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Bats of the Tunisian Desert: Preliminary Data Using Acoustic Identification and First Record of *Taphozous nudiventris* in the Country

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Abstract: Increasing aridity usually results in decreasing bat abundance and species richness, and the Saharan desert is an example of such impoverishment. Moreover, the harsh climatic and field conditions in this area restrict the feasibility of surveys. Therefore, the bat fauna of the Tunisian Sahara was unstudied until an expedition was conducted in May 2021. A total of seven species were recorded using passive bat detectors set mainly at water bodies, which concentrate bat activity. Echolocation calls of these species did not depart from published records for the Mediterranean area. Our data failed to identify the two ecomorphotypes of *Pipistrellus kuhlii* but confirmed the adaptability of this species to local conditions. For the first time in Tunisia, we recorded echolocation calls of *Taphozous nudiventris*, a species that has been rarely reported in North Africa. The highest species richness was identified at the largest wetlands of Oued Daghsen (Oued Dkouk Nature Reserve) and at Bordj el Khadra (only six and four species, respectively). Most Mediterranean species were recorded in the northern locality, while desert species were more active in the most southern one. The importance of water bodies for bats was confirmed once more. No sign of competition among species was detected, as the Mediterranean and desert-dwelling bat species were active at the same time. Additional surveys should be planned in order to enlarge the list of seven species recorded in only one week.

Keywords: Chiroptera; distribution; acoustic; activity; Sahara

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1. Introduction

Species richness in bats shows a classic latitudinal gradient from the temperate zones to the tropics, but not in Africa, where richness drops in the arid regions of North Africa and the Arabian Peninsula [1], rendering large parts of the Sahara desert void of bats [2]. As most bat species require access to water sources for drinking and often benefit from water-emergent insects [3], increasing aridity should result in decreasing bat abundance and species richness at local and regional scales [4]. Moreover, as some species need to drink directly after emerging from roosts, the proximity of roosts to water is the major factor of local occurrence [5]. Globally, bats in arid regions concentrate activity over open water [6], possibly exacerbating competitive interactions and influencing population numbers among coexisting species [4,7]. Both the size and accessibility of a water source influence whether a bat can drink from it and, as a consequence, the species richness of bats and activity [6,8].

The Sahara is the largest desert in the world, hosting 22 [9] or 26 [10] species of bats. According to [11], 23 species were recorded in the area excluding the Nile Valley, which benefits from the range extension of several tropical and Mediterranean species. However, only 11 species of bats have been reported from the core Sahara, where none is endemic. This number appears very low when compared with the 1462 bat species currently recognized in the world [12]. The species richness of Saharan bats has weakly increased in the last decades, whereas their distribution improved a lot after recent surveys, mainly in northern countries (syntheses in [13] for Algeria, [14] for Morocco, [15] for Libya, and [16] for Egypt).

In Tunisia, after two reviews [17,18], several studies improved our knowledge of the distribution, habitat, and seasonal activity of bats in the northern and central areas of the country [19–22]. The unique recent record for the Saharan area was collected during a tourist visit to Jbil National Park, Great Oriental Erg [23]. Therefore, it was a great opportunity to take part in a multidisciplinary expedition in the southernmost part of the country, where access is difficult and steadily controlled. The aim of our study was to survey bat assemblages along the way in order to investigate the occurrence of desert and mesic bat species, hypothesizing that the harsh conditions of the area would exclude the latter spatially and temporarily. Bat species richness should decrease along a gradient from north to south, whereas the overall bat activity and overnight activity pattern would especially depend on the available habitats. Moreover, the activity pattern of desert bat species should be independent of the availability of water, contrary to mesic bat species.

Due to the relatively short period of time devoted to the fieldwork, acoustic recording was the optimal method for obtaining enough results to investigate both hypotheses. However, scanty information is relevant for unambiguously identifying calls of bat species in the Sahara, so we performed several analyses focusing particularly on the most widely distributed species: *Pipistrellus kuhlii*. As a matter of fact, this species was until recently considered to be replaced in the Sahara by *P. deserti*, a smaller and lighter but very similar bat reported from other North African countries: Morocco, Algeria, Libya, and Egypt [24]. Recent genetic analyses involving both mitochondrial and nuclear markers showed that the latter was only an ecomorphotype of a North African subspecies of Kuhl's pipistrelle, *P. kuhlii marginatus* [25–27]. We then hypothesized that the smaller size of this desert form anticipates a different acoustic signature, as a relationship between size and echolocation calls has been reported for several genera of bats [28].

2. Material and Methods

2.1. Data Collection and Species Identification

From 14 to 20 May 2021, acoustic bat activity was sampled at six localities for eight sites of the Tunisian desert from the west of Dhaher to Grand Erg Oriental and Borj El Khadra (Table 1, Figure 1). The study area belongs to the lower arid and Saharan (upper and lower) bioclimatic stages with an annual average rainfall below 100 mm and a cold, dry, and windy winter and hot and arid summer. The most common soils are sand dunes and sandy limestone and gypsum soils [29].

