# Land use influence on chacma baboon (Papio ursinus) diet in South Africa using stable isotopes

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**Research Article**

**Keywords:** Carbon, Nitrogen, Anthropization, Habitat modification, Food availability, Garden Route

**Posted Date:** October 17th, 2023

**DOI:** https://doi.org/10.21203/rs.3.rs-3427689/v1

**Additional Declarations:** No competing interests reported.

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# Abstract

Anthropization processes affect wildlife feeding behaviours due to changes in resource availability related to land use and land cover change. To better understand the ecological responses of wildlife towards anthropogenic change, it is essential to evaluate whether human land use, characterized by high human-modified food availability, has an impact on wild animal feeding ecology. The chacma baboon (*Papio ursinus*) is interesting to study potential diet changes as it is largely present along a gradient of anthropized areas in Southern Africa. In this study, fecal samples from chacma baboon troops were collected in different land use habitats (peri-urban, agricultural and natural forest habitat) in the Garden Route, South Africa, and their isotopic ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) measured. Results showed significant differences between $\delta^{15}N$ ratios according to land use, indicating significant higher protein intake in areas with human influence in comparison to natural forest habitats. Furthermore, the large majority of the collected samples were contained within the bracket that reflect the $C_3$ ecosystem of the Garden Route region, with the exception of some samples showing higher $\delta^{13}C$ ratios associated with the consumption of anthropogenic foods (containing sugar, corn and wheat). The potential protein increase, as well as sources of $C_4$ plants present in the diets in anthropized areas suggests a visible dietary shift for this species between natural and transformed landscapes. In the future, it will be essential to determine whether and how the consumption of human-modified food could affect the health and associated fitness of chacma baboons.

# Introduction

The transformation of natural landscapes by human activities (Martínez-Fernández et al. 2015) has modified over half of the Earth's land surface (Foley et al. 2005; Hooke et al. 2012). Land use and land cover change (LULCC), including extensive clearing, the creation of pastures, croplands and urban settlements (Fahrig 2003; McKinney 2002) are the main drivers impacting ecosystems and causing drastic global and regional biodiversity collapse (Ellis et al. 2021; Foley et al. 2005; Sun et al. 2021; Turner et al. 2007; Zhang et al. 2007). For certain species, these transformed landscapes can create new niches and provide wild animals with other resources (Dale and Polasky, 2007; Eriksson 2013; Fleming and Bateman 2018).

In anthropized landscapes, the possible access to cultivated zones, gardens, kitchens and garbage has provided new opportunities for wildlife (Hulme-Beaman et al. 2016; Oro et al. 2013). Certain species have adapted or acclimated to these transformed areas, exploiting anthropogenic resources (Hulme-Beaman et al. 2016; Seoraj-Pillai and Pillay 2016; Webber 2017). For instance, wild boar (*Sus scrofa*) and vervet monkeys (*Cercopithecus aethiops*) are known to exploit croplands (Cancelliere et al. 2018; Lee and Lee 2019), carnivores such as San Joaquin kit foxes (*Vulpes macrotis mutica*) or coyotes (*Canis latrans*) exploit urban resources (e.g. garbage or compost; Newsome et al. 2010; Sugden et al. 2021) and commensal behaviour, notably as household and agricultural pests, has been observed in black rats (*Rattus rattus*) across different geographical areas on several occasions (Aplin et al. 2011). These changes cause direct modifications in wildlife diet, from the consumption of purely natural resources to the integration of more human-originated food (Murray et al. 2015). This can be a benefit to species, providing year-round food provisioning, reducing food and water deprivation during droughts or winters, or generally contributing to better individual condition. For example, a population of urban kit foxes presented higher cholesterol levels, a good indicator of energy intake (Harder and Kirk-patrick 1994), as well as reduced nutritional deprivation than rural ones in California (Cypher and Frost 1999). The integration of human resources into the diet of storks during periods of constrained resource availability has also been shown to lead to higher reproduction rates (Evans and Gawlik 2020). As another example, crop raiding behaviour in male elephants resulted in larger body size in adulthood (Chiyo et al. 2011), an important trait for this species during mating (Chelliah and Sukumar 2013). Despite certain benefits however, the consumption of human food has also been shown to have a negative impact on wildlife health. For instance, urban coyotes generally showed poorer average body condition as well as higher parasitic infection rates than rural coyotes in a study by Sugden et al. (2020). Reduced reproductive rates of birds (e.g. blue tits) are also associated with urban areas compared to populations in rural zones, linked to a lack of suitable diets for nestlings (Pollock et al. 2017; Seress et al. 2020).

The impacts of human resources on non-human primates appear to a lesser extent in the literature, even though primates often consume human resources (Strum 2010). It has been shown that wild primates obtain higher levels of essential nutrients relative to body weight than humans do through their diets (Milton 1999), but also that varying benefits can follow their consumption of anthropic food resources depending on the type of LULCC (Maibeche et al. 2015; Marty et al. 2020). An interesting primate species to better understand diet change in the presence of human resources is the chacma baboon (*Papio ursinus*), due to its adaptive capacity (Fischer et al. 2019). Baboons are opportunistic, omnivorous feeders that will eat anything from fruits, grasses, leaves or roots to invertebrates and even occasionally animal matter usually resulting from opportunistic hunting (Allan et al. 2022; Hoffman and O’Riain 2011; Schreier et al. 2019) and are highly adaptable to a wide range of habitats and environments (Johnson et al. 2015). They can be found across deserts, savannahs, forests and on the outskirts or within urban zones (Hoffman and O’Riain 2011, 2012; Johnson et al. 2015; Mormile and Hill 2017). With the encroachment of urban areas on natural habitats, encounters between humans and baboons have become prevalent in some areas, such as in the Western Cape of South Africa (Bracken et al. 2022a, b, 2023; Chowdhury et al. 2020; Lee and Priston 2005). In the Western Cape, as well as across South Africa, chacma baboons frequently raid croplands as well as people’s gardens, bins or houses (Hoffman and O’Riain 2011; Strum 2010; Walton et al. 2021), consuming resources of human origin. When the availability of rubbish is reduced, this affects the baboon’s raiding tendencies: Mazué et al. (2023) showed that when the rubbish resources were removed on regular foraging sites in a peri-urban area on the George Campus of the Nelson Mandela University (NMU), chacma baboons spent more time foraging for natural resources and less time in these more urban areas. The easy access to fruits, vegetables, meats, but also processed foods, refined sugars, added fats and oils may result in significant variations in their nutrient consumption and have unknown effects on their metabolisms. In this context, the objective of this present study was to evaluate whether human land use, characterized by high human modified food availability, has an impact on chacma baboon diet.

