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Twenty-five years of primate research in the Ndoki Forest

A brief history of primate research in the Ndoki forest

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Abstract

The Nouabalé–Ndoki National Park (NNNP) in Republic of Congo has become a beacon for conservation in Central Africa. This manuscript documents the arrival of primatologists, the establishment of field stations and major discoveries in primate behavior and ecology. Field stations were strategically established to study primate behavior in a variety of different contexts from stationary platforms to forest follows of habituated groups. The implementation of new technologies and analyses have also been a hallmark of research at Ndoki. Scientists are shaping a new era in primatology at NNNP by building on past successes and promoting the next generation of Congolese conservationists to address environmental challenges. Results have proven crucial in discussions with government and industry and led to conservation gains such as the inclusion of the intact forests of the Goualougo and Djéké Triangles into the NNNP. The research stations have also become essential for developing a long-term certified sustainable international gorilla tourism program. Despite the many advancements for conservation such as increased protection of forests, development of internationally recognized protocols and large-scale capacity building initiatives, there are reasons for considerable concern in the near- and long-term for primates and their forest habitats in the Ndoki landscape. To address these concerns, we emphasize the long history of forming partnerships with local communities. We also discuss shared overlap featuring multicultural and environmental use of forest resources that is likely to be crucial in championing the conservation of the Ndoki forests for the next 25 years and beyond.

Keywords Gorilla · Chimpanzee · Conservation · Park management · Intact forests

Introduction

Forty years ago, there was relatively little mention of the Congo Basin when the crisis of tropical forests and biodiversity loss was being discussed in global conservation forums (UNCED 1992). Urgent calls for halting deforestation were focused mainly on other regions of the world where there was evidence of tropical forests suffering large declines at alarmingly fast rates. Global conservation priorities also included protection of remaining intact forests and developing more informed forest management strategies. Regardless, large parts of east and west African forests had disappeared by the early 1990s (Ernst et al. 2010). While extractive industries have had a long history in Central Africa, there are still expansive forests lacking anthropogenic disturbance that contain abundant wildlife due to the comparatively low human population numbers. The region is also home to several primate species that had rarely been

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systematically studied in the wild (see Table 1), including western lowland gorillas (*Gorilla gorilla gorilla*) and central chimpanzees (*Pan troglodytes troglodytes*). Early research teams in northern Republic of Congo were led by primatologists, who we would argue have played disproportionately large roles in the conservation of the Nouabalé–Ndoki National Park.

The Nouabalé–Ndoki National Park (NNNP) has become a global icon for conservation. The government of the Republic of Congo has demonstrated a strong commitment to preserving forests and implementing innovative management strategies that benefit local peoples. There has also been a historical effort to coordinate transboundary conservation efforts in the Sangha Region, including government, industry, and NGO partners. To the north of the NNNP and neighboring Central African Republic are the Dzanga–Sangha Reserve and Dzanga–Ndoki National Parks, and to the west, Lobéké National Park in neighboring Cameroon (Fig. 1). Together, these protected areas comprise the transboundary Sangha Tri-National World Heritage Site featuring a combination of development, protection, and management activities spanning 746,309 ha.

Table 1 Primates of the Ndoki forest, ordered by conservation status and population trend

Scientific name	Common name	Conservation status	Population trend
Gorilla gorilla	Western gorilla	Critically endangered	Decreasing
Pan troglodytes	Chimpanzee	Endangered	Decreasing
Lophocebus albigena	Grey-cheeked mangabey	Vulnerable	Decreasing
Piliocolobus oustaleti	Oustalet's red colobus	Vulnerable	Decreasing
Cercopithecus nictitans	Putty-nosed monkey	Near threatened	Decreasing
Cercopithecus pogonias	Crowned monkey	Near threatened	Decreasing
Allenopithecus nigroviridis	Allen's swamp monkey	Least concern	Decreasing
Cercocebus agilis	Agile mangabey	Least concern	Decreasing
Colobus guereza	Guereza	Least concern	Decreasing
Cercopithecus cephus	Moustached monkey	Least concern	Unknown
Cercopithecus neglectus	De Brazza's monkey	Least concern	Unknown
Euoticus elegantulus	Southern needle-clawed galago	Least concern	Unknown
Arctocebus aureus	Golden angwantibo	Least concern	Unknown
Galagoides demidoff	Demidoff's dwarf galago	Least concern	Stable

Mitani 1990a, 1990b; Morgan et al. 2023; IUCN Red List

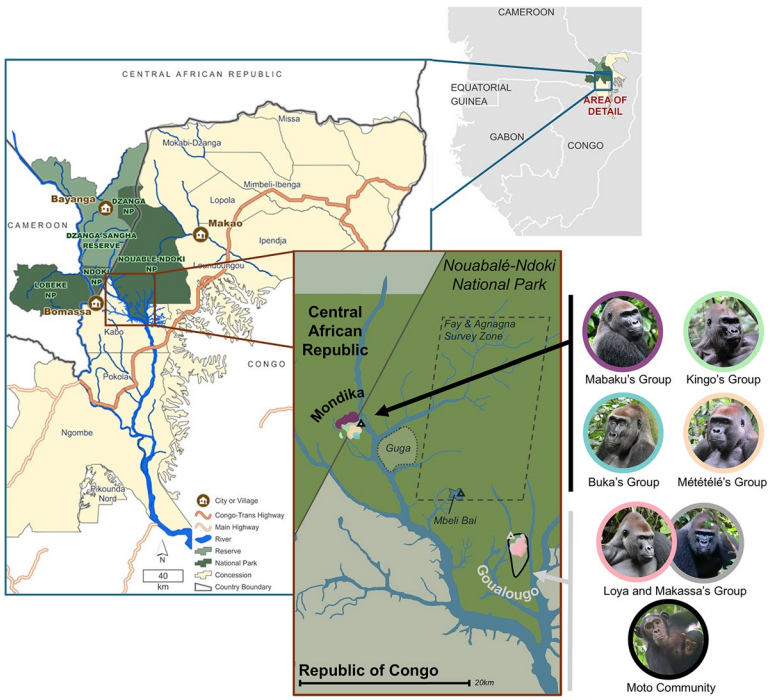

Fig. 1 Map of the Ndoki region. The Sangha Tri-national conservation area is shown in shades of green and located in areas across Republic of Congo, Cameroon and Central African Republic. The inset map show primate study sites in the Ndoki forests. Research and monitoring of great apes at Goualougo, Mondika and Mbeli Bai focus on identifying individuals and monitoring their social groups over time. The home ranges of habituated gorilla groups at Mondika overlap considerably which facilitate studies of intergroup dynamics. In Goualougo, the Loya–Makassa gorilla group ranges within the Moto chimpanzee community home range which makes it possibly to study the factors influencing gorilla and chimpanzee coexistence

Early success became a reality in 1993 with the creation of the NNNP. A landscape approach was established by the Congolese government in collaboration with Wildlife Conservation Society (WCS), local communities and industrial partners focusing on the neighboring production forests to buffer the NNNP from external threats through land management measures (Fay 1997; Ruggiero 2012). To achieve this goal, the consortium sought empirical information on which to base decisions regarding monitoring and protection of biodiversity. Multi-species landscape scale surveys, as well as more focused research efforts, contributed to informing policies, practices, audits, and management plans in this region (Clark et al. 2012; Morgan et al. 2013). While threats and opportunities have evolved over the past decades, we recount how research stations focusing on great apes have aided in preserving primates in a remarkable conservation stronghold.

