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Thirty years of arboreal wildlife trends in an African rainforest under evolving threats and researchers' presence

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ABSTRACT

Long-term wildlife monitoring is necessary to inform adaptive management and assess conservation measures. The long-term presence of researchers may also indirectly induce positive effects for wildlife conservation by deterring harmful activities, such as hunting and resource extraction. However, long-term research is challenging and thus rare. Here, we assess long-term trends of wildlife near a research station that was established, abandoned, and reestablished. We conducted monthly surveys of arboreal wildlife from 1995 to 1999 and 2017 to 2024 in a protected Cameroonian rainforest where illegal hunting is common. Coinciding with the initial establishment of the research station, the relative abundance of 10 out of 12 arboreal species (hornbills, primates, and parrots) increased from 1995 to 1999. However, the station closed in 1999, and by 2017, the relative abundance of many species had decreased compared to levels in 1999. Finally, no species increased in relative abundance after the station reopened in 2017; instead, many declined between 2017 and 2024. Although we lack control sites, these results suggest that researchers' presence can sometimes have a protective effect, but also that this effect can be variable and limited depending on circumstances. The declining trends from 1999 to 2024 align with the evolving state of hunting in Central Africa, which is shifting toward increased commercial hunting and the use of guns that are more effective than snares for harvesting arboreal species. We recommend providing sustained support for research stations, collaborating with local communities to reduce bushmeat hunting, and enhancing enforcement against the international trade of hornbill casques and pet parrots.

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1. Introduction

Humans are impacting terrestrial wildlife communities globally, often due to hunting and habitat degradation (Dirzo et al., 2014; Johnson et al., 2017). Conservation efforts and protected areas aim to minimize these threats (Rodrigues and Cazalis, 2020), but success can vary, and results are context- and species-specific (Hoskins et al., 2020; Laurance et al., 2012; Sonhaye-Ouyé et al., 2022). Long-term wildlife monitoring is fundamental for assessing the need for, and effectiveness of, conservation measures and informing adaptive management. Furthermore, long-term presence of researchers and associated infrastructure, such as field stations, have been shown to sometimes deter local resource extraction and thus support conservation (Eppley et al., 2024). Unfortunately, long-term research is challenging and thus rare, particularly in countries with limited funding or tumultuous politics (De Silva, 2016; Magurran et al., 2010; Nuttall et al., 2022).

The Living Planet Index suggests long-term wildlife trends are decreasing globally (WWF, 2020), but site-specific work reveals variation in the population dynamics of different tropical wildlife species, often dependent on local human context like hunting methods, laws and enforcement, taste preferences, and taboos (Brittain et al., 2022; Luskin et al., 2014). For example, in three protected areas in Cambodia, terrestrial species decreased over ten years, while arboreal species did not, likely due to ground-based threats such as snares and hunting dogs (Groenenberg et al., 2023; Nuttall et al., 2022). In two nearby protected areas in Tanzania, the monkey populations decreased in one and remained stable in the other due to differences in management (Barelli et al., 2023). Studies have also examined population trends under various contexts, such as wars (Daskin and Pringle, 2018), natural disasters (Walker et al., 2023), resource availability (Bush et al., 2020), researcher presence (Piel et al., 2015), zoonotic disease outbreaks (Morelle et al., 2020), and human pandemics (Burton et al., 2024). This site-, species-, and context-dependency motivate the need for more long-term monitoring, particularly for species that lack long-term data. Here, in a Cameroonian protected rainforest facing evolving hunting threats, we assess long-term trends of arboreal wildlife around a research station that closed and later reopened.

Population trends for arboreal tropical wildlife are typically less understood than those of terrestrial species, largely due to difficulties sampling in dense environments and the relatively rare use of arboreal camera trapping. Arboreal frugivores play crucial ecological roles as seed dispersers, influencing plant distribution, genetic diversity, forest structure, forest regeneration, and carbon storage (Rogers et al., 2021). Seed dispersers are especially important in African tropical forests, where up to 90 % of tree species are dispersed by animals (Osuri et al., 2016). Here, we monitored arboreal wildlife in the Dja Faunal Reserve (hereafter referred to as "Dja"), a protected Afrotropical forest in southeast Cameroon and a UNESCO World Heritage Site, but where there are still significant hunting and poaching activities (Bruce et al., 2018a, 2018b). Primates are often hunted for bushmeat (Muchaal and Ngandjui, 1999), hornbills are hunted for bushmeat and to trade their casques internationally (Su et al., 2024), and grey parrots are captured to be trafficked for the international pet trade (Tamungang, 2016).

Within the Dja (5260 km^2), we monitored arboreal species in a 25 km^2 area around the Bouamir Research Station, which was opened in 1993, closed in 1999, and then reopened in 2016. While researchers provide knowledge, their physical presence can sometimes also have a localized protective effect on wildlife populations by deterring activities like illegal hunting and poaching. In a National Park in Côte d'Ivoire, signs of poaching decreased toward the research area while primate and duiker encounter rates increased, especially for threatened and over-harvested species (Campbell et al., 2011). Similarly, in an unprotected Tanzanian forest, snare encounter rates decreased closer to a research base station and mammal encounter rates increased each year since the arrival of researchers (Piel et al., 2015). Research stations also often feature the presence of anti-poaching rangers, which was true at Bouamir Research Station. Thus, field stations can provide a high conservation return on investment (Eppley et al., 2024), but this necessitates further research (Laurance, 2013). In the Dja, it remains unclear whether the Bouamir Research Station has a protective effect, and whether it can vary due to circumstances across its tumultuous history.

