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Original Study

Fatine Lasgaa*, Farid Bounaceur and Stéphane Aulagnier

Feeding ecology of two rodent species, *Ctenodactylus gundi* and *Ctenodactylus vali* (Ctenodactylidae), in North-western Algerian Sahara

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Abstract: We investigated the feeding ecology of the two *Ctenodactylus* species, *Ctenodactylus gundi* and *Ctenodactylus vali*, in the Bechar region (North-western Algerian Sahara) over a two-year period, using microhistological analysis of faecal samples, including the first quantitative data on the diet of *C. vali*. Both species are strictly herbivorous, feeding on leaves, fruits, seeds, stems, and flowers. *Ctenodactylus gundi*, which inhabits semi-arid regions, exhibited a broad and opportunistic diet (27 plant species), whereas *C. vali*, found in more arid regions, showed a more specific diet, dominated by Amaranthaceae. Both diets reflect local and seasonal plant availability following rainfalls, with mainly *Chrysanthemum macrocarpum* and *Capparis spinosa* for *C. gundi*, *Haloxylon scoparium*, *Atriplex halimus* and *Salsola vermiculata* for *C. vali*. Although competitive interactions may occur, differences in both diets seem mainly due to climatic conditions that support the parapatric range of the two species.

Keywords: diet; seasonal variation; arid environment; Rodentia; gundis

1 Introduction

As a consequence of climate change, which can exacerbate desertification (Shukla et al. 2019), arid lands have experienced more intense warming and drying over the past 40 years compared to other biomes (Zhou et al. 2016). Given the strong relationship between primary productivity and precipitation, aridification dramatically reduces productivity across trophic levels (Chesson et al. 2004). Moreover, warming may cause phenological shifts (e.g., earlier plant growth), potentially leading to trophic mismatches (Post et al. 2008).

In hot deserts, interannual variation of precipitation is extreme, often fluctuating ten-fold between years (Schwinning and Sala 2004; Van Etten 2009). Water remains the most critical limiting resource for desert organisms (Greenville et al. 2014; Pavey and Nano 2013). Precipitation is known to indirectly shape herbivore populations, including rodents, through its effects on primary productivity and food availability, thereby influencing survival and reproductive outcomes (Ernest and Brown 2001; Letnic and Dickman 2006; Meserve et al. 2003). In such low-productivity areas, where precipitation is scarce and unpredictable, rodents adopt diverse dietary strategies to cope with harsh environmental challenges (Kerley 1992). For instance, granivory is prevalent among desert rodents in North America, whereas omnivory and herbivory dominate among desert rodents of Australia, South Africa and South America (Campos et al. 2001; Giannoni et al. 2005; Kerley 1992; Murray et al. 1999).

More generally, rodents exhibit spatiotemporal variability in their dietary preferences, reflecting local resource availability, seasonal changes, and ecological pressures (Brown and Heske 1990; Jakšić and Yáñez 1983; Meserve et al. 2003). Such variations are closely tied to the spatial and temporal food resource availability, which shapes the feeding strategies and ecological interactions of rodent species (Jakšić and Yáñez 1983; Mulungu et al. 2011), and ultimately influences reproductive success and population

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dynamics (Bomford 1987). Moreover, when resources are abundant, rodents become selective, specializing in high-value foods critical for reproduction; when resource are scarce, they broaden their diet to include a wider array of food items (Mulungu et al. 2011). In North African arid and semi-arid areas, research on diet of rodents mainly focused on Gerbillinae (e.g. Adamou-Djerbaoui et al. 2013; Petter 1961; Zaime and Gautier 1989) and Muridae (e.g. Khammes and Aulagnier 2007). Recently, the feeding ecology of two Ctenodactylidae, *Ctenodactylus gundi* (Rothmann, 1776) and *Massoutiera mzab* (Lataste, 1881), has been investigated (Lasgaa et al. 2021, 2023). However, these species live in distant areas and under very different bioclimatic conditions, preventing studying resource partitioning, the differential use of food resources among species (Pianka 1974). On the contrary, the two species of the genus *Ctenodactylus* live in close areas of North-western Africa, exhibiting quite similar anatomical and physiological adaptations to desert environments (George 1974, 1981; Gouat 1988a; Gouat and Gouat 1982; Grenot 1973; Petter 1961; Séguignes 1979).

Ctenodactylus gundi inhabits rocky slopes from Morocco to Libya, preferring natural rock crevices over burrowing for shelter (Gouat and Gouat 1983). The species is usually recorded in multimale-multifemale social groups with at least one reproductive male (Gouat 1988a; Honigs and Greven 2003; Séguignes 1979), in semi-arid to arid habitats between 230 and 1,700 m a.s.l., where annual precipitation ranges from 100 and 400 mm (Gouat and Gouat 1983; Séguignes 1983).

In contrast, *Ctenodactylus vali* (Thomas, 1902) more southern, fragmented habitats including sand dunes and saltbush areas across Morocco, Algeria and Libya, separated by over 1,000 km (Gouat 2013). In Algeria, it is found from Beni Abbès to Beni Ounif between 600 and 1,000 m a.s.l., typically along wadis (Gouat 1988a; Gouat and Gouat 1982, 1983). *Ctenodactylus vali* seems more tolerant of hyperarid, sparsely vegetated environments, although food availability likely limits its southern range (Gouat and Gouat 1984; Petter 1961). Its range is characterized by mean annual precipitation less than 100 mm (Gouat 1988a). However, crucial aspects of its natural history, such as diet, remain poorly documented.

This study aimed to investigate for the first time the feeding ecology of both species in contiguous areas of North-western Algerian Sahara. In this desert environment, where food resources are limited and subject to strong seasonal fluctuations, how do the two closely related rodent species adapt their feeding strategies to ensure survival and reproduction? Specifically, what are the spatial and temporal variations in their diets, and to what extent does the availability of plant resources influence their trophic behaviour under these extreme conditions?

2 Materials and methods

2.1 Study area

Investigations were carried out in two stations of the wilaya of Bechar (Figure 1). The first station, Chaabet Kelkoul, is located in the vicinity of Boukais (31.93359° N/02.51502° W), at 949 m a.s.l. The Saharan type climate is characterised by mild arid winter and hot, very dry summer with low rainfall (annual mean 2009–2018: 116.31 mm at Bechar). During the study period, the monthly rainfall exceeded 20 mm from April until October. The natural vegetation is composed of Mediterranean-type and desert type plants of Asteraceae (*Chrysanthemum macrocarpum* and *Launaea arborescens*), Brassicaceae (*Moricandia arvensis*), Anacardiaceae (*Pistacia lentiscus* and *Rhus tripartita*), Oleaceae (*Olea europaea*) and Amaranthaceae (*Haloxylon scoparium*). This station was inhabited by *C. gundi*.

