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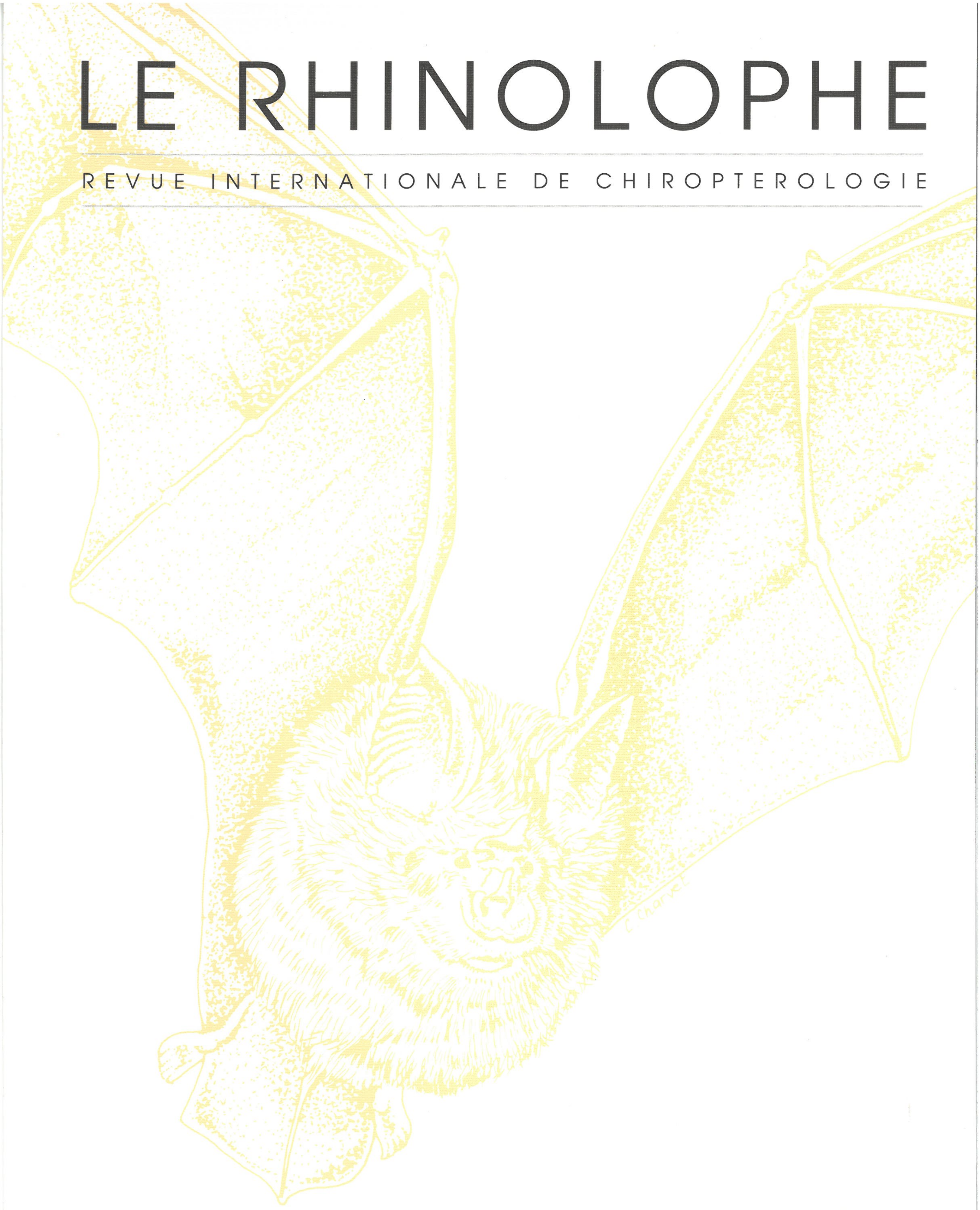

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First data on bat mortality in wind farms of Navarre (northern Iberian peninsula)

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Abstract. During the period 1998-2001, four wind farms located along mountain ridges of Navarre (northern Spain) were supervised. We found bat remains of 23 individuals which probably died due to collisions with wind turbines (19 were identified and belonged to five different species). All identified species were aerial-hawking bats. Both sexes were found in the same proportion. *Hypsugo savii* amounted to 62.5 % of all identified individuals. Eighty per cent of dead bats were found between August and the beginning of October, when dispersion and mating take place.

Key words: bat mortality, wind power, Iberian Peninsula, *Hypsugo savii.*

INTRODUCTION

In the last few years, the great concern about pollutant effects of oil, coal and natural gas has promoted the development of alternative energy sources, cleaner and renewable. As one of the best examples, wind power has recently experienced a huge expansion, with many wind farms being installed in developed countries.

Wind farms have been often installed without previous assessment of possible effects on the environment. This makes difficult to know interactions with local fauna. A number of studies have been done after installation of wind farms, once they were already working. Most studies have focused on the effects on birds, although some studies have recently evidenced bat mortality due to collisions with blades of wind turbines in Australia and the USA (Hall & Richards, 1972; Osborn *et al.*, 1996; Johnson *et al.*, 2000). In Europe, however, this kind of studies are very scarce, and until now no bat casualities in relation to wind turbines have been found (Bach *et al.*, 1999). It can be anticipated that bat populations are more vulnerable than bird ones, because of their low reproductive rate (usually lower than in birds) and their use of ultrasounds instead of sight to detect obstacles, impairing long distance location. Some authors (Bach et al., 1999; Rahmel *et al.*, 1999) have proposed several ways how wind farms might be affecting bat populations: emission of ultrasound, collision with blades, barrier effect (loss or displacement of flight-corridors) and loss of hunting areas.

The aim of this study was to investigate the effect of wind turbines on bats in Navarre (northern Spain). The use of wind power in this region has increased notoriously in the last few years and ambitious projects pretend that 50 % of energy consumption will be covered by wind power in 2005. Our purpose was to investigate: (i) whether bat species were involved in collisions with wind turbine blades, (ii) the mortality dates, and (iii) possible causes of collisions.

MATERIAL AND METHODS

During 1998-2000 we supervised four wind farms in central Navarre (northern Spain) totalling 198 wind turbines located along mountain ridges 600-1000 m high. Wind turbines consist of a tower (40-55 m high), a nacelle and a rotor with three blades (19.5-23.5 m long each). Between ground or topmost vegetation level and the lowest point reached by blades there are 16-32 m free of blade interference. Wind turbines work with wind speed ranging 4-25 m/s, and their power is 500-600 kW. Optimal rotation speed is 28-30 rpm. Since the four studied wind farms began to operate in different years, survey periods differed among farms (see Table 1 for detailed information concerning the four studied wind farms).

The study area belongs to the Eurosiberian biogeographic region. Pasture and scrub are predominant vegetation around these wind farms, although there are also some cereal fields. Wood patches (*Fagus sylvatica*, *Quercus faginea*, *Quercus ilex*, *Pinus sylvestris*, *Pinus nigra*) are common in the surroundings. Steep rocky slopes are present in two wind farms (Perdón and Selva).

A sample of wind turbines was randomly selected from every wind farm. In the same way as in previous studies (Gauthreaux, 1996; Osborn *et al.*, 1996; Anderson *et al.*, 2000), for every wind turbine we designed a survey circle with wind turbine in the centre and wind turbine maximum height (tower, nacelle and blades) as the radium.

Table 1 : Main characteristics of the studied wind farms.

Wind farm	Study period	Location UTM (10 x 10 km)	Number of wind turbines	% of surface surveyed
Perdón	1998-2001	30TXN03	40	25 %
Izko-Aibar	1999-2001	30TXN22-XN32	75	20 %
Salajones	1999-2001	30TXN31	33	18 %
Selva	2000-2001	30TXN60	50	11 %

Consequently, the radium varied according to wind turbine height, ranging 60-79 m. Some areas within the theoretical circles were not surveyed due to steep slopes or thick bushes, and we estimated percentage of area really surveyed in every wind turbine and farm. All distances were measured to the closest meter using a rangefinder. Search of bat carcasses was done on foot. In addition, we have collected and considered those dead bats found around the survey circles because every finding could give us important information. Precise location of all carcasses is shown in Table 2.

To determine if wind turbines caused differential mortality depending on the frequency of bat species we divided the minimun area that includes the four wind farms into 10 x 10 km UTM squares (a total of 20 squares). Then we checked the relationship (Spearman rank order correlation) between number of squares where each bat species was present (Alcalde & Escala, 1999 ; Alcalde, 1999) and number of dead individuals of each species (Zar, 1996). We used number of squares where each species was present because real abundance or density in the area is unknown.

Table 2 : Bat species and number of individuals found dead under wind turbines. * Individuals found dead outside sampled circles (see Methods for more details).

Wind farm	**Species**	**N of individuals**	**Sex**	**Date**
Salajones	*Hypsugo savii**	1	?	3.8.1999
	Hypsugo savii	1	♀	3.8.1999
	*Nyctalus noctula**	1	♂	12.8.1999
	Unidentified	1	?	24.9.1999
	Unidentified	1	?	5.10.1999
	*Pipistrellus kuhlii**	1	?	2.11.1999
	*Pipistrellus pipistrellus**	1	♂	21.8.2000
Perdón	*Eptesicus serotinus**	1	?	28.9.1998
	Hypsugo savii	1	♂	31.5.1999
	Hypsugo savii	1	?	16.8.1999
	Pipistrellus kuhlii	1	♂	24.8.1999
	Unidentified	1	?	3.9.1999
	Pipistrellus pipistrellus	1	♀	6.9.1999
	Pipistrellus pipistrellus	1	♂	5.9.2001
	Hypsugo savii	1	?	22.8.2001
Izko-Aibar	*Hypsugo savii**	1	♀	8.6.2000
	Hypsugo savii	1	♀	1.8.2000
	Hypsugo savii	1	♀	30.7.2001
Selva	Unidentified	1	?	31.5.2000
	Hypsugo savii	1	♂	9.8.2000
	Hypsugo savii	3	2♂, 1♀	17.8.2000

RESULTS

We found remains of 23 dead bats, of which only 19 could be identified. All identified bats belonged to five species (Table 2) and showed evident signs of violent crashes: bone fractures in head and extremities or body bruises with multiple fractures. The other four individuals were almost completely eaten, making species identification impossible with standard techniques. Fourteen out of 23 carcasses (60.9 %) were found entire, 6 (26.1 %) partially eaten by vertebrate scavengers, and 3 (13.0 %) partially eaten by invertebrate scavengers.

We have found no significant relationship between number of 10 x 10 km squares where each bat species was present (N=20) and number of individuals found dead for the 23 bat species present in the area (N=23; r_s=0.277; p>0.10). Sex was known only for 14 individuals, being males and females in the same number. Also the degree of maturity could be determined for 13 individuals, with 10 adults (76.9 %) and 3 youngs less than one year old (the 3 youngs were *Hypsugo savii*). For 22 individuals, distance between the place where carcass was found and closest wind turbine ranged 2-45 m (mean=13.0 m; SD=12.4 m).

Dead bats were found between the 31st of May and the 2nd of November (Table 2). Table 3 shows the number of surveys and the number of bat carcasses found in different periods of the year, corresponding to different phases of bat activities.

DISCUSSION

The absence of data on bat population gathered previous to wind farm installation makes difficult to know the true effect of wind turbines on original bat populations. However, this study shows 23 cases of bat mortality. Bone fractures and bruises found in bat carcasses suggest that collision with wind turbine blades was the most probable cause of this mortality. Although some authors (Bach *et al.*, 1999; Rahmel *et al.*, 1999) point out possible interactions between ultrasound emitted by bats and by wind turbines, this possibility can be ruled out in our study. Using an ultrasound-detector (S-25, Ultrasound Advice Ltd.) we have confirmed that wind turbines do not emit ultrasound in the range of frequencies used by bats in the area (14-115 kHz), at least when they were working properly. Moreover, since wind turbines are not floodlighted, they do not attract insects and, consequently, would not attract bats neither.

Some bird species may use wind turbines as resting or even nesting places (Osborn *et al.*, 1996), increasing the possibility of collision with the blades. Although Osborn *et al.* (1996) suggest that bats might use wind turbine towers as resting places during the night, this is not possible in the wind farms we have studied, because wind turbine towers were metallic with completely smooth surfaces. Between rotor and nacelle (the cab or housing that sits on top of the tower) there is a narrow groove, which does not seem suitable for bats, since the rotor is almost continuously spinning (except when there is no wind).

Eighty per cent of the dead bats were found between the 1st of August and the 5th of October (Table 2). This result is similar to those obtained in wind farms of Minnesota, where 85 % (Osborn *et al.*, 1996) or 97 % (Johnson *et al.*, 2000) of dead bats were found between mid-July and mid-September. Our result was not caused by a larger survey effort during late summer and early autumn, but was probably related to different bat activities (Table 3) and/or climatic factors. During this period we found 14 dead bats while surveying 950 wind mills, whereas during the rest of the year we found only three dead bats after surveying 2585 wind mills. Hence, the number of bats found in August-October was much larger than expected by chance (binomial test, n=17, p<0.001). In temperate regions, bats behave in a characteristic way during this period of the year: dispersal from breeding colonies with first flights of the young, beginning of mating season, and movements toward mating or wintering areas (Ransome, 1990). All these behaviours entail high bat dispersals and, as a consequence, higher risks of collision with wind turbines. Some individuals in our study could have died while dispersing, although the few carcasses found in

Table 3: Number of sampled circles and dead bats found in them in different periods.

Period	Activity	N circles surveyed	N dead bats
November-February	Hibernation	1037	0
March-May	Gestation	972	2
June-July	Breeding-rearing	576	1
August-October	Dispersion-mating	950	14
TOTAL		3535	17

other seasons suggest that resident bats (v.e. those living or just hunting in wind farm areas), can also be victims of blades. On the other hand, the weather changes in late summer, with the outbreak of storms; this might occasionally disturb the flight of bats.

Twenty-three bat species live in our study area (Alcalde & Escala, 1999; Alcalde, 1999), which can be classified in three categories according to their flight and hunting strategies: aerial-hawking, perch hunting and gleaning bats (Fenton, 1982). Interestingly, all bat carcasses we have found belonged to aerial-hawking species, which usually fly and hunt in open spaces; they might there be more vulnerable to wind turbines. Only 12 out of 23 bat species present in the study area are aerial-hawking species. However, all identified individuals found dead belonged to this group (5 species). This proportion is larger than expected by chance alone (binomial test, n=5, p=0.039).

Among the dead bats, three species (*E. serotinus*, *P. pipistrellus*, and *P. kuhlii*) are very common in the study area (Alcalde & Escala, 1999; Alcalde, 1999). These three species fly relatively low, usually under 10 m above ground level (Ahlén, 1990), and represent 31 % of all identified individuals. On the contrary, the other two species (*N. noctula* and *H. savii*) are scarce in the area (Alcalde & Escala, 1999; Alcalde, 1999), and usually fly much higher above ground level (Kronwitter, 1988; Zingg, 1988). In other studies carried out in Australia (Hall & Richards, 1972) and Minnesota (Johnson *et al.*, 2000) most dead bats found in wind farms belonged to relatively uncommon species: *Tadarida australis* and *Lasiurus cinereus* respectively. Both species fly at high altitude and catch their preys in flight in open areas (Norberg & Rayner, 1987). This suggests that some species, could be more vulnerable than others. The results in the present study also suggest that bat mortality caused by wind turbine blades differed depending on the species: 62.5 % of all identified individuals were Savi's pipistrelles (*H. savii*). This is the only species found in the four studied wind farms. Savi's pipistrelles are small bats (weight 5-10 g, wingspan 22-25 cm), very similar in colour (brown back and light-grey underneath) to other bat species living in the same area. Therefore, it is unlikely that Savi's pipistrelle carcasses were more easily detected by researchers than carcasses of other bat species. However, some behavioural traits can make it specially vulnerable to wind turbines.

