gave a favourable ethical opinion of the above application on the basis described in the application form, protocol and supporting documentation.

Additional approvals
This letter provides an ethical opinion only. You must not start your research project until all appropriate approvals are in place.

Amendments
Any substantial amendments to documents previously reviewed by the Committee must be submitted to the Committee via BIOSI-Ethics@cardiff.ac.uk for consideration and cannot be implemented until the Committee has confirmed it is satisfied with the proposed amendments. You are permitted to implement non-substantial amendments to the documents previously reviewed by the Committee but you must provide a copy of any updated documents to the Committee via BIOSI-Ethics@cardiff.ac.uk for its records.

Monitoring requirements
The Committee must be informed of any unexpected ethical issues or unexpected adverse events that arise during the research project.

The Committee must be informed when your research project has ended. This notification should be made to BIOSI-Ethics@cardiff.ac.uk within three months of research project completion.

Documents reviewed by Committee
The documents reviewed by the Committee were:

Document	Version	Date
SREC application form	v1	02/02/22
Participant Information Sheet	v1	02/02/22
Consent Form	v1	02/02/22
Research Project and Questionnaire	v1	02/02/22
Gatekeeper Letter	v1	02/02/22
Research Integrity Online Training Programme certification		02/02/22
for I Colmonero Marques Costeira and M Ferreira Da Silva		02/02/22
BIOSI SREC_answers to committee document		10/03/22
SREC application form	v2	12/04/22
Participant Information Sheet	v2	12/04/22
Consent Form	v2	12/04/22
Research Project and Questionnaire	v2	12/04/22
SREC application form	v3	26/09/22
DPIA	v2	26/09/22

Complaints/Appeals
If you are dissatisfied with the decision made by the Committee, please contact Dr Alan Watson in the first instance to discuss your complaint. If this discussion does not resolve the issue, you are entitled to refer the matter to the Head of School for further consideration. The Head of School may refer the matter to the Open Research Integrity and Ethics Committee (ORIEC), where this is appropriate. Please be advised that ORIEC will not normally interfere with a decision of the Committee and is concerned only with the general principles of natural justice, reasonableness and fairness of the decision.

Please use the Committee reference number on all future correspondence.

The Committee reminds you that it is your responsibility to conduct your research project to the highest ethical standards and to keep all ethical issues arising from your research project under regular review.

CARDIFF
UNIVERSITY
PRIFYSGOL
CAERDYD

You are expected to comply with Cardiff University's policies, procedures and guidance at all times, including, but not limited to, its Policy on the Ethical Conduct of Research involving Human Participants, Human Material or Human Data and our Research Integrity and Governance Code of Practice.

Yours sincerely,

Dr Alan Watson
Chair of the School of Biosciences Research Ethics Committee

Cc BIOSI-Ethics@cardiff.ac.uk

Instituto da Biodiversidade e das Áreas Protegidas (IBAP) -
Dr. Alfredo Simão da Silva

To Whom It May Concern

This letter confirms that IBAP (Instituto para a Biodiversidade e ÀreasProtegidas, Guiné-Bissau) has been cooperating with researchers working for primate conservation Guinea-Bissau for the last two decades. IBAP supports and is involved in all the initiatives aiming at wildlife and natural habitats preservation within the national territory.

Therefore, I confirm through this letter that IBAP is a partner of the project ***Ethnobiological and genomic insights on traditional management practices of insular mammals by the bijagó ethnic group in Guinea-Bissau and its implications to non-human primate conservation*** **(2020-2024).**

IBAP will collaborate with **Ivo Colmonero-Costeira** and the project researchers' team and will support the activities implemented in Guinea-Bissau.

Yours faithfully,

[redacted]

Dr. Justino BIAI
Director General of IBAP

Tel. 00 245 95 580 38 49
E-mail:justinobiai.ibap@gmail.com

Avenida Dom SettimioArturoFerrazzetta. Caixa Postal 70 Bissau
Tel. (245) 95 580 38 50
Guiné-Bissau
Site: www.ibapgbissau.org

ANNEX II

Past controversies on taxonomic identity of the spot-nosed monkey in Guinea-Bissau, West-Africa: implications for conservation management

Ivo Colmonero-Costeira*, Nia Evelyn Thomas*, Muhamed Lamino Djaló, Nelson Fernandes, Cecilia Veracini, Tânia Minhós, Susana Costa, Michael William Bruford, Isa-Rita Maria Russo, Rui Moutinho Sá**, Maria Joana Ferreira Da Silva**

* First co-authors; ** last co-authors

Ivo Colmonero-Costeira (Corresponding author, orcid.org/0000-0001-9914-0713) ONE, Organisms and Environment Division, School of Biosciences, Cardiff University, Cardiff, United Kingdom; CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Universidade do Porto, Vairão, Portugal; BIOPOLIS, Program in Genomics, Biodiversity and Land Planning, CIBIO, Vairão, Portugal; CIAS, Department of Life Sciences, Universidade de Coimbra, Coimbra, Portugal; institutional address: Sir Martin Evans Building, The Museum Ave, Cardiff CF10 3AX, United Kingdom; e-mail: colmonerocosteirai@cardiff.ac.uk

Nia Evelyn Thomas (orcid.org/0000-0003-4412-4286) ONE, Organisms and Environment Division, School of Biosciences, Cardiff University, Cardiff, United Kingdom

Muhamed Lamino Djaló Ganogo, Guinea-Bissau

Nelson Fernandes Ganogo, Guinea-Bissau

Cecilia Veracini (orcid.org/0000-0002-2036-0447) Centre for Public Administration and Public Policies, Institute of Social and Political Sciences, Universidade de Lisboa, Lisbon, Portugal

Tânia Minhós (orcid.org/0000-0003-0183-1343) CRIA, Centre for Research in Anthropology (CRIA-FCSH/NOVA), Lisbon, Portugal; Departamento de Antropologia, Faculdade de Ciências Sociais e Humanas – NOVA FCSH; Lisbon, Portugal

Susana Costa (orcid.org/0000-0002-2766-0135) CIAS, Department of Life Sciences, Universidade de Coimbra, Coimbra, Portugal

Michael William Bruford (orcid.org/0000-0001-6357-6080) ONE, Organisms and Environment Division, School of Biosciences, Cardiff University, Cardiff, United Kingdom

Isa-Rita Maria Russo (orcid.org/0000-0001-9504-3633) ONE, Organisms and Environment Division, School of Biosciences, Cardiff University, Cardiff, United Kingdom

Rui Moutinho Sá (orcid.org/0000-0001-6407-4541) Centre for Public Administration and Public Policies, Institute of Social and Political Sciences, Universidade de Lisboa, Lisbon, Portugal

Maria Joana Ferreira da Silva (https://orcid.org/0000-0001-6747-9827) CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Universidade do Porto, Vairão, Portugal; BIOPOLIS, Program in Genomics, Biodiversity and Land Planning, CIBIO, Vairão, Portugal; ONE, Organisms and Environment Division, School of Biosciences, Cardiff University, Cardiff, United Kingdom

Abstract

Biodiversity management policies equip relevant parties with the legal basis to act upon the unsustainable use of these resources. In Guinea-Bissau two species of spot-nosed monkey have been suggested to occur – the spot-nosed monkey (*Cercopithecus petaurista* Schreber, 1774), and the putty nosed monkey (*Cercopithecus nictitans* Linnaeus, 1766), respectively. The last extant populations of the spot-nosed monkeys in Guinea-Bissau are thought to be restricted to the Bijagós Archipelago and to be threatened by hunting. Despite unclear taxonomic identification, only the putty-nosed monkey was included as a fully protected species under national legislation. In this work we aimed to elucidate the taxonomic identity of the spot-nosed monkey in the Bijagós Archipelago. We reviewed the information presented in faunistic reports (1939-2004) and other relevant literature. Additionally, we gathered presence data over the last 13 years, and we used DNA barcoding (mitochondrial *cytochrome b* and HVRI) to identify faecal samples to the species level. The review of the faunistic reports suggests both species nomenclatures were used interchangeably in older records and could be linked with the usage of non-native vernacular nomenclature. Local testimonies, observations, and molecular identification confirm that the taxonomic identity of the species is the spot-nosed monkey (*C. petaurista*). Current legislation should be updated to include the species in the fully protected species list. This study highlights the importance of correcting misleading taxonomic information, often perpetuated in national policies, that could lead to decreased legal protection of rare species with high conservation value.

Keywords *Cercopithecus petaurista*, *Cercopithecus nictitans*, Guenons, Non-invasive sampling, DNA barcoding, Bijagós Archipelago.

Introduction

Policy is one of the five categories of conservation actions aimed at reducing the extinction risk of species proposed in the IUCN/CMP Conservation Actions Needed Classification Scheme (IUCN-CMP, 2012). While biodiversity and trade conventions such as CITES protect endangered species against unsustainable exploitation at an international level, national laws and policies allow the establishment of a basal layer of protection and equip local decision makers with the legal basis to act upon the main sources of unsustainable use (IUCN-CMP, 2012). However, the efficiency of species protection legislation depends on how well designed the law itself is in meeting the desired outcome. For example, by using the correct taxonomic identity of the target species (e.g., Gibbs et al., 2011; Gates et al., 2013).

