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Abstract

The seasonal variations of the diet of the desert Trident leaf-nosed bat, *Asellia tridens*, were investigated using dropping analyses during the whole year 2015 in the Timimoun region, south-western Algerian Sahara. We identified one order of arachnids (Araneae) and ten orders of insects: Coleoptera, Hymenoptera, Diptera, Orthoptera, Mantodea, Hemiptera, Isoptera, Ephemeroptera, Blattodea and Odonata in a decreasing rank. Coleoptera (31.07%) were Carabidae, Curculionidae, Chrysomelidae, Tenebrionidae, Aphodidae, Scarabaeidae, and Histeridae. Hymenoptera (21.31%) were Formicidae, Myrmicidae and Vespidae, Diptera (13.78%) were Culicidae and Tabanidae, and Orthoptera (11.40%) were Acrididae and Gryllidae. The autumn-winter diet (October to December) included a large amount of Odonata, Scarabaeidae, Blattodea, Acrididae and Myrmicidae. The spring-summer diet (February to August) was characterized mainly by Chrysomelidae, Vespidae, Tenebrionidae, Aphodidae and Araneae. As other desert bat species *A. tridens* displays a combination of opportunism and selective predation depending on the abundance of insect groups.

Keywords: *Desert, feeding ecology, season, Sahara, trident leaf-nosed bat*

Background

Understanding foraging habitats and feeding behaviour of bats has become increasingly recognized as crucial for the conservation of many species (Dietz et al. 2007). Foraging behaviour and diet vary among bat species, even among insectivorous bats (e.g. Beck 1995; Vaughan 1997; Smirnov & Vekhnik 2014) depending on dental and cranial morphology, wing shape, echolocation call frequency and habitat (Neuweiler 2000; Altringham 2011; Weterings & Umponstira 2014). Hill and Smith (1984) identified three general categories of foraging styles used by bats to capture insects: aerial insectivory, foliage gleaning and terrestrial acquisition. Alternate classifications were then suggested by, among others, Findley (1993), Patterson et al. (2003) and Denzinger and Schnitzler (2013) who suggested seven bat guilds

from open-space aerial foragers to narrow-space passive/active foragers on the basis of foraging behaviour and echolocation signals. Studying the diet of 15 species of European bats, Smirnov and Vekhnik (2014) also identified seven, but different, guilds. Although insectivorous bats mainly feed on insects, some of them feed on spiders, crustaceans and even scorpions (Altringham 2011). Their diet differs both in space and time and changing it could reflect a change in strategy by the bats or different prey abundances (Fenton 1982), insectivorous bats being mainly opportunistic feeders (Fenton & Morris 1976).

The trident leaf-nosed bat, *Asellia tridens* (Geoffroy, 1813), is highly adapted to arid environments and the most common species in the arid and Saharan North Africa (Aulagnier 2013). This bat is widely spread from the Western Sahara and Sahel savannah to Pakistan

through the Arabian Peninsula (Simmons 2005; Aulagnier 2013). It forages low by slow-hawking with rapid twists and turns and presumably by ground gleaning, but it was observed foraging around palm trees, buildings and over water (Jones et al. 1993; Whitaker et al. 1994; Dietz et al. 2007). *A. tridens* was recorded to feed mainly on medium-sized Coleoptera, Hymenoptera, Orthoptera, Diptera and Lepidoptera (Jones et al. 1993; Whitaker et al. 1994; Feldman et al. 2000; Benda et al. 2001, 2006, 2012, 2014; Whitaker & Yom-Tov 2002; Amichai et al. 2013; Žďárská 2013). Even if each of these authors did not survey for a long period and sometimes analysed a small number of samples (faeces or stomach), they reported important variations in diet, both locally from Gambia (Jones et al. 1993) to Iran (Benda et al. 2012), and seasonally from spring to autumn (Žďárská 2013). Identifying the main factor forthese variations remains difficult, and no study was extended over a whole year, including winter when bats are still active [e.g. Koch-Weser (1984) in Burkina Faso, Aulagnier and Destre (1985) in Morocco].

