Conservation implications of dietary strategies in the critically endangered Acacia gazelle (*Gazella arabica acacia*)

Abstract

Animals consume different foods in specific quantities and ratios to meet a multi-dimensional nutrient target that maximizes their fitness. Attempts to reach this target in an ever-changing nutritional landscape often influence animal foraging behavior, habitat choice, and food-web interactions. Consequently, understanding the nutritional ecology of a species is instrumental in developing efficient management plans for its conservation. We quantified the dietary considerations of a critically endangered population of Acacia gazelles (*Gazella arabica acacia*) in Southern Arava, Israel, and compared their diet and nutrition to that of the sympatric Dorcas gazelle (*Gazella dorcas*), using behavioral observations coupled by nutritional and secondary metabolite quantification, and morphological measurements of trees. Acacia gazelles mainly consumed resources from two umbrella-thorn acacia (*Vachellia tortilis*) subspecies that differed in morphology, nutritional composition, and phenology. Gazelles maintained a rather narrow nutritional intake target year-round despite the dynamic dietary landscape, tightly regulated their protein intake, and prioritized consumption of non-structural carbohydrates. They did so by adjusting the consumption of leaves, pods, and flowers, following the differential phenology of the two *Vachellia* trees. The sympatric Dorcas gazelles generally avoided the thorny *Vachellia* subspecies and consumed more halophytic shrubs and less tree foliage than Acacia gazelles. Despite these dietary differences, the two gazelle species converged to a similar intake target. We conclude that suitable habitats for Acacia gazelle reintroduction must include sympatric populations of the two *V. tortilis* subspecies, that nutritional deficiency is unlikely to play a major role in explaining the slow rate of population recovery, and that attempts to limit Dorcas gazelle's population size may be redundant due to the seemingly low competition between the two gazelle species.

Introduction

Wildlife feed on various foods in specific ratios and quantities to meet a multifaceted nutrient intake target that maximizes their fitness (hereafter "intake target"; Simpson & Raubenheimer 2012; Solon-Biet et al. 2014; Raubenheimer & Simpson 2018). Attempts to meet this target may regulate animals' spatial activity and behavior (Charnov 1976; Seagle & McNaughton 1992; Johnson et al. 2017), and influence interactions with competitors, natural enemies, and anthropogenic risks (Kohler & McPeek 1989; Pettersson & Brönmark 1993; Weber 2001; Kay et al. 2010). A key step in understanding the ecology of endangered species is thus to uncover their dietary considerations (Birnie-Gauvin et al. 2017).

Human activities have dramatically changed the natural environment, altered the abundance, quality, and distribution of food resources, and limited their accessibility to wild animals (Acevedo-Whitehouse & Duffus 2009). These changes may prevent animals from meeting their intake target, adversely affecting their population dynamics (Armstrong & Perrott 2000; López-Bao et al. 2010). Managers tend to address these general concerns using supplementary feeding as a precautionary measure. This is despite growing evidence that supplementary feeding may negatively affect the population it is intended to help (Carrete et al. 2006; Blanco et al. 2011; Martínez-Abraín & Oro 2013), or the recipient ecosystem at large (Cortés-Avizanda et al. 2009a, 2009b). Managers can minimize these double-sided risks by revealing the dietary strategies of wildlife in nature, and by integrating this knowledge into conservation plans.

Attempts to quantify nutritional needs and other dietary considerations of wildlife in the field traditionally focused on a single currency such as biomass, energy, or protein consumed (Schoener 1971; Charnov 1976; White 1993). However, natural foods are complex mixtures of macronutrients and micronutrients in varying levels of availability and digestibility. Animals often need to ingest several food types, and occasionally digestive assistant agents (DAA) to meet their multidimensional nutritional target (Zaguri et al. 2024). Thus, focusing on a single food currency may provide only a limited understanding of the animals' true dietary considerations (Belovsky 1984; Simpson et al. 2004; Felton et al. 2009a, 2018). Despite this well-accepted realization, the lack of adequate methods to quantify wildlife intake targets in the field largely prevents adopting this approach for conservation. Progress in nutritional ecology, and especially the development of the right-angled mixture triangle (RMT) method that uses proportions rather than amounts of foods consumed to quantify wildlife intake targets marked a breakthrough in our ability to use nutritional ecology to inform conservation

(Raubenheimer 2011; Raubenheimer et al. 2015). Yet despite the clear potential, RMT was used almost exclusively in primate research (Raubenheimer et al. 2015; Johnson et al. 2017; Takahashi et al. 2019; DePasquale et al. 2023), and only rarely to quantify intake targets of endangered wildlife including ungulates (Raubenheimer et al. 2014; Spitzer et al. 2023). In these rare cases, the limited ability to directly observe the animal feeding behavior and to quantify the nutritional composition of foods has led to the development of proxy methods like fecal (Nie et al. 2015; Hecker et al. 2021; Spitzer et al. 2023) or rumen and gut content analyses (Felton et al. 2021) to quantify the diet, and the use of crude nutritional estimates at the species level to assess the food nutritional content (Costello et al. 2016; Shrestha et al. 2020; Spitzer et al. 2023, 2024). These proxy methods are informative but produce less accurate and temporally dubious intake target estimates that are less applicable for conservation.

Focusing solely on the nutritional composition without considering other food characteristics may produce an incomplete understanding of animals' dietary considerations and may lead to erroneous conservation decisions. Plants are often defended by various chemical (e.g., tannins; alkaloids; salts) and physical defenses (e.g., thorns; opaline phytoliths; trichomes), and include components of little nutritional value (e.g., lignin, Barboza et al. 2009). These traits may alter herbivores' ability to ingest and digest foods, possibly influencing the herbivore's dietary choices (Freeland & Janzen 1974; Cooper & Owen-Smith 1986). Consequently, attempts to uncover the dietary strategies of endangered ungulates must include quantification of plant traits that may influence food choice.

Our goal was to assist in the recovery of a critically endangered Acacia gazelle (*Gazella arabica acacia*) population by exploring the gazelle dietary strategy using classic and modern approaches. Acacia gazelles are a genetically unique and geographically isolated population of Arabian gazelles (*Gazella arabica*, Hadas et al. 2015; IUCN SSC Antelope Specialist Group 2017). This remnant population of about 40 individuals is restricted to two small floodplains in the Yotvata Nature Reserve, Southern Arava, Israel, and struggles to recover despite substantial conservation efforts like water, food supplementation, and interventions to reduce predation and competition (Shalmon 1991; Blank 1996, 2000; Polak et al. 2023). Historical references suggest a much larger distribution before the 1950s when the entire population was almost extirpated by hunting (Mendelssohn 1974), Yet, not enough is known about the historic distribution to predict these gazelles' habitat requirements. In 2006, the Israel Nature and Parks Authority (INPA) enclosed the remaining 13 gazelle individuals within a 3.5 km^2 predator-proofed enclosure together with 82 Dorcas gazelles (*Gazella dorcas*) that presumably compete

with the Acacia gazelles for food (Shalmon et al. 2020; Breslau et al. 2020). Thus, another goal of the project was to compare the diets and intake targets of the two gazelle species.

To reveal their dietary strategy, we observed the Acacia gazelles' natural foraging behavior in monthly intervals for one year and collected samples from all plants consumed, and from similar reference resources that were not consumed. We used a similar protocol to assess the Dorcas gazelle dietary strategy during the summer months. We characterized the chemical composition of all samples using wet chemistry and Near Infra-Red Spectroscopy (NIRS). We then used right-angled mixture triangles (Raubenheimer 2011) to estimate the gazelle nutritional intake target. We measured the physical traits and tannin composition of the two *Vachellia* trees to identify the traits of individual trees that make them more palatable. We compared the Acacia gazelle diet and nutrition to those of the sympatric Dorcas gazelle to reveal the degree of resource competition between the two species.

