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Testudo graeca graeca feeding ecology in an arid and overgrazed zone in Morocco

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Abstract

Terrestrial chelonians of arid regions are frequently faced with highly variable food quality and/or quantity and these problems could be aggravated in overgrazing areas. Then, it is crucial for species conservation to possess precise data on feeding ecology. In this paper, we provide the first quantitative data on *Testudo graeca graeca* feeding ecology, in the central Jbilets (Morocco). Diet composition was obtained by faecal analysis and compared to plant assemblages in the field. Interestingly, *T. g. graeca* seems rather a specialist herbivorous tortoise. The five main plant species found in faecal samples (*Leontodon saxatilis* (Asteraceae); *Malva parviflora* (Malvaceae); *Astragalus cruciatus*, *Medicago hispida* and *Lotus arenarius* (Fabaceae)) represent 70% of the identified material and are highly preferred whereas several other plant species, common in the field (e.g. *Eryngium ilicifolium* (Ombellifereae); *Emex spinosus* (Polygonaceae); *Spergula flaccida* Caryophyllaceae)) are actively avoided. Fabaceae made up 27% of the diet and may be important forbs in the diet of terrestrial tortoise owing to their high nutritional value. The diet composition of *T. g. graeca* suggests that diet overlap may occur between domestic ungulates and tortoises in overgrazed landscape and could

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generate a competition context. However, *T. g. graeca* seems to focus its foraging effort under the spiny shrubs where the impact of overgrazing is strongly attenuated.

Keywords: Diet selection; Faecal analysis; Herbivory; Spur thighed tortoise; Competition

1. Introduction

The Mediterranean Spur-thighed tortoise *Testudo graeca graeca* is the unique terrestrial tortoise in Morocco. Populations have declined substantially by habitat changes due to human activities (e.g. agriculture, overgrazing, deforestation) (Bayley and Highfield, 1996; Slimani et al., 2001). Various studies have already been conducted on population dynamics (Bayley and Highfield, 1996; El Mouden et al., 2001; Slimani et al., 2001), general ecology (Lambert, 1969, 1981, 1983), geographic variations (Highfield, 1990a, b) and impact of trade (Highfield, 1994; Bayley and Highfield, 1996). Unfortunately, food habits are still poorly known and limited to brief notes in the literature (Cobo and Andreu, 1988; Highfield, 1989; Bayley and Highfield, 1996; Andreu et al., 2000). Precise qualitative and quantitative information about tortoise feeding ecology are nevertheless fundamental to conservation purpose in overgrazing area.

Several methods have been developed to evaluate the composition of herbivore diets: direct observation of animal foraging behaviour, and indirect methods of dietary reconstitution (alkane technique, stomach and faecal analysis). The direct observation of animals, when possible, is the more accurate sampling method but is exposed to several potential problems. It could be very difficult to identify precisely the items consumed by an individual and the presence of the observer can change the behaviour of animals (Gordon, 1995). This method is classically time-consuming and the observer can only sample a small number of individuals at a time (Gordon, 1995). This problem is particularly cumbersome to study Testudines species due to their sporadic activity and infrequent foraging behaviour (Lagarde et al., 2002, 2003). Nevertheless, direct observations of free ranging tortoises can be relatively straightforward and fruitful for diet and diet selection analysis, especially for desert tortoises (Jennings, 1993, Lagarde et al., 2003). Unfortunately, tortoises often forage under dense vegetation cover, and are therefore very difficult to observe. Then, indirect methods of feeding analysis provide helpful surrogates.

The faecal analysis method is the more widely used technique for determining herbivore diets indirectly (Baumgartner and Martin, 1939; Hercus, 1960; Stewart, 1967; Sparks and Malechek, 1968; Chapuis, 1980; Varva and Holechek, 1980; Garcia-Gonzalez, 1984; Macdonald and Mushinsky, 1988; Milton, 1992; Mason et al., 1999; Loehr, 2002). This technique can provide useful information on qualitative and quantitative aspects of herbivore diets (Chapuis and Didillon, 1987) despite the potential bias due to differential digestibility of plant species (Stewart, 1970; Varva et al., 1978; McInnis et al., 1983).

Then, the aim of our study is to give preliminary results about feeding ecology and diet diversity of *T. g. graeca* in an arid and overgrazed area in Morocco, using the faecal analysis technique.