In Guinea-Bissau, West Africa, the taxonomic identity of the spot-nosed monkeys is subject of great controversy in national faunistic inventories and subsequently for national conservation policies. Ten or eleven non-human primates (hereafter primates) have been listed to occur in the country, the number of species depending on if one or two species of spot-nosed monkey are recognised (i.e., *Cercopithecus petaurista* Schreber, 1774, and *Cercopithecus nictitans* Linnaeus, 1766; Gippoliti & Dell'Omo, 2003; Karibuhoye, 2004).

The spot-nosed monkey, *C. petaurista* (Fig. 1), is a quadrupedal frugivorous guenon that lives predominantly in the top layer of the forest canopy (McGraw, 2000). *Cercopithecus petaurista* has been grouped into the superspecies *Cephus* (Grubb, 2003; Guschanski et al., 2013) which includes *Cercopithecus cephus* (Linnaeus, 1758)*, Cercopithecus ascanius* (Audebert, 1799)*, Cercopithecus erythrotis* (Waterhouse, 1838)*, Cercopithecus erythrogaster* (Gray, 1866)*, Cercopithecus sclateri* (Pocock, 1904). *Cercopithecus petaurista* can be distinguished from the other species by a characteristic triangular patch of white hair on its nose and by white hair on its cheek ruffs and underside. The primate's back, flanks and outer upper limb surfaces are covered by golden olive-brown hairs. *Cercopithecus petaurista* is currently divided into two subspecies (Groves, 2001) – the western spot-nosed monkey (*Cercopithecus petaurista buettikoferi* Jentink, 1886), distributed from Guinea-Bissau and eastern Senegal to the Sassandra River in Côte d'Ivoire, and the eastern spot-nosed monkey (*Cercopithecus petaurista petaurista* Jentink, 1886), ranging from the Sassandra River to the western part of Togo (Fig. 1). The range limits of the two subspecies coincide with the Cavally River on the Liberia-Côte d'Ivoire border, although hybrids have been observed further west, between the Cavally and the Nzo River (Oates, 2011).

Another highly arboreal West-African guenon featuring a characteristic patch of white hair on its nose is the putty-nosed monkey, *C. nictitans* (Fig. 1). *Cercopithecus nictitans* has been considered a geospecies (Oates, 2011), including the subspecies *Cercopithecus ninctitans stampflii* (Jentink, 1888), *Cercopithecus nictitans insolitus* (Elliot, 1909), *Cercopithecus nictitans ludio* (Gray, 1849), *Cercopithecus nictitans martini* (Waterhouse, 1838) and *Cercopithecus nictitans nictitans* (Linnaeus, 1766)*,* or alternatively grouped under *C. n. martini* and *C. n. nictitans* (Groves, 2001; Grubb, 2003). *Cercopithecus nictitans* spp. occurs in dry and moist forests as disjunct populations in northern Liberia and Côte d'Ivoire and in a more continuous manner from Osse River in western Nigeria to the northern part of the Congo Basin (Fig. 1). They can also be found on Bioko Island, Equatorial Guinea (Oates, 2011). All the subspecies have a bulbous nose with an oval-shaped patch of white hair (Fig. 1), but in contrast to *C. petaurista*, the crown, shoulders and back are dark grey marked with olive-yellow hairs, and *C. nictitans* does not have fringes of white hair below its ears nor the conspicuous white ruff. *C. nictitans* is larger than *C. petaurista* (weight: 7 kg vs. 4-5 kg. adult males and 4 kg vs. 2.5-3 kg females, respectively, (Oates, 2011). Both species have been recently upgraded to Near Threatened status in the latest IUCN assessment due to the ever-increasing impact of hunting and habitat loss throughout their geographic ranges (Cronin et al., 2020; Matsuda Goodwin et al., 2020).

Primates in Guinea-Bissau are generally threatened by habitat loss and bushmeat hunting (Casanova & Sousa, 2007; Minhós et al., 2016, 2023; Ferreira da Silva et al., 2018). Primates are hunted in large numbers (Minhós et al., 2013) and traded in urban bushmeat markets and at bars/restaurants as a snack between alcoholic drinks (Ferreira da Silva et al. 2021b). Furthermore, there are important gaps in the published literature on the taxonomic identity, distribution, and conservation status for most species, which can severely hinder conservation management by international and local authorities. This is particularly the case for forest-dwelling, elusive, small-bodied primate species, which are not considered a focus for global conservation efforts and consequently for research in conservation biology (cf. Ferreira da Silva et al., 2020). The conservation of the spot-nosed monkey in the country is thought to be particularly dire. The last extant populations are thought to be restricted to islands in the Bijagós Archipelago. Based on the latest regional surveys and narratives of local inhabitants, the species is currently very rare or even extinct from areas in mainland where it had been previously reported (Cufada Lagoon Natural Park, Colmonero-Costeira 2023; Dulombi National Park, Bersacola et al., 2018). Regardless of the recognised need for conservation, the taxonomic identity of the primate remains unclear (Gippoliti & Dell'Omo, 2003). Despite the controversy, only *C. nictitans* has been included in the national list of fully protected species (i.e., species which are illegal to hunt under any circumstances, Decree-law No.21/1980 approving the Hunting Regulation).

This study aims to gather information on the spot-nosed monkey to allow national organizations to update and improve conservation policies and action plans. Specifically, we aimed to 1) review contemporary historical literature regarding the presence and taxonomic identity of the spot-nosed monkey in Guinea-Bissau; 2) elucidate the taxonomic identity of the spot-nosed monkey using testimonies of local inhabitants, observations recorded over the last 13 years, and molecular identification of non-invasive faecal samples collected at the Bijagós Archipelago using DNA barcoding tools.

Study Site

Guinea-Bissau is a small West African country (36,125 km^2) composed of a continental area and the Bijagós Archipelago, comprising approximately 88 islands (Rebelo & Catry, 2011). The islands are located a few kilometres away from the mainland and the vegetation types replicate the ones found in mainland coastal areas (e.g., mangrove forests, palm groves and woodland savannah and small areas of sub-humid forests resembling forest patches at Cufada Lagoons National Park; (Catarino et al., 2008). In 1996, UNESCO recognised the bio-cultural diversity of the Bijagós Archipelago, establishing the Biosphere Reserve of Archipelago Bolama-Bijagós

(ABBBR). Two national parks (Orango Islands National Park – ONP – and João Vieira e Poilão Marine National Park – JVPMNP) and a marine protected area (Urok Islands Communitarian Marine Protected Area – UCMPA) are formally recognized in the Archipelago (Fig. 1). On mainland Guinea-Bissau, five protected areas have been delimited (Fig. 1).

Methods

Historical recount of the taxonomy of the spot-nosed monkey in Guinea-Bissau

Published literature on the spot-nosed monkey in Guinea-Bissau is virtually non-existent (cf. Colmonero-Costeira et al., 2019). As such, we conducted a grey literature review to establish a timeline of changes of the spot-nosed monkey's taxonomy in the country. We searched for any past records of spot-nosed monkeys in Guinea-Bissau such as reports of zoological missions to the country, and post-graduate dissertations (master and doctoral theses) and other literature in our personal collections that mentioned the spot-nosed monkey . We focused on contemporary reports from 20th-21st century as these are the reports that were most likely used as a scientific basis for the redaction of contemporary law decrees on hunting regulation in Guinea-Bissau. The collections of historical reports to be consulted were based on advice from experts in the field of historical literature collections related to primates in Europe and African countries, African Portuguese-speaking countries included.

Additionally, we expanded our search to the National Library of Portugal to include anthropological records on the *Bijagó* ethnic group where possible mentions of the primates and their characteristics were made. Here, we searched for the key words '*Bijagó**' and 'Arquipélago dos Bijagós'. Search results were appraised initially by subject followed by an appraisal of the index. Non-written materials were excluded. Index entries regarding the socio-cultural uses of mammals, *Bijagó* art, artefacts and ceremonies were read in full. We conduced our literature search at the National Library of Portugal from 26th to 30th of July 2021.

Assessment of taxonomic identity and species occurrence

Our expeditions took place on the largest islands of the Bijagós Archipelago with suspected occurrence of the spot-nosed monkey *sensus lato* over a time span of thirteen years (2010-2023): Canhabaque (2010, 2013, 2016, 2022), Caravela, Uno, Uracane, Galinhas (2016), Bubaque, Rubane (2022, 2023).

To collect presence data (visual and/or derived from molecular data, see below) we initially identified the areas frequently used by primates (e.g., sleeping, and foraging sites) with the help of chieftains, local guides and villagers from villages located in proximity to forest fragments. Pinpointed locations were visited to collect geo-referenced presence records (visuals, footprints, vocalizations) and faecal samples for DNA extraction and analysis. We remained at each of the locations for at least 30 minutes. When observed, individuals were identified based on morphological characteristics portrayed in the Kingdon pocket guide to African mammals (Kingdon, 2005). Additionally, during the last survey (ICC, 2022) we asked local chieftains and other knowledgeable inhabitants (e.g., hunters) to identify the species of primates living in proximity to the villages using the same field guide.

Faecal samples were preserved until DNA extraction using one of the following methods: immersion in RNAlaterTM (InvitrogenTM, USA), 99% ethanol (Sigma-Aldrich, USA), DMSO, or the “two- step” in 99% ethanol and silica protocol (Roeder et al., 2004). Tissue/blood samples were collected opportunistically whenever carcasses were found in the local villages. These were preserved in 99% ethanol (Sigma-Aldrich, USA). All samples were stored at room temperature until DNA extraction. All molecular methods concerning faecal samples were conducted in dedicated non-invasive facilities. Faecal DNA was extracted using the Qiagen Stool Kit® (Qiagen, Germany) with some modifications to the manufacturer’s protocol (Ferreira da Silva et al., 2014). The DNA from blood and tissue samples was extracted using DNeasy Blood & Tissue Kit (Qiagen, Germany) following the manufacturer’s protocol.

