

Primate adaptations and evolution in the southern African Rift Valley

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Introduction and Background

Gorongosa National Park in central Mozambique offers an unparalleled setting for the study of primate adaptations to complex and highly dynamic environments. Located at the southern end of the East African Rift System, Gorongosa hosts a mosaic of forests, woodlands, grasslands, swamps, rivers, and a major lake, Lake Urema, which fluctuates extensively with the seasonal cycles (Figures 1, 2).¹ Renowned biologist E.O. Wilson has described Gorongosa as “ecologically the most diverse park in the world”.² The park is home to five species of nonhuman primates, among them 219 troops of baboons,³ whose phenotypic diversity suggests an extended history of admixture between chacmas (*Papio ursinus*) and yellow baboons (*P. cynocephalus*) (Figure 3).⁴ With its dynamic mix of environments in the African Rift Valley, and highly adaptable primates, Gorongosa brings to mind the vegetation mosaics in which Pliocene and Pleistocene hominins evolved.⁵

Gorongosa thus provided an ideal setting to bring together a broad interdisciplinary group of scientists to discuss “New perspectives on primate adaptations to complex environments and implications for early human evolution.” The occasion was a workshop funded by the Wenner-Gren Foundation and hosted by Gorongosa National Park on 23-25 July 2019. The Wenner-Gren Foundation has sponsored about 165 symposia and workshops over the past 67 years, but this

was only the third time such an event was held in Africa. The workshop included 36 researchers and students (from 20 institutions in 11 countries) with expertise in primatology, zoology, natural history, ecology, botany, genetics, genomics, paleontology, paleoanthropology, archeology, and geology (Figure 4). The event was open to the public, so researchers, students, and staff working in the park, among them many young Mozambicans, attended the workshop and participated in the discussions. Holding such an event in Mozambique was a milestone for a country with great potential in primatology, paleontology, and paleoanthropology, and allowed Mozambican scholars and students to establish new collaborations for future research and training.

Key questions

The central aim of the workshop was to set new directions for future theoretical and empirical research on primate adaptations to complex environments. The objective was to shed light on three interrelated questions at the interface of primatology, genetics, and paleoanthropology: 1) Are there identifiable behavioural patterns in primate responses to complex and dynamic environmental conditions? 2) How can we use studies of population structure and inter-population genetic introgression in wide-ranging primates to understand similar processes in hominin evolution? 3) How can we best integrate new concepts and insights from the study of living primates with a better understanding of hominin evolution and its environmental context?

The Paleo-Primate Project Gorongosa

The workshop opened with an introduction to Gorongosa National Park by Marc Stalmans, the Director of Scientific Services, who described Gorongosa's mosaic habitats as miombo woodlands, tall limestone gorge forests, *Combretum* open woodlands, *Acacia* woodlands, as well as extensive edaphic and secondary grasslands, with the highly dynamic Lake Urema at the heart of the park, fed by major rivers from Mount Gorongosa on the western shoulder of the

Rift Valley. Rising up to 1863 m, Mount Gorongosa itself is an ecological island of Afromontane rainforest, with a highly endemic flora and fauna. After Mozambique's devastating civil war (1977-1992), the park has been undergoing a highly successful wildlife restoration program and a renaissance of research.⁶⁻⁸ It is in this context that in 2016 Susana Carvalho launched the long-term Paleo-Primate Project with the overarching goal of understanding the evolutionary history of the region, with a focus on living primates, as well as archeological and paleontological research. At the workshop, Carvalho discussed how this project integrates studies of modern primate behaviour, genetics, and morphology, with new archeological excavations in Gorongosa's extensive karstic system, as well as new Miocene fossil sites on the eastern shoulder of the rift ([Figure 1](#)).⁹ Carvalho and colleagues saw the potential to focus on baboon behavior to learn more broadly about the processes by which primates adapt to complex and dynamic conditions, and about behavioral innovations that might emerge under particular ecological pressures. For example, one of the effects of the civil war was a severe decline of the park's carnivore communities, but lions are making a significant recovery in population size, leopards are returning, and wild dogs have been successfully reintroduced ([Figures 5, 6](#)). Thus, Gorongosa now offers a natural experiment to document how primate behaviour varies with different levels of predation pressure. Researchers are also documenting predation events and carrying out osteological surveys and collections across different environments. Jacinto Mathe, a young Mozambican scholar, discussed the first results of this neotaphonomic approach, and demonstrated that there are intriguing differences in mammalian abundances between bone surveys and aerial surveys of living animals. The bone surveys may be better at capturing species that are difficult to see and count from the air, and thus provide a supplementary method to estimate faunal distributions and abundance. These opening presentations were followed by in-depth talks and discussions of the three main themes/questions of the workshop.