Each site was surveyed for one whole different night under favorable weather conditions (no rain, no strong wind) using automatic echolocation call recording at fixed points starting 30 min before sunset and lasting 30 min after sunrise. Two bat detectors were available: a Batlogger M (Elekon, Luzern, Switzerland) and a Song Meter SM2+ (Wildlife Acoustic, Inc. Concord, Massachusetts, U.S.A.), which was connected to a BMX–US1 microphone (Biotope, France) with a 3 m cable.

Real-time recordings were made at a sampling frequency of 384 kHz and an activation frequency of −18 bB and 8 Hz. Recorded sequences were unzipped, analyzed, and split into 5 s sequences with Kaleidoscope (Wildlife Acoustic, Inc. Version 4.1.0a). Only 5 s sequences containing bat calls were analyzed using the real-time analysis software BatSound, v.3.10 (Petterson Elektronik AB), for spectrogram analyses. We used a simple frequency of 38.400 samples/s, 16 bits/sample, and selected 512 pt FFT with a Hamming window for analysis [30]. Recorded calls, including feeding and drinking buzzes [31], were manually identified to species level using the shape and several parameters of calls based on the unpublished sound library of R. Dalhoumi collected in different places in Tunisia [22]. Based on the shape, we distinguished constant-frequency calls (CF), quasi-constant-frequency calls (QCF), frequency-modulated calls (FM), and combinations of these components. Then, we measured the following characteristic parameters: start frequency (SF), end frequency (EF), frequency of maximum energy (FMAXE), duration of call (D), and inter-pulse interval (IPI) [28]. Identifications were ascertained by comparisons with data previously published for southern Mediterranean bat species.

Table 1. Main characteristics (coordinates and biotopes) of localities of the Tunisian desert sampled for bats in May 2021.

Habitats		GPS Coordinates	Biotopes
Oued Dkouk Nature Reserve		32.624197, 10.308822	Open habitat, Oued Daghsen bed with small lakes of salt water from Aïn Edkouk. The vegetation is sparse and represented by *Tamarix gallica*, *Limonium pruinosum*, *Phragmites australis*, *Sarcocornia fruticosa*, and *Frankenia pulverulenta*.
Senghar Jabbes National Park	Lighted place	31.958655, 9.547339	Open habitat lighted with a lamp fixed to a wall.
	Small trough	31.940659, 9.528980	Open habitat including an artificial small trough.
Lorzet		31.765947, 10.347375	Small artificial trough near old human buildings.
Ain Rhziza		31.657026, 9.659167	Open habitat including a water lake (50 m^2) surrounded by groves of *Tamarix aphylla* and *T. gallica.*
Ain Skhouna		30.622722, 10.031079	Open habitat corresponding to an isolated greenery (less than 0.5 ha) in the desert close to a hot spring. The vegetation cover includes *Tamarix aphylla*, *Phragmites australis*, *Juncus maritimus*, *Tetraena alba*, *Phoenix dactylifera*, *Retama sphaerocarpa*, *Imperata cylindrica*, *Stipagrostis pungens*, and *Oudneya africana*.
Bordj el Khadra	Reed bed	30.254260, 9.558299	Open habitat including a small sewage water body. The vegetation includes *Phragmites australis*, *Tetraena alba*, *T. geslinii*, and *Tamarix gallica.*
	Oasis	30.250482, 9.558967	Semi-open habitat inan old abandoned oasis. The vegetation cover is dominated by *Phoenix dactylifera*, *Eucalyptus* spp., *Acacia* spp., *Heliotropium curassavicum*, *Tamarix aphylla*, *Cistanche violacea*, *Tetraena alba*, *T. geslinii*, and *Frankenia pulverulenta*.

2.2. Data Analysis

Bat activity was estimated by counting the number of passes [32]. A bat pass was defined as a single or several calls emitted by a single animal during a 5 s interval [28]. Within each night, we considered 19 periods of 30 min to investigate activity patterns; the number of bat passes recorded during each period was used as a proxy of bat activity. Feeding and drinking buzzes were also investigated in order to evaluate the resources sought by bats in the different sampled habitats. Call recordings were used to calculate species richness at each site. We used Chi-square tests to assess differences in bat activity among sites and among periods of the night at four sites where bats were particularly active.

We also performed analyses in order to possibly identify the two ecomorphotypes of *P. kuhlii* in the whole sample and at each site using exploratory statistics (principal component analyses and Gaussian mixture models) performed in R software [33]. We also compared the call parameters among four sites where bats were particularly active using Kruskal–Wallis tests, as data were not normally distributed, followed by ad hoc multiple paired comparisons.

Figure 1. Bat sampling sites in May 2021 in the Tunisian desert. 1: Oued Dkouk Nature Reserve, 2: Senghar Jabbes National Park, 3: Lorzet, 4: Ain Rhziza, 5: Ain Skhouna, and 6: Bordj el Khadra.