Molecular species identification was obtained following a DNA barcoding approach. We amplified either a 402 bp fragment of the mitochondrial *cytochrome b* gene (*cytb*) or a 387 bp fragment of the mitochondrial hypervariable region I (HVRI) by polymerase chain reaction (PCR). The usage of the *cytb* gene in DNA barcoding has the advantage of being highly represented in reference databases (e.g., GenBank:

https://www.ncbi.nlm.nih.gov/genbank/) with many African mammal species having one or more reference sequences (Gaubert et al., 2015). To obtain a geographically representative molecular identification of the spot-nosed monkey occurring across multiple islands of Bijagós Archipelago, the bulk of our DNA samples were assigned to the species level using the HVRI fragment. This allowed to include previously generated mtDNA data for the species (Thomas, 2011; Colmonero-Costeira et al., 2019). We produced reference HVRI sequences by co-amplifying a subset of the samples for both *cytb* and HVRI mtDNA regions. This step was needed as many guenon species such as the spot-nosed monkey are lacking reference HVRI sequences in the GenBank database. The *cytb* fragments were amplified using the primer pairs GVL14724, 5’ GATATGAAAAACCATCGTTG 3’, and GVH15149 5’ CTCAGAATGATATTTGTCCTCA 3’ (Gaubert et al., 2015). HVRI fragments were amplified using LCERCOHVRI, 5’ CGTGCATTACTGCTAGCCAAC 3’ and HCERCOHVRI 5’ GGGATATTGATTTCACGGAGGA 3’ (Colmonero-Costeira et al., 2019), respectively. The PCR reactions were conducted in a total volume of 10 µL containing 1X MyTaq^{TM} Mix (Bioline, UK), 0.2 µM of forward and reverse primer, 1-2 µL of DNA extract and molecular grade water ensure a final volume of 10 µL. We used a T100TM 96 Well Thermal Cycler (Bio-Rad, USA) for the PCRs. We followed the cycling conditions by Gaubert et al. (2015) for *cytb* amplification. The HVRI cycling conditions started with a Taq activation step at 95ºC for 15 minutes, followed by 40 cycles of denaturing step at 94ºC for 30 seconds, annealing at 58ºC for 30 seconds and extension at 72ºC for 30 seconds. The final cycling step corresponded to a final extension at 72ºC for 15 minutes. The PCR amplifications were tested in 2% agarose gels stained with GelRedTM (Biotium, USA) at 300V and visualised with a Gel DocTM XR+ Gel Documentation System (Bio-Rad, USA). Positive amplifications were purified by 1 µL (1/4 ratio) of Exonuclease I (20 UµL-1) and FastAP (1 UµL-1) (Thermo Fisher ScientificTM, USA), following the manufacturer’s protocol. Fragments were sequenced uni or bi-directionally on a 3130XL automated sequencer (Applied BiosystemsTM, USA) using the BigDyeTM Terminator v3.1 Cycle Sequencing Kit (Applied BiosystemsTM, USA). Sequences were manually corrected using Geneious Prime v2022.2 (Biomatters). We aligned the mtDNA fragments using Geneious in-built automatic alignment algorithm. All sequences were trimmed to the size of the shortest sequence. Bad quality sequences were removed. Several post-sequencing procedures to avoid for the inclusion of ghost mitochondrial haplotypes with nuclear origin (NumtS) were employed: nucleotide positions containing double electrophoretic peaks were coded as missing data regardless of the over-representation of a specific nucleotide over the other; we translated the *cytb* sequences to screen for the presence of erroneous STOP codons (Haran et al., 2015). The genetic data was produced in 2021.

To disentangle between *C. petaurista* and *C. nictians,* we submitted the sequenced *cytb* fragments to BLAST (Basic Local Alignment Search Tool) on the NCBI database (https://blast.ncbi.nlm.nih.gov). Additionally, we retrieved *cytb* sequences from both species deposited on GenBank (https://www.ncbi.nlm.nih.gov/genbank/). *Cytochrome b* sequences from Guinean baboons (*Papio papio*) were included in the alignment as an outgroup. The phylogenetic relationships between sampled and reference haplotypes were inferred using maximum likelihood (ML), as implemented in IQ-TREE web server (http://iqtree.cibiv.univie.ac.at; Nguyen et al., 2015; Trifinopoulos et al., 2016). We identified the best-fit model of molecular evolution using ModelFinder implemented in IQ-TREE (Kalyaanamoorthy et al., 2017). Model choice was based on BIC. The statistical significance was estimated with the Shimodaira-Hasegawa approximate likelihood ration test (SH-aLRT; Guindon et al., 2010) and 9,999 ultrafast bootstrap (UFBoot) replicates (Hoang et al., 2018). To evaluate if the sampled HVRI haplotypes belonged to the same taxonomic unit as the reference sequences, we used the assemble species by automatic partitioning (ASAP; Puillandre et al., 2021) species delimitation method. Compared to other species delimitation methods ASAP is based solely on genetic distances, making it appropriate when a priori knowledge on the putative number of species sampled or species identity is scarce (Puillandre et al., 2021). ASAP analysis was run on ASAPweb server (https://bioinfo.mnhn.fr/abi/public/asap) using Kimura K2P model of molecular evolution and remaining parameters set to default. Delimitation results were evaluated based on asap-scores, and partition and group p-values.

Results

Historical recount of the taxonomy of the spot-nosed monkey in Guinea-Bissau

We were able to establish a timeline of changes in the taxonomy of the spot-nosed monkey using five reports of faunistic surveys conducted in Guinea-Bissau during the mid to late 20th century. Our grey literature search at the National Library of Portugal retrieved 20 works out of which, eight were excluded based on subject (e.g., health, education), four were excluded based on the index. We read selected sections of the eight-remaining works in full. Two works mentioned the spot-nosed monkey. We included one research paper and one PhD thesis from our personal collections (Supplementary Material 1).

The oldest record found was the report by Monard (1939) who acknowledged the rumoured existence of a form of *Cercopithecus nictitans* (Linnaeus, 1766) in the *Bijagó* Archipelago (pg. 137). The monkey is referred by the author as *petit singe à nez blanc* in French. The authors were unable to survey the archipelago. Thus, Monard (1939) reports the occurrence of the species as unconfirmed hearsay. Frade and collaborators (1946) reported a species named *macaco Bijagó* in Portuguese, classified as *Cercopithecus nictitans petaurista* (Schreber). The primate was described as “a monkey that exists in the Rubane Island and not in the Bubaque Island” (Frade et al., 1946, pg. 351). Chardonnet (1983) reported the first visual observations of spot-nosed monkeys on mainland Guinea-Bissau in the areas surrounding the Corubal River in the Dulombi region (pg. 98). The author named the primate in French as *petauriste butikogei* and classified the species as *Cercopithecus petaurista bultikogei* (Schreber). Later, Limoges (1989) carried out a country-wide faunal inventory to determine species presence and their distribution areas. The author mentioned two distinct species of spot-nosed monkey on mainland Guinea-Bissau – *Cercopithecus nictitans stampflii* (Jentink, 1888) and *Cercopithecus petaurista petaurista* (Schreber, 1774). The photographs of the individuals observed during the expedition are not presented and the morphological features used to identify and distinguish between the two species are not clearly stated. Nevertheless, the authors stated to have followed the Collins field guide to the mammals of Africa (Haltenorth & Diller, 1985). *Cercopithecus nictitans stampflii* is named as *le hocheur* or *pain à cacheter* in French, *Cercopiteco maior* in Portuguese and *macaco-Bijagó* or *nariz branco* in Creole (Limoges, 1989, pg. 18). The author reported that two social groups of six individuals each were observed "in palm tree groves in the Cufada area" (Limoges, 1989, pg. 106, Table III). Limoges (1989) added that *C. n. stampflii* was the species previously described to occur in the Bijagós Archipelago only and that this record in Cufada could be the result of a recent range expansion from the closely located islands (pg. 18). Regarding *C. p. petaurista*, the authors acknowledge the existence of the species in mainland Guinea-Bissau based on the reports by Chardonnet (1983). However, its presence was not confirmed during transects in the Dulombi region, despite the high sampling effort (Limoges, 1989). Thibault (1993) carried out another faunistic survey in areas which are now part of the Dulombi National Park and described two species of spot-nosed monkey. However, the nomenclature used was different from that of Limoges (1989). *Cercopithecus petaurista petaurista* (Schreber, 1774) – which was named by the author as *hocheur à nez blanc* in French, *cercopiteco menor* in Portuguese, *nariz branco* in Creole and *pakonru* in Fula-Futa, and *C. n. stampflii* (Jentink, 1888), named as *hocheur* in French, *cercopiteco maior* in Portuguese, *macaco Bijagó* in Creole and *tsalacuru* in Fula-Futa.

