



## Land use influences the diet of chacma baboons (*Papio ursinus*) in South Africa

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### ABSTRACT

Anthropization affects wildlife feeding behavior 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 wildlife feeding ecology. The chacma baboon (*Papio ursinus*) is an interesting study subject for 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 habitats with distinct land uses (peri-urban, agricultural and natural forest habitat) in the Garden Route, South Africa, and their carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotopic ratios were measured. Results showed significant differences between  $\delta^{15}\text{N}$  ratios according to land use, suggesting a shift towards higher protein intake in areas with human influence in comparison to natural forest habitats. The large majority of the collected samples reflected the  $\text{C}_3$  ecosystem of the Garden Route region, with the exception of some samples in peri-urban habitats showing higher  $\delta^{13}\text{C}$  ratios, which could be associated with the consumption of anthropogenic foods (e.g. sugar or corn). The potential protein increase, as well as sources of  $\text{C}_4$  plants present in the diets in anthropized areas, suggest a dietary shift for this species between natural and transformed landscapes. In the future, it will be essential to determine whether and

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how the consumption of human-modified food could affect the health and associated fitness of chacma baboons.

## 1. 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 and Martín-Duque, 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 some wildlife species, these transformed landscapes may provide access to novel resources including food and shelter (Dale and Polasky, 2007; Eriksson, 2013; Fleming and Bateman, 2018; Hulme-Beaman et al., 2016; Oro et al., 2013; Seoraj-Pillai and Pillay, 2016; Webber, 2017). For instance, wild boars (*Sus scrofa*) and vervet monkeys (*Chlorocebus pygerythrus*) are known to exploit croplands (Cancelliere et al., 2018; Lee and Lee, 2019) and 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). Commensal behavior, notably as household and agricultural pests, has also been observed in black rats (*Rattus rattus*) across different geographical areas on several occasions (Aplin et al., 2011).

Wildlife living in transformed habitats often exhibit marked changes in their diet and foraging behavior (Murray et al., 2015). For example, a population of urban kit foxes presented higher cholesterol levels, a good indicator of energy intake (Zhang et al., 2017), 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 (*Mycteria americana*) 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 behavior 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, the consumption of human food has also been shown to have a negative impact on wildlife health. For instance, urban coyotes have generally shown poorer average body condition as well as higher parasitic infection rates than rural coyotes (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 a suitable diet for nestlings (Pollock et al., 2017; Seress et al., 2020).

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). Variations in diet are evident in primates living near and interacting with humans and their resources, such as vervet monkeys (Loudon et al., 2014). An interesting primate species to study in order 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 from opportunistic hunting (Allan et al., 2022; Hoffman and O'Riain, 2011; Schreier et al., 2019). They are non-seasonal breeders (Dezeure et al., 2023) that are highly adaptable to a wide range of habitats and environments: the species 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; Lewis et al., 2018; 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, consuming resources of human origin (Fehlmann et al., 2017; Hoffman and O'Riain, 2011; Kaplan et al., 2011; Strum, 2010; Walton et al., 2021). 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, meat, but also processed foods, refined sugars, fats and oils, all typically found in human food waste, 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 quantify the change in diet of chacma baboons according to different land uses that are characterized by the availability of human-modified food.

Several methods can be used to study the diet of wildlife, 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) and can require baboon habituation, which is long, invasive and the reverse of what is necessary when trying to prevent baboons from raiding into cities. 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). Analyzing 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 ( $^{15}\text{N}/^{14}\text{N}$ ) and carbon ( $^{13}\text{C}/^{12}\text{C}$ ). 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  $\delta^{15}\text{N}$  isotopic ratios observed within feces may reflect consumption of dietary items with higher