Early research efforts

Some of the first researchers to document their study of primates in the Ndoki landscape were from Kyoto University of Japan. In October 1988, Masazumi Mitani conducted 32.6 km of reconnaissance surveys along elephant trails in what was then the Nouabalé–Ndoki forest management unit (FMU) including near a small fishing village called Bomassa, on the banks of the Sangha River. He reported the occurrence of ten diurnal primate species and was informed by local people of other nocturnal primate species (Mitani 1990). Botanical surveys were also initiated during this period to identify the plant foods of gorillas and chimpanzees in this region (Moutsambote et al. 1994).

Starting in 1989, Marcelin Agnagna and Michael Fay then led expeditions to document the abundance and ecology of western lowland gorillas across an expanded region of the Ndoki landscape. They employed line transect methodology, in which ape nests were surveyed along 401.6 km of line transects. A total of 326 gorilla nests were documented in the Ndoki, Motaba, Mbomo and Lake Mboukou areas of northern Congo. They found relatively high gorilla densities and unique landscape features where wildlife gathered, such as forest clearings that are referred to locally as "bais" (Fay et al. 1989, 1992). Subsequent reconnaissance surveys in an area known as the Goualougo Triangle south of the Nouabalé–Ndoki FMU between the Ndoki and Goualougo Rivers revealed that animals responded as if they were "naïve" to humans, indicating that anthropogenic pressures were not familiar in this ecosystem (Fay et al., 1990). Taken together, these expeditions highlighted the high conservation value of the Nouabalé–Ndoki FMU and put in place a strong scientific ethos that would become the foundation for some of the longest-running primate research projects in central Africa.

Guga research site

Studies of ape behavioral ecology at Ndoki by primatologists from Kyoto University began 1 year after Mitani's initial expeditions. Suehisa Kuroda and Tomoaki Nishihara arrived in Ndoki with the aim of establishing a long-term primate research project to inform models of human evolution. They were joined by Valentin Yako, Richard Malonga and other recent graduates of Marien Ngouabi University in Brazzaville, Republic of Congo. After initial missions, a research camp was established at Guga in an area that would eventually be included in the NNNP (Mitani et al. 1993). The researchers chose this area to observe chimpanzees inhabiting primary forest and western lowland gorillas frequenting a complex of forest clearings. The researchers built an elevated viewing platform in the trees at the edge of such a clearing to watch the animals as they entered the bai.

Initial observations by primatologists at Guga led to three areas of inquiry that are still relevant today. The first questions concerned the sociality of gorillas, and particularly the observed temporary subgrouping of western lowland gorilla social units that was initially interpreted as similar to the fission–fusion dynamics of chimpanzees and humans (Mitani et al. 1993). The second line of inquiry was about the extents of dietary overlap between sympatric gorillas and chimpanzees (Nishihara 1992, 1995), and the intriguing glimpses of cofeeding ape species in the same tree crown (Suzuki and Nishihara 1992; Kuroda et al. 1996). Thirdly, this research team published images of chimpanzee tools that differed from the material culture reported from ape populations in East or West Africa (Suzuki et al. 1995). There were also brief surveys of other primates, including black and white colobus monkeys and grey-cheeked mangabeys (Kuroda 1992; Onononga 1996). Importantly, a phenology circuit of trees was established at Ndoki and insect inventories were conducted to provide information on the abundance and seasonality of food resources for great apes. Due to civil instabilities, field investigations at Guga ended in 1997.

Mbeli Bai Gorilla Project

The scientific advancements pioneered at Guga and their study of gorillas in bais inspired similar methodology at Mbeli. Encompassing approximately 13 hectares, Mbeli Bai is one of the largest forest clearings in the Ndoki landscape. It is also the longest running study of western lowland gorillas. Multiple gorilla groups visit the clearing on a regular basis to forage on the lush herbaceous vegetation as well as socialize. A viewing platform was installed at the edge of the bai in 1994 and observations have been ongoing since. Since the beginning of the study, researchers have individually identified the gorillas who enter the clearing using binoculars, spotting scopes and cameras with zoom

lenses. A total of 626 gorillas have been monitored over the last 29 years (Villioth and Estienne 2023). Since the inception of the project, the population has largely increased over time (Robbins et al. 2022) apart from declines registered in 2015–2017 (Fig. 2). At the close of 2023, 184 individuals in 22 groups and 17 solitary silverbacks were observed at the clearing (Villioth and Estienne 2023). It is not only the sheer number of individual gorillas observed over the course of the study, what makes the Mbeli database special is that it includes details on life histories, including social relationships, maturation, mating, reproduction and rarer events like group formation, disintegration and death. While conducting observations from a stationary platform has some limitations, these longitudinal data on multiple groups provide novel insights into gorilla population dynamics (Parnell 2002a, b). Population monitoring is also being conducted on elephants and ungulate species who visit the peripheral forests as well as access the bai (Fishlock 2010). Like gorillas, the number of elephants visiting the clearing has also increased notably since the project's inception and suggest that this bai is unique by being both a "gorilla" and "elephant" clearing. More recently, researchers also began to expand primate research by studying putty-nosed monkeys in the forests around the clearing. Using acoustic playback techniques, these studies have provided novel information on the behavior and cognition of the most populous and widespread primate species in the Ndoki landscape (Mehon and Stephan 2021; Mehon et al. 2024 in review).

Interactions between gorilla groups are a notoriously challenging area of research because they require habituation of multiple groups and occur relatively rarely. Even in the early days of the Mbeli Bai Project, observers described two or more gorilla groups occupying the clearing as being a common occurrence. It was initially suggested that these groups were attracted to the opportunity to forage on *Hydrocharis chevalieri* which is an aquatic herb that flourishes within the clearing and along its periphery. However, it became apparent from observations at the bai that male and female gorillas were also taking advantage of opportunities for reproductive benefits. For adult male western lowland gorillas, competition with other males was apparent from male–male water displays in the bai (Parnell 2002a, b; Parnell and Buchanan-Smith 2001). With the open visibility of the bai, secondary sexual characteristics linked to life history traits and tenure lengths were also showcased (Breuer, et al. 2008). Similar to their eastern counterparts, male western lowland gorillas focus on gaining access to females as well as retaining female group members. These priorities of males explain, in part, the different rates of affinitive versus aggressive encounters between gorilla units observed in the clearing (Parnell 2002a).