The second station, Zaouia Fougania is located in the vicinity of Taghit (30.92539° N/02.04317° W) at 674 m a.s.l. The climate is also of the Saharan type, characterised by mild winter and hot, very dry summer with low rainfall (annual mean 2009–2018: 63.28 mm at Beni Abbes). During the study period, the rainiest month was August with 28.43 mm in 2017 and 49.28 mm in 2018. The desert type vegetation is composed of perennial plants meanly dominated by Amaranthaceae (*H. scoparium* and *Salsola vermiculata*), Brassicaceae (*Diplotaxis harra*), Capparaceae (*Capparis spinosa*) and Fabaceae (*Acacia tortilis raddiana*). This station was inhabited by *C. vali*.

2.2 Diet study method

The diet of both species was studied for a two-year period by micro-histological analysis of faeces collected every month from November 2016 to October 2018, for a total of 24 samples for each station. This non-invasive method was based on the specific identification of plant fragments (cuticles) in the faeces (Benamor et al. 2019, 2025; Bounaceur et al. 2023, 2024; Butet 1987; Chapuis 1979). The sites occupied by gundis were identified by the presence of piles of fresh faeces deposited by the colony of several adults and juveniles in the vicinity of rock shelters (George 1974; Gouat 1988a; Gouat and Gouat 1984). The study was therefore carried out on a population level because of the impossibility of assigning faeces to each individual. Each sample was randomly composed of 100–150 fresh faeces recognizable by their colour and shiny appearance, in different piles. Faeces were air-dried and stored in paper bags in the

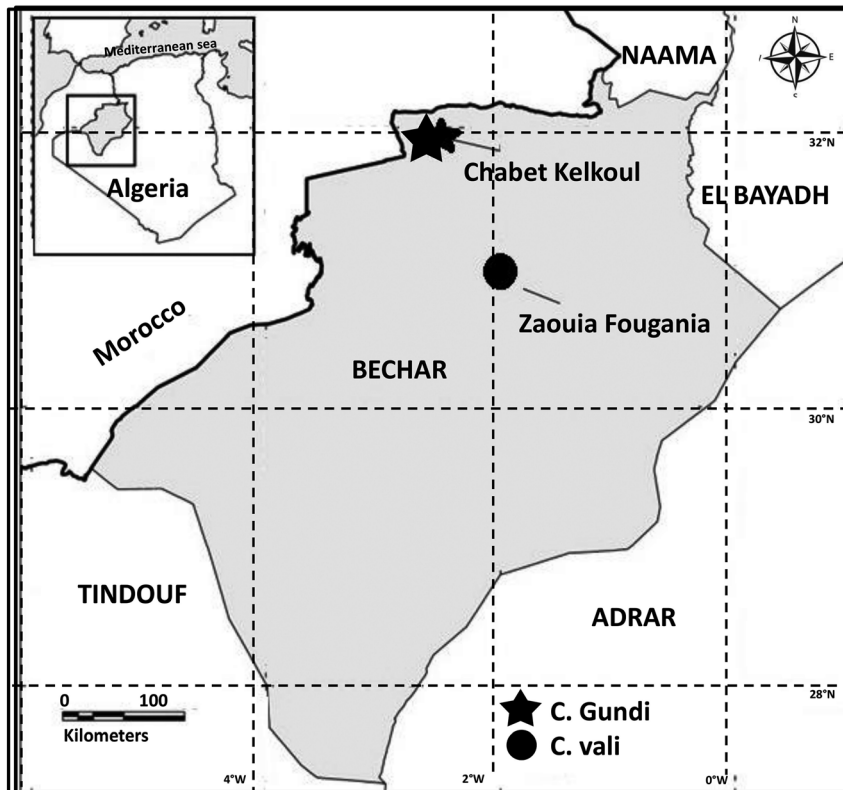


Figure 1: Location of study sites of *Ctenodactylus gundi* in Chaabet Kelkoul (Boukais, wilaya of Bechar) and *C. vali* in Zaouia Fougania (Taghit, wilaya of Bechar), North-western Algerian Sahara.

field. Preparation and identification of epidermis of a reference collection and of faeces is described in detail in Lasgaa et al. (2021).

2.3 Minimum number of representative faeces and fragments

Similarly to Lasgaa et al. (2021), the species richness was analysed in 100 fragments of epidermal cuticles of 1, 2, 3, 4, 5, 6, 7, 8, 9 and 10 faeces collected in March 2017 in each of the two study stations to estimate the sampling effort required. The accumulation curves in Figure 2 indicated that a plateau of 10 species was reached with 7 faeces for Chaabet Kelkoul and 9 faeces for Zaouia Fougania. As a precaution, 10 faeces were selected for each composite sample following Stewart and Stewart (1971).

Then, the species richness was analysed in sets of 50, 100, 150, 200, 250, 300, 350, 400, 450 and 500 fragments of epidermal cuticles in the same composite sample of 10 faeces to determine the sampling effort required. The accumulation curves indicate that the maximum number of species is 12 species for 250 fragments in both Chaabet Kelkoul and Zaouia Fougania (Figure 3). Therefore, 250 fragments were identified from 10 mixed faeces for each monthly sample.

2.4 Plant abundance

The evaluation of plant abundance was conducted in March 2017, this is the period of maximum development of annual plants in the area, and July 2017, the period of poverty of annual plants in the zone. The protocol was the same as in Lasgaa et al. (2021). The cover plant ratio ($CR\%$) for each species was calculated as $CR\% = 100/1,000 \times \sum_n R(i)$ with $R(i) = \pi d(i)^2/4$ of each plant species stem (i) at ground level with d : diameter of stem (Daget et al. 2010).

2.5 Data analyses

The diet of both species was quantified by relative abundance ($A\%$), calculated as: $A\% \text{ species } i = Ni \times 100/N$, where, Ni is the number of epidermal cuticles of species i , N the total number of epidermal cuticles.

Seasonal variations in the specific composition of the diet and the different parts consumed were analysed by Correspondence Factorial Analysis (CFA) calculated on the number of epidermal cuticles of each plant species for each station and each year of study. The CFA was followed by a cluster analysis on the first factorial coordinates using the Ward's grouping criterion (Saporta 2006).

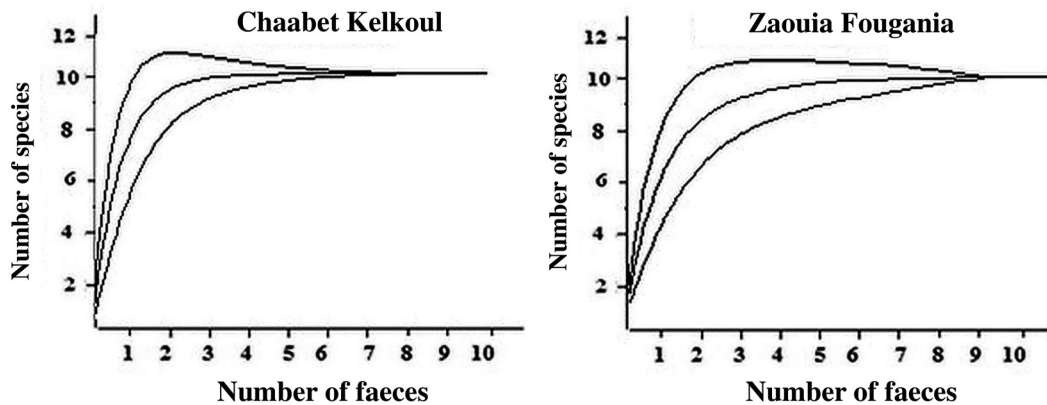


Figure 2: Accumulation curves of species richness (with 95% confidence interval) for determining the number of faeces representative of the diet of *Ctenodactylus gundi* in Chaabet Kelkoul (Boukais) and *C. vali* in Zaouia Fougania (Taghit), North-western Algerian Sahara.

