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Living with hyraxes: Biogeography and comparative ecology of West African *Fornasinius* beetles

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ABSTRACT

Among the flower beetles (Scarabaeidae, Cetoniinae), the Goliathini comprise several genera of medium and large-sized beetles widely distributed in sub-Saharan Africa. In this tribe, the genus *Fornasinius* Bertoloni, 1853 includes two species found in West Africa: *F. higginsi* (Westwood) and *F. klingbeili* Zöller, Fiebig, & Schulze. In this study, we present new data on the comparative ecology of these two species, including sex ratio, population structure by size, monthly activity patterns, and habitat features at two different spatial scales. These observations were conducted over a twenty-year period in Cote d'Ivoire, Ghana, and Togo. Both species exhibited similar overall population structure and morphometrics. They were characterized by a male-skewed adult sex ratio (with possible bias), male-larger sexual size dimorphism, and consistent population structure by size; the two species are seemingly parapatric (with the potential contact zone being separated in eastern Ghana by the Volta river and lake). Both are primarily found in the vicinity of trees that contained middens of hyraxes, such as *Dendrohyrax dorsalis* (*F. higginsi*), *D. interfluvialis* (*F. klingbeili*), and *Procavia capensis* (*F. klingbeili*). *Fornasinius higginsi* has been primarily observed in forest habitat, while *F. klingbeili* was found in both forests and Guinea savannahs. Occurrence sites of *K. higginsi* were predominantly characterized by higher tree cover, less bare areas and built-up zones. Although these beetles may be locally abundant within hyrax middens, they typically occur in only a relatively small number of sites within their preferred habitat. Monthly activity patterns differed between the two species. Adults of both species were observed throughout the year, sightings of *F. higginsi* were more common during the wet season, whereas *F. klingbeili* sightings were more frequent in the dry season. The observed differences in monthly activity patterns between these ecologically and morphologically similar species may help minimize interspecific competition in potential – yet unknown – sites of syntopy. Although some *Fornasinius* populations might be locally threatened by deforestation or overhunting of hyraxes, the careful management of hyrax populations should adequately ensure the conservation of these two beetle species.

Keywords: Africa; Ecology; Goliathiinae; Habitat; Interspecific competition; Population structure; Seasonality

1 | INTRODUCTION

The Goliath beetles in the genus *Fornasinius* Bertoloni, 1853 are a group of about seven relatively large-sized species (up to 68 mm long, including the clypeal apophysis) with distinctive morphology and large cephalic processes in the males. While previously included by some authors in genus *Goliathus* Lamarck, 1801 as a subgenus (Weibes 1968; Croizat, 1994; Maquart & Malec, 2017), *Fornasinius* is currently treated as a valid genus (De Palma, 2018). All *Fornasinius* species are found in sub-Saharan Africa (De Palma & Di Gennaro, 2017; De Palma & Takano, 2018; De Palma, 2018) and are heavily targeted in the international entomological trade. Despite this, these beetles have received little ecological study, with only scattered natural history data available (e.g., Maquart & Malec, 2017).

In this study, we utilize data gathered opportunistically over 20 years in Cote d'Ivoire, Ghana, and Togo, to provide information on the ecology of two apparently rare *Fornasinius* species: *F. higginsi* and *F. klingbeili*. We focus on monthly activity patterns, sex-ratio, population structure by size, and habitat characteristics/partitioning. These two species are morphologically similar (De Palma, 2018), and, despite having received attention from entomological collectors, have been extremely rare in collections (e.g., Lachaume, 1983) until the recent discovery of their association with hyrax middens.

The two West African *Fornasinius* species are entirely black, although sparse yellow cretaceous spots are often present on the elytra (Figure 1). *Fornasinius higginsi* males are readily distinguished from those of *F. klingbeili* by the very distinctive shape of the clypeal plate and clypeal horn; females display only minor differences in the anterior margin of the clypeus. Both species differ significantly from other members of the genus and arguably could be included in the now defunct genus *Sphyrorrhina* Nickerl, 1890 as a subgenus of *Fornasinius*.

In West Africa, the two *Fornasinius* species have a nearly continuous and parapatric distribution; *Fornasinius higginsi* recorded from western Cote d'Ivoire (Fediere et al., 1987) eastwards to the Volta region in Ghana, while *F. klingbeili* is found in Togo westwards to the Dahomey gap in Ghana (Maquart &

Malec, 2017). *Fornasinius aureosparsus* (van de Pool, 1890), a distantly related species, is found in south-eastern Nigeria, Cameroon and the Congo basin (De Palma, 2018). Given their parapatric distribution and similar habits, *F. higginsi* and *F. klingbeili* may serve as an interesting case study to examine patterns of coexistence and competition among Goliathine beetles in West African forest and savannah habitats.

In this paper, we aim to address the following key questions: (1) Given that the two West African *Fornasinius* species exhibit remarkable morphological similarity and are genetically related (M. De Palma, unpublished data), what ecological and/or biogeographic mechanisms have led to the separation of these species in otherwise analogous ecological niches? (2) Do potential differences in their ecological niches involve variations in annual phenology and/or habitat preferences? If so, are these differences observed at the site scale and/or the landscape scale? (3) Are the two species linked to middens of different hyrax species or do they occur in middens of a same hyrax species? (4) What are the conservation implications of our findings?

2 | MATERIALS AND METHODS

2.1 | Field protocol

All numerical data were obtained opportunistically between 2012 and 2022, during other fieldwork in Togo, Ghana, and Cote d'Ivoire (Figure 2). Qualitative and distribution records were gathered from 2000 to 2024. Beetles were recorded during surveys investigating aspects of the conservation and ecology of other animals, primarily reptiles.

The geographic coordinates of all observed beetles were recorded; however, these are not provided here for conservation reasons. This precaution is necessary because these beetles are heavily sought after by collectors for the entomological market trade.

We spent a total of 68 field days in sites in Ghana and Cote d'Ivoire (range of *F. higginsi*) and 609 field days in Togo (range of *F. klingbeili*). The number of field days per month in each country is given in Appendix Table A1.

We surveyed beetles across a wide range of potential habitats, including dry savannahs, wet rainforests, and mangroves. At each study site, we conducted random surveys from 06:00 to 24:00 local time, primarily targeting reptiles and amphibians but also searching for beetles. We ensured that similar amounts of time were spent in different habitats and under various weather conditions, from full sun to slight rain. Transects were walked concurrently by at least three individuals moving independently of each other.

In addition to recording live beetles, we documented individuals found dead on the ground. When an individual was found, we assessed the characteristics of the microhabitat and noted the presence of nearby hyrax groups. Hyrax middens in tree holes are often located at heights over 5 meters (our unpublished observations), making them difficult to examine directly. Therefore, we focused on checking the surrounding area for *Fornasinius* specimens or their remains on the ground.