We quantified long-term trends of twelve arboreal species (primates, hornbills, and grey parrots) around the Bouamir research station in the Dja using monthly non-linear trail transects conducted from 1995 to 1999 and from 2017 to 2024. We hypothesized that: 1) Most species would initially increase in relative abundance around the newly established research station (1995–1999) and again after its re-establishment (2017–2024), which may have discouraged nearby hunting. 2) Most species would experience population declines after the station closed in 1999, opening the way to hunters. This would be reflected in lower relative abundances in 2017 than in 1999. 3) Primates would suffer more immediate declines than hornbills due to local bushmeat preferences (Fa and Brown, 2009; Muchaal and Ngandjui, 1999). 4) Hornbills would suffer recent declines due to the increasing demand for African hornbill casques on illegal wildlife markets (Tinsman et al., 2025; Su et al., 2024), incentivizing hunters to target hornbills, especially the larger species.

2. Methods

2.1. Study site

The Dja Faunal Reserve in southeast Cameroon was founded in 1950 and covers 526,000 ha of tropical lowland rainforest. It has been classified as a UNESCO World Heritage Site since 1987 (Fig. 1). The reserve consists predominantly of primary lowland tropical rainforest and raffia palm swamps and is interspersed by rocky grassy inselbergs. It harbors over 100 mammal species, 350 bird species, and 270 tree species (Manfred and Ndjock, 2020; Bruce et al., 2018a, 2018b). Notably, it contains multiple endangered megafauna, including African forest elephants (*Loxodonta cyclotis*), western lowland gorillas (*Gorilla gorilla gorilla*), and central chimpanzees (*Pan troglodytes troglodytes*), which have all experienced population declines in the reserve since 1995 (Fankem et al., 2022; Fig. 1B). Although long-term studies have addressed these charismatic large species, less is known about the population changes of smaller arboreal species.

The Dja Faunal Reserve is surrounded by villages inhabited by Bantu and Baka communities. Although hunting in the Reserve is prohibited, illegal hunting and wildlife trafficking remain common. Hunters use guns and snares to acquire animals (Kamogne Tagne et al., 2022). The forest within the reserve is intact but encroaching agriculture, logging, and mining are increasingly putting pressure on habitats and animals (Fig. 2; Amin et al., 2023). We conducted our sampling within 5 km of the Bouamir Research Station, which is accessible by a 26 km footpath from the north of the reserve. Anti-poaching rangers (called "Eco-guards") are usually present within the station. The Bouamir Research Station was established in 1993, abandoned in 1999 due to a lack of funding, and then reestablished in 2016 (Zaunbrecher, 2021).

2.2. Study species

We surveyed for six species of hornbills: black-casqued hornbill (*Ceratogymna atrata; 1–1.6 kg*), white-thighed hornbill (*Bycanistes albotibialis; 1–1.4 kg*), Eastern piping hornbill (*B. fistulator sharpie; ~500 g*), Congo pied hornbill (*Lophoceros fasciatus; ~250 g*), Eastern long-tailed hornbill (*Horizocerus cassini*; ~250 g; insectivorous), and red-billed dwarf hornbill (*L. camurus*; ~100 g; insectivorous). All but the last two species are mainly frugivorous (Billerman et al., 2022). We surveyed five species of primates: black and white colobus (*Colobus guereza*), grey-cheeked mangabey (*Lophocebus albigena*), putty-nosed monkey (*Cercopithecus nictitans*), crowned guenon (*C. pogonias*), and moustached guenon (*C. cephus*). The primate species eat varying proportions of fruits,