Our results suggest no significant sex difference in mortality due to wind turbines (Table 2). Nevertheless, this conclusion needs confirmation, since sex ratio of bat populations in our study area is not known, and inter-species and inter-population variation in sex-ratio might be important (Hill & Smith, 1984).

In a parallel study on the detectability of dead passerines in the same wind farm area, only 6.2 % of passerine carcasses was found, with a mean permanence of less than 3 days in the field. Finding 23 dead bats might imply high mortality if we take into account this low carcass detectability (6.2 %). Moreover, this value was obtained for small passerine carcasses, but small birds are notably more conspicuous than bats due to their lighter coloration, and because feathers may fall off and spread around. Previous studies in wind farms of Minnesota (Johnson *et al.*, 2000) showed that dead bats were only eaten by insect scavengers, with carcasses remaining thus for a long time in the field. However, in the present study we have found six individuals (26 %) partially eaten by vertebrate scavengers. This role of vertebrate scavengers is also supported by the fact that the remains of four individuals only consisted of wing fragments. If we consider that most wind farms in the Iberian Peninsula are installed in mountainous areas, their effects on *N. noctula* and specially *H. savii* populations might be severe.

The 17 dead bats found within the sampled circles can be used to obtain a rough estimate of the annual killing in each wind farm (see Table 4). Assuming that the detectability for bats was similar to the detectability for birds (6.2 %), and keeping in mind that each farm was only partially surveyed, a conservative number of 620 bats can be estimated to be killed by the four wind farms annually.

Table 4: Findings in the sampled circles and estimations of mortality in each wind farm.

Wind farm	Dead bats found	Dead bats found (per year)	Wind turbines sampled	N bats dead in sampled areas (estimated/year)	N bats dead n wind farms (estimated/year)
Perdón	7	1.75	10	28	112
Izko	2	0.67	15	11	55
Salajones	3	1	5.9	16	89
Selva	5	2.5	5.5	40	364
TOTAL	17		36.4	95	620

More studies are needed to identify the effect of wind farms on every bat species and the way how these effects could be diminished. It should be compulsory to study bat populations in the areas where wind farms installation is planned. This would allow comparisons between the situation before and after the installation of wind turbines, which seems the best way of knowing the real effect of wind farms on bats.

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RÉSUMÉ

Durant la période 1998-2001, quatre parcs d'éoliennes situés le long de crêtes de montagne de Navarre (nord de l'Espagne) ont été examinés. Nous avons trouvé les restes de 23 chauves-souris, mortes probablement en raison de collision avec les pales des hélices (19 chauves-souris de 5 espèces différentes ont été identifiées). Toutes les espèces identifiées sont des chauves-souris chassant en milieu ouvert. Les deux sexes sont représentés en proportions égales. *Hypsugo savii* représente 62,5 % de toutes les chauves-souris identifiées. 80 % des chauves-souris mortes ont été trouvées entre août et début octobre.

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On a record of *Myotis alcathoe* in the region of Puy-de-Dôme, France

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Abstract. The re-examination of two preserved traffic-casualties from the region of Puy-de-Dôme in France revealed a specimen of *Myotis alcathoe*. Up to now, no other preserved animal of the species from France is known to be held in museum collections. The localities where the bats were found are described; external and skull measurements are given and compared with published data.

Key words: *Myotis alcathoe*, *Myotis mystacinus*, France, traffic casualties.

INTRODUCTION

The whiskered bats (species group of *Myotis mystacinus*) are composed of several species inhabiting the Palearctic and the Oriental regions. In Europe two species are distributed widely: the whiskered bat, *Myotis mystacinus* (Kuhl, 1819), and the Brandt's bat, *Myotis brandtii* (Eversmann, 1845). Two more European species were added recently: *Myotis aurascens* Kuzjakin, 1935 by Benda & Tsytsulina (2000) and *Myotis alcathoe* von Helversen & Heller, 2001 by von Helversen *et al.*, 2001.

Since the sympatric occurrence of *M. mystacinus* and *M. aurascens* has not been shown unambiguously, the species rank given to the poorly differentiated *M. aurascens* is still debated (Mayer & von Helversen, 2001). In contrast, *M. alcathoe* is well differentiated by external and skull characters and by genetic differences from all other species of the *mystacinus*-group.

Examination of museum specimens might provide further data on the distribution of this new species and give the possibility to verify characteristics useful for field identification of living bats. This is an essential requirement for ecological studies.

After the discovery of *Myotis alcathoe* in France (Ruedi *et al.*, 2002) I re-examined two specimens found as traffic casualties in 1992.

METHODS AND MATERIAL

Two dead whiskered bats were found as traffic casualties along the road D 941, east of the village St-Ours-les-Roches (north-east of Clermont-Ferrand, Département Puy-de-Dôme) within the area of the "Parc Naturel Régional des Volcans d'Auvergne".

The first specimen was found in the evening of 31 July 1992 between the Puy de Louchadière (1049 m a.sl.) and the Puy de Tressous (983 m a.sl.) on the south side of the road at an altitude of about 920 m a.sl. (coordinates: 45°51'4" N, 2°57'0" E). The locality is surrounded by natural deciduous forest. The bat had been killed most probably in the previous night, and showed a heavy injury in the hind parts of the body and several tears in the flight membranes. It was an adult female (growth plates of the phalanges were closed). After removing the innards, it was dried with opened wings and deposited in the collection of Christian Dietz and Isabel Schunger under the number CDIS-S 771.

The second individual was found in the evening of 2 August 1992 between St-Ours-les-Roches and the village of Le Vauriat, close to an old abandoned farmhouse. Wing membranes of this specimen and parts of the skin were already dry and the soft parts of the body quite rotten. It was also an adult female. No visible external injuries were observed. The innards were removed and the specimen dried with closed wings (CDIS-S 770).

After examination of the dried specimen, both skulls were removed and cleaned. The brain case of the second individual was broken.

The following measurements were taken with a Hommel mechanical calliper (+/- 0.1 mm): lengths of forearm including wrist (FA+), forearm excluding wrist (FA-), 5th finger excluding wrist (D5-), 3rd finger excluding wrist (D3-), thumb without claw (D1-), tibia (TibL) and hind foot without claws (HFL). Skull measurements were taken with an optical calliper (+/- 0.005 mm): greatest skull length (GSL), condylobasal length (CBL), zygomatic width (ZygW), mandible length (MDL) and lengths of upper and lower tooth row between canine and third molar (CM^3, CM_3).

The two specimens were compared with European whiskered-bat species held in the reference collections of the Staatliches Museum für Naturkunde Stuttgart (SMNS), collection of Prof. Otto von Helversen, Erlangen (OVH) and collection of Christian Dietz and Isabel Schunger (CDIS). The two French specimens were further compared with descriptions and measurements given by Benda & Tsytsulina (2000), von Helversen *et al.* (2001), Ruedi *et al.* (2002) and Benda *et al.* (2003).

RESULTS

The two bats are quite distinct from each other and differ in all measurements and all relevant external characteristics (Table 1).

The bat CDIS-S 771 has a colouration quite similar to *Myotis daubentonii* with a brown back and reddish-brown tips of the fur. The belly is greyish-white, no yellowish-brown hairs are found at the sides of the neck. The hair structure on the back is comparable to *M. daubentonii* and shorter than in *M. mystacinus*. The membranes of the wings and the tail are brownish, ears and tragus brown. The tragus reaches the notch of the outer margin of the ear but does not exceed it. The muzzle is relatively short. Ears are short, thumb and hind-feet are very small (see Table 1). The skull is small and delicate as shown by the measurements. The first (P^2) and second (P^3) upper premolars are located within the axis of the tooth row, the second premolar (P^3) is about half of the height of the first premolar (P^2). The cingulum of the third upper premolar (P^4) is well developed and reaches nearly the height of the tip of the second one (P^3). The paraconuli of the molars are well developed.

Colouration of the second bat CDIS-S 770 is light yellow-golden on the back with contrasting dark bases of hairs. General appearance is lighter than usual in German *M. mystacinus*. The belly is brownish-grey and the sides of the neck are yellowish-brown. Tragus and ears are uniformly dark black-brown; wing-membranes and the tail have the same dark colouration. The tragus clearly exceeds the notch in the outer margin of the ear by far. The ears are longer and all external measurements (Table 1) exceed those of the first specimen. The frontal part of the skull is built like in comparative *M. mystacinus*, it is larger than the skull of CDIS-S 771 and paraconuli are absent. The second upper premolar (P^3) is located within the axis of the tooth row and has about half the size of the first premolar (P^2). The cingulum cusp of the third upper premolar (P^4) is relatively low compared to the tip of the second one (P^3).

According to these very distinct characteristics, CDIS-S 771 is assigned to *M. alcathoe* and CDIS-S 770 to *M. mystacinus*.

Table 1: External and skull measurements of the two whiskered bats found as traffic casualties near St-Ours-les-Roches, France. External measurements are taken from the dried specimens. GSL and CBL are not available in CDIS-S 770 because the brain case is broken. Measurements of *Myotis alcathoe* from Greece (von Helversen *et al.*, 2001), France (Ruedi *et al.*, 2002) and Slovakia (Benda *et al.*, 2003) are given for comparison.

specimen	*M. mystacinus* CDIS-S 770	*M. alcathoe* CDIS-S 771	*M. alcathoe* Greece mean+/-SD (n)	*M. alcathoe* France mean (n)	*M. alcathoe* Slovakia min-max (n=2)
FA+ (mm)	34.1	31.1	-	-	32.5 - 32.9
FA- (mm)	32.7	30.0	31.4 ± 0.5 (13)	31.67 (20)	31.3 - 31.6
D5- (mm)	42.8	38.9	40.3 ± 1.3 (12)	41.58 (20)	40.2 - 41.0
D3- (mm)	54.4	51.5	51.4 ± 1.0 (10)	51.26 (20)	52.4 - 52.6
D1- (mm)	5.0	4.0	4.6 ± 0.3 (9)	3.95 (2)	4.2 - 4.4
TibL (mm)	15.7	13.5	13.4 ± 0.6 (8)	-	14.0 - 14.3
HFL (mm)	6.7	5.4	6.1 ± 0.3 (12)	-	5.3 - 5.6
GSL (mm)	-	12.50	-	-	12.66 - 13.18
CBL (mm)	-	12.13	12.3 ± 0.27 (7)	-	12.18 - 12.56
ZygW (mm)	8.45	8.24	8.13 ± 0.16 (7)	-	8.22 - 8.16
CM^3 (mm)	5.20	4.95	4.94 ± 0.09 (7)	-	4.90 - 4.98
MDL (mm)	10.02	9.48	9.5 ± 0.26 (7)	-	9.31 - 9.43
CM_3 (mm)	5.66	5.21	5.27 ± 0.16 (7)	-	5.20 - 5.31

DISCUSSION

M. mystacinus is a widespread species in France (Arthur & Lemaire, 1999; Tupinier & Aellen, 2001), and was found several times as traffic casualties (Arthur & Lemaire, 1999). *M. alcathoe* on the other hand has up to now only been known from a few localities in France. It was genetically established only in Charente-Maritime (Ruedi *et al.*, 2002), but suspected in Cantal, Haute-Loire, Puy-de-Dôme, Allier, Aube and Calvados (Jourde, 2000 opt. cit. in Ruedi *et al.*, 2002). No French specimen has been conserved as voucher so far (Ruedi *et al.*, 2002). The original description of *M. alcathoe* (von Helversen *et al.,* 2001) and the recent publications of new records of the species (Ruedi *et al.*, 2002; Benda *et al.*, 2003) give the possibility to discriminate *M. alcathoe* and *M. mystacinus* quite well according to external measurements, characters of the colouration, ear morphology and skull morphology as well.

I compared the two specimens found in 1992 with characteristics given in the above mentioned publications and with the genetically determined specimens of the type series (col. OVH, now deposited in the Senckenberg Museum Frankfurt). I also compared them with morphological descriptions, close-up photographs and drawings of three *M. alcathoe* caught in Bulgaria in 2003 (own data Schunger & Dietz), whose identities were verified genetically as well.

The bat found on 31 July 1992 (CDIS-S 771) could be clearly identified as *Myotis alcathoe*. External characters agree with the original description given by von Helversen *et al.* (2001) and with the information given by Ruedi *et al.* (2002) and Benda *et al.* (2003). All measurements, especially the species-specific lengths of thumb, tibia and hind feet, are within the currently known range given for *M. alcathoe* (Benda *et al.*, 2003) and are clearly smaller than those of the sibling species *M. mystacinus*. Additionally the paraconuli of the molars are well developed in CDIS-S 771, a situation typical for *M. alcathoe*. Conversely, they are usually absent in *M. mystacinus* (Benda & Tsytsulina, 2000). This specimen did not differ from those of the type-series of *M. alcathoe* (col. OVH) or from the three Bulgarian individuals. Skull measurements of this new French individual fully agree with data given for Greek and Slovak Alcathoe's bats. Variation of the up to now limited number of analysed skull measurements seems to be relatively low (Table 1).

In contrast, the second specimen (CDIS-S 770) is very distinct from the *M. alcathoe* (CDIS-S 771). In particular it is much bigger and shows all species-specific characters of *M. mystacinus*. External measurements correspond to the known range for that species (Benda & Tsytsulina, 2000; Benda *et al.*, 2003; Häussler, 2003). The colouration of its back is, however, much lighter and more golden than usually found in Central Europe and differs from all inspected voucher specimens (col. CDIS, OVH, SMNS). The skull size is larger than usually found among central European *M. mystacinus*, but correspond well with those given by Benda & Tsytsulina (2000) for the subspecies *M. mystacinus occidentalis* Benda, 2000. On the other hand, the colouration of fur is even more golden than in specimens from the type-locality of this subspecies (Linares de Riofrio, Salamanca, Spain, col. SMNS). However, considering the variability within *M. mystacinus*, it is not possible to assign this single specimen to a subspecies.

The newly reported record of *M. alcathoe* confirms the speculation of Jourde (2000 opt. cit. in Ruedi *et al.*, 2002) about the occurrence of this species in the region of Puy-de-Dôme. The location of the traffic casualty lies within the quite natural deciduous forest of the "Parc Naturel Régional des Volcans d'Auvergne", being in accordance with the habitat-information given by von Helversen *et al.* (2001), Ruedi *et al.* (2002) and Benda *et al.* (2003). The preferred habitats seem to be natural deciduous forests, very often in mountainous areas. Therefore, the species might be much more widespread than the limited data have suggested so far. *M. alcathoe* and *M. mystacinus* were found at the reported locality in sympatry; they occur most likely here in syntopy as well. This corresponds well to the situation found in Greece, Hungary (von Helversen *et al.,* 2001) and Bulgaria (own data Schunger & Dietz), where *M. alcathoe* was always found together with *M. aurascens* or *M. mystacinus.*

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Fréquentation des paysages sud-alpins par des chiroptères en activité de chasse

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Use of south-Alps landscape by hunting bats. Transects with bat detectors (heterodyne/time expansion) have been performed during 40 nights between 1993 and 2000, in the south of French Alps. Acoustics contacts of bats have been classified according to habitat, altitude (300 to 2500 m A.S.L.) and activity (hunting, transit). The results show that the activity level is not influenced by altitude up to 2200 m ; the 18 species contacted are more or less linked to landscapes (illuminated villages, forests, altitude meadows, lakes and rivers ...), with surprising results, especially for long-eared bats, which are more frequently contacted in wide open meadows above 1500 m.

