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Involvement of *Colobus polykomos* and *Procolobus verus* in polyspecific associations with other sympatric monkeys in Taï National Park, south-west Côte d'Ivoire

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Abstract

Polyspecific associations, observed in many vertebrates in natural environments, are particularly studied in primates of tropical forests due to the evolutionary and survival advantages they offer. However, understanding the associational dynamics between certain species, notably the King colobus and the Olive colobus in the Tai National Park (TNP) in Côte d'Ivoire, remains limited. Our study, based on a comprehensive analysis of ecological monitoring data from the TNP over 12 years, aimed to understand the associational dynamics of the King colobus, Olive colobus, and other Cercopithecines, as well as anthropogenic factors influencing their distribution in the TNP. The results reveal diverse associations among Cercopithecids in the TNP, involving up to seven species across the entire park. The Diana monkey stands out as a nuclear species, frequently associated with the King colobus. In contrast, the Olive colobus, due to its discreet nature, shows a low rate of observation in polyspecific associations. Our findings support the notion that primate associations follow an evolutionary trend primarily aimed at reducing the risk of predation. The study emphasizes the importance of understanding these associational dynamics to guide TNP management strategies, facing anthropogenic threats such as poaching. A more detailed approach, incorporating ethological aspects, is recommended for a better understanding of interactions among TNP primate species. These results lay the groundwork for future research to deepen the understanding of underlying mechanisms in these associations, contributing to the development of conservation strategies suitable for the complex environments of tropical forests.

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Introduction

Polyspecific associations, defined by the cohabitation of two or more animal species, are observed in natural environments among various vertebrates, including fish, birds, and mammals (Stensland *et al.*, 2003; Gatti *et al.*, 2021). This interspecific dynamic has been extensively studied in primates in the sub-Saharan African tropical forests (Buzzard, 2010; Kane and McGraw, 2017) and South America (Pinheiro *et al.*, 2011; De Carvalho Oliveira *et al.*, 2017).

While these associations may result from chance encounters between species, their evolutionary and survival significance has been recognized. Some polyspecific associations may be attributed to random encounters with limited evolutionary goals (Hutchinson and Waser, 2007; Whitesides, 1989), in-depth studies have revealed their importance. These associations offer significant advantages, primarily in terms of predator vigilance and access to food resources (Bryer *et al.*, 2013; Shaffer *et al.*, 2016). Although food competition increases with group size (Gogarten *et al.*, 2014; Kurihara and Hanya, 2015), polyspecific associations can be exempt from food competition (Smuts *et al.*, 1987) and even enhance food foraging for the involved species (Bryer *et al.*, 2013; Shaffer *et al.*, 2016). These advantages are particularly pronounced when associated species do not share the same food sources, as seen in frugivorous cercopithecines and folivorous colobines. Vigilance against predators is a crucial component of these associations, especially in species sometimes referred to as "nuclear" due to their role as anti-predator sentinels, alerting associated species (Amaral and Ragusa-Netto, 2008; Bangal and Sridhar, 2023). Although the term "nuclear species" may be confusing in some cases (Bangal and Sridhar, 2023) these species generally stand out with clearly perceptible alarm signals, distinctive movements, vibrant colors, and significant predator-detection abilities (Amaral and Ragusa-Netto, 2008).

In the Tai National Park (TNP) in Côte d'Ivoire, the Diana monkey (*Cercopithecus diana*) positions itself as a nuclear species, playing a central role in polyspecific associations with species such as the red colobus (*Procolobus badius*), Campbell's monkey (*Cercopithecus campbelli*), and the lesser spot-nosed monkey (*Cercopithecus petaurista*) (Bshary, 2001; Buzzard, 2006). However, among the eight species of Cercopithecidae present in the Tai National Park, the king colobus (*Colobus polykomos*) and the Olive colobus (*Procolobus verus*) are rarely studied in the context of polyspecific associations, despite being frequently observable throughout the park with the Diana monkeys. Understanding the associational dynamics of these two species among themselves and with other Cercopithecids in the park would provide a better understanding of the survival strategies of these monkeys, often challenging to observe in this environment. Additionally, information on the associational dynamics of cercopithecids in the TNP, subject to various types of anthropogenic aggression, would aid in better directing the park's management strategies, particularly in terms of ecological monitoring of primates.