The following habitat categories were considered for each observed individual:

i) DRS = dry (= Sudanese) savannah, characterized by a large dominance of drier grasslands interspersed with *Acacia* bushlands, and the Combretaceae and Caesalpinioideae trees. The herbaceous belt consists of mostly species of the genera *Andropogon* and *Hyparrhenia*, but on shallow soils also of *Loudetia* and *Aristida*.

ii) WES = wet (Guinean) savannah, that consists mainly of grasslands crossed with abundant trees and gallery forest strips alongside streams and on hillsides. *Lophira lanceolata* is among the dominant tree species found in this habitat type.

iii) DRF = semi-deciduous forest, that is characterized by some tree species exhibiting a partial shedding of leaves in the dry season. These forests are very diverse in terms of plant species and include the coexistence between humid forest species transgressing towards North and dry forest species transgressing towards South.

iv) PLT = plantation, mainly of cacao, coffee, banana, plantain, pineapple, cassava, yam, etc. These plantations are normally interspersed with few large trees and human settlements and are very disturbed and altered forest-derived habitats.

v) FTP = forest-plantation mosaic, is a mixed landscape with portions of territory similar to DRF and others to PLT.

vi) MAF = mature (and pristine) rainforest, consisting of patches of forests that have not been altered by humans in the last thirty years, with many trees more than 30 m height. These patches are typically sacred grooves, inner parts of community forests or legally protected areas.

vii) SEF = secondary or altered moist forest. This is typically the same vegetation type as MAF, but with a stronger/more recent human intervention. The number/density of very large trees (taller than 30 m height) is much smaller than in MAF, the average tree height is about 12-15 meters, and the surface is often crossed by paths and roads.

2.2 Sample sizes

None of the live specimens encountered were collected or sacrificed. Only those specimens that were found dead in the field were retrieved and saved for further analyses. In the following text, we define an "individual record" as the event observed during quantitative transects in which *Fornasinius* specimens were observed at a single point and at a single time (date and hour-of-the-day). Several individual records consisted of more than one specimen, including both live and remains of dead animals. However, all specimens found in the same locality and at the same time were considered as single records to avoid pseudoreplication in the analyses of activity patterns and habitat (at both spatial scales). In quantitative transects, we collected 77 individual records of *F. higginsi* and 39 individual records of *F. klingbeili.*

The 77 individual records of F. higginsi involved 105 measurable and sexually identifiable specimens, while the 39 individual records of *F. klingbeili* involved 44 measurable and sexually identifiable specimens. In the seasonality analyses, we included all individual records. For habitat analyses of *F. higginsi*, we excluded 14 out of 77 individual records because these involved individuals found squashed on roads or dead in ponds, making it impossible to define a clear habitat. The sample size for habitat analyses of *F. klingbeili* included a total of 50, since 11 additional individual records with habitat information were obtained outside the quantitative transect surveys. In addition to transect data, the biogeography analysis also incorporated data collected by one of the authors (M. De Palma) over more than two decades of research into African Goliath beetles.

The total body length of each beetle collected was measured from the tip of the clypeus to the apex of elytra. It is important to note that the total body length includes the cephalic horn present in male specimens. Therefore, a greater body length does not imply a greater body mass.

When analysing the monthly activity patterns, we only considered specimens encountered during random walks. We excluded individuals found dead and in small fragments, as it was not possible to determine the month(s) of their activity and death. However, we included some specimens from collections with reliable tags indicating the precise date of collection. All voucher specimens are deposited in the Entomological Collections of the Université de Lomé (Togo), Luiselli's collection in Rome (Italy), and De Palma's collection in Lausanne (Switzerland).

2.3 | Statistical analyses

Monthly activity patterns of adult beetles was analysed relative to monthly field effort. We first calculated the monthly relative sampling effort (MRSE) for each of the two species separately. We used a null hypothesis of equal encounter frequency among months. The MRSE was calculated using the following formula:

$$[1]\ \text{MRSE} = n \times 100 / N$$

where *n* represents the number of field days spent in that month in the study area, and *N* represents the total number of field days in that area. We then generated the expected number of beetles in each month by multiplying the total number of beetles of each species found during the entire research period by MRSE. Finally, we compared the observed number of beetles per month against the expected number using an observed-versus-expected χ^2 test. The same statistical design was applied in other field studies of beetles (see Dendi et al., 2023).

To evaluate the correlation between the activity of adult beetles and rainfall patterns, we used the number of rainy days per month as a proxy for rainfall. Rainfall data was obtained from Accra, Ghana (downloaded from <https://weatherspark.com/y/42322/Average-Weather-in-Accra-Ghana-Year-Round#Sections-Precipitation>, last accessed on 20 May 2022) for *F. higginsi*, and from Kara, Togo (<https://weatherspark.com/y/45806/Average-Weather-in-Kara-Togo-Year-Round#Sections-Precipitation>, last accessed on 20 May 2022) for *F. klingbeili*. We conducted a Spearman's rank correlation (r_s) test for each month, with the number of rainy days as the independent variable and percentage monthly observed adults as the dependent variable.

To evaluate habitat preferences of both species, we used two different approaches across two spatial scales: (i) the sighting site scale, and (ii) the landscape scale. For habitat preference at the sighting site scale, each beetle record was assigned to the dominant (or the most representative) of the seven habitat type categories described above, within a 200 m buffer around the capture site of each specimen. We assessed differences in sighting frequencies between habitats using observed-versus-expected χ^2 tests. Additionally, we calculated the habitat niche breadth for numerical data using Simpson's (1949) measure of niche breadth (B_s).

To analyze habitat preferences at the landscape scale, we utilized a GIS-based methodology with QGIS software version 3.32. For this analysis, we employed the LC Map of Africa 2016 raster layer, released by the European Space Agency (ESA) between October 2, 2017, and February 6, 2018, with a pixel size of 20 meters. The raster classifies land use into the following categories: 1 - Tree cover areas (TRC); 2 - Shrub cover areas (SHR); 3 - Grassland (GRS); 4 - Cropland (CRP); 5 - Aquatic or regularly flooded vegetation (VGA); 6 - Sparse vegetation (SPA); 7 - Bare areas (BAR); 8 - Built-up areas (BLT).

For each occurrence point, we created a square buffer area of 2.2 km per side. We used the "saga_histogram" algorithm to perform zonal statistics, which calculates the counts of each unique value from the raster layer within defined zones. This allowed us to count the number of pixels for each land use category at each beetle occurrence point and determine the percentage of occupancy for each land use category. To assess interspecific differences in the mean percentage occupancy of various land use categories, we employed a non-parametric Kruskal-Wallis ANOVA.

The sex ratio was evaluated using an observed-versus-expected χ^2 test. Intersexual differences in mean body sizes were assessed using a one-way ANOVA followed by Tukey HSD post-hoc tests for pairwise comparisons. We tested all variables for normality and homoscedasticity using a Shapiro-Wilk test, and if necessary, we log-transformed them before conducting any parametric analysis. All analyses were performed using PAST version 4.0 software, with all tests being two-tailed and alpha set at 5%.

3 | RESULTS

3.1 | Sex ratio and body length

Out of the total of 105 individuals of *F. higginsi* for which sex and body size were recorded, the observed sex ratio (males: females) was 1.92: 1 (χ^2 = 11.11, df = 1, P < 0.001). Data on body length and sex were also collected on 44 individuals of *F. klingbeili*, with a sex ratio of 1.44: 1, which was not significantly uneven (χ^2 = 1.45, df = 1, P = 0.228). The distribution of body lengths in the observed sample of the two species is shown in Appendix Figure A1.