Methods

Study site and gazelle populations

The study was conducted within the Acacia gazelle predator-proofed enclosure in Yotvata Nature Reserve, Israel (29°51'-29°53'N, 35°01'-35°03'E; Fig. 1). This hyper-arid site is located within the Jordan Rift Valley about 40 km north of the Gulf of Aqaba. The mean annual temperature is 24°C, and the average annual precipitation is 40.5 mm with big fluctuation between years. All precipitation occurs between October to May. The site includes two alluvial fans dominated by scattered *Vachellia* (formerly *Acacia*) trees and their common semi-parasite *Loranthus acaciae*. Several halophyte shrubs, mainly *Haloxylon salicornicum*, *Lycium shawii*, *Salsola imbricata,* and *Nitraria retusa*, dominate the exposed stony gaps between the *Vachellia* stands (Baharav 1982). Two *Vachellia* trees coexist in this site, both considered subspecies of *V. tortilis (V. tortilis tortilis and V. tortilis raddiana).* Locally, the two subspecies exhibit consistent differences in their chemical and physical traits, and habitat requirements (Halevy & Orshan 1972; Rohner & Ward 1997). Moreover, the two trees have very distinct phenology, producing flowers and fruits at different times (Halevy & Orshan 1973). Thus, we treated the two *Vachellia* trees as two distinct resources hereafter *V. tortilis* and *V. raddiana.*

The Acacia gazelle population of 35 individuals was first discovered at our study site in 1964. The population was discovered only after all other Acacia gazelle populations in Israel were extirpated. Since then, the INPA has attempted to restore the population using various

management interventions like supplementary feeding with natural or artificial foods, predator culling, and removal of calves in an attempt to establish a breeding colony in captivity. Despite those substantial efforts, the population failed to recover. In 2006, after a dramatic population decline, the INPA enclosed the remaining 13 gazelles together with 82 Dorcas gazelles (*Gazella dorcas*) in a 3.5 km^2 predator-proofed enclosure. By 2013, both Acacia and Dorcas gazelle populations reached a maximum density of 42 and 173 individuals, respectively. However, in the winter of this year, large parts of the fence were breached by flood water, enabling wolves to penetrate and kill about 30 Acacia gazelles and 65 Dorcas gazelles. Between 2015 to 2019 the INPA actively removed 161 Dorcas gazelles from the enclosure as a precautionary step against interspecific competition, leaving only 36 individuals in the enclosure. During 2022-2023 only about 30 Acacia gazelle and about 40 Dorcas gazelle inhabited the enclosure (Polak et al. 2023).

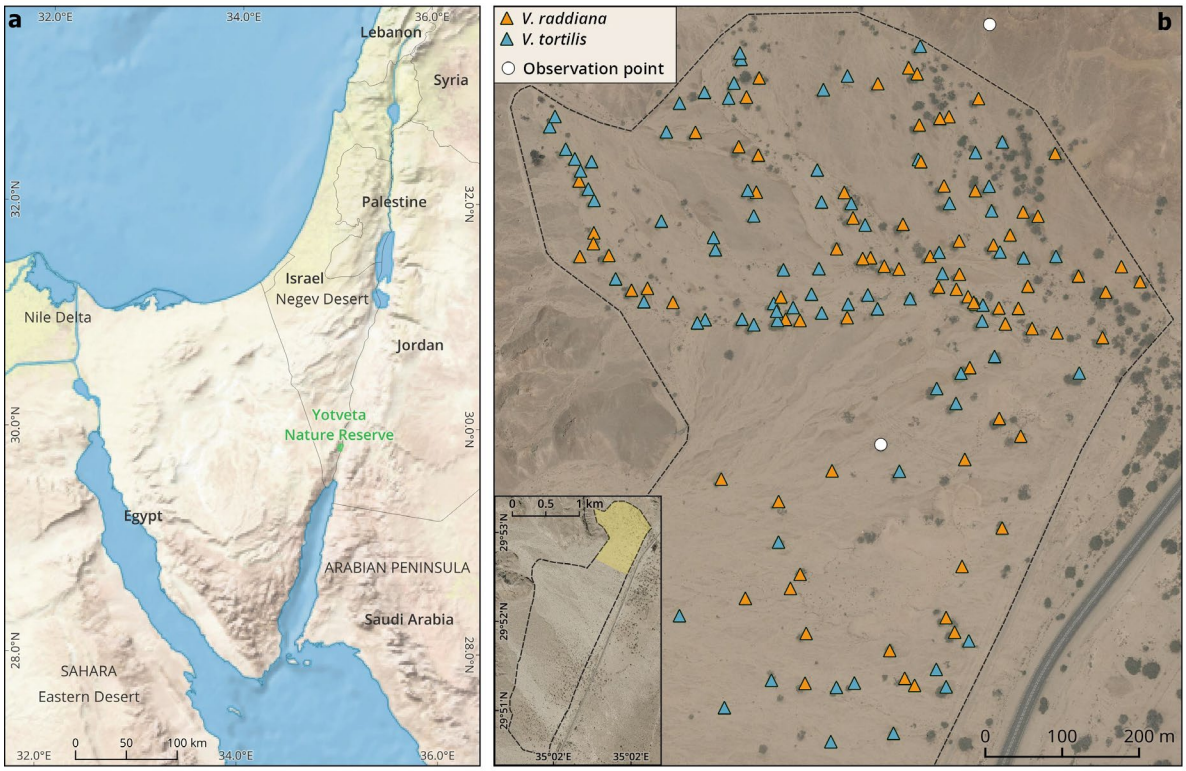

Fig. 1 Study site locality map showing the location of Yotvata NR (a), and the gazelle enclosure (b). the enclosure (bottom left) is presented with emphasis on the northern part (enlarged and highlighted) where observations were conducted. Marked in the northern part are the trees observed and sampled, colored by *Vachellia* subspecies, and the two hides used for observations. The Internal hide was used during morning sessions and the external hide was used during evening sessions.

136 Gazelle feeding observations and forage sampling

137 To assess the gazelle diet, we conducted monthly group observations of the gazelles'
138 feeding behavior in the northern part of the gazelle enclosure during 2022 and 2023. We
139 observed the gazelles' behavior during their peak foraging activity in the early morning and
140 late afternoon for a minimum of 3 consecutive days each month. For each individual plant
141 resource, we recorded the number, age, and sex of the feeding gazelles, the feeding time, and
142 feeding behavior (either from the ground or from the canopy). We used QField mobile
143 application to collect this data with its location into a QGIS project (see Appendix 1 for full
144 protocol and details).

145 To compare the foraging behavior of Acacia gazelles to that of Dorcas gazelles, we used
146 observational data on the foraging behavior of the two gazelle species that we collected at the
147 same site during the summer of 2014, prior to the Dorcas gazelle removal. These foraging
148 observations were conducted using continuous time-budget observations on focal individuals.

149 After each observation, we collected samples from all plant resources that were
150 consumed by the gazelles and immediately transferred them to our field lab. There, we weighed
151 and oven-dried the samples (60°C at least 48 h), and re-weighed them for dry mass estimations.
152 Following each observation session, we milled all samples through a 1 mm sieve using a
153 laboratory grinding mill (Kinematica POLYMIX PX-MFC 90D). We stored the milled samples
154 in the freezer until further analyses.

155 Chemical analyses

156 We used classic chemical quantification methods to estimate the nutritional content of
157 209 out of 400 collected food samples (Table S1). Samples were chosen based on quantity and
158 Near Infrared Spectroscopy (NIRS) unique spectra. Each of the 209 samples was analyzed for
159 total non-structural carbohydrates, crude protein, lipids, fiber fractions, ash, and tannin content.
160 The non-structural carbohydrates were quantified using the phenol-sulfuric assay with acid
161 extraction (Dubois et al. 1956; Landhäusser et al. 2018). For crude protein estimation, we
162 estimated the Nitrogen (N) content by combustion, using a Leco FP-528 Nitrogen Analyzer
163 (Michigan, USA), and multiplied the N content by the widely used 6.25 conversion factor
164 (Jones 1931; Rothman et al. 2012). Lipids were measured using ether extract in an ANKOM
165 Fat Analyzer (New York, USA). Fiber fractions were determined using the sequential detergent
166 fibers assay (Van Soest et al. 1991) in an ANKOM A200 Fiber Analyzer: Neutral Detergent
167 Fibers (NDF), which contains non-soluble fibers (hemicellulose, cellulose, and lignin), Acid

168 Detergent Fibers (ADF, cellulose and lignin), and Acid Detergent Lignin (ADL). Samples were
169 burned at 500–550°C for ash measurement (Rothman et al. 2012). Finally, the relative content
170 of condensed tannins was estimated using the acid-butanol assay after extracting samples with
171 70% acetone (Porter et al. 1985; Hagerman & Butler 1994; Rothman et al. 2009). Additionally,
172 we chose 56 samples of the food resources observed in 2014 (8-10 samples of each food
173 resource) for mineral quantification to assess the ash composition. Minerals were assessed via
174 atomic absorption spectroscopy after microwave digestion at Dairy One Commercial Forage
175 Laboratory (Ithaca, NY, USA). Nutrient estimations are presented on a 105°C dry matter basis.