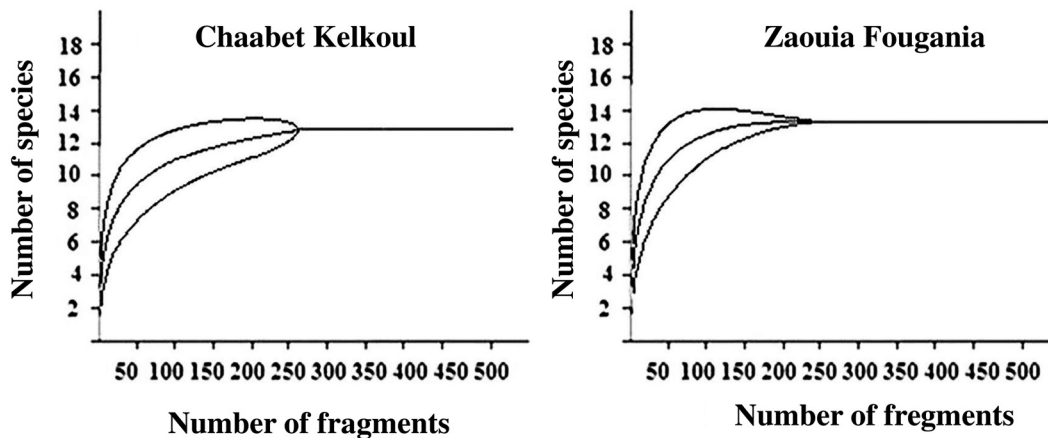


Figure 3: Accumulation curves of species richness (with 95% confidence interval) for determining the number of epidermal fragments representative of the diet of *Ctenodactylus gundi* in Chaabet Kelkoul (Boukais) and *C. vali* in Zaouia Fougania (Taghit), North-western Algerian Sahara.

Then, we estimated the diet preference of both species using the Ivlev's index which compares the relative abundance of the available food species in the environment and the choice of food consumed by the animal (Ivlev 1961). It was calculated as: $Ei = (A\% - CR\%)/(A\% + CR\%)$. This index varies from -1 to 0 for a negative selection and from 0 to $+1$ for a positive selection. All analyses were performed with PAST v.1.9 and Minitab v.12.2 softwares.

3 Results

3.1 Diet of the two gundis

Over the two studied years, *C. gundi* consumed a total of 27 plant species from 16 families in Chaabet Kelkoul, and *C. vali* consumed a total of 19 plant species from 13 families in Zaouia Fougania, with 10 shared species: *H. scoparium*, *Anvillea*

radiata, *L. arborescens*, *Perralderia coronopifolia*, *M. arvensis*, *C. spinosa*, *Gymnocarpos decander*, *Helianthemum lippii*, *Asphodelus tenuifolius* and *Lygeum spartum* (Tables 1 and 2).

In Chaabet Kelkoul, the most consumed plant species by *C. gundi* belonged to three families: Asteraceae with *C. macrocarpum* ($A\% = 31.03\%$), Capparaceae with *C. spinosa* ($A\% = 23.22\%$) and Caryophyllaceae with *G. decander* ($A\% = 11.60\%$). These three species accounted for 65.85 % of a diet composed by 48.02 % of fruits and seeds, 20.15 % of stems, 17.08 % of flowers, and 14.75 % of leaves.

In Zaouia Fougania, the most consumed plant species by *C. vali* belonged to two families: Amaranthaceae with *H. scoparium* ($A\% = 25.90\%$), *Atriplex halimus* ($A\% = 15.52\%$) and *S. vermiculata* ($A\% = 11.10\%$), and Apiaceae with *Ammodaucus leucotricus* ($A\% = 16.48\%$) (Table 2). These four species accounted for 69.00 % of a diet composed by 38.73 % of leaves, 34.60 % of fruits and seeds, 21.18 % of stems and 5.48 % of flowers.

Table 1: Relative abundance of each plant species (A%) in the diet of *Ctenodactylus gundi* in Chaabet Kelkoul (Boukais, wilaya of Bechar) from November 2016 to October 2018.

Families	Species	Nov. 2016 Oct. 2017 (A%)	Nov. 2017 Oct. 2018 (A%)
Anacardiaceae	<i>Pistacia lentiscus</i>	0.10	0.13
Amaranthaceae	<i>Haloxylon scoparium</i>	1.63	3.33
Asteraceae	<i>Anvillea radiata</i>	0.30	0.03
	<i>Artemisia herba-alba</i>	5.13	1.17
	<i>Bubonium graveolens</i>	0.00	0.23
	<i>Carduus</i> sp.	0.00	0.20
	<i>Chrysanthemum macrocarpum</i>	40.83	21.23
	<i>Launaea arborescens</i>	0.10	0.00
	<i>Perralderia coronopifolia</i>	0.03	0.00
Apiaceae	<i>Deverra scoparia</i>	0.00	0.03
	<i>Pituranthos chloranthus</i>	0.17	0.33
Brassicaceae	<i>Farsetia aegyptiaca</i>	7.20	8.63
	<i>Moricandia arvensis</i>	0.03	4.33
Capparaceae	<i>Capparis spinosa</i>	21.77	24.67
Caryophyllaceae	<i>Gymnocarpus decander</i>	5.30	17.90
Cistaceae	<i>Helianthemum lippii</i>	3.53	3.90
Fabaceae	<i>Retama raetam</i>	1.70	1.03
Globulariaceae	<i>Globularia arabica</i>	0.23	0.00
Lamiaceae	<i>Salvia aegyptiaca</i>	0.17	0.00
Liliaceae	<i>Asphodelus tenuifolius</i>	0.40	3.23
Plantaginaceae	<i>Plantago notata</i>	0.10	0.00
Plumbaginaceae	<i>Limoniastrum feei</i>	0.00	1.93
Poaceae	<i>Avena sterilis</i>	3.63	1.17
	<i>Hordeum mirinum</i>	4.63	1.80
	<i>Lygeum spartum</i>	0.27	3.33
Zygophyllaceae	<i>Fagonia glutinosa</i>	2.13	1.37
	<i>Fagonia microphylla</i>	0.60	0.00
Total		100	100

Table 2: Relative abundance of each plant species (A%) in the diet of *Ctenodactylus vali* in Zaouia Fougania (Taghit, wilaya of Bechar), from November 2016 to October 2018.

