Stable isotope series from elephant ivory reveal lifetime histories of a true dietary generalist

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Longitudinal studies have revealed how variation in resource use within consumer populations can impact their dynamics and functional significance in communities. Here, we investigate multi-decadal diet variations within individuals of a keystone megaherbivore species, the African elephant (Loxodonta africana), using serial stable isotope analysis of tusks from the Kruger National Park, South Africa. These records, representing the longest continuous diet histories documented for any extant species, reveal extensive seasonal and annual variations in isotopic—and hence dietary—niches of individuals, but little variation between them. Lack of niche distinction across individuals contrasts several recent studies, which found relatively high levels of individual niche specialization in various taxa. Our result is consistent with theory that individual mammal herbivores are nutritionally constrained to maintain broad diet niches. Individual diet specialization would also be a costly strategy for large-bodied taxa foraging over wide areas in spatio-temporally heterogeneous environments. High levels of within-individual diet variability occurred within and across seasons, and persisted despite an overall increase in inferred C4 grass consumption through the twentieth century. We suggest that switching between C3 browsing and C4 grazing over extended time scales facilitates elephant survival through environmental change, and could even allow recovery of overused resources.

Keywords: C4 grass; Kruger National Park; time series; tusks

1. INTRODUCTION

Within generalist populations, individuals may have flexible, overlapping ranges of resource use, or individuals may be niche specialists, each using only a subset of the population’s resource [1,2]. Although early theory predicted that, unless constrained by extrinsic factors, niche breadths of individuals should not differ from that of the whole population [2,3], there is growing evidence that individuals using narrow, specialized niches are a characteristic of populations of many species [4–9]. Such individualization of niches probably influences the strength of ecological interactions within and among species, and so can be an important mechanism for density-dependent population and community dynamics [5,10,11]. It also represents a source of variation for evolutionary divergence through natural selection [12]. Some generalist groups may, however, be indisposed to a strategy of reduced individual niche breadths if constraints act on individuals themselves. Dietary niches of mammalian herbivores are a likely example: nutritional constraints mean that individuals should consume a diverse range of plant foods to achieve sufficient nutrient uptake, or to minimize intake of single-species secondary compounds [13–15].

Among mammal herbivores, dietary generalism is expected to increase with body size, as larger species, because of their relatively lower metabolic demands, can accept foods of low nutritional value and thus broaden their niche breadths [16,17]. The largest herbivore, the...
African elephant *(Loxodonta africana)*, typifies this expectation. Field studies have shown that elephants, which as hindgut-fermenters should tolerate a wide array of plant food qualities [17], use a greater variety of woody plant species than sympatric browsers [18,19]. Moreover, elephants are mixed-feeders, able to switch between browse (trees, shrubs and forbs) and grass depending on seasonal and regional changes in the availability of these two plant food groups [17,20,21]. Although diet switching occurs even within individuals [22], the wide niche breadth of the species could imply that there is sufficient niche space for individuals within elephant populations to partition the resource.

Approaches to population structure require information about realized niche breadths of individuals. At the individual level, morphological comparisons are only indirect niche proxies, whereas short-term studies based on observational data or analysis of gut contents give false impressions of specialization if niche differences are stochastic and non-persistent [4]. Long-term information is necessary to partition true levels of within-individual from between-individual dietary variation [5–7]. Longitudinal dietary data are obtainable through stable isotope analysis of fast- versus slow-growing tissues [6,23] and from isotopic profiles along inert tissues, which archive dietary chronologies in successive growth layers [8,9,22,24]. Tusks of elephants and other proboscideans are an ideal material for long-term investigations because they grow continuously throughout the animal’s life, which may exceed 60 years. Sequential growth occurs along the pulp cavity, lengthening the tusk from the proximal end, in ordered growth layers of different time scales: in African elephants, these reflect annual (first order), weekly (second order) and daily (third order) growth [25,26]. Each growth order comprises alternating periods of faster and slower growth. For example, within first-order layers, wet and dry seasons appear optically as light (more dentine) and dark (less dentine) bands, respectively, under transmitted light [26] (figure 1). Serial isotope analyses along longitudinal and/or transverse growth axes of tusks have been exploited to reconstruct dynamic feeding behaviours in various extinct proboscideans [25,27,28].