Several methods exist to study diets in ecology, including direct observation or fecal analysis. These techniques yield accurate results but they can vary according to what is consumed and the digestibility of the latter (Matthews et al. 2020): some resources will appear in higher proportions in fecal samples than others depending on how easy they are to digest. Direct observation also often requires long periods of time (Jordan 2005), whereas non-invasive methods based on fecal samples, such as DNA metabarcoding and/or isotopic analyses, can counter this problem (Ando et al. 2020; Crowley et al. 2016; De Barba et al. 2014; O'Brien 2015). In the case of metabarcoding however, sample analysis can be costly and a broad list of plant/animal DNA sequences that could be consumed in the region would be necessary (Taberlet et al. 2018). Analysing isotopic ratios is therefore an interesting alternative, both less expensive and less time-consuming than other options, which explains why it is a recurrent method used in feeding ecology studies (Boecklen et al. 2011; Martínez del Rio et al. 2009; Taki et al. 2017). Common isotopes used for diet studies include nitrogen ($^{15}N/^{14}N$) and carbon ($^{13}C/^{12}C$). Nitrogen isotopes are a potential biomarker of protein source because tissue nitrogen derives almost entirely from dietary protein (for a review of isotopes as biomarkers see O'Brien 2015). Due to a stepwise increase with the trophic chain, variations of the $\delta^{15}N$ isotopic ratios observed within feces may reflect consumption of dietary items with higher protein content within the different LULCC based on what resources the baboons have access to. The carbon in plants derives from atmospheric $CO_2$ which is fixed during the process of photosynthesis. Differences in stable carbon isotope ratios therefore reflect the type of plants consumed based on their photosynthetic pathways ($C_3$, $C_4$ or CAM) due to differential fractionation of carbon isotopes during photosynthesis that leads to distinct $\delta^{13}C$ values (Ehleringer and Cerling 2002; Smith and Epsten 1971). Examining carbon and nitrogen ratios may therefore be a suitable method of assessing the potential contribution of human-derived foods to animal diet, comparing protein intake and the type of plants consumed between natural areas and those with anthropic resources (Penick et al. 2015).

To address the objective of this study, we obtained stable isotope ratios from fecal samples of chacma baboons, which would provide quantitative data on the types of plants and animal protein they consume. Baboons may be considered as opportunistic feeders (Allan et al. 2022; Schreier et al. 2019) and therefore the potential access to high protein sources such as meat and legumes in more anthropized areas (with crops, garbage or kitchens) may result in higher proportions of protein in their diet. We could expect that if the anthropized landscapes provide higher protein contents than the natural resources consumed by chacma baboons, the stable nitrogen isotope values would tend to be higher in these transformed landscapes. More positive $\delta^{13}C$ values for samples from anthropized areas may be associated with a higher consumption of $C_4$ plants that pervade human-derived foods (e.g. maize, sugarcane) as well as lipids when these types of resources are included in chacma baboon diets (Post et al. 2007). We could then expect to observe more positive $\delta^{13}C$ ratios from samples collected in more urbanized environments compared to natural landscapes. To evaluate whether transformed landscapes have an influence on chacma baboon diet, we collected fecal samples from chacma baboons along a gradient of land use in the Garden Route, South Africa, and studied stable isotopic ratio data, incorporating the surrounding landscape characteristics.

## Material and methods

# Study area

The study was conducted in the Western Cape, South Africa, across the Garden Route Biosphere Reserve (listed in the UNESCO's World Network of Biosphere Reserves; Pool-Stanvliet and Coetzer 2020) between George and Knysna, representing an area of 2000km² (Fig. 1a). The reserve is known for its unique and endemic biodiversity, such as afrotemperate forests, fynbos, as well as wetlands, mountains and coastal ecosystems. However, human presence has largely transformed the landscape in many places (Socio-Economic Profile: Garden Route District Municipality 2021), providing agricultural, forestry and touristic activities as well as the development of many urban settlements (e.g. Mossel Bay, George, Knysna). To protect the area, the Garden Route biosphere reserve, with the Garden Route National Park (GRNP) as a core area was created, preserving natural areas where biodiversity can prosper. Due to the complex landscape configuration that includes agriculture, logging, urban areas as well as natural vegetation, this IUCN type II protected area is very patchy and fragmented. Certain species, such as chacma baboons, can be found across all these different ecosystems, populating protected areas, rural zones as well as highly urbanized regions (Mormile and Hill 2017; Slater et al. 2018).

In the study area, three main contrasted locations were selected, a peri-urban, an agricultural and a protected area, hereafter referred to as Campus, Hoekwil and Knysna throughout this study (represented in red, purple and blue respectively in Fig. 1a). These three sampling areas represent different land use types. The first location (Campus) is located on the Nelson Mandela University Campus near the city of George, where there are many people, buildings (e.g. accommodation and cafeterias) and lawns, and is surrounded by natural forest and fynbos. The second location (Hoekwil) was situated in the agricultural area bordering the Garden Route National Park to the North of the Town named Hoekwil. This area mainly consisted of livestock pastures and croplands, with occasional buildings (accommodation and infrastructure). In the region, summer crops can include lucerne, maize and vegetables (CapeFarmMapper v 2.7). The third location (Knysna) was situated within the afrotemperate forest of the Knysna Section of the Garden Route National Park (GRNP).

Two subsites were established for each of these three main locations as replicates to account for troop preferences and intra-troop variation: Main and North for Campus (respectively light and dark red; Fig. 1b), Oakhurst and Woodville for Hoekwil (light and dark purple; Fig. 1b), Goudveld and Diepwalle sections of the GRNP for Knysna (light and dark blue; Fig. 1b). The two replicates for Campus represent two distinct troops, whereas the replicates for Hoekwil and Knysna were made up of one or more distinct troops each, and each replicate had varying proportions of land cover including within each of the three sites.

# Chacma baboon fecal sampling

Sampling took place between the 14th of February and the 1st of April 2022. fecal samples from baboons were collected during regular visits to each of the three locations over this period. Each location was visited two to three times a week. Sample collection was opportunistic, resulting in different sample sizes for both temporal and spatial replicates.

At the Campus, samples were collected on foot by retracing where the Main and North troops had been sighted by students or staff. At Hoekwil, footpaths and fences where the baboons were often sighted were scoured on foot. In the Knysna forest, road transects were followed by car in search of samples. Each sample was collected using gloves and inserted into plastic tubes or bags. At each sampling point the collection date, latitude, longitude, freshness of feces, location and subsite names were noted (SI 1). Samples were kept in a cooler box during the fieldwork each day before being frozen and stored at -20°C at NMU REHABS Laboratory until further analysis. Data collection and analyses were authorized by permits from SANParks (BERN-A/2020-008) and Cape Nature (CN44-87-16198), and the Section 20 of the Animal Diseases Act, 1984 (Act No 35 of 1984).

# Landscape characteristics surrounding each collected fecal sample

The study area (latitude: 630900–725500, longitude: 6214900–6263600) was represented using QGIS (3.18), under a WGS 84 – UTM 34S projection. It was characterized according to several landscape metrics: land cover, slope, elevation and length/number of roads. In order to characterize the landscape metrics in the area used by the baboons for feeding, we recorded them within a circle of 4km² defined around each fecal sample position, based on the highest daily distance covered by chacma baboons in the literature in South Africa (Hoffman and O'Riain 2011; Slater et al. 2018) and the observations of the baboon troops on NMU Campus in George by Maud Czerwinski et al. (unpubl. Manuscript).