With this perspective, our study relies on a comprehensive analysis of ecological monitoring data collected in the TNP over 12 years. The objective is to determine whether the associations between the King colobus, the Olive colobus, and other Cercopithecids result from chance or truly constitute a survival strategy for these two species. Furthermore, we will assess the influence of anthropogenic factors on the associational dynamics of these monkeys.

Material and methods

Study area

We conducted the study at the TNP, located in the southwest of Côte d'Ivoire, in the Cavally-Sassandra interfluve (Fig. 1). It is situated between 5°08' and 6°24' North latitude and between 6°47' and 7°25' West longitude (Boesch and Boesch-Achermann, 2000). Covering an area of 536,018 hectares (Tiedou *et al.*, 2018), this park is the oldest in the humid tropical forest zone of West Africa (Terborgh *et al.*, 2002). Due to its relatively large size, the TNP is subdivided into 5 sectors (Taï, V6, Soubré, Djapadji and Guiroutou) administered by the Office Ivoirien

des Parc et Réserves, the institution that manages protected areas in Côte d'Ivoire. This park harbors over a thousand vertebrate species belonging to various classes (Mammals, Birds, Reptiles, Fishes, and Amphibians), as well as countless invertebrates (Chatelain *et al.*, 2001). The park is home to 12 primate species, including eight Cercopithecids, of which three are Colobines and five are Cercopithecines, the focus of our study (Table 1). The climate in the Tai National Park is subequatorial, warm, and humid throughout the year. It is characterized by two rainy seasons, a major one (from March to June) and a minor one (from September to October), alternating with two dry seasons, a major one (from November to February) and a minor one (from July to August) (Collinet *et al.*, 1984).

