A recipe for recovery: Diet as a decisive tool in species conservation

Abstract

Animals consume 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*), and compared their diet and nutrition to that of the sympatric *Gazella dorcas,* using behavioral observations coupled with nutritional and secondary metabolite quantification, and morphological measurements of trees. Acacia gazelles mainly consumed resources from two subspecies of the umbrella-thorn acacia (*Vachellia tortilis*) that differ in morphology, nutritional composition, and phenology, and prioritized consumption of specific trees based on their nutritional and defensive traits. Gazelles maintained a narrow nutritional target, tightly regulated their protein intake, and prioritized consumption of non-structural carbohydrates. Dorcas gazelles consumed a very different diet from the Acacia gazelle, but 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 the seemingly low competition between the two gazelle species does not necessitate controlling the Dorcas gazelle population. Our work demonstrates the importance of nutritional ecology as a major conservation tool.

1. 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 and Raubenheimer, 2012). Attempts to meet this target in an ever-changing nutrient landscape may influence animals' spatial activity and behavior (Bazazi et al., 2010; Johnson et al., 2017), and affect their interactions with competitors, natural enemies, and anthropogenic risks (Coogan and Raubenheimer, 2016; Gazzola and Balestrieri, 2020; Kay et al., 2010; Machovsky-Capuska et al., 2019; Nie et al., 2019). Moreover, human activities may alter the abundance, quality, and distribution of food resources (Acevedo-Whitehouse and Duffus, 2009; Fehlmann et al., 2021; Hamann et al., 2021), possibly limiting wild animals from meeting their intake target (Armstrong and Perrott, 2000; López-Bao et al., 2010). Thus, uncovering the dietary and foraging considerations of endangered species in the wild is key to address the challenge of conserving them (Birnie-Gauvin et al., 2017).

We adopted this dietary-centric approach to assist in conserving a critically endangered Acacia gazelle (*Gazella arabica acacia*) population in the Southern Arava, Israel. Acacia gazelles are a genetically unique and geographically isolated population of Arabian gazelles (*Gazella arabica*; Hadas et al., 2015; Fig. 1). This remnant population of about 40 individuals is restricted to two small floodplains, and struggles to recover despite substantial conservation efforts (Blank, 2000, 1996; Polak et al., 2023; Shalmon, 1991). Historical references suggest a much larger distribution before the 1950s, when the entire population was almost extirpated by hunting (Mendelssohn, 1974). However, not enough is known about this historic distribution to predict the gazelles' habitat requirements and locate suitable reintroduction sites. In 2006, the last remaining 13 individuals were enclosed within a predator-proof enclosure, together with 82 Dorcas gazelles (*Gazella dorcas*), which presumably compete with the Acacia gazelles for food. It was hypothesized that nutritional limitations, due to intensifying competition and food shortage, might impede the population’s recovery (Breslau et al., 2020; Shalmon et al., 2020). Thus, revealing the Acacia gazelle's natural diet and nutritional needs, and comparing them to those of the Dorcas gazelle, may allow the development of an effective plan to save this unique population.

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 (Charnov, 1976; Schoener, 1971; 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; Felton et al., 2018, 2009a; Simpson et al., 2004). 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 (DePasquale et al., 2023; Johnson et al., 2017; Raubenheimer et al., 2015; Takahashi et al., 2019), and only rarely to quantify intake targets of other endangered wildlife, including ungulates (Raubenheimer et al., 2014; Spitzer et al., 2023). In these rare cases, the limited ability to directly observe the animal's feeding behavior and to quantify the nutritional composition of foods has led to the development of proxy methods like fecal (Hecker et al., 2021; Nie et al., 2015; 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., 2024, 2023). These proxy methods are informative but ignore temporal and intra-specific variation in the availability and nutritional content of food resources, leading to cruder intake target estimates that are less applicable for management purposes.

Focusing solely on the nutritional composition without considering other food characteristics may produce an incomplete understanding of animals' dietary considerations. 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 (Cooper and Owen-Smith, 1986; Freeland and Janzen, 1974). Consequently, attempts to uncover the dietary strategies of endangered ungulates must include quantification of nonnutritive plant traits that influence food choice.