The land cover raster layer was obtained from the South African National Land Cover Datasets (2018) of the South African Forestry, Fisheries and the Environment government website (DEFE, 2021) and clipped to the study area. The 73 classes from this layer were grouped into 10 (Fig. 1a) for simplification according to main types (*i.e.* natural forest, plantations, shrubland, grassland, waterbodies, wetland, barren land, cultivated land, built up and mines). The elevation raster at 30 meters was downloaded from SRTM products (Farr and Kobrick 2000, Shuttle Radar Topography Mission) and slopes were calculated within QGIS. The roads vector layer covering South Africa was obtained from the website of the Princeton University Library (International Steering Committee for Global Mapping, map issued in 2016). The percentage of land cover, as well as mean slope, elevation, road length and number of road segments was calculated within the buffer of each sample using QGIS (3.18). Finally, a principal component analysis (PCA) was performed considering these variables after removing those with a correlation higher than 0.8, to visualize the land use characteristics surrounding each sample.

# Stable isotope analysis for chacma baboon diet characterization

After being placed in a fridge for 24 hours to defrost, up to 10g of each sample used for the isotopic analyses was inserted into 20mL tubes and dried for 48 hours in an oven at 60°C at the NMU REHABS laboratory (following steps used by Caut et al. 2008; Codron et al. 2007; De Carvalho et al. 2019). These samples were then transported to the University of Pretoria where they were ground using a mortar and pestle and passed through a ½ mm sieve. The homogenized fecal samples were weighed out in aliquots of 0.9 mg and placed in tin capsules, which were pre-cleaned in toluene to avoid any potential contamination.

The isotopic ratios for carbon (C) and nitrogen (N) of these samples were analysed at the University of Pretoria, South Africa. Samples were combusted at 1,020°C using an elemental analyser (Flash EA 1112 Series) coupled to a Delta V Plus stable light isotope ratio mass spectrometer via a ConFlo IV system (all equipment supplied by Thermo Fisher, Bremen, Germany), housed at the University of Pretoria Stable Isotope Laboratory, Mammal Research Institute. Several samples were run in duplicate (every 13th sample) to verify the accuracy of the homogenization of the samples. Two laboratory running standards Merck Gel ($\delta^{13}C$ = -20.26‰, $\delta^{15}N$=7.89‰, C%=41.28, N%=15.29) and DL-Valine ($\delta^{13}C$ = -10.57‰, $\delta^{15}N$=-6.15‰, C%=55.50, N%=11.86) and a blank sample were run after every 11 unknown samples. The carbon and nitrogen ratios for the laboratory running (Merck and DL-Valine) standards were calibrated using the following PRIMARY standards: IAEA- CH-3 (Cellulose), IAEA-CH-6 (Sucrose), IAEA-CH-7 (Polyethylene foil), IAEA N-1 and IAEA N-2 (Ammonium sulfate), IAEA NO-3 (Potassium nitrate). All results were referenced to Vienna Pee-Dee Belemnite for carbon isotope values, and to air for nitrogen isotope values.

Results are expressed in delta notation using a per mil scale using the standard equation (Coplen 2011, Rapid Comm, in Mass Spectrometry): $\delta X(‰)=[(R_{sample} - R_{standard})/R_{standard} - 1]$ where X = $^{15}N$ or $^{13}C$ and R represents $^{15}N/^{14}N$ or $^{13}C/^{12}C$ respectively.

# Statistical analysis of diet variations

Statistical analyses were conducted using R (R Core Team 2020, version 3.6.3.) in RStudio (version 1.3.1093) to analyse and compare the isotopic patterns ($\delta^{15}N$ and $\delta^{13}C$) of chacma baboon diets in relation to land use over the three locations (Campus, Hoekwil, Knysna). Firstly, the data for each stable isotope ratio were summarized as mean and standard deviation values according to location and subsite. After carrying out Shapiro-Wilk and Levene tests, non-parametric Kruskal-Wallis tests were used to determine the significance of the location variable on the isotopic ratios of $\delta^{13}C$ and $\delta^{15}N$ followed by Dunn pairwise comparison tests to establish the significance of the differences between locations characterized by different landscapes and between the subsites of each location. A biplot was also created to visualize any variation in diet according to land use by comparing the $\delta^{13}C$ and $\delta^{15}N$ ratios by site. Finally, the differences between chacma baboon populations were tested across the gradient of anthropization created using the resulting axes of the PCA, using a linear model (LM) for the nitrogen and distribution plots for the carbon ratios.

To establish if grouping the subsites within each location had an impact on the results, an inter-troop analysis was carried out focusing on the subsites of the Campus (Main and North). The comparison between these troops within site was possible due to the intimate knowledge of the troops using the area through regular monitoring and research projects. Following Shapiro-Wilk and Levene tests, a Student's t-test was carried out on the Campus $\delta^{15}$N results and a Wilcoxon test for the $\delta^{13}$C.

## Results

### Sampling

A total of 231 baboon fecal samples were collected throughout the sampling period (Fig. 1a; Table 1). Within the Campus, a total of 98 samples were collected, 60 for the Main and 38 for the North subsites, representing two different troops of baboons monitored on the NMU campus. At the Hoekwil site, 28 samples were found, with 14 for each subsite (Oakhurst and Woodville). In Knysna, 105 were collected in total, 67 of which for the Goudveld subsite and 38 for the Diepwalle subsite. We selected 148 samples for analysis in this study, according to their freshness and to obtain a similar number of replicates per location (Table 1; SI 1). A total of 60 samples were selected for both Campus and Knysna, with 30 samples per subsite. The Hoekwil samples were used in their totality due to the limitation of samples available linked to difficulties in finding samples in these areas, amounting to a total of 28 (14 per subsite).

Table 1
Numbers of fecal samples collected, analyzed for land cover and analyzed for stable isotopes by location and subsite. The 146 samples chosen for the stable isotope analysis were chosen according to freshness and to obtain a representative number of replicates per location.

| **Location** | **Campus** | | **Hoekwil** | | **Knysna** | |
|---|---|---|---|---|---|---|
| **Subsite** | **Main** | **North** | **Oakhurst** | **Woodville** | **Goudveld** | **Diepwalle** |
| **Number of collected samples** | 60 | 38 | 14 | 14 | 67 | 38 |
| | 98 | | 28 | | 105 | |
| | 231 | | | | | |
| **Number of samples analyzed for land cover** | 30 | 30 | 14 | 14 | 30 | 30 |
| | 60 | | 28 | | 60 | |
| | 148 | | | | | |
| **Number of samples analyzed for isotopes** | 29 | 29 | 14 | 14 | 30 | 30 |
| | 58 | | 28 | | 60 | |
| | 146 | | | | | |

### Landscape and anthropization level characterization

The PCA biplot created by combining the landscape variables used in this study revealed that the 148 samples from the three locations (Campus, Hoekwil, Knysna) were characterized by distinct land cover (Fig. 2a). Three clusters emerged within this figure, grouping together the samples from each studied location. The first axis, which explained 41.1% of the variation, opposed the flatter areas dominated by agriculture (including irrigation dams) mostly present in Hoekwil with the area to the steeper slopes dominated by natural forests and characteristic of the Knysna site. On the other hand, the second axis of this PCA, explaining 30.5% of the variation, opposed the built up location (Campus) with the more natural and less built up areas (Hoekwil and especially Knysna; Fig. 2a). A gradient, going from land rich with infrastructure (Campus) to natural environments without human settlements (Knysna) via an intermediate, agricultural area (Hoekwil), could be distinguished along the second axis (Fig. 2a). This axis was therefore defined as the gradient of anthropization of the environment for the following diet analyses of chacma baboons, with more negative values representing the more natural areas, more positive values representing more urban zones and intermediate values representing the agricultural areas.