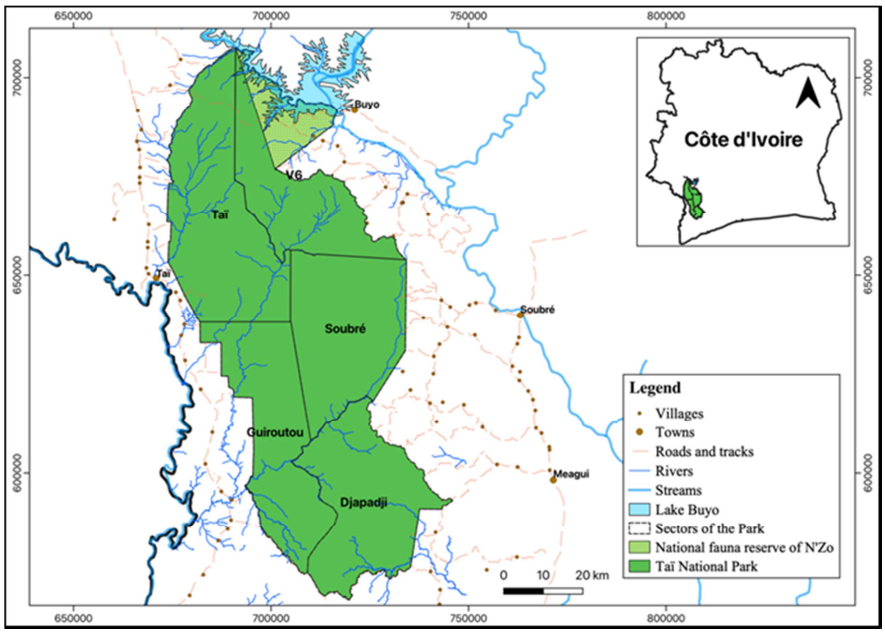

Fig. 1. Geographical location of the Taï National Park in Côte d'Ivoire

Table 1. List of the Cercopithecids living in the Taï National Park

Common name	Scientific name	Abbreviation	IUCN status 2023
Colobine			
Red colobus	*Piliocolobus badius* (Kerr, 1792)	Bad	Endangered
King colobus	*Colobus polykomos* (Zimmermann, 1780)	Pol	Endangered (EN)
Van Beneden's colobus	*Procolobus verus* (Van Beneden, 1838)	Ver	Vulnerable (VU)
Cercopithecine			
Diana's monkey	*Cercopithecus diana* (Linné, 1758)	Dia	Endangered (EN)
Campbell's Mone	*Cercopithecus campbelli* (Waterhouse, 1838)	Cam	Near Threatened (NT)
Lesser spot-nosed monkey	*Cercopithecus petaurista* (Schreber, 1774)	Pet	Near threatened (NT)
White-nosed Guenon	*Cercopithecus nictitans stampflii* (Waterhouse, 1838)	Nic	Endangered (EN)
Sooty Mangabey	*Cercocebus atys* (Audebert, 1797)	Aty	Vulnerable (VU)

Data collection

The data utilized in this study originate from the ecological monitoring database conducted at the TNP by the Ivorian Office of Parks and Reserves (OIPR) in collaboration with the Wild Chimpanzee Foundation. These data were collected over 12 years from May 2005 to September 2016 through counts along line transects (Buckland *et al.*, 1993). The data collection during these years was carried out by teams of 8 individuals with experience in primate species identification, including members of local communities, OIPR agents, and master's and doctoral students. To cover a greater distance per day, each team split into two groups of four people (two

assistants, one agent, and one student) before starting counts along line transects. Thus, each team covered two transects per day during each mission, which lasted 7 to 8 days, with two missions per month. In each phase (yearly), 294 transects oriented perpendicularly to the main watercourses and systematically distributed throughout the extent of the TNP were scheduled for ecological monitoring during the summer. Teams made maximum efforts to cover as many transects as possible. For example, in 2016, 291 transects out of 293 planned were covered, covering 569.48 km. In addition to transects, teams conducted reconnaissance walks to locate primate groups in areas difficult to access via transects, as suggested by some researchers (White and Edwards, 2000; Whytock *et al.*, 2021). The teams recorded the species identified and their geographical positions during ecological monitoring. In our study, we only considered data related to Cercopithecids species. Along the transects, observers also recorded indicators of human activities within the park including signs of poaching (camps, gun casings, gunfire sounds, and traps), old plantations, tree cutting (toothpick cutting, wood shavings, skidding sites), old gold mining sites, object left by human and tracks used for the illegal anthropic activities in the forest.

Data analysis

We analyzed polyspecific associations, considering at least two of the eight Cercopithecidea species living in the TNP. Subsequently, we extracted associations involving *Colobus polykomos*, *Procolobus verus,* or both species for a more in-depth analysis. In this extraction, we examined 52 types of associations involving two to seven cercopithecid species in the TNP. Each association involved *Colobus polykomos* and/or *Procolobus verus*. Specific composition data were organized into a presence-absence matrix, where the number "1" in the "i" row of a "j" column indicates that species "j" is present in the species group "i," and the number "0" indicates the absence of the considered species in the specified species group. We conducted three binomial logistic regression models, with the dependent variable being the presence-absence of *Colobus polykomos*, *Procolobus verus,* or both species, evaluated against the categorical variable "type of association." In our analysis of the signs of human activity, we focused mainly on the traps and gun blasts reported by observers. To ensure a single record of evidence over the years, observers systematically defused and removed all traps discovered in the forest, thus guaranteeing the consistency of evidence throughout the different phases of monitoring. However, integrating other indicators of human presence proved tricky, as some of these signs remain over time, potentially skewing the data and complicating accurate assessment. The data were processed using IBM STATISTIC SPSS Version 25.

Results

Occurrence of species in associations

During the study period, polyspecific associations among cercopithecids in the TNP were observed across the entire park (Fig. 2).