176 We then constructed a NIRS model for *Vachellia* leaves and pods of the two subspecies.
177 *Vachellia* flowers, *Loranthus* leaves and flowers and perennial shrubs were analyzed only by
178 wet chemistry and average nutrient content was applied, due to the low number of samples.

179 For NIRS analyses, we dried all samples for 48h. After homogenizing the sample, we
180 randomly took a ~50 mg subsample and added it to a 1 ml clear glass shell vial. We then
181 scanned all samples, using an Antaris II FT-NIR analyzer. We constructed two NIRS models
182 using TQ analyst software, the first model included absolute concentrations of all measured
183 macro-nutrients (Protein, Lipids, NSC, NDF, ADF, and ADL). The second model was for the
184 relative concentration of tannins. NIRS model's protocol and performances are presented in
185 Appendix 2.

186 Physical measurements of *Vachellia* trees

187 We randomly chose 20 *V. tortilis* and 20 *V. raddiana* trees in the northern part of the
188 enclosure. Half of the trees were observed browsed by Acacia gazelles during the winter when
189 mainly foliage is available. We randomly chose the 10 reference trees from all trees for which
190 we did not detect feeding in the previous year. For each tree, we divided the canopy into 4
191 equal-sized sections and measured 2 randomly chosen branches in each section. All sampled
192 branches were within the feeding range of an adult Acacia gazelle (up to 1.7 m, Fig. S1).
193 Following the protocol described by Rohner & Ward (1997), on each branch, we counted all
194 leaves and thorns >1mm within 50 cm from the branch distal end. We classified thorns as either
195 straight (spines) or curved (prickles) and the lengths of all thorns >5mm were measured
196 perpendicular to the branch. A sample of the 5 biggest leaves was measured for length and
197 width as well. We also noted the existence of browsing marks on each branch.

198 Data analysis

199 We estimated the Acacia gazelles' nutritional target and resources' composition using a
200 right-angled mixture triangle (Raubenheimer 2011), of the relative contents of the three main
201 macro-nutrients in the gazelle diet – Protein, non-structural carbohydrates (NSC), and
202 digestible fibers (calculated as NDF-ADL). We calculated the daily nutritional target by
203 multiplying each observation unit's (plant) nutritional values with the time and number of
204 gazelles spent feeding from it divided by the total daily feeding time. To unravel gazelle
205 regulation and prioritization of different macro-nutrients we conducted a permutation test for
206 the gazelles' intakes. We summarized each food resource mean nutritional concentrations and
207 its total feeding time in each observation session. Then, we permuted these feeding times. To
208 evaluate seasonal variation in gazelles' intake of NSCs and digestible fibers we performed a
209 Pearson's correlation test and fitted a linear model of the temperature effect. We obtained the
210 mean monthly minimal temperature from the daily ambient temperature measurements of the
211 nearest meteorological station in Yotvata, from August 2021 to April 2022 ("Meteorological
212 Database | Israel Meteorological Service" 2023).

213 We performed a Kruskal-Wallis test followed by a Bonferroni-corrected Conover-Iman
214 post-hoc test (Conover & Iman 1979) to compare the means of all macro-nutrients, minerals,
215 and tannins contents of the most prominent resources in the diets of both gazelle species as
216 observed in 2014 (i.e., *Vachellia* leaves and pods, *Haloxylon salicornicum*, and *Loranthus*
217 *acacia* leaves). We calculated fibers nutritional values (i.e. Hemicellulose, cellulose, and
218 lignin) by subtracting the chemical sequential fractions (NDF-ADF, ADF-ADL, ADL,
219 respectively). Since subtraction introduces a greater protentional error we report also the raw
220 values in the supplementary, where applicable.

221 For the physical traits measured, we averaged all traits for all branches of each tree. We
222 analyzed thorns data using counts within two length categories (with a 5 mm cutoff), resulting
223 in four thorns categories. Nutritional data were obtained for each tree from the NIRS model
224 predictive results, except for two *V. raddiana* trees which did not have nutritional data and were
225 therefore removed from this analysis. We used PCA to evaluate inter-specific variance between
226 *Vachellia* subspecies. To uncover differences between browsing categories we applied a
227 separate PLS Discriminant Analysis (PLS-DA, Barker & Rayens 2003) on each *Vachellia*
228 subspecies since the PCA revealed a large inter-specific variability. We standardized the data
229 before both ordinations. To estimate whether the separation between the two feeding categories

in the PLS analysis is significant, we performed two permutation tests on the feeding categories. First, we tested for cluster separation using the Mahalanobis distance between the two categories' centroids based on the pooled covariance matrix. We also tested for significance the proportion of explained variance between the feeding categories (R^2_y) and DR^2_y, correcting for false-negatives resulting from out-of-bounds estimation (Westerhuis et al. 2008). We used 1000 permutations and defined the p-value as the fraction of permutations greater than the chosen statistic. Last, we estimated each variable importance by randomly permuting it 1000 times and conducting the same analyses described. We compared the means of permutations R^2_y, DR^2_y, Mahalanobis distance between clusters, and the fraction of significant permutations for cluster separation.

All statistical analyses were conducted in R 4.3.0 software (R Core Team 2023). Linear models and correlation tests were performed using 'lm' and 'cor.test' functions from the 'stats' package. Kruskal-Wallis and Conover's tests were performed using 'kruskalTest' and 'kwAllPairsConoverTest' from 'PMCMRplus' package. PCA was fitted using 'prcomp' from 'stats' and PLS-DA was fitted using 'plsda' from the 'mixOmics' package (Rohart et al. 2017).

Results

Six different plant species were consumed by Acacia gazelles during the study. Their diet consisted mainly of different resources from two *Vachellia* subspecies, which together constituted about 88% of the annual gazelle diet, and no less than 70% of the monthly diet (Fig. 2). The consumed resources differed substantially in their nutritional and mineral content (Kruskal-Wallis $p<0.001$ for all, see tables S3 and S4 for post-hoc comparisons).

These two *Vachellia* subspecies differ substantially in their chemical and physical characteristics. *V. raddiana* trees have bigger leaves, while *V. tortilis* trees have higher densities of prickles, and higher concentrations of proteins and lipids in the leaves (Fig. S2). PCA results revealed high intra-specific variability in spines counts, and the contents of NSC, fibers, and tannin in the leaves of both subspecies (Fig. S2).

Vachellia subspecies differed also in their phenology. *V. tortilis* trees flowered while shedding their leaves in early summer, whereas *V. raddiana* trees started flowering in late summer and throughout the fall without completely shedding their leaves. *V. tortilis* pods developed immediately after the blooming period and ripened in late summer, while *V. raddiana* green pods remained on the branches during winter and ripened only in the next spring (Fig. 3c). *V. tortilis* produced flowers and fruits in shorter and more synchronized time

windows than *V. raddiana* (Fig. 3c). The rate of gazelles' visits to the *Vachellia* trees, and their relative feeding time were tightly associated with the above-listed phenological differences (Fig. 3). For instance, gazelles seemed to prioritize feeding on flowers when those were available. During June while green pods of *V. raddiana* were still available, the gazelles switched to feeding almost exclusively on the *V. tortilis* flowers during the peak blooming period (Fig. 3).