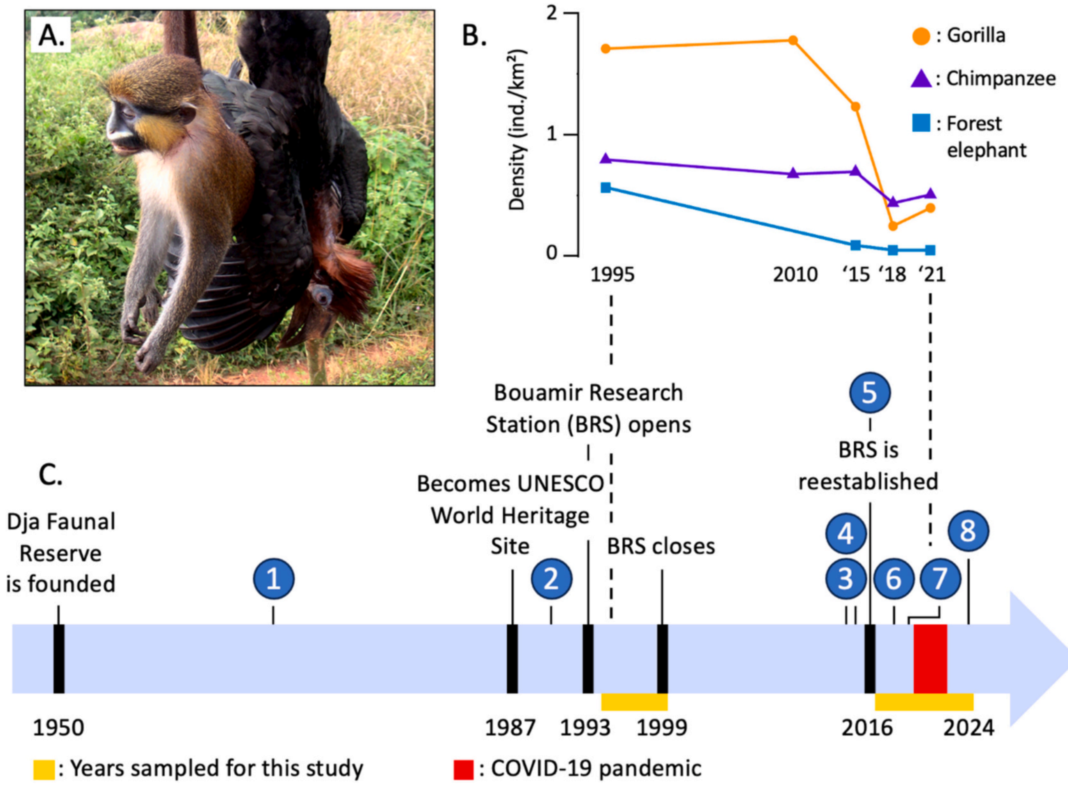

Fig. 1. Timeline of the Dja Faunal Reserve since its founding and trends for terrestrial megafauna. A) Photo of hunted moustached guenon and female black-casqued hornbill (2001; credit Benjamin Wang). B) Densities of elephants, gorillas, and chimps in the Dja (Bruce et al., 2018a; Fankem et al., 2022). C) Timeline of notable events in the Dja with details as follows. 1: Industrial logging around the reserve starts (1970), 2: Logging intensifies around the reserve (1990; Betti, 2004), 3: Seizure of 39 ivory tusks from poachers (IUCN, 2014), 4: 16 hunting camps found in the reserve (Steyn, 2015), 5: The Anglophone Crisis civil war starts in Cameroon (2016), 6: Seizure of 106 ivory tusks from poachers (WWF, 2018), 7: A baby chimp is rescued from poachers (Epanda, 2019), 8: A baby gorilla is rescued from poachers (Nfor, 2024). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

leaves, seeds, and invertebrates, while colobus are primarily folivores (Poulsen et al., 2001). We also surveyed the endangered African grey parrot (*Psittacus erithacus*). See Fig. 2 for illustrations and IUCN Red List listing.

2.3. Wildlife surveys

We conducted repeated non-linear transect surveys on the trails in a 25 km^2 area surrounding the Bouamir Research Station from 1995 to 1999 and 2017 to 2024 (Fig. 2C). Trail transects were walked two to four times per month by teams of two observers that included at least one Indigenous Baka researcher. The Baka have a hunter-gatherer heritage and are renowned for their excellent knowledge of the forest and its ecology. Observers recorded visual and auditory detections of twelve canopy wildlife species with their date, time, and location (trail name for 1995–1999, GPS for 2017–2024). Over 50 different observers participated throughout the length of this study. Pairs of observers included at least one experienced observer to train new observers. Surveys were typically conducted in the morning, from 6 am to 11 am. Observers walked no more than four hours each day. We removed observations with estimated distances larger than 500 m (although not all observations had this level of detail). Some trail transects slightly changed between 1999 and 2017. Surveys were limited to trails around the research station and are therefore not representative of the reserve as a whole.

2.4. Analysis

We calculated a relative abundance index (RAI) based on encounter rates for each species for each surveyed month by adding all detections and dividing by the number of kilometers walked that month (for yearly averages in RAIs see Tables S1 and S2 in ementary materials). It was not possible to use a Distance Sampling analysis to account for detection probability because distance estimates between the observer and the animal were not consistently taken nor deemed suitably accurate when taken (Fig. S3). We therefore refrain from comparing RAI values between different species due to differences in detectability (i.e., larger RAI in one species versus another does not necessarily mean higher abundance). However, we can compare population trends within species. Encounter rates have been used in multiple past studies on primate and hornbill populations and there have been strong relationships reported between encounter rates and density estimates for African grey parrots (Holbech et al., 2018; Lwanga et al., 2011; Marsden et al., 2016).

We quantified population trends using Generalized Additive Models (GAMs). We compared single-species GAMs with and without (null model) a variable for time (sequential number increasing from first to last surveyed month) and selected the best model based on the Akaike Information Criterion (AIC; Table S3 in ementary materials). To evaluate if trends were significantly positive or negative at a given time, we assessed the slopes of these GAMs (1st derivatives) and observed where the confidence intervals overlap with the zero line (nonsignificant) and where they do not (significant increasing or decreasing trend in RAI) (Fig. S1 and S2 in ementary materials). To test for differences in trends between all hornbills and all primates (excluding grey parrots), we fit a multi-species GAM with variables for time and for group (hornbill versus primate) and a random intercept for species. Lastly, we assessed each species' averaged seasonal variation in RAI from January to December (Fig. S4 and S5 in ementary materials). All analyses were conducted in R version 4.4.2 (R Core Team, 2022).