Based on early observations from Mbeli, the risk of infant mortality up to 3 years of age is quite high compared to estimates in mountain gorillas (Robbins, et al. 2004). However, death resulting from infanticide appears to be low as mothers with offspring were observed to successfully immigrate into neighboring groups without lethal male aggression (Stokes et al. 2003; Manguette et al. 2020). These findings do not concur with patterns of immigration and associated infant mortality events among mountain gorillas of the Virungas

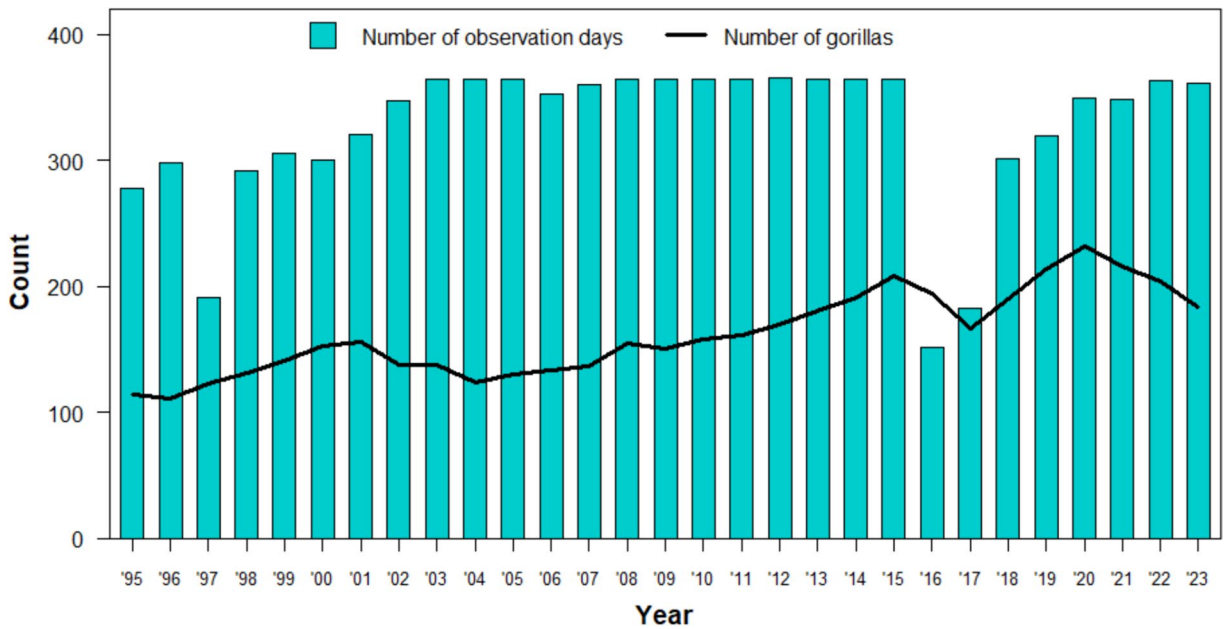

Fig. 2 Number of Mbeli Bai gorillas and number of observation days (*y*-axis) over time (*x*-axis) at the clearing. The number of individual gorillas observed increases overtime apart from decreases in the early 2000s and a 2 year period from 2015 to 2017

(Watts 1989). Due to reduced threat of infanticide by males, females at Mbeli may exercise more choice and time in making group transfer decisions. The bai setting offers females an important vantage point for assessing dispersal options (Manguette et al. 2020). As an example, one female at Mbeli has transferred between groups on at least twelve occasions (Manguette et al. 2020).

The low risk of infanticide may also help explain the rarity of multimale gorilla groups, which is another notable difference between Mbeli gorillas and mountain gorilla populations. By some estimates, roughly 40% of mountain gorilla groups are multimale social units (Harcourt and Stewart 2007). Based on a 6-year study, the majority of Mbeli males (88%) emigrated from their natal group (Robbins et al. 2004) which is far higher than male dispersal events in mountain gorillas (Robbins 1995) The presence of co-resident males in breeding groups is explained in terms of benefits such as protection for group members or influencing decisions of females on choosing in which group to reside. Female mountain gorillas are more likely to join multimale groups than those led by a single dominant male in the Virungas (Watts 2000). In contrast, female gorillas at Mbeli have rarely had the option of transferring into social units with two dominant males (Parnell 2002b) as only two social units have been recorded featuring a multimale structure and existed only briefly (Robbins, et al. 2004). Female western lowland gorillas generally transfer to groups with younger males and prefer transferring to groups with fewer females (Stokes et al. 2003; Manguette et al. 2020).

Observations in the clearing also offer a rare window into questions that have been raised about the potentially multilevel societies of gorillas. This is yet another area where long-term monitoring of known individuals and group membership can have broader implications on understanding western gorilla sociality. Over the years, Mbeli gorillas from different social units have been observed to socialize and merge groups on occasion within the bai and forest edges (Parnell 2002a). These observations prompted further questions as to what extent neighboring groups socialized and if western gorilla society had broader social networks or a larger sense of "community" (Parnell 2002a). Subsequent research on western lowland gorillas has provided evidence of multi-level sociality with social groups nested within larger units (Morrison et al. 2019). As western lowland gorillas only spend 1% of their time in bais (Parnell 2020a), studies in the forest setting are essential in furthering our understanding of great ape societies.

Mondika Gorilla project

Exploring the influence of resource availability on lowland gorillas in the diverse forests of central Africa was among the prescient topics prompting Dian Doran's initiation of the Mondika Gorilla Project in 1995 (Doran and McNeilage 1998). By establishing a field station in the Djeke Triangle forests along the border of the Central African Republic and Republic of Congo, Doran positioned the research program between the Guga and Mbeli field sites from which many of the novel observations of gorilla socioecology and interpretations of subgrouping were being reported. Primatologists across the region were making efforts to habituate a group of western lowland gorillas to the presence of humans (Lope, Gabon: Tutin and Fernandez 1991; Bai Houkou, Central African Republic: Blom 1998; Lossi, Republic of Congo: Bermejo 1996; Mondika, Republic of Congo: Doran-Sheehy et al. 2007; Teberd et al. 2023). Most previous work on gorillas in this region had relied on indirect traces (remains of food items consumed by gorillas, fecal analysis), whereas habituation would enable researchers to conduct daily follows through the forest to observe all aspects of gorilla daily life. Such efforts proved to be extraordinarily impactful for science and conservation, for example, by allowing the world to follow silverback Kingo and his group for more than three decades.