3. Results

3.1. Species Identification

A total of 5721 bat echolocation sequences were recorded from seven bat species including four Mediterranean species and a species new for Tunisia (Table 2). Among the six species that were easily identified, one emitted CF/FM calls with a frequency of maximum energy (FMAXE) of 118.90 ± 1.54 kHz, within the range of the desert-dwelling trident leaf-nosed bat, *Asellia tridens* (Table 3). Three species emitted FM/QCF calls with an FMAXE of 12.16 ± 0.81 kHz, 25.76 ± 1.03 kHz, and 42.91 ± 1.91 kHz, supporting the identification of the European free-tailed bat, *Tadarida teniotis*, the isabelline serotine, *Eptesicus isabellinus*, and the Kuhl's pipistrelle, *Pipistrellus kuhlii*, respectively. The last two species emitted FM calls with an FMAXE of 22.97 ± 2.80 kHz and 28.10 ± 1.20 kHz in the first harmonic, suggesting the recording of the Hemprich's long-eared bat, *Otonycteris hemprichii*, and the Maghrebian long-eared bat, *Plecotus gaisleri*, respectively.

Table 2. The number of bat passes, feeding (between brackets), and drinking buzzes (italics) in some localities of the Tunisian desert collected in May 2021. D: desert-dwelling species, M: Mediterranean species.

Species \ Locality	Oued Dkouk Nature Reserve	Ain Rhziza	Ain Skhouna	Bordj el Khadra	
				Reed Bed	Oasis
Asellia tridens D	-	-	-	5	81 (17)
Tadarida teniotis M	21	-	-	-	-
Eptesicus isabellinus M	113 (3)	-	-	-	-
Pipistrellus kuhlii M, D	702 (36)	2304 (621–*42*)	18 (4)	379 (18)	1212 (105)
Plecotus gaisleri M	3	-	-	2	-
Otonycteris hemprichii D	12 (1)	-	-	10	-
Chiroptera sp.	12	-	-	-	-
Total	**903**	**2967**	**22**	**414**	**1415**
Species richness	6	1	1	4	2

Table 3. Frequency and time parameters of echolocation calls for six bat species of the Tunisian desert. CS: call structure, CF: constant frequency, FM: frequency modulated, QCF: quasi-constant frequency, N: number of measured calls, S: number of analyzed sequences, SF: start frequency; EF: end frequency; FMAXE: frequency of maximum energy; D: duration; IPI: inter-pulse interval. Mean ± sd values are shown above the range.

Species	CS	N (S)	SF (kHz)	EF (kHz)	FMAXE (kHz)	D (ms)	IPI (ms)
Aselia tridens	CF/FM	94 (94)	-	105.22 ± 3.56 [93.4–112.3]	118.90 ± 1.54 [113.0–122.3]	9.47 ± 1.74 [5.7–12.8]	48.60 ± 13.33 [23.8–89.2]
Tadarida teniotis	FM/QCF	11 (11)	13.20 ± 1.76 [11.4–16.7]	11.71 ± 0.70 [11.1–12.8]	12.16 ± 0.81 [11.3–13.0]	14.25 ± 2.06 [10.7–17.3]	772.13 ± 179.48 [634.9–1095.0]
Eptesicus isabellinus	FM/QCF	109 (109)	38.74 ± 8.21 [25.8–61.8]	24.28 ± 1.01 [21.8–26.4]	25.76 ± 1.03 [23.3–27.9]	12.44 ± 2.63 [7.2–18.5]	241.01 ± 74.08 [104.5–483.2]
Pipistrellus kuhlii	FM/QCF	1940 (1940)	59.60 ± 10.97 [39.7–101.6]	42.13 ± 1.91 [36.8–48.4]	42.91 ± 1.91 [36.9–49.5]	6.10 ± 1.18 [3.6–11.8]	181.81 ± 82.16 [8.4–716.5]
Otonycteris hemprichii	FM	18 (18)	46.68 ± 6.35 [30.7–55.9]	17.72 ± 1.40 [15.7–18.9]	22.97 ± 2.80 [18.9–27.7]	6.49 ± 1.54 [4.0–8.4]	200.92 ± 61.65 [112.2–313.9]
Plecotus gaisleri	FM	5 (5)	43.00 ± 4.27 [38.1–48.3]	20.06 ± 3.46 [15.7–24.3]	28.10 ± 1.20 [26.4–29.7]	3.44 ± 0.66 [2.3–4.0]	135.30 ± 42.12 [85.6–186.2]

The seventh bat species, recorded from 20:07 to 20:14 in Oued Dkouk Nature Reserve, produced long QCF multiharmonic calls (Figure 2) with an FMAXE of 23.17 ± 0.80 kHz measured at the second harmonic (Table 4). Both criteria identified the naked-rumped tomb bat *Taphozous nudiventris*.