More recently, Gippoliti and Dell'Omo (2003) carried out a primate-dedicated country-wide survey. The authors discarded the hypothesis that *C. nictitans* would be present in Guinea-Bissau. They observed spot-nosed monkeys, identified as *C. p. buettikoferi* (Jentink, 1886) on Rubane and Caravela Islands; in the latter, the species was feeding on tall trees over groups of *Cercopithecus campbelli,* Waterhouse, 1838 (Gippoliti & Dell'Omo, 2003). At that time, the species was thought to be present on the Rubane, Canhabaque, Caravela, Galinhas, Uno and Uracane Islands and on the mainland in Cufada Lagoons NP and the Dulombi NP (Gippoliti & Dell'Omo, 2003) but not in Cantanhez Forest NP (Gippoliti & Dell'Omo, 1996). Karibuhoye (2004) compiled information on diversity and threats faced by Guinea-Bissau's mammals. She acknowledged *Cercopithecus nictitans* (Linnaeus, 1766) as part of the national list of primates based on the record by Crawford Cabral (1997) and Limoges (1989). Nevertheless, Karibuhoye (2004) made the remark that occurrence of *C. nictitans* in Guinea-Bissau is doubtful. On the other hand, the authors presented visual evidence of the occurrence of *Cercopithecus petaurista* (Schreber, 1774) in Canhabaque Island, Bijagós Archipelago.

We found two mentions of primates in ethnographic literature on the Bijagós Archipelago. Primates were associated with spiritual and cultural traditions either by being represented in dances or decorations of the *balobas*, the local ceremonial venues (Scantamburlo, 1991). We found references to the spot-nosed monkey as part of the oral tradition of the *Bijagó* of Uno Island (Paiva, 1990). According to the legend, a small monkey with a characteristic white spot on its nose was said to have been the first player of the *bombolom*, a local percussion instrument fundamental to several local ceremonies (Paiva, 1990). No details were given on the taxonomic identity of the primates. Additionally, other visual/morphological details that could be used to identify the primate taxonomically or the morphological features of the primates depicted were not present apart from the white spot on the primate's nose.

Taxonomic identity

We visually identified spot-nosed monkeys eleven times between 2010-2022 – two observations in Caravela, one in Uno, one in Bubaque, three in Rubane, and four in Canhabaque (Supplementary Fig. 1). Additionally, we photographed one recently hunted individual and one infant being kept as a pet at Canhabaque (Fig. 2). We visually classified the primates as spot-nosed monkeys (*Cercopithecus petaurista* Schreber, 1774). At Canhabaque, local inhabitants coherently identified the occurring primate as spot-nosed monkey rather than the putty-nosed monkey. Inhabitants from Bubaque Island stated that the spot-nosed monkey occurred in both Bubaque and nearby Rubane Island.

We molecularly identified three tissue samples, one blood and eight faecal samples as spot-nosed monkey using *cytb*-based DNA barcoding. After aligning and trimming to the shortest sequence, sequence length was of 385 bp. Only one haplotype was found (GB Hap1). When processed through NCBI's BLAST tool, we found that the GB Hap1 had a high percentage of identity to GenBank sequence vouchers JQ256982 (*C. p. buettikoferi*; 99.48% identity), JQ256983 (*C. p. petaurista*; 99.22% identity) and JQ25693 (*C. p. petaurista*; 98.18% identity). Based on BIC, the model of molecular evolution TN+I with empirical base frequencies was selected for the phylogenetic tree reconstructed based on the 385 bp fragments of the *cytb* gene. The GB Hap1 was sorted into the *Cercopithecus petaurista* spp. clade rather than the *Cercopithecus* *nictitans* spp. clade (Fig. 2). However, phylogeny within the *C. p.* spp clade was highly unresolved with no clear divergence between both subspecies (Fig. 2).

Using HVRI, we identified a total of 134 faecal samples as spot-nosed monkey (49 this study, 39 from Colmonero-Costeira and collaborators (2019), and 46 from Thomas (2011); Fig. 3). The identified faecal samples were collected at 25 geographically independent locations (distanced ≥ 1 km) that likely represent different ranging primate groups (average 5.36 samples per independent location) – two in Caravela, five in Uno, three in Uracane, 11 in Canhabaque and four in Galinhas (Supplementary Fig. 1). After alignment, trimming and removal of low-quality sequences, the final sequence alignment length was of 290 bp. We found 28 different haplotypes with a total of 52 polymorphic sites. Species delimitation analysis using ASAP suggested that the single-species hypothesis was not rejected for any of the proposed lineage partitionings ($p = 0.83$).

Discussion

In this study, we established a timeline of changes in the taxonomical classification of the spot-nosed monkey. To clarify taxonomic incongruencies, we compiled a comprehensible amount of visual and molecular information on the taxonomic identity of Guinea-Bissau's spot-nosed monkey that could potentially lead to the strengthening of the local protection of the primate through local policy making.

The faunistic surveys conducted in the country during the 20th century are inconsistent regarding the occurrence of two species of spot-nosed monkey. We found that between 1939 and 1989, nomenclatures for the putty-nosed monkey (*C. nictitans*) and the spot-nosed monkey (*C. petaurista*) were used interchangeably to describe the primates found in either the Bijagós Archipelago and mainland Guinea-Bissau (Cufada and Dulombi regions). Furthermore, the scientific nomenclatures used to designate the spot-nosed monkey contained specific epithets that were used to distinguish between the two forms in another point in time (e.g., *Cercopithecus nictitans petaurista* in Frade, 1946, and *Cercopithecus nictitans stampflii* and *Cercopithecus petaurista petaurista* in Limoges, 1989).

Through the contradictory reports on the two forms of spot-nosed monkeys we can summarise that 1) the authors designate spot-nosed monkey using vernacular names in non-native languages (Portuguese and French); 2) these vernacular names converge mainly into two names whose tentative English translations would be “white-nosed monkey” and “shaking monkey” regardless of chosen scientific nomenclature (Supplementary Table 1); 3) documents lacked detailed morphological descriptions of the observed specimens. In some of these reports, records were based on dubious depictions of the species. For example, Limoges (1989) used the Haltenorth and Dillier (1985) mammals of Africa field guide to train the survey teams who claimed to have observed both *C. nictitans* and *C. petaurista*. However, the set of images presented in Limoges (1989)’s methodology section of the report used to identify the spot-nosed (*C. petaurista*) lack key diagnostic features of the primate or are wrongly depicted (e.g., facial mask and the white cheek ruffs).

A credible identification of the species could not be based in the ethnographic studies on the livelihood and belief systems of the local ethnic group since the revision of these works did not provide detailed morphological features of the primates inhabiting the Bijagós Archipelago. However, the spot-nosed monkey is part of the socio-cultural repertoire of the *Bijagó* ethnic group, to which most of the local communities inhabiting the archipelago belong to.

The visual observations of both live and hunted specimens suggest that one single species of spot-nosed monkey – the spot-nosed monkey – occurs on the islands. Moreover, using DNA barcoding tools, we provided molecular evidence that the most likely taxonomic identity of the spot-nosed monkey in the Bijagós Archipelago, Guinea-Bissau is the spot-nosed monkey (*C. petaurista* Schreber, 1774*)*. *Cytochrome b* sequences showed a high percentage of identity with GenBank vouchers identified as *C. petaurista* spp. and were phylogenetically closer to *C. petaurista* spp. than to *C. nictitans* spp.. By co-amplifying a subset of samples for both *cytb* and HVRI mitochondrial regions we guaranteed the crossover between *C. petaurista* spp. *cytb* sequences and the three HVRI databases here conjoint (Thomas, 2011; Colmonero-Costeira et al., 2019; this study). The species partitioning analysis conducted on the HVRI haplotypes sampled across the different islands suggests that all samples analysed are from a single taxonomic unit (Puillandre et al., 2021). Taken together, our results suggest that the presence of the putty-nosed monkey in the Bijagós Archipelago is unlikely, as suggested by the more recent surveys in the region (Gippoliti & Dell'Omo, 2003; Karibuhoye, 2004). The most north-western populations of this species can be found in northern Liberia and Ivory Coast, where the distribution is patchy (Oates, 2011). Although unlikely, it could still be argued that the species that was last observed in mainland Guinea-Bissau 30 – 40 years ago (Chardonnet, 1983; Limoges, 1989; Thibault, 1993) was the putty-nosed monkey because the range of this species could have been wider than the currently described distribution and relict populations exist in north-western African forests, namely in Guinea-Bissau mainland, for which our work gives no input (cf. Gippoliti & Dell'Omo, 2003).

In Guinea-Bissau, formal protection against hunting is established in two forms – the delimitation of protected areas, where commercial hunting is forbidden (Decree-law No.3/1997, Decree-law No.5-A/2011), and law regulating hunting practices (Decree-law No.21/1980, Decree-law No.2/2004), which limits hunting of highly threatened taxa across the country. The primates mentioned in national decree-laws that specifically assures total protection against commercial hunting (Decree-law No.21/1980 approving the Hunting Regulation) are the western chimpanzee (*Pan troglodytes verus*, Schwarz, 1934), the black-and-white colobus (*Colobus polykomos*, Zimmermann, 1780) and the putty-nosed monkey (*C. nictitans* Linnaeus). The exclusion of the spot-nosed monkey from the Decree-law No.21/1980 list of integrally protected species is probably a consequence of the incongruent nomenclature employed to designate both spot-nosed monkey species in the previous faunistic surveys.