Stable isotopes in consumer tissues archive dietary and other resource use axes because tissues reflect the isotope composition of the sources from where they are derived. $^{13}$C/$^{12}$C ratios in body tissues approximate relative proportions of $^{13}$C-depleted C$_3$ and $^{13}$C-enriched C$_4$ biomass consumed around the time of tissue formation, which for herbivores living in African and some other subtropical savannahs, translates almost directly to the relative proportions of browse (C$_3$) and grass (C$_4$) in the diet [29–31]. Although carbon isotope composition of C$_3$ and C$_4$ plants can vary substantially over environmental gradients, these effects were relatively small within a single savannah reserve (Kruger National Park, South Africa, where mean annual rainfall varied by only approximately 300–700 mm across habitats), and are therefore unlikely to influence dietary interpretations, even from historical records [32]. Herbivore $^{15}$N/$^{14}$N ratios are difficult to interpret quantitatively, because while they reflect the $^{15}$N composition of diet, $^{15}$N-abundances are also influenced by diet quality, ecophysiological adaptation and condition, and climate factors [33–36]. Patterns of $^{18}$O/$^{16}$O variation reflect climate, generally increasing with aridity, but may be further influenced by differences in how animals acquire water, dietary $^{18}$O/$^{16}$O composition and physiology [25,37–39]. Animal tissues differ with respect to the time interval over which diet information is captured in the tissues and, more relevant to the present study, in the dietary component(s) they reflect. In skeletal material, the protein phase (collagen) records only the animal’s protein source, owing to biochemical routing during tissue...
synthesis, whereas carbonate in the mineral phase (apatite) represents a mixture of all dietary constituents [40].

Here, we investigate long-term individual patterns of resource use in elephants, based on stable isotope profiles in ivory dentine of 14 individuals from Kruger Park. Our analyses yielded decade-long diet histories for each individual, with the total record spanning virtually the entire twentieth century (ca 1903–1993). We predicted that chronologies would reveal extensive dietary variability within individuals, and test whether this variability precludes the possibility for individual specialization to occur within an elephant population: if so, most of the variation in isotope data should occur within rather than between individuals. We also investigate environmental correlates (region/habitat, season and climate) of isotopic, and hence dietary, dynamics within individuals, and how these factors contributed to overall long-term diet trends.

2. MATERIAL AND METHODS

(a) Tusk samples, chronologies and stable isotope profiles

We sampled tusks on display in the elephant museum at Letaba restcamp in Kruger Park (Letaba Elephant Hall, LEH; six individuals), from the ivory stockpiles at Skukuza restcamp in Kruger Park (SKZ; seven individuals), and the Transvaal Museum, Pretoria (TM; one individual; see electronic supplementary material, table S1). Where both tusks were available (LEH), we sampled from the longest (less-abraded) of the pair to include more of the early years of life; inevitably, however, several years of growth are lost from the distal end of tusks owing to abrasion [26]. Samples were either 10 mm thick transverse sections (SKZ; figure 1a), or 10 mm diameter cores (LEH, TM; figure 1b; sampled with a hole saw attached to a power drill), removed from multiple points along the longitudinal axis where possible.

Chronologies were established by counting first- and second-order growth bands in tusk sections, the latter under 40× magnification using Incident Light Microscopy (ILM; Reichert-Jung Polyvar Pol Dual Incident/Transmitted Light Microscope). For ILM, sections were polished with silicon carbide paper (220–1200 mesh grit; Buehler flat bed rotary power drill), removed from multiple points along the longitudinal axis where possible.