2. Materials and methods

2.1. Study area

The study site is a 33 ha area located in the central Jbilet mountains about 25 km north of Marrakech, in the western of Morocco (31°37′N, 8°02′W, altitude: 580 m above sea level). The study site is located in an arid region, with mean annual rainfall of about 240 mm and most precipitation occurring between September and February (El Mouden et al., 1999; Znari et al., 2002). Average air temperature in the hottest month (July) can reach 39 °C and the minimal annual temperature is normally above 0 °C (Emberger, 1933; Le Houérou, 1989). Vegetation consists mainly in spreaded bushes of Jujube (*Ziziphus lotus*), with some widely separated Acacia (*Acacia gummifera*) (typical arid vegetation) and Retams (*Retama monosperma*). Most of habitat is open, hard bare ground with stony soils on the flats and low hillsides that surround small sandy, pebbly or stony wadis (riverbeds). Seasonal over-grazing by domestic livestock (sheep and goat) strongly affects the vegetation structure. A simple visual inspection of study area reveal two major and different plant assemblages: a relatively rich and diversified plant community under Jujube, protected against over-grazing by the spiny structure of this shrub, and a lesser diversified plant community out of the Jujube, with a low percent of plant cover.

2.2. Vegetal cover

The study was performed in spring 2002 (May–June), during the period of maximum activity for tortoises. All plant species represent in the study area were collected and identified at the species level, with the help of previous botanical studies (Nègre, 1961, 1962; Quezel and Santa, 1962, 1963).

To describe the vegetation structure, the percentage of plant cover for each species was measured in 43 quadrats (1 m^2) placed at 100 m from each other along six parallel lines established in the study area. Nine quadrats were sampled under jujube shrubs, 34 quadrats were set up out of the jujube shrubs, broadly reflecting the actual proportion occupied by each major types of habitat in the study site.

2.3. Faecal analysis

Captured animals were considered as juveniles when midline carapace length was less than 100 mm (Slimani et al., 2001), the minimum size observed at maturity. Adult were sexed using classical dimorphic characters for *Testudo* (Andreu et al., 2000; Bonnet et al., 2001; El Mouden et al., 2001). The faecal samples were obtained during the animal's manipulation and collected with a metallic pincer disinfected with alcohol in order to avoid diseases and parasites transmission between individuals.

To allow species recognition of faecal plant fragments, a reference collection of upper, lower leaves and caudal epidermis were realized. Epidermises were obtained by mechanical separation on fresh plant material with a scalpel under a microscope. Then, each fragment were placed in potassium chloride for 10 min, rinsed in distilled water, mounted on microscope slides and photographed under an optic microscope (320 ×).

A total of 44 faeces were collected during the study period (seven juveniles, 19 males, 18 females). The faecal samples were stored in alcohol until analysis. In order to eliminate the effect of fragment size, each faecal sample was ground in a mortar and then passed through 0.8 and 0.4 mm sieves. The 0.4 and 0.8 fraction was dispersed in 50% glycerine solution. Three microscope slides were prepared for each sample and examined at 100 × and/or 200 × magnification under an optical microscope by two observers. Three horizontal traverses (2 × 60 mm) were scanned with 2 mm between traverses. The fragments in each traverse were identified to species level by comparing them to the reference collection, using epidermal characteristics (shape, size and arrangement of epidermal cells, stomata and hairs) and counted. The three slides results for each sample were pooled. The total fraction of unknown fragments remains low ($7 \pm 3.5\%$).

2.4. Statistics

Due to small sample sizes and to the absence of normality in the distribution of the data, we used Kruskall Wallis tests to compare the numbers of plant species and the percentages of plant cover under and out of the jujube plant communities.