By the mid-2000s, findings from Mondika were published showing that gorilla diets consisted not only of terrestrial herbaceous vegetation like those in other central African forests (Remis 1994; Doran, et al. 2002; Rogers et al. 2004) but that gorillas also consumed notable amounts of ripe fruit in this lowland environment (Doran-Sheehy et al. 2009). These frugivorous foraging tendencies positioned western gorillas closer to chimpanzees on the dietary continuum, rather than closer to mountain gorillas who are more folivorous (Clutton-Brock and Harvey 1977; Rogers et al. 2004; Harcourt and Stewart 2007; Doran-Sheehy et al. 2009; Tutin and Fernandez 1993). This preference for fruit was hypothesized to have direct implications on the travel and social behaviors of lowland gorillas, both within and between groups. While initial reports of the range use of a single gorilla group at Mondika showed an expansive area covered (Doran-Sheehy et al. 2004), subsequent monitoring including multiple groups however detailed an annual average home range of 5.39 km^2 ($n = 31$) that remain stable over years (Judson et al. 2024). Larger social groups do maintain more expansive home ranges that overlap at Mondika, supporting arguments that western gorillas may face greater socioecological constraints compared to mountain gorillas (Robbins and Robbins 2018). While the average home ranges are similar in size to eastern gorillas that consume mostly herbs, it does not preclude goal-directed foraging for discrete food patches like fruiting trees as documented in other primates (Garber 1989). In fact, analyses of daily travel follows revealed that Mondika gorillas display a heightened spatial awareness of the location of key resources like preferred food patches over time (Salmi et al. 2020; Scarry et al. 2023). This includes foraging focused

on consuming "truffles" concealed underground at particular locals within monodominant *Gilbertiodendron dweveri* forests (Fig. 3) (Abea et al. this issue). Mondika gorillas returned year after year to the same resources indicating the presence of memory-based foraging.

Goal-directed foraging by neighboring groups could affect rates at which groups come into close proximity to other groups, and even compete between groups. However, interunit encounters of gorillas at Mondika were not found to be driven by resources like seasonally and asynchronously available fruits or abundance of herbs over a 5-year period (Cooksey et al. 2020). Instead, findings indicate defense of mates was more influential in dictating between-group competition (Cooksey et al. 2020). Social factors also influence space use strategies with the degree of intergroup home range overlap being the most influential factor in the timing and co-occurrence of neighboring groups at Mondika (Judson et al. 2024). Perhaps the most telling aspect of these inter-group observations is the common occurrence of tolerant and even affiliative interactions between neighboring

Fig. 3 "Soil scratching" for fungi growing in the root matrix within *Gilbertiodendron d.* forests requires patient foraging behavior by gorillas such as this adult male in the Djéké Triangle (**a**, Photo credit G. Duvot WCS/GTAP). Chimpanzees in the Ndoki forest use modified "fishing probes" to access termites from their mounds (**b**, Photo credit W.Burrad-Lucas/WCS). Chimpanzees use multiple tools to open beehives to access honey. In this photo, a chimpanzee uses a modified branch to lever-open the entrance of a hive (**c**, Photo credit S.BroganWCS/GTAP)

gorilla groups that may even scaffold into stable social relationships that are maintained for several years (Mondika unpublished data). Overall, the intergroup interactions observed during follows of groups through the forest at Mondika corroborate those documented at Mbeli Bai.

Gorilla communities

However, a surprising revelation from forest-based observations is that some dyads develop strong social relationships not only within but between groups. This challenges long-held notions of gorillas being asocial. Age and sex are key factors in determining gorilla group dynamics, with young males engaging most often in playful interactions with peers (Cooksey et al. 2024 in review). More interestingly, black-back males produce the largest impacts to the social connectivity within and between neighboring social units (Cooksey et al. 2024 in review). These extended social ties support early assessments indicating the existence of extended male networks at Mondika based on genetic relatedness (Bradley et al. 2004). Females also negotiate relationships between groups, particularly in cases where interactions may occur with their natal group (Cooksey et al. 2024 in review). Together, these observations bolster arguments for the existence of a larger gorilla "community" (Parnell 2002b).

The implications of an intergenerational component to gorilla social niche construction should not be overlooked. Further, we should avoid exclusively focusing on the roles of males. Any degree of social ties between neighboring silverbacks would presumably support an environment of tolerance between groups, which would have secondary implications for other group members, both in the present and future time scales. Forty percent of female group members are related which indicates non-random group selection among adult females (Bradley et al. 2007). Immatures and juveniles are also important actors within groups who have been observed to initiate and maintain contacts between groups. One can predict that relationships formed among immatures and information gained through their social interactions could have future benefits to them as adults. However, there are also potentially elevated health risks of pathogen exchange between groups that could have negative outcomes (Cooksey et al. 2023). Progress has been made in elucidating the ecology and behavior of western lowland gorillas which inform comparisons with other species of great apes, including chimpanzees that live in sympatry with western gorilla populations.

The Goualougo Triangle Ape Project

At the end of the twentieth century, detailed knowledge of coexisting central chimpanzee populations was also lacking (Tutin 2001). Analysis of indirect signs showed similar general ecological tendencies in dietary composition as well as nest building behaviors to eastern (*Pan troglodytes schweinfurthii*) and western chimpanzees (*Pan troglodytes verus*) (Tutin and Fernandez 1993). These initial findings were instructive but did not provide the level of detail needed to assess variation across the chimpanzee range. For example, Eastern chimpanzees were habituated at Gombe (Goodall 1986) and Mahale (Nishida 1990) Tanzania in the 1960s; and Western chimpanzees at Tai, Ivory Coast (Boesch and Boesch-Achermann 2000) and Bossou, Guinea (Sugiyama and Koman 1979). Initiation of the Goualougo Triangle Ape Project (GTAP) in northern Republic of Congo by David Morgan and Crickette Sanz was inspired by the opportunity to shed light on this little-studied subspecies of great ape. Importantly, this was the first chimpanzee research site that was launched with a conservation emphasis from the outset and a strong focus on interdisciplinary research that included anthropology, ecology, botany, epidemiology and other perspectives. Also integral was the emphasis on identifying national scholars to lead research efforts in ape density estimation (Jean Robert Onononga, Crepin Eyana, Wen Mayoukou), botanical surveys (Sydney Ndolo Ebika, Davy Koni) and other key topics.