The distribution of body length in the observed sample of the two species is given in Appendix Figure A1. In both species, there was a significant male-larger sexual size dimorphism, driven by the presence of the cephalic horn in the males (Figure A1; *F. higginsi* – males: 53.1 ± 4.7 mm, median = 54 mm, n = 69; females: 45.9 ± 3.3 mm, median = 46 mm, n = 36; *F. klingbeili* – males: 52.3 ± 6.1 mm, median = 51.5, n = 25; females: 48.1 ± 5.7 mm, median = 47 mm, n = 19. A) (after log-transformation, $t = 8.33$, $P < 0.0001$ for *F. higginsi* and $t = 2.33$, $P < 0.05$ for *F. klingbeili*). A one-way ANOVA (on log-transformed body size measurements) followed by Tukey HSD post-hoc test revealed that male size did not differ significantly between species (Tukey = 1.18, $P = 0.836$), and the same was true for the female size (Tukey = 2.233, $P = 0.394$).

3.2 | Apparent abundance and **Seasonality**

Considering only the individuals encountered during our transect walks, we recorded 63 individuals of *F. higginsi* and 50 individuals of *K. klingbeili*. The number of individuals observed relative to field effort was higher in *F. higginsi* (0.93 individuals per field day in appropriate habitat) than in *F. klingbeili* (0.07 individuals per field day.

Adults of both species were observed throughout most of the year. However, *F. higginsi* was not sighted in September-October, and *F. klingbeili* was not sighted in September (Figure A2). The frequency of monthly sightings was significantly uneven in *F. higginsi* ($\chi^2 = 62.52$, df = 11, $P < 0.0001$), with peaks higher than expected in March, April, and May (wet season) and lower than expected in September to December (the last phase of the wet season and the dry season; Figure 3).

Similarly, the frequency of sightings of *F. klingbeili* was also significantly uneven ($\chi^2 = 56.73$, df = 11, $P < 0.0001$), with peaks higher than expected in November, December, and January (dry season) and negative peaks in June to September (wet season; Figure 3). There was no correlation between monthly sighting frequency of and the number of rainy days per month in *F. higginsi* ($r_s = 0.049$, $P = 0.879$). However, the activity of *F. klingbeili* was inversely correlated to the monthly number of rainy days ($r_s = -0.633$, $P < 0.05$). Monthly activity patterns differed significantly between species ($\chi^2 = 48.1$, df = 10, $P < 0.0001$).

3.3 | **Habitat**

3.2.1. Habitat at sighting site scale

Although the two species occurred in various habitats, particularly in SEF (Figure 4), there were significant interspecific differences ($\chi^2 = 25.6$, df = 4, $P < 0.0001$). *Fornasinius higginsi* was observed more frequently in MAF, while *F. klingbeili* was more commonly found in DRS (Figure 4). Habitat niche breadth was much broader in *F. klingbeili* compared to *F. higginsi*, with respective values of 4.596 and 2.733 (B_s).

Except for a few individuals found dead along roads and paths, most individuals from both species (including preyed specimens) were discovered under hollow shafts with middens of *Dendrohyrax interfluvialis* (*F. klingbeili*) and of *D. dorsalis* (*F. higginsi*), particularly *Dialium guineense* trees. However, *F. klingbeili* was also found in rocky sites where there were *Procavia capensis kerstingi* middens, particularly in the DRS habitat. Height above ground of tree cavities where hyraxes made their middens (and therefore used by these beetles) ranged from 5 to 13 m. This made it impossible for us to examine the different hollows. However, we identified seven trees regularly used by hyrax in Cote d'Ivoire, 11 in Ghana, and 32 in Togo. In these, we found remains of *F. higginsi* in the immediate vicinity of six trees in Cote d'Ivoire (85.7%), nine in Ghana (81.8%), while *F. klingbeili* were found nearby nine of the surveyed trees in Togo (28.1%).

3.2.2. Habitat at landscape scale

Land use categories for each beetle occurrence site of the two *Fornasinius* species at the landscape scale are shown in Table 1. The two species differed significantly in terms of the percent coverage of the various land use categories in their respective presence sites (Kruskal Wallis ANOVA, $P < 0.0001$), with significant differences being for: (i) tree cover representing a much higher percentage of land use in *F. higginsi* occurrence sites and (ii) bare areas and built up areas appearing with significantly higher percentages in *F. klingbeili* occurrence sites (Figure 5):

4 | DISCUSSION

4.1 General considerations

The two species of *Fornasinius* beetles examined in this study showed both similarities and significant statistical differences in their ecological traits. These similarities likely stem from conservative traits associated with the evolutionary history of Goliathiinae beetles. These traits include aspects of population structure, such as similar patterns in body size distribution among individuals, as well as morphometrics, specifically the larger size in terms of total length of males compared to females (sexual-size dimorphism). In other genera of the Goliathini, males also tend to be larger than females primarily due to their hypertrophic cephalic processes (e.g. genus *Dicronorhina,* Lekkerkerk & Krikken, 1986 and De Palma, 2011; genus *Goliathus*, Jiang et al., 2012; genus *Mecynorhina,* Christiansen, 2013 and De Palma et al., 2024; genus *Eudicella*, Vendl et al., 2018) These processes serve as signals of a mating system based on male-male combat for access to females (Björkman et al., 2009). Sexual selection likely contributes to the increase in male body size, as larger body size and success in sexual combat are often correlated in larger animals (Shine, 1978, 1994; Berry & Shine, 1980).

We observed that males outnumbered females, although this difference was statistically significant only in *F. higginsi*. A skewed operational sex ratio may be associated with intense sexual competition among these beetles. This could be because females are a limited resource, confined to a relatively small area where many males are actively competing. However, our estimates of sex ratios may be biased by our sampling modality. In fact, we have considered only the specimens encountered along the transects, in which the sex-ratio may have been unbalanced to favor males due to their lower philopatry and habit to flutter and disperse in search of females with which to mate. Conversely, females are more philopatric and may remain in the nests of hyraxes rather than disperse. In support of this hypothesis, the data collected by one of us (M. De Palma) inside a hyrax midden in Ghana indicate that the majority of the specimens were females.

4.2 *Fornasinius* beetles and hyrax middens

We frequently observed these beetles under, or in the vicinities of, trees that housed hyrax middens, but they were rarely found in areas without hyrax. This suggests that the beetles are confined to small areas within dense forest habitats, unlike other Goliathiinae species that are more widely distributed. Because we couldn't access the various tree cavities with hyrax middens, our survey likely underestimated the abundance of these beetle species. We did, however, find remains of *F. higginsi* near almost all (>90%) of the trees used by *Dendrohyrax interfluvialis*, indicating that this species is widespread wherever the hyraxes accumulate their middens. Local hunters in eastern Ghana also suggest that multiple *Fornasinius* specimens, both adults and larvae, may inhabit each tree cavity used by hyrax individuals for their middens. So, although their density may be locally high, they are confined to small areas within the appropriate habitat. The percentage of trees with hyraxes that also have *F. klingbeili* was significantly lower (<30%), suggesting that this species is either less common than *F. higginsi* or less frequently associated with hyrax middens. Currently, it is unknown whether *Fornasinius* species are obligate hosts of hyrax species, as we found them in some sites apparently without any hyrax populations. However, the presence of hyraxes is often associated with the presence of these beetles. Nor can it be ruled out that these beetles may also occasionally associate with the latrines of other forest mammals, and that this explains the reason for the observation of individuals in sites without the apparent presence of hyraxes. For instance, we observed in southern Nigeria two adults of the closely-related *Fornasinius aureosparsus* at least than 1 m from a African civet's (*Civettictis civetta*) latrine, suggesting that they were just dispersing out of it. However, the storage time of the latrines is essential for the maintenance of a stable population of beetles. Therefore, it can be hypothesized that the latrines of any other species can only be used by *Fornasinius* species occasionally and in suboptimal environmental conditions.