The data collected from faecal analysis were explored in two separate ways (1) the frequency of occurrence which was the proportion of faecal samples containing a given plant species and (2) the percent of each plant species in the diet. The proportion (p_i) of a given plant species 'i' in tortoise's faeces was calculated as the percentage of the number of epidermis fragment for each plant species relative to the total of the number of epidermis fragment we counted. Then, we calculated the mean p_i in tortoise's faeces for males, females and juveniles. Similarly, taxonomic availability in the study site (q_i) was calculated as the percentage of plant cover for each plant species relative to the total percentage of plant cover for each quadrat. Then, we calculated the mean q_i for the 43 quadrats we collected, and separately the mean q_i for quadrat under Jujube and quadrat out of Jujube. We used Hunter's index ($H_i = p_i/q_i$, Hunter, 1962) to distinguish preferred ($H_i > 1$) from avoided plant species ($H_i < 1$). Preference or avoidance were considered as statistically significant if the 95% confidence limits of mean p_i did not overlap the confidence limits of mean q_i. This statistical procedure was preferred to a simple contingency table with χ^2 tests because it takes into account the spatial heterogeneity of the vegetation and inter individual diet heterogeneity (Lagarde et al., 2003). The proportional similarity index (PSI = $1\text{-}0.5\ \Sigma_i|p_i - q_i|$) of Feisinger et al. (1981) was used to estimate to what extent *T. g. graeca* is a specialized or generalized diet. PSI can range from 1 when animals consume any plant at their disposal to minimal 'q_i' when they narrowly select their food (Feisinger et al., 1981).

Mean values were given with their standard deviation, and differences were considered statistically significant at $P<0.05$. All statistical tests were performed using Statistica 5.1.

3. Results

3.1. Spatial variations in plant community

We identified 88 different plant species in our study area. The vegetation structure strongly diverged between quadrats performed under (UJ) and out of the Jujube (OJ). The mean plant species number and the total percent of recovery were significantly higher in UJ quadrats (mean = 90.2%) than in OJ quadrats (mean = 36.7%, Table 1). Species assemblage differed strongly between the both plant communities (Table 2).

3.2. Diet composition and food selection

We identified 34 different plant species in *T. graeca* diet. Because of the absence of significant differences between males, females and juveniles faecal samples, the results were pooled for subsequent analysis. Some invertebrate (insects and molluscs) fragments were found in 21% of faeces analysed.

Hunter's index calculation (Table 3) and the comparisons of the 95% confidence limits of mean p_i and of mean q_i (Table 2) suggest that eight plant species were significantly preferred and seven plant species significantly avoided (Table 2). The five main plant species recovered in faeces (*Leontodon saxatilis* (Asteraceae); *Malva parviflora* (Malvaceae); *Astragalus cruciatus*, *Medicago hispida* and *Lotus arenarius* (Fabaceae) represented about 70% of the identified material (Table 2). *L. saxatilis* seemed to be the most commonly consumed item (28%) followed by *M. parviflora* and *A. cruciatus* (15% each); these three species were regularly recorded (in more than 75% of the faeces analysed). *T. g. graeca* showed marked preferences for these five species, *Scorpiurus sulcata* was also a very common food item (Tables 2 and 3).

Table 1
Comparison between plant communities under and out of the jujube

	Under jujube	Out of jujube	K–W-test
Number of plant species	17.1 ± 7.3 (7–31)	10.9 ± 3.5 (4–19)	**5.98; $P = 0.01$**
Percentage of plant cover	90.2 ± 24.1 (48.8–112.0)	36.7 ± 17.1 (10.9–90.2)	**16.98; $P < 0.001$**

The mean number of plant species and the mean percentage of vegetation cover were given ± SD with min-max in parentheses. Kruskall–Wallis statistics were given in boldface when significant differences were detected between plant communities.

Table 2
Mean (±SD) plant availability (% of total vegetation cover) in the study site and percentage of species in the diet of *Testudo graeca graeca* during the spring 2002