Microsamples were drilled in 1 mm increments along the growth axis of tusk sections (figure 1a, b, d) using a diamond-tipped microdrill with a 1 mm Burr (covering approx. 14 weeks of growth; figure 1c and electronic supplementary material, table S1). A portion of each dentine powder sample was treated in a 0.2 M HCl solution to isolate the organic (collagen) fraction, according to methods described by Sealy [41]. These were analysed for 13C/12C and 15N/14N ratios by combustion in an automated Elemental Analyzer (Carlo Erba, Milan) and introducing the CO2 and N2 gases to a Finnigan MAT 252 Mass Spectrometer (Finnigan, Bremen) via a continuous flow-inlet system. Molar C:N ratios of these samples were between 2.7 and 3.8, within the expected range for biological proteins [42]. Dentine powder from seven individuals was also treated for analysis of the inorganic (carbonate) phase by exposure to a 1.5 per cent sodium hypochlorite solution (50% bleach, 50% water). Carbonate 13C/12C and 18O/16O ratios were analysed from dry CO2 gas released to the mass spectrometer after reaction with phosphoric acid at 70°C and cryogenic distillation in a Kiel II autocarbonate device. Results are presented in delta (δ) notation in parts per thousand (%) relative to the Vienna PeeDee Belemnite (VPDB; δ13C, δ18O) and atmospheric N2 (δ15N) standards; standard deviations of repeated measures of working standards were less than 0.1‰ for δ13C, 0.2‰ for δ18O and 0.3‰ for δ15N (collagen standards were Merck Gel, Valine, and a laboratory-calibrated chocolate powder; carbonate standards were NBS-18, and two laboratory-calibrated marble standards).

(b) Data analysis

Microsamples were viewed under ILM in order to assign each observation in the data series to a specific year (by counting first-order growth bands) and season (wet or dry, corresponding to light or dark portions of annual growth bands, respectively). The series for each ivory section included multiple years, and both dry and wet seasons were represented for almost all years (2.77 observations per year, on average; electronic supplementary material, table S1). To minimize pseudoreplication, series were summarized as means per season per year. Gaps (n = 6) within series were filled by taking the median of the three adjacent cells on either side. δ13C series were corrected for twentieth-century decreases in atmospheric δ13CO2 using the exponential model described in an earlier paper [43].

We assessed environmental correlates of isotopic variation within individuals using general linear models including season, year and climate effects. Climate proxies were annual rainfall (data from Kruger Park Scientific Services) and sunspot activity (data available at ftp://ftp.ngdc.noaa.gov/STP/SOLAR_DATA/SUNSPOT_NUMBERS/INTER NATIONAL/yearly/YEARLY.PLT), both of which influence savannah vegetation patterns [44,45]. Lag terms were introduced as additional covariates to account for serial correlation; however, because some series are relatively short, we only present results accounting for single-order persistence, i.e. δXn−1 (including second-order persistence made no substantial difference to the results). Season × year interactions within individuals were never significant (p > 0.05), so they were omitted from the final analyses. Overall significance of each effect was assessed with Fisher’s global test [46], which provides a combined P-value for n independent tests of the same null hypothesis (based on the observation that, from the series P1, P2, ..., Pn, the quantity ∑n−1i=2 ln Pi is distributed as an χ2 with 2n degrees of freedom).

To compare within- versus between-individual variation in the data, we used variance components analysis (VCA) to partition sources of variation in mixed effects models, where the random effect individual is nested within region (Northern Kruger Park, n = 8, or South, n = 6) [20]. Season was included as a fixed effect, and year as a covariate. Second- and third-order interactions between categorical effects were included: non-significant (p ≥ 0.05) interactions were removed.
and the models re-evaluated without them. In all, the VCA partitioned three sources of variability: between individuals (nested within region), individual × season interactions (when included) and within individuals (residual error).