In Algeria, *A. tridens* is quite common in caves, other underground shelters (e.g. subterranean irrigation channels), and buildings from the whole desert zone to the Saharan Atlas in the north (Kowalski & Rzebik-Kowalska 1991). So it was reported as one of the 16 mammal species inthe Timimoun region (Boukhemza et al. 1994) where we found a colony of 300 bats which occupies the same underground cavity all year round. This finding allowed the opportunity to regularly collect droppings and study the seasonal variations of the diet of *A. tridens* in one locality. This is the first time that the feeding ecology of this bat species was monitored in North Africa. We hypothesized that, as most insectivorous desert species, *A. tridens* may have a broad diet and hunt prey depending on the seasonal cycle of insect species abundance.

Materials and methods

Study area

The study took place in El Hadj Guelmane oasis (N 29° 25′31.188″, E 0°16′35.976″), 18 km north of Timimoun (Adrar governorate, central Sahara). Annual rainfall in the study area is low (22.5 mm) and mainly occurs during winter and spring. The summer is dry and hot (mean temperature of the hottest month: 24.5°C, maximum: 46.0°C) (Allal–Benfekih 2006).

The area is a sandy landscape consisting of dunes of the Western Erg and palm groves. The dominant plant species is the date palm *Phoenix dactylifera*. In the oasis, the understory includes some fig trees *Ficus* sp., pomegranate trees *Punica granatum*, vineyards *Vitis vinifera* and Rosaceae (Karimi 2016). The ground is more or less covered by *Aristida pungens*, *Danthonia forskahlii*, *Phragmites communis*, *Arundo plinii*, *Panicum turgidium* (Souttou 2010), vegetable crops and fodder plants. Outside the cultivated area, sandy banks are sprinkled with *Euphorbia guyoniana*; some acacia trees (*Acacia arabica* and *A. raddiana*) surviving in dry wadis and dayas. There, a monospecific colony of ca. 300 *Asellia tridens* was discovered in an underground cavity of an old castle, in the resort of Ksar Abdennour. The colony, females and males, roosted in the cavity all around the year.

Methods

The diet of *Asellia tridens* was investigated from 10 g of droppings (ca. 60) collected twice per month from January to December 2015 under both female and male colonies when they segregate inside the roost from March to July. A sheet of paper was placed underneath and removed each fifteen days to collect all droppings and store them dry in a tube. In the laboratory, they were soaked a few minutes in 70% ethanol to sterilize them and, after softening, spread individually, using two dissecting needles under a 40 × 10 binocular microscope. The content of each dropping was spread in a Petri dish and dried. The chitinous remains of arthropods were separated according to their form and colour in order to identify and count prey items under a microscope. We identified remains to the lowest taxonomical level possible with the aid of identification keys (McAney et al. 1991; Shiel et al. 1997) and the reference collection of the Superior National Veterinary School in Algiers (Zoology laboratory). *Asellia tridens* has strong jaws and powerful upper canines (Aulagnier 2013); arthropod remains in droppings are tiny and particularly difficult to identify at a taxonomic level under the family or even the order. Taxonomy follows Misof et al. (2014). For quantitative analyses, identifications were restricted to family (or order) level. Results were expressed in terms of relative frequency (% F), calculated as the ratio of the number of items for a taxon to the total number of items identified. We performed a Factorial Correspondence Analysis (FCA) on the two-week numbers of items for each taxon followed by a hierarchical classification on factorial co-ordinates of time variable using PAST 1.37 (Hammer et al. 2001) in order to identify

unsupervised seasonal patterns. This analysis identified subsequently two and four seasons that were compared using chi-square tests; the significance level was 0.05.

Results

Annual diet

We identified a total of 2806 items belonging to 10 insect and one arachnid orders (Table I), however insects dominated the faecal fragments as the 36 Araneae items accounted for only 1.28% of items. The most abundant order was Coleoptera (31.08%) which were mainly Carabidae (9.23%), Curculionidae (4.89%), Tenebrionidae (4.81%), Scarabaeidae (4.70%) and Aphodidae (4.13%). The main additional prey were Hymenoptera (21.31%) including Formicidae (13.22%), Myrmicidae (2.99%) and Vespidae (2.42%), Diptera (13.79%) with Culicidae (7.84%) and Tabanidae (5.97%), and Orthoptera (11.40%) with Acrididae (4.49%) and Gryllidae (2.39%). Mantodea, Hemiptera, Isoptera, Ephemeroptera, Blattodea and Odonata accounted for 21.13% of prey.

Table I. Annual diet of *Asellia tridens* at El Hadj Guelmane, Timimoun (Algerian Sahara) from January 2015 to December 2015: orders/families identified in droppings, relative frequency (F%) calculated as the ratio number of items from a taxon (Nb Items)/total number of identified items.