Estimating ape density and habitat use

Since there was very little information on the ecology of this region, the first aim was to develop a baseline understanding of the distribution and abundance of great apes across the Goualougo Triangle watershed and neighboring forests. As described in Morgan et al. 2006, the 525 km^2 study area was stratified into study zones designed to assess ape density and habitat use across different conservation contexts (pristine forest with no disturbance, active logging zone, zone adjacent to active logging zone). Line transects and botanical plots were placed systematically to produce independent abundance estimates in each zone for long term monitoring. This was to facilitate detection of changes in ape abundance estimates and habitats in relation to protection status and/or anthropogenic disturbances, such as road construction, mechanized logging and the presence of research, community use and tourism activities.

Baseline nest counts indicated a relatively high abundance of chimpanzees and gorillas in the intact forests, compared to reports from other central and west African sites (Morgan et al. 2006). These initial survey efforts also revealed aspects of ape nest surveys that could be improved to more precisely estimate the abundance of sympatric apes, such as site-specific decay rates (Morgan et al. 2016) and methods to distinguish nests of different ape species (Sanz et al. 2007b). With the imminent arrival of forestry in the once-logged study zone, we conducted repeated surveys along the same transects in the logging concession zone

to implement a before, during and after assessment of the impact of selective logging on apes. Both chimpanzees and gorillas were adversely affected by timber extraction, but neither chimpanzee nor gorilla occurrence was dictated by anthropogenic impacts alone, as both species-maintained fidelity to their ecological preferences via flexible coping strategies (Morgan et al. 2019). Although the study spanned 5 years, continued monitoring of repeated selective logging on the great apes and their environment is necessary and ongoing to determine the long-term impacts.

As mentioned above, the research teams studying apes in the forest and conducting line transects realized that there was an urgent need to improve the accuracy and precision of the transect methodology on which ape density estimates are based. More specifically, we found that 75% of ape nests recorded on transects were not directly attributed to either gorillas or chimpanzees. Synthesizing insights from our direct observations of apes building nests, we developed a predictive model to distinguish between the nests of sympatric apes which increased the precision of resulting ape abundance estimates (Sanz, et al. 2007). Another aspect of ape nest surveys that reduced their accuracy was the generalization of nest conversion factors from other study sites. Both nest creation and decay rates for gorillas and chimpanzees were generalized across study sites because of the intensive and costly effort to generate such information for specific sites. Given the importance of these conversion factors to the long-term monitoring across the Ndoki landscape, a 9-month study was conducted to quantify species-specific nest decay times in Ndoki. For this study, Jean Robert Ononga detected and monitored the disappearance of 1035 nests observed along line transects. Nest decay rates differed between habitats but showed fewer differences between ape species than previously suggested (Morgan, et al. 2016). Nest creation rates were calculated from daily follows from the first community of central chimpanzees to be identified and followed on a daily basis. The resulting conversion factors have improved the reliability and precision of transect studies across the Sangha Tri-National, Ndoki–Likouala and Odzala–Kokoua landscapes. Outcomes from these studies have also played critical roles in lobbying for the protection of these endangered apes and their forest environments (Brncic et al. 2018; Strindberg et al. 2018).

Chimpanzee tool use and culture

Drawing insights from the landmark studies of chimpanzee tool-using behaviors by Jane Goodall in East Africa and Christophe Boesch in West Africa, Morgan and Sanz predicted that the chimpanzees of the Goualougo Triangle would have a unique tool repertoire and material culture. Our discoveries included not only the different types of tools used by this population of central African chimpanzees, but also how they teach this information to younger individuals. Tools varied in task difficulty from simple leaf sponges for gathering water to complex tool sets that were used to access and extract termites from subterranean nests (Sanz et al. 2004). In total, more than 22 different tool behaviors have been documented, indicating Goualougo chimpanzees have one of the largest and most diverse tool repertoires reported for *Pan troglodytes* and indeed the animal kingdom (Sanz and Morgan 2007a). Another notable aspect of the tool-using behavior of Goualougo chimpanzee is the brush-tip modification of fishing probes that results in increased efficiency in harvesting prey (Sanz et al. 2009b). The subterranean context however first requires the chimpanzee to access the nest with a puncturing stick and then follow this tool action with a modified fishing probe (Fig. 3b). This specific tool-set and associated actions provide an example of cumulative cultural knowledge in the chimpanzee.

The tool using propensities of Goualougo chimpanzees also have important implications for understanding the transmission of information over time and across generations (Musgrave et al. 2019). For 20 years, we have monitored chimpanzee visitation to termite mounds. It is at these tool-using sites where individuals encounter tool traces left behind by previous visitors. The presence of such tools effectively passes along ecological legacies to others who visit the nest via social learning opportunities through local and stimulus enhancement, but also to future generations via niche construction (Sanz et al. 2019). Interactions with others at these tool sites is also an important aspect of teaching tool skills (Musgrave et al. 2019). Through a combination of observational learning, handling of discarded tools and sharing of tool items, future generations of Goualougo tool-users are shaped at these centers of learning. By comparison, chimpanzee mothers at Gombe are less likely to act as models or share tools with their close kin (Musgrave et al. 2019). These differences between populations in social facilitation of tool using skills could be related to the complexity of the task. These findings and research were at the forefront of what became a second wave of surveys to document chimpanzee tool traditions across the range of *Pan*, an effort made more feasible by camera trapping technology that was first pioneered in the study of chimpanzee behavior ("Chimpcams") in the Goualougo Triangle (Sanz et al. 2004).

The skilled techniques and impressive multiple tool assemblages of the Goualougo chimpanzees are not limited to the terrestrial biome. These apes use multiple tools in the high canopies of trees to access honey from the hives of stingless bees. In fact, these trees are among the largest in the forests of Africa (Bastin 2015). After identifying a beehive, the chimpanzees manufacture a wooden pounding club from nearby branches to create an access point in the hive (Fig. 3c). Once the hive has been breached, another

tool will be made from smaller twigs to dip into the hive to gather the honey and brood. Such honey gathering tool sets appear to be a behavioral trait of chimpanzees inhabiting Central Africa (Fay 1994; Bermejo and Illera 1999; Hicks et al. 2005; Boesch et al. 2009; Sanz and Morgan 2009a; Sanz and Morgan 2013). Identifying the specific mechanisms that promote and maintain such cultures remains an ongoing research focus at Goualougo, Mondika and beyond.

Chimpanzee sociality

Having longitudinally followed the Moto chimpanzee community in the Goualougo Triangle across contexts in the forest and using camera traps for in-depth investigations of their tool use and cultural transmission, this site can offer new perspectives on the influence of fission–fusion sociality on the expression and possible accumulation of cultural variants. From several years of matched data collection across these modes of observation, Funkhouser et al. (2024) adopted the concept of social niche construction to explore the potential for individual behavioral strategies within fission–fusion systems to produce differences in social complexity both at the individual and group level across feeding contexts. Specifically, we examined patterns of individual behavioral strategies in the construction of social niches across asynchronous *Ficus* feeding events and termite=gathering visits in this community of central African chimpanzees. While reporting some of the first accounts of social behavior for this sub-species, we also elucidated how social niche construction produces different patterns of relationships and social complexity across contexts that are stable in their expression over many years, and likely offer functional benefits. Such benefits likely include the presence of social niche specialists who function as models to focus the context- or skill-specific learning of conspecifics in chimpanzee communities.