Echolocation calls of *P. kuhlii* were highly variable, including different types from QCF to deep FM with a bandwidth ranging from 0 to 58.3 kHz and the FMAXE ranging from 36.9 to 49.5 kHz (Table 5). However, the principal component analyses and Gaussian mixture models failed to link the variability in any call parameter to differences between the two ecomorphotypes. Echolocation calls were also quite variable among the four main sites where the species was recorded (Oued Dkouk Nature Reserve, Ain Rhziza, and Bordj el Khadra reed bed and oasis) for the five measured parameters according to the Kruskal–Wallis tests, which were all highly significant (Supplementary Material, Table S1). Start frequency was higher at Ain Rhziza than at the other sites according to ad hoc multiple paired comparisons. The FMAXE and end frequency were different among sites, except between Bordj el Khadra reed bed and Bordj el Khadra oasis. The differences among sites for duration and interpulse intervals were not so informative.

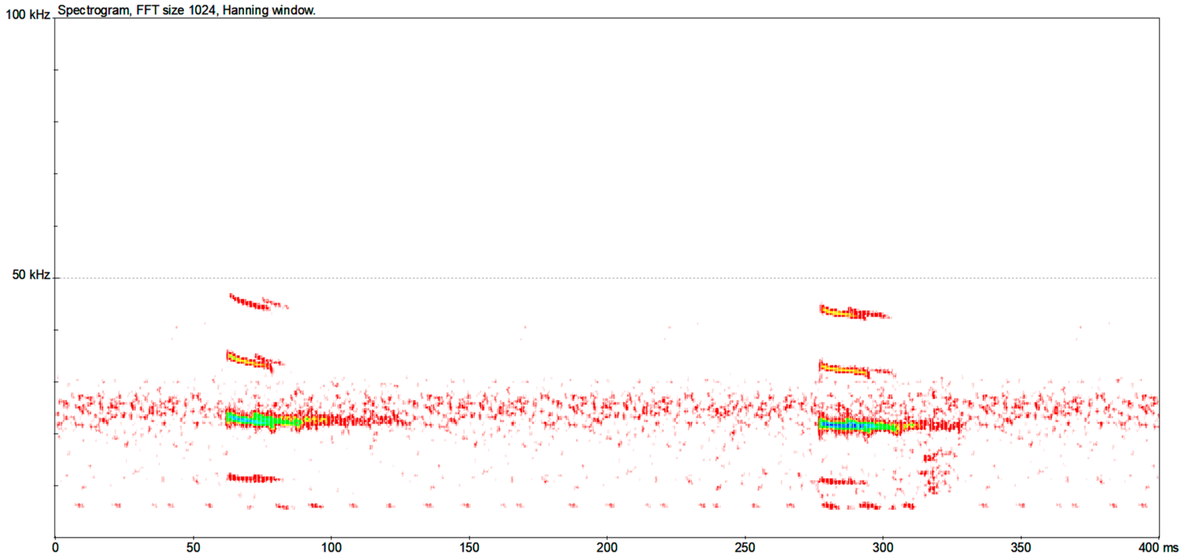

Figure 2. Two calls of *Taphozous nudiventris* recorded in May 2021 in Oued Dkouk Nature Reserve (southern Tunisia).

Table 4. Call parameters measured from 7 sound sequences (22 signals) of *Taphozous nudiventris* recorded in the Tunisian desert, in Jordan (Benda et al., 2010), and the Near East (Hackett et al., 2017). Q1 and Q3 are the lower and upper quartiles.

Parameters	Mean ± SD	Range	Median	Q1	Q3	Jordan	Near East
SF (kHz)	23.67 ± 1.09	21.8–26.3	23.4	23.2	23.6	26.1 ± 1.0	24.39 ± 1.55
EF (kHz)	22.42 ± 0.72	21.7–23.6	22.0	21.8	23.3	22.2 ± 0.6	22.80 ± 1.29
FMAXE (kHz)	23.17 ± 0.80	21.7–24.9	23.3	23.2	23.5	24.5 ± 0.5	23.38 ± 1.31
D (ms)	18.86 ± 3.32	13.1–26.4	18.5	16.6	20.6	15.4 ± 2.6	12.99 ± 3.50
IPI (ms)	420.17 ± 168.4	153.1–719.0	398.8	344.6	548.0	363.9 ± 115.1	-

Table 5. Frequency and time parameters of echolocation calls for *Pipistrellus kuhlii* at four sites of the Tunisian desert. N: number of measured calls, SF: start frequency, EF: end frequency; FMAXE: frequency of maximum energy; D: duration; IPI: inter-pulse interval. Mean ± sd values are shown above the range, and the median is shown in the third raw.