Order	Family	Nb Items	F%
Araneae		36	1.28
Odonata		58	2.07
Ephemeroptera	Ephemeridae	92	3.28
Orthoptera	Family unidentified.	76	4.52
	Acrididae	141	4.49
	Gryllidae	103	2.39
Mantodea	Mantidae	127	5.03
Blattodea	Blattidae	126	2.70
Isoptera	Termitidae	67	3.67
Hemiptera		123	4.38
Hymenoptera	Family unidentified.	259	2.67
	Formicidae	137	13.22
	Myrmicidae	32	2.99
	Vespidae	135	2.42
Coleoptera	Carabidae	116	9.23
	Curculionidae	132	4.89
	Chrysomelidae	61	1.14
	Tenebrionidae	75	4.81
	Aphodidae	371	4.13
	Scarabaeidae	68	4.70
	Histeridae	84	2.17
Diptera	Culicidae	220	7.84
	Tabanidae	167	5.97
Total		**2806**	**100**

Seasonal variations

The inertia of the two first axes of the FCA was respectively 32.53% and 14.41%. The first axis clearly separated an autumn-winter diet (October to December) including a large amount of Odonata, Scarabaeidae, Blattodea, Acrididae, and Formicidae and Myrmicidae from a spring-summer diet (February to August) characterized mainly by Chrysomelidae and Tenebrionidae, Vespidae, Aphodidae and Araneae (Figure 1). The second half of September and the first half of January were transitional but associated with the autumn-winter diet by the hierarchical classification. This analysis clearly identified a winter diet (November-December) on one side, and an early spring diet (second half of January to first half of March) on the other side. The second axis slightly contrasted a spring diet (second half of January to May) with Chrysomelidae and a summer diet (June to the first half of September) with Gryllidae.

The difference between autumn-winter and spring-summer diets (Table II) was highly significant (chi-square test = 118.56, dl = 22, p < 0.001). The major contributions to this difference were already listed above. When considering only orders the difference was again highly significant (chi-square test = 31.59, dl = 10, p < 0.001); the autumn-winter diet including more Odonata, Blattodea and Isoptera, and less Mantodea and Coleoptera than expected under the null hypothesis.

The winter diet (Table III) was also significantly different from the autumn and early spring diet (chi-square test = 36.17, dl = 20, p = 0.015) due mainly to the low numbers of Odonata, Carabidae and Tenebrionidae. At last, the early spring diet differed from the summer diet too (chi-square test = 41.80, dl = 22, p = 0.007). This early spring diet was characterized by lower numbers of Araneae, Orthoptera Gryllidae, Hymenoptera Vespidae and Coleoptera Curculionidae and higher numbers of Acrididae and Formicidae. When considering only orders, the difference was also significant between the autumn and early spring diets (chi-square test = 21.25, dl = 10, p = 0.019) due mainly to a large amount of Odonata in the winter. The difference was not significant between the early spring and the late spring-summer diets (chi-square test = 6.68, dl = 10, p = 0.756).

Discussion

As previously reported (Jones et al. 1993; Whitaker et al. 1994; Feldman et al. 2000; Benda et al. 2001, 2006, 2012, 2014; Whitaker & Yom-Tov 2002;
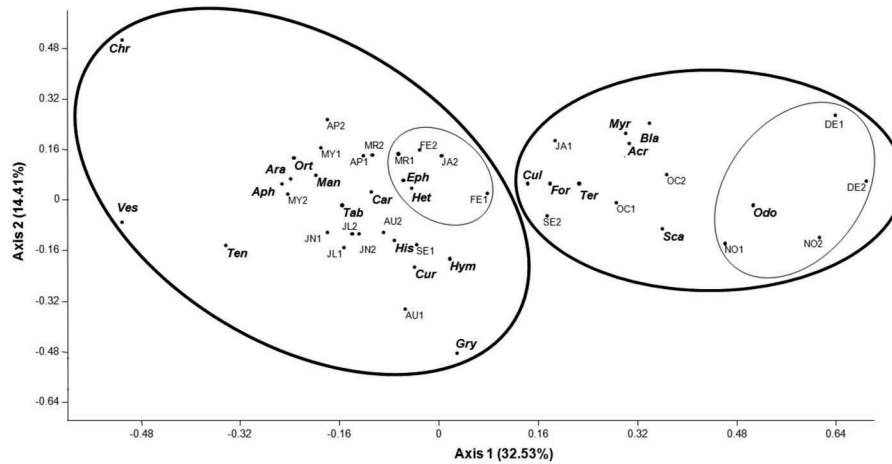
Figure 1. Plot of the two first axes of the Factorial Correspondence Analysis (FCA) projecting order/family prey items (acronyms in bold are given in Table II) of *Asellia tridens* at El Hadj Guelmane, Timimoun (Algerian Sahara) and collecting dates from JA1: first half of January to DE2: second half of December (JA: January, FE: February, MR: March, AP: April, MY: May, JN: June, JL: July, AU: August, SE: September, OC: October, NO: November, DE: December).