Taxon	% of plant cover			Faecal samples		
	Total plant cover	Under jujube	Out Jujube	Mean number of fragments	Occurrence	% of occurrence
Aizoaceae						
Aizoon hispanicum	1.15±6.80(−0.89–3.18)	1.02±2.47(−0.06–2.63)	0.08±0.42(−0.06–0.23)	0.03±0.12(0.00–0.07)	3	6.8
Aizoon canariense	**26.11±27.92(17.76–34.45)**	2.53±4.05(−0.12–5.17)	**32.32±28.78(22.65–42.00)**	**0**	0	0
Alsinoideae						
Spergula flaccida	**3.53±7.06(1.42–5.64)**	**8.80±10.25(2.11–15.50)**	**1.75±3.00(0.74–2.76)**	**0.10±0.41(−0.02–0.22)**	5	11.4
Caryophyllaceae						
Fagonia cretica	1.06±4.00(−0.13–2.26)	5.25±9.34(−0.85–11.35)	0	0.03±0.20(−0.03–0.09)	1	2.3
Spergularia marginata	2.75±7.10(0.63–4.87)	2.13±5.12(−1.21–5.48)	3.07±8.05(0.36–5.77)	7.30±11.26(3.97–10.63)	36	81.8
Chenopodiaceae						
Chenopodium murale	0.27±0.76(0.05–0.50)	**1.77±2.49(0.14–3.39)**	0.02±0.12(−0.02–0.06)	0.02±0.11(−0.02–0.05)	1	2.3
Asteraceae						
Anacyclus radiatus	**1.51±2.73(0.69–2.33)**	**8.05±11.76(0.37–15.73)**	**0.74±0.99(0.41–1.08)**	**0**		0
Calendula algeriensis	0.38±1.21(0.02–0.75)	1.52±2.37(−0.02–3.07)	0.09±0.38(−0.03–0.22)	0.05±0.34(−0.05–0.15)	1	2.3
Leontodon saxatilis	**0.99±2.56(0.23–1.76)**	**1.14±3.42(−1.09–3.37)**	**0.97±2.31(0.19–1.74)**	**27.91±18.37(22.48–33.33)**	42	95.5
Scolymus hispanicus	**0.65±1.91(0.08–1.22)**	**2.31±3.37(0.10–4.51)**	0.23±1.13(−0.15–0.61)	**0**	0	0
Asteraceae sp	0.46±2.05(−0.15–1.07)	2.19±4.21(−0.56–4.94)	0	0	0	0
Convolvulaceae						
Convolvulus althaeoides	0.22±1.13(−0.12–0.56)	1.08±2.41(−0.49–2.66)	0	0	0	0
Brassicaceae						
Biscutella didyma	0.38±1.72(−0.13–0.89)	0.81±2.06(−0.54–2.15)	0.03±0.15(−0.02–0.08)	1.21±4.37(−0.08–2.50)	14	31.8
Sinapsis arvensis	0.37±1.57(−0.01–0.84)	2.66±4.83(−0.50–5.81)	0	0	0	0
Notoceras bicorne	**1.14±1.56(0.67–1.60)**	1.76±2.04(0.42–3.09)	**1.12±1.50(0.62–1.63)**	**2.92±4.19(1.69–4.16)**	32	72.7
Geraniaceae						
Erodium guttatum	0.27±1.16(−0.08–0.62)	1.25±2.49(−0.38–2.88)	0.02±0.13(−0.02–0.07)	0.01±0.06(−0.01–0.03)	1	2.3
Fabaceae						
Medicago hispida	**0.05±0.20(−0.01–0.11)**	**0.11±0.25(−0.05–0.27)**	**0.04±0.22(−0.04–0.11)**	**5.75±9.85(2.84–8.66)**	36	81.8
Medicago laciniata	**12.52±14.59(8.16–16.88)**	2.61±3.30(0.46–4.77)	**14.29±16.70(8.68–19.90)**	**1.27±5.33(−0.30–2.85)**	5	11.4

Table 2 (*continued*)