## Stable isotope signatures and distributions according to the level of anthropization

Out of the 148 fecal samples, 146 were analysed for $\delta^{15}N$ and $\delta^{13}C$ (SI 1) due to reduced quality of two samples. When combining the carbon and nitrogen ratios, the resulting biplot showed that the samples from the three locations had different nitrogen and carbon isotopic ratios (Fig. 2b). The widest range of isotopic ratios belonged to the Campus, the smallest to Knysna, with intermediate values for Hoekwil, resembling the Campus for its $\delta^{15}N$ and Knysna for its $\delta^{13}C$ (Fig. 2b). Low values of $\delta^{15}N$ and $\delta^{13}C$ tended to characterize the Knysna samples, going from − 0.02 to 3.12‰ for nitrogen and − 29.96 to -23.53‰ for carbon (Table 2). A wide range of $\delta^{15}N$ (from 0.55 to 5.15‰) combined with low values of $\delta^{13}C$ (from − 29.82 to -25.67‰) characterized those of Hoekwil (Table 2). A more intermediate profile characterized the Campus samples, yielding a wider range of $\delta^{15}N$ (0.66 to 5.31‰) and wider ranges of $\delta^{13}C$ (-29.26 to -17.92‰) than the other locations (Table 2).

Table 2

Summary statistics (including minimum, maximum, mean and standard deviation SD) for isotopic ratios of Nitrogen and Carbon in the 146 analysed fecal samples by location and subsite.

| | **δ15N (‰)** | | | | **δ13C (‰)** | | | |
|---|---|---|---|---|---|---|---|---|
| **Location** | **Min** | **Max** | **Mean** | **SD** | **Min** | **Max** | **Mean** | **SD** |
| **Campus** | **0.66** | **5.31** | **2.68** | **1.08** | **-29.26** | **-18.99** | **-26.38** | **1.84** |
| Main | 1.95 | 5.31 | 3.36 | 0.92 | -29.09 | -21.98 | -26.43 | 1.42 |
| North | 0.66 | 3.70 | 1.97 | 0.71 | -29.26 | -18.99 | -26.34 | 2.22 |
| **Hoekwil** | **0.55** | **5.15** | **2.55** | **1.21** | **-29.82** | **-25.67** | **-28.13** | **0.93** |
| Oakhurst | 2.24 | 5.15 | 3.34 | 0.72 | -29.82 | -27.54 | -28.65 | 0.62 |
| Woodville | 0.55 | 4.29 | 1.75 | 1.08 | -28.90 | -25.67 | -27.60 | 0.91 |
| **Knysna** | **-0.02** | **3.12** | **1.58** | **0.69** | **-29.96** | **-24.24** | **-28.03** | **0.80** |
| Goudveld | 0.62 | 3.12 | 1.65 | 0.70 | -29.96 | -24.24 | -27.92 | 0.91 |
| Diepwalle | -0.02 | 3.08 | 1.51 | 0.69 | -29.72 | -27.01 | -28.14 | 0.67 |

A significant increase in the $\delta^{15}$N ratios was visible along with the level of anthropization of the environment across the land use gradient (R = 0.45, P-value = $1.4e^{-08}$; Fig. 2c), created using the second axis of the PCA from Fig. 2a. The samples collected at the Campus (highest proportion of built up land cover), characterized by the highest anthropization levels, showed higher ratios of $\delta^{15}$N. The samples from Hoekwil (highest proportion of agriculture), with lower levels of built up land cover, presented intermediate $\delta^{15}$N numbers. The Knysna samples (highest proportion of forest), reflecting the lowest anthropization levels and more natural habitat, showed the lowest values for $\delta^{15}$N. The majority of the Campus samples, as well as all those from Hoekwil and Knysna, reflected an isotopic signature between about − 30‰ and − 24‰ for $\delta^{13}$C values (specific to $C_3$ plants), except four of the Campus samples that possessed slightly higher values (Fig. 2d). Higher values correspond to the more urban areas.

The data for both $\delta^{15}$N and $\delta^{13}$C were found to be non-parametric (Shapiro-Wilk, p-value = 3.89e-4 for $\delta^{15}$N and 1.50e-12 for $\delta^{13}$C) with unequal variances between the three locations (Levene, Pr(> F) = $7.59e^{-4}$ for $\delta^{15}$N and $1.01e^{-2}$ for $\delta^{13}$C). Kruskal-Wallis tests indicated that at least one location was significantly different from the others for nitrogen (chi-squared = 32.97, df = 2, p-value = $6.92e^{-08}$) and carbon (chi-squared = 57.92, df = 2, p-value = $2.65e^{-13}$). Post-hoc Dunn tests revealed that the Knysna samples significantly differed from both the Campus (p-value = 1.04e-07) and Hoekwil (p-value = $4.77e^{-04}$) samples for nitrogen (Fig. 3a), whereas for carbon ratios, the Campus samples were significantly different from both Hoekwil (p-value = $8.88e^{-09}$) and Knysna (p-value = $3.28e^{-11}$; Fig. 3b). According to these tests, nitrogen ratios did not significantly differ between Hoekwil and Campus samples (Dunn, p-value = $4.53e^{-01}$), nor did Knysna and Hoekwil for carbon samples (Dunn, p-value = $6.77e^{-01}$).

# Isotopic distribution variations between troops at the Campus site

The resulting PCA biplot for the inter-troop analysis on the two subsites of the Campus (Main and North troops) showed little difference in distribution according to land use. The landscape surrounding the samples only differed slightly along the first axis according to the troop, which accounted for 70.9% of the variation (Fig. 4a). The Main troop samples tended towards higher levels of built up land use as well as the presence of roads, whereas the North troop spanned a wider range across the axis, going from built up to more natural landscapes (Fig. 4a).

Despite these limited differences in the landscapes used by these two troops of baboons, $\delta^{15}N$ nitrogen ratios of the fecal samples from these two subsites varied significantly (Student's t-test, t = 6.50, df = 57, p-value = 1.09e-08) and according to the level of land use created using the first axis of the inter-troop PCA biplot (Fig. 4a and Fig. 4b). Higher $\delta^{15}N$ values were associated with the Main troop (1.95 to 5.31‰; Table 2), which is represented by built up land cover and higher anthropization levels. The North troop nitrogen ratios had a wider range, spanning from ratios similar to those of the Main samples down to lower values of $\delta^{15}N$ along with the anthropization level and towards areas characterized by more natural forests (0.66 to 3.70‰; Table 2).