The available information on taxonomy and distribution is also likely to be outdated or incorrect for most mammals in Guinea-Bissau. Destruction of infrastructure over the last fifty years has led to a discontinuity of research and scientific data and resources to be spread across reports and grey literature in national and international repositories and libraries. Similar incongruencies in the taxonomy and occurrence were found for other primates. For instance, the sooty mangabey (*Cercocebus atys* Audebert, 1797) was considered extinct in the country since the 1980's but its presence and range was recently confirmed through a combination of geo-referenced visual records and non-invasive DNA barcoding (Ferreira da Silva et al., 2020).

Additionally, the occurrence of two species of baboons (*Papio papio* Desmarest, 1820, and *Papio anubis* Lesson, 1827) is frequently claimed (e.g., Bout & Ghiurghi, 2013) but only one species was confirmed in a regional molecular-based survey (Ferreira da Silva et al., 2014). Therefore, updating the list of primates present in National Parks in Guinea-Bissau should be considered a priority and subject of systematic research since it is basal to any measure of protection in the National Action plan. The use of interdisciplinary methodologies, such as in this work, is proving adequate for cases in countries in which scientific data is not centralized or available in digital repositories.

Implications for the conservation of the spot-nosed monkey in Guinea-Bissau

The 12 years of visual and molecular occurrence data confirms the presence of the spot-nosed monkey in Caravela, Uno, Uracane, Canhabaque, Bubaque and Galinhas, Rubane, and Bubaque Islands, and is concordant to the occurrence estimates suggested in previous studies (Reiner & Simões, 1999; da Silva, 2001; Gippoliti & Dell'Omo, 2003; Colmonero-Costeira et al., 2019; Supplementary Fig. 1). Overall, this work suggests that the confirmed area of distribution of the spot-nosed monkey in Guinea-Bissau is the insular territories with an area amounting to less than 500 km^2, and currently is not included in any of the archipelago's protected areas nor is it on the list of integrally protected species as declared in Decree-law No.21/1980. As such, the primate is not under formal protection against over-exploitation in Guinea-Bissau. The spot-nosed monkey has been overlooked by conservationists and researchers, mainly due to its large occurrence range and apparent high behavioural resilience to habitat disturbance. However, the species is increasingly rare in the Bijagós Archipelago due to possibly unsustainable hunting (Colmonero-Costeira, 2019). This work does not suggest the exclusion of the putty-nosed monkey from the list of formally protected primates until its presence on mainland Guinea-Bissau is further investigated but highlights the need to urgently review the list of formally protected species in Guinea-Bissau and the inclusion of the spot-nosed monkey.

Further work should assess the long-term viability of the insular *C. petaurista* populations using population genetic health indicators (e.g., genetic diversity, population substructure and demographic trends), as well as the investigating the sustainability of current hunting rates.

Author contributions Conceptualization: Maria Joana Ferreira da Silva, Rui Sá, Michael William Bruford; Data collection logistics: Maria Joana Ferreira da Silva, Rui Sá, Ivo Colmonero-Costeira; Historical species accounts data collection: Ivo Colmonero-Costeira, Maria Joana Ferreira da Silva, Cecilia Veracini, Susana Costa; Molecular data production and analysis: Ivo Colmonero-Costeira, Nia Evelyn Thomas; Writing - original draft preparation: Ivo Colmonero-Costeira, Maria Joana Ferreira da Silva; Writing - review and editing: Nia Evelyn Thomas, Isa-Rita Maria Russo, Tânia Minhós, Susana Costa, Rui Sá, Cecília Veracini; Funding acquisition: Maria Joana Ferreira da Silva, Tânia Minhós, Ivo Colmonero-Costeira, Rui Sá; Supervision: Maria Joana Ferreira da Silva, Susana Costa, Michael William Bruford, Isa-Rita Maria Russo, Cecilia Veracini, Tânia Minhós, Rui Sá.

Acknowledgments We are grateful to the field guides of the *Bijagó* community that facilitated the execution of this work. We thank the Guinea-Bissau governmental agency Instituto de Biodiversidade e Áreas Protegidas (IBAP) for permits and logistical support during fieldwork to I. Espinosa and H. Foito for logistical support in Bissau.

Funding This work was supported by Portuguese national funds through FCT - *Fundação para a Ciência e a Tecnologia,* under project PRIMATOMICS (PTDC/IVC-ANT/3058/2014) and was carried out under the scope of project PRIMACTION, funded by the Born Free Foundation, Chester Zoo Conservation Fund, Primate Conservation Incorporated, CAROSI, Cápsulas do Norte, Camarc, JA-Rolhas e Cápsulas. The fieldwork season of 2022 was supported by Primate Conservation Incorporated, USA (PCI# 1694), the Genetics Society, UK and the project NORTE- 01-0145-FEDER-000046 supported by Norte Portugal Regional Operational Programme (NORTE2020), under the PORTUGAL 2020 Partnership Agreement, through the

European Regional Development Fund (ERDF). ICC was supported by FCT doctoral fellowship (SFRH/BD/146509/2019) and MJFS worked under a FCT contract (CEECIND/01937/2017). The authors have no competing interests to declare that are relevant to the content of this article.

Ethical Standards Biological data collection was conducted non-invasively to minimize ethical concerns of research with primates. All tissue samples were collected opportunistically from carcasses hunted by the local inhabitants for their personal use. All the work carried out in Guinea-Bissau was approved by a governmental agency (IBAP). We informed local communities on our research aims and requested consent to conduct and publish our data from local chieftains. The enquiries to local inhabitants regarding the species identity of primates occurring in the vicinities of the villages received ethical approval from Cardiff University, UK, BIOSI SREC (ref: BIOSI SREC 22 11-01). Exportation and importation of tissue samples was authorised by the Guinea-Bissau and Portuguese CITES authorities, respectively (ref: Nº062/DGFF/2018). The exact locations of the sampled primate groups are not presented as a precaution against exploitation but can be requested to the corresponding author.

Nucleotide sequence data Sequence data newly produced in this manuscript and sequences from Colmonero-Costeira et al., (2019) and Thomas (2011) have been deposited in GeneBank https://www.ncbi.nlm.nih.gov/genbank/), accession numbers XXXX – XXXX.

References

Bersacola, E., Bessa, J., Frazão-Moreira, A., Biro, D., Sousa, C. & Hockings, K.J. (2018) Primate occurrence across a human-impacted landscape in Guinea-Bissau and neighbouring regions in West Africa: using a systematic literature review to highlight the next conservation steps. *PeerJ*, 6, e4847.

Bout, N. & Ghiurghi, A. (2013) *Guide des mammiferes du Parc National de Cantanhez, Guinée-Bissau*. Acção para o Desenvolvimento & Associazione Interpreti Naturalistici ONLUS, Rome, Italy.

Campredon, P., Cuq, F., Giraudet, E., Giraudet, J., Goulemon, F., Pennober, G. & Silva, A.S. da (2001) *Un Système d'Ínformation Géographique pour l'áide à la gestion intégrée de l'árchipel des Bijagos (Guinée-Bissau). Notice de la carte, constitution et exploitation du SIG*. Géosystèmes-CNRS, Plouzané, France.

Casanova, C. & Sousa, C. (2007) *Action Plan for the Conservation of Chimpanzees, red western colobus and king colobus in Guinea-Bissau Republic*. IBAP, Guinea-Bissau.

Catarino, L., Martins, E.S., Basto, M.F.P. & Diniz, M.A. (2008) An Annotated Checklist of the Vascular Flora of Guinea-Bissau (West Africa). *Blumea - Biodiversity, Evolution and Biogeography of Plants*, 53, 1–222.

Chardonnet, B. (1983) *Gestion de la faune sauvage Africaine Proposition d'un project en Guinee-Bissau*. PhD thesis, Faculte de Medicine de Créteil, Créteil, France.

Colmonero-Costeira, I. (2019) *Insights into insular primates: conservation genetics of Cercopithecus petaurista buettikoferi, Cercopithecus campbelli and Chlorocebus sabaeus in the Bijagós Archipelago, Guinea-Bissau*. MSc thesis, Universidade do Minho, Braga, Portugal.

Colmonero-Costeira, I., Minhós, T., Djaló, B., Fernandes, N. & Ferreira da Silva, M. (2019) Confirmação da ocorrência de primatas não-humanos no Arquipélago dos Bijagós com base em técnicas de identificação molecular. *Sintidus*, 2, 145–179.

Cronin, D.T., Maisels, F., Gadsby, E.L., Gonedelé Bi, S., Ikemeh, R. & Imong, I. (2020) *Cercopithecus nictitans*. In *The IUCN Red List of Threatened Species* 2020. dx.doi.org/10.2305/IUCN.UK.2020-1.RLTS.T4224A222904443.en.

Direção-Geral da Função Pública (1990) *Decree-law No.21/1980*, Bissau, Guinea-Bissau.

Direção-Geral da Função Pública (1997) *Decree-law No.3/1997*, Bissau, Guinea-Bissau.

Direção-Geral da Função Pública (2004) *Decree-law No.2/2004*, Bissau, Guinea-Bissau.

Direção-Geral da Função Pública (2011) *Decree-law No.5-A/2011*, Bissau, Guinea-Bissau.

Ferreira da Silva, M.J. (2016) *Protecting the Western Chimpanzee and threatened primates from logging and illegal hunting in Guinea-Bissau: Eighteen months progress report*. Unpublished report. CIBIO, Vairão, Portugal.

Ferreira da Silva, M.J., Camará, M., Egeter, B., Minhós, T., Bruford, M.W., Godinho, R. (2021) Using meta-barcoding tools to monitor primate meat consumption at dedicated establishments in Guinea-Bissau, West Africa. *ARPHA Conference Abstracts*, 4, e65575.