Taxon	% of plant cover			Faecal samples		
	Total plant cover	Under jujube	Out Jujube	Mean number of fragments	Occurrence	% of occurrence
Astragalus cruciatus	**0.02 ± 0.11(−0.01–0.06)**	**0.08 ± 0.24(−0.08–0.23)**	**0.01 ± 0.05(−0.01–0.03)**	**14.37 ± 18.02(9.04–19.70)**	34	77.3
Lotus arenarius	**0.09 ± 0.36(−0.02–0.20)**	**0.00**	**0.12 ± 0.42(−0.02–0.27)**	**3.57 ± 5.96(1.81–5.33)**	25	56.8
Scorpiurus sulcata	**0.06 ± 0.29(−0.03–0.14)**	**0.00**	**0.07 ± 0.32(−0.04–0.18)**	**2.37 ± 5.58(0.72–4.01)**	18	40.9
Malvaceae						
Malva parviflora	**1.09 ± 4.62(−0.29–2.47)**	**2.34 ± 2.74(0.55–4.13)**	**0.96 ± 5.15(−0.77–2.69)**	**15.22 ± 14.79(10.85–19.58)**	38	86.4
Ombellifereae						
Eryngium ilicifolium	**20.21 ± 16.68(15.23–25.20)**	**7.83 ± 6.68(3.46–12.19)**	**23.33 ± 18.16(17.22–29.43)**	**0**	0	0
Ammi majus	0.40 ± 1.61(−0.08–0.88)	1.92 ± 3.22(−0.18–4.02)	**0**	**0.27 ± 0.64(0.08–0.45)**	12	27.3
Plantaginaceae						
Plantago amplexicaulis	**0.15 ± 0.64(−0.04–0.34)**	1.24 ± 2.62(−0.47–2.95)	**0**	**2.82 ± 4.84(1.39–4.25)**	28	63.6
Polygonaceae						
Emex spinosus	**7.20 ± 10.30(4.12–10.28)**	2.92 ± 3.74(0.47–5.36)	**8.93 ± 11.29(5.13–12.73)**	**0.40 ± 1.20(0.05–0.76)**	11	25.0
Scrophulariaceae						
Linaria sagittata	0.49 ± 3.24(−0.47–1.46)	2.36 ± 7.08(−2.26–6.98)	0	0	0	0
Linaria bipartita	0.40 ± 0.91(0.13–0.67)	0	0.54 ± 1.08(0.18–0.91)	0.11 ± 0.76(−0.11–0.34)	1	2.3
Solanaceae						
Solanum nigrum	0.58 ± 3.77(−0.55–1.70)	4.27 ± 12.82(−4.10–12.65)	0	0	0	0
Poaceae						
Festuca sp.	3.19 ± 5.84(1.45–4.94)	**0.06 ± 0.13(−0.03–0.15)**	**3.75 ± 5.29(1.98–5.53)**	**1.01 ± 2.34(0.32–1.70)**	12	27.3
Brachypodium distachyum	2.36 ± 6.38(0.46–4.27)	10.99 ± 13.36(2.27–19.72)	**0.14 ± 0.46(−0.01–0.30)**	**3.52 ± 3.86(2.38–4.66)**	34	77.3
Cynodon dactylon	1.11 ± 7.26(−1.06–3.28)	0	0.26 ± 1.52(−0.25–0.77)	0	0	0
Stipa retorta	0.01 ± 6.62(−0.22–3.74)	7.05 ± 13.49(−1.76–15.87)	0.13 ± 0.38(0.00–0.26)	0	0	0
Liliaceae						
Asphodelus tenuifolius	2.34 ± 5.12(0.81–3.87)	1.34 ± 1.57(0.31–2.37)	2.56 ± 5.56(0.69–4.43)	0.79 ± 1.84(0.25–1.33)	19	43.2
Others	4.74 ± 5.99(2.95–6.53)	10.61 ± 9.57(4.36–16.86)	4.42 ± 4.21(3.00–5.83)	6.76 ± 3.50(5.72–7.79)	–	

Ninty-five per cent confidence intervals are indicated in brackets. Occurrence represents the number of faecal samples containing the item. The availability for each plant species in the study site was given in boldface when a significant difference was detected with the percentage of species in the diet. Data are based on 43 quadrats analyzed for plant availability (34 out of the Jujube and 9 under the Jujube) and 44 faecal samples of wild foraging tortoises.

Table 3
Hunter's index calculated for different plant species observed in the *Testudo g. graeca* diet in the Central Jbilets (Morocco)

Taxon	Hunter's index		
	Total plant cover	Under Jujube	Out Jujube
Aizoaceae			
Aizoon hispanicum	0.03	0.03	0.38
Aizoon canariense	0	0	0
Alsinoideae			
Spergula flaccida	0.03	0.01	0.06
Caryophyllaceae			
Fagonia cretica	0.03	0.01	—
Spergularia marginata	2.66	3.43	2.38
Chenopodiaceae			
Chenopodium murale	0.07	0.01	1.00
Asteraceae			
Anacyclus radiatus	0	0	0
Calendula algeriensis	0.13	0.03	0.56
Leontodon saxatilis	28.08	24.48	28.77
Scolymus hispanicus	0	0	0
Asteraceaea sp	0	0	—
Convolvulaceae			
Convolvulus althaeoides	0	0	—
Brassicaceae			
Biscutella didyma	3.19	1.49	40.33
Sinapsis arvensis	0	0	—
Notoceras bicorne	2.57	1.66	2.61
Geraniaceae			
Erodium guttatum	0.04	0.01	0.50
Fabaceae			
Medicago hispida	155.0	52.27	143.75
Medicago laciniata	0.10	0.49	0.09
Astragalus cruciatus	718.50	179.63	1437.0
Lotus arenarius	39.67	—	29.75
Scorpiurus sulcata	39.50	—	33.86
Malvaceae			
Malva parviflora	13.96	6.50	15.85
Ombellifereae			
Eryngium ilicifolium	0	0	0
Ammi majus	0.68	0.14	—
Plantaginaceae			
Plantago amplexicaulis	18.80	2.27	—
Polygonaceae			
Emex spinosus	0.06	0.14	0.04
Scrophulariaceae			
Linaria sagittata	0	0	—
Linaria bipartita	0.14	0.03	0.61
Solanaceae			
Solanum nigrum	0	0	—