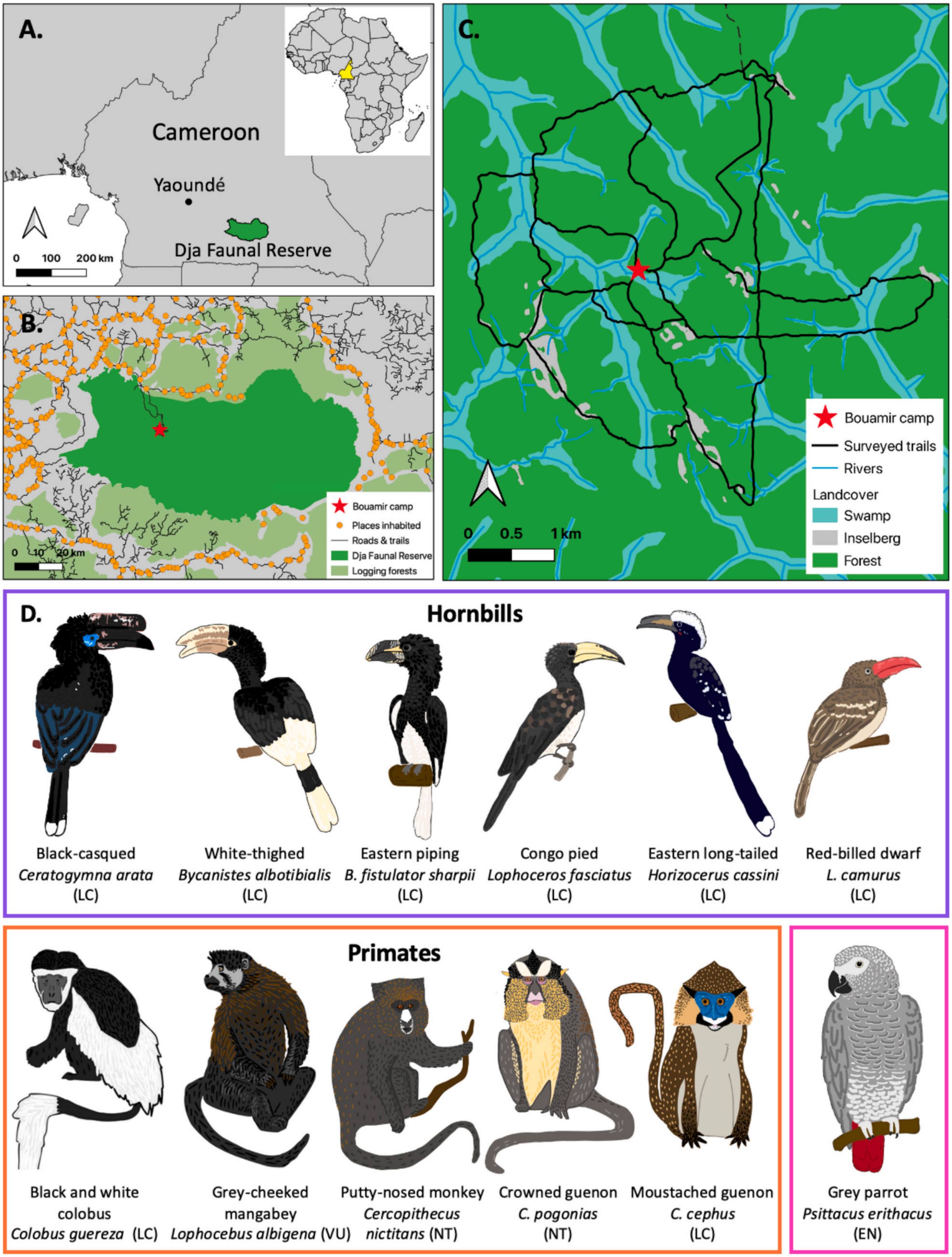

Fig. 2. A) Location of the Dja Faunal Reserve in Cameroon. B) Detailed land cover of the reserve and surrounding areas. The orange dots show inhabited locations, the pale green represents logging forests, and the red star is the Bouamir Research Station. C) Map of the study area surrounding the research station and the surveyed trails. D) Studied species and their IUCN Red List category (illustrations by Bastien Dehaudt). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3. Results

3.1. Single-species population trends

We surveyed 132 months and 13,303 km of trail transects in total from 1995 to 1999 and 2017 to 2024. All species showed significant changes in RAI from 1995 to 2024 (GAM: null model ΔAIC >2 and $p < 0.05$ for time variable effective degrees of freedom "edf"), except moustached guenons, which did not show a significant difference. Detailed model summaries are reported in the ementary materials (Table S3).

All six hornbill species showed an increase in RAI from 1995 to 1999 when the research station was first opened (Figs. 3 and S1). The four larger hornbill species (black-casqued, white-thighed, piping, and Congo pied) had similar RAI in 2017 compared to 1999 after the station had been closed, but showed significant decreasing trends from 2017 to 2024 after it was reopened (Figs. 3A-D and S1A—D). The two smaller hornbill species (long-tailed and red-billed dwarf) had a slightly lower RAI in 2017 than in 1999 and had almost no significant increasing or decreasing trends from 2017 to 2024 according to 1st derivatives (Figs. 3E-F and S1E—F). No significant punctuated changes occurred for hornbills during the COVID-19 period from 2020 to 2022.