Analyses were carried out separately for each isotope series, as well as for a subset of the $\delta^{13}$Ccollagen series of only those individuals for which $\delta^{13}$Ccarbonate data are available ($n = 7$). We used additional GLMs (accounting for single-order persistence) to evaluate correlations between isotope series, within individuals and globally. Statistical analyses were performed using STATISTICA v. 8.0 [47].

3. RESULTS
(a) Sources of variation within individuals
Detailed descriptive and inferential statistics about this level of variation are given in the electronic supplementary material, tables S3–S7. In the collagen data series, mean $\delta^{13}$C values of individuals reflect diets comprising largely C3 browse ($-20.6\%^{\circ}$ to $-18.6\%^{\circ}$) throughout life, but the time-series demonstrate wide variability within individuals ($4.3\%^{\circ}$ on average, but up to $6.6\%^{\circ}$ in some, indicating switches in dietary C3/C4 composition by magnitudes of approx. 30–50%, or more; figures 2 and 3). Much of the within-individual variation is derived from a seasonal effect ($p < 0.05$ in 11 individuals; average $\eta_2 = 0.730$; Fisher’s global $p < 0.0001$), appearing as regular cycles throughout each sequence. This cyclicity is consistent with diet switches between C3 browse-dominated diets in dry seasons (lower $\delta^{13}$C values in the dark part of first-order growth bands; mean $\delta^{13}$Ccollagen $= -19.9^{\circ} + 0.71$ s.d.) to increased C4 grass consumption in wet seasons ($-18.7^{\circ} + 0.93^{\circ}$). Two individuals also show a significant increase in $\delta^{13}$Ccollagen over time (figures 2f and 3f; $p < 0.01$), and the trend, although weak (average $\eta_2 = 0.142$), is globally significant (Fisher’s $p < 0.001$). Moreover, the trend persists in models that account for differences between individuals (table 1; $p = 0.025$), which implies that, in general, the population shifted to slightly higher C4 grass intake through the twentieth century. There is no effect of annual rainfall (Fisher’s global $p = 0.563$) or sunspot activity (Fisher’s global $p = 0.394$) on within-individual variation in $\delta^{13}$Ccollagen data, suggesting that while climate may have been a major factor underlying diet shifts across seasons, it did not influence C3/C4 composition of elephant diets over the long term.
The $\delta^{15}$N series also show variability within individuals (mean range = 2.8‰; figures 2 and 3). There is a significant, but relatively weak, seasonal effect in these series ($p < 0.05$ in six individuals; average $\eta^2 = 0.126$; Fisher's global $p < 0.0001$). There is also evidence for a directional shift in $\delta^{15}$N values over time in three individuals, which is globally significant (Fisher's $p < 0.001$). However, in this case, neither the seasonal nor long-term trend effects persist in models accounting for differences between individuals (table 1; $p = 0.642$ and 0.534), probably because the direction of the changes is not consistent in all individuals sampled. In addition, the $\delta^{15}$N series are not related to either climate proxy (Fisher's global $p = 0.607$ and 0.723 for annual rainfall and sunspot activity, respectively).

In carbonate data, the $\delta^{13}$C series also correspond to C$_3$-dominated diets (individual means ranged from $-12.5$ to $-10.2$‰), with fluctuations within individuals of approximately 3.3‰ on average (figure 3). This variation is somewhat smaller than that of the $\delta^{13}$C$_{collagen}$ series, and suggests diet switches by only approximately 10–30% C$_3$/C$_4$ consumption through life. Accordingly, the seasonal effect in the $\delta^{13}$C$_{carbonate}$ series, while significant (Fisher's global $p < 0.001$), is much weaker (average $\eta^2 = 0.302$) than in the $\delta^{13}$C$_{collagen}$ series. By contrast, the former show a stronger long-term trend of increasing $\delta^{13}$C—and hence increasing C$_4$ grass consumption—through time (Fisher's global $p < 0.001$; average $\eta^2 = 0.399$). The long-term, and also the seasonal, signal in the $\delta^{13}$C$_{carbonate}$ series persists even when differences between individuals are accounted for ($p < 0.001$; table 1).