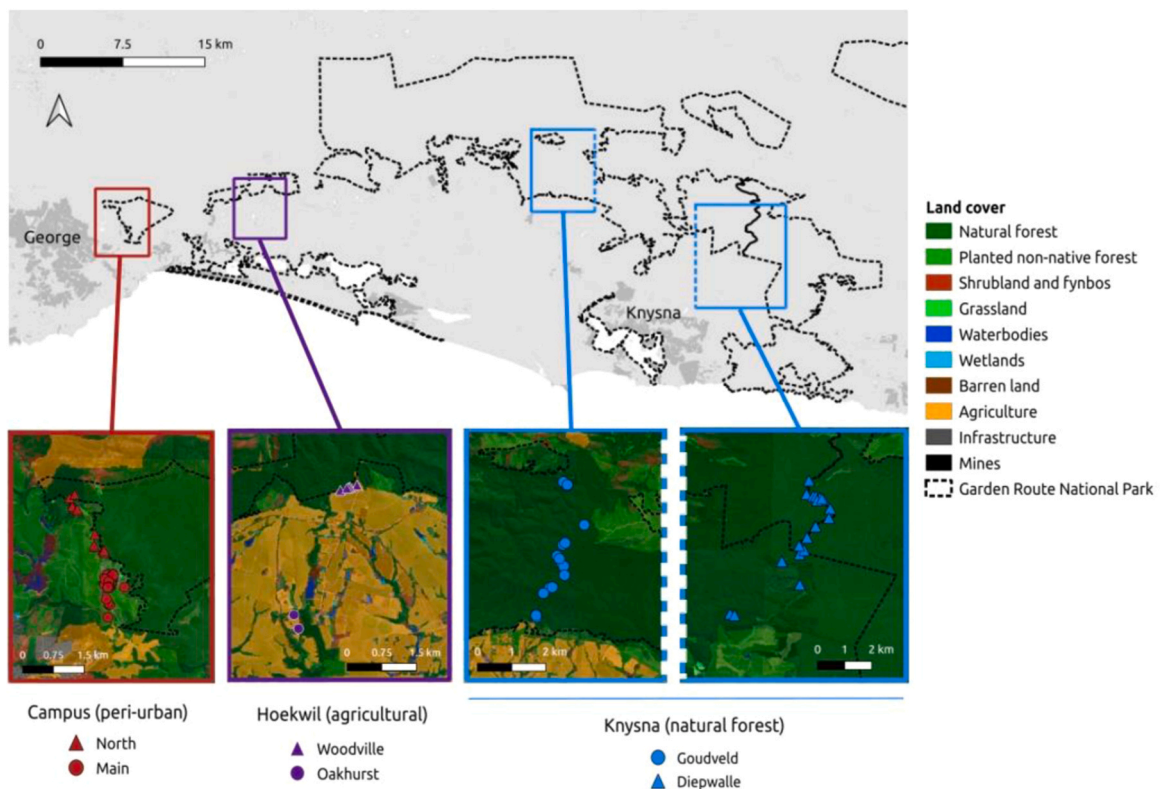
protein content within the different LULCC based on what resources the baboons have access to. The carbon in plants derives from atmospheric CO<sub>2</sub> which is fixed during the process of photosynthesis. Differences in stable carbon isotope ratios therefore reflect the type of plants consumed based on their photosynthetic pathways (C<sub>3</sub>, C<sub>4</sub> or CAM) due to differential fractionation of carbon isotopes during photosynthesis that leads to distinct δ<sup>13</sup>C values (Ehleringer and Cerling, 2002; Smith and Epstein, 1971). Examining carbon and nitrogen ratios may therefore be a suitable method of assessing ecological niches (Flaherty and Ben-David, 2010) and 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 evaluate whether transformed landscapes have an influence on chacma baboon diet, we collected fecal samples from chacma baboons along a gradient of land uses (peri-urban, agricultural and natural forest) in the Garden Route, South Africa. We then assessed the stable isotopic ratios of the feces for nitrogen and carbon, which would provide quantitative data on the types of plants and animal matter they consume, incorporating the surrounding landscape characteristics. As opportunistic feeders, the potential access to high protein sources such as meat and legumes in highly anthropized areas (crops, garbage or kitchens) may result in higher proportions of protein in their diet. If food items in anthropized landscapes provide higher protein content than the natural resources consumed by chacma baboons, the stable nitrogen isotope values would be higher in these transformed landscapes. More positive δ<sup>13</sup>C values for samples from anthropized areas may be associated with a higher consumption of C<sub>4</sub> 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 therefore expected that baboons in the peri-urban site would have higher δ<sup>15</sup>N and δ<sup>13</sup>C ratios than the agricultural one, which in turn would have higher δ<sup>15</sup>N and δ<sup>13</sup>C ratios than the natural forest site, indicating an increase of δ<sup>15</sup>N (hypothesis H1) and δ<sup>13</sup>C (hypothesis H2) with increasing anthropization.