Gorilla sociality

Our long-term studies of gorillas in the Goualougo Triangle have also shown that in contrast to the single-male breeding group structure observed at Mbeli and Mondika multi-male groups do occur, indicating that single-male breeding groups are not the only configuration present in other areas. The Loya gorilla group is a multi-male social unit that has persisted for years since the arrival and first documentation of a group takeover by an external silverback. While several multi-male social groups have been observed in the region, their formation was because of late natal dispersal of mature males and the durations of these groups were not long-lasting (see Robbins et al. 2004). Before the disintegration of the Kingo group at Mondika the social unit was an all-male group of mixed-aged individuals. There is likely a combination of ecological and social factors driving the existence of a two-silverback group in Goualougo. Male mating competition as well as elevated levels of population densities (Caillaud et al. 2020) could support the formation of two-silverback groups but observations of such competitive events have not been recorded in gorillas at Mondika nor at Mbeli Bai. This is despite an Mbeli Bai gorilla population growth rate doubling in known individuals over the last 25 years (Robbins et al. 2022). The Mbeli population increase is based on direct observations from a localized forest clearing and may not provide an accurate assessment of changes in the overall population. To answer population level questions on the number of individuals with great confidence requires additional evaluation techniques.

Great ape coexistence

Taking up the initial inquiry of coexisting apes (Kuroda 1992; Suzuki and Nishihara 1992; Kuroda et al. 1996), Morgan and Sanz documented observations of interactions among gorillas and chimpanzees. The quality of these observations significantly improved after a group of gorillas was habituated within the home range of the Moto chimpanzee community. The "Loya" gorilla group has been followed on a daily basis since 2014, making Goualougo the first and only field station to feature two species of great ape that can be studied by direct observations in the same locality due to their spatial overlapping home ranges. This provided an unprecedented opportunity to study whether these apes showed preference for certain social partners of the other species and if these relationships were consistent over time. Over a 20-year period, we observed more than 300 interspecific interactions that ranged from predominant play to infrequent aggression (Sanz et al. 2022). The strength and persistence of social relationships also indicates a depth of social awareness and a myriad of between-species social transmission pathways previously not imagined. Certain types of interactions may also afford unique development opportunities that extend the individual's social, physical and cognitive competencies. Ongoing research investigating transmission pathways of beneficial, socially learned cultural behaviors as well as potentially harmful outcomes such as the spread of infectious disease are ongoing avenues of study.

Ndoki great ape and monkey density estimates

A foundational monitoring component of longitudinal assessments in Africa are transect surveys of great ape nests and diurnal primates to inform population dynamics (Chapman et al. 2023). At present, at least an estimated 7000 km of transects across approximately 33,000 km of northern Congo forest and swamps have been realized since

the creation of the park. The most recent ape surveys in the landscape come from the Djéké Triangle, an area that has scantly received much attention in terms of ape nest surveys. Ape nest counts in this forest revealed high gorilla and chimpanzee abundances in comparison to neighboring forests (Table 2). While density estimates for both species vary over short time periods, both species populations are stable (Mayoukou et al. 2024 in review). What also remains consistent is gorilla densities tend to be higher in terra firma forests featuring open canopy (Morgan, et al. 2006; Stokes, et al. 2010), whereas chimpanzees prefer nesting in closed canopy terra firma forests as well as monodominant stands of *Gilbertiodendron dweverei* forests (Morgan et al. 2006; Stokes et al. 2010). Ape abundances also vary across space and time, with distance from anthropogenic impact being an important factor. Lower densities of apes are generally documented in closer proximity to human disturbances. Temporal aspects such as time since exploitation of timber also influence densities of chimpanzees, with lower numbers of this species found in more recently logged forests (Morgan, et al. 2018; Stokes, et al. 2010). Conversely, gorilla abundances tend to be higher in once- and twice- logged forests, which corresponds with this species' preference for more open canopy habitat (Stokes et al. 2010).

Diurnal monkey populations at Ndoki also change depending on habitat type and anthropogenic factors. Based on line transect surveys in the Goualougo Triangle and wider NNNP, Putty-nosed monkey, Crowned monkey, and Grey-cheeked mangabey show a wide distribution and high encounter rate across intact forests (Table 2). Wider scale surveys in 2002 and 2006 in unlogged and logged forests in logging concessions did not indicate significant differences in the relative abundances of Putty-nosed monkey or Grey-cheeked mangabey (Clark et al. 2012). However, more intensive surveys in one of the CIB–OLAM concessions revealed primate densities to be an estimated 30% lower than those in the neighboring NNNP (Poulsen et al. 2011). Follow-up surveys in 2016–2017 also indicated concerning declines in relative primate abundances in forests, particularly those surrounding towns like Pokola and Kabo (Brncic, et al.

Table 2 Density estimates and encounter rates of great apes and monkeys in the Ndoki forest

Species	Stratum	Forest status	Measure of abundance	Abundance (95% CI)
Western lowland gorilla (*G. g. gorilla*)	NNNP[a]	Unlogged	Density	1.02 [0.59–1.77]
	Goualougo Triangle[b]	Unlogged	Density	2.34 (1.83, 2.99)
	Djéké Triangle, 2016[c]	Unlogged	Density	2.15 [1.36–3.40]
	Djéké Triangle, 2018[c]	Unlogged	Density	1.19 [0.78–1.82]
	Kabo FMU[a]	Logged	Density	2.16 [1.02–4.56]
	Pokola FMU[a]	Logged	Density	4.08 [2.27–7.36]
	Loundougou FMU[a]	Logged	Density	0.78 [0.34–1.77]
	Mokabi FMU[a]	Logged	Density	0.15 [0.05–0.45]
Central chimpanzee (*P. t. troglodytes*)	NNNP[a]	Unlogged	Density	1.03 [0.61–1.71]
	Goualougo Triangle[b]	Unlogged	Density	0.3–1.0
	Djéké Triangle, 2016[c]	Unlogged	Density	0.75 [0.52–1.09]
	Djéké Triangle, 2018[c]	Unlogged	Density	0.61 [0.40–0.92]
	Kabo FMU[a]	Logged	Density	0.39 [0.24–0.66]
	Pokola FMU[a]	Logged	Density	0.34 [0.14–0.82]
	Loundougou FMU[a]	Logged	Density	0.48 [0.25–0.90]
	Mokabi FMU[a]	Logged	Density	0.05 [0.02–0.13]
Putty-nosed monkey (*Cercopithecus nictitans*)	NNNP[d]	Unlogged	Density	79.7 [62.1–102.3]
	Goualougo Triangle[e]	Unlogged	Encounter rate	1.6
	Kabo FMU[d]	Logged/hunted	Density	0.37 [24.4–56.8]
Crowned monkey (*Cercopithecus pogonias*)	NNNP[d]	Unlogged	Density	34.9 [24.8–49.1]
	Goualougo triangle[e]	Unlogged	Encounter rate	0.5
	Kabo FMU[d]	Logged/hunted	Density	23.3 [15.9–34.2]
Mustached monkey (*Cercopithecus cephus*)	NNNP[d]	Unlogged	Density	39.7 [27.8–56.6]
	Kabo FMU[d]	Logged/hunted	Density	28.3 [15.9–50.1]
Grey-cheeked mangabey (*Lophocebus albigena*)	NNNP[d]	Unlogged	Density	49.5 [34.8–70.3]
	Goualougo Triangle[e]	Unlogged	Encounter rate	1.9
	Kabo FMU[d]	Logged/hunted	Density	14.9 [6.6–33.5]