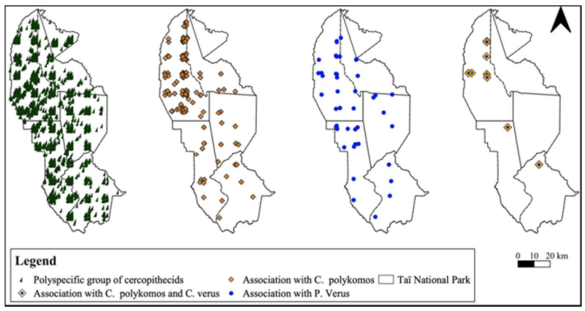

Fig. 2. Distribution of polyspecific associations involving *Colobus polykomos*, *Procolobus verus* and both species at TNP from 2005 to 2016

These associations involved *Cercocebus atys*, *Cercopithecus campbelli*, *Cercopithecus nictitans*, *Cercopithecus diana*, *Cercopithecus petaurista*, *Colobus polykomos*, *Piliocolobus badius*, and *Procolobus verus*. The associations involving *Colobus polykomos* (X^2=178.57; df=19; p<0.001) were visible over a large area of the TNP (Fig. 2), like associations involving *Procolobus verus* (X^2=183.69; df=19; p<0.001), though less represented (Fig. 2c) than those involving *Colobus polykomos*. On the other hand, associations involving both species were rare

and had limited representation in the TNP (Fig. 2d). The few observations of these associations involving *Colobus polykomos* and *Procolobus verus* (X^2=100.31; df=19; p<0.001) were recorded in the Taï, Guiroutou, and Djapadji sectors.

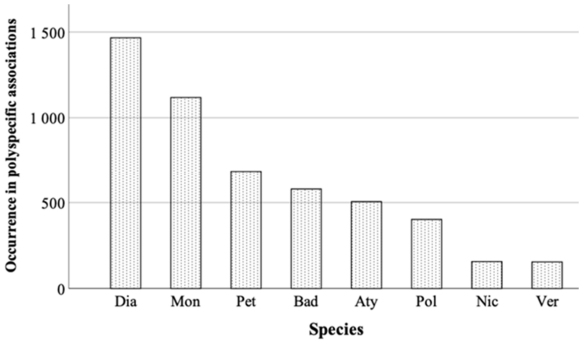

Fig. 3. Occurrence of each cercopithecid species in polyspecific associations at TNP

Aty= *Cercocebus Atys*; Bad= *Piliocolobus badius*; Cam= *Cercopithecus campbelli*; Dia= *Cercopithecus diana*; Pet= *Cercopithecus petaurista*; Pol= *Colobus polykomos*; Nic= *Cercopithecus nictitans*; Ver= *Procolobus verus*

A total of 1997 association records were documented, with *Cercopithecus diana* and *Cercopithecus campbelli* being the most prevalent species, each appearing in more than 1000 associations (Fig. 3). *Colobus polykomos*, with 402 records, was more frequently observed than *Procolobus verus,* which had 155 records.

Primate associations involving Procolobus verus and/or Colobus polykomos in the TNP

Among the 510 polyspecific associations analysed in this study the association between *Cercopithecus diana* and *Colobus polykomos* was the most frequent, with over 60 observations (Fig. 4). Following this, we observed associations such as *Piliocolobus badius*, *Cercopithecus diana, Colobus polykomos*; *Piliocolobus badius, Cercopithecus campbelli, Cercopithecus diana* and *Colobus polykomos*; *Cercopithecus campbelli, Cercopithecus diana, Colobus polykomos*, and *Cercopithecus diana, Cercopithecus petaurista, Colobus polykomos* each with over 20 observations. Associations involving *Colobus polykomos* were more frequently observed in the TNP compared to those involving *Procolobus verus,* which, in each case, had fewer than 20 observations. There were very few associations involving species, *Colobus polykomos* and *Procolobus verus,* in our observations. Associations involving these two species accounted for less than 1% of association observations, ranking them among the least frequently observed associations within the TNP.