## 2. Material and methods

### 2.1. 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 2000 km<sup>2</sup> (Fig. 1). The reserve is known for its unique and endemic biodiversity, such as afrotemperate forests, fynbos, as well as



**Fig. 1.** Study area and collected samples (Garden Route, Western Cape, South Africa). The first map shows the three study locations in relation to the Garden Route National Park. A zoom on each location shows the distribution of where samples were collected and the surrounding landscape composition for all six subsites (Main and North, Oakhurst and Woodville, Goudveld and Diepwalle). Source: SANLC, 2018 - EPSG 32734.

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 and preserve natural areas where biodiversity can prosper, the Garden Route biosphere reserve was created, with the Garden Route National Park (GRNP) as a core area. Due to the complex landscape configuration that includes agriculture, forestry, urban settlements 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 to compare different levels of anthropic transformation: a peri-urban area, an agricultural area and a protected area, hereafter referred to as Campus, Hoekwil and Knysna throughout this study (represented in red, purple and blue respectively in Fig. 1). These three sampling areas represent mosaics of different land use types which differ in relative proportions of the ten different land uses that have been identified in this region. The first location (Campus) is located on the Nelson Mandela University (Saasveld Campus) near the city of George, where there are many people most of the year round, 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 GRNP 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, planted pastures and vegetables, from fallow land in winter (CapeFarmMapper v 2.7). The third location (Knysna) was situated within the afrotemperate forest of the Knysna Section of the 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. 1), Oakhurst and Woodville for Hoekwil (light and dark purple; Fig. 1), Goudveld and Diepwalle sections of the GRNP for Knysna (light and dark blue; Fig. 1). 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. The Knysna subsites were situated in two different areas of the GRNP with similar land cover (natural forest) to be certain that there was no overlap in troops since the dynamics of these baboon populations are not well known (Fig. 1).

## 2.2. Chacma baboon fecal sampling

Sampling took place at the end of summer/beginning of autumn, 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 (Table S1). Samples were kept in a cooler box during the fieldwork each day before being frozen and stored at  $-20^{\circ}\text{C}$  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).

A total of 231 baboon fecal samples were collected throughout the sampling period (Fig. 1; 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; Table S1). 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. NB: The 148 samples used for the isotopic analysis were chosen according to freshness and to obtain a representative number of replicates per location. Two samples (one from Main and one from North) were removed after the isotopic analysis due to poor quality.

Location	Campus		Hoekwil		Knysna	
	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 and isotopes	30	30	14	14	30	30
	60		28		60	
	148					

### 2.3. 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 4 km<sup>2</sup> circle defined around each fecal sample position. Dietary isotopes from fecal samples have a short turnover time (Martins et al., 2012) and tend to represent what passes through the digestive system without being incorporated into the body. The 4 km<sup>2</sup> buffer zone surrounding the samples was therefore based on the highest daily distance covered by chacma baboons in the literature in South Africa, particularly in the Western Cape (Hoffman and O’Riain, 2011, 2012; 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 (Department of Forestry, Fisheries and the Environment (DFFE), 2021) and clipped to the study area. The 73 classes from this layer were grouped into 10 (Fig. 1) for simplification according to main types (*i.e.* natural forest, plantations, shrubland, grassland, waterbodies, wetland, barren land, cultivated land, infrastructure and mines). The elevation raster at 30 m 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 4 km<sup>2</sup> buffer of each sample using the zonal statistics plugin within QGIS (3.18; following similar steps to Alders, 2023). 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. These included the land use variables (plantation, infrastructure, barren land, lawn, fynbos, cultivated/pasture, waterbodies, natural forest), mean slope and road length.