Table II. Seasonal diet of *Asellia tridens* at El Hadj Guelmane, Timimoun (Algerian Sahara) from January 2015 to December 2015 according to seasons identified by the first level of a hierarchical classification performed on the co-ordonates of a factorial correspondence analysis: relative frequency of orders/families identified in droppings. Jan: January, Sep: September; 1: first half of the month, 2: second half of the month. The main items contributing to a chi-square test are in bold.

Order	Family	Acronyms	Autumn-Winter Sep2 - Jan1	Spring-Summer Jan2 - Sep1
Araneae		Ara	1.22	1.30
Odonata		Odo	**3.21**	1.72
Ephemeroptera	Ephemeridae	Eph	2.90	3.39
Orthoptera	Family unidentified.	Ort	**2.60**	5.11
	Acrididae	Acr	6.11	4.00
	Gryllidae	Gry	2.60	2.32
Mantodea	Mantidae	Man	3.36	5.53
Blattodea	Blattidae	Bla	**4.27**	2.23
Isoptera	Termitidae	Ter	5.04	3.25
Hemiptera		Het	4.43	4.37
Hymenoptera	Family unidentified.	Hym	2.75	2.65
	Formicidae	For	**16.34**	12.27
	Myrmicidae	Myr	**4.58**	2.51
	Vespidae	Ves	**0.15**	3.11
Coleoptera	Carabidae	Car	7.48	9.76
	Curculionidae	Cur	5.34	4.74
	Chrysomelidae	Chr	**0.15**	1.44
	Tenebrionidae	Ten	**1.98**	5.67
	Aphodidae	Aph	**2.44**	4.65
	Scarabaeidae	Sca	**7.33**	3.91
	Histeridae	His	1.53	2.37
Diptera	Culicidae	Cul	9.77	7.25
	Tabanidae	Tab	4.43	6.42

Amichai et al. 2013; Žďárská 2013), *Asellia tridens* mainly feeds on insects even if we found some spider remains as Whitaker and Yom-Tov (2002) did in the Jordan valley (Israel). As in these studies, except for a very small sample from the Dead Sea (Whitaker et al. 1994), Coleoptera were the most abundant. As in several species of insectivorous bats (e.g. Graclik & Wasielewski 2012; Smirnov & Vekhnik 2014),

Table III. Seasonal diet of *Asellia tridens* at El Hadj Guelmane, Timimoun (Algerian Sahara) from January 2015 to December 2015 according to seasons identified by the third level of a hierarchical classification performed on the co-ordonates of a factorial correspondence analysis: relative frequency of orders/families identified in droppings. Jan: January. Mar: March. Sep: September. Oct: October. Nov: November. Dec: December; 1: first half tof the month. 2: second half of the month. ⋆ includes also Jan1. The main items contributing to chi-square tests within the seasons are in bold.