Theme 1: primate behaviour in complex environments

Baboons provide a striking example of an anthropoid primate that is widely distributed, ecologically adaptable, and behaviorally flexible.¹⁰ Baboon research in Africa has a long and distinguished history,¹¹⁻¹⁴ but until now the baboons of Gorongosa had never been studied, even though with 219 troops (and many thousands of individuals), the park likely holds one of the highest concentrations of these primates in Africa. A series of presentations introduced the workshop participants to the emerging work on Gorongosa baboons. Dora Biro discussed the team's work on possible cultural behaviors in relation to bark stripping; Lynn Lewis-Bevan discussed social and ecological factors in relation to baboon ranging patterns in a floodplain environment, and Philippa Hammond presented work on the changing landscapes of fear in a troop of woodland baboons by analyzing vocalizations and vigilance patterns. The concept of landscapes of fear affecting the ranging and behavior of primates was discussed in depth by Russell Hill based on his team's work at the Lajuma Research Centre in the Soutpansberg Mountains of South Africa.^{15,16}

The workshop was privileged to have representatives from some of the longest ongoing baboon study sites in Africa. Susan Alberts brought to bear the decades of research at Amboseli National Park in Kenya, where baboons were first studied in 1963,^{12,17} and Anthony Collins brought to the discussion his nearly 50 years of experience at Gombe National Park in Tanzania, where baboons share their habitats with chimpanzees. It is only through long-term studies such as these that researchers can study evolutionary processes in action. At Amboseli, for example, we have learned that females with long life spans have overall higher offspring survival than females with shorter life spans.

The diversity of habitats in which baboons live was highlighted by Alecia Carter's study of baboons in the edges of the Namib Desert at the Tsaobis Nature Park in Namibia, where she has documented information acquisition through dynamic social networks.¹⁸ Variation in baboon social systems was eloquently presented by Julia Fischer, who discussed the nested multi-level society of Guinea baboons from the "neglected West".¹⁹ Fischer's work at Niokolo Koba National Park in Senegal reveals that the Guinea baboon social system is in some

fundamental features similar to that of hamadryas baboons. Guinea baboons are organized in reproductive units consisting of one male with several females and their young, with several of these reproductive units forming a “party”, and several parties forming a “gang”. Gangs are formed by a core of closely related males, and females tend to transfer between gangs. Compared to other baboon species, Guinea baboons show lower levels of male-male aggressiveness, and compared to hamadryas they have more female freedom.

Thus, baboons took center stage at the workshop, and not only as a topic of discussions: during the course of the meetings, baboons would often peek into the lecture theatre or jump across its roof, above the participants' heads. We had the rare opportunity of discussing these amazing primates with renowned baboon specialists while observing baboon behavior right before our eyes.

Theme 2: primate genetics/genomics and hybridization

Baboons have become important in studies of the evolutionary processes that lead to population divergence, speciation, and hybridization in primates.^{10,20-22} Adding to the social complexity inherent in primate societies and the environmental complexity of the Gorongosa ecosystem is the apparently mixed origin of the Gorongosa baboons. Our recent work indicates that Gorongosa harbors chacma baboons descended from populations that experienced some historical gene flow from yellow and/or Kinda baboons. Whether gene flow is still ongoing is an urgent research question. Felipe Martínez and Thomas Püschel presented their study on the morphological variation in Gorongosa baboon populations. Gorongosa baboons exhibit features that are diagnostic of the grayfooted chacma baboon (*Papio ursinus griseipes*), but they also exhibit features frequently seen in yellow and Kinda baboons. The morphometric analysis of the skull shows that their phenotype is a mosaic of features from yellow and grayfooted baboons²³. Maria Joana Ferreira da Silva and colleagues presented their study on Gorongosa baboon population structure and genetic diversity estimates using non-invasive DNA samples and mtDNA and STR genetic markers. At the mtDNA level, Gorongosa baboons fall within the

northern chacma clade, formed by grayfooted baboon populations (from Namibia and Botswana).²⁴ Using STR data, da Silva and colleagues estimated high levels of genetic diversity, comparable to that of yellow baboons and *Papio* hybrid zones elsewhere. They also found a gradient of genetic variation from Gorongosa to the Zambezi River (located 150 km to the north). Cristian Capelli and colleagues presented a preliminary analysis of the first baboon whole-genome from Gorongosa indicating high nuclear diversity. Further analyses will reveal if, when, and to what extent baboons in the region experienced gene flow with other chacma groups and hybridization with other baboon species.