### 2.4. Stable isotope analysis for chacma baboon diet characterization

After being placed in a fridge for 24 h to defrost, up to 10 g of each sample used for the isotopic analyses was inserted into 20 mL tubes and dried for 48 h 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 analyzed at the University of Pretoria, South Africa. Samples were combusted at 1020°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 ( $\delta^{13}\text{C} = -20.26\text{‰}$ ,  $\delta^{15}\text{N} = 7.89\text{‰}$ , C% = 41.28, N% = 15.29) and DL-Valine ( $\delta^{13}\text{C} = -10.57\text{‰}$ ,  $\delta^{15}\text{N} = -6.15\text{‰}$ , 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):  $\delta X(\text{‰}) = [(R_{\text{sample}} - R_{\text{standard}}) / R_{\text{standard}} - 1]$  where X = <sup>15</sup>N or <sup>13</sup>C and R represents <sup>15</sup>N/<sup>14</sup>N or <sup>13</sup>C/<sup>12</sup>C respectively.

### 2.5. 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 analyze and compare the isotopic patterns ( $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ) 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  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ . This was 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, according to hypotheses H1 and H2. A kernel utilization density (KUD) estimator was used to look at niche overlap between  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  ratios by location (based on Eckrich et al., 2020). Finally, the differences between chacma baboon populations were tested across the gradient of anthropization created using the resulting axes of the PCA. Linear models (LM) were used to represent the nitrogen, using the gradient of anthropization axis from the PCA, and distribution plots were used for the carbon ratios because they showed the best distribution of plant type by location. A perMANOVA test was also run using the vegan package (version 2.6–4) in RStudio comparing locations and subsites for combined  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  ratios. It is important to note that the fecal samples were not attributed to specific individuals and can therefore not be controlled for individual variation, since this can be affected by other aspects (*e.g.* hierarchy) and could potentially increase variation in the samples (Marty et al., 2020, Oelze et al., 2022).

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  $\delta^{15}\text{N}$  results and a Wilcoxon test for the  $\delta^{13}\text{C}$ .

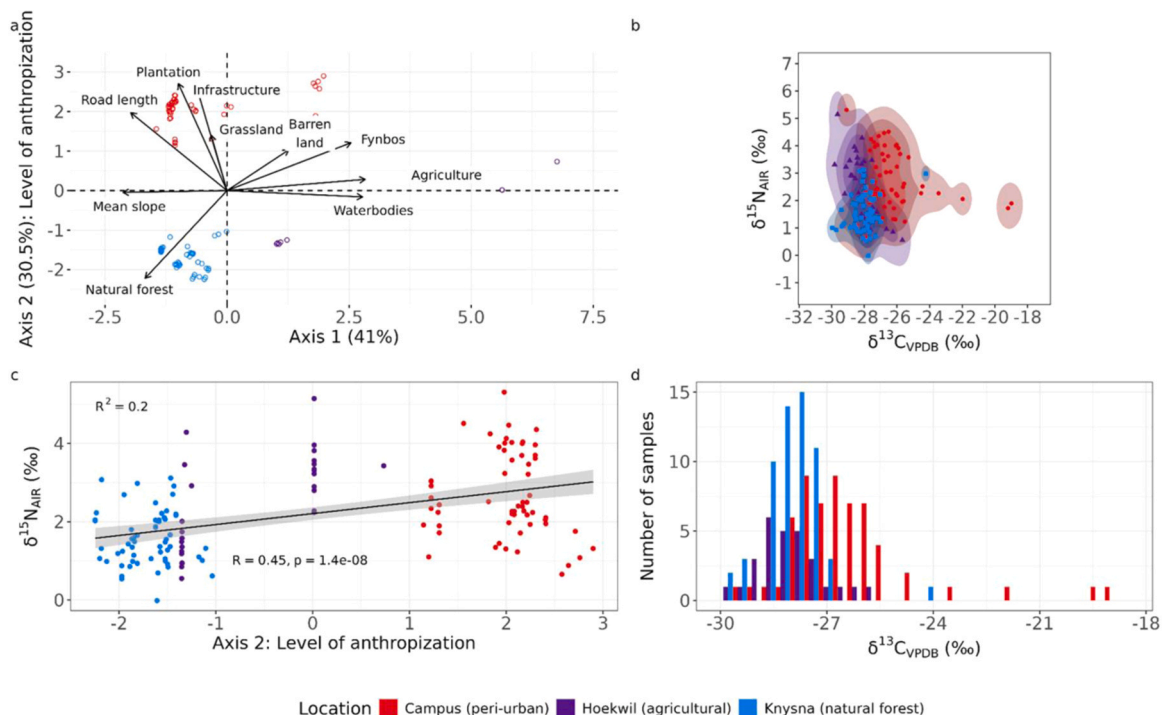
### 3. Results

#### 3.1. 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 infrastructure location (Campus) with the more natural and less infrastructure 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.