The carbon $\delta^{13}C$ ratios of these two subsites reflected a similar distribution to those of all three locations: no significant differences were present between the two troops, whose ratios were contained between − 24‰ and − 30‰ (Wilcoxon, W = 450, p-value = 0.83; Fig. 4c; SI 1). It is noticeable that the highest $\delta^{13}C$ values of two subsite samples of the Campus were specific to the North troop (Fig. 4c).

# Discussion

In South Africa, chacma baboons are highly present in anthropized landscapes, possibly most notably in the Western Cape province. In Cape Town, as well as across the Garden Route region, chacma baboons and humans often occupy overlapping habitats, where increased conflicts have been reported associated mostly to stealing food (Chowdhury et al. 2020; Mormile and Hill 2017). Hoffman and O'Rian showed that Cape peninsula baboon troops present in human-modified habitats are associated with increased events of observed stealing from people's houses and visiting the bins around settlements (Hoffman and O'Riain 2012). Mazue et al. also described that the Main troop living on the campus of Nelson Mandela University (George Campus), representing a peri-urban area, was responsible for an unexpected number of raids: 70 raids were recorded within a two-week study (unpublished data, 2016). Overall, it appears that the fragmentation and the modification of their natural habitats has pushed chacma baboons to co-exist with humans within modified landscapes, where new human-modified food resources are easily available, which could have an impact on their foraging behaviour. In the present study, the analysis of nitrogen and carbon stable isotopic ratios in chacma baboon troops inhabiting a gradient of human-modified landscapes in the Garden Route region showed significant differences in their diet in terms of protein and plant intake.

## A shift towards higher protein intake in anthropized areas

It is well known that $^{15}N/^{14}N$ ratios in mammalian excrements are related to a combination of variables, driven by the complexity of the nitrogen cycle (Handley and Raven 1992). The latter leads to a variety of $\delta^{15}N$ patterns in soil and plants that are consumed by animals higher up the trophic chain. When consumed, $^{15}N$ is preferably incorporated into tissues over $^{14}N$, creating a stepwise increase with each trophic level and also increasing with protein intake (Handley and Raven 1992; Schoeninger and DeNiro 1984; Sponheimer et al. 2003). In the present study, the $^{15}N/^{14}N$ results showed significantly higher protein intake for chacma baboons in landscapes transformed by human activity, *i.e.* on the Campus with built up land cover and in Hoekwil with agricultural zones (Fig. 2c and 3a). This suggests that the chacma baboon populations known to live in close contact with human populations in the Garden Route have been shifting their diet to a richer nitrogen pattern when inhabiting more anthropized lands. This is the case whether agricultural or peri-urban, a result probably associated with the easier access to human-modified resources. Such results could be explained by the easy access to protein sources in such areas, such as garbage bins, meat detritus from the cafeteria on the Campus site or the houses and farmsteads around the Hoekwil area. Particularly on Campus, the kitchens and bins provide regular food for the baboons almost all year round, including remaining meals from students that contain large amounts of meat that would not be accessible to them in the wild. This observation was even confirmed when considering the smaller scale of the Campus site, where higher values of $\delta^{15}N$ were observed to be associated with the Main troop, in comparison to the North one (Fig. 4b). This chacma baboon Main troop is followed daily by monitors and has been reported to spend considerable time on George Campus where they regularly visit buildings and bins (Mazué et al. 2023), which could again explain the differences observed between the Main and the North troops at the Campus location regarding nitrogen intake. This study showed that the nitrogen ratios in the fecal samples, and therefore protein intake, were significantly highest in the populations inhabiting the most anthropized areas where the most buildings, built up land cover and transformed landscape for agriculture can be observed and where a higher access to human modified food highly composed of meat is present.

Some studies have also described higher protein intake by wild animals inhabiting human-modified environments, such as rats, that have been shown to consume more protein-rich resources in anthropized areas (Guiry and Buckley 2018). While these studies showed the same pattern and confirmed that certain wild animal populations inhabiting anthropogenic landscapes present higher protein intake in comparison to natural ones (Guiry and Buckley 2018), others described different patterns with either lower nitrogen intake in anthropized environments or no significant difference in relation to landscape use. Some birds and carnivorous mammal species such as foxes or coyotes have been found to possess protein-poor diets in anthropized areas in comparison to populations in rural zones (Francis et al. 2021; Heiss et al. 2009; Murray et al. 2015; Newsome et al. 2010; Scholz et al. 2020). Moreover, a study from Nabugabo Field Station in central Uganda showed that for vervet monkeys consuming crops, there were no resulting variations in protein, fibre or lipid composition in comparison to wild populations (Cancelliere et al. 2018). The same pattern has been observed for wild boars, for which similar protein levels have been described across a gradient of modified landscapes, even though the species has been proven to be present near human settlements (Cahill et al. 2012; Stillfried et al. 2017). The work from Gámez et al. (2020) also evidenced that overall, $\delta^{15}N$ ratios did not differ between urban and rural or wild land predators suggesting that the protein intake was not influenced by landscape modifications. It then appears that depending on the species studied and probably the geographic location of the study, wild animals respond differently to human modified resources. In the present study, the results reveal a significant shift toward higher protein intake in chacma baboons' diet inhabiting anthropized areas in South Africa, but this will need to be confirmed through replicates along the same landscape gradient in multiple troops.

# Variations in plant consumption patterns across anthropized areas

It is well established that $C_3$ plants tend to have lower $^{13}C/^{12}C$ ratios than $C_4$ plants: the $\delta^{13}C$ values of $C_3$ plants range from − 34 to -22‰ and those of $C_4$ plants from − 16 to -10‰ (Basu et al. 2015). In the Garden Route temperate region, it has been shown that most trees and shrubs follow the $C_3$-photosynthetic pathway (Ehleringer and Cerling 2002), so we could expect chacma baboon's diet living in natural forest to be richer in $C_3$ than in $C_4$ plants. The results obtained in this study showed that the large majority of the collected samples were contained within the bracket that reflect a $C_3$ ecosystem, suggesting that as expected the overall consumption of the chacma baboon troops studied was made up of $C_3$ plants (Fig. 2d). However, small variations have to be considered regarding the $\delta^{13}C$ isotopic ratios, as some samples collected at the highly anthropized Campus location possessed a higher proportion of $C_4$ plants than those from Hoekwil and Knysna, suggesting more consumption of $C_4$ components during recent foraging by certain individuals (Fig. 2d). This could be associated with the fact that higher $\delta^{13}C$ isotopic ratios can be explained by the consumption of anthropogenic foods that are known to contain large quantities of $C_4$ plants (*i.e.* sugar, corn and wheat; Gámez et al. 2020; Nicholson and Cove 2022; Post et al. 2007). The same pattern has been observed for instance in eurasian red squirrels (*Sciurus vulgaris*) that consumed more sugar in urban zones (Wist et al. 2022). In the present study, the overall consumption of the chacma baboon troops studied was made up of $C_3$ plants with for a significantly higher $\delta^{13}C$ ratios in the Campus suggesting that the troops in this area may have access to and consume a higher proportion of $C_4$ plants (*i.e.* sugar, corn and wheat), presumably due to the access to garbage and kitchens, as described previously for nitrogen.