The use of hyrax middens by *Fornasinius* beetles is similar to that of other cetonids that use bird nests for larval development (Choi et al., 2018; Zbyryt & Oleksa, 2018), and that may be even obligate hosts of their avian nests (Zbyryt & Oleksa, 2018). Tropical cetoniinae may also develop in termite nests (Touroult & Le Gall, 2013), but we have not observed any *Fornasinius* specimen nearby termite nests.

Hyrax species, both *Dendrohyrax* spp. and *Procavia capensis*, are scattered throughout West Africa, which influences the distribution of *Fornasinius* species. Further investigation of hyrax middens may reveal whether the association between these beetles and mammals is obligatory or facultative. The occurrence of *F. klingbeili* in *Dendrohyrax* middens was previously reported by Maquart & Malec (2017). It's worth noting that *Hegemus pluto* and *Argyrophegges kolbei* from East Africa also use the middens of *Heterohyrax brucei* and *Dendrohyrax dorsalis*, respectively (Di Gennaro, 2014), indicating that these two *Fornasinius* species are not unique among goliathini beetles in having their life cycle linked to hyrax middens.

4.3 Habitat and biogeography implications

Our study documented that *F. klingbeili* occurs in dry open forests in the Kara region in central Togo, as well as in dense deciduous forests in the Togo hills and in the lowland dry forest in the Togodo area. Thus, it is apparently a habitat generalist, as suggested by the relatively high value of its habitat niche breadth. Conversely, *F. higginsi* shows less generalist behaviour in habitat use, typically dwelling in dense forests. These patterns are clearly confirmed also at the landscape scale: the occurrence sites of *K. higginsi* were characterized by a higher percentage of tree cover areas and less of bare areas and built-up areas. The distribution of *F. higginsi* closely follows that of *Dendrohyrax dorsalis* in Cote d'Ivoire and that of *F. klingbeili* follows the distribution of *Dendrohyrax interfluvialis* in Togo and even in eastern Ghana as it seems to be present only east of the Volta lake and the former Volta river (Oates et al., 2022). Like other species of the same genus (Milner & Harris, 1999), the two *Dendrohyrax* species are moist evergreen and semi-deciduous forest dwellers (Jones, 1978; Djossa et al., 2012). Therefore, the density of the two *Fornasinius* species is likely to be higher in moist evergreen and semideciduous forests than in other habitat types. These two types of forests are also those with higher Cetoniinae species diversity in Ghana (Mudge et al., 2012). Given that *D. interfluvialis* occurs between the Volta and Niger Rivers, including the south of the Republic of Benin throughout the "Dahomey Gap" (sensu Salzmann and Hoelzmann, 2005) and even close to Benin City in western Nigeria (Oates et al., 2022), and that *F. klingbeili* has already been recorded from relatively open dry forest-savannah mosaics in Togo (Maquart & Malec, 2017; this study), we predict that *F. klingbeili* may also occur in Benin and western Nigeria, where its presence has not been reported so far. At the same time, it is very likely that *F. higginsi* is widespread also in Liberia and eastern Sierra Leone, in the regions where the forest cover is still adequate.

Based on the above-considerations, the distribution of *F. higginsi* should be very similar to the classic pattern of the West African species of the Upper Guinean Forest block (Oates et al., 2004; Mallon et al., 2015), while that of *F. klingbeili* would not be limited to the Dahomey Gap but could perhaps also penetrate the humid forests of the Lower Guinean forest block, west of the Niger River. From a biogeographical point of view, all *Fornasinius* species have, in Africa, a parapatric distribution. In this sense, the two species studied are no exception. Unfortunately, there is no data on the separation zones between the ranges of the two target species in eastern Ghana. These areas have been enormously modified by the creation of Lake Volta, the largest artificial lake in the world, and the natural landscape has changed so much that it is impossible nowadays to reconstruct the dynamics of their past distribution on a fine scale.

4.4. Seasonal activity patterns

Both *Fornasinius* species were year-round active. Although adult sightings occurred almost every month, a more in-depth analysis, controlling for field effort, revealed substantial interspecific differences: *F. higginsi* was more frequently encountered on the ground during the wet season, and *F. klingbeili* during the dry season. We hypothesize that the individuals found on the ground are those that disperse in search of new mating sites, and therefore, their monthly frequency of sightings may correlate with their above-ground activity intensity. Since these beetles are found year-round inside the hyrax middens (tree cavities often placed at over 10 m from the ground), we cannot exclude the possibility that the number of individuals found on the ground (often just recently dead) may not directly correlate with their activity intensity inside the tree cavities.

Niche theory cannot explain the different activity patterns we uncovered in the two species. In fact, the nearest presence localities for the two species (Kwahu escarpment as the easternmost site for *F. higginsi* and Hohoe and the Kadjebi district as the westernmost sites for *K. klingbeili*) are about 155 km apart, now separated by Lake Volta. Therefore, it seems that the former Volta river and the westernmost part of the Dahomey Gap separated the ranges of these two species. However, in the gap area between the two *Fornasinius*, both *Dendrohyrax interfluvialis* and *Procavia capensis* are known to occur (Kingdon et al., 2013; Oates et al., 2022). Therefore, we cannot exclude the possibility that the ranges of the two species may be closer than they appear, or even be sympatric in a few sites. As regards the interspecific relationships between these two species, there are no data available. However, their distribution can be predicted to be strictly parapatric due to highly competitive potential occurring between the two species. In fact, both have a very peculiar niche (inhabiting hyrax middens) and hyrax populations are scattered in the environment, probably providing a limited resource to these beetles. Nonetheless, it would be interesting to verify whether, in the areas where both *Dendrohyrax interfluvialis* and *Procavia capensis* do co-occur, also both *Fornasinius* species may coexist, perhaps by partitioning the niche using each a given species of hyrax. However, this hypothesis remains purely speculative.