We addressed many of these methodological considerations by observing the Acacia gazelles' foraging behavior in the field, by collecting samples from all plants consumed and from similar reference resources that were not consumed, and by measuring the morphological

traits and tannin composition of *Vachellia* trees. We characterized the chemical composition of all samples using wet chemistry and Near Infra-Red Spectroscopy (NIRS), and employed the RMT method to estimate the gazelle nutritional intake target. Using a similar protocol, we assessed the Dorcas gazelle diet and intake target, and compared them to those of the sympatric Acacia gazelle.

2. Methods

2.1 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 fluctuations 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 tortilis* subspecies coexist in this site *(V. tortilis tortilis and V. tortilis raddiana).* Locally, the two subspecies exhibit consistent differences in their chemical and morphological traits, and habitat requirements (Halevy and Orshan, 1972; Rohner and Ward, 1997). Moreover, the two trees have very distinct phenology, producing flowers and fruits at different times (Halevy and Orshan, 1973). Thus, we treated the two *Vachellia* trees as two distinct resources, hereafter *V. tortilis* and *V. raddiana.*

An Acacia gazelle population of 35 individuals was first discovered at our study site in 1964. This population was discovered only after all other Acacia gazelle populations in Israel were extirpated. Since then, the Israel Nature and Parks Authority (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, the fence was 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 our field observations (2021-2023) only about 30 Acacia gazelle and about 40 Dorcas gazelle inhabited the enclosure (Polak et al., 2023).

2.2 Gazelle feeding observations and forage sampling

To assess the gazelle diet, we conducted monthly group observations of the gazelles' feeding behavior for a minimum of 3 consecutive days each month. We observed the gazelles' behavior from two hides during their peak foraging activity in the early morning and late afternoon. We recorded the number, age, and sex of feeding gazelles, the feeding time, and whether gazelles were feeding from the ground or from the canopy, along with the exact location and type of each food resource (see Appendix 1 for details). After each observation, we collected samples from all plant resources that were consumed by the gazelles and immediately transferred the samples to our field lab. There, we weighed and oven-dried the samples (60°C, 48 h), and re-weighed them for dry mass estimations. We milled all samples through a 1 mm sieve using a laboratory grinding mill (Kinematica POLYMIX PX-MFC 90D), and stored the milled samples in the freezer until further analyses.

To compare the diet of Acacia gazelles to that of Dorcas gazelles, we used continuous time-budget observations on focal individuals of the two gazelle species. We collected this data in the summer of 2014, prior to the Dorcas gazelle removal, using the same hides as in the 2021-2022 observations.

2.3 Chemical analyses

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

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

We constructed a NIRS model for *Vachellia* leaves and pods of the two subspecies. *Vachellia* flowers, *Loranthus* leaves and flowers, and perennial shrubs were analyzed only by wet chemistry and average nutrient content was applied, due to the low number of samples. For NIRS analyses, we dried all samples for 48h. After homogenizing the sample, we transferred a ~50 mg subsample into a 1 ml clear glass shell vial and scanned each sample using an Antaris II FT-NIR analyzer. We constructed two NIRS models using TQ analyst software. The first model included absolute concentrations of all measured macro-nutrients (Protein, Lipids, NSC, NDF, ADF, and ADL). The second model was for the relative concentration of tannins. NIRS model's protocol and performances are presented in Appendix 2.

2.4 Physical measurements of *Vachellia* trees

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

2.5 Data analysis

We estimated the Acacia gazelles' nutritional target and resources' composition using a RMT (Raubenheimer, 2011), of the relative contents of the three main macro-nutrients in the

gazelle diet – Protein, NSC, and digestible fibers (calculated as NDF-ADL). We calculated the daily nutritional target by multiplying each observation unit's (plant) nutritional values with the time and number of gazelles spent feeding from it divided by the total daily feeding time. To unravel gazelle regulation and prioritization of different macro-nutrients we conducted a permutation test for the gazelles' intakes. We summarized each food resource's mean nutritional concentrations and its total feeding time within each observation session. Then, we permuted these feeding times.