Dietmar Zinner discussed the phylogeography of African savanna monkeys. The historical dynamics of savanna habitats explain the geographic pattern of many African species. In the case of baboons, speciation started around 2 Ma but gene flow across lineages occurred multiple times.²² *Papio* mtDNA lineages indicate a north-south split. The oldest mtDNA lineages are found in southern Africa and, thus, the range expansion of baboons occurred from south to north in agreement with the fossil record.²⁵ In turn, the distribution of baboon mtDNA lineages correlates well with geography but not taxonomy. The incongruence between nuclear and mtDNA is the result of several episodes of male-driven, introgressive hybridization within *Papio*.^{24,26} Clifford Jolly discussed the evolutionary origins of male philopatry in hamadryas and Guinea (H-G) baboons in contrast to female philopatry in chacma, olive, Kinda, and yellow (COKY) baboons. Jolly argues that male philopatry is fundamental to other behavioral traits and a basic precondition for the evolution of the multi-level societies. It was not an ecological adaptation but rather an adaptation to the rapid expansion of the proto H-G populations. In this scenario, the population's geographical range was expanding south to north as troops at the front edge increased in size, fissioned, and sent colonists forward into open territory. The lack of troops beyond the frontier would have favored males that stayed and attempted to breed in their natal group. This 'frontier' hypothesis for the evolution of large and substructured groups in northern baboons implies that male philopatry was a feature of the common ancestor of all northern baboons, but only in hamadryas and Guinea baboons has it survived later introgression, principally by male olive baboons (*P. anubis*).

Theme 3: hominin paleoenvironments

Research on the environments of early hominins emphasizes the importance of dynamic and heterogeneous ecosystems as the fundamental substrate on which key hominin adaptations emerged in Africa.^{27,28} The workshop had several presentations and lively discussions on this topic. In a splendid talk with the title of “Mozambique in island Africa”, Jonathan Kingdon described “the big picture” and the role of major basins, with the Congo basin and a series of lesser basins down the eastern coast of Africa playing major roles in the continent's biogeography. Basins can function to group endemic communities while a giant, year-round river, such as the Congo, may act as a barrier that isolates species. Kingdon discussed how the interplay of geology, climate, adaptation, and dispersal led to the patterns of diversification we see in mammals today, with a predominant humid center-west biogeographic realm, and a drier longitudinal south-east realm. As the lead-editor of the six-volume *Mammals of Africa*²⁹ and a lifetime spent in eastern Africa, Kingdon has unmatched first-hand knowledge of many of the continent's 1,111 species of mammals. He discussed his hypothesis of hominin origins in the eastern coastal forests,³⁰ an idea that is receiving renewed attention.³¹ In this light, the new fossil sites from Gorongosa acquire special importance, as they sample Miocene woodlands/forests in a coastal paleoenvironment,⁹ and will allow for the testing of hypothesis about mammalian evolution in wooded coastal regions.

René Bobe provided an overview of early hominin environments. Bobe showed that paleontological sites reconstructed as highly dynamic and heterogeneous paleolandscapes are more likely to have a high *abundance* of hominins, as at Kanapoi around 4 Ma,³² or a high *diversity* of hominins, as in the Koobi Fora Formation between 2.0 and 1.4 Ma, when up to four hominin species co-existed in a single basin.⁵ One of the key elements running through the discussions of early hominin paleoenvironments was the importance of water. Linda Marchant provided an insightful discussion of the role of water throughout our evolutionary history. Potable water is, and has been, a precious and often scarce resource, one that is fundamental

to our survival. She drew from her extensive research on wild chimpanzees to illustrate how these primates may dig wells in dry streambeds, use leaf sponges, or suck on tubers for moisture. Chimpanzees also make use of a range of other fresh-water resources: they use tools to scoop algae and “fish” for fresh-water crabs. Early hominins may have relied on similar approaches to obtain water and forage at the water’s edge. Marchant also discussed the role of hydro-refugia as a buffer against the increasingly unpredictable climates of the African late Miocene and Plio-Pleistocene.³³ During periods of aridity, hominins (and other water-dependent mammals) would have stayed close to fresh-water refugia, and during wet periods they would have dispersed more widely. An appreciation of the critical role of water was also highlighted by Richard Wrangham, in a collaborative presentation with Andrew Cunningham, emphasizing that wet habitats are more important than often considered in human evolution. Wrangham outlined a model in which a Miocene ape inhabiting forests could have adapted to living outside the forests in environments similar those provided by the Okavango Delta, with year-round fruit trees and wet herbs. He further developed the delta hypothesis³⁴ discussing how the abundant Okavango baboons provide a model of how a species like the chimpanzee could adapt to these habitats. Marc Stalmans commented that Gorongosa might also provide a model of a highly productive environment that could, in theory, support ape populations. Gorongosa today does not harbor any apes, but has three species of anthropoid primates: baboons, vervets, and Samango monkeys. Sarah Elton described how these three primates co-occur in many parts of southern Africa, and she traced back the evolutionary history of primate communities into the Pliocene. In her presentation, “Living together in complex environments”, she discussed the roles of adaptation, niche partitioning, and ecological neutral theory in structuring primate communities. She emphasized that neutral processes may play an important role in structuring primate communities in complex habitats.