The $\delta^{18}$O series varied widely within individuals (by 5.3‰ on average), but in this case, the variability was not because of a seasonal effect (Fisher's global $p = 0.874$). A positive long-term trend was detected in the $\delta^{18}$O series (Fisher's global $p = 0.016$). Neither $\delta^{13}$C$_{carbonate}$ nor $\delta^{18}$O were related to annual rainfall (Fisher's global $p = 0.927$ and 0.336); $\delta^{13}$C$_{carbonate}$ was not related to sunspot activity (Fisher's global $p = 0.962$), and although the $\delta^{18}$O series was related to sunspot activity (Fisher's global $p < 0.001$), the trend is reversed between the two individuals for which it is significant.

Figure 3. Stable isotope profiles along ivory sections of eight individual elephants from Kruger Park (TM 10046 stored at the Transvaal Museum, Pretoria; the other samples are from stockpiles at Skukuza within Kruger Park. Black circles, $\delta^{13}$C$_{collagen}$; grey circles, $\delta^{15}$N; black triangles, $\delta^{13}$C$_{carbonate}$; grey triangles, $\delta^{18}$O). Symbols are means per season per year: closed symbols indicate microsamples from the dark portions of annual growth bands (dry seasons), open symbols represent light portions (wet season growth). $\delta^{14}$C data are adjusted for twentieth-century depletion of atmospheric $^{13}$CO$_2$ [43].
Table 1. Mixed effects models and variance components analysis of $\delta^{13}C$ series in African elephant ivory dentine collagen (14 individuals; numbers in parentheses are results from only those individuals with $\delta^{13}C$carbonate data) and dentine carbonate (seven individuals).

<table>
<thead>
<tr>
<th>effect</th>
<th>$F$</th>
<th>$p$</th>
<th>variance component</th>
<th>% explained</th>
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<td>region</td>
<td>28.465,1,540</td>
<td>&lt;0.0001 (&lt;0.8918)</td>
<td>0.153 (0.312)</td>
<td>13.8 (31.9)</td>
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<td>individual (region)</td>
<td>11.295,1,540</td>
<td>&lt;0.0001 (&lt;0.0001)</td>
<td></td>
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<tr>
<td>season</td>
<td>214.387,1,540</td>
<td>&lt;0.0001 (&lt;0.0001)</td>
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<td>region $\times$ season</td>
<td>10.433,1,540</td>
<td>0.0013 (&lt;0.01)</td>
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<td>&lt;0.0001 (n.a.)</td>
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<td>5.036,1,540</td>
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<td>0.813 (0.667)</td>
<td>73.4 (68.1)</td>
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<td>season</td>
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<td>$\delta^{13}C_{\text{carbonate}}$</td>
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<tr>
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<td>$\delta^{18}O$</td>
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(b) Sources and relative magnitude of variation between individuals

The wide isotopic variability within individuals suggests broad, overlapping niche breadths. Indeed, the majority of variation in the collagen data is attributable to within-individual components (73.4% and 70.0% for $\delta^{13}C$ and $\delta^{15}N$ series, respectively; table 1), even accounting for differences across regions, seasons and years. Between-individual components of variation are significant for both datasets ($p < 0.0001$; table 1), but differences are limited to a few individuals only. In the $\delta^{13}C_{\text{collagen}}$ series, differences between individuals—and between Kruger Park regions—arise because three individuals from the South have lower mean $\delta^{13}C_{\text{collagen}}$ values than the others (unequal N post-hoc tests, $p < 0.05$; see individuals Kambaku, Phelwana and TM-10046 in electronic supplementary material, table S3). The region $\times$ season interaction seems to occur because of a weaker seasonal signal in the north: this is consistent with short-term trends based on faecal $\delta^{13}C$ data, which showed higher levels of $C_4$ grazing and smaller seasonal switches (less-extensive dry season browsing) in northern Kruger Park habitats [20]. Between-individual differences in the $\delta^{15}N$ series occur because three individuals from the North have higher means than most other individuals in the dataset (unequal N post-hoc tests, $p < 0.05$; see individuals Dzombo, Ndulamiti and Shingwedzi in electronic supplementary material, table S3).