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

For the morphological traits measured, we averaged all traits for all branches of each tree. We analyzed the thorns data using counts within two length categories (with a 5 mm cutoff), resulting in four thorns categories. Nutritional data were obtained for each tree from the NIRS model predictive results, except for two *V. raddiana* trees which did not have sufficient nutritional data and were therefore removed from this analysis. We used PCA to evaluate inter-specific variance between *Vachellia* subspecies. To uncover differences between browsing categories we applied a separate PLS Discriminant Analysis (PLS-DA, Barker & Rayens 2003) within each *Vachellia* subspecies since the PCA revealed a large inter-specific variability. We standardized the data 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). Last, we estimated each variable importance by randomly permuting it and conducting the same analyses. 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). 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).

3. 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. 2a). 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).

The two *Vachellia* subspecies differed substantially in their chemical and physical characteristics. *V. raddiana* trees had bigger leaves, while *V. tortilis* trees had higher densities of prickles, and higher concentrations of proteins and lipids in the leaves (Fig. S2). PCA results revealed high intra-specific variability in spine 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. 2b, 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. S3). This tight intake target

was reached despite substantial differences in resource availability (Fig. 3, Fig. 2). 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. S4). Similarly, we observed no selective feeding for digestible fibers (p=0.29, Fig. S4). However, the permutations test revealed 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). During summer, gazelles increased their relative NSC intake by prioritizing *V. tortilis* NSC-rich flowers (Fig. 2). Still, gazelles kept their tight protein intake by consuming *V. raddiana* pods and leaves from both *Vachellia* 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. S5). The browsed and un-browsed *V. tortilis* trees differed substantially (Fig. 4a, M_d=3.28, p=0.014). The variation in the browsing category explained by the model was 75%-78% 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. 4a,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 (Fig. 4b). Using raw analytical fiber fractions instead of the nutritionally calculated fractions slightly decreased the performances of both models, but it remained significant for *V. tortilis* (Fig. S6).

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. 5a). Acacia gazelles fed more on the foliage from both *Vachellia*s, 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. 5a). 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 Dorcas gazelles (Fig. 5b). 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. 5b), 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 gazelles' diet, had higher Na, Mg, and K content (Table S4), hence also significantly higher ash content compared to all 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 consumed higher quantities of tannins and less salt than Dorcas gazelles.

4. Discussion

Our goal was to reveal the dietary considerations of the critically endangered Acacia gazelle 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). Gazelles preferred browsing on *V. tortilis* individuals with higher protein content, more leaves, and lower density of big prickles over trees with bigger and more fibrous 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 canopies, Dorcas gazelles' diet included more halophytic shrubs and almost no *V. tortilis* resources. Both gazelles consumed *V. raddiana* resources, but Dorcas gazelles ate primarily from the ground and less from the canopy compared to Acacia gazelles.

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

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

When examining diets and food preferences researchers often use resource species as a basic unit, neglecting intraspecific variability that could be substantial (Chapman et al., 2003; Lawler et al., 1998; Rothman et al., 2012). Acacia gazelles chose to forage on specific trees and ignored others, likely due to intraspecific variation in tree traits. The preferred *V. tortilis* trees were richer in protein and NSC relative to fibers and had high densities of small leaves and lower densities of prickles relative to the un-browsed trees. We hypothesized that in their

attempt to improve foraging efficiency, gazelles consider both the nutritional intake and the feeding costs. Understanding palatability variation across trees is necessary when estimating an area carrying capacity since not all potential resources are being used in similar ways (DeGabriel et al., 2014). Moreover, the nutritional content and chemical and physical defenses can vary with tree age and in response to browsing pressure (Fornara and Du Toit, 2007; Gowda, 1997; Nzimande et al., 2022; Rohner and Ward, 1997). Thus, gazelles may experience nutritional limitations even if the number of trees and the foliage availability may erroneously suggest ample forage. We suggest that the nutritional and defensive traits of trees should be monitored to prevent such convoluted density-dependent reduction in resource quality and accessibility. This recommendation is especially relevant when the population is fenced.

The diet of the sympatric Acacia and Dorcas gazelles varied substantially, suggesting limited interspecific competition for food resources. Our continuous observation of Acacia gazelle individual-foraging from the summer of 2014 revealed a similar diet composition and nutritional intake to that observed in the summer of 2022 using a different observation approach. We found that Acacia gazelles consumed foliage, flowers, and pods from the canopy of the two *Vachellia* subspecies, and ate the abundant parasitic plant *Loranthus acaciae*. In comparison, the diet of the sympatric Dorcas gazelle included almost exclusively *V. raddiana* resources collected from the ground. Halophytic shrubs constituted 30% of the Dorcas gazelle's diet in comparison to only 7.2% in the Acacia gazelle's diet. Despite these large dietary differences, their protein intake converged to similar values, and their intake of carbohydrate sources differed only slightly between the two gazelle species, suggesting similar physiological needs.