[a]Stokes et al. 2010; [b]Morgan et al., 2006; [c]Mayoukou et al. 2024; [d]Poulsen et al. 2011; [e]Unpublished data

2018). Whether the low rates of detecting primates in these forests is based on real declines in individuals or species within these hunting zones employing anti-predation strategies that make observations by observers less likely remains to be explored. Roughly 66% of primate species globally are in danger of extinction (listed as Vulnerable, Endangered, and Critically Endangered) (IUCN 2024). Given primates are now among the most often observed prey of hunters in the Ndoki landscape (Poulsen, et al. 2009) more research on the underlying factors driving this demand and associated risks needs increased attention.

Mitigating health risks

The risk of emerging infectious diseases to primates in the Ndoki forests has been of concern since the initiation of the field stations. The late 1990s and early 2000s brought dramatic changes in local ape populations in Odzala–Kokoua National Park and surrounding forests as a result of Ebola and anthrax outbreaks (Walsh et al. 2003; Leroy et al. 2004; Bermejo et al. 2006; Leendertz et al. 2006). The long-term research sites not only provide a valuable conservation and research presence in the forest, but also serve as critical outposts for detecting and monitoring pathogens among wildlife and in the environment. The potential role of field sites as sentinels was highlighted by the sudden die-off of hundreds of known gorillas (Bermejo et al. 2006) that could have gone undetected if not observed by scientists in real time (Gillespie et al. 2008; Calvignac-Spencer et al. 2012; Lonsdorf et al. 2022). As a result, a unique partnership was forged between primate researchers and the Wildlife Conservation Society to address health concerns in the region affecting wildlife and human populations. The holistic One Health approach at Ndoki includes multiple activities, from daily health monitoring of primate field teams to systematic observational health assessments of known apes. This collaborative effort has also led to the development of policies and protocols to deter disease spread.

At a regional level, results also indicate the apes are susceptible to Human Respiratory Virus (HRV) and that simultaneous outbreaks in spatially close groups of gorillas in the Sangha Tri-National (TNS) may originate from different human strains (Jochum et al. 2024). In accordance with the IUCN's Primate Specialist Group's "Best Practice Guidelines for Health Monitoring and Disease Control in Great Ape Populations" (Gilardi et al. 2015), specific "Field Protocols for Disease Prevention and Health Monitoring" were developed for Mondika and Goualougo. Results from our monitoring of gorilla health have revealed an increased likelihood of clinical symptoms during periods of low fruit availability in gorillas and that adult male gorillas show the highest prevalence of respiratory signs (Cooksey et al. 2023). These new results are important considering the development of international and domestic gorilla-based tourism planned for sites like the Djéké Triangle, as well as those already in place in the TNS and Odzala–Kokoua National Park. While gorilla-based tourism can provide significant economic incentives through income, protection, and employment opportunities, the negative health and behavioral effects on the gorillas can also be considerable (Palacios et al. 2011; Mazet et al. 2020; Gessa and Rothman 2021; Costa et al. 2023). Given the examples from east Africa, gorilla tourism at Ndoki will need to be managed with the well-being of the apes, the sites and local human population central to achieving positive and sustained tourism outcomes.

Preserving intact forests

Historically, the low human population and remote nature of this region contributed to significant conservation gains. The most notable of these outcomes was the expansion of the NNNP by 360 km^2 through the incorporation of the Goualougo and Djeke Triangle into the park as a result of the combined efforts of the government, WCS and the field stations (Morgan and Sanz 2003; Morgan et al. 2023). These successes are also in part due to the industrial logging firm CIB–OLAM and its commitment to Forest Stewardship Council (FSC) certification and responding to the environmental recommendations of WCS. CIB–OLAM was the first in the region to voluntarily adhere to the FSC with the Kabo concession certificate in 2003, which was then expanded to three other concessions encompassing 2 million ha of forest. This is among the largest FSC-certified tropical forest regions in the world. Forestry practitioners and conservation scientists also developed a synergistic collaboration to integrate gorilla and chimpanzee needs into timber and land management policies (Morgan et al. 2020). Specific recommendations to improve existing best practice guidelines and FSC certification standards aim to safeguard these protected species (Morgan and Sanz 2007; Morgan et al. 2013). The near-term environmental benefits of certification have been verified across the certified concessions with primate populations largely remaining stable (Clark et al. 2009; Stokes et al. 2010; Morgan et al. 2018).

The diversity and abundance of primate species is an indication these forests are of high quality to the diurnal primate community. There are other measures based on environmental information such as remote sensing data that indicate the NNNP and surrounding landscape is of high forest integrity (Grantham et al. 2020). Elevated assessment scores in attributes such as tree canopy coverage, forest continuity, and distance from human disturbance suggest the NNNP supports corresponding high abundances of biodiversity, and ecosystem services (Hansen et al. 2019). Further, genetic studies of apes in and around the study area show genetic continuity

and gene flow throughout these forests (Fünfstück et al. 2014; Fünfstück and Vigilant 2015) reflecting the forests' integrity and importance for ape ecology. Protected status alone, however, does not ensure reduced deforestation particularly in environments where parks become increasingly isolated (DeFries et al. 2005). The REDD agenda (Reducing Emissions from Deforestation and Degradation) seeks to mobilize countries to reduce deforestation and protect existing forests. In northern Congo, forest clearance however is not widely practiced and the incentives for implementing REDD initiatives remain low. As a consequence, the long-term preservation of forests even designated national park status remain concerning. To meet this challenge the High Integrity Forest (HIFOR) initiative seeks to incentivize the continued protection of intact forests landscapes (IFL) and the environmental services like carbon sequestration, water security, and biodiversity derivatives. (https://www.wcs.org/our-work/climate-change/forests-and-climate-change/hifor). To do so will take collaborating with the Wildlife Conservation Society scientists to combine these recently developed analytical tools for mapping forest integrity with smaller scale ecological components that clarify what important forest attributes are at risk of being lost. Ground-based studies on primate resource use, phenology, and botanical surveys from the Goualougo and Mondika field stations will assist in identifying these forest components that are of conservation value to wildlife and humans alike. The Congo Basin is defined by the presence of large- statured trees (Bastin et al. 2015) and the Ndoki forests specious emergent tree layer is notable. Over 100 species reaching the largest size classes (tree stratum reaching 80 cm diameter and above) populate the forest canopies in this region (Harris et al. 2021). Informing the creation of standardized metrics representing important local environmental services such as large trees from baseline forest assessments is critical not only for protected intact forests, but also for those under threat in concessions and multi-use zones exposed to repeated exploitation.