This method seems very efficient, as it permits to collect more information than with other inventory techniques, especially about habitat preferences for hunting bats.

Key words : Bat detector, application of acoustic identification, hunting habitats, mountain habitats, 18 species, Alps, France.

INTRODUCTION

Les chiroptères européens forment un groupe diversifié d'espèces au régime insectivore plus ou moins spécialisé. Des différences d'adaptation (liées à la forme des ailes et des oreilles, à la taille et au poids, au type de sonar …) impliquent l'utilisation de différentes strates aériennes et structures d'habitats au sein d'un paysage.

Situées à un niveau élevé dans la pyramide alimentaire, les chauves-souris constituent de bons indicateurs de biomasse pour divers groupes d'arthropodes, avec leurs plantes-hôtes et prédateurs associés. Le nombre et le spectre des espèces de chiroptères en un lieu donné, associés à un indice mesurant leur activité de chasse, devraient permettre une évaluation de cette biomasse.

La difficulté d'étudier l'activité des chiroptères (espèces petites, nocturnes, volantes et inaudibles) est aujourd'hui atténuée par la mise au point d'une technique (détection des ultrasons émis par les individus en vol) et d'une méthode associée (identification acoustique des espèces et de leur type d'activité). Il est donc désormais possible, moyennant un protocole adapté, de mettre en évidence le niveau d'activité des différentes espèces tout au long de la saison de chasse dans plusieurs types d'habitats. Les résultats permettent de hiérarchiser les paramètres influençant la fréquentation des milieux par les chauves-souris (Ahlén & Baagøe, 1999 ; Barataud, 1999 ; Boonman, 1996 ; de Jong, 1995 ; Hayes, 1997 ; Moeschler & Blant, 1990 ; Vaughan *et al.,* 1997 ; Walsh & Mayle, 1991).

MATÉRIEL ET MÉTHODE

De 1993 à 2000, durant la période de mi-juillet à fin août, 40 soirées ont été consacrées à des transects ou points d'écoute au détecteur ; 11 grands types de milieux de montagne ont été inventoriés, en bordure ou au sein de la zone centrale du Parc National du Mercantour (Alpes, France). Les 1670 contacts acoustiques recueillis sont répartis par types de milieux, tranches d'altitude et types d'activité, afin de dresser un schéma d'occupation des paysages montagnards en été, pour les 18 espèces inventoriées.

Récolte et identification des données acoustiques

Le décodage des ultrasons était effectué grâce à deux détecteurs Pettersson D980 (hétérodyne et expansion de temps). Les séquences sonores étaient stockées sur un magnétophone DAT Sony TCD-D7, notamment celles présentant des difficultés d'identification immédiate.

Les séances d'écoute débutaient dès le crépuscule pour une durée de 4 heures environ et se déroulaient, selon la configuration du terrain, tantôt à poste fixe, tantôt le long de transects. Le temps d'écoute était divisé en tranches de 5 minutes, à l'intérieur desquelles étaient notés l'altitude, le milieu dominant et le ou les contacts éventuels de chiroptères. L'objectif était de connaître le temps exact passé dans chacun des milieux et tranches d'altitude, ceci dans le but d'établir des moyennes du nombre de contacts en fonction de chacun de ces paramètres.

Un contact correspond à une séquence acoustique bien différenciée, quelle que soit sa durée. Un même individu chassant en aller et retour peut ainsi être noté plusieurs fois, car les résultats quantitatifs expriment bien une mesure de l'activité et non une abondance de chauves-souris. Lorsque les émissions de plusieurs individus sont en recouvrement, le nombre de contacts noté correspond au nombre de séquences perceptibles. Les contacts, selon la qualité de réception (durée, intensité), étaient attribués à une espèce, un genre, un groupe d'espèces ou à un chiroptère indéterminé, ainsi qu'à une activité de transit, de chasse ou inconnue.

La détermination est réalisée sur la base des résultats d'une étude menée en France depuis 1988 (Barataud, 1996, 2001). A l'heure actuelle, dans de bonnes conditions d'écoute et avec un détecteur à expansion de temps, 25 espèces sur les 33 présentes en France sont identifiables, les autres étant regroupées par paire ou trio d'espèces d'un même genre. Chacune de ces 25 espèces utilise dans des conditions données des signaux de structure type, jugée discriminante. Lorsque ces signaux, sous des pressions environnementales ou sociales, sont soumis à des variations rendant possible un recouvrement avec une ou plusieurs autres espèces, la détermination est alors limitée à un groupe d'espèces.

Les limites actuelles de la technique du détecteur ne permettent pas de différencier *Rhinolophus mehelyi* de *R. hipposideros*, *Plecotus auritus* de *P. austriacus* et *P. macrobullaris, Myotis myotis* de *M. blythii, Nyctalus noctula* de *N. lasiopterus*. C'est ainsi qu'elles apparaissent regroupées par paire ou trio (selon les régions considérées) au sein des résultats

L'activité de chasse est décelée grâce à la présence d'accélérations dans le rythme des impulsions, typiques de l'approche d'une proie (Griffin *et al.*, 1960). La notion de transit est indiquée par une séquence sonore au rythme régulier, typique d'un déplacement rapide dans une direction donnée, d'un vol linéaire, mais sur une distance inconnue. Ce peut être simplement un changement de terrain de chasse dans une même vallée, ou un trajet plus long, inter-valléen ou de type migratoire. Quelle qu'en soit la signification, le transit indique que le milieu traversé n'offre pas les conditions éventuellement recherchées par l'animal pour son alimentation à cet instant précis. Ce type d'activité est plus aisé à discerner chez une espèce audible de loin (*Nyctalus* sp., *Eptesicus* sp., *Tadarida teniotis, Vespertilio murinus, Hypsugo savii)*, car la séquence, ainsi plus longue, permet de révéler un vol en ligne droite sur 200 mètres minimum (sans retour, ni séquence de capture de proie). C'est ainsi que généralement la plupart des contacts d'activité indéterminée concerne des petites espèces audibles dans un faible rayon.

Points d'écoute et transects

Le point d'écoute à poste fixe pose occasionnellement un problème de quantification des contacts, lorsqu'une ou plusieurs chauves-souris volent continuellement à l'intérieur du rayon de perception du détecteur : la séquence sonore continue devrait se résumer alors à un contact unique, ce qui exprime mal le niveau élevé d'activité des animaux (on compte arbitrairement dans ce cas un contact toutes les dix secondes pour chaque individu présent). Cependant, la méthode du point d'écoute est la seule utilisable sur des milieux ponctuels (plan d'eau de faible surface, lumière artificielle isolée ou col en montagne par exemple) impossibles à parcourir en transects.

Lorsqu'on compare les nombres de contacts par unité de temps, récoltés successivement lors de points d'écoute et de transects, sur un même site, une même soirée dans des milieux équivalents, on obtient des résultats tantôt similaires, tantôt en faveur de l'une ou de l'autre technique (Barataud, 2000). Il n'apparaît ainsi aucune tendance prévisible influençant l'indice d'activité.

Il ne semble donc pas que le choix de la technique, entre point d'écoute et transect, influence quantitativement les résultats (de Wijs, 1999). Ainsi le choix a été fait de fusionner les deux dans l'exploitation des données. Cependant, la particularité des cols d'altitude dans leur rôle de lieu de transit privilégié inter-valléen a justifié de séparer les points d'écoute sur cols des transects en milieux similaires – landes et rochers sur pentes (Tableau 2).

Dans le Tableau 1, l'ordre d'énumération des espèces a été choisi en fonction de leurs affinités bioclimatiques, afin de mieux visualiser un éventuel gradient dans les colonnes de totaux en % pour chaque unité biogéographique. Le premier groupe (de *E. nilssonii* à *V. murinus*) comprend des espèces tolérantes aux climats continentaux et nordiques ; le deuxième (*B. barbastellus* à *E. serotinus*) inclut des espèces à large distribution, sans affinités particulières ; enfin les espèces du troisième groupe (*R. hipposideros* à *T. teniotis*) sont relativement à franchement thermophiles.

Analysé à partir des études phytogéographiques d'Ozenda (1981 ; 1985) et du document interne « Principes d'aménagement du PNM » (1998), le massif du Mercantour peut se résumer en trois grandes influences biogéographiques :

- **alpine ou intra-alpine :** air froid et sec amené du nord par les Alpes ; cette influence concerne plus particulièrement les secteurs Haute-Ubaye et Haute-Tinée. La zone intra-alpine se caractérise par une très forte xéricité ; elle est représentée par le pin à crochets et le mélèze à l'étage alpin avec quelques beaux peuplements de pin cembro (Vésubie) et une série interne de pin sylvestre (Ubaye) à l'étage montagnard,

Tableau 1 : Peuplements spécifiques par secteurs géographiques. Chaque chiffre indique le nombre de sites où l'espèce a été contactée.

Influences biogéographiques	Influence alpine			Influence pré-ligure				Influence haute-provençale				Carrefour d'influences
Secteurs (n. de sites prospectés) Espèces	Ubaye (n=4)	Haute-Tinée (n=6)	**TOTAL %**	Vésubie (n=4)	Haute-Roya (n=6)	Basse-Roya & Bevera (n=5)	**TOTAL %**	Haut-Var (n=7)	Haut-Verdon (n=5)	Moyenne-Tinée (n=6)	**TOTAL %**	Vallon de Mollières (n=2)
Eptesicus nilssonii		1	**10 %**		1		**6,6 %**	2			**11,7 %**	
Myotis nattereri	2	4	**60 %**		2		**13 %**	2	1	2	**29,4 %**	2
Myotis mystacinus		2	**20 %**	2	1		**20 %**		1		**5,8 %**	1
Nyctalus noctula/lasiopterus								1			**11,7 %**	
Vespertilio murinus	1		**10 %**		1		**6,6 %**		1		**5,8 %**	
Barbastella barbastellus					2	1	**20 %**			1	**5,8 %**	1
Plecotus sp.	3	3	**60 %**	2	1	1	**26 %**	5	4	5	**82,3 %**	2
Myotis daubentonii(bechsteinii)	4	4	**80 %**	3	6	3	**80 %**	5	5	3	**76,4 %**	2
Myotis myotis/blythii						1	**6,6 %**					
Pipistrellus pipistrellus	4	5	**90 %**	4	5	5	**93 %**	5	5	5	**88,2 %**	2
Eptesicus serotinus	1		**10 %**					1		1	**11,7 %**	
Rhinolophus hipposideros						1	**6,6 %**	1			**5,8 %**	
Nyctalus leisleri	1	1	**20 %**	3	4	3	**66 %**	3	5	3	**64,7 %**	2
Rhinolophus ferrumequinum						1	**6,6 %**					
Myotis emarginatus												1
Pipistrellus kuhlii	2	2	**40 %**	4	6	5	**100 %**	2	2	2	**35,2 %**	
Hypsugo savii	4	6	**100 %**	4	6	4	**93 %**	7	5	5	**100 %**	2
Tadarida teniotis	1	2	**30 %**	2	2	2	**40 %**	5	1	4	**58,8 %**	
TOTAL nbre d'espèces	10	10		8	12	11		12	10	10		9

- **haute-provençale :** saisons sèches méditerranéennes caractéristiques : Haut-Verdon, Haut-Var et Moyenne-Tinée. La zone haute-provençale se caractérise par de fortes remontées d'essences méditerranéennes comme le chêne pubescent jusque dans l'étage collinéen (supraméditerranéen),
- **pré-ligure :** chaleur et saisons sèches méditerranéennes et humidité venue de l'est (Haute-Vésubie et Roya-Bevera). Terminaison sud-orientale de la zone haute-provençale, la zone pré-ligure s'en distingue par la dominance de l'Ostrya (charme-houblon) à l'étage collinéen (unique en France) et la présence du pin mugo à l'étage subalpin.

Dans les Tableaux 2 et 3, l'ordre d'énumération des espèces a été choisi en fonction de leur comportement de chasse (connu par la bibliographie existante et les expériences de terrain), afin de rendre plus visible au sein des tableaux d'éventuelles tendances convergentes parmi les groupes suivants :

- espèces au vol agile, évoluant généralement au sein ou à proximité immédiate du feuillage : *Rhinolophus hipposideros, Myotis emarginatus, M. nattereri, M. mystacinus, Plecotus* sp. (concernant *M. bechsteinii :* cette espèce étant très rare dans la région prospectée, les contacts légendés *M. daubentonii/bechsteinii* concernent plus probablement la première espèce),
- espèces de lisière, fréquentant souvent la forêt mais plutôt en suivant les écotones (bordures de rivière ou de retenue d'eau, allées forestières, parcelles au sol dégagé, lisières sur milieu ouvert) : *Myotis daubentonii, Rhinolophus ferrumequinum, M. myotis, Barbastella barbastellus, Pipistrellus pipistrellus, P. kuhlii, Eptesicus serotinus*,
- espèces de haut-vol, évoluant généralement au-dessus de la végétation et jusqu'à plusieurs centaines de mètres de hauteur *: Hypsugo savii, Eptesicus nilssonii, Vespertilio murinus, Nyctalus leisleri, N. noctula/lasiopterus, Tadarida teniotis.*

RÉSULTATS

Le Tableau 1 montre le nombre d'espèces (moy. = 6) rencontrées par secteurs administratifs du Parc national – ceux-ci ayant été arbitrairement regroupés selon les trois types d'influences bioclimatiques – ainsi que le nombre de sites par secteur où elles furent contactées.

Mille six cent septante contacts ont été récoltés, sur 165 heures 50 minutes d'écoute, la moyenne générale est donc de 10 contacts/heure (Tableaux 2, 3). Quatre-vingt-cinq % des contacts ont permis une identification spécifique certaine et 9,7 % une identification limitée à un groupe d'espèces. L'activité de chasse représente 74,5 % des contacts, celle de transit 7 %.

Les indices d'activité (en contacts/heure) ne peuvent être comparés entre espèces que lorsque celles-ci émettent des signaux d'intensités voisines :

- Au sein du groupe d'espèces (n=7) à intensité d'émission faible (de *R. hipposideros* à *R. ferrumequinum* dans les Tableaux 2 et 3), le nombre total de contacts est de 302. Le complexe *M. daubentonii/bechsteinii* arrive en tête avec 52,3 % des contacts. Le genre *Plecotus* est bien représenté, avec 22,8 % des contacts. *M. nattereri* arrive en troisième position d'abondance avec 9,2 % des contacts.
- Le groupe de 4 espèces (de *M. myotis/blythii* à *P. kuhlii*) à intensité moyenne cumule 545 contacts. *P. pipistrellus* domine largement avec 65,3 % des contacts, suivie de *P. kuhlii* avec 33,2 %.
- Le groupe des 7 espèces (*E. serotinus* à *T. teniotis*) à intensité forte cumule 757 contacts. *H. savii* est très abondante avec 73,3 % des contacts, suivie de loin par *N. leisleri* (13,8 %) et *T. teniotis* (11 %).

Le Tableau 2 montre que la proportion d'activité de chasse est forte dans tous les milieux boisés, mais le record (95,6 %) appartient aux villages éclairés. Cependant, ces derniers lieux rassemblent une des plus faibles diversités d'espèces (7 seulement avec 4 espèces représentant 98,8 % des contacts en ce milieu). Les villages sans lumière concentrent par contre une activité inférieure à la moyenne.