Similar physiological needs of sympatric species that feed on 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 spines and prickles, especially those of *V. tortilis*. On the other hand, Dorcas gazelles need to cope with high salt levels and fluctuations in food availability. Our results suggest that the two sympatric gazelle species evolved to consume different diets, hence experience low interspecific competition. 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 coincide with this conclusion.

Our comparative observations were conducted during summer and fall. Thus, our inferences 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, 1982, 1980), 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 *Vachellia*s' 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. 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 (Blank, 2000; Mendelssohn et al., 1997; Shalmon, 1991). 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.

4.1 Conclusions and management implications

We used a nutritional geometry approach to uncover Acacia gazelles' dietary considerations in attempts to guide conservation efforts. Acacia gazelles forage predominantly on two *Vachellia* subspecies that provide crucial resources at different seasons. 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. Acacia gazelles' specialization on *Vachellia* resources 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

411 gazelles (Shalmon et al., 2020). Instead, our findings reveal low interspecific competition
412 between the two gazelles. Thus, we recommend postponing the seemingly unjustified removal
413 of Dorcas gazelles from the enclosure that may counterintuitively harm the Acacia gazelles by
414 denying potential anti-predatory benefits (e.g., social vigilance, dilution effect). We also found
415 that Acacia gazelles selectively feed on certain *Vachellia* individuals and identified the possible
416 traits that affect this selection for *V. tortilis* but not for *V. raddiana*. Since trees subject to
417 different browsing pressures may change the expression of these traits, continuous monitoring
418 is important. We recommend monitoring the *Vachellia* recruitment, canopy height, and
419 defensive traits, to prevent density-dependent limitations and identify otherwise obscured
420 reductions in resources' accessibility and quality. Our case study highlights the benefit of
421 adopting a nutritional ecology approach to guide management and reintroduction plans for
422 endangered wildlife.

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Figures:

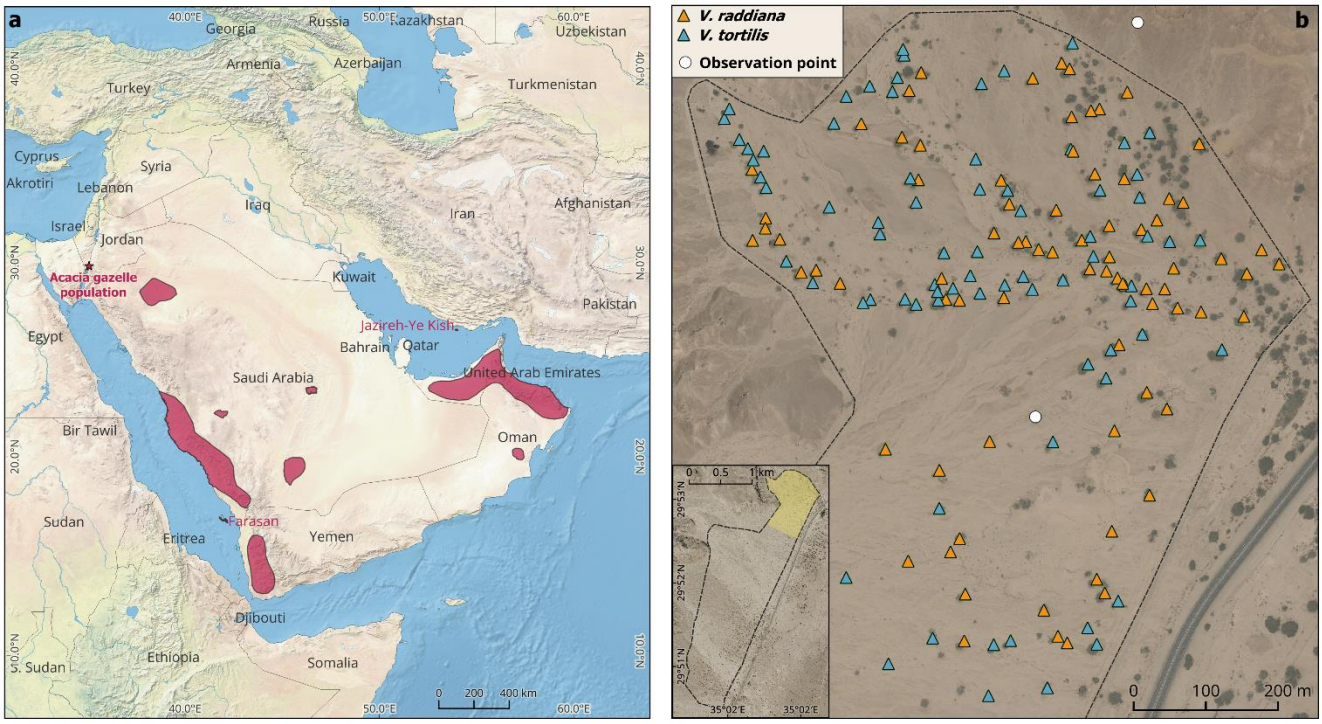

Fig. 1 Study site locality map. (a) Distribution of *G. arabica* populations (IUCN SSC Antelope Specialist Group., 2017). The studied Acacia gazelle population is marked with a star. (b) Acacia gazelle enclosure. The entire enclosure (bottom left) is presented with emphasis on the northern part (enlarged and highlighted), where most observations were conducted. The perimeter fence is marked with a dashed line. Triangles are the trees observed and sampled, colored by *Vachellia* subspecies. The two hides used for observations are marked with white circles. The Internal hide was used during morning sessions, and the external hide was used during evening sessions.