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

The Campus had the largest isotopic niche, Knysna the smallest and Hoekwil an intermediate size (Fig. 2b, Table S2). While the Campus and Hoekwil baboons' isotopic niches only partially overlapped with the others, the Knysna baboons' niche was nearly completely encompassed by the others (over 80 % by both the Campus and Hoekwil; Fig. 2b, Table S2). The Campus had the least overlap with the other two locations, with a wider range of both nitrogen and carbon ratios (Fig. 2b, Tables S1 and S2). A significant increase in the  $\delta^{15}\text{N}$  ratios was visible along with the level of anthropization of the environment across the land use gradient ( $R^2 = 0.29$ ,  $R = 0.45$ ,  $p\text{-value} < 0.001$ ; Fig. 2c), created using the second axis of the PCA from Fig. 2a. The samples collected at the Campus (highest proportion of infrastructure land cover), characterized by the highest anthropization levels, showed higher ratios of  $\delta^{15}\text{N}$ . The samples from Hoekwil (highest proportion of agriculture), with lower levels of infrastructure land cover, presented a wider variation of



**Fig. 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 Kernel Utilization Density with 50, 75 and 95 % confidence intervals, (c) nitrogen ( $\delta^{15}\text{N}$ ) according to the anthropization level (i.e. the coordinates of the second axis of the corresponding PCA) and (d) the distribution of the carbon ratios ( $\delta^{13}\text{C}$ ).

$\delta^{15}\text{N}$  numbers, with lower values resembling those of Knysna and higher ones resembling those of the Campus. The Knysna samples (highest proportion of forest), reflecting the lowest anthropization levels and more natural habitat, showed the lowest values for  $\delta^{15}\text{N}$ . The majority of the Campus samples, as well as all those from Hoekwil and Knysna, reflected an isotopic signature between about  $-30\text{‰}$  and  $-24\text{‰}$  for  $\delta^{13}\text{C}$  values (specific to  $\text{C}_3$  plants), except four of the Campus samples that possessed slightly higher values (Fig. 2d).

Kruskal-Wallis tests indicated that at least one location was significantly different from the others for nitrogen and carbon. Post-hoc Dunn tests revealed that the Knysna samples significantly differed from both the Campus and Hoekwil samples for nitrogen ( $p$ -values  $< 0.001$ ; Fig. S1a), whereas for carbon ratios, the Campus samples were significantly different from both Hoekwil and Knysna ( $p$ -values  $< 0.001$ ; Fig. S1b). The perMANOVA results showed significant differences for the subsites when combining  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  results ( $p$ -value  $< 0.001$ ). When comparing the two troops on Campus, Kruskal-Wallis tests again indicated that at least one site was significantly different from the rest. The Dunn tests showed that for nitrogen, two subsites differed from the rest (Main and Oakhurst, Fig. S1c) whereas the two Campus subsites (Main and North) stood out from the rest for carbon (Fig. S1d).