Four out of five primate species (black and white colobus, grey-cheeked mangabey, putty-nosed monkey, and crowned guenon) also showed an increase in RAI from 1995 to 1999 when the research station was first opened (Figs. 4 and S2). These same four primate species had lower RAI in 2017 compared to 1999 after the station had been closed. Only crowned guenon showed significant decreases from 2017 to 2024 after the station reopened. The other three species showed non-significant changes (Figs. 4A-D and S2A—D). The moustached guenon was the only species for which the null model was the best and showed no significant changes in RAI throughout (Fig. 4E and Table S3). The endangered grey parrot decreased linearly from 1995 to 2024 (−0.0011 RAI/month; Figs. 4F and S2F). No significant changes occurred for primates or grey parrots during the COVID-19 period from 2020 to 2022.

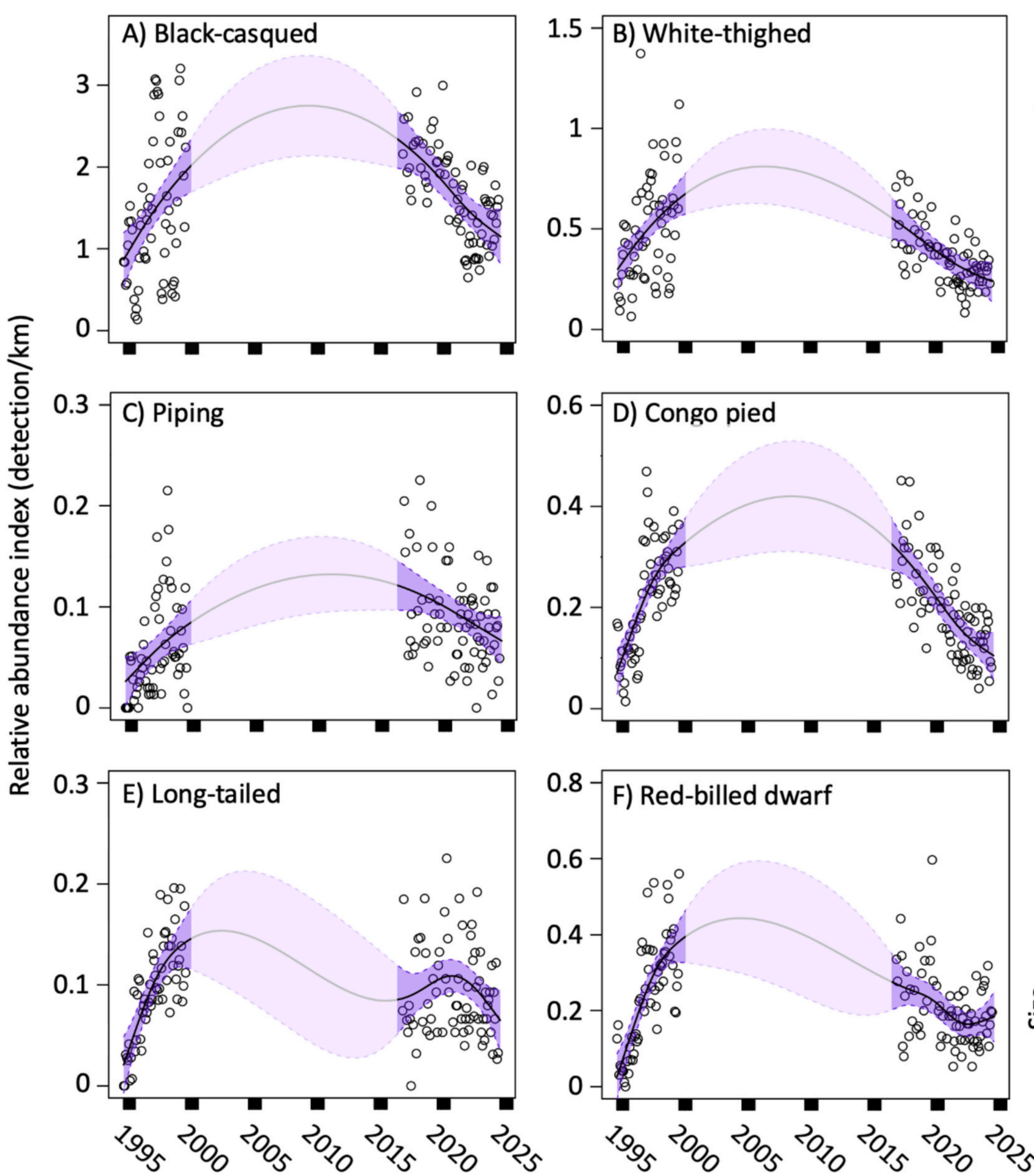

Fig. 3. Trends in RAI for each hornbill species from 1995 to 2024. Points show the RAI (encounter rates) of that species during a surveyed month and black lines represent the estimated trends from the single-species generalized additive models. Solid black lines indicate significance ($p < 0.05$) of time on RAI, while the dashed black line indicates non-significance ($p > 0.05$) (significant for all species in this figure). The purple shading shows the 95 % confidence intervals. We note the gap in sampling from 2000 to 2016 (faded). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.2. Hornbills versus primates