Ferreira da Silva, M.J., Godinho, R., Casanova, C., Minhós, T., Sá, R. & Bruford, M.W. (2014) Assessing the impact of hunting pressure on population structure of Guinea baboons (Papio papio) in Guinea-Bissau. *Conservation Genetics*, 15, 1339–1355. Springer Netherlands.

Ferreira da Silva, M.J., Kopp, G.H., Casanova, C., Godinho, R., Minhós, T., Sá, R., et al. (2018) Disrupted dispersal and its genetic consequences: Comparing protected and threatened baboon populations (Papio papio) in West Africa. *PLoS ONE*, 13, e0194189.

Ferreira da Silva, M.J., Paddock, C., Gerini, F., Borges, F., Aleixo-Pais, I., Costa, M., et al. (2020) Chasing a ghost: notes on the present distribution and conservation of the sooty mangabey (Cercocebus atys) in Guinea-Bissau, West Africa. *Primates*, 61, 357–363.

Frade, F., Bacelar, A. & Gonçalves, B. (1946) *Trabalhos da Missão Zoológica da Guiné: Relatório da missão zoológica e contribuições para o conhecimento da fauna da Guiné Portuguesa*. Junta de Investigações do Ultramar, Lisbon, Portugal.

Gates, K.K., Kerans, B.L., Keebaugh, J.L., Kalinowski, S. & Vu, N. (2013) Taxonomic identity of the endangered Snake River physa, Physa natricina (Pulmonata: Physidae) combining traditional and molecular techniques. *Conservation Genetics*, 14, 159–169.

Gaubert, P., Njiokou, F., Olayemi, A., Pagani, P., Dufour, S., Danquah, E., et al. (2015) Bushmeat genetics: Setting up a reference framework for the DNA typing of African forest bushmeat. *Molecular Ecology Resources*, 15, 633–651.

Gibbs, H.L., Murphy, M. & Chiucchi, J.E. (2011) Genetic identity of endangered massasauga rattlesnakes (Sistrurus sp.) in Missouri. *Conservation Genetics*, 12, 433–439.

Gippoliti, S. & Dell'Omo, G. (1996) Primates of the Cantanhez Forest and the Cacine Basin, Guinea-Bissau. *Oryx*, 30, 74–80.

Gippoliti, S. & Dell'Omo, G. (2003) Primates of Guinea-Bissau, West Africa: distribution and conservation status. *Primate Conservation*, 19, 73–77.

Groves, C.P. (2001) *Primate Taxonomy*. Smithsonian Institution Press, Washington, D.C., USA.

Grubb (2003) Assessment of the Diversity of African Primates. *International Journal of Primates*, 24, 1301–1357.

Guindon, S., Dufayard, J.F., Lefort, V., Anisimova, M., Hordijk, W. & Gascuel, O. (2010) New algorithms and methods to estimate maximum-likelihood phylogenies: Assessing the performance of PhyML 3.0. *Systematic Biology*, 59, 307–321.

Guschanski, K., Krause, J., Sawyer, S., Valente, L.M., Bailey, S., Finstermeier, K., et al. (2013) Next-generation museomics disentangles one of the largest primate radiations. *Systematic Biology*, 62, 539–554.

Haltenorth, T. & Diller, H. (1985) *Collins Field Guide to the Mammals of Africa including Madagascar*. William Collins Sons & Co Ltd., London, UK.

Haran, J., Koutroumpa, F., Magnoux, E., Roques, A. & Roux, G. (2015) Ghost mtDNA haplotypes generated by fortuitous NUMTs can deeply disturb infra-specific genetic diversity and phylogeographic pattern. *Journal of Zoological Systematics and Evolutionary Research*, 53, 109–115.

Hoang, D.T., Chernomor, O., Von Haeseler, A., Minh, B.Q. & Vinh, L.S. (2018) UFBoot2: Improving the ultrafast bootstrap approximation. *Molecular Biology and Evolution*, 35, 518–522.

IBAP (2022) *Áreas Protegidas.* ibapgbissau.org/index.php/areas-protegidas [accessed 25 November 2022].

IUCN-CMP (2012) *Conservation Actions Classification Scheme (Version 2.0)*. iucnredlist.org/resources/conservation-actions-classification-scheme [accessed 17 February 2023].

IUCN (2022) *The IUCN Red List of Threatened Species* 2022. iucnredlist.org [accessed 23 November 2022].

Kalyaanamoorthy, S., Minh, B.Q., Wong, T.K.F., Von Haeseler, A. & Jermiin, L.S. (2017) ModelFinder: Fast model selection for accurate phylogenetic estimates. *Nature Methods*, 14, 587–589.

Karibuhoye, C. (2004) *Mammal Conservation status and Prospects for community-based wildlife management in coastal Guinea-Bissau, West Africa*. PhD thesis, Georg-August-Universität Göttingen, Gottingen, Germany.

Kingdon, J. (2005) *The Kingdon pocket guide to African mammals*. Princeton University Press, Princeton, N.J., U.S.A.

Limoges, B. (1989) *Résultats de l'inventaire faunique au niveau national et propositions de modifications à la loi sur la chasse*. Ministério do Desenvolvimento Rural e da Agricultura, Bissau, Guinea-Bissau.

Matsuda Goodwin, R., Segniagbeto, G., Waife, E., Osei, D., Koné, I., Gonedeé, B. & Oates, J.F. (2020) *Cercopithecus petaurista. The IUCN Red List of Threatened Species* 2020. dx.doi.org/10.2305/IUCN.UK.2020-2.RLTS.T4225A17945536.en

McGraw, W.S. (2000) Positional behavior of Cercopithecus petaurista. *International Journal of Primatology*, 21, 157–182.

Minhós, T., Borges, F., Parreira, B., Oliveira, R., Aleixo-Pais, I., Leendertz, F.H., et al. (2023) The importance of well protected forests for the conservation genetics of West African colobine monkeys. *American Journal of Primatology*, 85, e23453.

Minhós, T., Chikhi, L., Sousa, C., Vicente, L.M., Ferreira da Silva, M., Heller, R., et al. (2016) Genetic consequences of human forest exploitation in two colobus monkeys in Guinea Bissau. *Biological Conservation*, 194, 194–208. Elsevier B.V.

Minhós, T., Wallace, E., Ferreira da Silva, M.J., Sá, R.M., Carmo, M., Barata, A. & Bruford, M.W. (2013) DNA identification of primate bushmeat from urban markets in Guinea-Bissau and its implications for conservation. *Biological Conservation*, 167, 43–49.

Monard, A. (1939) *Résultats de la mission scientifique du Dr Monard en Guinée Portugaise 1937-1938*. Arquivos do Museu Bocage, Lisbon, Portugal.

Nguyen, L.T., Schmidt, H.A., Von Haeseler, A. & Minh, B.Q. (2015) IQ-TREE: A fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution*, 32, 268–274.

Oates, J.F. (2011) *Primates of West Africa: A Field Guide and Natural History.* Conservation International, Arlington, U.S.A.

Paiva, M.C. (1990) *Artefactos Bijagós: O 'nós' e o 'outro' - das construções de alteridade nos discursos em torno de artefactos de uma população insular da África Ocidental*. MAnth, Universidade Técnica de Lisboa, Lisbon, Portugal.

Puillandre, N., Brouillet, S. & Achaz, G. (2021) ASAP: assemble species by automatic partitioning. *Molecular Ecology Resources*, 21, 609–620.

Rebelo, R. & Catry, P. (2011) O arquipélago dos Bijagós (Guiné-Bissau) - valores de biodiversidade e potencialidades para a investigação científica. *Ecologia*, 2, 8–15.