At a smaller scale, a few samples from the most anthropized subsites (on Campus) particularly stood out, possessing higher $\delta^{13}C$ values, which could be as discussed above the result of higher $C_4$ plant consumption by specific individuals (Fig. 4c). This raises the possible influence of other factors including social behaviour that could contribute to variations in diet in primates that can influence carbon intake. Indeed, adult males of several macaque species have been shown to consume more human resources than adult females, younger and lower ranked individuals (Maibeche et al. 2015, Marty et al. 2020). Focusing management (*i.e.* monitors) on certain high ranking individuals may be helpful to reduce their consumption of human resources, but can also provide lower ranking individuals with easier access to these resources (Bracken et al. 2022b), thereby failing to reduce conflict with humans. To address such questions, future studies should integrate stable isotope analyses with complementary behavioural analyses to get a better understanding of the chacma baboons' behavioural ecology and to establish better strategies for conflict management.

# Perspectives and future impacts

This present study showed that land use influences chacma baboons' diet, with a shift in anthropized environments toward a globally significant higher nitrogen and for some individuals higher carbon patterns. This quantitative analysis gives a first picture of land use impact on this species diet, however we are still far from identifying exactly what chacma baboons consume in different environments. In this context, future studies should combine stable isotope analysis with observation and/or DNA metabarcoding in order to extract the precise composition and species richness of the baboon's diet along multiple land uses.

Moreover, seasonal variations can also account for differences in carbon ratios in baboon diet across the year: Lewis et al. (2018) provided results that showed that summer and autumn $\delta^{13}C$ ratios were higher than those in winter and lowest in spring. In the future, studies should therefore also focus their efforts on the analysis of the stable isotopic ratios of larger sampling size and of fecal samples collected over several seasons to avoid missing any individual or seasonal effects (Mychajliw et al. 2022).

This study has shown that chacma baboons consume more human resourced foods in more anthropogenic landscapes, and it has previously been described that despite some benefits, the shift in trophic niche associated with human-modified resources can also be detrimental to many wild animals. Unfortunately, to date health studies tend to revolve around humans and few have focused on the extent and direct impacts that the consumption of anthropogenic food by wild animals can have on their health. Several diseases found in humans (e.g. obesity, cardio-metabolic or cardiovascular risks, cancer, type-2 diabetes) are linked to the consumption of processed foods, refined sugars, certain grains or fats (Elizabeth et al. 2020; Monteiro et al. 2018; Popkin et al. 2020) that, according to this study, species such as chacma baboons have increasing access to. The question is now to determine what specific human-modified resources non-human primates are consuming in urban and peri-urban areas, and if this is causing health problems (e.g. short or long term diseases; Sapolsky and Share 2004) as well as affecting other aspects of their lives (i.e. behavioral, social, physiological, stress; Bracken et al. 2022b; Chowdhury et al. 2020; Mazué et al. 2023). Understanding these effects is important for future management in the growing context of human-wildlife encounters and conflict.

# Declarations

### Statements & Declarations

**Supplementary Information** The online version contains supplementary material available at XXX

**Acknowledgements** We are grateful to SANParks for allowing and participating in data collection throughout this study. We would especially like to thank all SANParks personnel who provided us with not only access and guidance throughout the park, but who became personally involved in the research project, particularly Nathan and Dylan. We also thank the Wildlife Ecology Lab and the students that participated in data collection and analysis, namely Eloise Krisch, Sinayo Lungile, Brittany McClear, Tessa Raw, Markus Woesner, Bianca Coulson and especially the NMU Campus Baboon Monitors, Dietre Stols, Liyabona Ntlokwana, Nusheen Brenner and Abulele Sixonxo who provided us with remarkable insight into the Campus baboon habits. Thank you to all the people who provided details on troop locations throughout the Garden Route and granted us access to their properties, including the Oakhurst Farm and the personnel of the Woodville Trading Store.

**Funding** This work was supported by the funding of Virginie Rougeron from Centre National de la Recherche Scientifique, REHABS International Research Laboratory.

### Data availability and material

**Ethics declarations** Data collection was possible according to SANParks (BERN-A/2020-008) and Cape Nature (CN44-87-16198) permits, and analysis was allowed under the Section 20 of the Animal Diseases Act, 1984 (Act No 35 of 1984).