### 3.3. Isotopic distribution variations between troops at the Campus site

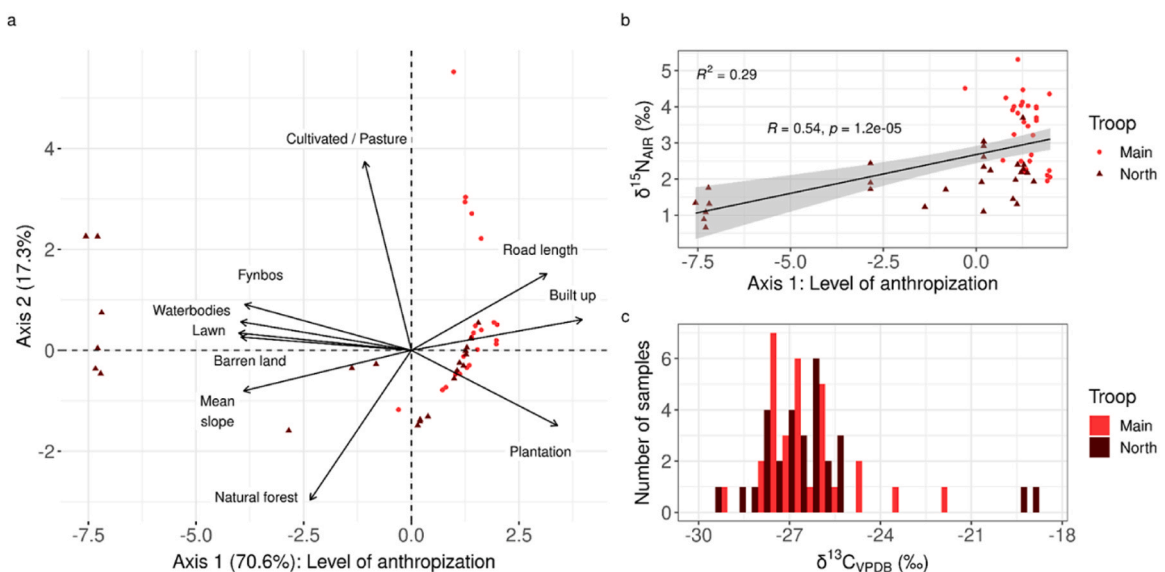
The resulting PCA biplot for the inter-troop analysis on the two subsites of the Campus (Main and North troops) showed little difference in distribution according to land use. The landscape surrounding the samples only differed slightly along the first axis according to the troop, which accounted for 70.9 % of the variation (Fig. 3a). The Main troop samples tended towards higher levels of infrastructure land use as well as the presence of roads, whereas the North troop spanned a wider range across the axis, going from infrastructure to more natural landscapes (Fig. 3a).

Despite these limited differences in the landscapes used by these two troops of baboons,  $\delta^{15}\text{N}$  nitrogen ratios of the fecal samples from these two subsites increased with the level of anthropization created using the first axis of the inter-troop PCA biplot ( $R^2 = 0.29$ , Student's  $t$ -test,  $t = 6.50$ ,  $df = 57$ ,  $p$ -value  $< 0.001$ ; Fig. 3a and b). Higher  $\delta^{15}\text{N}$  values were associated with the Main troop (1.95–5.31 ‰; Table S1), which was represented by infrastructure 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  $\delta^{15}\text{N}$  along with the anthropization level and towards areas characterized by more natural forests (0.66–3.70 ‰; Table S1).

The carbon  $\delta^{13}\text{C}$  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  $-24\text{‰}$  and  $-30\text{‰}$  (Wilcoxon,  $W = 450$ ,  $p$ -value = 0.83; Fig. 3c; Table A.11). It is noticeable that the highest  $\delta^{13}\text{C}$  values of two subsite samples of the Campus were specific to the North troop (Fig. 3c).

## 4. 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



**Fig. 3.** (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 ( $\delta^{15}\text{N}$ ) for the 58 fecal samples according to the anthropization level (i.e. the first axis of the corresponding PCA). (c) Distribution of the carbon isotopic ratios ( $\delta^{13}\text{C}$ ) for the 58 fecal samples.

increased conflicts have been reported, mostly associated with stealing food (Chowdhury et al., 2020; Mormile and Hill, 2017). Increased observations have been made of Cape peninsula baboon troops in human-modified habitats stealing from people's houses and visiting the bins around settlements (Hoffman and O'Riain, 2012). Mazué et al. (2023) also described that the Main troop living on the George Campus of Nelson Mandela University, 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 and which could have an impact on their foraging behavior. Even if there are important costs in living in anthropized habitats in term of stress (Chowdhury et al., 2020), risk of mortality (Fehlmann et al., 2017) or injury (Beamish and O'Riain, 2014), the benefit of getting higher protein content food might overcome such costs. 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.