	Oued Dkouk N. R. N = 541	Ain Rhziza N = 143	Bordj el Khadra Reed Bed N = 196	Bordj el Khadra Oasis N = 1037
SF (kHz)	58.66 ± 11.02 38.4–101.6 57.3	64.37 ± 13.28 47.3–100.8 60.4	58.99 ± 12.83 41.2–92.0 57.2	59.39 ± 9.96 39.8–100.5 57.8
EF (kHz)	40.36 ± 1.32 36.8–45.6 39.9	40.82 ± 1.75 37.8–45.6 40.2	42.65 ± 1.45 38.4–45.6 42.8	43.14 ± 1.48 39.7–48.4 43.3
FMAXE (kHz)	41.19 ± 1.38 36.9–46.3 41.3	42.27 ± 1.75 38.6–46.3 41.8	43.41 ± 1.53 39.9–47.3 42.8	43.81 ± 1.58 39.7–49.5 43.4
D (ms)	6.00 ± 1.14 4.0–11.8 5.9	5.70 ± 0.85 4.0–9.5 5.7	5.86 ± 1.36 4.0–11.0 5.6	6.25 ± 1.19 3.6–10.6 6.2
IPI (ms)	165.16 ± 76.28 8.4–563.5 169.5	138.42 ± 58.35 42.4–275.6 111.5	169.64 ± 76.18 61.3–716.5 184.2	198.76 ± 85.03 56.5–528.6 195.5

3.2. Species Richness and Bat Activity Patterns

Even if bats were mainly detected at water bodies, the activity and richness varied among sites, with no bat being detected at three sites (Senghar Jabbes National Park lighted place and small trough and Lorzet). The highest bat activity was recorded above the permanent water lake at Ain Rhziza, and the highest bat richness was recorded along the northernmost Oued Daghsen in Oued Dkouk Nature Reserve (n = 6). Only one bat species was detected at Ain Rhziza and Ain Skhouna, i.e., *P. kuhlii*, which was the most active species at the other sites. The other species were recorded either in Oued Dkouk Nature Reserve or at Bordj el Khadra (reed bed and oasis), a unique site where *A. tridens* was detected. *T. teniotis* and *E. isabellinus* were only detected in Oued Dkouk Nature Reserve. Calls of *P. gaisleri* and *O. hemprichii* were recorded in the reed bed of Bordj el Khadra and in Oued Dkouk Nature Reserve.

The overnight activity of bats was significantly different among sites and periods (Chi-square tests, $p < 0.001$, Table S2) with a huge peak in activity between 20:50 and 21:20 at Ain Rhziza (*P. kuhlii*) and Bordj el Khadra reed bed (*P. kuhlii* + *O. hemprichii*), whereas the activity peaked between 20:20 and 20:50 in Oued Dkouk Nature Reserve and between 22:50 and 23:20 in Bordj el Khadra oasis (Figure 3). In Oued Dkouk Nature Reserve, *P. kuhlii* was active overnight, *E. isabellinus* in the first part of the night (20:20–23:50), and *T. teniotis* in the second part (01:50–04:50). In Bordj el Khadra oasis, *P. kuhlii* was active overnight, and *A. tridens* was active between 20:20 and 00:50 (Figure 4). Feeding and drinking buzzes were mainly recorded at Ain Rhziza (621 feeding + 42 drinking buzzes) between 19:50 and 02:15, peaking between 21:50 and 22:20. Feeding buzzes were also recorded in Oued Dkouk Nature Reserve (36 for *P. kuhlii* between 19:50 and 22:20, 3 for *E. isabellinus*, 1 for *O. hemprichii*) and Bordj el Khadra reed bed (18 for *P. kuhlii*).