Les lacs bordés d'arbres sont l'habitat naturel présentant l'indice le plus fort, et la chasse y représente 82,7 % de l'activité totale.

Si les indices d'activité ne peuvent être comparés entre les espèces ayant des intensités d'émission différentes, il est cependant possible de comparer la nature et l'amplitude des différences intraspécifiques d'utilisation de plusieurs types d'habitats. La Figure 1 montre que les espèces au vol agile (genres *Myotis* et *Plecotus*) fréquentent moins les milieux éclairés que l'ensemble des autres milieux, au contraire des espèces de lisière ou de haut-vol (genres *Pipistrellus, Eptesicus, Nyctalus*).

Le degré de fermeture du milieu (voir Fig. 2, excluant les milieux anthropisés) semble avoir une influence sur le peuplement spécifique. Le genre *Myotis* paraît lié à la végétation arborée et il semble d'autant plus contacté que celle-ci est dense.

Le genre *Plecotus* se distingue du groupe des espèces au vol agile (en théorie liées au couvert forestier), puisqu'il affiche un modèle d'occupation du paysage similaire à celui de *N. leisleri*, qui est au contraire une espèce de haut-vol. En effet, la proportion des contacts d'oreillards en milieux ouverts (31,9 %) est étonnante pour des espèces liées au feuillage, même si presque un tiers de ces contacts représente des transits (la proportion de transits de *Plecotus* en paysages boisés n'est que de 12,7 %).

Tableau 2 : Peuplements spécifiques et indices d’activité par types de milieux. Les chiffres entre parenthèses correspondent aux nombres de contacts classés par types d’activité ; dans l’ordre : chasse, transit, activité indéterminée.

Types de paysages	Ouvert sans eau		Ouvert avec eau		Semi-ouvert avec eau		Semi-ouvert sans eau		Fermé	Anthropisé		TOTAL	
Milieux Espèces	Col sur pelouse et rochers	Pelouse, prairie et pierriers	Ruisseau sur pelouse	Lac sur pelouse	Lac avec arbres	Ruisseau avec arbres	Friche et lande arbustive	Lisière et forêt clairsemée	Forêt dense	Village sans lumière	Village éclairé	Nbre contacts	% au sein de chaque classe d’espèces
Rhinolophus hipposideros								(1) - (2)				(1) - (2)	2
Myotis emarginatus						(1) - -						(1) - -	0,6
Myotis nattereri					(5) - -	(5) - (2)		(6) - -	(8) - -	(1) - (1)		(25) - (3)	19,4
Myotis mystacinus		(1) - -			(1) - -	(1) - (2)		(1) - (1)	(6) - (1)			(10) - (4)	9,7
Myotis sp.	- (1) -	(2) - (5)	(1) - -	(1) - -	- (1) -	(1) - (5)		(2) (1) (3)	(1) (1) (4)			(8) (4) (17)	20,1
Plecotus sp.	(1) (3) (4)	(2) (2) (8)	- (1) -	- (1) -	(4) - (1)	(3) (1) (3)		(8) (5) (10)	(5) - (5)	- - (1)	- - (1)	(23) (13) (33)	47,9
Myotis daubentonii/bechsteinii					(2) - -	(14) - (4)	(2) - -	(15) (1) (4)	(30) (3) (12)	(1) - -		(64) (4) (20)	12,4
Myotis daubentonii				(3) (2) -	(37) - (1)	(11) - (3)		(8) (1) (2)	(2) - -			(61) (3) (6)	9,8
Rhinolophus ferrumequinum								- - (1)				- - (1)	0,1
Myotis myotis/blythii									(1) - -			(1) - -	0,1
Barbastella barbastellus		(1) (3) -					- - (1)	(1) - (1)				(2) (3) (2)	0,9
Pipistrellus pipistrellus		(15) (1) (7)	- (2) (1)	(10) (1) (1)	(18) - (1)	(38) (1) (6)	(4) (1) (4)	(58) (6) (18)	(73) (3) (16)	- (1) (2)	(67) - (1)	(283) (16) (57)	50,2
Pipistrellus kuhlii		(5) (4) (2)		- - (3)	(8) - -	(6) (1) (4)	(16) (5) (1)	(16) - (7)	(21) - (3)	(3) - (1)	(74) - (1)	(149) (10) (22)	25,5
Eptesicus serotinus	- (2) -				- (1) -			(1) - -				(1) (3) -	0,5
Hypsugo savii	(19) (7) (2)	(86) (3) (6)	(5) - -	(10) (2) (3)	(16) (4) (3)	(25) (1) (5)	(7) - (1)	(144) (10) (14)	(86) (3) (9)	- - (1)	(82) - (1)	(480) (30) (45)	67,8
Eptesicus nilssonii	- (1) -			(4) - (1)	(1) - -						(2) - -	(7) (1) (1)	1,1
Vespertilio murinus								(2) (1) -	(1) - -			(3) (1) -	0,4
Nyctalus leisleri	(9) (1) (2)	(11) (1) (1)		- - (1)	(4) (2) (1)	(1) - (7)	- - (3)	(1) (4) (10)	- (1) (2)	(1) (1) (1)	(32) - (8)	(59) (10) (36)	12,8
Nyctalus noctula/lasiopterus	- (1) -											- (1) -	0,1
Tadarida teniotis	(4) (9) (3)	(18) - (2)				- - (1)		(17) - (3)	(21) - (1)	- (1) -	(3) - -	(63) (10) (10)	10,1
Chiroptera sp.		- - (6)		- (2) (3)	- (2) (3)	(1) (2) (4)		(3) (1) (15)	- - (18)	- - (1)		(4) (7) (50)	7,4
TOTAL	(33) (25) (11)	(141) (14) (37)	(6) (3 (1)	(28) (8) (12)	(96) (10) (10)	(107) (6) (46)	(29) (6) (10)	(284) (30) (91)	(255) (11) (71)	(6) (3) (8)	(260) - (12)	(1245) (116) (309)	
Temps cumulé	7h30'	23h55'	4h30	9h	7h55'	21h30'	6h	45h45'	31h10'	2h15'	6h20'	165h50'	
Nb. de contacts/heure	9,2	8	2,2	5,3	14,6	7,4	7,5	8,8	10,8	7,5	42,9	10	

Tableau 3 : Peuplements spécifiques et indices d’activité par tranches d’altitudes. Les chiffres entre parenthèses correspondent aux nombres de contacts classés par types d’activité ; dans l’ordre : chasse, transit, activité indéterminée.

Altitudes Espèces	300 à 499 m	500 à 699 m	700 à 899 m	900 à 1099 m	1100 à 1299 m	1300 à 1499 m	1500 à 1699 m	1700 à 1899 m	1900 à 2099 m	2100 à 2299 m	2300 à 2520 m	TOTAL
Rhinolophus hipposideros				- - (2)		(1) - -						(1) - (2)
Myotis emarginatus						(1) - -						(1) - -
Myotis nattereri		(1) - -		(1) - -		(4) - -	- - (3)	(10) - -	(8) - -	(1) - -		(25) - (3)
Myotis mystacinus						(1) - -	- - (2)	- - (1)	(6) - (1)	(3) - -		(10) - (4)
Myotis sp.	(1) - -	(1) - (1)			- - (1)	(1) - -	- (1) (4)	(2) (2) (3)	- - (4)	(3) - (3)		(8) (4) (17)
Plecotus sp.					- - (1)	- - (4)	(6) (2) (7)	(7) (2) (3)	(6) (2) (8)	(3) (4) (9)	(1) (3) (1)	(23) (13) (33)
Myotis daubentonii/bechsteinii	(1) - (1)			- - (1)	(1) - (1)	(8) - -	(13) (1) (8)	(24) (2) (8)	(16) (1) -	(1) - (1)	- - (1)	(64) (4) (20)
Myotis daubentonii	(5) - -	(1) - -				(17) - -	(22) - (1)	(8) (1) (4)	(3) - (1)	(5) (2) -	- (1) -	(61) (3) (6)
Rhinolophus ferrumequinum	- - (1)											- - (1)
Myotis myotis/blythii						(1) - -						(1) - -
Barbastella barbastellus							- - (1)	(1) (2) -	(1) (1) (1)			(2) (3) (2)
Pipistrellus pipistrellus	(9) (1) (2)	(6) - (1)		- - (1)	(18) (1) (3)	(28) - (4)	(63) (4) (18)	(92) (2) (15)	(48) (5) (9)	(19) (3) (4)		(283) (16) (57)
Pipistrellus kuhlii	(24) (5) (1)	(1) (1) (1)	(5) - (1)	(18) - (1)	(36) - (1)	(17) - (3)	(5) (1) (4)	(30) (3) (4)	(12) - (2)	(1) - (4)		(149) (10) (22)
Eptesicus serotinus									(1) (1) -	- (1) -	- (1) -	(1) (3) -
Hypsugo savii	(6) - -	- (1) (2)	(1) - -	(3) - -	(10) - (1)	(11) - (1)	(67) (5) (10)	(150) (7) (9)	(156) (8) (16)	(66) (7) (5)	(10) (2) (1)	(480) (30) (45)
Eptesicus nilssonii								(2) - -	- (1) -	(1) - -	(4) - (1)	(7) (1) (1)
Vespertilio murinus							- (1) -		(3) - -			(3) (1) -
Nyctalus leisleri	(2) - (2)	- - (2)	- - (2)	(3) (1) (1)	(16) - (4)	(5) - (3)	(9) (3) (12)	(1) (2) (2)	(3) (2) (6)	(20) (2) (2)		(59) (10) (36)
Nyctalus noctula/lasiopterus									- (1) -			- (1) -
Tadarida teniotis				(1) - (1)	(1) - -	(2) (1) (1)	(6) - (1)	(12) (1) (1)	(38) (2) (4)	(1) (1) -	(2) (5) (2)	(63) (10) (10)
Chiroptera sp.		- - (1)		- - (1)	- - (1)	- - (3)	(1) - (21)	(1) (3) (12)	(2) - (6)	- (4) (5)		(4) (7) (50)
TOTAL	(48) (6) (7)	(10) (2) (8)	(6) - (3)	(26) (1) (8)	(82) (1) (13)	(97) (1) (19)	(192) (18) (92)	(340) (27) (62)	(303) (24) (58)	(124) (24) (33)	(17) (12) (6)	(1245) (116) (309)
Temps cumulé	4h50’	1h55’	1h20’	3h25’	7h55’	12h10’	37h15’	30h50’	29h45’	25h45’	10h40’	165h50’
Nb. de contacts / heure	12,6	10,4	6,7	10,2	12,1	9,6	8,1	13,9	12,9	7	3,2	10

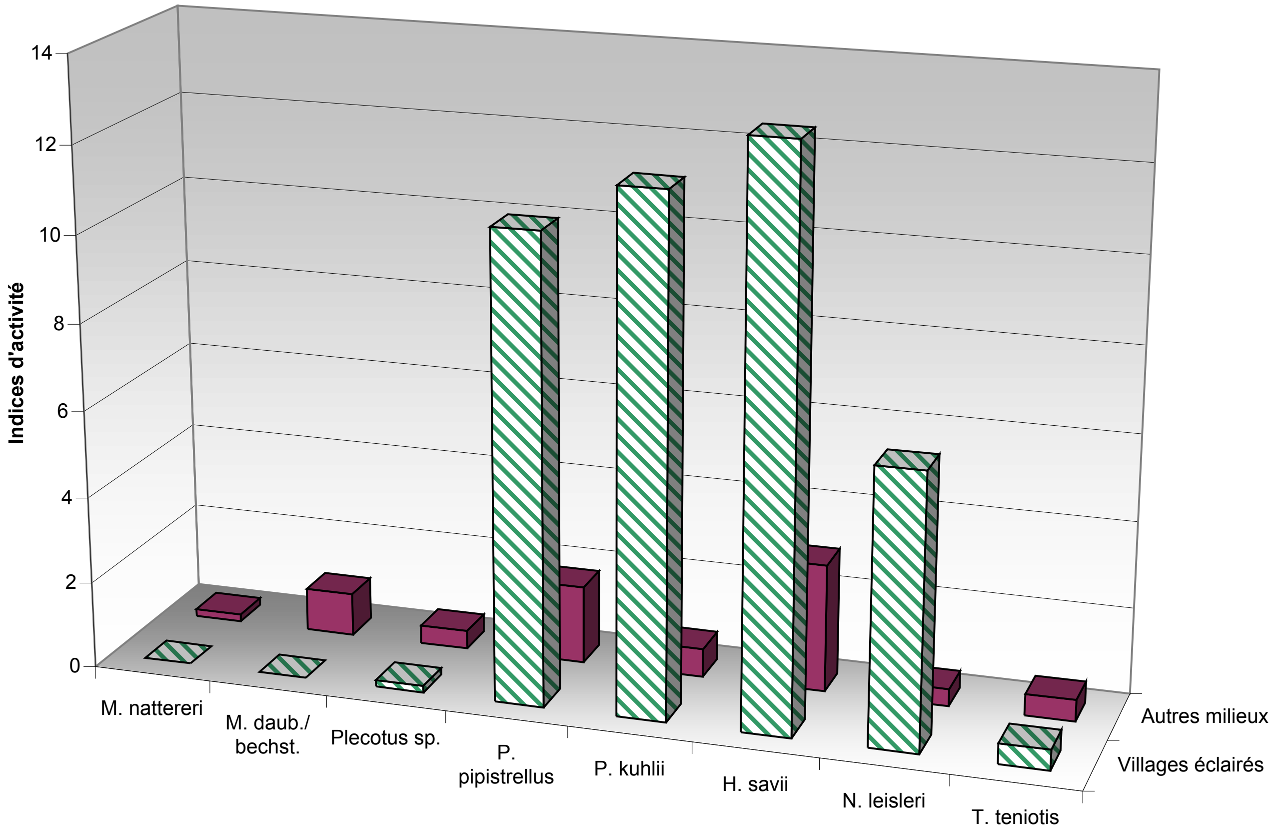

Fig. 1 : Comparaison des indices d’activité globale obtenus en villages éclairés et dans l’ensemble des autres milieux.