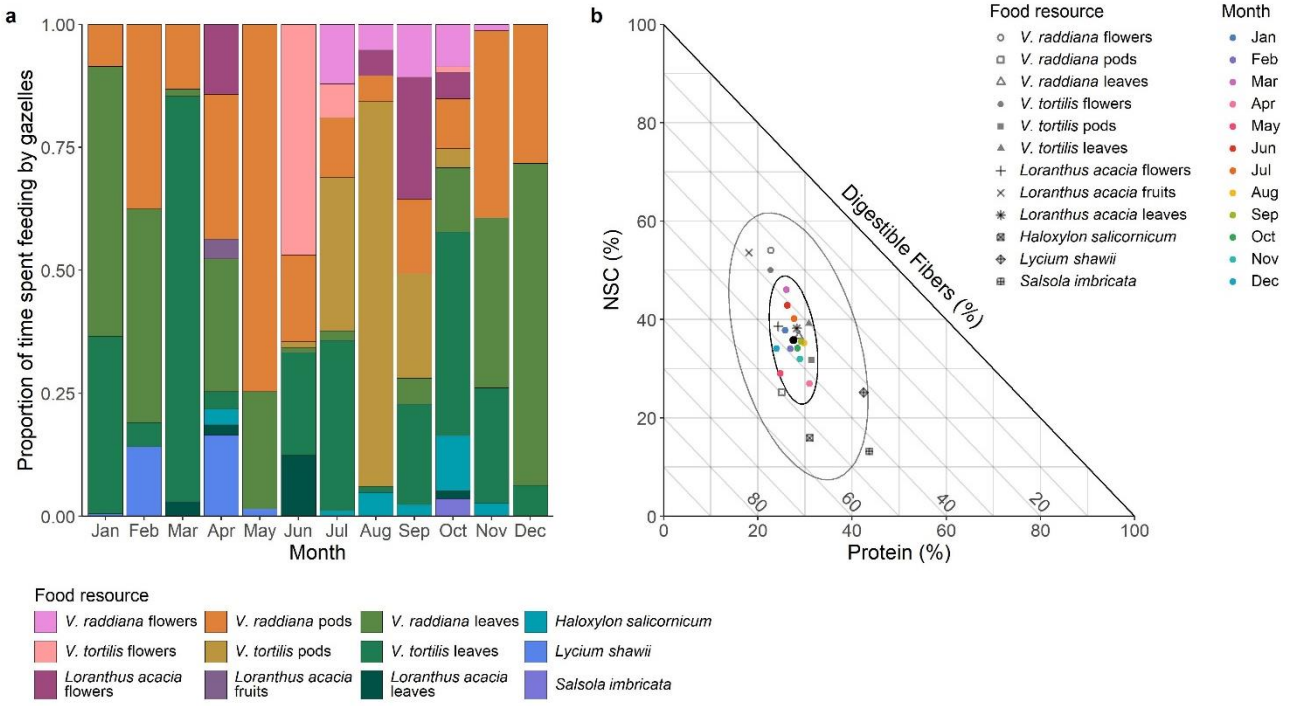

Fig. 2 Diet & nutrition of Acacia gazelles. (a) Distribution of food resources' monthly utilization. (b) Right-angled Mixture Triangle (RMT) of the relative concentrations of the three major macro-nutrients in the Acacia gazelles' diet – Digestible fibers (hemicellulose+cellulose), non-structural carbohydrates (NSC), and protein. Diagonal (Z) axis values are written in italics above the X-axis. Mean monthly intakes are colored by month and the mean annual intake is in black. In gray are the mean annual nutritional values of the different food resources in the gazelle diet. Ellipses represent the 95% confidence interval of the mean intake in black, and the mean nutritional value of all resources in gray.