Families	Species	Nov. 2016 Oct. 2017 (A%)	Nov. 2017 Oct. 2018 (A%)
Amaranthaceae	<i>Atriplex halimus</i>	21.90	9.67
	<i>Haloxylon scoparium</i>	23.10	27.53
	<i>Salsola vermiculata</i>	11.03	11.37
Apiaceae	<i>Ammodaucus leucotricus</i>	14.07	18.83
Asphodelaceae	<i>Asphodelus tenuifolius</i>	0.10	0.07
Asteraceae	<i>Anvillea radiata</i>	1.03	0.07
	<i>Launaea arborescens</i>	0.57	0.67
	<i>Perralderia coronopifolia</i>	0.00	0.07
Brassicaceae	<i>Diplotaxis harra</i>	3.00	3.23
	<i>Eurca sativa</i>	0.00	0.07
Boraginaceae	<i>Moltkia ciliata</i>	0.00	0.03
Capparaceae	<i>Capparis spinosa</i>	4.67	0.87
Caryophyllaceae	<i>Gymnocarpus decander</i>	8.93	4.37
Cistaceae	<i>Helianthemum lippii</i>	1.23	4.33
	<i>Moricandia arvensis</i>	1.23	0.20
Fabaceae	<i>Acacia tortilis raddiana</i>	2.60	3.13
Poaceae	<i>Lygeum spartum</i>	5.70	5.87
Resedaceae	<i>Reseda alba</i>	0.17	1.07
Urticaceae	<i>Forskhelea tenacissima</i>	0.67	8.57
Total		100	100

3.2 Feeding preferences of both species

In Chaabet Kelkoul, the available vegetation consisted of 47 herbaceous species for 53.21 % of coverage in March, and 19 herbaceous species for 40.48 % of coverage in July. The 13 species consumed by *C. gundi* in March composed 71.79 % of the vegetation cover, and the 11 species consumed in July composed 71.09 % of the vegetation cover (Table 3). In March, 8 species were positively selected, including 6 of the most consumed plant species: *C. macrocarpum*, *C. spinosa*, *Artemisia herba-alba*, *H. lippii*, *Fagonia glutinosa* and *Hordeum mirinum*. Four of the most abundant species were negatively selected: *L. arborescens*, *M. arvensis*, *R. tripartita* and *H. scoparium*. In July, 8 species were also positively selected, including 4 of the most consumed plant species: *C. macrocarpum*, *C. spinosa*, *G.*

decander and *H. mirinum*. Five of the most abundant species were negatively selected: *Olea europea*, *A. radiata*, *A. herba-alba*, *L. spartum* and *Retama raetam*. The most consumed species, *C. macrocarpum* and *C. spinosa*, were positively selected in March and in July, whereas *A. herba-alba* was positively selected in March and negatively selected in July.

In Zaouia Fougania, the available vegetation consisted of 22 herbaceous species for 6.38 % of coverage in March, and 18 herbaceous species for 4.43 % of coverage in July. The 13 species consumed by *C. vali* in March composed 97.85 % of the vegetation cover, and the 10 species consumed in July composed 89.91 % of the vegetation cover (Table 4). In March, 6 species were positively selected, including 4 of the most consumed plant species: *A. halimus*, *L. spartum*, *A. leucotricus* and *G. decander*. Three of the most abundant species were negatively selected: *A. tortilis raddiana*, *H. scoparium* and *M. arvensis*, and two species were consumed in a proportion of availability: mainly *S. vermiculata*, and *D. harra*. In July, 7 species were positively selected,

Table 3: Relative abundance of each plant species (*A%*) in the diet of *Ctenodactylus gundi* in Chaabet Kelkoul (Boukais) in March and July 2017; cover plant ratio (*C%*), percentage of cover plant ratio (*CR%*) and Ivlev's electivity index (*Ei*) calculated as: $Ei = (A\% - CR\%)/(A\% + CR\%)$. This index varies from -1 to 0 for a negative selection and from 0 to $+1$ for a positive selection.

Family	Species	March				July			
		<i>A%</i>	<i>C%</i>	<i>CR%</i>	<i>Ei</i>	<i>A%</i>	<i>C%</i>	<i>CR%</i>	<i>Ei</i>
Amaranthaceae	<i>Anabasis articulata</i>	–	0.11	0.21	–1.00	–	–	–	–
	<i>Fredolia aretioides</i>	–	0.03	0.06	–1.00	–	–	–	–
	<i>Haloxylon scoparium</i>	0.80	3.76	7.07	–0.80	3.20	2.07	5.12	–0.23
Anacardiaceae	<i>Pistacia lentiscus</i>	–	2.01	3.78	–1.00	–	1.08	2.68	–1.00
	<i>Rhus tripartita</i>	–	4.63	8.70	–1.00	–	1.89	4.67	–1.00
Apiaceae	<i>Deverra scoparia</i>	–	0.01	0.03	–1.00	–	–	–	–
	<i>Pituranthos chloranthus</i>	–	0.05	0.10	–1.00	0.80	–	–	1.00
Asclepiadaceae	<i>Periploca laevigata</i>	–	2.36	4.44	–1.00	–	1.04	2.57	–1.00
Asteraceae	<i>Anvillea radiata</i>	–	0.53	1.01	–1.00	–	3.39	8.37	–1.00
	<i>Artemisia herba-alba</i>	14.00	2.09	3.93	0.56	4.80	10.78	26.64	–0.69
	<i>Bubonium graveolens</i>	–	0.19	0.35	–1.00	–	–	–	–
	<i>Carduus</i> sp.	–	0.38	0.72	–1.00	–	0.12	0.30	–1.00
	<i>Chrysanthemum macrocarpum</i>	34.80	7.47	14.04	0.42	46.40	–	–	1.00
	<i>Launaea arborescens</i>	–	7.88	14.80	–1.00	–	0.09	0.22	–1.00
	<i>Launaea mucronata</i>	–	1.89	3.56	–1.00	–	–	–	–
	<i>Perralderia coronopifolia</i>	–	0.26	0.49	–1.00	–	0.20	0.50	–1.00
Boraginaceae	<i>Echium horridum</i>	–	0.01	0.02	–1.00	–	–	–	–
Brassicaceae	<i>Diplotaxis harra</i>	–	1.99	3.74	–1.00	–	–	–	–
	<i>Farsetia aegyptiaca</i>	0.80	0.79	1.48	–0.30	2.40	–	–	1.00
	<i>Moricandia arvensis</i>	0.40	5.44	10.23	–0.92	–	–	–	–
Capparaceae	<i>Capparis spinosa</i>	20.80	0.91	1.71	0.85	20.40	1.26	3.12	0.74
Caryophyllaceae	<i>Gymnocarpus decander</i>	2.00	0.22	0.41	0.66	10.40	–	–	1.00
Cistaceae	<i>Helianthemum lippii</i>	11.20	0.95	1.79	0.72	0.80	0.24	0.60	0.14
Ephedraceae	<i>Ephedra alata</i>	–	0.10	0.19	–1.00	–	–	–	–
Fabaceae	<i>Ceratonia siliqua</i>	–	1.50	2.82	–1.00	–	–	–	–
	<i>Retama raetam</i>	0.80	1.88	3.54	–0.63	2.40	3.67	9.08	–0.58
Globulariaceae	<i>Globularia arabica</i>	0.80	0.49	0.92	–0.07	–	0.42	1.03	–1.00
Lamiaceae	<i>Salvia aegyptiaca</i>	–	0.03	0.05	–1.00	–	0.19	0.46	–1.00
	<i>Teucrium polium</i>	–	0.02	0.03	–1.00	–	0.36	0.88	–1.00
Liliaceae	<i>Asphodelus tenuifolius</i>	–	0.21	0.40	–1.00	–	–	–	–
	<i>Dipcadi serotinum</i>	–	0.00	0.00	–1.00	–	–	–	–
Oleaceae	<i>Olea europaea</i>	–	1.64	3.07	–1.00	–	5.65	13.96	–1.00
Plantaginaceae	<i>Plantago notata</i>	–	0.00	0.00	–1.00	–	–	–	–
Plumbaginaceae	<i>Limoniastrum feei</i>	–	0.34	0.64	–1.00	–	1.02	2.53	–1.00
Poaceae	<i>Avena sterilis</i>	0.80	0.01	0.02	0.95	0.80	–	–	–
	<i>Hordeum mirinum</i>	6.00	0.34	0.64	0.81	7.60	–	–	–
	<i>Lygeum spartum</i>	–	1.70	3.19	–1.00	–	4.22	10.43	–1.00
	<i>Stipa</i> sp.	–	0.11	0.21	–1.00	–	2.76	6.81	–1.00
Polygonaceae	<i>Rumex vesicarius</i>	–	0.33	0.62	–1.00	–	–	–	–
Resedaceae	<i>Randonia africana</i>	–	0.08	0.14	–1.00	–	–	–	–
	<i>Reseda alba</i>	–	0.20	0.38	–1.00	–	–	–	–
Urticaceae	<i>Forsskaolea tenacissima</i>	–	0.00	0.00	–1.00	–	–	–	–
Zygophyllaceae	<i>Fagonia glutinosa</i>	6.80	0.06	0.12	0.97	–	–	–	–
	<i>Fagonia microphylla</i>	–	0.19	0.36	–1.00	–	–	–	–
Total		100	53.21	100		100	40.48	100	