The variation in the gazelle's monthly nutritional intake was much smaller than the variation in the nutritional landscape (Fig. 4, Table S3). Gazelles achieved this tighter balance by eating differentially from the different available food resources. For example, in February the gazelles ate *V. raddiana* leaves from the canopy and pods from the ground, as well as *L. Shawii* leaves in order to reach their nutritional target (Fig. 2, Fig. 4, Fig. S3). This tight intake target was reached despite substantial differences in resource availability (Fig. 3, Fig. 4). From all macro-nutrients measured, protein intake varied the least (Table S3). The permutation test shows no significant selection for protein-rich foods (p=0.43). Thus, the precise protein intake may reflect the smaller variation in protein compared to other macro-nutrients in the consumed resources (Fig. S5). Similarly, we observed no selective feeding for digestible fibers (i.e. hemicellulose+cellulose, p=0.29, Fig. S5). However, the permutations test found that gazelles strongly select for non-structural carbohydrates, as the observed intake was significantly higher than the expected intake by random feeding (p=0.11, we consider this a significant result since we permuted the intakes between consumed resources, depicting evolutionary resource selection).

We observed a negative correlation between the monthly intake of NSC and digestible fibers (r=-0.54, 95% CI [-0.85,0.043], t_{10}=-2.0263, p=0.07; Fig. 5a). Gazelles tended to consume higher daily proportions of digestible fibers as monthly temperature decreased (slope=-0.22 [-0.47,0.034], R^2=0.1, $F_{1,28}$=3.143, p=0.087 for both). In the coldest months (January-February) gazelles increased both NSC and fiber intakes (Fig. 5a). Using NDF measure showed similar patterns for temperature effect on NDF consumption (slope=-0.30 [-0.53, -0.062], R^2=0.2, $F_{1,28}$=6.725, p=0.015 for both) and NDF to NSC trade-off (r=-0.55 [-0.85,0.034], t_{10}=-2.0866, p=0.064). This seasonal fiber intake was not confounded by available resources as different ratios could have been achieved in each season (Fig. 5b). In March, gazelles consumed a high NSC to digestible fibers ratio that substantially deviated from this general pattern. This was possibly because gazelles consumed large quantities of *V. tortilis* leaves during this time (Fig. 2). Leaves and pods had a relatively low protein content during

March than in other months, but *V. tortilis* leaves had proportionally the highest protein content (Fig. S4), suggesting that attempts to regulate protein intake may cause this dietary change. During summer, gazelles increased their relative NSC intake by prioritizing *V. tortilis* carbohydrates-rich flowers (Fig. 2, Fig. 4). Still, gazelles kept their tight protein intake by consuming *V. raddiana* pods and *Vachellia* leaves from both subspecies.

We observed variation in the use of individual *Vachellia* trees, of both subspecies, where some trees were heavily browsed while others were ignored (Fig. S6). The browsed and un-browsed *V. tortilis* trees differed substantially (Fig. 6a, M_d=3.28, p=0.014). The variation in the browsing category explained by the model was 75%-78%, depending on the type of fit-measure, and was significantly higher than random for both fit-measures (R^2_y=0.75, DR^2_y=0.78, p=0.021, 0.019, respectively). The separation was mainly along the first ordination axis (LV1) driven predominantly by the high fiber fractions and bigger leaf size (expressed as width and length measures) of the un-browsed trees, and the higher protein as well as higher number of leaves of the browsed trees (Fig. 6a,c). Browsed trees were also characterized by having a lower density of big prickles, and un-browsed trees had a relatively higher density of small prickles. Hemicellulose, big prickles, and protein were the variables that their randomization had a major effect on the model performance and cluster separation (Table S5). We did not find significant differences between the browsed and un-browsed *V. raddiana* trees (M_d=2.74, R^2_y=0.67, DR^2_y=0.72, p=0.14, 0.13, 0.11, respectively; Fig. 6b). Using raw analytical fiber fractions instead of the nutritional calculated fractions slightly decreased the performances of both models, but it remained significant for *V. tortilis* (Fig. S7).

We found major differences between the diet compositions of the two gazelle species. Acacia gazelle foraged predominantly on two *Vachellia* subspecies while Dorcas gazelles' diet included more shrubs, especially *Haloxylon salicornicum*. When feeding from the two *Vachellia* trees, Acacia gazelles consumed a much higher proportion of *V. tortilis* in comparison to Dorcas gazelles which fed almost exclusively from *V. raddiana* (Fig. 7a). Acacia gazelles fed more on the foliage from both *Vachellias*, while Dorcas gazelles fed predominantly on *V. raddiana* pods and flowers from the ground. Additionally, Acacia gazelle fed on *Loranthus acacia* while Dorcas gazelle did not use this resource (Fig. 7a). Despite the large dietary differences the two Gazelle species converged to a similar intake target. Both gazelle species achieved very similar protein intake, but Acacia gazelles reached higher NSC and lower digestible fibers than *G. dorcas* (Fig. 7b). Our two independent measurements of Acacia Gazelle intake targets in the presence of high (2014) and low (2022) sympatric Dorcas gazelle

densities revealed very similar estimations (Fig. 7b), suggesting that intra-specific competition had minimal influence on Acacia gazelle dietary considerations.

We observed consistent differences in ash and tannin levels between the diets of the two gazelle species. The halophyte *H. salicornicum* which constituted a major part of Dorcas gazelle's diet, had higher Na, Mg, and K content than all other plant resources (Table S4). The differences in the concentration of these salts likely explain why ash content in *H. salicornicum* was much higher than in other plant resources ($p<0.03$; Table S3). Leaves of the two *Vachellia* trees had significantly higher tannin content compared to all other resources ($p<0.001$ for all; Table S3), suggesting that Acacia gazelles potentially consumed higher quantities of tannins and less salt than Dorcas gazelles due to higher ingestion of *Vachellia* leaves and lower ingestion of *H. salicornicum*.

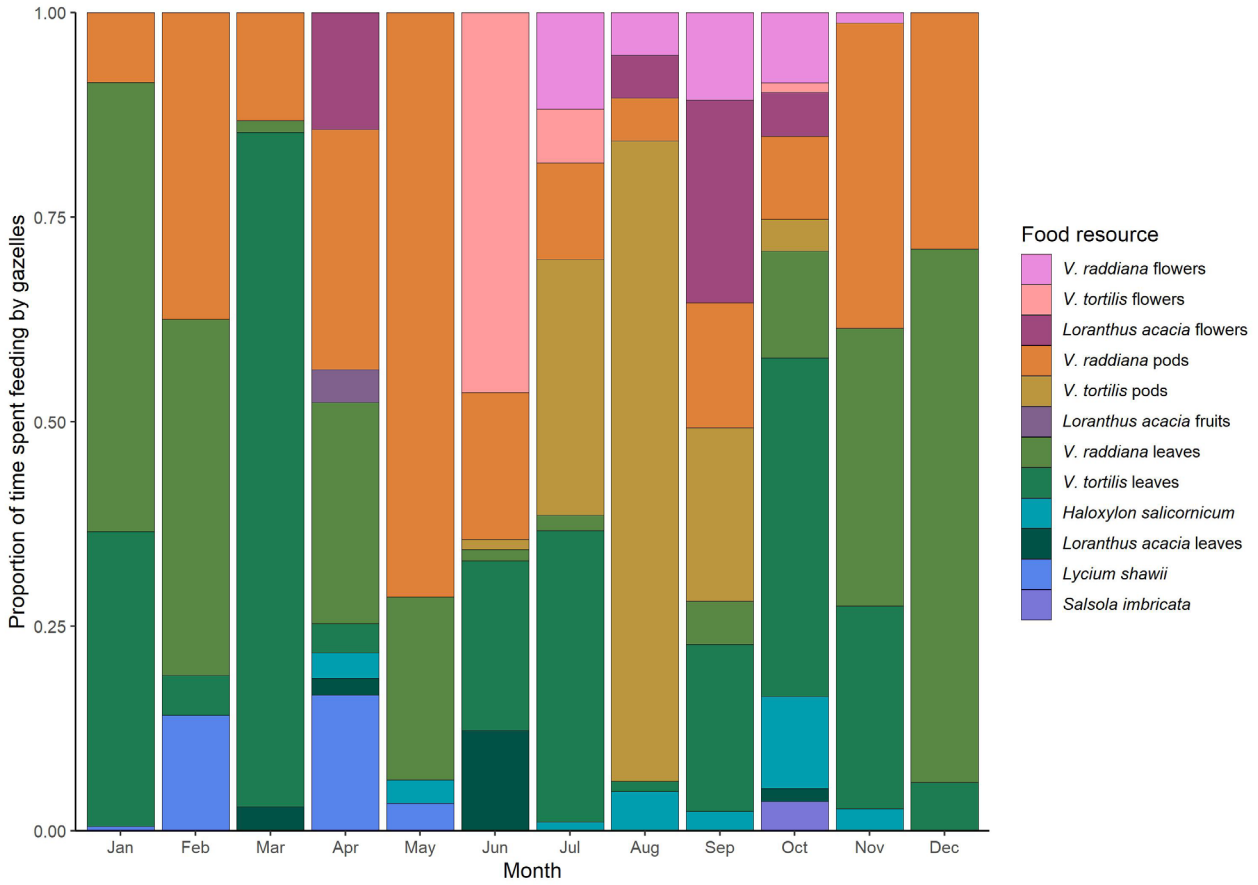

Fig. 2 Distribution of different food resources utilization by Acacia gazelles throughout the year. Proportions were calculated based on the time spent feeding from each resource.