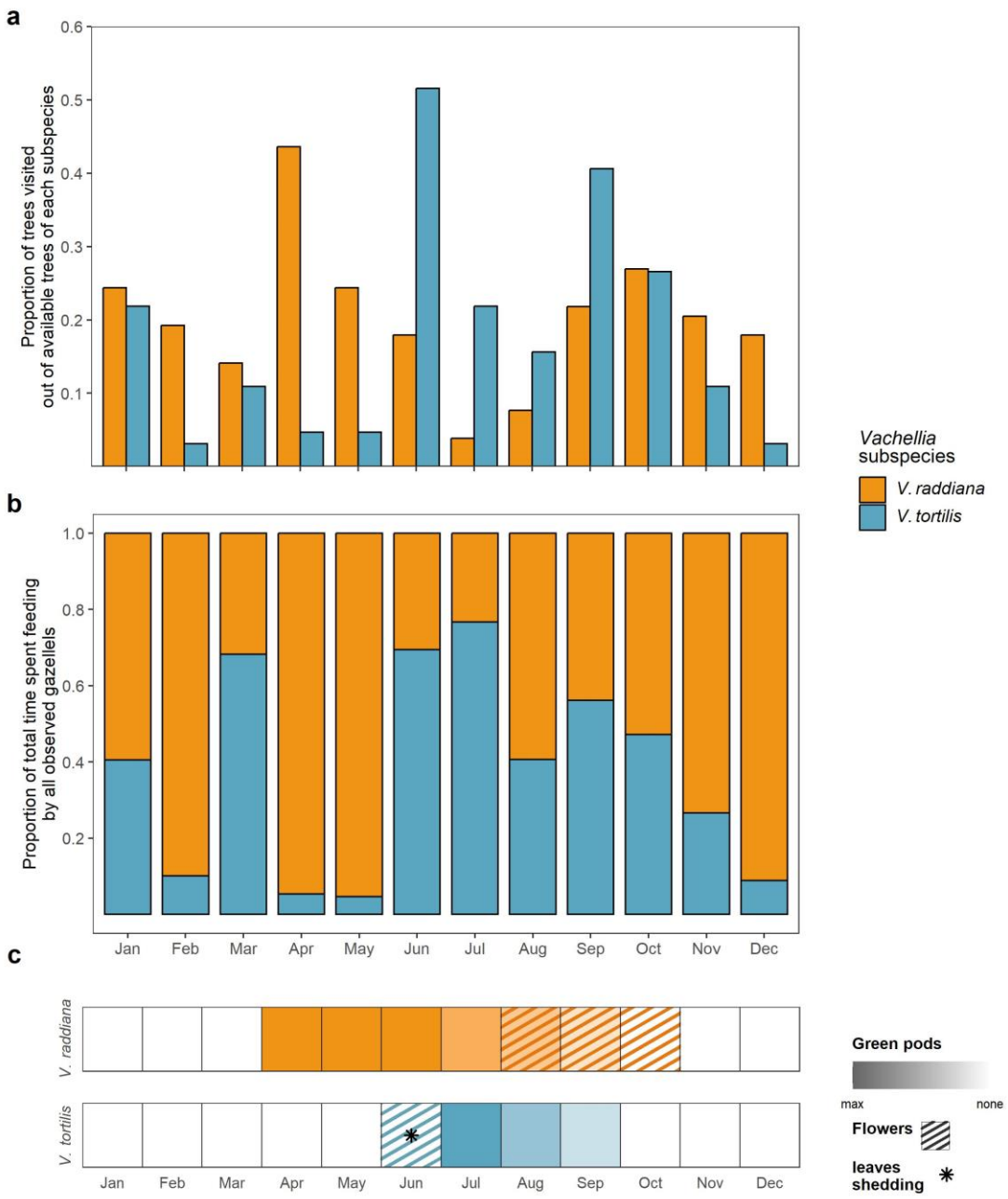

Fig. 3 Acacia gazelles' response to *Vachellia* phenological changes. (a) The number of different trees utilized of each subspecies out of the total trees of that subspecies identified in the northern part of the enclosure. (b) Proportional time spent each month feeding from each *Vachellia* subspecies.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