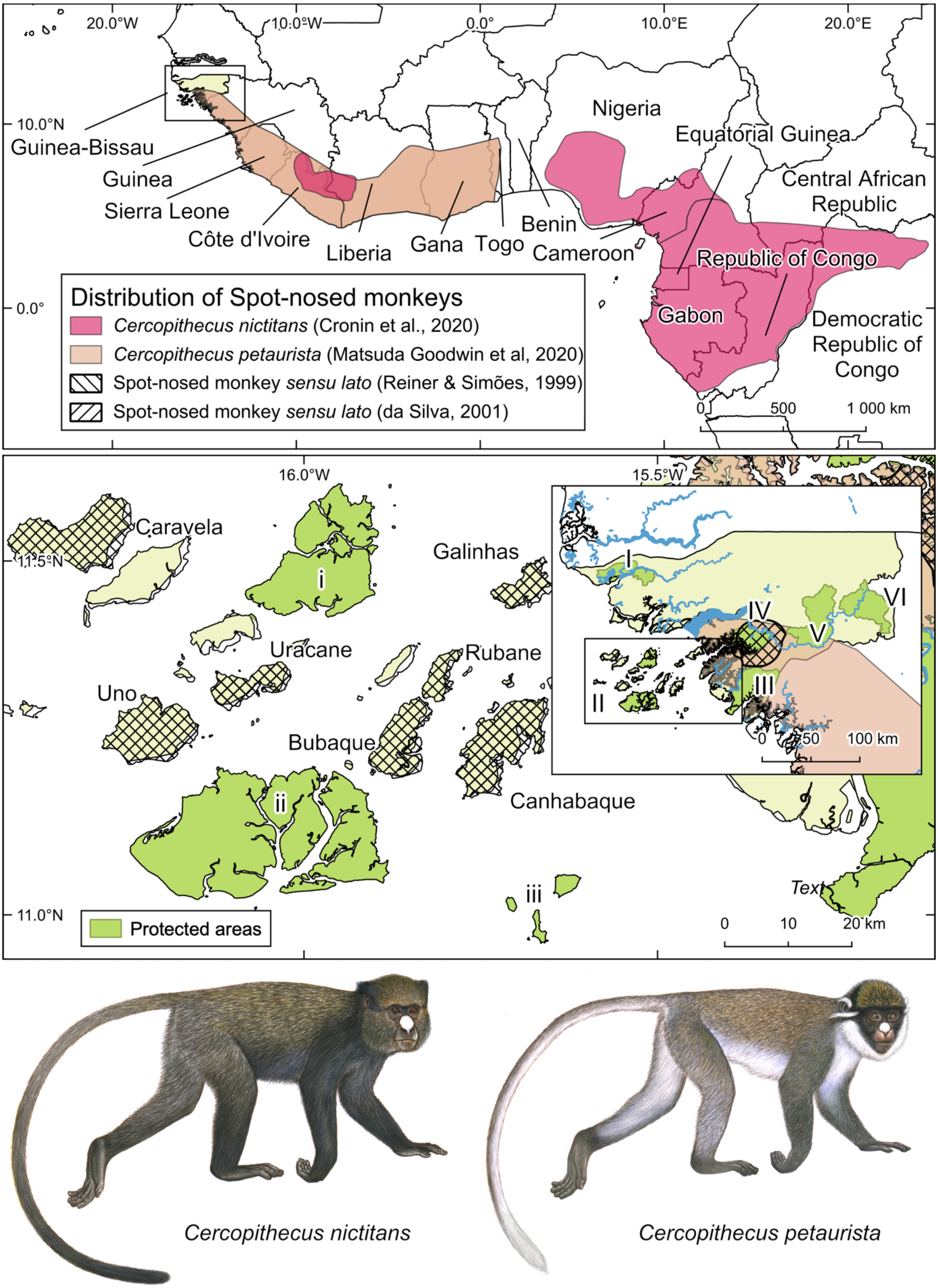
Reiner, F. & Simões, P. (1999) *Mamíferos Selvagens da Guiné-Bissau*. Projeto Delfim - Centro Português de Estudos dos Mamíferos Marinhos, Lisbon, Portugal.

Scantamburlo, L. (1991) *Etnologia dos bijagós da ilha de Bubaque*. Instituto de Investigação Científica Tropical, Lisbon, Portugal.

Thibault, M. (1993) *Parc National de Dulombi*. Ministère de L'Agriculture et du Dévelopment rural and CECI, Bafatá, Guinea-Bissau.

Thomas, N.E. (2011) *Mitochondrial DNA variation of the lesser spot-nosed guenon (Cercopithecus petaurista) from the Canhabaque island, Bijogo Archipelago, West Africa*. BSc thesis, Cardiff University, Cardiff, U.K.

Trifinopoulos, J., Nguyen, L.T., von Haeseler, A. & Minh, B.Q. (2016) W-IQ-TREE: a fast online phylogenetic tool for maximum likelihood analysis. *Nucleic Acids Research*, 44, W232–W235.



Cercopithecus nictitans

Cercopithecus petaurista

Fig. 1 Distribution of the spot-nosed in Guinea-Bissau, West Africa. The species distribution area was drawn based on regional surveys by Reiner and Simões (1999) and da Silva (1994). The global distributions of the putty-nosed monkey, *Cercopithecus nictitans*, and the spot-nosed monkey, *Cercopithecus petaurista* are represented (IUCN polygons, 2022). The maps depict protected areas established in Guinea-Bissau (IBAP, 2022): I) CRMNP, Cacheu River Mangroves Natural Park; II) BBBR, Bolama Bijagós Biosphere Reserve; III) CFNP, Cantanhez Forests National Park; IV) CLNP, Cufada Lagoons Natural Park; V) DNP, Dulombi National Park; VI) BNP, Boe National Park; i) UCMPA, Urok Communitarian Marine Protected Area; ii) ONP, Orango National Park; iii) JVPMNP, João Vieira and Poilão Marine National Park. Illustrations copyright 2022 Stephen D. Nash/IUCN SSC Primate Specialist Group. Used with permission.

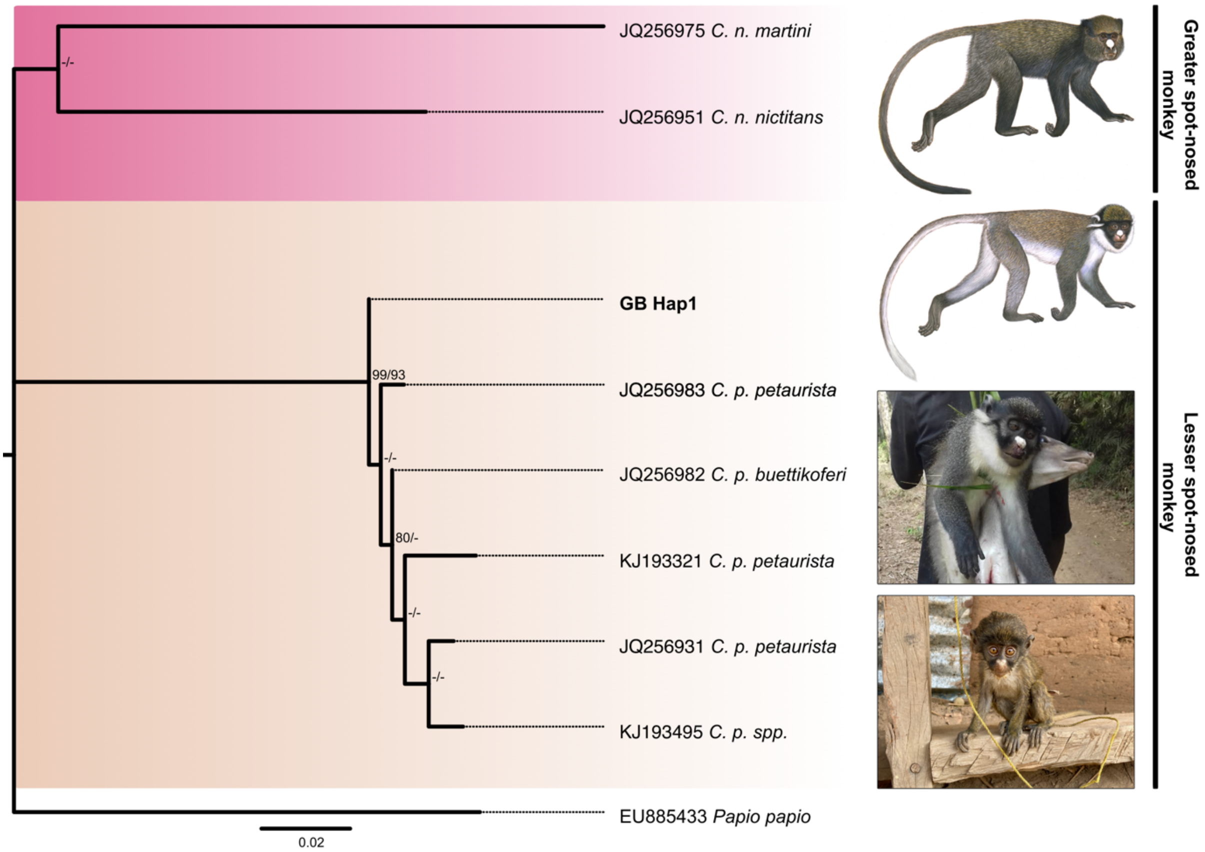
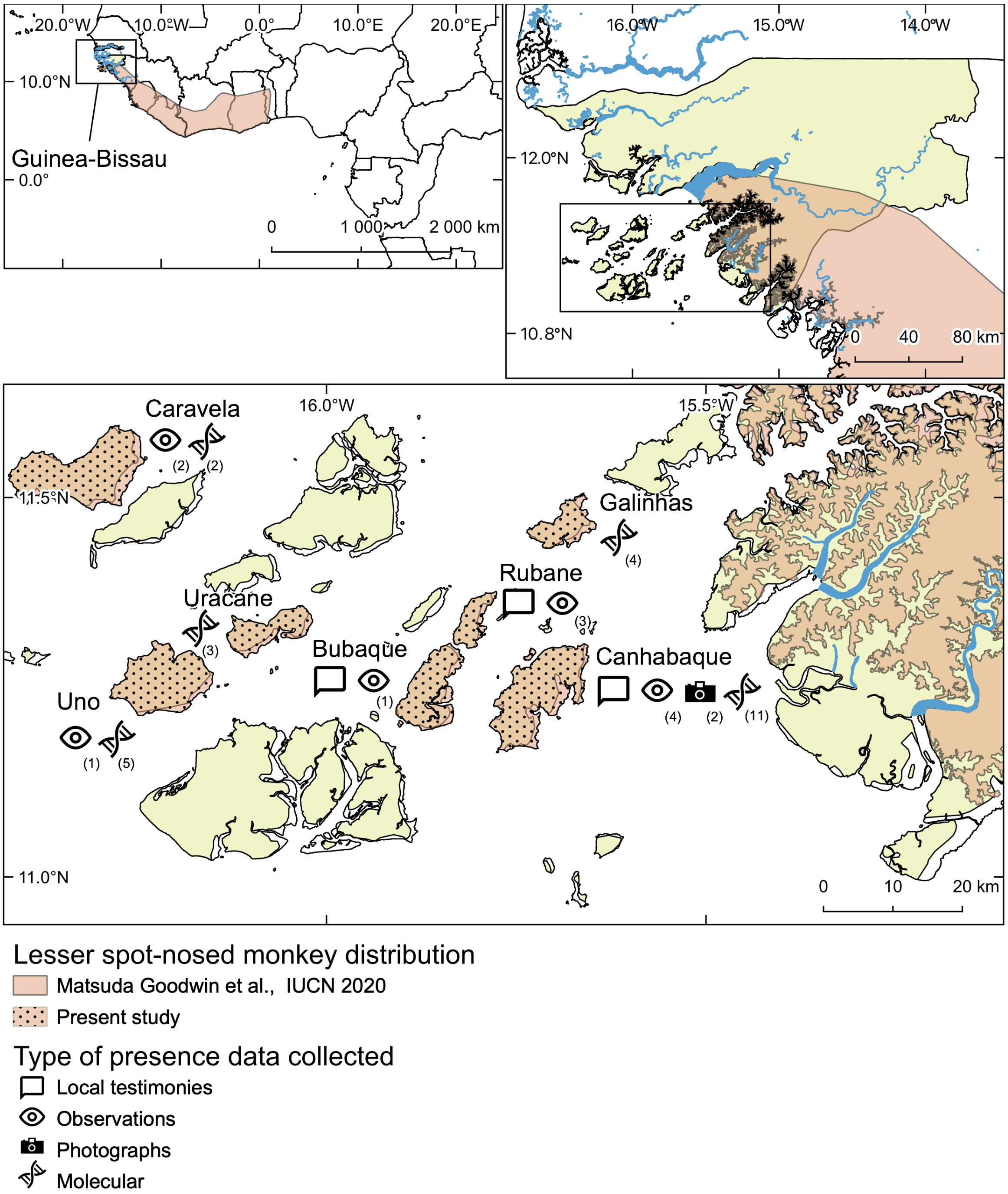