including 5 of the most consumed plant species: *A. halimus*, *G. decander*, *S. vermiculata*, *L. spartum* and *A. leucotricus*. One of the most abundant species was negatively selected: *Attractylis babelii*, and two species were consumed in a

proportion of availability: *H. scoparium* and *C. spinosa*. The most consumed species were positively selected in March and July, except *S. vermiculata* which was not selected in March.

Table 4: Relative abundance of each plant species (A%) in the diet of *Ctenodactylus vali* in Zaouia Fougania (Taghit) in March and July 2017; cover plant ratio (C%), percentage of cover plant ratio (CR%) and Ivlev's selectivity index (Ei) calculated as: $Ei = (A\% - CR\%)/(A\% + CR\%)$. This index varies from -1 to 0 for a negative selection and from 0 to +1 for a positive selection.

Family	Species	March				July			
		A%	C%	CR%	Ei	A%	C%	CR%	Ei
Amaranthaceae	<i>Atriplex halimus</i>	19.60	0.03	0.50	0.95	19.20	0.02	0.45	0.95
	<i>Haloxylon scoparium</i>	7.20	1.33	20.82	-0.49	20.40	1.00	22.59	-0.05
	<i>Salsola vermiculata</i>	24.80	1.41	22.06	0.06	12.00	0.10	2.31	0.68
Apiaceae	<i>Ammodaucus leucotricus</i>	10.00	0.02	0.30	0.94	10.80	-	-	1.00
Apocynaceae	<i>Pergularia tomentosa</i>	-	0.12	1.85	-1.00	-	-	-	-
Asteraceae	<i>Anvillea radiata</i>	1.60	0.06	0.89	0.29	-	0.19	4.33	-1.00
	<i>Atractylis babilii</i>	-	0.00	0.07	-1.00	-	0.35	7.99	-1.00
	<i>Launaea arborescens</i>	-	0.32	4.95	-1.00	-	0.02	0.43	-1.00
	<i>Perralderia coronopifolia</i>	-	0.01	0.13	-1.00	-	0.03	0.72	-1.00
Boraginaceae	<i>Moltkia ciliata</i>	-	0.00	0.02	-1.00	-	0.01	0.22	-1.00
Brassicaceae	Brassicaceae sp.	-	0.00	0.06	-1.00	-	-	-	-
	<i>Diploaxis harra</i>	4.40	0.27	4.25	0.02	-	-	-	-
	<i>Moricandia arvensis</i>	1.20	0.60	9.44	-0.77	2.40	0.06	1.37	0.27
Capparaceae	<i>Capparis spinosa</i>	3.20	0.14	2.17	0.19	8.00	0.24	5.45	0.19
Caryophyllaceae	<i>Gymnocarpus decander</i>	5.20	0.14	2.16	0.41	13.20	0.01	0.27	0.96
Cistaceae	<i>Helianthemum lippii</i>	2.00	0.15	2.37	-0.08	1.60	0.03	0.77	0.35
Fabaceae	<i>Acacia tortilis raddiana</i>	2.80	1.41	22.15	-0.78	1.20	2.09	47.31	-0.95
Lamiaceae	<i>Salvia aegyptiaca</i>	-	-	-	-	-	0.08	1.89	-1.00
Liliaceae	<i>Asphodelus tenuifolius</i>	-	0.01	0.13	-1.00	-	0.02	0.37	-1.00
Poaceae	<i>Lygeum spartum</i>	17.60	0.26	4.00	0.63	11.20	0.13	2.87	0.59
Polygonaceae	<i>Rumex vescauiis</i>	-	0.01	0.23	-1.00	-	-	-	-
Resedaceae	<i>Reseda alba</i>	-	0.02	0.30	-1.00	-	0.01	0.30	-1.00
Urticaceae	<i>Forskalea tenacissima</i>	0.40	0.08	1.18	-0.49	-	0.02	0.38	-1.00
Total		100	6.38	100		100	4.43	100	

3.3 Seasonal and interannual variations of the diet-specific composition

In Chaabet Kelkoul, the first axis of the CFA (27.74 % of variance) mainly opposed the two surveyed years (Figure 4), with most differences being supported by poorly consumed species, except a higher consumption of *C. macrocarpum*, *A. herba-alba*, *H. mirinum* and *Avena sterilis* the first year, *G. decander*, *M. arvensis* and *A. tenuifolius* the second year. The second axis of the CFA (14.90 % of variance) is mainly supported by the consumption of *Farsetia aegyptiaca* in December 2016.

In Zaouia Fougania, the first axis of the CFA (31.63 % of variance) opposed the months from July to October 2018, associated with a high consumption of *Forskalea tenacissima*, to the other months and species (Figure 5). The second axis of the CFA (17.81 % of variance) mainly isolated the months March–May 2017 and December 2017–March 2018 associated with a high consumption of *H. lippii*, and secondary of *D. harra*. These CFA support a seasonal variation of diet higher for *C. vali* than for *C. gundi*, and an

interannual variation of diet lower for *C. vali* than for *C. gundi*.