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# Figures

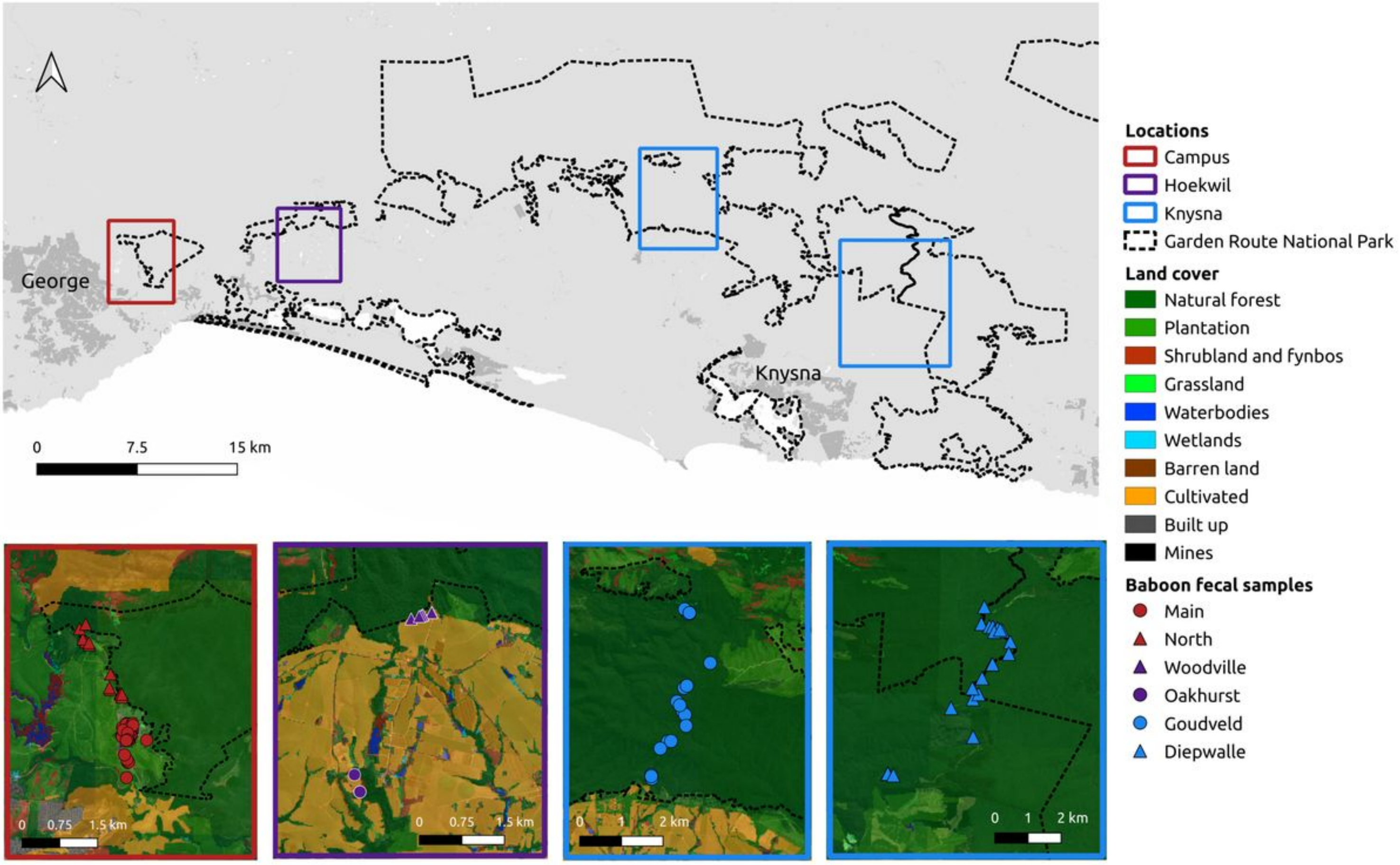
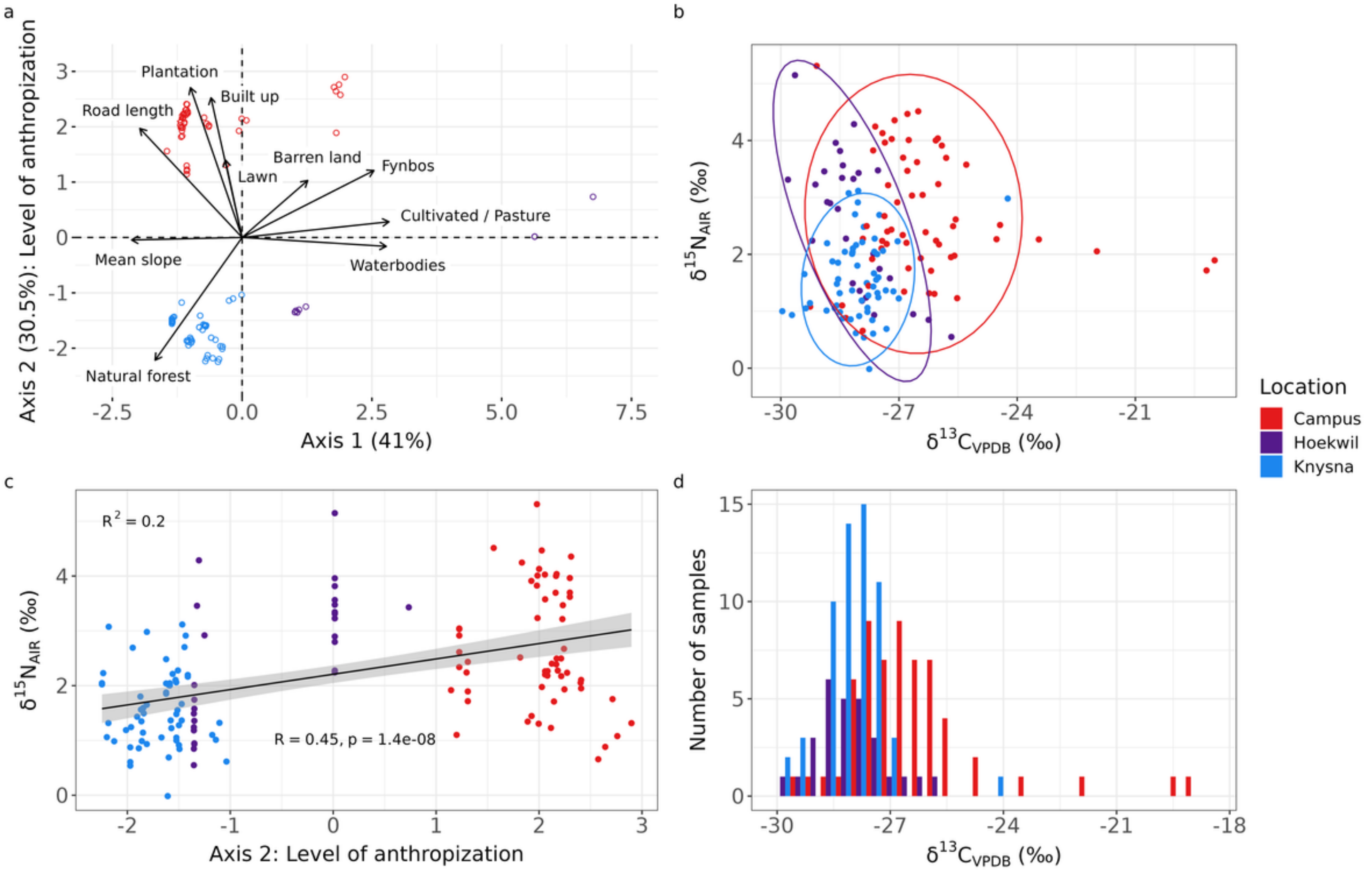