Table 3 (*continued*)

Taxon	Hunter's index		
	Total plant cover	Under Jujube	Out Jujube
Poaceae			
Festuca sp.	0.32	16.83	0.27
Brachypodium distachyum	1.49	0.32	25.14
Cynodon dactylon	0	—	0
Stipa retorta	0	0	0
Liliaceae			
Asphodelus tenuifolius	0.34	0.59	0.31

However, the tortoises actively avoided *Spergula flaccida*, *Eryngium ilicifolium*, and *Anacyclus radiatus*. For nine plant species (*Aizoon canariense*, *Ammi majus*, *Brachypodium distachyum, Chenopodium murale*, *Emex spinosus*, *M. laciniata*, *Notoceras bicorne, Plantago amplexicaulis*, *Scolymus hispanicus*) conventional significance for selectivity was reached in one plant community solely (Table 2). Finally, a more puzzling result (inconsistent trend under and out of the Jujube) was obtained for a single species (*Festuca sp.*) (Table 2). It should be noted however that these eight plant species was only rarely found as a food item (0–3.5% of identified fragments).

The PSI was always less than 0.25 (0.20 when considering the overall plant community, and 0.24 and 0.17 when focussed on under the Jujube and out of the Jujube plant communities, respectively), indicating that *T. g. graeca* is a rather selective herbivore.

4. Discussion

4.1. Dietary

Our study provides the first quantitative data on the feeding ecology of *T. g. graeca* using faecal analysis method. The obtained data indicate clearly that *T. g. graeca* is essentially herbivorous, with 34 different species identified in the faeces. This result agree with the general tendency founded in most Testudinidae species, though some occasionally take other material, including fungi, invertebrates, carrion, bones and soil (Pritchard, 1979; Moskovits and Bjorndal, 1990; Milton, 1992; Rall and Fairall, 1993; Bayley and Highfield, 1996). Such diversity may allow the Spur-thighed tortoise to reach an adequate balance of nutrients by ingesting a wide variety of plants (until 18 plant species in single faeces sample). Therefore, diet mixing in herbivores can greatly increase digestibility of dry matter, organic matter and energy sources (Bjorndal, 1991). In addition to these wild plant species, the diet of *T. g. graeca* also include a wide variety of cultivated plants (lucerne, potato leaves, tomatoes, lettuce, etc.) in the Agadir region (Bayley and Highfield, 1996). According to these authors, the loss of vegetal cover and drought contributed to increase tortoise population densities around the intensively farmed areas and then changed their feeding habits by consuming the cultivated species. In Spain, Andreu (1987) recorded 88 plant species in the diet of Spur-thighed inhabiting the Doñana Park. This number of plant is high compared to the 34 plant species found in our study. This could be due to local bio-climatic conditions. Nevertheless, the major constituents of tortoise diets in the two area (Jbilets and Doñana) were essentially composed on Asteraceae, Fabaceae and Poaceae.

4.2. Is T. g. graeca a generalist or a specialist feeder?

Our results suggested that five plant species made up 70% of the diet (*L. saxatilis*, *A. cruciatus*, *M. parviflora, M. hispida*, *L. arenarius)*. Surprisingly, these main plant items consumed correspond to relatively under represented species in plant community and other ones like *A. canariense* and *E. ilicifolium* are very abundant in the environment during the study period (represent 46% of the total vegetal cover) and highly avoided (0% in the diet). This suggest that Spur-thighed tortoise strongly select its food, and the PSI (Feisinger et al., 1981) confirmed this tendency (PSI < 0,25 in all the cases): *T. g. graeca* in the Jbilets during spring is rather a specialist herbivorous species. This strongly contrasts with other studies but one (*Gopherus agasizzii*: Jennings, 1993), where Chelonian species are generally at midway between a specialist and a generalist herbivore (*G. polyphemus*: MacDonald and Mushinsky, 1988, *Geochelone pardalis*: Mason et al., 1999, *G. denticulata* and *G. carbonaria*: Bjorndal, 1989; Moskovits and Bjorndal, 1990, *T. horsfieldi*: Lagarde et al., 2003).