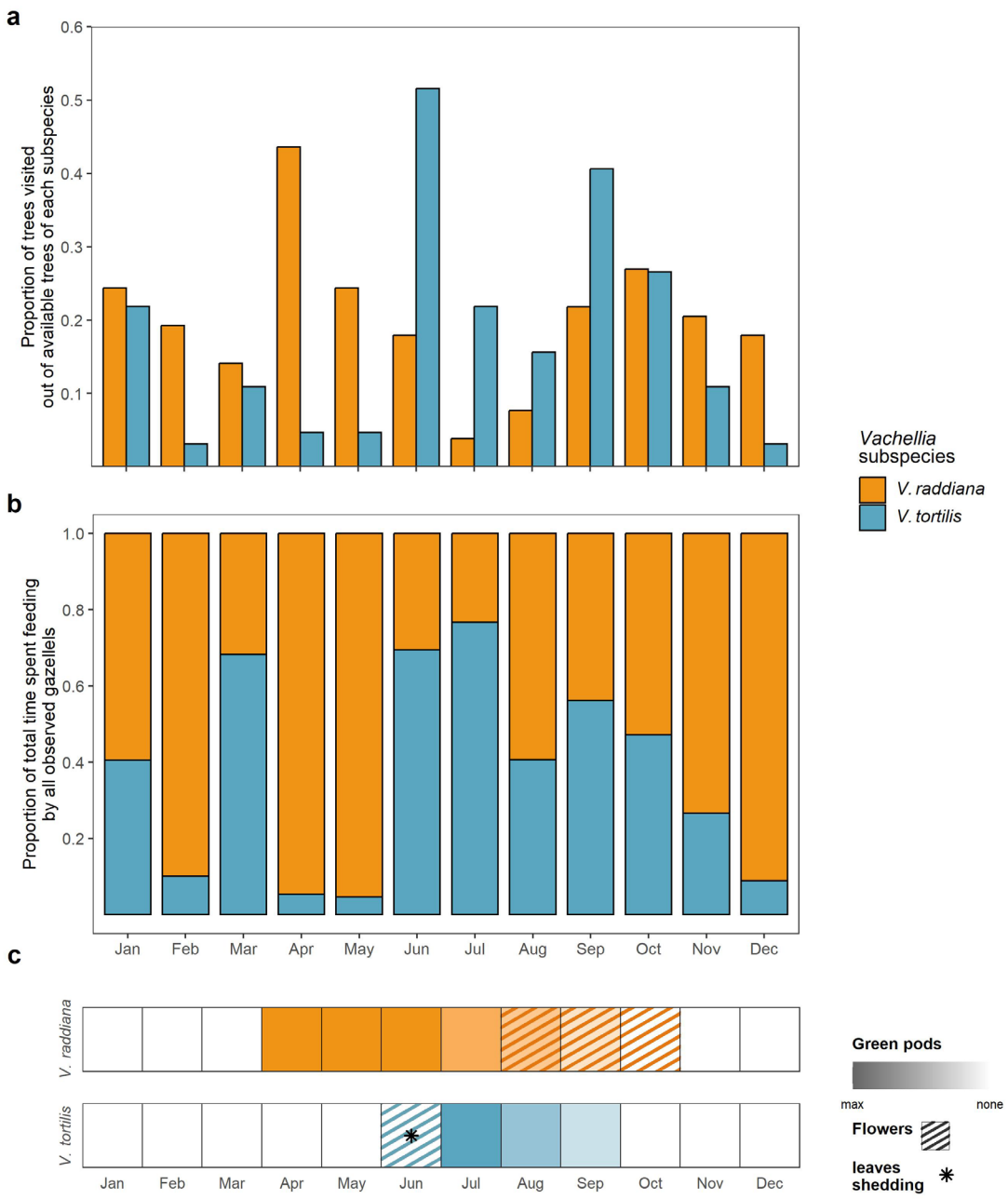

Fig. 3 Acacia gazelles' response to *Vachellia* phenological changes. (a) the number of different trees utilized of each subspecies out of the total trees of that subspecies identified in the northern part of the enclosure. (b) proportional time spent each month feeding from the two *Vachellia* subspecies. (c) Phenological state throughout the year of both *Vachellia* subspecies.

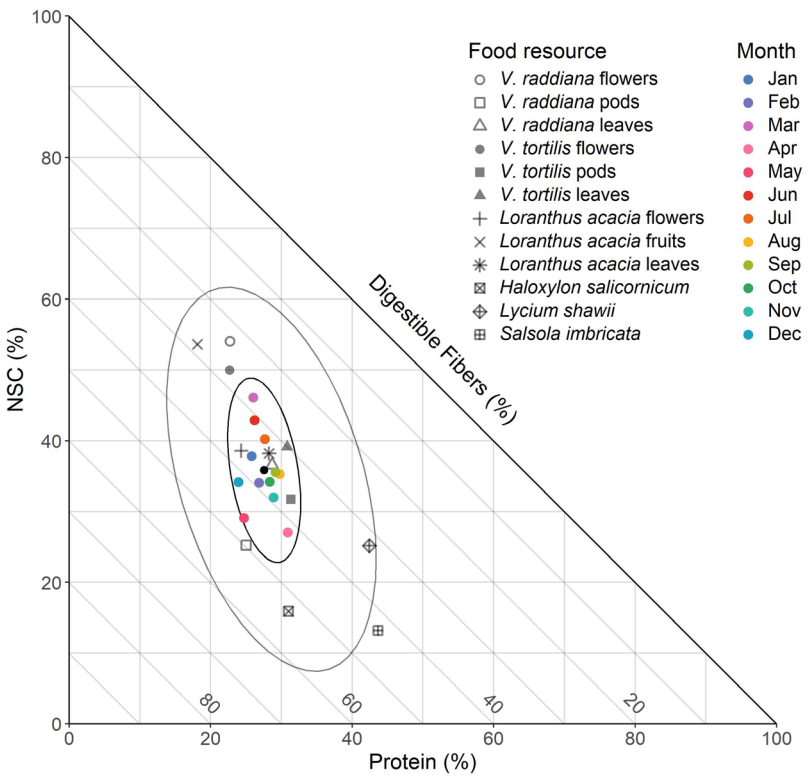

Fig. 4 Right-angled Mixture Triangle (RMT) of the relative concentrations of the three major macro-nutrients in the Acacia gazelles' diet – Digestible fibers (hemicellulose+cellulose), non-structural carbohydrates (NSC), and Protein. Diagonal (Z) axis values are written in italics above the X-axis. Points are the mean monthly intake colored by month and the mean annual intake in black. In gray are the mean annual nutritional values of the different food resources in the gazelle diet. Ellipses represent 95% confidence interval of the mean intake in black, and the mean nutritional value of all resources in gray.