Order	Family	Autumn	Winter	Early spring	Late spring-Summer
		Sep 2–Oct 2⋆	Nov 1–Dec 2	Jan 2–Mar 1	Mar 2–Sep 1
Araneae		**1.76**	**0.39**	**0.47**	1.51
Odonata		1.51	5.84	1.40	1.80
Ephemeroptera	Ephemeridae	3.27	2.33	3.49	3.37
Orthoptera	Family unidentified.	3.27	1.56	6.05	4.88
	Acrididae	4.77	8.17	**5.58**	3.60
	Gryllidae	2.01	3.50	**0.70**	2.73
Mantodea	Mantidae	3.77	2.72	4.65	5.75
Blattodea	Blattidae	3.52	5.45	2.09	2.27
Isoptera	Termitidae	4.77	5.45	3.49	3.20
Hemiptera		5.53	2.72	5.35	4.13
Hymenoptera	Family unidentified	2.26	3.50	2.09	2.79
	Formicidae	16.08	16.73	**16.05**	11.33
	Myrmicidae	4.27	5.06	3.02	2.38
	Vespidae	0.25	0.00	**0.93**	3.66
Coleoptera	Carabidae	9.05	**5.06**	11.86	9.24
	Curculionidae	6.03	4.28	**3.02**	5.17
	Chrysomelidae	0.25	0.00	1.16	1.51
	Tenebrionidae	**3.02**	**0.39**	5.58	5.69
	Aphodidae	2.76	1.95	3.26	5.00
	Scarabaeidae	6.53	8.56	3.72	3.95
	Histeridae	1.26	1.95	3.26	2.15
Diptera	Culicidae	9.30	10.51	6.74	7.38
	Tabanidae	4.77	3.89	6.05	6.51

Coleoptera were the main prey in spite of seasonal variations of food availability. Scarabaeidae and Carabidae were also reported by Whitaker and Yom-Tov (2002), but not Curculionidae, Tenebrionidae and Aphodidae, which were possibly gathered in the group "other", and Chrysomelidae were less abundant in the Timimoun samples.

The main additional prey differed among the studies. In our study Formicidae were the main prey even if they accounted for a small volume. Hymenoptera were also abundant in two Israeli studies (Whitaker et al. 1994; Feldman et al. 2000) where they were not identified at the family level. Myrmecophagy could be associated to poor environments as in arid and desert areas (Znari & El Mouden 1997; Znari et al. 2000). Our third most consumed insect order was Diptera (Culicidae and Tabanidae). These are among the most abundant nocturnal insects detected by high frequency calls with short wavelengths (Jones & Rydell 1994), and *A. tridens* emits CF/FM calls including a CF-frequency between 108 and 124 kHz (Gustafson & Schnitzler 1979; Jones et al. 1993). Diptera were also abundant in two other Israeli studies (Whitaker & Yom-Tov 2002; Amichai et al. 2013), Chironomidae being the most numerous due to mass emergences from local fish-ponds in summer.

Orthoptera were the fourth most consumed insect order by Timimoun *A. tridens* colony. Together with Coleoptera, they are typical prey of gleaners (Patterson et al. 2003). They were also abundant in two Israeli samples (Whitaker et al. 1994; Whitaker & Yom-Tov 2002) and two Syrian samples (Benda et al. 2006). Contrary to our study, the main additional prey were Heteroptera (Hemiptera) in one Israeli sample (Amichai et al. 2013) and one Omani sample (Žďárská 2013), together with Auchenorrhyncha (Hemiptera) in one Syrian sample (Benda et al. 2006) and two Iranian samples (Benda et al. 2012). However the main difference is the absence of Lepidoptera at Timimoun while this group was the second one in the Jordan valley (Whitaker & Yom-Tov 2002), in Gambia (Jones et al. 1993) and two Syrian samples (Benda et al. 2006), and even the first group in a small sample from the Dead Sea (Whitaker et al. 1994). This difference can be explained by the semi-desert environment of the later sites whereas Timimoun is

located in a harsh desert. If we add Trichoptera, Neuroptera and Dermaptera (Feldman et al. 2000; Whitaker & Yom-Tov 2002; Benda et al. 2006) to Blattodea, Mantodea, Odonata and Ephemeroptera to the list of incidental prey of *A. tridens*, we confirm that this bat has a broad diet and could be considered as a "generalist" species following Smirnov and Vekhnik (2014). Despite a specialized foraging strategy reported by Jones et al. (1993), Whitaker et al. (1994) and Amichai et al. (2013), *A. tridens* hunts whatever prey is available at its foraging site as most insectivorous bat species do (Fenton 1982). This combination of behaviour and diet has been recorded in most desert bat species studied so far: *Antrozous pallidus* in Arizona (Fenton & Morris 1976) and Sonora in New Mexico (Bell 1982), *Rhinopoma microphyllum, R. hardwickii* and *Nyctinomus aegyptiacus* in Rajasthan, India (Advani 1981, 1982a, 1982b), *R. microphyllum* and *R. cystops* in Israel (Whitaker & Yom-Tov 2002), *Otonycteris leucophaea* in Kirghistan (Arlettaz et al. 1995) and *Otonycteris hemprichii* Israel (Fenton et al. 1999).