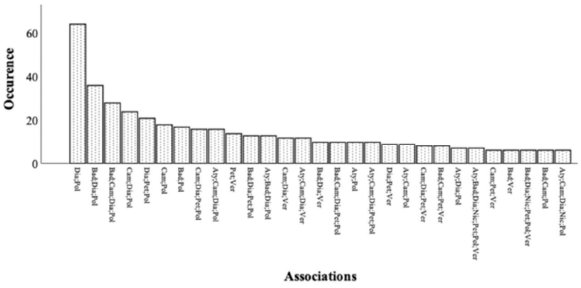

Fig. 4. Main polyspecific associations between TNP cercopithecids

Aty= *Cercocebus atys*; Bad= *Piliocolobus badius*; Cam= *Cercopithecus campbelli*; Dia= *Cercopithecus diana*; Pet= *Cercopithecus petaurista*; Pol= *Colobus polykomos*; Nic= *Cercopithecus nictitans*; Ver= *Procolobus verus*

Association between Colobus polykomos, Procolobus verus, and other sympatric monkeys

In the polyspecific associations recorded during the study, *Colobus polykomos* was more frequently associated with other cercopithecids compared to *Procolobus verus* (Fig. 5). Both species, either together or separately, were most frequently observed with *Cercopithecus diana*, showing a significant proportion of associations between *Colobus polykomos* and *Cercopithecus diana*. In this study, *Cercopithecus nictitans* was the least associated species with both *Colobus polykomos* and *Procolobus verus*. No associations were observed exclusively between *Procolobus verus* and *Colobus polykomos*. Of the two species, *Colobus polykomos*, in 63% of cases, was more frequently observed in associations than *Procolobus verus,* which accounted for 28% of cases (Fig. 6). The two species were rarely seen together in polyspecific associations within the TNP.

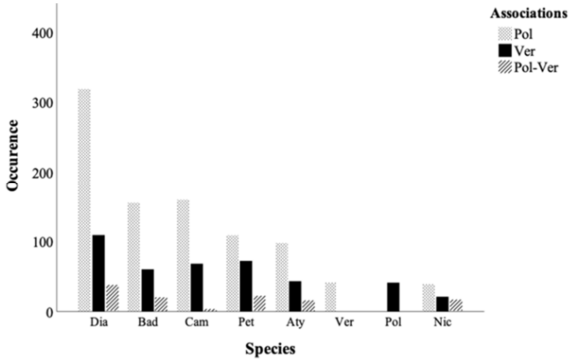

Fig. 5. Proportion of sightings of *Colobus polykomos*, *Procolobus verus* and both species in associations which each species of Cercopithecids at TNP

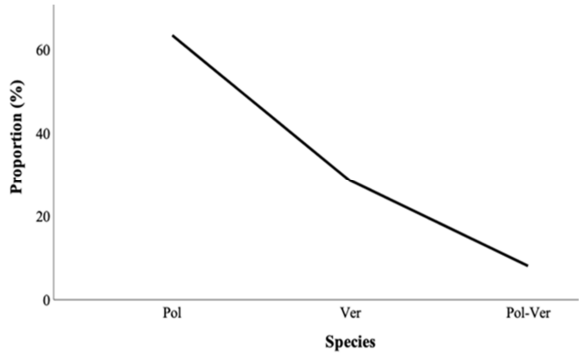

Fig. 6. Proportion of sightings of *Colobus polykomos*, *Procolobus verus* and both species in polyspecific associations of Cercopithecids at TNP