4.5 Conservation implications

According to our observations, we conclude that the survival of these mammals will protect *Fornasinius* populations because their life cycle is closely linked to three hyrax species, D. *interfluvialis*, *D. dorsalis,* and *P. capensis.* Although opportunistically eaten by people, these hyrax species are not easily found by human hunters and are not among the main prey species hunted for meat (Oates et al., 2022). This is likely due to their cryptic, mainly nocturnal and arboreal habits, as well as their solitary foraging activities (Djossa et al., 2012). Furthermore, *Dendrohyrax* spp. and *Procavia capensis* are not threatened in Togo (Amori et al., 2016) or in West Africa in general (Oates et al., 2022), suggesting that neither of the two *Fornasinius* species are currently facing serious threats. Additionally, these beetles are not collected by local communities due to their low cultural and/or subsistence value. While the international entomological market may exploit the wild populations of both species (which are sold at a relatively high price in the northern world), it is unlikely to pose a serious threat to these species at the global scale. However, the loss of forest habitat, particularly the cutting of hollow shafts used by hyrax individuals, may be a local threat as it could affect their mammalian "hosts" (Oates et al., 2004; Poorter et al., 2004; Critical Ecosystem Partnership Fund, 2015). Therefore, habitat protection is crucial for the conservation of these beetle species. Overall, although some *Fornasinius* populations might be locally threatened by deforestation or perhaps overhunting of hyraxes, we conclude that for both species a red listing of LC/NT should be adequate.

4.5 Limitations of the study and future steps of the research

The present study, although consisting of a sample size sufficient to conduct robust statistical analyses, is certainly limited by the fact that the research was carried out in only a few presence sites within the ranges of the two *Fornasinius* species. This was because, while *Fornasinius* species were common at sites of occurrence, it was nevertheless difficult to find new locations of occurrence, especially for *F. klingbeili*. For many of the statistical analyses carried out by us, considering the number of individuals observed in the same site as independent would have caused biases due to pseudoreplication (Heffner et al., 1996; Chaves & Chaves, 2010) given that the various individuals probably all came from a single source (a certain hyrax midden within a specific hollow tree). Therefore, the significance of our conclusions may be affected by the small number of surveyed sites.

Regarding future studies, it will be necessary to verify the generality of our observations with a larger sample of presence locations. Additionally, exploring the ecological relationships between hyraxes and *Fornasinius* beetles in more detail will be appropriate, for example, by using technologies such as camera traps placed near hyrax middens. These future studies will have to verify whether the cohabitation between hyraxes and *Fornasinius* beetles is obligated, and above all if, as it seems at the current state of our research, each species of *Fornasinus* is linked to a specific species of *Dendrohyrax*.

Increasing collaboration between mammalogists and entomologists is essential to better study the ecology and conservation of both hyraxes and *Fornasinius* beetles. Both are subject to the same type of threat (habitat loss) but also face species-specific threats (overhunting for subsistence in the case of hyraxes and harvesting for the international entomological market in the case of beetles). Finally, a formal "threats analysis" approach, as recently performed on threatened turtles (Luiselli et al., 2024a, 2024b), would be extremely important for defining future management and conservation planning.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

REFERENCES

Amori, G., Segniagbeto, G.H., Decher, J., Assou, D., Gippoliti, S., Luiselli, L. 2016. Non-marine mammals of Togo (West Africa): an annotated checklist. *Zoosystema*, 38, 201-244.

Berry, J.F., & Shine, R. (1980). Sexual size dimorphism and sexual selection in turtles (Order Testudines). *Oecologia*, 44, 185-191.

Bertoloni, G. (1853). Illustrazione dei prodotti naturali del Mozambico. *Memorie della Reale Accademia delle Scienze dell'Istituto di Bologna*, 4: 343-363.

Björkman, C., Gotthard, K., & Pettersson, M.W. (2009). Body size. In Encyclopedia of insects, pp. 114-116. Academic Press, New York.

Choi, C. Y., Nam, H. Y., Park, C. R., & Lee, W. S. (2018). Life cycle of *Anthracophora rusticola* (Coleoptera: Cetoniidae) from the commensal nests of Chinese Sparrowhawks (*Accipiter soloensis*). *Journal of Asia-Pacific Entomology*, 21, 25-28.

Chaves, L. F., & Chaves, L. F. (2010). An entomologist guide to demystify pseudoreplication: data analysis of field studies with design constraints. *Journal of medical entomology*, 47, 291-298.

Christiansen, P. (2013). Larval growth rates and sexual differences of resource allocation in the cetoniine scarab *Mecynorhina polyphemus* Fabricius 1781 (Coleoptera: Scarabaeidae: Goliathini). *Journal of Natural History*, 47(19-20), 1287-1307.

Critical Ecosystem Partnership Fund (2015). *Guinean Forests of West Africa Biodiversity Hotspot*. CEPF, New York.

Croizat, L. (1994). Observations on the biogeography of the genus *Goliathus* (Insecta: Coleoptera). *Kirkia*, 15, 141-155.

Dendi, D., Rugiero, L., Luiselli, R., Fa, J. E., Amori, G., & Luiselli, L. (2023). Phenology, sex-ratio and protandry in three stag beetle species (Lucanidae) from central Italy. *Journal of Natural History*, 57 (33-36), 1540-1558.

De Palma, M. (2011). Identification of *Scarabaeus micans* Drury and taxonomic notes on *Dicronorhina* Hope, with description of a new species (Coleoptera, Scarabaeidae, Cetoniinae). *Cetonimania,* NS 2, 5-36.

De Palma, M. (2018). Taxonomic revision of genus *Fornasinius* Bertoloni, 1853 with description of new taxa (Scarabaeidae, Cetoniinae). *Entomologia Africana*, 23, 2-18.

De Palma, M., & Di Gennaro, C. (2017). Description of *Fornassinus hermes* sp. nov. (Coleoptera, Cetoniidae, Goliathini). *Entomologia Africana*, 22, 31–38.

De Palma, M., & Takano, H. (2018). Identification of the Goliath beetles *Fornasinius fornasini* Bertoloni and *Fornasinius hauseri* Kraatz (Scarabaeidae: Cetoniinae). BioRxiv preprint doi: https://doi.org/10.110.

De Palma, M., Takano, H., Leonard, P., & Bouyer, T. (2024). Taxonomic revision of *Mecynorhina* Hope, 1837 and allied African genera with simple or bifurcate horns (Coleoptera, Scarabaeidae, Cetoniinae, Goliathini). *Entomologia Africana*, 29, 11-32.

Di Gennaro, C. (2014) *Hegemus pluto* (Raffray, 1880): repartition, biologie et description de nouvelles sous-espèces (Coleoptera, Cetoiniidae, Goliathini). *Entomologia Africana*, 19, 47–58.

Djossa, B.A., Zachee, P., & Sinsin, B.A. (2012). Activity patterns and habitat use of the western tree hyrax (*Dendrohyrax dorsalis*) within forest patches and implications for conservation. *Ecotropica,* 18, 65–72.

Heffner, R. A., Butler, M. J., & Reilly, C. K. (1996). Pseudoreplication revisited. *Ecology*, 77, 2558-2562.

Fediere, G., Dauthuille, D., & Lery, X. (1987). *Cetoines de la Cote d'Ivoire*. Orstom, Abidjan.

Kingdon, J., Happold, D., Hoffmann, M., Butynski, T., Happold, M., & Kalina, J., eds. (2013). *Mammals of Africa (Volume 1): introductory chapters and Afrotheria*. London: Bloomsbury

Jiang, L., Dong, B., Liu, X., & Liu F, & Zi, J. (2012). Structural origin of sexual dichromatic coloration and luster in the beetle *Goliathus cacicus*. *Chinese Science Bulletin,* 57, 3211-3217.

Jones, C. (1978). *Dendrohyrax dorsalis. Mammalian Species,* 113, 1–4.