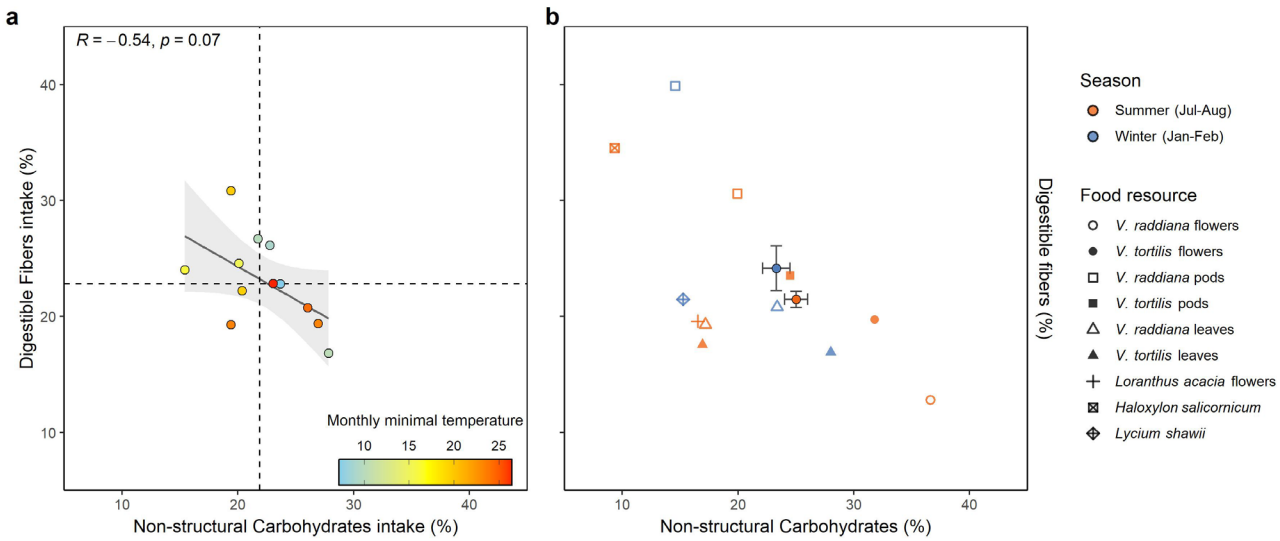

Fig. 5 Relationships between temperature and the intake of fiber and NSC. (a) NSC to fibers monthly intake colored by the monthly mean minimal temperature. Dashed lines are the annual nutritional target of each macro-nutrient (b) NSC to fiber mean intake and food resources available for the two coldest and two hottest months. Error bars are the standard error (n=4 days in summer and winter).

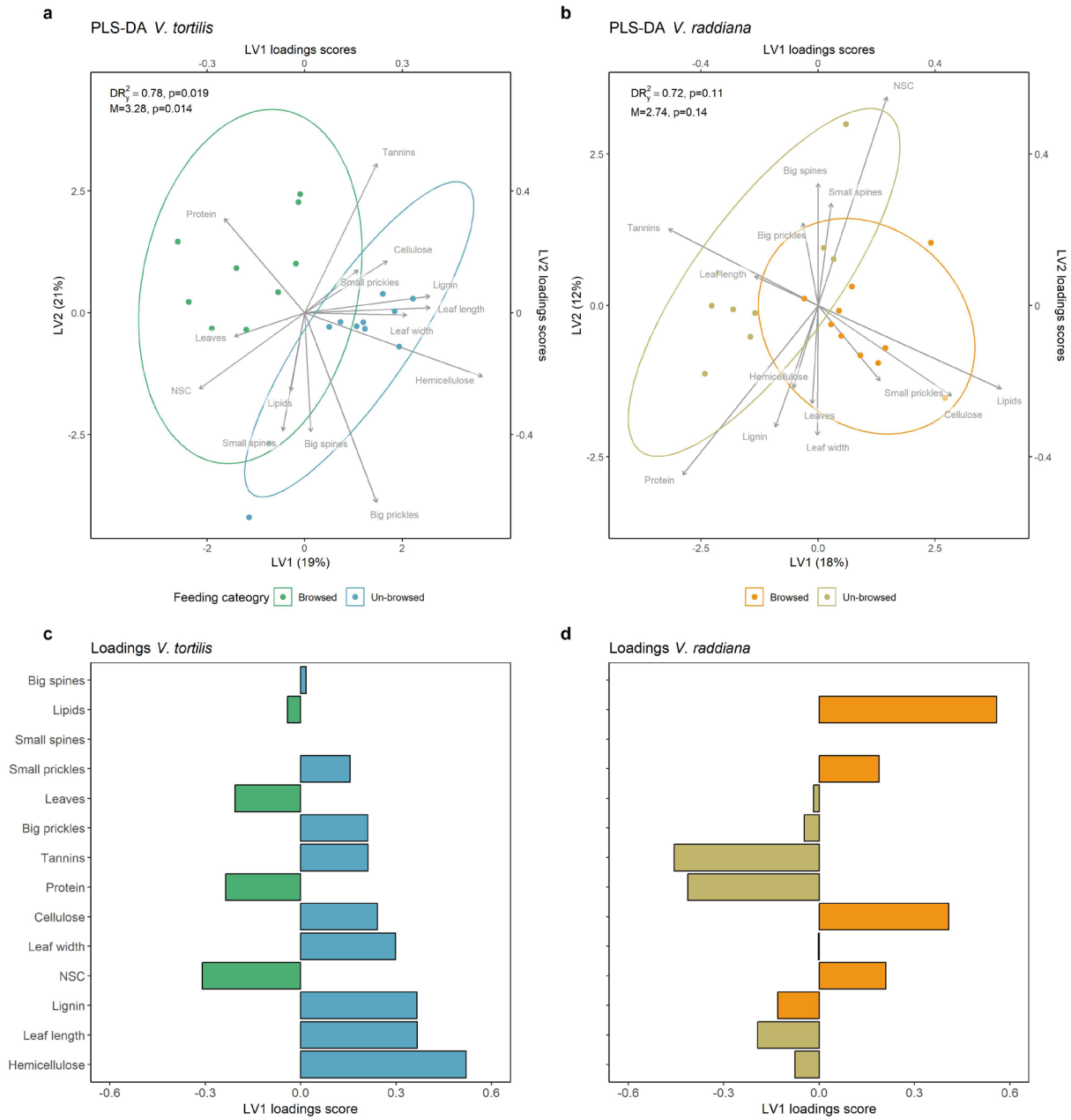

Fig. 6 PLS-DA ordination results. a;b. biplots for both *Vachellia* subspecies. Gray arrow sizes are equivalent to the loading scores for each ordination variable. Percentages on the axes are the variations explained by each. c;d. Loading scores of the first component are colored by the feeding category in which the median is maximum for each variable.