3.4 Seasonal and interannual variations of the diet parts consumed

In Chaabet Kelkoul, the first axis of the CFA (61.53 % of variance) mainly opposed the months April–July 2017 (Figure 6), associated with a high consumption of flowers ($A\% = 47.6$ in June 2017), to the other months and parts, with leaves particularly abundant from September to March both years (e.g. $A\% = 37.2$ in January 2017, 32.4 in March 2017). The second axis (24.86 % of variance) weakly opposed the consumption of fruits and seeds, mainly in November and December both years and the consumption of leaves in January and March 2017.

In Zaouia Fougania, the first axis of the CFA (46.19 % of the variance) mainly stands out the consumption of flowers from January to June 2018 (Figure 7). The second axis (37.98 %) is even less informative.

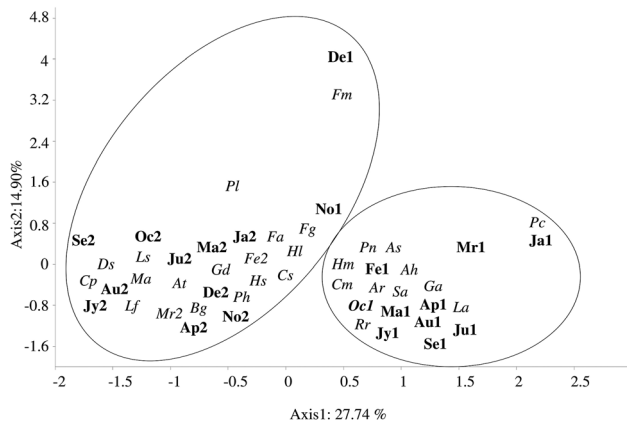


Figure 4: Monthly variations of the plant species consumed by *Ctenodactylus gundi* in Chaabet Kelkoul (Boukais), from November 2016 to October 2018, first axes of the CFA and first groups identified by automatic classification according to Ward's criterion... Ah: *Artemisia herba-alba*, Ar: *Anvillea radiata*, As: *Avena sterilis*, At: *Asphodelus tenuifolius*, Bg: *Bubonium graveolens*, Cm: *Chrysanthemum macrocarpum*, Cp: *Carduus sp.*, Cs: *Capparis spinosa*, Ds: *Deverra scoparia*, Fa: *Farsetia aegyptiaca*, Fg: *Fagonia glutinosa*, Fm: *Fagonia microphylla*, Ga: *Globularia arabica*, Gd: *Gymnocarpus decander*, Hl: *Helianthemum lippii*, Hm: *Hordeum mirinum*, Hs: *Haloxylon scoparium*, La: *Launaea arborescens*, Lf: *Limoniastrum feei*, Ls: *Lygeum spartum*, Ma: *Moricandia arvensis*, Pc: *Perralderia coronopifolia*, Ph: *Pituranthos chloranthus*, Pl: *Pistacia lentiscus*, Pn: *Plantago notata*, Rr: *Retama raetam*, Sa: *Salvia aegyptiaca*. Ja: January, Fe: February, Mr: March, Ap: April, Ma: May, Ju: June, Jy: July, Au: August, Se: September, Oc: October, No: November, De: December. 1: month of the first year, 2: month of the second year.

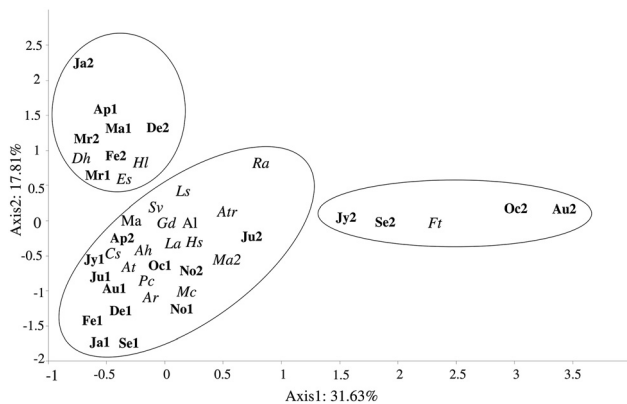


Figure 5: Monthly variations of the plant species consumed by *Ctenodactylus vali* in Zaouia Fougania (Taghit) from November 2016 to October 2018, first axes of the CFA and first groups identified by automatic classification according to Ward's criterion. Ah: *Atriplex halimus*, Al: *Ammodaucus leucotricus*, Ar: *Anvillea radiata*, At: *Asphodelus tenuifolius*, Atr: *Acacia tortilis raddiana*, Cs: *Capparis spinosa*, Dh: *Diplotaxis harra*, Es: *Eurca sativa*, Ft: *Forskhalea tenacissima*, Gd: *Gymnocarpus decander*, Hl: *Helianthemum lippii*, Hs: *Haloxylon scoparium*, La: *Launaea arborescens*, Ls: *Lygeum spartum*, Ma: *Moricandia arvensis*, Mc: *Moltkia ciliata*, Pc: *Perralderia coronopifolia*, Ra: *Reseda alba*, Sv: *Salsola vermiculata*.

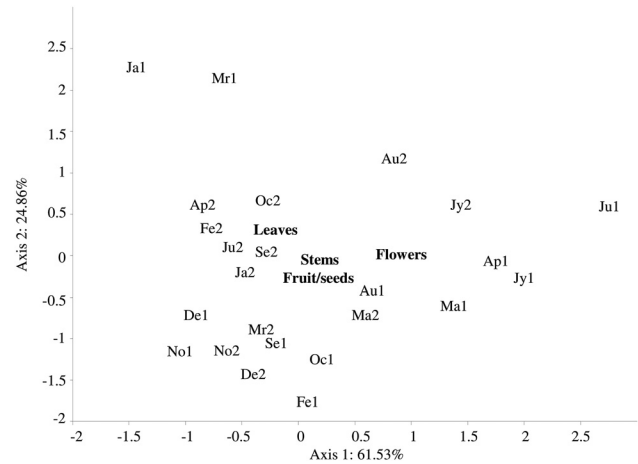


Figure 6: Monthly variations of the parts of plants consumed by *Ctenodactylus gundi* in Chaabet Kelkoul (Boukais) from November 2016 to October 2018.

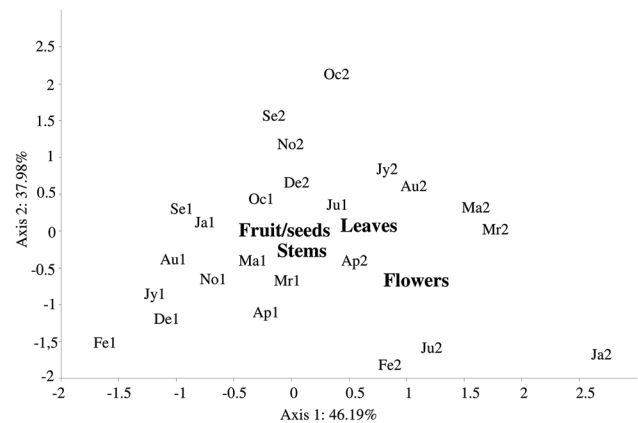


Figure 7: Monthly variations of the parts of plants consumed by *Ctenodactylus vali* in Zaouia Fougania (Taghit) from November 2016 to October 2018.