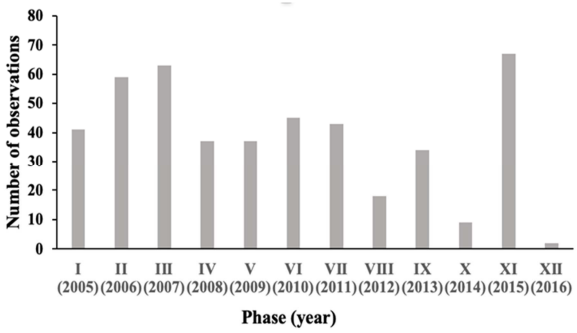

Fig. 7. Occurrence of poaching indices in the TNP

Anthropogenic threats

A total of 455 poaching indices (mainly traps and gunfire sounds) were recorded within the TNP from 2005 until 2016, with peaks in 2006, 2007, and 2015, where over 50 indices were recorded each year (Fig. 7). In 2012 and 2014, were the years with the lowest number of indices recorded, with below 20 indices in 2012 and below 10 indices in 2014. Despite these variations, there was no significant difference in the number of records between years (X^2= 10.846, df= 10, p= 0.3696). The poaching indices were observed across the entire extent of the TNP (Fig. 8). In addition to the signs of poaching, several other signs of human aggression (old plantations, some rare gold mining site in the sector of soubré) have also been observed in the TNP.

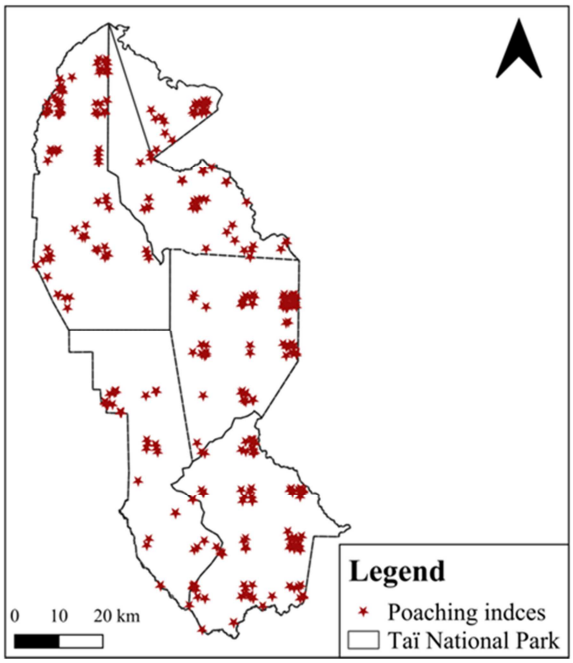

Fig. 8. Distribution of signs of poaching in the TNP from 2005 to 2016

Discussion

Our results highlight that the eight species of cercopithecids can be involved in polyspecific associations. In these associations, it was possible to observe between two and seven different species together. This observation reflects the specific primate diversity of this park, characterized by a habitat allowing primate survival and social dynamics within this ecosystem.

In these associations, the Diana Monkey was the most frequently observed species, confirming its nuclear role, as observed in several studies in the TNP (Bshary, 2001; Buzzard, 2006). The king colobus was the most frequently observed species in associations with the Diana Monkey, possibly justified by their different use of food resources, with one being

frugivorous (Kane and McGraw, 2017) and the other folivorous (Dasilva, 1994). However, another frugivorous species, the Campbell's monkey, was often observed with the Diana Monkey, which could be explained by the remarkable dietary flexibility that certain species, like the Diana Monkey, exhibit in these polyspecific associations (Kane and McGraw, 2017). Alongside *Colobus polykomos* and *Piliocolobus badius* was also frequently associated with *Cercopithecus diana*. As demonstrated by Noë and Bshary (1997), the association between *Piliocolobus badius* and *Cercopithecus diana* has a strategic aspect against predation by chimpanzees. The frequent association of *Colobus polykomos* with these two species suggests that it benefits from this anti-predator strategy. Our observations affirm that the involvement of *Colobus polykomos* in polyspecific associations among cercopithecids in the TNP is not a random occurrence. However, more in-depth behavioral observations will contribute to a better understanding of the associative dynamics of *Colobus polykomos* with other primates in the TNP.