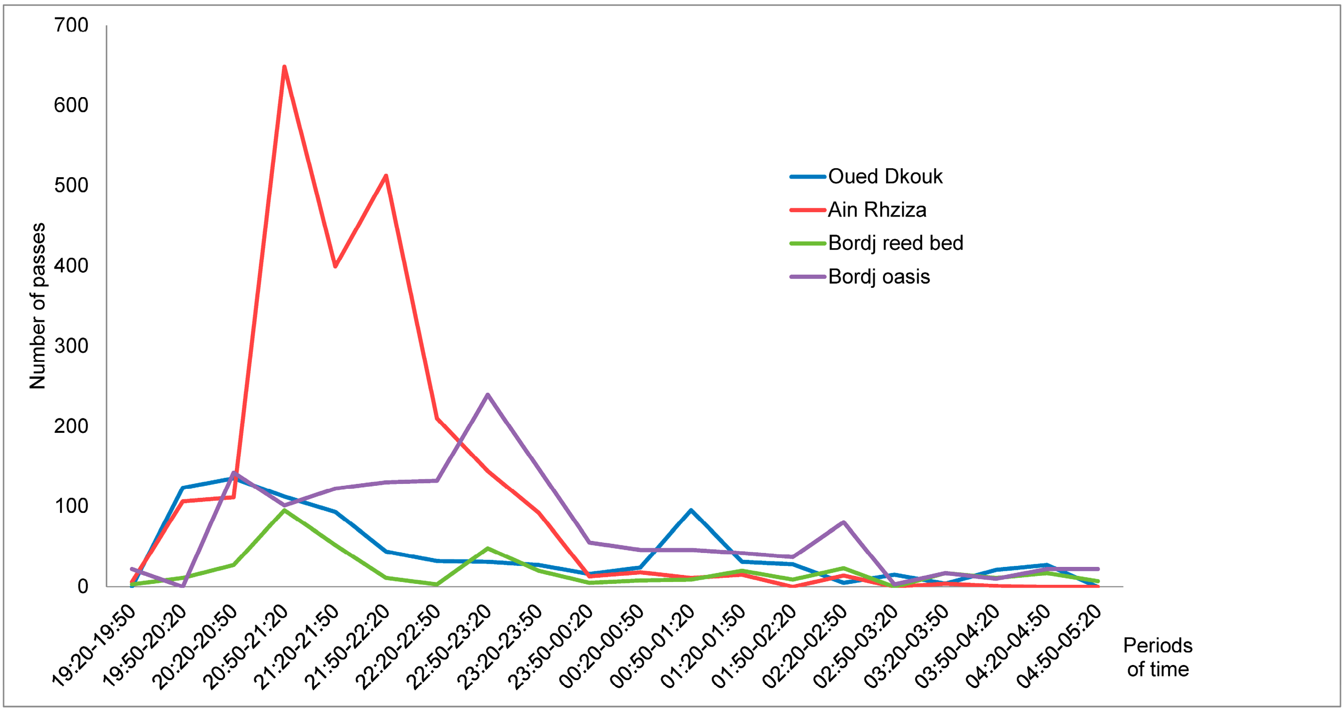

Figure 3. Night activity (number of passes per 30 min) of bats recorded in May 2021 at four localities of the Tunisian desert. Automatic echolocation call recording started 30 min before sunset and lasted 30 min after sunrise.

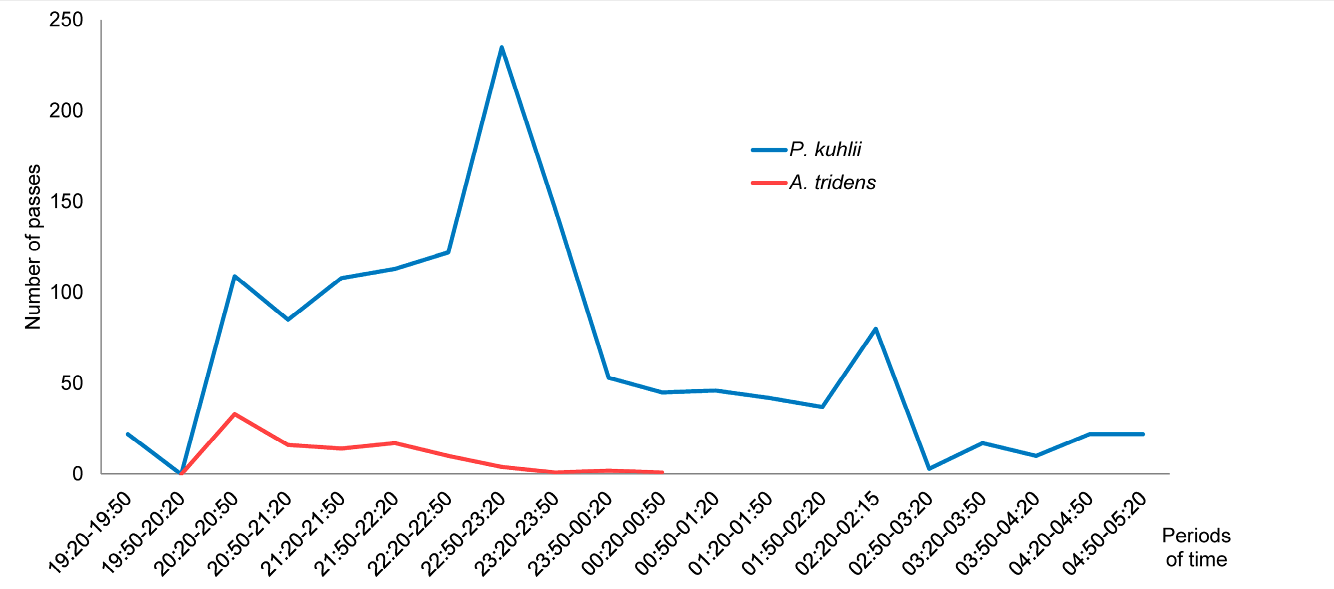

Figure 4. Night activity (number of passes per 30 min) of *Pipistrellus kuhlii* and A*selllia tridens* recorded in May 2021 at Bordj el Khadra oasis (Tunisian desert). Automatic echolocation call recording started 30 min before sunset and lasted 30 min after sunrise.

4. Discussion

4.1. Echolocation Calls of Bats in the Tunisian Desert

The identification of bat species from their echolocation call type and parameters was facilitated by huge differences among them and the low number of species expected at the northern edge of the Sahara [11]. The only CF/FM calls were identified as *A. tridens* by its FMAXE, which is only similar to that of the lesser horseshoe bat, *Rhinolophus hipposideros*, the only bat that emits calls at more than 110 kHz in the area [34,35]. However, the latter emits FM-CF-FM and almost longer calls (39.7 ± 13.2 and 24.74 ± 7.99 kHz, [34,35]). Moreover, similar calls of this species have already been reported in Tunisia [36].