#### 4.1. A shift towards higher protein intake in anthropized areas

It is well known that  $^{15}\text{N}/^{14}\text{N}$  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  $\delta^{15}\text{N}$  patterns in soil and plants that are consumed by animals higher up the trophic chain. When consumed,  $^{15}\text{N}$  is preferably incorporated into tissues over  $^{14}\text{N}$ , 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, consistent with hypothesis H1, the  $^{15}\text{N}/^{14}\text{N}$  results showed significantly higher protein intake for chacma baboons in landscapes transformed by human activity, i.e. on the Campus with infrastructure land cover and in Hoekwil with agricultural zones (Figs. 2c and 3b) and particularly within two subsites (Main and Oakhurst, Fig. S1b). This suggests that the chacma baboon populations known to live in close contact with human populations in the Garden Route have seen a dietary shift with a richer nitrogen pattern when inhabiting more anthropized lands. This is the case whether the land transformation is agricultural or peri-urban, a result probably associated with the easier access to human-modified resources. These results could be linked to potentially easier access to protein sources in these 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  $\delta^{15}\text{N}$  were observed to be associated with the Main troop, in comparison to the North troop (Fig. 3b). The Main troop was 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). This could explain the differences observed between the Main and the North troops at the Campus location regarding nitrogen intake. Concerning the higher nitrogen ratios in Hoekwil, the agricultural sampling zone included pastures and crops that could potentially be fertilized with products that can increase  $\delta^{15}\text{N}$  ratios (e.g. manure or compost) in the consumer (Bateman and Kelly, 2007, CapeFarmMapper v 2.7). This present study showed that the nitrogen ratios in the fecal samples, and therefore most likely animal protein intake or plants with high  $\delta^{15}\text{N}$  ratios, were significantly higher in the populations inhabiting the most anthropized areas. These areas are where the most buildings, infrastructure land cover and transformed landscape for agriculture were observed and where there was easier access to human-modified food with large quantities of meat or plants with high  $\delta^{15}\text{N}$  ratios.

Other studies have also described higher protein intake by wild animals inhabiting human-modified environments (e.g. rats, Guiry and Buckley, 2018). Similar to this study, Codron et al. (2006) also showed that fecal samples from chacma baboons in Kruger Park who came into contact with people and their food had higher  $\delta^{15}\text{N}$  values than those who exhibited less interactions with humans. 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, others have 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 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, several studies have also shown no variations in protein and  $\delta^{15}\text{N}$  ratios between modified and natural landscapes across a wide range of animals: vervets monkeys, wild boars, wild land predators (Cahill et al., 2012; Cancelliere et al., 2018; Gámez et al., 2022; Stillfried et al., 2017). It appears that depending on the species studied and possibly the geographic location of the study and reason, wild animals respond differently to human-modified resources. Urban environments can also be used for different reasons, such as refuges from predators, that would not necessarily result in a change in diet (Aronson et al., 2016; Møller, 2012). 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.

#### 4.2. Variations in plant consumption patterns across anthropized areas

It is well established that  $\text{C}_3$  plants tend to have lower  $^{13}\text{C}/^{12}\text{C}$  ratios than  $\text{C}_4$  plants: the  $\delta^{13}\text{C}$  values of  $\text{C}_3$  plants range from  $-34$  to  $-22$  ‰ and those of  $\text{C}_4$  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  $\text{C}_3$ -photosynthetic pathway (Ehleringer and Cerling, 2002). We could therefore expect the diet of chacma baboons living in natural forest to be richer in  $\text{C}_3$  than in  $\text{C}_4$  plants. The results obtained in this study showed that the large majority of the collected samples were contained within the bracket that reflect a  $\text{C}_3$  ecosystem across the different land uses. This suggests that the overall consumption of the chacma baboon troops was made up of  $\text{C}_3$  plants (Fig. 2d), not supporting H2. However,



small variations have to be considered regarding the  $\delta^{13}\text{C}$  isotopic ratios: some samples collected at the highly anthropized Campus location possessed values that were outside of both the  $\text{C}_3$  and  $\text{C}_4$  brackets (around  $-19\%$ , Figs. 2d and 3c). This could indicate a higher proportion of  $\text{C}_4$  plants within these samples and therefore a higher consumption of  $\text{C}_4$  components during recent foraging by certain individuals in the Campus, but without becoming a majority of  $\text{C}_4$  plants.