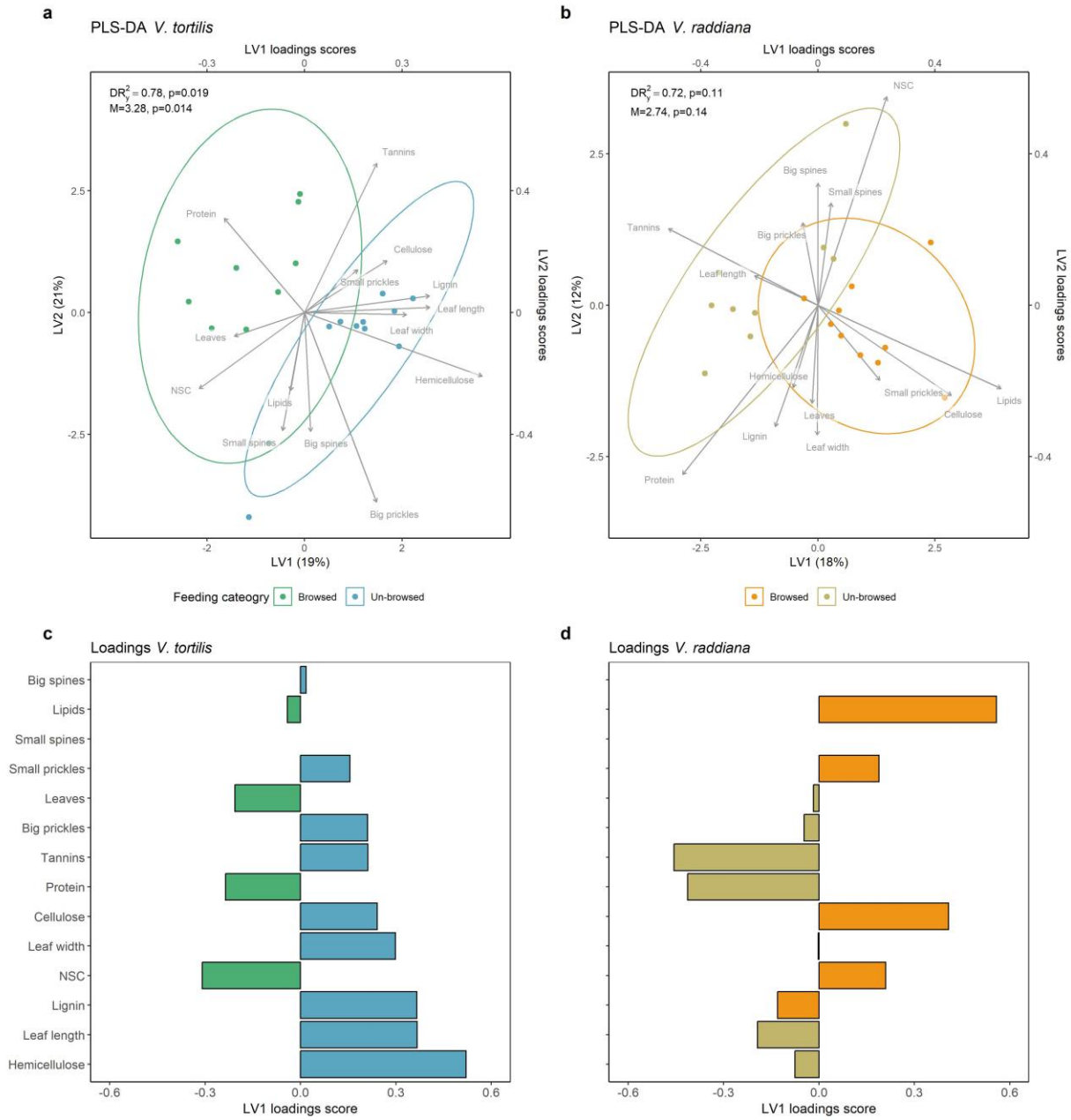

Fig. 4 PLS-DA ordination results. a;b. biplots for both *Vachellia* subspecies. Gray arrow sizes are equivalent to the loading scores for each ordination variable. Percentages on the axes are the variations explained by each. c;d. Loading scores of the first component are colored by the feeding category in which the median is maximum for each variable.

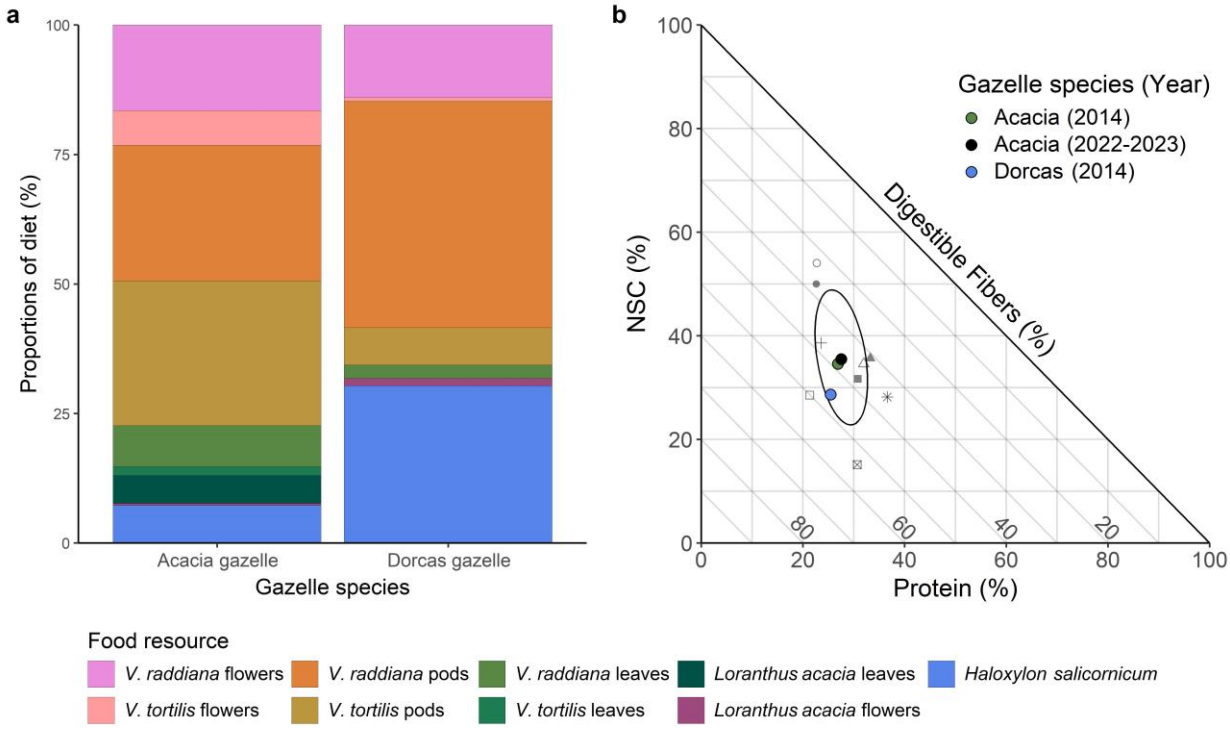

Fig. 5 Comparison of diets (a) and nutritional targets (b) of the two gazelle species. Colored intakes are calculated based on 2014 dietary observations and 2021-2022 mean resources nutritional content for August-October. The black intake and gray food resources are the same as in Fig. 2b.