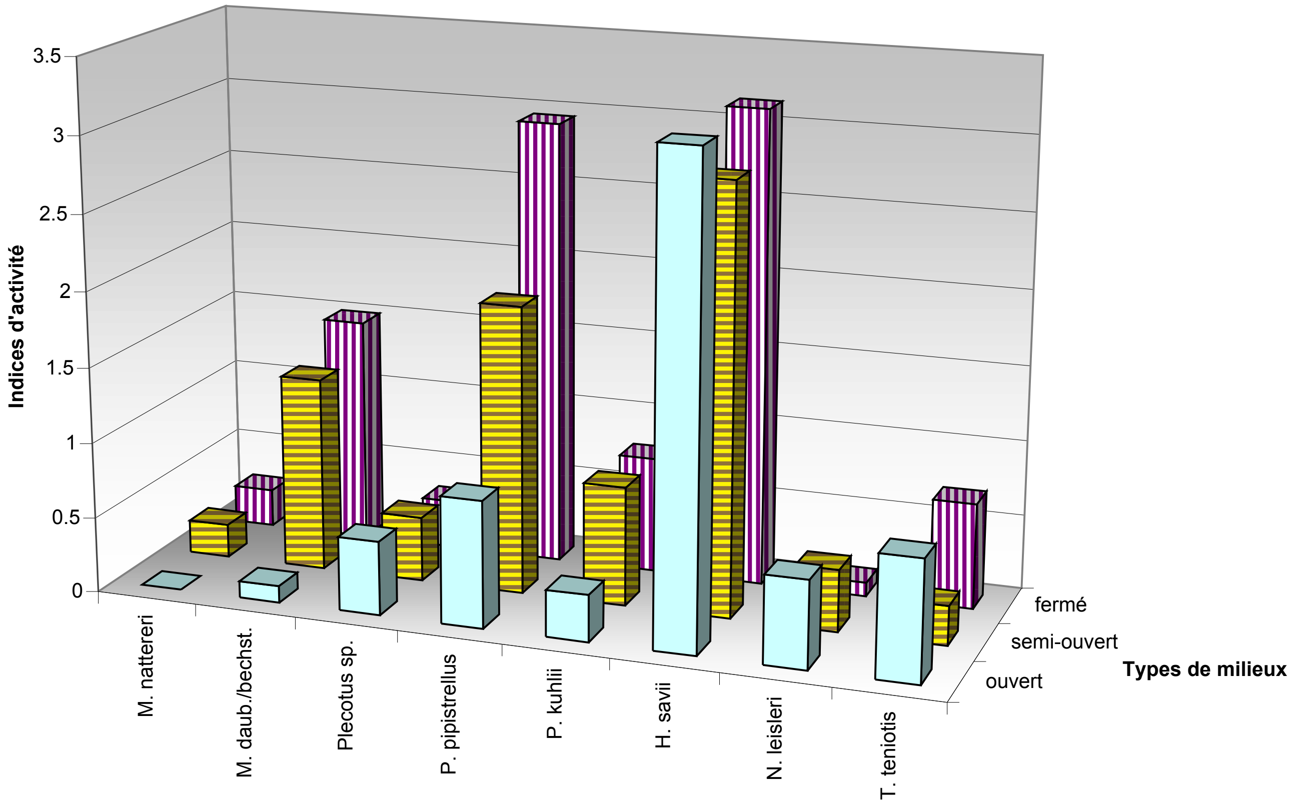

Fig. 2 : Comparaison de l’indice d’activité globale en fonction de l’ouverture du milieu.

Une Analyse Factorielle des Correspondances, suivie d'une classification hiérarchique, confirme l'attachement : de *P. pipistrellus* et *P. kuhlii* aux villages éclairés, de *M. daubentonii* aux milieux humides, de *T. teniotis* et *Plecotus* sp. aux pelouses et aux prairies ; le genre *Myotis* forme un ensemble lié aux milieux forestiers plus ou moins humides.

Le Tableau 3 montre que l'indice d'activité reste relativement élevé même au-dessus de 2000 m, avec une bonne proportion d'activité de chasse par rapport à l'activité globale jusqu'à 2300 m.

L'indice d'activité de chasse, toutes espèces confondues, ne diminue pas de manière significative (p>0,5) avec l'élévation de l'altitude (Fig. 3). L'influence méditerranéenne remontant dans la plupart des vallées du massif du Mercantour doit considérablement nuancer les effets limitants liés à l'altitude. Ainsi, à fin juillet 1998 dans la haute-vallée de la Roya, certains transects ont recueilli 28 à 38 contacts par heure entre 1900 et 2200 m d'altitude.

P. kuhlii, en dépit de quelques données remarquables (2190 m à Valmasque et 2200 m au Lac Vert de Fontanalbe en Roya), se raréfie très nettement au-dessus de 1500 m. La diminution de son indice d'activité avec l'élévation de l'altitude (Fig. 4) s'avère très significative (p< 0,01).

La grande majorité des contacts d'oreillards concerne des altitudes supérieures à 1500 m. L'augmentation de l'activité avec l'altitude pour ce taxon (voir Fig. 5) est très significative (p<0,01). On pourraît suspecter cette constatation d'être biaisée par la proportion relativement importante des contacts d'oreillards en milieux ouverts (Fig. 2), en supposant que la représentation de ces derniers augmente avec l'altitude. Il est à ce titre important de préciser que le temps de prospection consacré aux habitats forestiers reste dominant même au-dessus de 1500 m (62 % du temps total entre 1500 et 2520 m), et ne baisse drastiquement qu'à partir de 2000 m (34 % du temps total entre 2000 et 2520 m).

Enfin, quelques espèces ont été notées à des altitudes inhabituelles :

- *R. hipposideros* à 1460 m en chasse sous le col de Barels (Haut-Var)
- *M. emarginatus* à 1320 m en chasse dans le vallon de Mollières (Moyenne-Tinée).

COMMENTAIRES

Répartition en fonction des influences bioclimatiques

La fréquence d'apparition (total % dans Tableau 1) des espèces au sein de chaque région bioclimatique correspond bien aux valeurs attendues dans quelques cas :

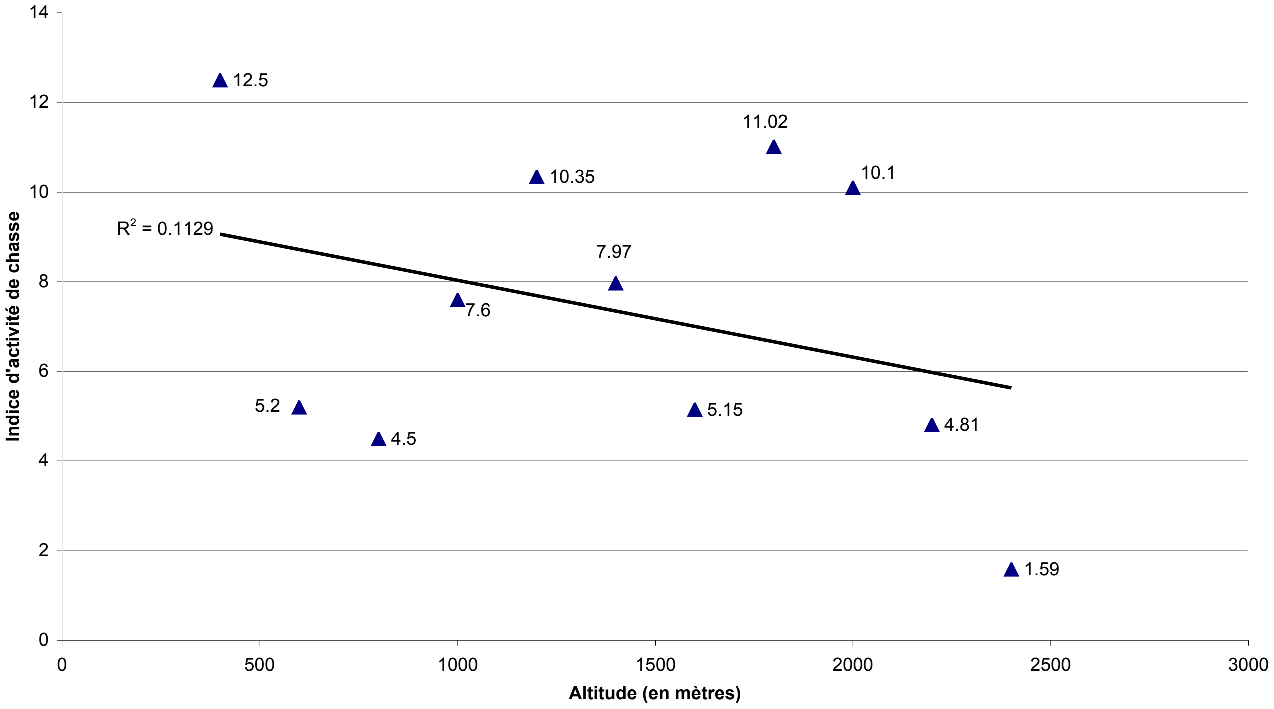

Fig. 3 : Évolution de l'activité de chasse (toutes espèces confondues) en fonction de l'altitude.

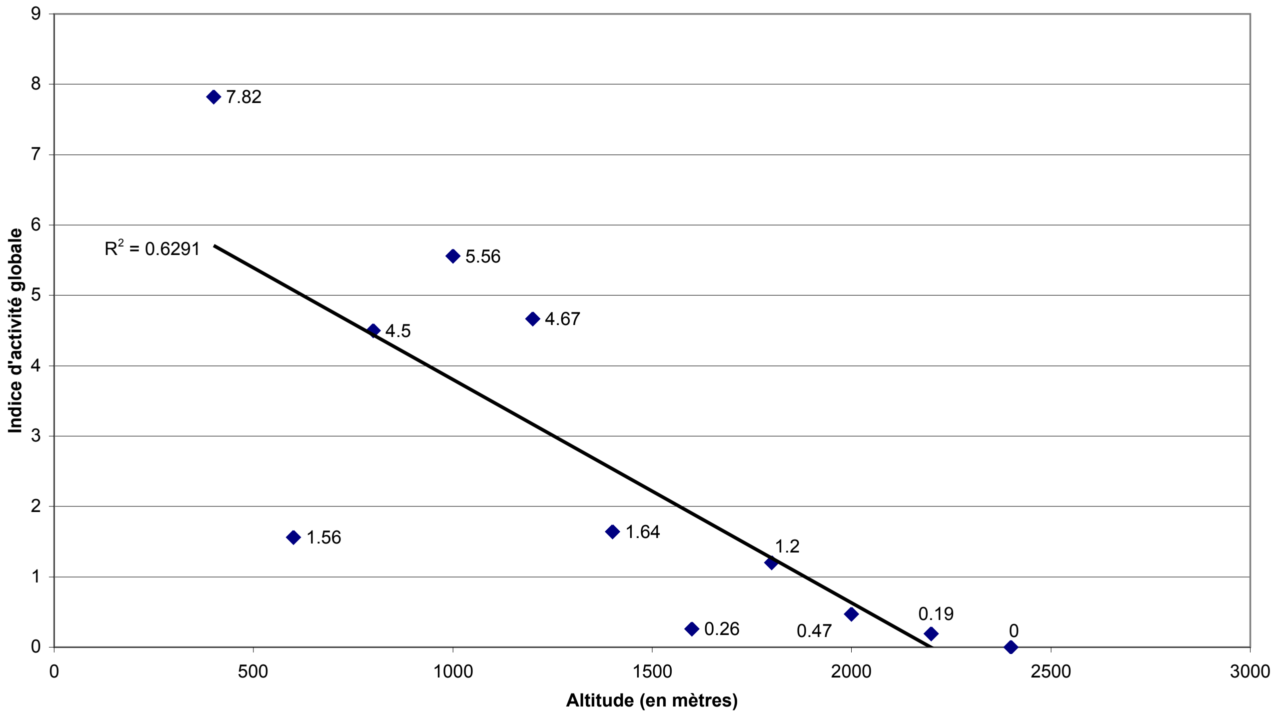

Fig. 4 : Évolution de l'indice d'activité globale de *Pipistrellus kuhlii* en fonction de l'altitude.

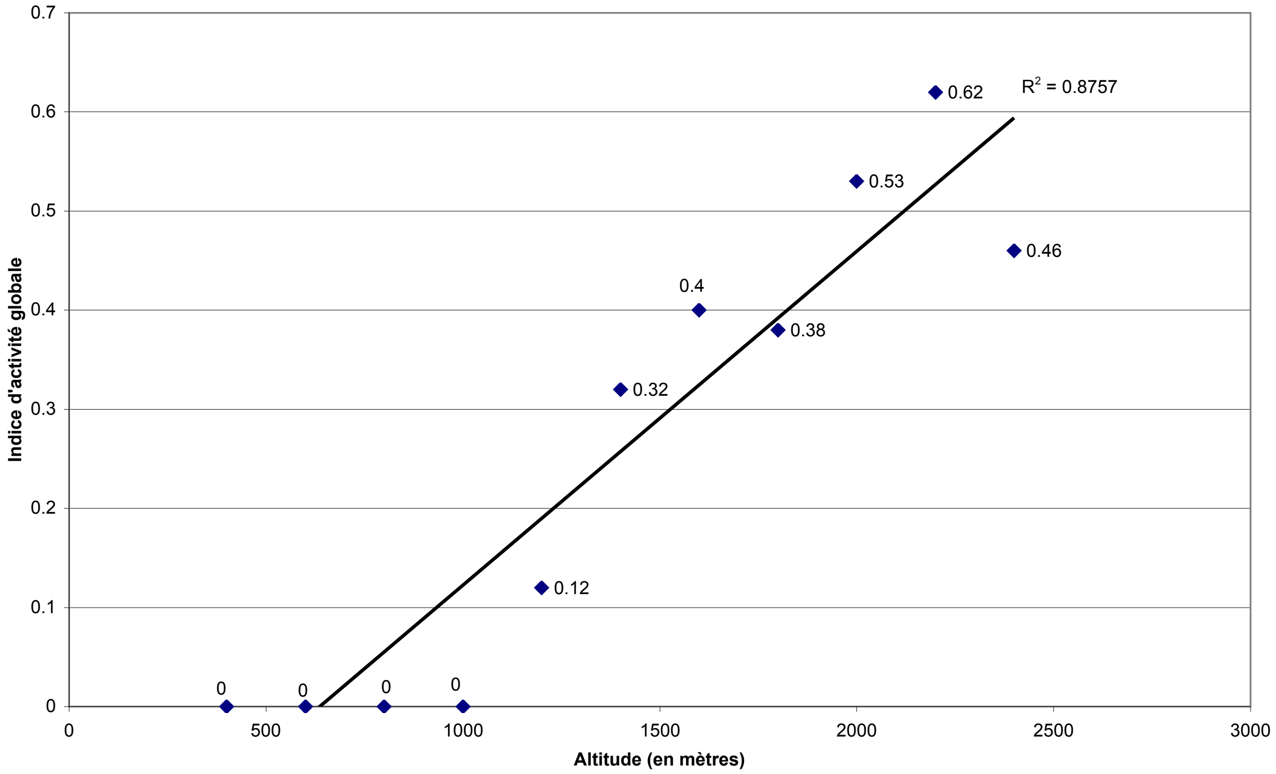

Fig. 5 : Évolution de l'indice d'activité globale de *Plecotus* sp. en fonction de l'altitude.

- *M. nattereri*, rare dans toute l'Europe méridionale (Mitchell-Jones *et al.*, 1999), fréquente ici surtout les forêts de mélèzes sous influence alpine (notamment en Haute-Tinée qui concentre 42,8 % des contacts de cette espèce) ;
- *N. leisleri* (plus abondante au sud de la France qu'au nord, elle semble également limitée par l'altitude) et *T. teniotis* qui est franchement thermophile car inapte à une hypothermie profonde et prolongée (Arlettaz *et al.*, 2000) sont plus présents au sud et à l'ouest, dans les vallées les moins froides. La même tendance a été observée dans les Alpes centrales (Barataud, 1994) ;
- aucune différence n'apparaît par contre pour les espèces communes à large distribution, comme *P. pipistrellus* et *M. daubentonii* (respectivement présents dans 93 et 81 % des sites au total).

Le genre *Plecotus* semble plus présent dans les vallées chaudes et sèches (influence provençale), surtout si l'on considère que les contacts dans les secteurs alpins concernent principalement des individus en transit sur des cols. Malgré son intensité d'émission faible à moyenne, il fut contacté sur 49 % des sites.

À l'opposé, les cas de *P. kuhlii* et *H. savii* sont plus surprenants.

Concernant *P. kuhlii*, la valeur la plus faible se rencontre dans la région à priori la plus favorable (influence haute-provençale), car sous influence méditerranéenne type. Pourtant, c'est dans les secteurs du Haut-Var et du Haut-Verdon que le nombre de villages éclairés (milieu préferentiel de l'espèce) prospectés est le plus important ; il ne semble donc pas qu'il y ait un biais lié aux habitats visités.