The FM/QCF calls were particularly distinctive for three species. *Tadarida teniotis* emitted the lowest calls in a similar range as in Morocco [34], Algeria [37], and Malta [38], among other Mediterranean countries. These calls identify this free-tailed bat with regard to the Egyptian free-tailed bat, *Nyctinomus aegyptiacus*, reported once in Tunisia [23], which emits calls of higher frequencies (FMAXE: 19.6 ± 1.6 kHz in Morocco [39]). The call frequencies of *E. isabellinus* were still higher, fell within the range of individuals recorded in Morocco [34], and were only slightly higher than individuals recorded both in Algeria and Spain [37,40].

Pipistrellus kuhlii emitted different types of echolocation calls, including FM calls within a range of frequencies higher than the two previous species, which was only previously reported in the northern Sahara in Algeria [41]. Concerning the frequency of maximum energy including all types of calls, even if QCF calls are usually lower than true FM calls [28], it was higher in the Tunisian desert than in any other part of the Mediterranean range of the species (e.g., Italy [42], Pantelleria [43], Greece [44], Malta [38], the Near East [45], Jordan [46], Syria [47], or northern Algeria [37]), including northern Tunisia (R. Dalhoumi, unpublished data). The only similar frequencies come from central Algeria [41]. At the northern edge of the Algerian Sahara, the reported frequencies were even higher and suggested a possible identification of the two ecomorphotypes [41], which was not possible with our recordings. This discrepancy could be due to differences in sound analyses, which would require the analyses to be performed again by a unique operator. Moreover, bats of the desert ecomorphotype should be recorded after hand identification, which requires finding roosts or mist-netting, which is a challenge in a desert habitat.

Instead of identifying the two ecomorphotypes within the large variety of recorded echolocation calls, we evidenced profound differences among sites, suggesting some adaptation to each habitat type. Such adaptability has also been investigated in *P. kuhlii* among different behavioral contexts: emergence from a roost, commuting to and from foraging sites, foraging, and returning to a roost [48]. In our short field investigations, it was not possible to identify precisely this behavioral context, but feeding buzzes were mostly recorded at Ain Rhziza (20.9% of recorded sequences vs. 4.5% and 7.9% at Bordj el Khadra reed bed and oasis, respectively). The presence of a large lake (for the area) is assuredly attractive for these bats, which also emitted drinking buzzes. Then, Ain Rhziza can be identified as a foraging site for the pipistrelle, whereas Bordj el Khadra could be more of a commuting site, as suggested by a high proportion of QCF calls, which are absent at Ain Rhziza.

The last FM calls exhibiting several harmonics identified two Plecotini species that were already recorded in the northern Sahara. *O. hemprichii* emits longer calls of lower frequencies than *P. gaisleri* in our sample and in their whole range. Frequencies of the first harmonic, the call duration, and interpulse intervals of *O. hemprichii* fall within the reported ranges from Morocco [34], Malta [38], Pantelleria [43], Sinai [49], the Near East [45], and Jordan [46]. The recordings are less numerous for *P. gaisleri*, according to the smaller range of this species, which is still disputed [50]. Nevertheless, our very few sequences do not depart from reported data from Morocco [34,51], Malta [38], and Pantelleria [43] for all parameters, even if frequencies are the lowest and duration and interpulse interval the highest. Such differences could be due to the usually low number of analyzed sequences for a bat that is difficult to record and/or different methods of sound analysis, as it can be suspected for the two Moroccan sets (SF = 51.4 $\pm$ 1.1 kHz [34] vs. 41.7 kHz [51]).

4.2. Bat Assemblage and Activity Pattern

With only eight overnight acoustic surveys at eight sites with two bat detectors, we recorded seven bat species including a new species for Tunisia. This list is somewhat short when compared with the 21 species reported in the country [17,18,23]. Such low richness has already been reported in another Tunisian area of the northern Saharan border, the Dghoumes National Park [22]. These results support the hypothesis of declining bat richness in desert areas (e.g., [1,52]), which has already been reported from Egyptian and mainly Libyan oases [15,53–55]. Bat richness is slightly higher in the northern Algerian Sahara [41] and much higher in Near East deserts [3,56–58]. The short duration of the survey is assuredly a limitation as several desert-dwelling species, such as *Rhinopoma cystops* or *Vansonia rueppellii*, which have been reported in central Tunisia [20,22], were not recorded. Even if spring is assuredly the best season for sampling bats, previous studies showed that some species can be detected only at other times of the year depending on the site [20,41].

Our records extend the range of four Mediterranean bat species (*P. kuhlii*, *E. isabellinus*, *P. gaisleri*, and *T. teniotis*). *P. kuhlii* is the most widespread species in Tunisia [17] and was always the most active bat in previous studies in central and northern Tunisia [19–22], in Egypt and Libyan oases [15,53–55], and in northern Algerian Sahara [41]. However, this extent and numbers benefit from the adaptation of *P. kuhlii* to desert conditions, with an ecomorphotype that has long been considered a valid species (but see [15,25–27]). The three other Mediterranean species are also widely distributed in central and northern Tunisia [17,18], even if they have been less recorded than the pipistrelle due to the hazards in finding of their roosts, which was the main survey method in the past.