The Van Beneden's colobus has been less frequently observed in association with the Diana's monkey compared to other primates. However, it has been confirmed that *Procolobus verus* has a strong tendency to associate with *Cercopithecus diana* as part of an evolutionary strategy to reduce the risk of predation (Whitesides, 1989; Oates and Whitesides, 1990). The low rate of observed associations of *Procolobus verus* with other cercopithecids in the TNP could be linked to the sampling method used for data collection in our study. We analyzed ecological monitoring data primarily aimed at assessing animal species populations in the TNP to refine the park's management strategy. In this case, the relevance of primate behavioral information is incomplete. Moreover, *Procolobus verus* typically lives in small groups of less than 10 individuals, being the smallest of all colobines, with adult males averaging 4.7 kg and adult females 4.2 kg (Oates, 1988), and displaying very dull colors. These factors increase the difficulty of observing this species within the TNP, which is a habitat of dense evergreen forest, also explaining the rare observations of associations between *Procolobus verus* and *Colobus polykomos*. Furthermore, this species, although having a repertoire of varied unitary and combined calls, does not emit a long call that would allow ecological monitoring agents to easily detect it (Bene *et al.*, 2012, 2007). We suggest incorporating an ethological component to the methodology of the ecological monitoring program of the TNP to facilitate data acquisition on the associative dynamics of primates in the protected area. We also encourage the investigation of *Procolobus verus* in polyspecific primate groups, including *Cercopithecus diana*, during ecological monitoring phases. Our study emphasizes the importance of a more detailed approach to understanding interactions between primate species in the TNP and the environmental factors that could influence these relationships.

Despite the significant number of human presence indices distributed throughout the entire TNP, we observed associations among several species of cercopithecids across the park. This suggests that, through the years, the level of protection in the TNP remain relatively satisfactory, creating favourable conditions for the viability of primate populations in this park. However, ongoing efforts are essential because certain activities remain highly dangerous for wildlife habitat, notably old gold mining sites, old plantations, and areas of true cutting. The relatively low number of poaching reports in 2014 may be attributed to the widespread fear and disruption caused by the Ebola fever outbreak in West Africa during that time (Nyenswah *et al.*, 2014; Fa *et al.*, 2019). This hypothesis gains credence when considering the significant surge in poaching indices recorded in 2015, likely spurred by a large influx of poachers into the TNP following the subsiding of the Ebola epidemic. The existing aggressions in the TNP demand a strengthening of protective measures, especially regarding poaching, which might be the most significant threat to the biodiversity of the TNP according to OIPR. This is not only the case of TNP, but poaching has been repeatedly confirmed as a major cause of biodiversity loss across the world

(Estrada *et al.*, 2017; Ferreguetti *et al.*, 2023). It is important to emphasize that the encounter rates of human signs observed during the period of this study has notably been reduced particularly from 2015 to 2016 due to the conservation effort made by the OIPR. At the same time, efforts are still needed since some of those illegal activities, in particular poaching, can take on considerable proportions again, as was observed during phase XI. Specific sectors within the TNP require considerable protection efforts, with a particular focus on the sector of Soubré where, in addition to poaching threats, most of the old illegal gold panning sites have been recorded.

Conclusion

Our study has provided insights into the polyspecific associations among cercopithecid species within the Taï National Park (TNP). Notably, *Colobus polykomos* and *Procolobus verus* are frequently involved in these associations, particularly with the *Diana Monkey*, supporting earlier research that underscores the complexity of these primate social structures. The diversity of these associations reflects the rich primate biodiversity of the park, shaped by habitat conditions that foster survival and interaction. However, our study also highlights gaps in data collection, particularly concerning *Procolobus verus*, whose association rates may have been underrepresented due to the study's methods. Additionally, our observations underline the need for sustained conservation efforts in the face of ongoing threats like poaching and illegal activities that could destabilize this primate community.

Recommendations

We recommend incorporating ethological studies into ecological monitoring to better understand the dynamics of polyspecific associations, particularly for *Procolobus verus*. Strengthening anti-poaching measures, especially in high-risk sectors like Soubré, is crucial given the resurgence of illegal activities post-Ebola. Future research should focus on key species such as *Colobus polykomos* and *Procolobus verus*, examining the environmental and behavioral factors driving their interactions. Continuously refining conservation strategies will be essential to address both immediate human threats and ensure long-term habitat preservation in the TNP.

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