Feeding opportunism constitutes an adaptation to changing environmental conditions, and *Asellia tridens* seemed to adapt its feeding ecology to local, and probably seasonal, prey availability and abundance (Amichai et al. 2013). Seasonal variations of prey in the Timimoun Region were prominent during our study. They were probably a response to seasonal changes in abundance of each category of prey, which is related to water and vegetation availability in the Sahara (Rebelo & Brito 2006).

Seasonal variations of the diet of *A. tridens* were investigated for the first time, but for comparisons we can refer to similar studies of desert bat species, unfortunately not in the Sahara and not in the same harsh conditions. For instance in Rajasthan the diets of *Rhinopoma microphyllum, R. hardwickii* and *Nyctinomus aegyptiacus* changed along the four identified seasons (Advani 1981, 1982a, 1982b) with huge species differences. So Coleoptera were the main prey (ca. 40%) for *R. microphyllum* in the winter and post-monsoon season, for *R. hardwickii* only in the post-monsoon season and for *N. aegyptiacus* in the summer and winter. Isoptera were the main prey (24–48%) for the three species in the monsoon season. Finally, Orthoptera were the main prey (23–26%) for *R. hardwickii* in the summer and winter. We did not record such differences in the seasonal diet of *A. tridens* at Timimoun. When pooling families, Coleoptera were less abundant prey than for those sympatric species, particularly in winter (22.19% vs 28.90–32.71% in the three other seasons) and

Hymenoptera were always the secondary prey with a slight difference between the summer (20.16%) and the winter (25.29%). Diptera and Orthoptera also displayed slight differences, 12.09–14.40% and 10.05–13.23% respectively. The main differences were observed for the large amount of Odonata and Blattodea in the winter. This abundance of Odonata may be related to the migration of some species such as *Hemianax ephippiger* which concentrates in the Sahara during the cold season before moving to more northern regions in the spring (Dumont 1977, 1988; Dumont & Desmet 1990). Blattodea are also an available group of insects in the winter in the area, so they were also among the main prey of the desert hedgehog *Paraechinus aethiopicus* (Loumassine 2014) and the second insect prey of the barn owl *Tyto alba* (Belkacem 2017).

Most Coleoptera families (Chrysomelidae, Tenebrionidae, Aphodidae and Carabidae) were less abundant in the winter, except Scarabaeidae whose reproduction is favoured by mild and cool weather (Haloti et al. 2006). Formicidae and Myrmicidae were main prey too. With the high number of Termitidae, this result shows that this season is poor in large insects which are the main prey of *A. tridens* according to Whitaker et al. (1994). The consumption of Acrididae can be related to the migration of the desert locust to oases (Ould Elhadj 2002; Allal–Benfekih 2006; Kara-Toumi et al. 2010).

During spring, Formicidae were still a major component of the diet together with Acrididae which are more common during this season (Souttou 2010). However, Araneae and Vespidae, which are not active during the cold season, were less hunted than in the summer, as well as Curculionidae and Gryllidae, the latter reaching the last larvae stages (Lakhdari et al. 2015). These seasonal variations support the model in which certain predators tend to specialize when resources become abundant in environment by searching profitable and common prey (Boukhemza et al. 1994).

Conclusions

Apparently, *Asellia tridens* has a large geographic range both in latitude and longitude, overlaying different temperature and precipitation conditions which presumably impact the number and diversity of arthropods at each location (Kunz 1974; Jones & Rydell 1994; Moosman et al. 2012). These variations are overcome by a broad diet even if this bat mainly hunt terrestrial prey, Coleoptera and

Orthoptera, as most Saharan bat species do (Benda et al. 2012). Emergence and abundance figures for each prey items should be further investigated. Besides, soft-bodied prey items could be identified by DNA barcoding.

We consider that, according to the presence of the colony throughout the year, this site does not present food restrictions that the species cannot deal with. Yet, as the Sahara could experience the fastest climate change among world deserts (Loarie et al. 2009), global warming and increasing aridity will affect arthropod resources for bats. Whereas *A. tridens* still form large colonies in the North-African desert, conservation measures should be undertaken, at least for protecting their roosts, as part of optimised conservation suggested by Brito et al. (2014).

Acknowledgements

Authors' contributions

Availability of data and materials

All material is stored in the University of Tiaret. Raw data are provided in the tables.

Disclosure statement

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