La région sud-est (Pré-Ligure), au climat sous influence méditerranéenne mais plus humide, semble particulièrement favorable à *P. kuhlii*, puisqu'on la rencontre même dans les hautes vallées. Au total, sa présence a été notée dans 58 % des sites, ce qui est remarquable étant donné les altitudes prospectées.

Le cas d'*H. savii* semble plus simple à interpréter. Certes elle présente en Europe une répartition méridionale (Mitchell-Jones *et al.*, 1999), et l'on aurait pu s'attendre à un déséquilibre des fréquences d'apparition en faveur des secteurs les plus chauds. En fait elle fut présente dans 98 % des sites. Ceci s'explique certainement par ses affinités rupestres qui en font aussi une espèce typique de la zone minérale des montagnes méridionales. Elle est dominante au-dessus de 1500 m d'altitude (Tableau 3), et ceci quel que soit l'habitat. Dans les secteurs les plus froids, elle trouve certainement refuge le jour dans les falaises exposées au sud.

Le cas du vallon de Mollières est intéressant. Il se situe au carrefour des trois influences, ce qui laissait présager l'existence d'une faune plus diversifiée que dans les autres vallées. On y rencontre effectivement aussi bien *M. emarginatus* que *M. nattereri*, ce dernier ayant une fréquence d'apparition aussi forte que *N. leisleri*, ce qui n'est le cas dans aucun autre secteur. Le nombre de 9 espèces sur seulement 2 transects est également remarquable.

Plusieurs espèces *(E. nilssonii, V. murinus, N. noctula/ lasiopterus)* sont ici hors de leur aire de reproduction connue. La rareté des contacts pour ces chiroptères pourtant facilement audibles grâce à leur forte intensité d'émissions, ne plaide pas en faveur de l'hypothèse d'une population autochtone.

Répartition en fonction des types d'habitats

La différence de peuplements spécifiques entre les zones éclairées et les autres milieux semble être la règle (Tableau 2). Les espèces de lisière et de haut-vol, souvent qualifiées d'opportunistes, ont sans doute développé une stratégie de recherche de concentrations de proies, quitte à parcourir de grandes distances, le coût énergétique de ces déplacements étant faible pour de bons voiliers (Jaberg, 1998 ; Leuthold & Jaberg, 2000). De plus, leur système sonar est parfaitement adapté à la recherche de proies (même petites) à moyenne ou longue distance (Waters *et al.*, 1995). Ces espèces deviennent donc des « spécialistes » des lampadaires (ces derniers attirant par phototropisme de nombreux diptères et lépidoptères), et ce phénomène semble favoriser leurs populations, au dépens des autres espèces dont les stratégies de chasse (repérage à courte distance de proies liées au feuillage) interdisent une telle adaptation (Rydell & Racey, 1995).

Dans une étude menée en Suède, ces derniers auteurs montrent que le nombre d'espèces fréquentant les lampadaires (5, avec absence des genres *Plecotus* et *Myotis*) est très inférieur à celui rencontré dans la campagne environnante (10), ce qui est conforme à nos résultats.

Dans notre étude, seul *T. teniotis* semble, parmi les chasseurs de haut-vol, être moins lié aux lumières artificielles, même si son activité y est équivalente à celle de tous les autres milieux réunis (Fig. 2).

L'indice d'activité dans les villages sans lumières est similaire à ceux de la plupart des milieux semi-ouverts ; il est en outre près de six fois inférieur à l'indice en villages éclairés, ce qui confirme que ce sont bien les lumières et non les habitations ou d'autres résultantes des activités humaines qui expliquent de telles concentrations de chauves-souris en chasse (Rydell, 1991).

La proportion relativement élevée des contacts d'oreillards en milieu ouvert (Fig. 2) peut être due au fait qu'ils émettent dans ces circonstances des signaux d'intensité moyenne (comparable à celle d'une pipistrelle), ce qui peut induire une surestimation de l'activité dans ces habitats, aux dépens des milieux forestiers où leurs émissions sont plus faibles.

D'une façon générale, seules les espèces agiles ont une forte proportion de leur activité en milieu ouvert. Elles n'affichent cependant pas de preferendum marqué pour ces derniers (à l'exception peut-être de *N. leisleri*). Ceci peut s'expliquer par leur mode de chasse en vol élevé, exploitant le plancton aérien groupé en essaims, dérivant au gré des thermiques et des vents. Ces espèces sont donc certainement peu en lien direct avec le type de végétation présente au sol.

Les différences d'indices d'activité entre les habitats de milieu ouvert peuvent paraître surprenantes (Tableau 2). L'eau, courante ou stagnante, s'avère souvent être un facteur favorisant l'abondance d'insectes, et par conséquent celle de chauves-souris. C'est le contraire ici et deux hypothèses peuvent expliquer ce phénomène :

- le nombre important de transits sur les cols augmente l'activité générale dans ce milieu, même si la proportion de chasse n'y est pas négligeable : les caractéristiques physiques des cols peuvent favoriser la concentration d'insectes en essaims, amenés par dérive aérienne ;
- les milieux ouverts en montagne se rencontrent surtout à des altitudes supérieures à 1800 m, et dans ce contexte le moindre abaissement de température limite ou stoppe l'activité des insectes et de leurs prédateurs. Les lacs et ruisseaux, situés en fond de cuvette ou vallon, génèrent des courants froids qui pourraient être la cause des indices très bas rencontrés dans ces biotopes.

La différence d'indice entre ruisseaux et lacs bordés d'arbres tient certainement au caractère torrentiel des cours d'eau de montagne, peu propice à de fortes diversité et abondance d'insectes dont le stade larvaire est aquatique, notamment les diptères qui constituent un des taxons clés dans le régime alimentaire des chiroptères européens (Beck, 1994-95 ; Vaughan, 1997).

La forêt dense présente un indice conforme à la moyenne générale. Mais des différences sont apparues selon les années : en 1995 dans le Haut-Verdon et en 2000 en Haute-Tinée, les températures fraîches lors des inventaires semblent avoir influencé le niveau d'activité en sous-bois, nettement supérieur ces années-là par rapport aux autres. Cette valeur de refuge des forêts est liée à la température, plus élevée de un à plusieurs degrés par rapport aux milieux ouverts, ce qui peut maintenir ou augmenter l'activité des insectes (Duvergé & Jones, 1994). Ce phénomène doit être particulièrement important en montagne durant toute la saison de chasse des chiroptères.

Répartition altitudinale

La répartition altitudinale des villages éclairés prospectés, étant donné l'indice très élevé de ce type d'habitat, peut influencer les résultats dans certaines tranches d'altitude : c'est entre 900 et 1299 m, et surtout de 1700 à 1899 m, que les indices peuvent être biaisés par la présence de villages. Mais la tranche 1900 à 2099 m, qui compte parmi les indices les plus élevés (Tableau 3), ne doit rien aux lumières artificielles. Il y a donc bien une richesse intrinsèque des habitats naturels au-dessus de 2000 m.

Le genre *Plecotus* semble plus abondant en altitude que dans les basses vallées. La majorité des contacts se rapporte donc certainement à *P. macrobullaris* et *P. auritus*, car *P. austriacus* ne monte guère en altitude, y compris dans le sud de l'Europe : Favre (2003) le situe principalement en-dessous de 1300 m dans les Alpes du sud, et en Espagne il ne dépasse pas 1600 m (Swift, 1998). *P. macrobullaris*, de découverte récente (Kiefer & Veith, 2001 ; Spitzenberger *et al.*, 2003) est connu actuellement des Alpes et des Pyrénées, et passe pour être strictement montagnard. *P. auritus* a été capturé dans les Alpes du sud jusqu'à 1600 m (P. Favre, comm. pers.). Il est possible que certaines notes montagnardes attribuées à *P. auritus* avant 2001 concernent en réalité *P. macrobullaris* : dans les Pyrénées, *P. auritus* est une des espèces les plus fréquemment capturées au filet au-dessus de 1500 m en vallée d'Ossau (Masson & Sagot, 1988) et même entre 2000 et 2500 m en Ariège (Bertrand, 1992).

La distinction de ces espèces n'étant pas à l'heure actuelle possible au détecteur, nous ne pouvons esquisser ici aucune répartition en fonction de l'altitude et de l'habitat. Simplement, la forte proportion de contacts en altitude rend probable la présence de *P. macrobullaris* sur les secteurs prospectés. La fréquence d'apparition d'oreillards en pelouse alpine pourrait indiquer une tendance de cette dernière espèce à exploiter ces milieux, *P. auritus* étant reconnu comme essentiellement forestier (Swift, 1998).

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RÉSUMÉ

Durant 40 soirées réparties entre les étés 1993 et 2000, des transects et points d'écoute ont été menés dans divers types de paysages alpins, entre 300 et 2500 m d'altitude. Les contacts acoustiques de chiroptères, relevés grâce à un détecteur hétérodyne et expansion de temps, ont été

classés en fonction du type de milieu, d'activité, et de l'altitude. Les résultats montrent un indice d'activité peu dépendant de l'altitude jusqu'à environ 2200 m, le niveau d'activité de certaines espèces comme l'oreillard étant même positivement corrélé à l'altitude. Les grands types de milieux (anthropisés, forestiers, ouverts, humides ou non) montrent également des regroupements spécifiques particuliers : les espèces de lisière ou de haut-vol (genres *Pipistrellus*, *Hypsugo*, *Nyctalus*) fréquentent surtout les villages éclairés, à l'inverse des espèces manœuvrables (genres *Myotis*, *Plecotus*). Le genre *Plecotus* est fréquemment contacté en pelouses sommitales.

Les résultats montrent également l'efficacité de cette méthode dans des milieux difficiles à inventorier grâce aux méthodes classiques, et ses prolongements sur une meilleure connaissance de l'occupation des habitats par les chiroptères.

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Découverte d'un jeune grand murin (*Myotis myotis*) albinos en Corrèze (19) (France) : essai de synthèse sur les cas d'albinisme des chiroptères en Europe

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Abstract. After an albino mouse-eared Bat (*Myotis myotis*) discovery in France, we have searched for another cases of mouse-eared Bat's albinism. Our synthesis has an one-fold objective : to publish unknown or unpublished data about Chiroptera albino with French and European data.

Key words : Chiroptera, albinism, France, Europe.

INTRODUCTION

L'albinisme chez les chiroptères reste un phénomène rare surtout lorsqu'il est total. Les cas relatés par les naturalistes et les abondantes publications concernent bien souvent des dépigmentations partielles, appelées généralement « albinisme partiel » (Caire & Thies, 1988 ; Cerveny, 1980 ; Cheng & Lin, 2002 ; Dorst, 1957a ; Dulic & Mikuska, 1968 ; Gaisler & Pokorny, 2002 ; Haensel, 1968, 1972 ; Haensel & Nest, 1989 ; Heddergott, 1999 ; Holsworth, 1988 ; Hsu, 1997 ; Jones, 1973 ; Laar, 1994 ; Matis & Pjencak, 1998 ; Obara, 1983 ; Pryswitt, 1997 ; Suter & Kuhn, 2003 ; Weidner, 1994).

Rappelons que l'albinisme est une anomalie héréditaire résultant de l'absence partielle ou totale de pigment, par défaut de mélanine, qui se manifeste par la décoloration de la peau, des poils et de l'iris. L'albinisme total chez les chiroptères est ainsi caractérisé par une fourrure uniformément blanche sur la totalité du corps, et par le museau, les ailes et les yeux rosés ou rouges (Haensel, 1972 ; Uieda, 2000, 2001).

DÉCOUVERTE D'UN GRAND MURIN ALBINOS EN CORRÈZE

Une convention entre *Electricité de France* (*EDF*) et *Limousin Nature Environnement* signée en 2002 permet aux naturalistes d'accéder aux différentes installations hydroélectriques (barrages, usines) du Limousin. Ainsi, le 4 juillet 2003, nous avons été autorisés à procéder au recensement des colonies de chiroptères présentes dans le Barrage du Chastang [St Martin-la-Méasne/Servières-le-Château (Corrèze-19)] situé dans les Gorges de la Dordogne. Ces colonies de reproduction sont parmi les plus importantes du Limousin, que ce soit pour le grand murin ou le petit rhinolophe. Nous avons alors dénombré 659 grands murins (*Myotis myotis*) dans les bajoyers et 125 petits rhinolophes (*Rhinolophus hipposideros*) dans les sous-sols, alors que le 5 juillet 2002 leurs effectifs étaient respectivement de 601 (dont 366 adultes) et de 80 (dont 70 adultes) individus.

C'est au cours de ce dénombrement de juillet 2003 que nous avons remarqué la présence d'un jeune grand murin (*Myotis myotis*) albinos. Cet individu semblait particulièrement gêné par la lumière de notre lampe. Dans un premier temps, il chercha à se dissimuler au sein de ses congénères, puis il s'isola de l'essaim lors de notre décompte de la colonie. Cet individu présentait les caractéristiques morphologiques d'un jeune de l'année. De plus, au cours du dénombrement de l'été 2002, il n'y avait aucun grand murin albinos présent dans cette colonie. Malheureusement, ignorant où hiberne cette importante colonie de grands murins, nous n'avons pas retrouvé cet animal au cours de l'hiver 2003-2004, pas plus qu'au cours de la saison de reproduction 2004.

DISCUSSION/SYNTHÈSE

La seule observation détaillée et publiée d'une chauve-souris albinos en France remonte à 1957 (Dorst, 1957b) et concerne un rhinolophe euryale (*Rhinolophus euryale*). Il s'agit d'un exemplaire conservé au Muséum National d'Histoire Naturelle sans que l'on connaisse précisément la date et le lieu de sa capture.

On dénombre cependant en France **dix** autres observations, connues soit par des clichés photographiques ou par des témoignages ayant parfois fait l'objet de courtes notes dans des bulletins d'associations naturalistes (Tabl. 1).

En Europe, 34 spécimens pour 12 espèces ont été observés (Tabl. 2).

Le grand murin (*Myotis myotis*) est très peu représenté. Seulement 4 individus ont été observés en Europe auparavant par :

- Aellen : le spécimen apparaît dans l'ouvrage de Denise Tupinier (Aellen *in* Tupinier, 1989), sans précision de lieu et de date ;
- Andera : en 1982, en Bohème (Tchécoslovaquie), Andera a photographié un grand murin (*Myotis myotis*) albinos avec un insecte dans la bouche, (*Mammals Image Gallery*, www.emporia.edu/biosci/msl/chiro.htm). Il semble cependant que cette dernière observation n'ait pas fait l'objet d'une publication.
- Dietz & Schunger : un jeune grand murin a été découvert en Allemagne en 2001, il semble qu'il n'ait jamais été revu depuis.
- Cart : l'individu albinos a été observé deux années consécutives dans une colonie de mise bas dans le Nogentais [Aube-10 (France)] (Cart, 2003).

Selon le dernier inventaire concernant l'albinisme des chauves-souris réalisé par Uieda (2000), 65 spécimens représentant 39 espèces ont été recensés à ce jour de par le monde. A ce décompte, nous avons ajouté les quelques découvertes récentes ou oubliées concernant l'Europe ainsi que quelques découvertes sur les autres continents (Tabl. 3).

Ainsi, si nous cumulons les découvertes réalisées en Europe et ces dernières observations à l'inventaire de Uieda, le recensement des chiroptères d'un albinisme total est de **98** spécimens pour **52** espèces.