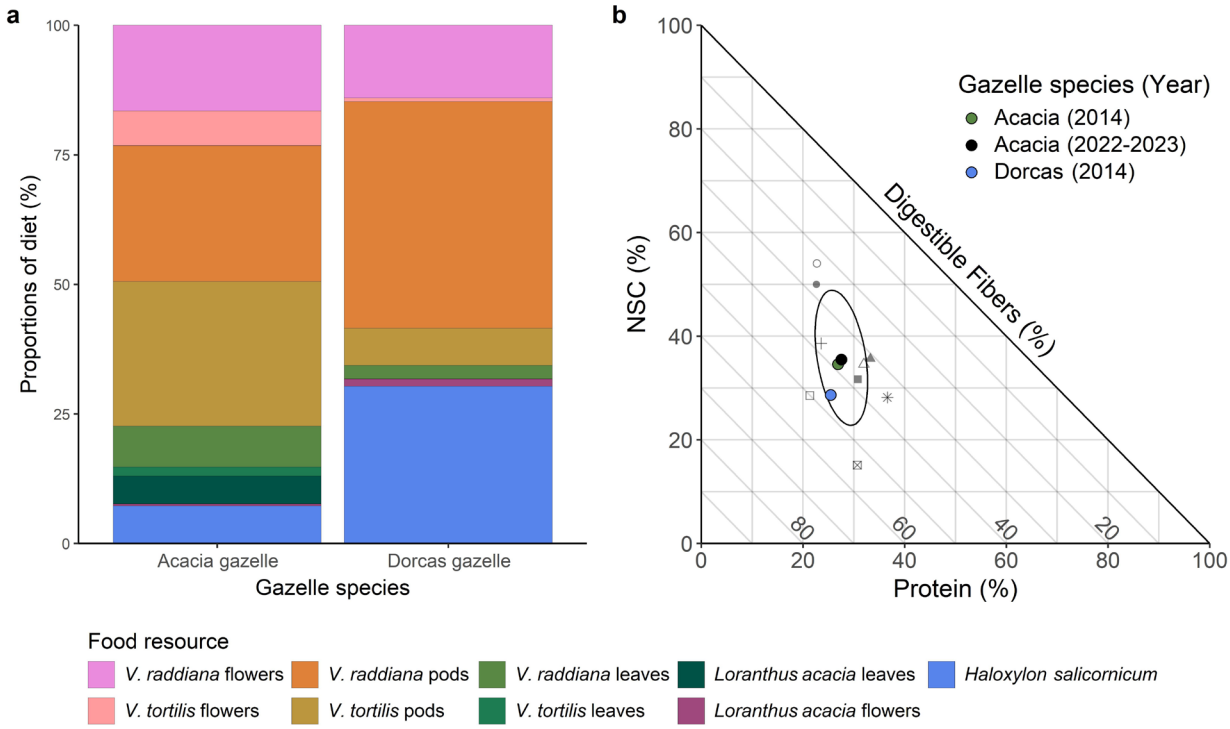

Fig. 7 Comparison of diets (a) and nutritional targets (b) of the two gazelle species. Colored intakes are calculated based on 2014 dietary observations and 2021-2022 mean resources nutritional content for August-October. The black intake and gray food resources are the same as in Fig. 4.

Discussion

Our goal was to reveal the dietary considerations of the critically endangered Acacia gazelle in an attempt to assist population recovery and identify suitable habitats for reintroduction. We found that Acacia gazelles feed almost exclusively on resources from two *Vachellia* trees that differ in their phenology, nutritional composition, and defensive traits. The Acacia gazelles maintained a tight nutritional intake year-round, despite an ever-changing broader nutritional landscape. Specifically, Acacia gazelles regulated protein intake and prioritized consumption of non-structural carbohydrates (NSC). We also found that Acacia gazelles increased their fiber consumption in the cold season at the expense of NSC consumption. Gazelles preferred browsing on *V. tortilis* individuals with higher protein content, more leaves, and lower density of big prickles over trees with more fibers, bigger leaves, and high density of small prickles. Despite a similar preference pattern, we failed to identify what dictates the differential use of *V. raddiana* trees. The diet of Acacia gazelles differed substantially from that of the sympatric Dorcas gazelles. While Acacia gazelles used the two *Vachellia* subspecies and fed from their tree canopy, Dorcas gazelles' diet included more halophytic shrubs and almost no *V. tortilis* resources. Dorcas gazelles ate less from the canopy compared to Acacia gazelles, and used *V. raddiana* resources primarily by collecting them from

356 the ground. Consequently, Acacia gazelle consumed more tannin-rich foods and had to deal
357 with the high density of prickles and thrones, while Dorcas gazelles consumed more salt-rich
358 foods.

359 Acacia gazelle kept a precise multidimensional nutritional intake across seasons despite
360 a broader nutritional landscape and large seasonal fluctuations in the availability of food
361 resources. Protein intake was about 17% across seasons and showed the least variation in
362 comparison to other nutrients. To our best knowledge, such tight regulation of protein
363 consumption in wild herbivores was documented only in primates (Felton et al. 2009c, 2009b;
364 Hou et al. 2021; Takahashi et al. 2021). A common presumption in the herbivore-plant literature
365 is that herbivores must prioritize the consumption of protein-rich foods to fulfill their protein
366 demand (Milton 1979; Mattson 1980; White 1993). This presumption is based on the
367 acknowledged mismatch between the low protein content of many plant resources and the
368 herbivores' high physiological protein demand. We, however, found no evidence that gazelles
369 attempted to maximize protein ingestion to achieve the precise protein intake. We, therefore,
370 suggested that similarly high protein content in many available food resources allows these
371 gazelles to maintain tight protein intake while prioritizing the consumption of other important
372 nutrients (Codron et al. 2007; Felton et al. 2016; Ganzhorn et al. 2017).

373 Acacia gazelles prioritized consumption of NSC-rich foods, such as Vachellia flowers,
374 and aimed to increase NSC intake whenever possible. Prioritization of non-protein energy over
375 protein was observed in primates (Rothman et al. 2011) and in other ungulates (Asher et al.
376 2011; Felton et al. 2016), However, these studies found that attempts to ingest more NSC-rich
377 foods come at the expense of protein regulation. We found that Acacia gazelle can
378 simultaneously maintain a precise protein intake while prioritizing NSC intake. To increase
379 NSC intake, gazelles must feed on both *Vachellia* subspecies that provide flowers and ripe
380 fruits at different times. Consequently, a good habitat for Acacia gazelles must include
381 sufficiently large populations of both *Vachellia* subspecies. *V. raddiana* and *V. tortilis* co-occur
382 mainly along the Jordan Rift Valley, south of the Dead Sea (Halevy & Orshan 1972). This may
383 explain why the historic distribution of Acacia gazelles was limited to this area (Mendelssohn
384 1974), while the distribution of the sympatric Dorcas gazelle is much wider and includes
385 diverse desert habitats (Yom-Tov 2016).

386 The general pattern of maximizing NSC consumption was slightly disrupted by the
387 seasonal changes in fiber consumption. The relative intake of these two carbohydrate sources

388 varied across seasons in association with the monthly average minimal temperature and was
389 affected by resource availability. Gazelles consumed proportionally more structural
390 carbohydrates (digestible fibers; NDF) in the winter and increased intake of non-structural
391 carbohydrates in the warmer seasons. These dietary changes seem intentional since the
392 nutritional landscape allowed tighter regulation of fibers and NSC in both seasons. Our findings
393 coincided with ungulate studies that found higher fiber consumption during cold periods. These
394 studies hypothesized that the increase in fiber consumption is an undesirable outcome of
395 resource scarcity or a costly byproduct of attempts to prioritize consumption of other nutrients
396 (Stolter et al. 2005; Verheyden-Tixier et al. 2008, for example). This realization builds upon a
397 common assumption of browsing theory that higher fiber content characterized by low
398 digestible energy has lower physiological value for herbivores (Milton 1979; Van Soest 1994).
399 Instead, we suggest that increased fiber consumption in cold periods may assist gazelles to
400 thermoregulate. Fermentation of structural carbohydrates produces more heat than that
401 produced by digestion of simple carbohydrates (Armstrong & Blaxter 1956; Cowsert &
402 Montgomery 1969; Reynolds et al. 1991; Van Soest 1994). For example, the heat increment of
403 feeding in white-tailed deer fawns can substitute up to 100% of their thermoregulation
404 requirements. This effect was stronger for fawns that were fed on natural fiber-rich browse than
405 those fed on NSC-rich pellets (Jensen et al., 1999). The domestic livestock literature supports
406 this notion and recommends using lower fiber-to-NSC feed ratio as a way to improve livestock
407 thermoregulation efficiency during warm seasons (John & Webster 1978; West 1999; Conte et
408 al. 2018). Understanding the dietary considerations that are influenced by variations in animals'
409 thermoregulatory needs is crucial for designing artificial diets and preventing adverse
410 consequences of unsuitable supplementary feedings. Future studies should focus on the
411 mechanistic details of this potentially important and thus far largely neglected dietary
412 consideration by manipulating the feed under various climatic conditions and measuring the
413 herbivores' dietary and physiological responses.