Examining single-species models, most primate species had a lower RAI in 2017 compared to 1999, while most hornbill species had a similar RAI in 1999 and 2017 but started decreasing after 2017 (Figs. 3, 4, S1, and S2). However, the multi-species GAM (n = 1452; Deviance explained = 81.9 %; R^2_{adj} = 0.807) did not find a significant difference in the trends between hornbills and primates (edf = 2.445; ref. df = 10; p = 0.078) when grouping species (Fig. 5). Instead, time since the first survey (edf = 7.568; ref. df = 9; p < 0.001) and the species random intercept (edf = 9.783; ref. df = 10; p < 0.001) explained RAI trends.

4. Discussion

The long-term wildlife trends in this study suggest a complex story involving fluctuating researcher presence and evolving hunting threats. We found strong positive trends in encounter rates from 1995 to 1999 for 10 out of 12 species of canopy vertebrates. This is possibly due to the newly created Bouamir Research Station, which may have had a protective effect on wildlife by deterring illegal hunting. However, we lack baselines and controls to conclude this with certainty. We hypothesize that this increase in relative abundance was primarily driven by lower mortality from hunting, and potentially higher detectability (via

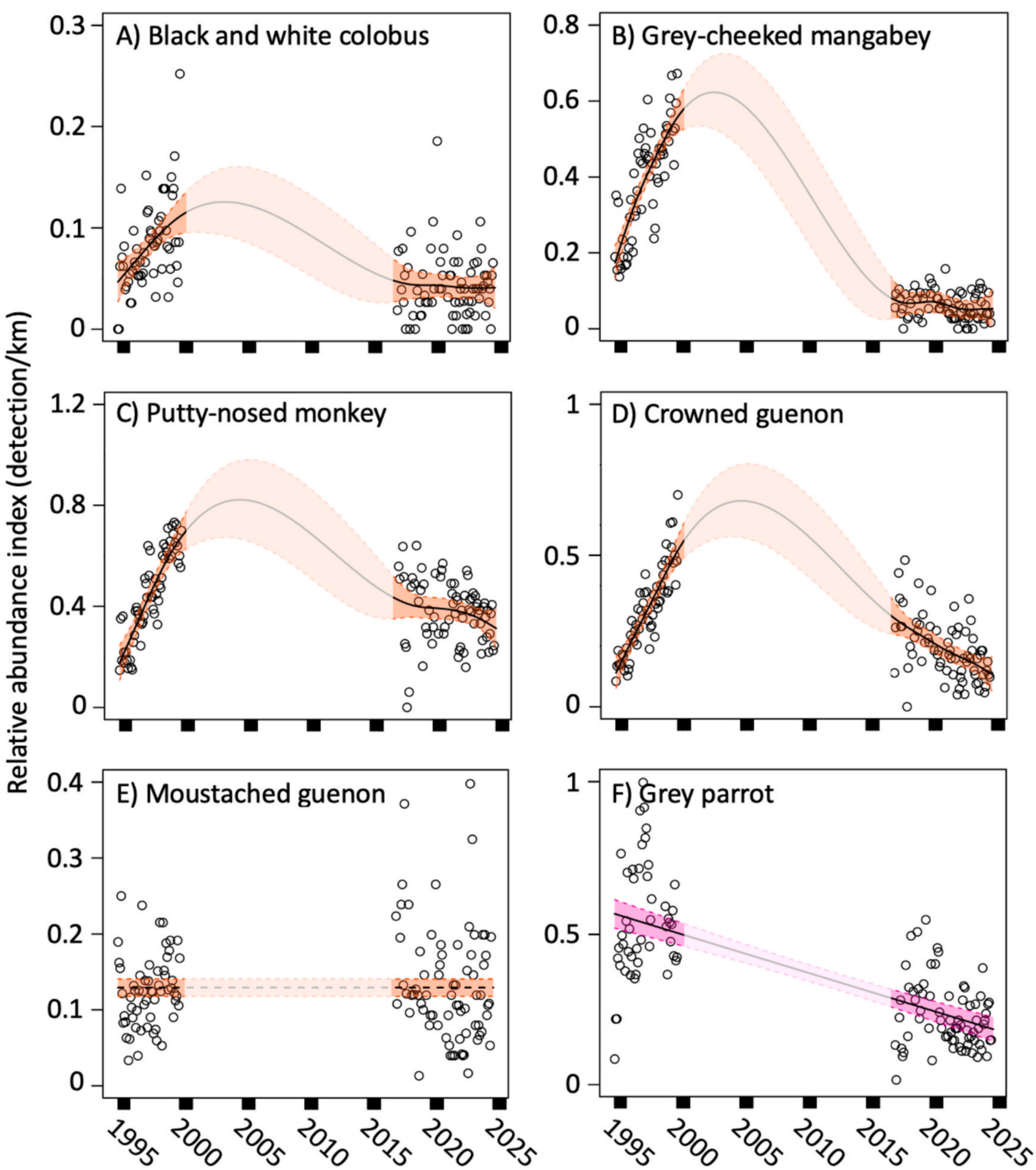

Fig. 4. Trends in RAI for primates and grey parrots from 1995 to 2024. Interpretations follow Fig. 3.