Fig. 2 Taxonomic identity of the spot-nosed monkey in the Bijagós Archipelago, Guinea-Bissau, West Africa. A maximum likelihood tree based on 385 bp of fragment of the *cytb* gene alignment is presented. The *cytb* haplotype sampled in the Bijagós Archipelago is represented in bold. Other *cytb* sequences retrieved from the GenBank (https://www.ncbi.nlm.nih.gov/genbank/) for *C. nictitans* and C. *petaurista spp.* are represented by their individual assession numbers. A *cytb* sequence from Guinea baboon (*Papio papio*) was included as outgroup. Nodes were annotated with SH-aLRT and UFBootstrap support values. Only SH-aLRT and UFBootstrap values above 80% and 90%, respectively, are shown. Photographed individuals at the Bijagós Archipelago were included as well as illustrations to aid visual identification. Illustrations copyright 2022 Stephen D. Nash/IUCN SSC Primate Specialist Group. Used with permission.



Supplementary Fig. 1 Estimated distribution of the spot-nosed monkey (*Cercopithecus petaurista spp.*) in Guinea-Bissau, West Africa. The global distribution of the species is represented (IUCN polygons, 2022). Islands with confirmed presence display a dotted light brown background. The types of presence data collected at each sampled island are represented by the icons. The numbers in brackets correspond to the number of independent data collection events or locations according to the different types of presence data collected.

Supplementary Table 1. Literature included in the study

Year	Authors	*Title*	Journal/Publisher	Inclusion
1939	Monard A.	*Résultats de la mission scientifique du Dr Monard en Guinée Portugaise 1937-1938*	Arquivos do Museu Bocage, Lisbon, Portugal	Read in full, included
1946	Frade F., Bacelar A. & Gonçalves B.	*Trabalhos da Missão Zoológica da Guiné: Relatório da missão zoológica e contribuições para o conhecimento da fauna da Guiné Portuguesa*	Junta de Investigações do Ultramar, Lisbon, Portugal	Read in full, included
1983	Chardonnet B.	*Gestion de la faune sauvage Africaine Proposition d'un project en Guinee-Bissau*	PhD thesis, Faculte de Medicine de Créteil, Créteil, France	Read in full, included
1989	Limoges B.	*Résultats de l'inventaire faunique au niveau national et propositions de modifications à la loi sur la chasse*	Ministério do Desenvolvimento Rural e da Agricultura, Bissau, Guinea-Bissau	Read in full, included
1993	Thibault M.	*Parc National de Dulombi*	Ministère de L'Agriculture et du Dévelopment rural and CECI, Bafatá, Guinea-Bissau	Read in full, included
2003	Gippoliti S. & Dell'Omo G.	Primates of Guinea-Bissau, West Africa: distribution and conservation status	*Primate Conservation*, 19.	Read in full, included
2004	Karibuhoye	*Mammal Conservation status and Prospects for community-based wildlife management in coastal Guinea-Bissau, West Africa*	PhD thesis, Georg-August-Universität Göttingen, Gottingen, Germany	Read in full, included
1991	Scantamburlo L.	*Etnologia dos bijagós da ilha de Bubaque*	Instituto de Investigação Científica Tropical, Lisbon, Portugal	Read in full, included
1990	Paiva M.C.	*Artefactos Bijagós: O 'nós' e o 'outro' - das construções de alteridade nos discursos em torno de artefactos de uma população insular da África Ocidental*	MAnth, Universidade Técnica de Lisboa, Lisbon, Portugal	Read in full, included

1960	Castelo Branco F.	*Um caso de semelhança instrumental em povos diferentes : as fechaduras de madeira de Portugal e dos Bijagós e Papéis* (Guiné Portuguesa)	Agência Geral do Ultramar, Lisbon, Portugal	Excluded based on index
1975	Teixeira da Mota A.	Actividade marítima dos Bijagós nos séculos xvi e xvii	Junta de Investigações Científicas do Ultramar, Lisbon, Portugal	Read in full, not included
1963	Countinho da Costa F.M.	*Contribuição para o estudo do regime alimentar dos bijagós*	Missão de Estudo e Combate da Doença do Sono, Bissau, Guinea-Bissau	Read in full, not included
1994	Kipp E.	Guiné Bissau: aspectos da vida de um povo	Editorial Inquérito, Lisbon, Portugal	Read in full, not included
1994	Có M-D.S.M.	Mudanças recentes da linha de costa e dos ecossistemas costeiros da ilha de Bubaque (Arquipélago dos Bijagós)	Master thesis, Universidade do Algarve, Faro, Portugal	Excluded based on index
1947	Lima A.J.S.	Organização económica e social dos Bijagós	Centro de Estudos da Guiné Portuguesa, Bissau, Guinea-Bissau	Read in full, not included
1928	Pinto J.V.	Relatório sobre uma visita sanitária feita aos Bijagós	Imprensa Nacional, Bolama, Guinea-Bissau	Excluded based on subject
1964	Mateus E.O.	Análise da variância e teste t de caracteres métricos da cabeça de Bijagós	Junta das Missões Geográficas e de Investigações do Ultramar, Lisbon, Portugal	Excluded based on subject
1955	Vieira R.A.	Estudo dos grupos sanguíneos dos indígenas Bigagós da Guiné Portuguesa: contribuição para o estudo da sua soro-antropologia	Centro de Estudos da Guiné Portuguesa, Bissau, Guinea-Bissau	Excluded based on subject
1957	Vieira R.A.	Pesquisa de vitamina C na urina dos indígenas Bijagós da Guiné Portuguesa	Centro de Estudos da Guiné Portuguesa, Bissau, Guinea-Bissau	Excluded based on subject

2003	Fernandes A.	Gonçalo nos Bijagós	Arteplurar, Cascais, Portugal	Excluded based on subject
2009	Madeira J.P.C.B.	A gestão do espaço e da propriedade tradicional no Arquipelágo dos dos Bijagós	Master thesis, Instituto Superior de Ciências Sociais e Políticas, Universidade Técnica de Lisboa, Lisbon, Portugal	Read in full, not included
2009	Oliveira S.	Educação para todos: Urok - Arquipélago de Bijagós - Guiné-Bissau	Instituto Marquês de Valle Flôr, Lisbon, Portugal	Excluded based on subject
2011	Estácio A6 .J.E.	Nha *Bijagó*: respeitada personalidade da Sociedade Guineense, 1871-1959	AlfaPrint, Sintra, Portugal	Excluded based on subject
2011	Polet F.	Dinâmicas e impactos da expansão do turismo no Arquipélago dos Bijagós, Guiné Bissau: lições para AMPC UROK	Instituto Marquês de Valle Flôr, Lisbon, Portugal	Excluded based on subject
2016	Pape D. & Andrade R.R.	Bijagós: património arquitectónico	Tinta da China, Lisbon, Portugal	Excluded based on index
2006	Bordonaro, L.I.	Living at the margins. Youth and modernity in the Bijagó islands (Guinea-Bissau)	PhD thesis, University Insitute for Social Sciences, Business Studies and Technologies	Excluded based on index
2018	Ferreira, M.	Sons da tradição: registo da tradição musical de três etnias da Guiné-Bissau, Manjacos, Balantas-brassa e Bijagós (de Bubaque)	AEGUI – Associação de Escritores da Guiné-Bissau, Bissau, Guinea-Bissau.	Read in full, not included