CONCLUSION

Les observations d'individus albinos sont souvent ponctuelles et rarement réitérées. Or, au cours de nos recherches bibliographiques, nous avons remarqué que toutes les découvertes ne font malheureusement pas l'objet de note ou de petit article détaillés. Nous avons tenté de faire une première synthèse européenne de ces observations en espérant inciter les chiroptérologues à publier leurs découvertes insolites.

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RÉSUMÉ

Suite à la découverte d'un jeune grand murin (*Myotis myotis*) albinos en France, nous avons recherché les cas d'albinisme recensés pour cette espèce. Notre synthèse s'est efforcée de rendre publique ces données peu connues ou non publiées relatives aux chiroptères albinos. Celle-ci ne se limite pas aux observations françaises mais rassemble également des données européennes.

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Tableau 1 : Liste des chiroptères albinos observés en France.

Espèce	Nombre	Année	Lieu	Pays	Source
Rhinolophus hipposideros	1	1995-1997 ?	Haute-Saône	France	Roué, *comm. pers.* (photo)
Rhinolophus ferrumequinum	1	1986	Chartres Eure-et-Loire	France	Photo de Lustrat *in* Fontanel, 2001
Rhinolophus ferrumequinum	1	2002	Vallée de l’Indre	France	Frontera, 2002 (note)
Rhinolophus ferrumequinum	1	2002 ?	Morbihan	France	Farcy, *comm. pers.*
Rhinolophus euryale	1	Fin XIX^{e} s. - début XX^{e} s.	Maine-et-Loire	France	Dorst, 1957b
Myotis myotis	1	2000-2001	Aube	France	Cart, 2003 (note)
Myotis myotis	1	2003	Corrèze	France	Présent article
Myotis emarginatus[1]	1	2002/2003	Picardie	France	Huet, *comm. pers.* (photo)
Miniopterus schreibersii	2	2002 ?	Bouches-du-Rhône	France	Hacquart, *comm. pers.*

[1] Cet individu uniformément clair, ne semble pas être à proprement dit un « albinos », mais il présente plutôt le résultat d’une dépigmentation généralisée de son pelage. (Huet, *comm. pers.*).

Tableau 2 : Liste des chiroptères albinos observés en Europe.

Espèce	Nombre	Année	Lieu	Pays	Source
Rhinolophus hipposideros	1	1950-1960 ?	Vallée de la Meuse	France	Redant, *comm. pers.* (stocké à Ramioul)
Rhinolophus hipposideros	1	1995	?	Slovaquie	Horacek, 1995
Rhinolophus hipposideros	1	1995-1997 ?	Haute-Saône	France	Roué, *comm. pers.* ;
Rhinolophus hipposideros	1	2002 –2003	Huy – province de Liège	France	Redant, 2002.
Rhinolophus ferrumequinum	1	1986	Chartres Eure-et-Loire	France	Lustrat *in* Fontanel, 2001
Rhinolophus ferrumequinum	1	2002	Vallée de l’Indre	France	Frontera, 2002
Rhinolophus ferrumequinum	1	2002 ?	Morbihan	France	Farcy, 2003, *comm. pers.*
Rhinolophus euryale	1	Fin XIX^{e} s. – début XX^{e} s.	Maine-et-Loire	France	Dorst, 1957b
Myotis myotis	1	1939 ?	?	?	Aellen *in* Tupinier, 1989
Myotis myotis	1	2001	?	Allemagne	Dietz & Schunger, 2001
Myotis myotis	1	1982	Bohème	Tchécoslovaquie	Andera,1982
Myotis myotis	1	2000-2001	Aube	France	Cart, 2003
Myotis myotis	1	2003	Corrèze	France	Présent article
Myotis daubentonii	1	?	Böhmerwald	Tchécoslovaquie	Cerveny, 1977, 1980 ; Cerveny & Bürger, 1977
Myotis daubentonii	1	?	Böhmerwald ?	Tchécoslovaquie ?	Cerveny *in* Schober & Grimmberger, 1991

Myotis daubentonii	1	1968	Viborg	Danemark	Egsbaek *in* Haensel, 1968
Myotis daubentonii	1	1985	Miedzyrzecki Rejon Umocniony	Pologne	Jaros, *comm. pers.*
Myotis daubentonii	1	2002	Gonzen	Suisse	Suter & Kuhn, 2003
Myotis nattereri	1	1998	Norfolk	Grande Bretagne	Goldsmith, 1998
Myotis nattereri	1	2001	Grodziec	Pologne	Jaros, *comm. pers.*
Myotis bechsteini	1	1993	?	Tchécoslovaquie	Zukal *et al.*, 1994
Myotis emarginatus	1	2002/2003	Picardie	France	Huet, *comm. pers.*
Eptesicus serotinus	1	1953-1957	Vreschen-Bokel	Allemagne	Havekost *in* Haensel, 1968
Eptesicus serotinus	1	1957-1958	Kleinkneten	Allemagne	Havekost *in* Haensel, 1968
Eptesicus serotinus	1	1970	?	Allemagne	Stratmann, 1971
Eptesicus serotinus	1	1975 ?	?	Allemagne	Cerveny, 1977, 1980
Eptesicus serotinus	1	2003	Süd Brandenburg (Lübben	Allemagne	Pelz, 2004
Eptesicus serotinus	1 mâle	2002-2003	Sniaty (proche de Poznan)	Pologne	Laskowska, 2002 ; Jaros, *comm. pers.*
Pipistrellus pipistrellus	1	1976	?	Allemagne	Cerveny, 1977
Pipistrellus pipistrellus	1	2000	?	Allemagne	Sendor, 2001
Miniopterus schreibersii	2	2002 ?	Bouches-du-Rhône	France	Hacquart, *comm. pers.*
Plecotus auritus	1	1990	Berlin/Wannsee	Allemagne	Lehnert, 1991
Plecotus auritus	1	2000	Nunhem	Pays-Bas	Buys *et al.* 2000a-b

Tableau 3 : Liste complémentaire des chiroptères albinos observé sur les autres continents.

Espèce	Nombre	Année	Lieu	Pays	Source
Carollia perspicillata	1	([1990 ? 2000)	Réserve naturelle des Nouragues ?	Guyane française	Charles-Dominique *et al.*, 2001
Eptesicus fuscus	quelques individus	XXe s.	?	U.S.A.	Baker, 1983
Myotis macrodactylus	1	1990	?	Japon	Harada *et al.*, 1991
Miniopterus schreibersii bassanii [2]	1	1999	Bat Cave - Naracoorte	Australie	Lumsden, 2001
Nycteris nana	1	1997	?	Zaïre	Nowak, 1997
Rhinophylla pumilio	1	1993 ?	Réserve Naturelle des Nouragues ?	Guyane française	Charles-Dominique *et al.*, 2001
Scotophilus leucogaster	1	2000 ?	Monts Nuba - Kordofan	Soudan	Fahr, 2001
Taphozous georgianus	1	1980	Arnhemland escarpment	Australie	Swamson, 1980

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[2] 2e mention pour cette espèce dont un individu avait été découvert par Smith en 1968.

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Cas d'une prédation d'une chauve-souris par une grenouille (genre *Rana*) en Creuse (Limousin, France)

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En juillet 1999, c'est dans le village de St Georges-la-Pouge (23) que Madame Rufflet découvre ce cas surprenant : une grenouille morte, flottant dans une mare, tenant dans sa gueule une chauve-souris, morte elle aussi. Mais ce n'est qu'en septembre 2001 que celle-ci me présente les deux photographies qu'elle a prises de cette « prédation » d'une chauve-souris par une grenouille.

A notre connaissance, une seule référence bibliographique mentionne la capture d'une chauve-souris européenne par une grenouille. Brosset relate, en effet, le cas d'une grenouille verte (*Rana esculenta*) pêchée à la ligne, régurgitant une jeune pipistrelle au moment où le pêcheur décroche l'hameçon (Brosset, 1966, p. 117-119). Dans le cas présent, les clichés photographiques réalisés ne permettent pas une identification certaine des animaux: la grenouille appartient probablement à l'espèce *Rana esculenta*, seule espèce du genre *Rana* de couleur verte sur ce site (G.M.H.L., 2000). Quant à la chauve-souris, de par sa forme générale, sa taille, la forme de son museau et de ses oreilles, il s'agit vraisemblablement d'un vespertilionidé, pipistrelle commune *(Pipistrellus pipistrellus)*, pipistrelle de Kuhl (*Pipistrellus kuhli),* ou murin de Daubenton *(Myotis daubentoni),* espèces considérées communes autour de ce village (G.M.H.L., 2000).

Si ce phénomène semble très rare en Europe, par contre ailleurs dans le monde la prédation des chauves-souris par les grenouilles est observée assez régulièrement. Ainsi, en Asie, la grenouille *Rana tigrina* happe des oiseaux mais aussi des chiroptères; en Amérique du Nord, les *Rana catesbeiana* et *Rana pipiens* peuvent aussi en avaler (Brosset, 1966, p. 117-119); en Amérique du Sud, d'autres espèces, comme les *Leptodatylus myersi* et *Bufo guttatus,* attendent aux sorties de gîtes les chauves-souris afin de les capturer (Charles-Dominique *et al.*, 2001, p. 51).

Remercions Madame Rufflet qui a eu l'amabilité de nous faire part cette observation remarquable.

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5. European Bat Detector Workshop
Forêt de Tronçais – Allier (France) – 21-25.08.2002

Depuis 15 ans, l'European Bat Detector Workshop, concomitant au Symposium Européen sur les chauves-souris organisé tous les 3 ans, permet de faire le point sur les avancées en matière d'étude des chiroptères grâce aux ultrasons.

Cet atelier est l'occasion pour l'ensemble des naturalistes passionnés de se rencontrer et de confronter leurs découvertes lors de séances en salle et de sorties sur le terrain.

La cinquième édition a été réalisée conjointement par l'association Chauve-Souris Auvergne, la Société Française pour l'Etude et la Protection des Mammifères et l'association Bats. Les dernières études et méthodes d'identification des différentes espèces de chauves-souris ont été présentées. Le comité d'organisation a souhaité publier les actes correspondants dans un numéro du Rhinolophe afin de permettre à un plus grand nombre de lecteurs de profiter de ces nouveautés. La majorité des présentations effectuées lors de ce workshop sont jointes sur un CDRom pour vous permettre d'en bénéficier.

Créé par un groupe d'amis sur le coin d'une table, au cœur de la forêt de Tronçais en automne 1999, ce workshop fut un agréable moment de rencontres et d'échanges sur ce thème cher à nous tous: les chauves-souris !

For fifteen years, the European Bat Detector Workshop, a event comcomitant to the European Bat Symposium which is organized every three years, takes stock of the innovation on bats studies using echolocation.

This workshop is an opportunity for every bat lovers to meet and compare their discoveries during seminaries and fieldworks.

The fifth edition was conducted jointly by the Chauve-Souris Auvergne association, the French society for the study and the protection of mammals (S.F.E.P.M.) and the Bats association. The last studies and methods for bat identification were presented. In order to make this information available to everyone, the organisation committee wished to publish the workeshop's acts in a issue of Le Rhinolophe. Moreover, a CDrom which contains must of the workshop's presentations is enclosed to this issue.

Created during the automn 1999 by a group of friends around a table, in the heart of the forest of Tronçais, this workshop was a nice moment to exchange ideas on this theme so dear to us : bats.

Comité d'organisation/*Organisation committee* : Michel Barataud, Pascal et Sylvie Giosa – Chauve-Souris Auvergne, Philippe Jourde & Sébastien Y. Roué.

Soutiens/*Supports* : Ministère de l'Ecologie et du Développement Durable
Direction Régionale de l'Environnement d'Auvergne
Conseil Régional d'Auvergne
Conseil Général d'Allier
Office National des Forêts

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Bat detectors

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Abstract. This paper discusses the role of bat detectors in the study of bat behaviour and their identification. All bat detectors work on the principle of receiving echolocation calls using ultrasonic-sensitive microphones and electronically processing these signals. The three main methods are : heterodyne, frequency division and time-expansion. Some detectors use only one method whereas others can be switched between different types. Each method is described and the advantages and limitations discussed with respect to actual bat calls.

PC-based acoustic analysis software has become increasingly available. These techniques, and their influence on the interpretation of signals, are also considered. Acoustic analysis is most commonly applied to time-expansion recordings. A basic understanding of the techniques used is essential because the software allows various parameters to be changed which can, in turn, influence the interpretation of signals. Some of the common parameters are presented.

Problems associated with the identification of bats are discussed, along with some of the methods used to improve confidence in identification.

INTRODUCTION

A bat detector converts the inaudible, ultrasonic echolocation calls of bats into an audible sound which can be listened to or recorded. Bat detectors can assist in the study of bats by determining whether bats are foraging in the immediate area, to assess the foraging activity or number of bats present, and to assist in their identification. While bat detectors are undoubtedly of enormous benefit to those working on bats, it is important to understand their limitations since many factors can influence the interpretation of the data. In addition, with the falling cost and increasing power of personal computers, and the increased availability of sound analysis software, it is now possible to undertake acoustic analysis of sounds recorded using bat detectors. Such analyses can also introduce biases in the interpretation of recorded signals, and consequently it is important to understand how these analysis techniques work, and how they affect the results.

DETECTOR TYPES

All detectors have a microphone which is sensitive in the ultrasound region. The echolocation calls of bats are picked up by the microphone, and relayed to some electronic circuitry which will convert the high frequency signals into lower frequency ones. These circuits work in three different ways : heterodyne, frequency division and time expansion. The type of circuit used depends on the detector, some detectors use only one method, other can switch between different types. All have advantages and disadvantages.

Heterodyning

Heterodyning is basically the same process by which high frequency radio-waves are converted into low frequencies and output as sound in portable radios. This is why some designs of home-made bat detectors can be made by converting radios. The principle of operation works as follows :

1. The detector has an internal oscillator which produces a square wave. The frequency of this square wave depends on the position of the tuning dial of the detector. Call this frequency f1.
2. The microphone of the detector picks up the echolocation call of the bat and converts it into an electronic signal. Call this signal f2. Because the call from the bat varies in frequency and amplitude, so does f2.
3. A mixer circuit combines the two signals together, producing an output that has four components, a frequency which is the sum of f1 and f2, one which is the difference between f1 and f2 and the original f1 and f2 signals.
4. A filter allows only the lower 5 kHz to 10 kHz signal components to pass, meaning that all of the f1, f2 and f1+f2 signals are removed, and only the lower frequency components (difference between f1 and f2) is allowed to pass.
5. The signal is then passed to an amplifier and sent to the speaker.

By way of example, say that the internal oscillator produces a signal of 45 kHz (f1), and the detector picks up the echolocation call of a Pipistrelle, which sweeps down in frequency from 100 kHz to 43 kHz (f2). The mixer will mix the incoming signal with the oscillator producing a signal which sweeps from 145 kHz to 98 kHz (the f1 + f2 signal), and one which sweeps from 55 kHz to -2 kHz (the f1 – f2 signal). The signal at -2 kHz represents a 2 kHz signal which is switched in phase by 180°. The higher frequency (f1 + f2) signal is removed by a filter, and the lower frequency one allowed to pass. This signal is then amplified prior to being sent to the speaker. The end result is signals around 47-43 kHz will produce an audible output of around 2 kHz, while those of a higher frequency will not. What happens in most detectors is anything above about 5 kHz from the tuned signal is filtered out from the signal. This gives the bandwidth of the detector, so a heterodyne detector with a bandwith of 10 kHz, when tuned to 45 kHz, will pick up bats from 50 kHz to 40 kHz (5 kHz above and below the tuned frequency). A narrower bandwidth gives better frequency identification at the cost of reduced overall sensitivity as more sound energy is discarded. In theory, if heterodyne detectors are tuned to a particular frequency, the output should be 0 kHz, and therefore not heard. In practice, as the bat signal sweeps in frequency, there is enough sound energy either side of the tuned frequency to produce an output.