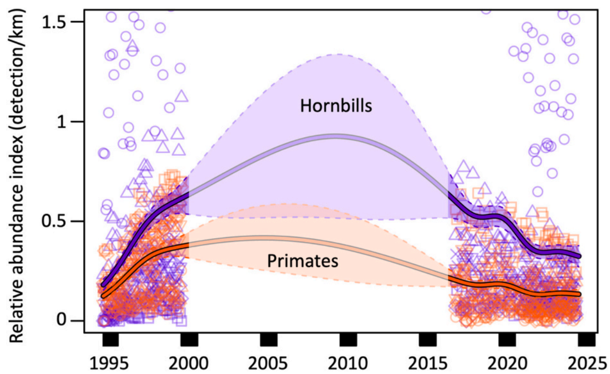

Fig. 5. RAI trends for all hornbill and primate species from 1995 to 2024. Purple symbols show the monthly RAI for hornbills: circles = black-casqued, triangles = white-thighed, squares = piping, upside down triangles = Congo pied, diamonds = long-tailed, crosses = red-billed dwarf. Orange symbols show the monthly RAI for primates: circles = black and white colobus, diamonds = grey-cheeked mangabey, squares = putty-nosed monkey, upside down triangles = crowned guenon, triangles = moustached guenon. The colored shading shows the 95 % confidence intervals. As RAI does not account for variation in detectability among species, the interpretation should focus on the trends and not the values (i.e., hornbills are not necessarily more abundant than primates). We note the gap in sampling from 2000 to 2016 (faded). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

reduction in fear of humans). The station closed in 1999 due to a lack of funding, and we found that most primate species had lower relative abundance in 2017 than in 1999. This suggests that these populations suffered strong hunting pressures during the absence of researchers. This is also supported by reports that hunters occasionally used the abandoned field station as a camp (B. C. Wang, personal communication, March 2025). We had expected that encounter rates would increase again after the reopening of the station in 2016; however, no wildlife species showed increasing trends from 2017 to 2024, and some even decreased, suggesting that potential protective effects from researchers can be limited depending on circumstances.

Several co-occurring factors may explain why the presence of researchers after the reopening of the field station in 2016 no longer deterred hunting, at least not enough to offset hunting pressures and cause higher encounter rates. First, hunters may have lost some of their apprehensions toward researchers and may be less avoidant of areas near the field station. Second, subsistence hunting has always been prevalent in the area, but this has likely increased alongside the growth in local human populations bordering the Dja (Brittain, 2019; Masanja, 2014). Third, there has also been a rise in commercial bushmeat sales and poaching across central Africa to satisfy growing urban and rural demands (Fa and Brown, 2009; Tagg et al., 2015; Ichikawa et al., 2017; Bruce et al., 2018a; Brittain, 2019). Fourth, hunting methods in the area have been evolving, with increased frequency of gun use, which are more effective for harvesting arboreal wildlife than traditional methods like snares (Abernethy et al., 2013; Ávila et al., 2019). This is partly due to the rise in commercial hunting, and species hunted with guns are almost four times more likely to be sold than eaten (Brittain, 2019). Furthermore, while it is easy for researchers to remove snares they encounter without risk (and often during the day), it is unadvisable to approach hunters armed with guns, especially at night. The rise in gun use is supported by anecdotal reports of increasing gunshots being heard at the field station in the last several years (Thomas B. Smith, personal communication, April 2025). Thus, while it is possible that there would have been steeper declines without the station reopening, its protective effect was not strong enough to counteract the increased and modernized hunting pressure on arboreal vertebrates.

While we believe that researchers' protective effect is a credible explanation for the initial trends, we lack temporal or spatial baselines required for causal proof (e.g., data prior to the opening of the station or at a second location in the reserve). Thus, we cannot exclude the possibility that factors aside from hunting and the researchers' presence contributed to the opposing wildlife trends observed among the two periods when the field station was open. Namely, changes to biophysical, climatic, or ecological factors could have affected wildlife populations, such as the hypothesized long-term decline in Afrotropical rainforest fruit production (Bush et al., 2020). While we find this plausible, we believe it represents a relatively minor factor since hunting has consistently been attributed as the dominant factor in central African wildlife trends, including at our study site (Fa and Brown, 2009; Tagg et al., 2015; Ichikawa et al., 2017; Bruce et al., 2018a; Brittain, 2019). Change in detection probability through time and observer effect may also have influenced these trends. Increasing trends for particular species may be driven by habituation to humans, although this would also suggest a reduction in hunting. Some observers' skills may have improved throughout this study, although over 50 different observers participated over the study duration and RAIs did not increase from 2017 to 2024. To better understand the effects of the Bouamir Station on wildlife, we suggest pairing sampling with new surveys at control sites far from the station.