Forest change and exploitation

Even with these successes there are multiple reasons for considerable concern in the near- and long-term for primates and their forest habitats in the Ndoki landscape. The forests neighboring the NNNP and indeed the whole of middle-northern Congo are in a state of transition with some areas already experiencing a third cycle of selective exploitation. Using the Hansen et al. (2013) data set, based on Landsat images at 30 m resolution in habitat with > 20% tree cover, forest loss was calculated between 2000 and 2021. Between those two survey periods there was a cumulative loss/degradation across eight concessions of 142,433 ha of forest. Forest change varied between logging concessions, with Kabo and Loundougou–Toukoulaka experiencing relatively low levels of forest degradation with an estimated 1% and 2% decline, respectively, whereas concessions more distant from NNNP, like Mimbeli and Ngombe, experienced elevated levels of change with a 5% and 7.6% decline, respectively (Ayina et al. 2023).

Forest clearance associated with linear infrastructure like logging roads is far more apparent and potentially just as significant to primate conservation for a variety of reasons. Over the last 25 years, there has been a surge in road construction in the landscape (Laporte, et al. 2007; Kleinschroth, et al. 2017). The period between 2013 and 2020 showed especially notable change, with an estimated 650 km^2 of IFL forests surrounding the NNNP being lost to route establishment (Morgan 2020). However, roads can be of benefit to the local and national economy as well as human population via accessibility to services. As part of a nationwide program to develop "economic growth for all" in the fight to eliminate poverty and hunger, Route Nationale #2 (or the "Trans-Congo Highway") will be extended and tarmacked, eventually linking the capital cities of Brazzaville in Republic of Congo and Kinshasa in the Democratic Republic of Congo to Central African Republic and the capital of Bangui 2,440 km away to the north. The highway will build upon the existing logging road network that bisects regions previously devoid of human settlements and domestic travel. In the early 2000s, when the forestry road network began expanding, a population increase of nearly 70% occurred, comprised largely of migrants to five logging concession towns (Poulsen et al. 2012). Improving the infrastructure and accessibility for domestic and commercial travel will stimulate an expanded engagement with regional and international markets, as well as potentially trigger a second influx of migrants to towns in previously remote forest regions. It also has the added risk of creating unsustainable demands on wildlife, including bushmeat, with data indicating species are already being hunted at unsustainable levels (Poulsen et al. 2009). Bushmeat market surveys indicate primates are the second most commonly observed species group hunted behind duikers in concessions bordering the NNNP (Poulsen et al. 2012). An increasing human population in the Ndoki region, largely composed of migrants relying on indiscriminate hunting practices, could lead to resource scarcity, which can imperil biodiversity (Cawthorn and Hoffman 2015) and threaten the conservation gains that have been made to date.

Traditional ecological knowledge and community collaboration

A crucial and largely overlooked approach across all of the Ndoki long-term field stations has been the local partnerships and involvement of Congolese nationals in all research and conservation activities. In particular, the indigenous

people's deep commitment to preserving these forests and sharing local Traditional Ecological Knowledge (TEK) has directly contributed to the success of both research and conservation over the past 25 years. The early generations of researchers have had impactful careers in conservation, with many now holding important positions as directors, conservators, professors, and project managers. These collaborative partnerships were the product of successful protection resulting from applied research and responsible resource use which in turn led to conservation jobs and revenue generation from the informative monitoring activities at the long-term field stations. This approach, which emphasizes developing the next generations of conservationists, has expanded as have jobs associated with protecting the larger biodiversity assets of the NNNP and forests. These colleagues have also acted as valuable role models and their leadership has diversified and strengthened responses to the opportunities and threats facing forests and primates. Scientific results from these collaborative engagements have also led to Goualougo and Mondika being among the top three percent of tropical field stations in publication output (Eppley et al. 2024). The scientific output not only bolsters the primate and conservation literature, but also local leadership in primary authorship positions. The percentage of publications from Republic of Congo with local primary authors has been lower than in sub-Saharan African countries (Tuyisenge et al. 2023).

The primates of the Ndoki landscape will once again face an uncertain future if protection measures and human communities outside the park's periphery fail to flourish. As in the past, present-day research team members can once again play an important role in meeting the challenges facing the Ndoki forests. Expanding engagement to peripheral community levels and translating the hard-earned conservation-oriented scientific information to messaging and actions that align with these communities will have far reaching conservation implications (Estrada et al. 2022). These are the communities that are likely to embody the values of long-term stewardship, communal obligation and authority in managing a significant proportion of Africa's forested lands and resources (Garnett et al. 2018). Given primates and particularly apes have long been incorporated in the spiritual traditions and beliefs of local indigenous peoples (Köhler 2005; Oishi 2013; Duda et al. 2017; Kohler and Brondizio 2017), they provide the avenues for local researchers to initiate dialogues in collaboration with community development actors.

Collaborative management approaches with local communities around the NNNP have had positive outcomes in identifying locations of cultural value and resource importance (Poynton 2012). Sharing the multicultural information we have learned at the field stations is a starting point for further community engagement. These connections will also ensure the inclusion and recognition of their knowledge and traditions when developing environmental and social monitoring tools. Importantly, there is also a concerted effort among primatologists in developing standards on how the cultures concept can be applied to existing conservation frameworks and policy initiatives (Carvalho et al. 2022).

Cultures are in decline, and we risk losing these rich legacies that have developed over millennia if we do not preserve the environments in which they emerge and are maintained. There is increasing realization that the lives and livelihoods of humans and wildlife are intertwined. This may involve shared plant resources or material use including resources with traditional and cultural legacies (Ellis et al. 2021). Regardless of the species or the specific cultural trait, there is an urgent need for broader and more effective conservation. Such actions to restore shared resource connections while safeguarding humans, primates and the Ndoki landscape will ensure that these primate communities exist for the next 20 years and beyond.

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