Higher  $\delta^{13}\text{C}$  isotopic ratios could be explained by the consumption of anthropogenic foods that are known to contain large quantities of  $\text{C}_4$  plants (e.g. sugar or corn; Gámez et al., 2022; Nicholson and Cove, 2022; Post et al., 2007) which are easily accessible from garbage and kitchens, as described previously for nitrogen. The same pattern has been observed in eurasian red squirrels (*Sciurus vulgaris*) that consumed more sugar in urban zones (Wist et al., 2022) or vervet monkeys who had higher  $\delta^{13}\text{C}$  ratios related to anthropogenic disturbance, particularly from raiding  $\text{C}_4$  plantations (sugarcane and maize, Loudon et al., 2014). On the other hand, the large number of samples from the Campus and the agricultural samples that still reflected an overall  $\text{C}_3$  diet could also be due to the presence of  $\text{C}_3$  plants within human foods (e.g. wheat or rice, Shewry and Hey, 2015) or in the surrounding agricultural areas.

Primate diets can also be affected by factors other than just resource availability (e.g. age, sex, dominance rank), which could affect the  $\delta^{13}\text{C}$  results in the samples according to each individual (Bracken et al., 2022; Maibeche et al., 2015; Marty et al., 2020). For example, adult males of several macaque species have been shown to monopolize resources, consuming more human resources than adult females, younger and lower ranked individuals (Maibeche et al., 2015, Marty et al., 2020). A similar explanation could be possible in this instance, where only a few individuals (e.g. high-ranking) would have had access to sufficient amounts of  $\text{C}_4$  plants for it to be noticeable in the fecal  $\delta^{13}\text{C}$  ratios. 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 behavioral analyses to get a better understanding of the chacma baboons' behavioral ecology and to establish better strategies for conflict management.

#### 4.3. Perspectives and future impacts

This present study showed that land use influences chacma baboons' diet, with a shift in anthropized environments toward globally significant higher nitrogen ratios, and for some samples higher carbon patterns. It is interesting to note that despite the significant difference in both C and N isotopic ratios between sites, the nitrogen profile for the agricultural area resembled that of the peri-urban area, whereas its carbon profile was more similar to the natural isotopic profile. It could be that within the peri-urban area, baboons consume more protein whereas within the agricultural site they consume more N-fixing plants; regarding the type of plant ( $\text{C}_3$  or  $\text{C}_4$ ), they would be consuming more  $\text{C}_3$  plants in the agricultural area. The peri-urban location tended to show the highest isotopic ratios, suggesting the highest consumption of human-derived foods. 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. Conducting similar studies in other cities, agricultural and natural areas would be interesting to determine whether the same patterns are observed. A more in depth analysis of the differences between the different studied environments (i.e. the available food) could also provide a more specific understanding of the variations in consumption.

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  $\delta^{13}\text{C}$  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), or on other tissues (e.g. hair) that cover larger time windows such as used in Loudon et al. (2014).

This study suggests a higher consumption of human-derived foods by chacma baboons. While they inhabit human-modified landscapes, the species is still linked to the remaining natural areas, in which they might increase the consumption of fallback foods (i.e., non-preferred food items in natural areas; Marshall and Wrangham, 2007) compared to more preserved areas, resulting in a different pattern of isotopic values. In terms of conservation and human-baboon conflicts, this study indicates that baboons can indeed consume quite a lot of human-modified food when available and therefore aims at highlighting the importance of preventing baboons accessing food in urban areas in order to both avoid conflicts in cities and to protect them from such unsuitable resources. 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. Health effects linked to living in close contact with humans have been studied in primates such as baboons: Drewe et al. (2012) reported likely exposure to human viruses and Ravasi et al. (2012) revealed that baboons and humans share parasites with both authors attributing these pathogens to sharing space with humans. Unfortunately, to date health studies linked to human resources 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, even though it has been shown that the consumption of human resources can affect baboon physiology (Altmann et al., 1993). 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 now is 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, such as short or long term diseases (Sapolsky and Share, 2004) or gut microbiomes (Moy et al., 2023), 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.

### 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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### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

### Data availability

The sample data can be found in the supplementary file published alongside this article (Table A.1).

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### Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2024.e03100](https://doi.org/10.1016/j.gecco.2024.e03100).

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