4 Discussion

4.1 Diet of two generalist but selective herbivores

Our results confirm that both species are strict herbivores as it was reported in the literature (Gouat 1988a; Grenot 1973; Lasgaa et al. 2021; Meddour 2019; Petter 1961; Séguignes 1979).

However, in Chaabet Kelkoul fruits and seeds were the most abundant parts of plants in the diet of *C. gundi*, together with a large amount of dry flowers, whereas in the Aurès region, it was mainly composed of green parts of plants (e.g. 52.74 % and 67.86 of leaves in Baniane and Bazem, respectively), and few flowers (1.11 % and 3.58 %) (Lasgaa et al.

2021). This difference is primarily linked to the immediate availability of trophic resources, as the species exploits all plant parts accessible in its environment (Lasgaa et al. 2021). So, the high proportion of seeds support the clear trend toward increased seed consumption by most rodents in arid conditions (Campos et al. 2001; Degen et al. 1997; Giannoni et al. 2005; Lasgaa et al. 2023; Murray et al. 1999; Petter 1961; Reichman 1977; Yip and Dickman 2023). For example, *Meriones crassus* and several other gerbilline includes a quantity of seeds which varies based on the availability of green vegetation (Bar et al. 1984; Kam et al. 1997), and these species may prey upon arthropods in harsh conditions (Bar et al. 1984; Hadjoudj 2020). In North American deserts, small mammals often specialize in seeds during periods of food abundance in arid and semiarid ecosystems of central New Mexico, seeds accounting for ca. 50 % of the total dietary intake for 15 rodent species (Hope and Parmenter 2007). Granivory is also predominant among rodents inhabiting Australian deserts (Murray et al. 1999). However, contrary to most of these granivore rodents which forage nocturnally due to consideration of water balance (Khokhlova et al. 2005), *C. gundi* is active during daytime.

There was no previous quantitative study of the diet of *C. vali*; Petter (1961) and Gouat (1988a) only reported that this species primarily consumes the green parts of plants., which is partly confirmed by our results as leaves were the most consumed parts of plants in Zaouia Fougania. According to our results, both plant-eating species undoubtedly fit the trophic level 'herbivore' according to Kissling et al. (2014) (diet category 'omnivore' according to Verde Arregoitia and D'Elia 2021), but *C. gundi* would belong to the dietary guild 'granivore', and *C. vali* to the dietary guild 'folivore' (Kissling et al. 2014). The main consumption of fruits and seeds by *C. gundi* is surprising as gundis have a very long digestive tract with a huge caecum that clearly differs from the short digestive tract of granivore species (Gouat 1993). This can be the sign of an opportunistic feeding strategy.

The consumption of 27 plant species from 16 families by *C. gundi* in Chaabet Kelkoul confirms the generalist diet supported by Lasgaa et al. (2021). Unsurprisingly, the most consumed species, and plant families, were different in the previous studies in the Aurès region where a high variability among sites was recorded (Lasgaa et al. 2021; Meddour 2019), and only *A. herba-alba* (A% = 33.13 in Baniane, Lasgaa et al. 2021) was also consumed in our study site. These results confirm the weak importance of the vegetation composition in the habitat of *C. gundi* (Gouat and Gouat 1983). At the family level, Asteraceae of different species were a major food resource in all sites. Such diet variations were previously observed by Séguignes (1979), and later by Gouat and Gouat (1987), due to huge differences of vegetation along a

range extending along 1,500 km of mountain areas, the habitat of *C. gundi* (Gouat 1988a). This flexibility may be particularly advantageous in arid environments where resource availability is unpredictable and heterogeneous (Giannoni et al. 2005; Meserve 1981; Reichman 1977).

The consumption of 19 plant species from 13 families by *C. vali* in Zaouia Fougania also suggests a generalist diet previously inferred by Gouat (1988a) who nevertheless watched animals eating only 7 species from 6 families at Djeniene Bou Rezg in the Naâma region. Three of the most consumed species belong to the family Amaranthaceae (A% = 52.52), with *H. scoparium* as the main species, differing from the species reported by George (1974) and Gouat (1988a). By comparison with *C. gundi*, this smaller variety of consumed plant species can be related to the very arid biotopes of this gundi, locally exhibiting a limited floristic diversity (23 species) and low vegetative cover (6.38 %). Other rodents from arid regions, such as certain *Meriones*, have adapted their diets to food availability (Adamou-Djerbaoui et al. 2013; Zaim and Gautier 1989).

Both species showed a marked preference for certain plant species, indicating a degree of selective feeding behaviour despite the limited food availability typical of desert environments. In the Aurès massif, the diet of *C. gundi* included 16 out of 27 plant species in Baniane (6 preferred species), 20 out of 40 plant species in Bazem (15 preferred species, Lasgaa et al. 2021). With 8 preferred out of 44 available plant species and the avoidance of two abundant plant species in March in Chaabet Kelkoul, *C. gundi* was more selective. However, the selectivity was different in July when there were 8 preferred out of only 19 available plant species, and almost when four abundant species were not in the diet. Such result suggests that plant species availability should be surveyed every month in the future.

In Djeniene Bou Rezg site, Gouat (1988a) watched *C. vali* consuming only 7 out of 65 available plant species, a selectivity higher than in Zaouia Fougania, where the vegetation is poorer (22 and 18 available plant species in March and July, respectively). It is worth recalling that in the latter site only one abundant plant species in July was not consumed. Such different pattern between sites was reported for *M. mzabi*, another Saharan Ctenodactylid, which consumed 14 plant species at Chaabet Tidakine with three species accounting for 25 % of the diet, and 20 plant species at Oued Izarwaz with *Pulicaria* sp. accounting for more than 50 % of the diet (Lasgaa et al. 2023).

With 52.52 % of Amaranthaceae in diet, *C. vali* could be considered a specialist species in Zaouia Fougania. Specialist species are defined as those consuming a single food type disproportionately to its environmental availability (Feinsinger et al. 1981), with consumption exceeding 50 % for one

plant group (Giannoni et al. 2005). Among the Saharan rodents *Psammomys obesus* (Cretzschmar, 1828) which feeds almost exclusively on Amaranthaceae (formerly Chenopodiaceae) (Daly and Daly 1973; Fichet-Calvet et al. 1999; Petter 1961; Zaime and Gautier 1989) is a true specialist. In recent studies, dietary specialists are herbivores exhibiting unique behaviours or physiological and morphological adaptations to digest challenging plants (Shipley et al. 2009). Well, *P. obesus* has renal adaptations, such as enlarged vascular bundles, an extended inner medulla, and a distinctive renal pelvis morphology, allowing for highly concentrated urine and efficient urea recycling (Kaißling et al. 1975), which is not the case of *C. vali*. If Petter (1961) also reported the prevailing consumption of Amaranthaceae by *C. vali* in Beni Abbès, George (1974) did not mention any plant species of this family in the diet, and Gouat (1988a) listed only *Haloxylon articulatum* among seven species. As we previously reported for *C. gundi* and *M. mzabi* (Lasgaa et al. 2021, 2023), the feeding ecology of most desert rodents is highly environment dependant (Mulungu et al. 2011).