Lachaume, G. (1983). *The Beetles of the World 3: Goliathini 1*. Sciences Nat, Paris.

Lekkerkerk, R.W., & Krikken, J. (1986). Taxonomic review of the afrotropical genus *Dicronorhina* Hope, with notes on its relatives (Coleoptera, Cetoniidae). *Zoologische Verhandelingen,* 233, 1-46.

Luiselli, L., Demaya, G. S., Benansio, J. S., Ajong, S. N., Behangana, M., Marsili, L., ... & Battisti, C. (2024a). Searching priorities for a species at the brink of extinction: Threats analysis on the critically endangered Nubian Flapshell Turtle (*Cyclanorbis elegans*). *African Journal of Ecology*, 62, e13256.

Luiselli, L., Le Duc, O., Van, T. P., Xuan, T. N., Dang, P. B., Kuchling, G., ... & Battisti, C. (2024b). A threat analysis for the world's most threatened turtle (*Rafetus swinhoei*). *Journal for Nature Conservation*, 78, 126577.

Mallon, D. P., Hoffmann, M., Grainger, M. J., Hibert, F., Van Vliet, N., & McGowan, P. J. (2015). *An IUCN situation analysis of terrestrial and freshwater fauna in West and Central Africa.* Occasional paper of the IUCN species survival commission, 54, 40.

Maquart, P.O., & Malec, P. (2017). On the distribution and natural history of a rarely encountered species: *Goliathus (Fornasinius) klingbeili* Zöller, Fiebig, & Schulze, 1995 (Coleoptera: Scarabaeidae: Cetoniinae). *Zootaxa*, 4341 (3), 441–444.

Milner, J.M., & Harris, S. (1999). Activity patterns and feeding behaviour of the tree hyrax, *Dendrohyrax arboreus*, in the Parc National des Volcans, Rwanda. *African Journal of Ecology,* 37, 267–280.

Mudge, A. D., Orozco, J., Philips, T. K., & Antoine, P. (2012). The cetoniine fauna of the Upper Guinean forests and savannas of Ghana (Coleoptera: Scarabaeidae: Cetoniinae). *Terrestrial Arthropod Reviews*, 5, 113-174.

Oates, J.F., Bergl, R.A., Linder, J.M. (2004). Africa's Gulf of Guinea forests: biodiversity patterns and conservation priorities. *Advanced Applied Biodiversity Sciences*, 6, 1-91.

Oates, J. F., Woodman, N., Gaubert, P., Sargis, E. J., Wiafe, E. D., Lecompte, E., ... & Bearder, S. K. (2022). A new species of tree hyrax (Procaviidae: *Dendrohyrax*) from West Africa and the significance of the Niger–Volta interfluvium in mammalian biogeography. *Zoological Journal of the Linnean Society*, 194, 527-552.

Poorter, L., Bongers, F., & Lemmens, R.H.M.J. (2004). West African forests: introduction. In: Poorter L, Bongers F, Kouamé FN', Hawthorne WD, eds. *Biodiversity of West African forests: an ecological atlas of woody plant species*. Wallingford: CABI, 5–14.

Salzmann, U., & Hoelzmann, P. (2005). The Dahomey Gap: an abrupt climatically induced rain forest fragmentation in West Africa during the late Holocene. *The Holocene,* 15, 190–199.

Shine, R. (1978). Sexual size dimorphism and male combat in snakes. *Oecologia,* 33, 269-277.

Shine, R. (1994). Sexual size dimorphism in snakes revisited. *Copeia*, 1994, 326-346.

Shultz, S., & Roberts, D. (2013). *Dendrohyrax dorsalis*: western tree hyrax. In: Kingdon, J., Happold, D., Hoffmann, M., Butynski, T., Happold, M., & Kalina, J., eds. *Mammals of Africa (Volume 1): introductory chapters and Afrotheria.* London: Bloomsbury, 155–157.

Simpson, E.H. (1949). Measurement of diversity. *Nature*, 163, 688.

Touroult, J., & Le Gall, P. (2013). Fruit feeding Cetoniinae community structure in an anthropogenic landscape in West Africa. *Journal of Insect Conservation*, 17, 23-34.

Vendl, T., Šípek, P., Kouklík, O., & Kratochvíl, L (2018). Hidden complexity in the ontogeny of sexual size dimorphism in male-larger beetles. *Scientific Reports,* 8, 1-10.

Weibes, J. T. (1968). Catalogue of the Coleoptera Cetoniidae in the Leiden Museum. 1. *Goliathus* Lamarck, sensu lato. *Zoologische Mededelingen*, 43(3), 19-40.

Zbyryt, A., & Oleksa, A. (2018). The first observation of obligate saproxylic chafer larvae inside white stork *Ciconia ciconia* nest. *Journal of Insect Conservation*, 22, 795-797.

TABLE 1. Summary of the habitat features of each occurrence site of the two Fornasinius species at the landscape scale. Symbols: Tree cover areas (TRC); Shrubs cover areas (SHR); Grassland (GRS); Cropland (CRP); Vegetation aquatic or regularly flooded (VGA); Sparse vegetation (SPA); 7 - Bare areas (BAR); Built up areas (BLT). Geographic coordinates are not given for conservation reasons.

Genus	Species	Country	Locality	TRC	SHR	GRS	CRP	VGA	SPA	BAR	BLT
Fornasinius	*higginsi*	Ghana	Ankasa Forest reserve	99.30%	0.01%	0.00%	0.69%	0.00%	0.00%	0.00%	0.00%
Fornasinius	*higginsi*	Ghana	Kwahu	86.35%	0.04%	4.04%	9.41%	0.00%	0.00%	0.00%	0.00%
Fornasinius	*higginsi*	Ghana	Kwahu plateau	76.10%	0.00%	4.09%	19.80%	0.00%	0.00%	0.00%	0.00%
Fornasinius	*higginsi*	Ghana	Kyebi	52.42%	0.00%	2.58%	36.99%	3.63%	0.00%	0.00%	4.09%
Fornasinius	*higginsi*	Ghana	Kyebi	80.35%	0.00%	0.50%	16.48%	1.14%	0.00%	0.00%	1.41%
Fornasinius	*higginsi*	Cote d'Ivoire	Tai Forest	99.33%	0.00%	0.00%	0.67%	0.00%	0.00%	0.00%	0.00%
Fornasinius	*higginsi*	Cote d'Ivoire	Tai Forest	100.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Fornasinius	*higginsi*	Cote d'Ivoire	Banco	54.00%	0.00%	0.00%	15.81%	25.05%	0.00%	0.00%	2.76%
Fornasinius	*higginsi*	Cote d'Ivoire	Danané	86.84%	0.00%	2.41%	10.73%	0.03%	0.00%	0.00%	0.00%
Fornasinius	*klingbeili*	Togo	Badou	74.74%	0.16%	3.60%	6.36%	0.00%	0.00%	0.00%	15.10%
Fornasinius	*klingbeili*	Togo	Kara	5.63%	1.60%	3.40%	11.53%	0.00%	0.00%	0.06%	77.79%
Fornasinius	*klingbeili*	Togo	Togodo forest	13.08%	2.66%	83.44%	0.83%	0.00%	0.00%	0.00%	0.00%
Fornasinius	*klingbeili*	Togo	Bénali	91.42%	1.58%	0.64%	6.36%	0.00%	0.00%	0.00%	0.00%
Fornasinius	*klingbeili*	Togo	Kpété Béna	91.42%	1.58%	0.64%	6.36%	0.00%	0.00%	0.00%	0.00%
Fornasinius	*klingbeili*	Togo	Klouto	82.25%	1.56%	2.08%	13.51%	0.00%	0.00%	0.00%	0.61%