While most hornbill and primate species showed similar trends over the 30-year study period, there were still variations among species driven by unique factors affecting specific species. First, the abandonment of the research station and the increase of commercial hunting using guns likely explain the declines in four out of the five primate species between 1999 and 2017. The exception was the moustached guenon, which was the only species without significant trends. This may be because they are comparatively more cryptic than other guenon species, such as the larger and louder putty-nosed monkey (Kingdon, 1980; Kümpel et al., 2008), or they may be better able to tolerate some hunting pressure (Matthews and Matthews, 2002). For hornbills, most species had similar relative abundance in 1999 and 2017, but then decreased from 2017 to 2024, especially the four larger species. This drop is likely due to a recent spike in the illegal trade of African hornbill casques to replace declining ies from Asia, caused by the increasing rarity of certain Asian hornbills and lower regulations in Africa (Su et al., 2024). Finally, the endangered African grey parrot is the only species that had a linear decrease in relative abundance without any signs of increase at any period. Instead of being hunted, grey parrots are captured and trafficked for the international pet trade. They are among the most intensively traded parrot species and have suffered severe declines across West and Central Africa (Davies et al., 2022). Our results thus suggest that their decline is ongoing, even in a UNESCO-listed protected forest reserve.

There are limitations to our interpretations due to the methodology employed to survey these arboreal vertebrates. Using a relative abundance index based on encounter rates does not account for variations in detection probability. However, our approach controls for the main drivers of detection variability by comparing the same species over time at the exact same locations (controlling for changes in detectability due to habitat) and sampling evenly throughout the years (controlling for seasonal changes). Nonetheless, we cannot compare RAI values across different species and therefore cannot determine if one species is more abundant than another. We also cannot assess how species' fear toward humans changed over time, which could be influenced by changing hunting pressures or the presence of researchers. Lastly, we were unable to account for variations among observers due to the high number of participants (>50) and the presence of multiple observers for each transect.

Arboreal frugivores are keystone seed dispersers, and their decline in the Dja and Central Africa may affect future plant distribution, forest structure, and carbon storage (Dehaudt et al., 2024; Rogers et al., 2021). Ten of the species surveyed are at least partially frugivorous and contribute to the seed dispersal of tropical plants. Hornbills in the Dja were previously found to disperse seeds of over 50 different species of plants, with some species consistently moving seeds more than 500 m from parent trees. Their gut passage also results in viable seed germination (Holbrook and Smith, 2000; Whitney et al., 1998). Similarly, arboreal primates in the reserve were found to disperse over 60 different species of plants, retain seeds for at least 20 h on average, and defecate seeds viable for germination (Poulsen et al., 2001). Therefore, the decline of these seed dispersers is worrisome, and this is especially true considering that their populations in 1995 were likely already lower than in the past (Soga and Gaston, 2018).

There are several options that may help mitigate the declining wildlife trends we observed in the Dja over the last decades. First is the enforcement of existing prohibitions on hunting, such as through increased funding and efficacy of the Cameroonian Ecoguard program. However, we note that forbidding hunting in some tropical forests is delicate when local livelihoods and health depend on wild meat (Golden, 2009). Effective enforcement of hunting regulations thus requires the willing participation of local communities and the co-design of desirable livelihood and wild meat alternatives, presenting opportunities for participatory conservation interventions. Second, there are positive ways to reduce hunting pressures, such as creating alternative income with microenterprise and skill training programs (Van Velden et al., 2020), promoting education (Friant et al., 2015), encouraging local communities to participate in citizen science (Larson et al., 2016), and providing access to family planning options (Ripple et al., 2016). Third, increasing international regulations and deterrents for the trade of African hornbill casques and pet grey parrots would contribute to protecting these species. Lastly, our work adds to a growing collection of studies suggesting a positive effect of research stations on wildlife, although this effect may be limited depending on the circumstances. We highlight the importance of sustained support for research sites to maintain this protective effect.

CRediT authorship contribution statement

Bastien Dehaudt: Writing – review & editing, Writing – original draft, Visualization, Software, Project administration, Methodology, Formal analysis, Data curation, Conceptualization. **Ruksan Bose:** Project administration, Methodology, Investigation, Data curation. **Jean Jacques Avoto:** Investigation. **Stephanie Brittain:** Writing – review & editing. **Tom Bruce:** Writing – review & editing. **Emily K. Chen:** Writing – review & editing, Investigation, Data curation. **Francis A. Forzi:** Writing – review & editing, Investigation, Data curation. **Britta D. Hardesty:** Writing – review & editing, Investigation, Data curation. **Kimberly M. Holbrook:** Writing – review & editing, Investigation, Data curation. **Aaron M. Lamperti:** Writing – review & editing, Investigation, Data curation. **V. Thomas Parker:** Writing – review & editing, Investigation, Data curation. **John R. Poulsen:** Writing – review & editing, Investigation, Data curation. **Nicholas J. Russo:** Writing – review & editing. **Ernest Simpoh:** Investigation. **Benjamin C. Wang:** Writing – review & editing, Investigation, Data curation. **Kenneth D. Whitney:** Writing – review & editing, Investigation, Data curation. **Thomas B. Smith:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Matthew Scott Luskin:** Writing – review & editing, Writing – original draft, Validation, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare no conflicts of interest related to this work.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2025.111475.

Data availability

The data and R code are available on FigShare repository at 10.6084/m9.figshare.29642459.

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