414 When examining diets and food preferences researchers often use resource species as a
415 basic unit neglecting intraspecific variability that could be substantial (Lawler et al. 1998;
416 Chapman et al. 2003; Rothman et al. 2012). Acacia gazelles chose to forage on specific trees
417 and ignored others suggesting an intraspecific preference. The preferred *V. tortilis* trees were
418 richer in protein and carbohydrate relative to fibers and had high densities of small leaves and
419 lower densities of prickles relative to trees that were not used. We hypothesized that in their
420 attempt to improve foraging efficiency gazelles consider both the nutritional intake and the

421 feeding costs. Understanding palatability variation across trees is necessary when estimating
422 an area carrying capacity since not all potential resources are being used in similar ways
423 (DeGabriel et al. 2014). Moreover, the nutritional content and chemical and physical defenses
424 are plastic traits that can vary with age and level of browsing pressure that the tree experienced
425 (Gowda 1997; Rohner & Ward 1997; Fornara & Du Toit 2007; Nzimande et al. 2022). High
426 browsing pressure may reduce tree recruitment, altering the stand age structure and may force
427 trees to invest more in anti-browsing defenses. These changes may generate a positive feedback
428 loop in which gazelle may respond to these changes by browsing more on less defended trees.
429 Thus, gazelle may experience nutritional limitations even if the number of trees and the foliage
430 availability may erroneously suggest ample forage. We suggest that nutritional and defense
431 traits of trees should be monitored to prevent such convoluted density-dependent reduction in
432 resource quality and accessibility. This recommendation is especially relevant when the
433 population is limited in space.

434 We found similar intraspecific variation in the use of *V. raddiana* trees but failed to
435 identify what traits are associated with the gazelle preference. *V. raddiana* has higher phenolics
436 and condensed tannins concentrations than *V. tortilis* (Rohner & Ward., 1997), suggesting those
437 chemical compounds may play an important role in *V. raddiana*'s defense against herbivory
438 and may affect gazelles' browsing preference in this subspecies. Our measurements of defense
439 compounds did not allow testing this plausible hypothesis as a more elaborate secondary
440 metabolite profile is required. *V. raddiana* has lower thorn densities and a much bigger leaf size
441 than *V. tortilis*. Thus, these traits may play a much lesser role in predicting gazelle foraging
442 preference in this subspecies. Blank (2005), who also noticed intraspecific variation in
443 *Vachellia* use by Acacia gazelles, attributed this variation to differences in resource abundance
444 (i.e., quantities of flowers and pods). We only used trees that were browsed for leaves during
445 winter to minimize the possible effects of these confounding factors. Nevertheless, resource
446 quantity may still affect our results regarding *V. raddiana* as dry pods can still be present below
447 trees during winter. Future work should consider these potential sources of variation when
448 exploring the intraspecific variation in *V. raddiana* use by Acacia gazelle.

449 The diet of the sympatric Acacia and Dorcas gazelles varied substantially, suggesting
450 limited interspecific competition for food resources. Our continuous observation of Acacia
451 gazelle individual-foraging from the summer of 2014 revealed a similar diet composition and
452 nutritional intake to that observed in the summer of 2022, using a different observation
453 approach. We found that Acacia gazelles consumed relatively high proportions of foliage from

the two *Vachellia* subspecies, ate the abundant parasitic plant *Loranthus acaciae,* and ingested pods of the two *Vachellia* subspecies in similar proportions. In comparison, the diet of the sympatric Dorcas gazelle was dominated by *V. raddiana* pods collected from the ground, a much lower proportion of *V. tortilis* pods, and just a small portion of *V. raddiana* leaves. Halophytic shrubs constituted 30% of the Dorcas gazelle's diet in comparison to only 7.2% percent in the Acacia gazelle's diet. Despite these large dietary differences, the protein intake of the two gazelle species converged to similar values and the intake of carbohydrate sources differed only slightly between the two gazelle species, suggesting similar physiological needs.

Similar physiological needs of sympatric species that are met by ingestion of different diets may suggest dietary niche separation that requires specific adaptations. Acacia gazelles forage high in the canopy by standing only on the hind legs or by leaning with the front legs on low branches (Blank 2005). These gazelles have to cope with high tannin levels and presumably other chemical defenses and avoid the thorns and prickles, especially those of *V. tortilis* that may limit foraging efficiency. On the other hand, Dorcas gazelles mainly consume halophytic plants and dry resources found under *Vachellia* trees and largely ignore resources from *V. tortilis* canopies. Consequently, needing to cope primarily with high salt levels and fluctuating and unpredictable food availability. Altogether our results suggest that the two sympatric gazelle species evolved to consume different diets. Our findings that Acacia gazelles' diet and nutritional intake did not differ before and after the sharp drop in the sympatric Dorcas gazelle population density coincided with this conclusion, suggesting limited inter-specific competition between the two gazelle species.

Our comparative observations were conducted during summer and fall. Thus, our inference of low interspecific competition between the two gazelle species may be limited to these seasons. We also found that Acacia gazelles increased consumption of *V. raddiana* in the winter, possibly intensifying competition with the Dorcas gazelles. However, previous work showed that Dorcas gazelles tend to substantially decrease the use of *V. raddiana* during the winter (Baharav 1980, 1982), supporting our conclusion of dietary niche separation between the two gazelle species. Acacia gazelles specialize in feeding from *Vachellia* trees and switch between subspecies and their resources to maintain a tight nutritional target. Tracking both *Vachellias'* phenology may allow this gazelle species to avoid seasonal nutritional shortages in this unpredictable hyper-arid environment. Moreover, *Vachellia* trees supply resources that are less prone to fluctuations in availability between years compared to annual plants or small perennial shrubs, which other herbivores rely upon. Stability in resource quality and quantity

may support a high reproductive rate allowing Acacia gazelles to calve in all seasons and even twice a year (Shalmon 1991; Mendelssohn et al. 1997; Blank 2000), as we have also observed. Other gazelle species, including the sympatric Dorcas gazelle, exhibit a synchronized seasonal reproduction peak that is tightly timed to match the annual peak in resource availability (Baharav 1983; Yom-Tov 2016). Thus, Acacia gazelles may have greater reproductive potential than Dorcas gazelles, but, are limited to a more specific habitat where the two *Vachellia* subspecies are present.

Conclusions and management implications

We used a nutritional geometry approach to uncover Acacia gazelles' dietary considerations in attempts to guide this critically endangered population's recovery. Acacia gazelles forage predominantly on two *Vachellia* subspecies that provide crucial resources at different times. Acacia gazelle's macro-nutritional intake varied little between months in 2021-2022 and was similar to that observed in the summer of 2014. This enforces confidence in the estimated intake representing nutritional needs and suggests that since Acacia gazelles were able to reach it year-round, currently, the population does not suffer from a nutritional deficiency that requires supplement feeding. However, in case of future needs, identifying this precise intake target may enable managers to provide feed that meets the species-specific needs. Our findings that gazelle alternate fiber and NSC, possibly to improve thermoregulation efficiency may further assist in this effort and should be considered whenever exploring the nutritional ecology of wild ungulates. Acacia gazelles' specialization on *Vachellia* resources suggests a higher reproductive potential than that of other desert ungulates. This specialization, however, also poses a potential obstacle to the population's recovery, since the two *Vachellia* subspecies coexist only in alluvial fans along the Jordan Rift Valley, south of the Dead Sea. This restricted habitat is diminishing in an unprecedented way due to agricultural expansion. Reintroductions of Acacia gazelles may thus necessitate a broader conservation plan to expand the protection of their unique habitat. It was hypothesized that similar physiological needs may induce intense interspecific competition for food between the two sympatric gazelles (Shalmon et al., 2020). Instead, our findings suggest Acacia gazelles feed a different diet than Dorcas gazelles and overall experience low interspecific competition that does not affect their diet or nutrition. Thus, we recommend postponing the seemingly unjustified removal of Dorcas gazelles from the enclosure that may counterintuitively harm the Acacia gazelles by denying potential anti-predatory benefits (e.g., social vigilance, dilution effect) and by potentially reducing selection against plant species that are less important for this species. We also found

that Acacia gazelles selectively feed on certain *Vachellia* individuals and identified the possible traits that affect this selection for *V. tortilis* but not for *V. raddiana*. Since trees subject to different browsing pressures may change the expression of these traits, continuous monitoring is important. We recommend monitoring the *Vachellia* recruitment, canopy height, and defensive traits, to prevent density-dependent limitations and identify otherwise obscured reductions in resources' accessibility and quality. Our case study highlights the benefit of adopting a nutritional ecology approach to guide management plans for endangered wildlife.

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