FIGURE 1. The two study species: *Fornasinius higginsi* (a) female, b) male) from Banco forest, Cote d'Ivoire, *Fornasinius klingbeili* (c) female, d) male) from Missahohé forest, Togo

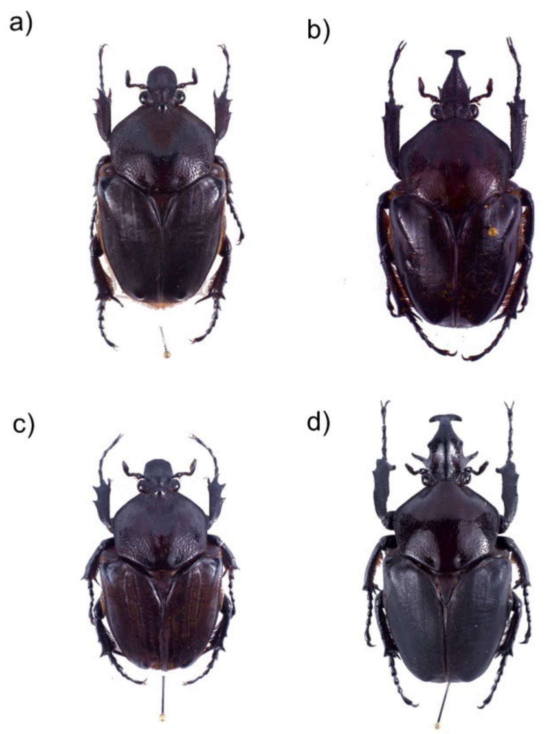


FIGURE 2 Map of Cote d'Ivoire, Ghana and Togo showing the sites of quantitative transects of *Fornasinius higginsi* and *F. klingbeili* during the present study, and the landuse of the region.

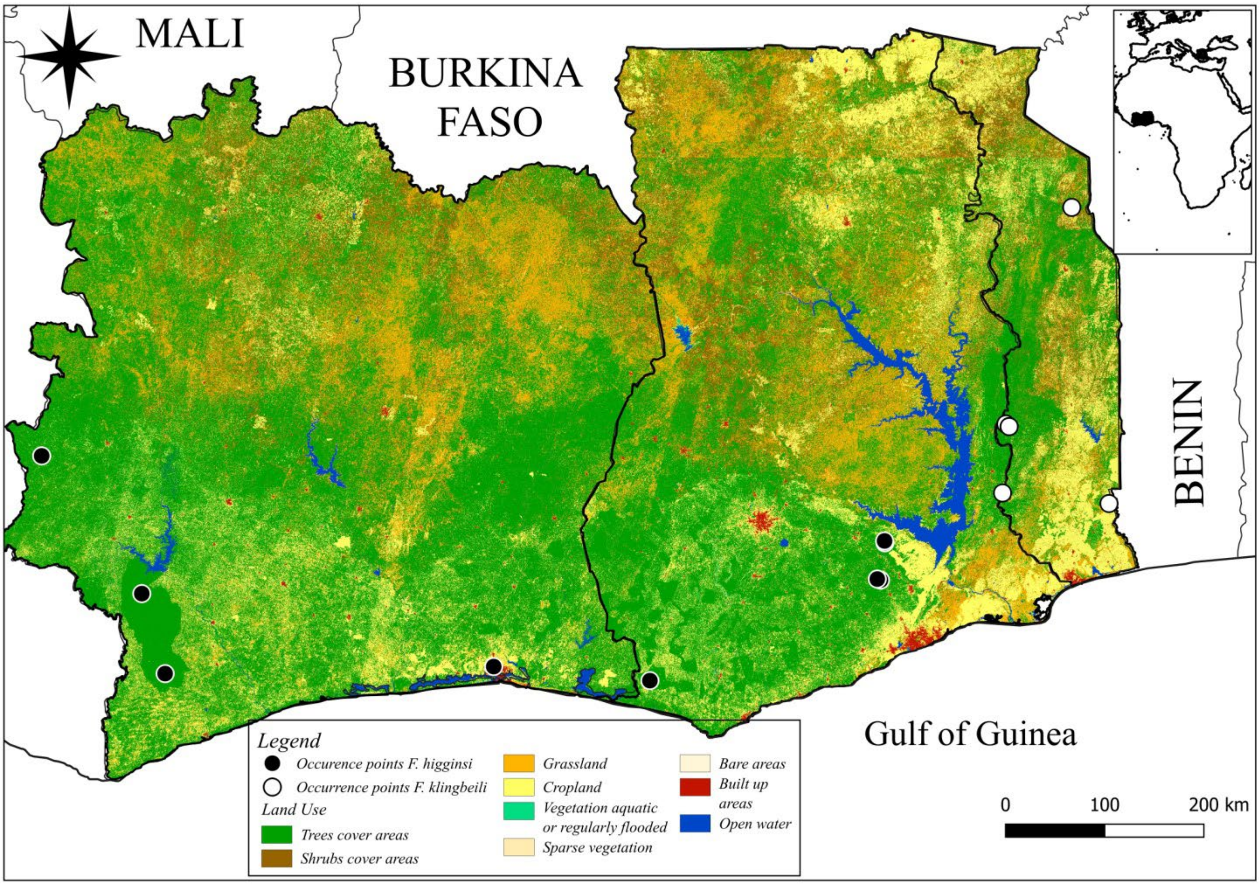


FIGURE 3. Monthly activity patterns of *Fornasinius higginsi* and *F. klingbeili* expressed as number of individuals observed during the study transects versus those expected on the basis of the relative monthly field effort. For statistical details, see the text

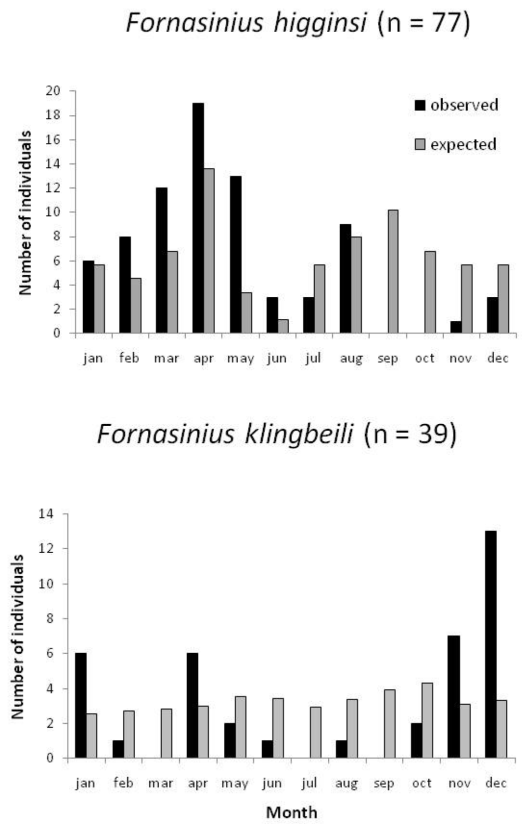


FIGURE 4. Distribution of the two *Fornasinius* species across habitat types at the sighting site scale. Symbols: DRS = dry savannah, WES = wet savannah, DRF = dry forest, PLT = plantation, FTP = forest-plantation mosaic, MAF = mature (and pristine) forest, SEF = wet secondary or altered forest.