In the carbonate data, isotopic differences between individuals emerge because of higher mean $\delta^{13}C$ (as for the $\delta^{13}C_{\text{collagen}}$ series), and lower mean $\delta^{18}O$ values, among individuals from the North than in the South. The variance accounted for by the between-individual components in the carbonate data is higher than recorded in the collagen data (>45% in both cases; table 1), probably because of the small number of individuals in this dataset ($n = 7$), the relatively short time-series for each animal (often 10–15 years), and because several individuals lived during different periods of the twentieth century (figure 3). Despite these confounding factors, within-individual components still account for more than 50 per cent of the variation in carbonate data.

4. DISCUSSION

(a) Constraints to foraging strategy

These data reveal little evidence for individualized isotope niches in elephants. The high level of within-individual variation and relatively low level of between-individual variation in $\delta^{13}C_{\text{collagen}}$ values observed here contrast with patterns recorded for many taxa in other environments, including highly diverse marine systems [8,9]. Thus, individual elephants do not partition the $C_3$ browse/$C_4$ grass resource available to the population. The higher between-individual variation found in the $\delta^{13}C_{\text{carbonate}}$ series (but still accounting for less than 50% of the total variance) is probably because these data are represented by only a few individuals ($n = 7$) over somewhat different time periods, and cannot be taken as evidence for individualization of dietary niches within a single population. It is possible that specialization in elephants occurs at
scales other than C₃ browsing and C₄ grazing, if, for example, individuals differ in plant species or plant parts used. However, the ivory δ¹⁵N and δ¹⁸O series also had higher within- than between-individual variance components, indicating that elephants do not partition these isolate niche axes either. Another possibility is that niche differentiation across individuals is not evident in our data because the majority of animals sampled (for which sex information is available) were males, which have largely solitary lifestyles. Niche separation might be more prevalent among individuals in herds. Yet we found similarly high within-individual variation in δ¹³C profiles of elephant tail hairs (ranges up to 5.0‰; 96% of the variation explained by the within-individual component), based on a sample of 19 individuals from herds in the North and in the South of Kruger Park, including both sexes and all age classes (electronic supplementary material). Comparably high within-individual isotopic variability has also been reported from tail hairs of male and female elephants from East Africa [22].

Our result contrasts with findings of several recent studies in a variety of carnivorous, omnivorous and non-mammalian herbivore taxa [4–6,8,9]. While much research effort is currently focused on conditions leading to individual niche specialization [7], our findings indicate that this strategy must exclude at least large-bodied herbivores; conditions favouring individual generalism also warrant consideration. Our prediction was that disparity between elephant strategies and those of various other animal groups arises because mammalian herbivores are nutritionally constrained to maintain broad dietary niche breadths. Hence, a herbivore specializing on a narrow range of foods would probably translate into energetic losses for the individual [15]. This should affect niche structure of all mammal herbivore populations, but may be most prevalent in larger species that cannot be particularly selective feeders because of their gross morphology necessitating, for example, large bite sizes (cf. [48]). Ecological constraints probably also play a role. For example, savannah herbivores live in habitats in which their food sources are unevenly distributed across spatio-temporally heterogeneous landscapes [44], where—nutritional constraints aside—individualization of dietary niches could emerge in populations of smaller herbivore species affected by density-dependent factors like resource limitation, or even predation [49]. But for large-bodied species like elephants, which forage over wide areas at daily and seasonal scales, encounter rates with a narrow range of food items are likely to decline as foraging strategies become increasingly fine-grained over larger areas [50], making individualization in heterogeneous landscapes an unprofitable strategy.