4.3. Why T. g. graeca select its food?

The major factors influencing feeding selectivity in herbivorous species seems to be principally the energetic, hydric and toxic contents of plants consumed (see Pyke, 1984 for a review and Moskovits and Bjorndal, 1990; Mason et al., 1999; Lagarde et al., 2003). Belovsky (1981) and Owen-Smith and Novellie (1982) recognized that concentrations of specific nutrients in potential foods may play a significant role in determining diet choice. Bjorndal (1980) found that the herbivore sea turtles, *Chelonia mydas*, select a food with both high protein and low lignin content to increase digestibility. Garner and Landers (1981) predicted *G. polyphemus* diet selection according to nutritional compound. They considered the Fabaceae as the most important forbs in the diet both because of a high nutritional value. Another study on *G. agassizii* (Jennings 1993) showed similar results: four species of Fabaceae (*Lotus* and *Astragalus* species) were among the most highly preferred plant species and represented about half of the seasonal diet of the tortoises. In the present study too, within eight plant species significantly preferred by *T. g. graeca,* four are Fabaceae representing 27% of total diet. *E. illicifolium* is probably unpalatable and hard to digest by herbivores (Floret, 1988) because of its thorny leaves (external defence mechanisms) and then highly avoided by tortoise. The present study showed that *T. g. graeca* consumes some plants (e.g. *M. parviflora*, *Solanum nigrum,* *A. majus, Anagalis arvensis and C. murale*) which could be toxic for mammalian herbivores because of toxic contents (Halsey, 1998; Forshaw, 2000; Knight and Walter, 2002). The occurrence of potentially toxic items in the diet has been documented in other Chelonian species (*T. hermanni*: Longepierre and Grenot, 1999; *Eretmochelys imbricata*: Meylan, 1988; *T. graeca*: Andreu et al., 2000; *T. horsfieldi*: Lagarde et al., 2003) and has been interpreted as anti-helminthic strategy (Satorhelyi and Sreter, 1993; Longepierre and Grenot, 1999, Lagarde et al., 2003).

Despite the consumption of some plants species that could be toxic for mammalian herbivores, the present study indicated that in our study area, *T. g. graeca* feed mostly on plant species that are also appreciated by the domestic mammals (Floret, 1988). Then, competition for food between tortoises and domestic mammals could occur in overgrazing areas and in such a context, spiny shrubs may represent a crucial protection for tortoises feeding resources.

4.4. Where *T. g. graeca* forage?

For several (10 out 34) plant species, the significance of plant selection and/or the Hunter selectivity indexes differs when comparing the diet of the tortoises under and out of the Jujube shrubs. However, these problematic plant species represent only a marginal part of the diet of the tortoises (0–3.5% of the plant fragments identified). It is therefore difficult to consider that the inconsistency in some of our results reflects a real change in the feeding selectivity of the tortoises. More likely, the abundance of such plants strongly differs between the two plant communities and/or, *T. g. graeca* prefers to forage under Jujube, where the global feeding resources are more abundant and diversified.

4.5. Methodological bias and perspectives

We focussed our study on the spring period. It could be very useful to study the feeding preferences seasonal variations. But nevertheless, spring is the period of maximum activity level and then the period of maximum food intake.

Faecal analysis was classically considered as a limited method in describing diet composition quantitatively (Rice, 1970; Slater and Jones, 1971; McInnis et al., 1983; Gordon, 1995), due to differential digestion rates of plant species and the typically high proportion of unidentified cuticle remains occurring in the faeces. Nevertheless, in our results, the percentage of unidentified remains (6.6%) and the percentage of wrong recognition ($7 \pm 3.5\%$) were low. Of course, we cannot exclude problems of differential digestibility of plant items and we need additional analysis to confirm the major pattern we found: *T. g. graeca* seems a rather specialist herbivorous species.

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