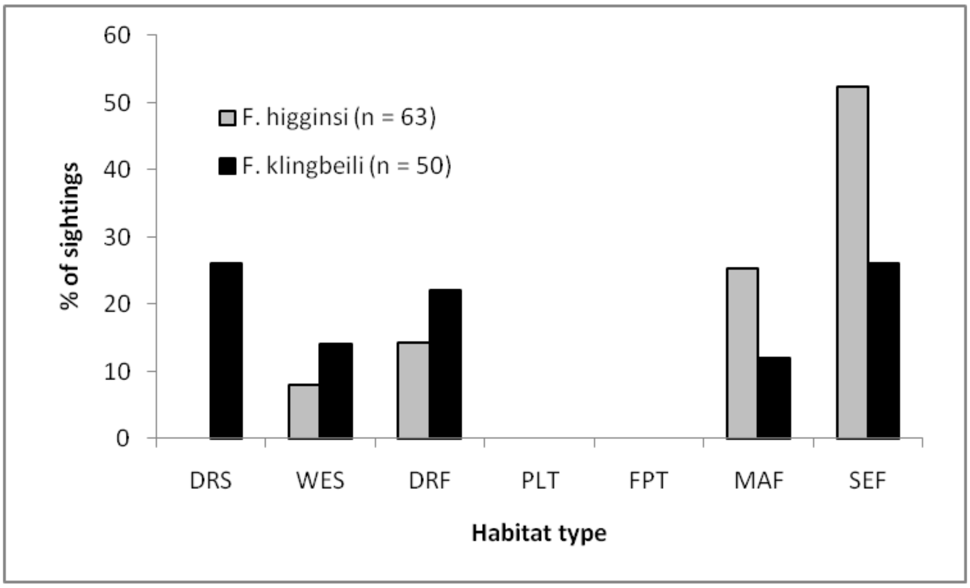
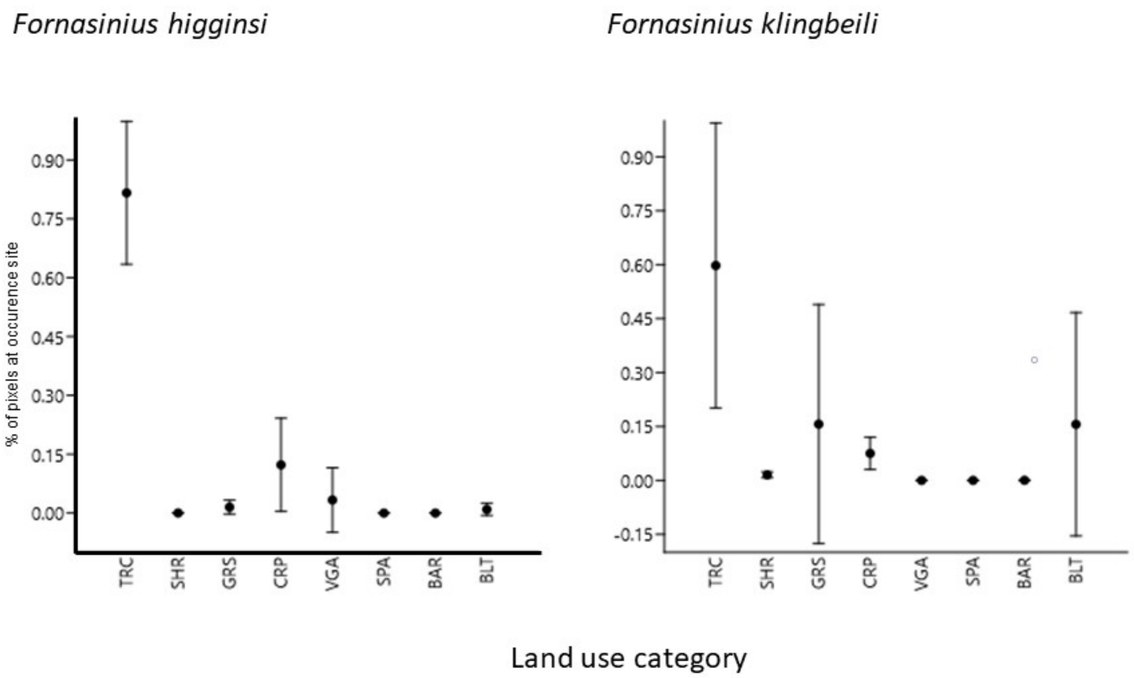


FIGURE 5. Means and Standard Deviation of the land use categories of each occurrence site of the two *Fornasinius* species at the landscape scale. Symbols: Tree cover areas (TRC); Shrubs cover areas (SHR); Grassland (GRS); Cropland (CRP); Vegetation aquatic or regularly flooded (VGA); Sparse vegetation (SPA); 7 - Bare areas (BAR); Built up areas (BLT).



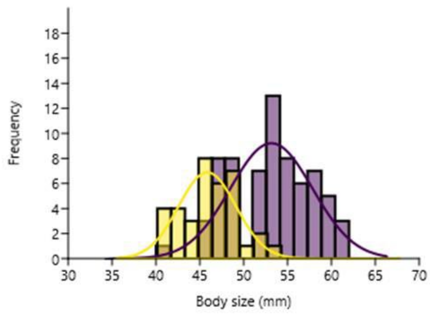
APPENDIX

TABLE A1 Field effort (number of days) per month, spent by the team within the range of the two study species.

	Ghana + Cote d'Ivoire	Togo	TOTAL
	F. higginsi	*F. klingbeili*	
January	5	40	45
February	4	42	46
March	6	44	50
April	12	47	59
May	3	55	58
June	1	54	55
July	5	46	51
August	7	53	60
September	9	61	70
October	6	67	73
November	5	48	53
December	5	52	57
TOTAL	68	609	677

FIGURE A1. Population structure-by-size in the two *Fornasinius* species studied here. For statistical details, see the text. Yellow = females; purple = males.

Fornasinius higginsi – males = 69, females = 36



Fornasinius klingbeili – males =25, females = 19

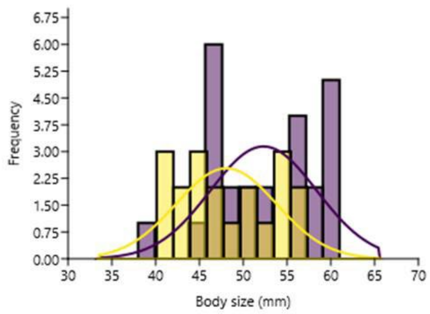


FIGURE A2. Monthly activity of *Fornasinius higginsi* and *F. klingbeili* (expressed as percentage of observed individuals per month with Standard Error). For statistical details, see the text