Interspecific competition is a major factor shaping rodent distribution especially in arid environments where food resources are limited (Polis 1991). Such interactions may lead to ecological partitioning of habitats or resources, thereby facilitating the coexistence of multiple sympatric or parapatric species (MacArthur and Levins 1967; Rosenzweig 1974). So, dietary preferences can facilitate species coexistence through niche differentiation (Pianka 1974), notably for rodent species in desert environments (Harris 1986; Joel 1989; Li et al. 2024). In the case of *C. gundi* et *C. vali* the weak overlap in food selection suggests that competition between species is likely to be low even if food is limited (as a source of energy and water), as is often the case in desert ecosystems (Heske et al. 1994). More assuredly, the social structure of *C. gundi* enables the species to outcompete *C. vali* in areas where food is locally abundant (Gouat 1988b). So, the two species exhibit a parapatric distribution (Gouat 1988b), *C. vali* inhabiting more southern latitudes than *C. gundi* (George 1981; Gouat 1988a; Gouat and Gouat 1984; Séguignes 1979). In this context, *C. gundi* expands into more southern sites only where plant availability is increasing (Gouat 1988b), explaining the sparse distribution of *C. vali* across the rocky areas of the north-western Saharan margin (George 1981; Gouat 1988a; Séguignes 1979).

4.2 Seasonal and interannual variations in diet

Differences between the diets of the two species extend to temporal variations. In Chaabet Kelkoul, the diet of *C. gundi*

mainly differed between the two years, whereas in Zaouia Fougania, the diet of *C. vali* was characterized by a seasonal hazard. Both variations, can be related to the rainfall events. *Ctenodactylus gundi* relies predominantly on perennial plant species, supplementing its diet with the seasonal development of annual plants (Gouat 1988a; Lasgaa et al. 2021; Séguignes 1979). This was the case after substantial rainfalls in November and December 2016 in Bechar, and the subsequent main consumption of *C. macrocarpum* from January to October 2017, a dry period. From December 2017 to October 2018, rainfalls were more regular and supported the main consumption of *C. spinosa* and *G. decander*. These perennial plants, even when dry, can serve as a food resource throughout the year (Grenot 1973), but seems to be more appetizing after rainfalls.

The main variation of the *C. vali* diet from July to October 2018 is linked to substantial rainfalls after at least eight months of drought in Beni Abbes, and to the high consumption of *F. tenacissima*. The incidental variations from March to May 2017, and from October 2017 to March 2018 can be related to very dry periods. Interannual differences were less pronounced due to a more regular distribution of rainfall, peaking in August. A marked dietary seasonality has also been reported in various herbivorous rodent species inhabiting arid environments, including the ctenodactylid *C. gundi* (Gouat and Gouat 1987; Lasgaa et al. 2021; Séguignes 1979) and *M. mzabi* (George 1988; Gouat 1988a; Lasgaa et al. 2023), and also *M. crassus* Sundevall, 1842 (Degen et al. 1997), *Microcavia australis* (I. Geoffroy and d'Orbigny, 1833) (Sassi et al. 2011), and *Rhombomys opimus* (Lichtenstein, 1823) (Liu et al. 2012).

The consumed plant parts displayed some seasonal variations in the diet of both species. Flowers were particularly eaten from April to July 2017 by *C. gundi*, and from January to June 2018 by *C. vali*, all these months being dry. On the opposite, *C. gundi* ate the largest amount of leaves from September to March both years after the main rainfalls. In the Aures massif, the consistent year-round consumption of leaves and stems by *C. gundi* also peaked in autumn and winter, the consumption of flowers in spring (Lasgaa et al. 2021). Such seasonal pattern was associated to the development of different vegetative parts known to occur in many desert rodents (Bar et al. 1984; Degen et al. 1997; Zaime and Gautier 1989). Well, in Chaabet Kelkoul and Zaouia Fougania, the consumption of flowers was particularly high during dry months. Such discrepancy can be explained by the averred consumption of flowers of Asteraceae or Apiaceae long after they had dried as the issue of an opportunistic feeding strategy relying on persistent plant parts which offer longer-term availability (Bozinovic 1997; Degen et al. 1997; Murray et al. 1999; Zaime and Gautier 1989). This capacity to shift dietary composition in response to the

seasonal availability of different plant organs reflects an adaptive strategy to arid ecosystems (Meserve et al. 1988; Stafford Smith and Morton 1990).

5 Conclusions

This study provides new insights into the feeding ecology of *C. gundi* in arid environments of southwestern Algeria, and the first quantitative diet of *C. vali*. Our findings confirm that both species are strict herbivores and adapt to variations of vegetation availability, but they exhibit distinct dietary strategies. Opportunistic, *C. gundi* consumed a wide range of plant species, including a large amount of seeds, as most desert rodents. In contrast, living in harsher conditions and sparse vegetation, *C. vali* consumed a smaller range of plant species, including maliny leaves, with a strong appetite for Amaranthaceae, suggesting physiological adaptations to exploit halophytic vegetation.

Despite these differences, both species exhibited selective feeding behaviour, influenced by local floristic composition and environmental conditions. The weak dietary overlap does not support interspecific competition. However, the flexibility observed in *C. gundi* may act as a key factor in its competitive advantage over *C. vali*, potentially limiting the range expansion of the latter across the Saharan Atlas (Gouat 1988b).

This work contributes significantly to our understanding of how desert rodents adapt to the challenges of life in arid environments and provides a foundation for future studies on the feeding ecology and conservation of desert species. Future research should focus on the physiological adaptations underlying dietary specialization in *C. vali* and the potential impacts of climate-induced habitat shifts on the competition dynamics between the two *Ctenodactylus* species.

At last, this study highlights the strong influence of environmental variability, particularly tainfalls and subsequent vegetation dynamics, on diet of desert rodents. Given that climate change should modify plant distribution and availability, understanding trophic interactions is critical for predicting the long-term viability of desert adapted rodents (Blumstein et al. 2025).

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Informed consent: Informed consent was obtained from all individuals included in this study.

Author contributions: Fatine Lasgaa collected and analyzed the faeces, performed statistic analyses and wrote a draft of the paper. Farid Bounaceur supervised the work, performed the statistic data, wrote the draft and corrected the manuscript. Stéphane Aulagnier suggested statistical analyses and wrote the final version of the paper.

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Data availability: All material is stored in Ecole Normale Supérieure de Kouba, Laboratoire d'Ecobiologie Animale. Raw data are provided in the tables. The data that support the findings of this study are available from the corresponding author, Fatine Lasgaa., upon reasonable request.

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