(b) Evidence and implications for long-term diet switching

The ability to switch frequently between browsing and grazing gives elephants an advantage in surviving environmental perturbations, and may help them to survive future environmental change. Previous studies of historical diet patterns of elephants yielded equivocal results. Stable carbon isotope data for Amboseli National Park, Kenya, implied an increased C₄ grass intake from the early 1970s to the late 1980s [51], whereas data for Tsavo National Park, Kenya, implied a constant diet regime over 50 years [52]. Our result indicates that such disparity could arise because of the enormous variation that occurs within individuals. Long-term trends would thus be difficult to detect in the absence of continuous diet records such as those used here. Even in this instance, although the result is statistically significant (p = 0.025), the long-term trend of increasing C₄ grass consumption is only weakly evident in the ivory δ¹³Ccollagen series (figure 2). However, the δ¹³Ccarbonate series depicts a stronger trend of increasing δ¹³C (and hence increasing C₄ grass intake) through the twentieth century (with smaller amplitudes of seasonal diet switching). A hypothetical time-series model (electronic supplementary material) suggests that the smaller seasonal signal in the δ¹³Ccarbonate (and δ¹⁸O) series could be related to slower isotope turnover rates in this material, but this cannot account for the differences in trend at decadal scales. Rather, the weaker trend in the δ¹³Ccollagen series probably arises because these data under-represent increases in C₄ grass consumption owing to the relatively low protein content of this resource [40]. Consistent with this hypothesis is the fact that regressions of δ¹³Ccollagen on δ¹³Ccarbonate series, while revealing a significant correlation between them (Fisher’s global p < 0.0001), showed slopes generally shallower than 1.0 (electronic supplementary material, figures S4, S7 and table S7). Thus, while the trend of increasing C₄ grass intake through time is weak in the δ¹³Ccollagen series (amounting to ca 1‰ over the 90-year period), the stronger trend in the δ¹³Ccarbonate series represents the true long-term diet shift (amounting to ca 2–3‰, i.e. ca. 15–20% increase in the C₄ grass component of elephant diets). Nonetheless, this pattern may only be driven by increases in C₄ grass consumption by a few individuals in our dataset, and the trend requires further study.

For a species widely considered as having keystone effects on biodiversity in its habitats, long-term ecological insights are sought-after [53]. Our finding that some Kruger Park elephants increased C₄ grass consumption rates through time—possibly reflecting a general shift, although this requires confirmation (see above)—implies that they experienced either increased availability of high quality and abundant grasses [21], or reductions in tree cover and tree species diversity [20]. A number of global or local environmental changes in the twentieth century could have contributed to such habitat modifications. The δ¹³Ccollagen and δ¹³Ccarbonate series were significantly and positively related to the δ¹⁵N and δ¹⁸O series, respectively (Fisher’s global p < 0.0001 and p < 0.001, respectively; electronic supplementary material, table S7). Both the latter proxies are predicted to increase with aridity, a climate shift that may have driven the long-term diet switch. However, ascribing cause-and-effect to such relationships is only speculative, because the shift in δ¹⁵N and δ¹⁸O series may merely be a product of the switch to increased C₄ grass intake. For example, grass leaves are often ¹⁸O-enriched relative to tree foliage due to them being better irradiated than tree foliage (besides uppermost canopy leaves) [54]. Elephants themselves are a more likely cause of the inferred diet switch because of increased densities and their impacts on woody vegetation [21,44,53]. This could suggest a cyclic feedback system similar to that proposed by Caughley [55], whereby diet switching over long time scales allows recovery of the
initial resource (tree populations, in this case), a process that would be crucial for understanding elephant–plant interactions, and for conservation policy.

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