The two desert-dwelling bat species, *O. hemprichii* and *A. tridens*, were both previously reported from arid central Tunisia [17,18]. Their presence is not surprising, even if the latter was only recorded at Bordj el Khadra, whereas it was particularly active in several places in the Dghoumes National Park [22] and in the northern Algerian Sahara [41]. *O. hemprichii* is more rarely reported in North Africa [51,59], and our records extend its Saharan range.

Surprisingly, we recorded echolocation calls of a seventh species, which can only be identified as *T. nudiventris*. The end frequency was similar in Jordan and the Near East, while the start frequency was slightly lower than in both countries, and the peak frequency was similar to that in the Near East only [45,46]. Our record extends the known distribution of a species that is mainly distributed in mid-African savannas, the Middle East, and the Indian Peninsula. Reported in the central Algerian Sahara [60,61] and oases in the Libyan desert in Egypt [55], there were only two records from the northern edge of the Sahara: one in Morocco [62] and one in Algeria [63], both from owl pellets.

Overall, the bat assemblage in southern Tunisia is unbalanced in favor of Mediterranean species, mainly in the northernmost site (Oued Dkouk Nature Reserve), contrary to the Negev desert, where nine of the twelve species of bats are associated with arid areas [3]. The expansion of Mediterranean species into the desert is partly due to the introduction of artificial water bodies for sustaining human settlements [6,8] since non-desert species of bats must drink on a daily basis and more frequently compared with desert-dwelling bats [8]. Indeed, in our survey, bat activity was almost limited to water bodies and their associated vegetation, confirming the importance previously reported in Tunisia [20,22,64] and more widely (e.g., [6,8,65–67]). However, no bat call was detected at the small artificial watering trough in Lorzet, and the bat communities were more diversified and their activities were more developed over the large water bodies in Oued Dkouk Nature Reserve and the wetland of Bordj el Khadra. Feeding buzzes were recorded at these sites and at Ain Rhziza, a small lake where *P. kuhlii* was particularly active at the beginning of the night, with most buzzes when insects are particularly abundant [68,69]. Such occurrence and activity of this pipistrelle was observed in the northern Algerian Sahara [41] and in the Negev desert [3], where it was shown to compete for the use of pools [70], resulting in temporal and spatial partitioning among local bat species [7]. If *P. kuhlii* was the unique bat species at Ain Rhziza, which could support a possible exclusion of desert species, *A. tridens* displayed a joint activity in the first part of the night in Bordj el Khadra oasis. *E. isabellinus* was also mainly active at the beginning of the night together with *P. kuhlii* in Oued Dkouk Nature Reserve, as it was previously recorded in central Tunisia [20]. The size, volume, and environment of water bodies also influence their use by some species. For example, *T. teniotis* requires large water bodies for maneuvering [8], which is the case in Oued Dkouk Nature Reserve and not in the other sites. In contrast, the only highly visited site without any water body, Bordj Khadra oasis, is covered by relatively rich vegetation compared with the other sites, which supports overnight activity, as it was already recorded at the northern Saharan border [22]. This shift in bat activity related to habitat within desert areas should be investigated further.

We provided preliminary data on bat distribution and richness in Tunisian desert areas. Together with the occurrence of seven different bat species, including one species new for Tunisia, the presence of *P. kuhlii deserti* was confirmed in the country. It also shown that the Oued Daghsen in Oued Dkouk Nature Reserve and the wetland of Bordj el Khadra are key habitats for the sustainability of bats in extreme conditions, thanks to the availability of water and prey associated with a diversity of micro-habitats. This list of species may be expanded by exploring other sites and/or by carrying out additional explorations in other seasons for a longer time. Feeding resources should also be investigated and, above all, bat roosts should be searched for in order to improve our knowledge of desert-dwelling bat species and the adaptation of Mediterranean ones to arid environments in the future prospects of climate change.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d15111108/s1, Figure S1: Boxplots of frequency and time parameters of echolocation calls for *Pipistrellus kuhlii* at four sites of the Tunisian desert: SF: start frequency (kHz), FMAXE: frequency of maximum energy (kHz), EF: end frequency (kHz), BW: bandwith (kHz), D: duration (ms), IPI: interpulse interval (ms). 1: Oued Dkouk Nature Reserve, 2: Ain Rhziza, 3: Bordj el Khadra reed bed, 4: Bordj el Khadra oasis; Figure S2: Night activity (number of passes per 30 minutes) of *Pipistrellus kuhlii* (blue), *Eptesicus isabellinus* (red) and *Tadarida teniotis* (green) recorded in May 2021 at Oued Dkouk Nature Reserve (Tunisian desert). Automatic echolocation call recording started 30 minutes before sunset and lasted 30 minutes after sunrise; Table S1: Frequency and time parameters of echolocation calls for *Pipistrellus kuhlii* at four sites in the Tunisian desert: Kruskal-Wallis tests and ad-hoc multiple paired comparisons.

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