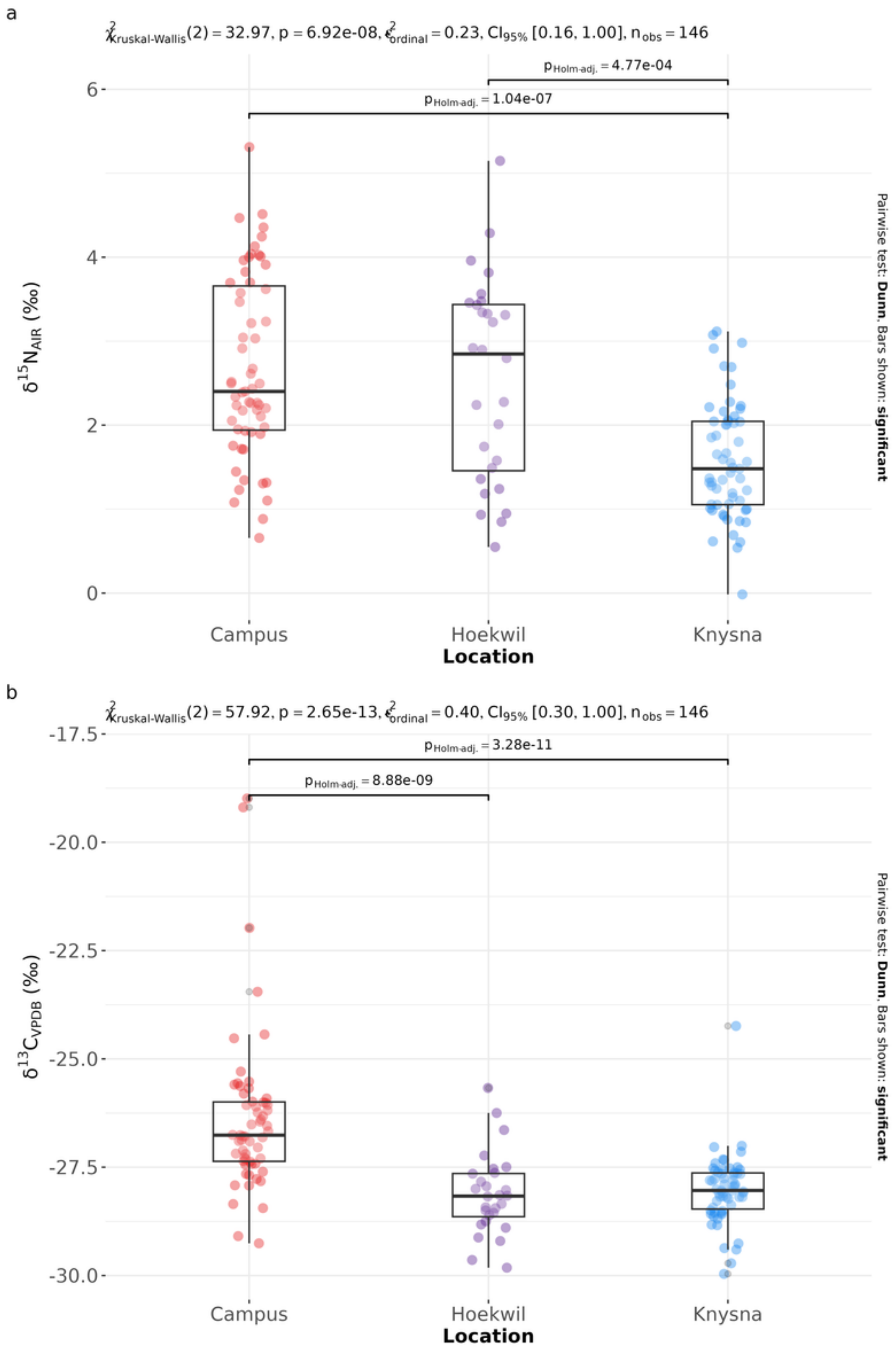
**Figure 1**

Study area and collected samples (Garden Route, Western Cape, South Africa). Map (a) shows landscape composition and the three study locations, along with the number of samples collected for each subsite. A zoom on each location (b) shows the distribution of where samples were collected for all six subsites (Main and North, Oakhurst and Woodville, Goudveld and Diepwalle). The red panel visualizes the most anthropized and built up area that is the Nelson Mandela University, named Campus. The purple panel represents the more intermediate anthropization level, the agricultural location called Hoekwil. The last two panels in blue represent the two subsites of the more natural environment within the Garden Route National Park, namely Knysna. Source: SANLC, 2018 - EPSG 32734.



## Figure 2

(a) PCA (Axes 1 and 2) land cover characteristics obtained around each of the 148 analyzed fecal samples across the three studied locations (Campus, Hoekwil and Knysna). Biplots of the isotopic ratios of the 146 analyzed fecal samples comparing (b) Carbon and Nitrogen (ellipse = 0.95), (c) nitrogen (δ15N) according to the anthropization level (i.e. the coordinates of the second axis of the corresponding PCA) and (d) the distribution of the carbon ratio (δ13C).



## Figure 3

Kruskal-Wallis tests for (a) nitrogen and (b) carbon including Dunn post-hoc tests comparing the three locations (Campus, Hoekwil and Knysna).

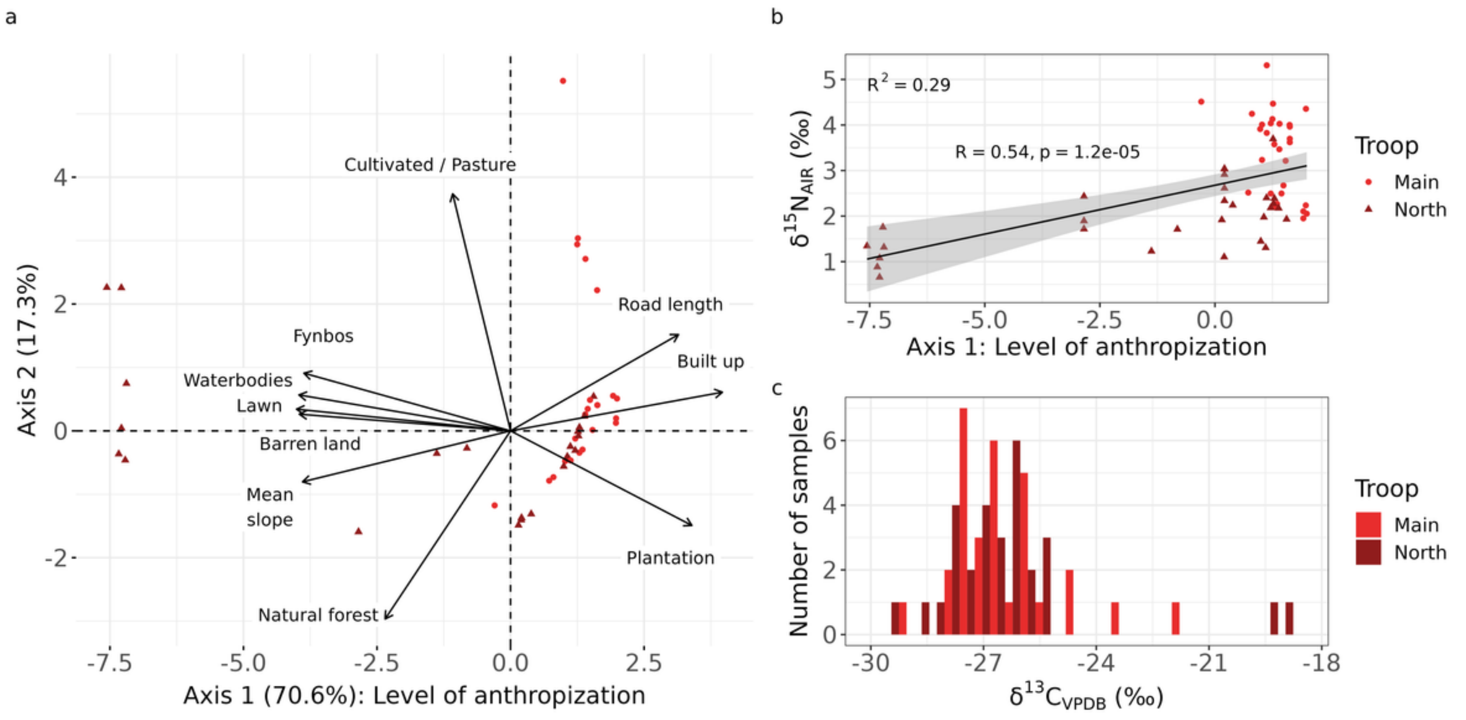


**Figure 4**

(a) PCA (Axes 1 and 2) of land cover variables and the 60 analyzed fecal samples for the two subsites on Campus (Main and North). (b) Nitrogen isotopic ratios (δ15N) for the 58 fecal samples according to the anthropization level (i.e. the first axis of the corresponding PCA; ellipse = 0.95). (c) Distribution of the carbon isotopic ratios (δ13C) for the 58 fecal samples.

## Supplementary Files

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- Supplementaryinformation.docx
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