One of the ways in which early hominins adapted to complex environments was through the use of tools. Katarina Almeida-Warren discussed primate technology in the context of ecological and foraging landscapes. Based on her studies of wild chimpanzees as a point of reference, she argued that chimpanzees’ reliance on percussive technologies produces a visible

archeological record, in some ways akin to the earliest known hominin tools.³⁵ Zeresenay Alemseged asked the question: did *Australopithecus* use tools? He provided answers based on the work at Dikika, Ethiopia, with evidence of the earliest stone-tool-modified bones dated to 3.4 Ma.^{36,37} Alemseged went on to discuss the morphological adaptations of *A. afarensis*, showing that the species had an ape-like scapula that reflected arboreal adaptations.³⁸ Thus, it is clear that early hominins evolved neither in closed canopy tropical rain forest nor in open savanna grasslands, but in intermediate, complex ecosystems composed of varying proportions of woodlands and grasslands usually close to permanent bodies of fresh water. Much of the data derives from key paleoanthropological sites along the East African Rift System, where variable topography, elevation, soil composition, temperature, and rainfall result in highly complex environments with high levels of biodiversity, both past and present. The study of living primates in these environments remains a key source of data and ideas for a better understanding of our own evolution.

Conclusions

This workshop brought to Gorongosa National Park a group of scholars that transcended traditional disciplinary boundaries to discuss primate adaptations to complex environments and their implications for understanding hominin evolution. The diverse tapestry of backgrounds amongst participants, and their openness to share their insights, produced lively discussions and rich exchanges of ideas. The workshop succeeded in generating future avenues for research, collaboration, and data sharing among primatologists, geneticists, and paleoanthropologists. Primatologists, for example, agreed on the importance of standardizing aspects of data collection so that they could carry out comparisons among widely separated sites. It is clear that we still have much to learn about the behavior of living primates, and that studies of primate ecology and behavior still have much to offer paleoanthropologists as they grapple with the fossil record. In turn, the time depth perspective of paleontologists can generate questions and hypothesis that can be tested with studies of living primates (e.g., what is the relationship between different levels of predation pressure and key aspects of primate

behavior?). The workshop bridged in creative ways the past with the present, paleoanthropology with primate behavior, and paleontology with genetics. Having had this event in Gorongosa was of critical importance to bring a new generation of Mozambican students and colleagues in direct contact with top primatologists, primate geneticists, and paleoanthropologists. There was consensus among participants that this kind of meeting is essential for generating new ideas and enriching the context of research across anthropological disciplines.

Presenters

Scholars who gave presentations at the workshop: Susan Alberts (Duke University), Zeresenay Alemseged (University of Chicago), Dora Biro (University of Oxford), René Bobe (Gorongosa National Park and University of Oxford), Cristian Capelli (University of Oxford), Tongai Castigo (Gorongosa National Park), Alecia Carter (Université de Montpellier), Susana Carvalho (University of Oxford and Gorongosa National Park), Anthony Collins (Gombe Stream Research Centre, Jane Goodall Institute), Maria Joana Ferreira da Silva (CIBIO-InBIO, Universidade do Porto, and Cardiff University), Sarah Elton (Durham University), Julia Fischer (German Primate Center), Philippa Hammond (University of Oxford), Russell Hill (Durham University), Clifford Jolly (New York University), Jonathan Kingdon (University of Oxford), Lynn Lewis-Bevan (University of Oxford), Linda Marchant (Miami University), Felipe Martínez (Pontificia Universidad Católica de Chile), Jacinto Mathe (University of Coimbra), Thomas Püschel (University of Oxford), Marc Stalmans (Gorongosa National Park), Katarina Almeida-Warren (University of Oxford), Richard Wrangham (Harvard University), Dietmar Zinner (German Primate Center).

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Figure captions

Figure 1: Gorongosa National Park at the southern end of the East African Rift System. This map shows the location of the Miocene fossil sites and the park’s extensive karstic system. Base image from <https://lab.wildcamgorongosa.org/>

Figure 2: Partial view of Lake Urema and its seasonally flooded grasslands. Woodlands are visible in the distance.

Figure 3: Gorongosa National Park baboon mother and offspring (Photo Bobe). There are 219 troops of baboons documented in the park.

Figure 4: Participants in the workshop “New perspectives on primate adaptations to complex environments and implications for early human evolution”.

Figure 5: lion and waterbuck on the Urema floodplain, Gorongosa National Park. Lion populations in the park are becoming more abundant. Currently there are 146 lions in the park (as of December 2019). Photo credit: Gorongosa National Park.

Figure 6: Wild dogs (or painted wolves) have been successfully reintroduced to Gorongosa National Park. Currently (December 2019) there are 52 wild dogs in the park. Photo: Brett Kuxhausen/Gorongosa Media.

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