Heterodyning allows high levels of amplification to be used, and as it looks only at a narrow range of frequencies, it is very sensitive and can detect bats over a considerable range. The disadvantage is it will only listen to part of the call at any one time, and in order to listen to other frequencies we have to adjust the tuning dial. This can however tell us at which frequency the call is loudest, and identify what the maximum and minimum call frequencies are. It also produces different sounds depending on the duration of the call in the tuning window. Depending on the shape of the FM sweep of the bat, sounds can be described as “wet slaps” or “dry crackles” and this may help with identification.

In many cases, the process of superheterodyning is used, in which case it is the higher frequency sum of f1 and f2 that is kept, this being passed to a narrow bandwidth amplifier, before being mixed with the signal from a second, fixed frequency oscillator to bring the frequency back down again to an audible one. Such a system allows much higher levels of amplification and hence better sensitivity.

Frequency division

One way in which to convert high frequencies into low ones is simple to divide the frequency by a fixed factor, usually a factor of 10. This converts 100 kHz to 10 kHz, and 20 kHz to 2 kHz and so on. This is done by taking the electrical output from the microphone of the bat detector and counting the number of cycles of the waveform. The number of cycles are counted using a technique known as zero-crossing. Each time the waveform goes from positive to negative, it is counted, and there are two zero-crossings per cycle of the waveform. On the first zero-crossing, the output circuitry rises, then waits for ten zero-crossings before falling again. This gives one output cycle to every ten input cycles, dropping the frequency by a factor of ten (see Fig. 1). The benefits of such a system are that it listens to all frequencies at

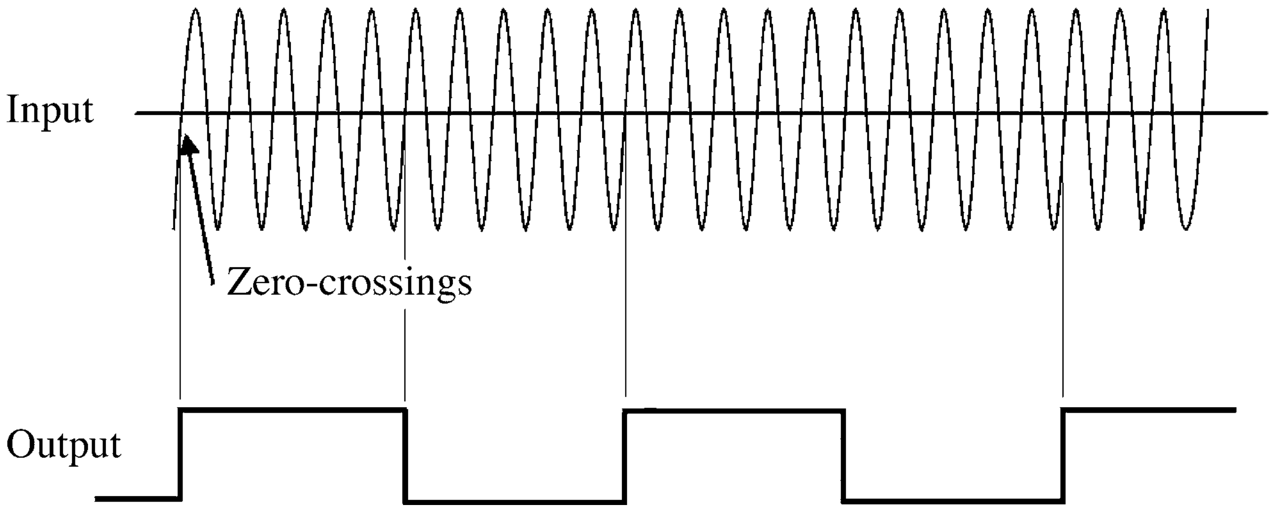

Fig. 1 : **How frequency division works.** The number of zero-crossings of the original signal is counted, and an output signal produced after a set number. This example produces a square wave output which is one tenth that of the original signal.

once. A bat will never be missed by having the tuning dial set to the wrong frequency. It is also possible to carry out some very basic computer analysis on such recordings. The disadvantages are that it becomes very difficult to identify bats by listening to the output, and it gives no information on maximum, minimum or peak frequencies just by listening. Such circuits are best reserved for cases when it is necessary to know whether any bats are present. A further confusing aspect depends on whether the echolocation call has strong harmonics present. Normally, with weak harmonics, they are not of sufficient amplitude to generate their own zero-crossings. However, when the bat is close or directly in front of the detector, the lower frequency harmonics can be so loud they generate their own zero-crossings. The result for a call which sweeps from 80 kHz to 20 kHz would be seen to sweep from 8 kHz down to 2 kHz, then when strong harmonics were present, the signal would suddenly double in frequency. Another problem with this type of circuit is that the amplifiers work over the full frequency range, not only amplifying the signals of interest, but also of any noise present, such as the sound of walking though grass, insect calls or the electronic noise of the circuits themselves. This generally gives a worse signal to noise ratio than the heterodyne types of detectors making bats more difficult to detect. Positive feedback can also occur between the speaker and the microphone. The microphone will pick up a signal which is processed by the circuitry and output from the speaker. The microphone then picks up the output from the speaker, processes it, and outputs it through the speaker and so on, creating a roaring or whining noise.

Time expansion

Another way of converting a high frequency signal to a lower one is to record it, and play it back at a slower speed. If a 100 kHz signal is recorded onto tape at 100 cm per second, and the tape is then replayed at 10 cm per second, the frequency of the signal will drop by a factor of ten. It will obviously also take ten times longer to replay. The limited length and speed of portable cassettes do not work like this, but this technique was actually used in the past, with large high speed tape recorders being taken into the field which could run at almost two meters of tape per second. Modern digital techniques mean that digital recording is now possible and the circuitry had become more portable in the field. The microphone picks up the echolocation call of the bat as before. Now however, the waveform of the signal is sampled by the digital circuitry, and the height of the waveform is taken at regular intervals which depends on the sampling rate (see Fig. 2). This is termed Analogue to Digital Conversion (A/D). The sampling rate must be at least twice the frequency of the signal we wish to sample (see later about aliasing). In most time-expanding detectors this rate is about 450 kHz. So, 450 000 times a second, the height of the waveform is taken, encoded as one of 256 height "steps" and stored in a digital memory. The 256 height steps corresponds to an encoding level of 8 bits because $2^8 = 256$. In contrast, CD quality sound encodes at 16 bit resolution which provides $2^{16} = 65\,536$ intensity steps between the loudest sound and the quietest sound. In practice, the difference in quality between using 8 or 16 bit in bat detectors is marginal as the electronic noise in the detector masks any benefit – we would just more accurately encode noise. Once the memory is full, which can take anything from a few milliseconds to a number of seconds, depending on the detector, the memory is emptied, but this time, at one tenth the rate it was filled. The height values are read out at 45 kHz, and from them, the waveform is reconstructed, only this time it will be ten times longer than the original, and with the frequencies dropped by a factor of ten. This is termed Digital to Analogue Conversion (D/A). The signal is now of the right frequency to be recorded onto portable tape recorders for later analysis.

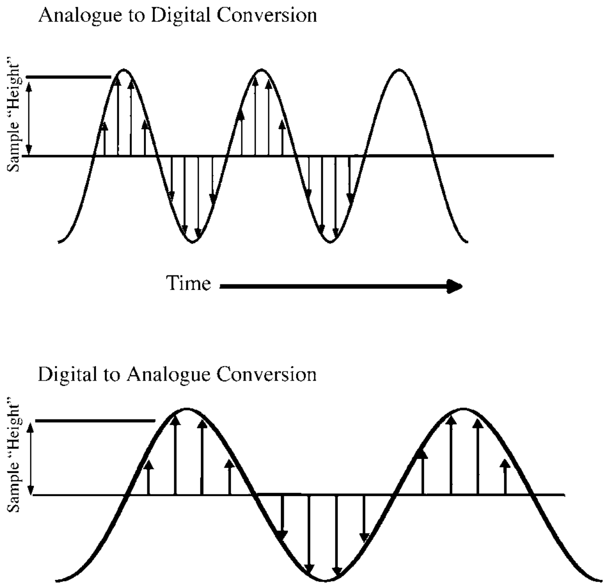

Fig. 2: **How a signal is sampled.** The height of the signal is measured at set intervals (governed by the sampling rate), and the height recorded as one of 256 levels.

The advantages of this system are it preserves all the characteristics of the recorded signal. The disadvantages are that another system needs to be used to detect the bat in the first place in order to capture the signal, and while the signal is replaying, another signal cannot be captured, so for 90 % of the time, the detector is not recording what is going on. Signals also have to be taken away for analysis as it is very difficult to assess species from listening to time-expanded outputs.

SOUND ANALYSIS

Sound analysis most particularly applies to recordings made from time-expanding detectors. While it is possible to analyse heterodyne recordings for measures of bat activity, little other information can be extracted from them. It is possible to analyse frequency divided information, but again, there are a number of signal processing issues that make this unwise since there are many opportunities for spurious frequency components to arise. Such problems limit the usefulness for species identification.

A number of commercial programs exist which allow the analysis of sound. There are also a number of shareware or freeware programs available via the internet. Many of these programs allow researchers to alter such things as the transform size, window type, overlap and a variety of other parameters. All of these things have a bearing on the final interpretation of the signal as to the frequency range observed, peak frequency and duration of the signal, so it is important to know what they do and how they affect the analysis of the signal.

Time and Frequency domains and the Fourier transform

The echolocation call of a bat consists of series of pulses of ultrasound. Researchers can ask questions about the time properties of these pulses such as when they occurred, what the time intervals are between them and how long they last. These questions have nothing to do with the frequency of sound the bat uses. They are therefore questions about what is called the *time domain*. Questions could also be asked about what frequencies the bats use. What is the maximum frequency, the minimum, what frequency do they use the most? These questions deal with the *frequency domain*. The time domain can be represented by looking at the waveform of a series of bat echolocation calls, or the waveform of one call only. It is difficult to tell which frequency the bat was using from a waveform only. Conversely it is possible to look at a power spectrum of a bat call, to see what the maximum frequency the bat used was, or the minimum or peak frequency. However, there is no information about when those frequencies occurred. In order to move from the time domain to the frequency domain, a mathematical process called a “Fourier transform” is used. Briefly, the Fourier transform takes a waveform and breaks it down into a number of superimposed sine waves, all of which have their own frequency, amplitude and phase. By looking at the different amplitudes of the different frequencies of sine waves, it is possible to work out which frequencies are the loudest components in the call. In practice the Fourier transform samples a number of points of the waveform, just as a time-expanding bat detector samples the waveform. If the number of points it takes is a power of 2, such as 64, 128, 256, 512, 1024, etc., then the maths becomes simpler and a fast Fourier transform (FFT) can be used, a solution that saves computational time. If a bat echolocation call is selected from a view of its waveform and a power spectrum is needed to find out what frequencies are in the call, a sound analysis program will look at the number of sampled points which are between the cursors used to select it. The program then rounds up the number of samples to the next power of two, divides those extra samples by two, and places one half before the first cursor, and one half after the last cursor, then performs the FFT on the signal. The result is a graph which shows what the amplitude level was of each frequency that could be identified between the cursors. It is meaningless to ask what was happening to the frequency within those cursors. In order to ask that question, it is necessary to look at what happens to frequency with time, as is shown in displays of a sonogram. These show the amplitude of the different frequency components with time. This joint time-frequency domain has a cost however. While in principle it is possible to know exactly the timing or the duration of an event in the time domain, or the exact peak frequency from a power spectrum, in the joint time-frequency domain, neither is accurate. The more accurately time information is needed, the less accurate will be the frequency information and vice versa.

Transform size

The accuracy with which either the time or the frequency domain is known is dependent on the transform size. The larger the transform size, such as a 2048 point transform, then the more accurate will be the frequency information, but the less accurate the time information. Conversely, a 64 point transform will provide more accurate time information, but less accurate frequency information. This is because a 64 point transform is taking a smaller section of time, so the time information is better, but it only has 64 points to work out what the frequency is, while a 2048 point transform takes a big section of time, but has longer to work out what the frequencies are, so is more accurate. This can be seen in Fig. 3. So, where bat echolocation calls need to be quantified for any form of multivariate analysis, it is best to extract time domain information from waveforms, and frequency domain information from power spectra, ensuring the transform size is held constant. In some analysis packages it is possible to standardise the transform length by generating a plot of power spectral density (PSD). In this case, a transform of standard length is slid across the signal of interest, and at specified points will generate a power spectrum. These are then averaged at the end.

Sonograms are generated in a similar way. A transform of a specified length (usually 128, 256 or 512 points) is

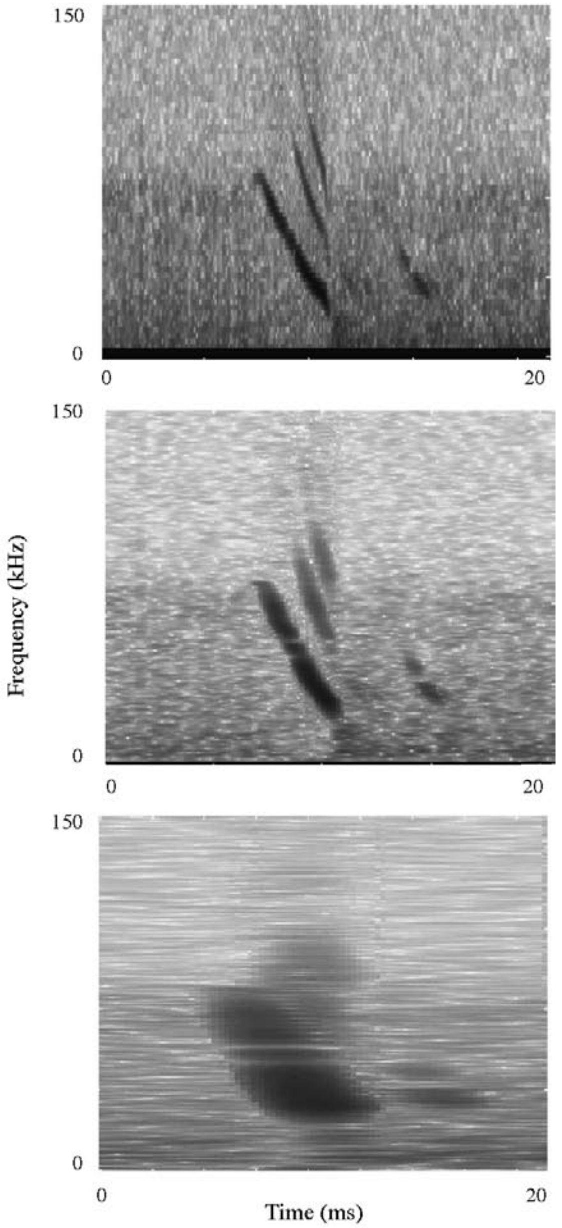

Fig. 3 : Sonograms showing the effect of different transform lengths on the ability to resolve time features (i.e. the duration of the signal), and frequency features (i.e. what the peak frequency is). The top figure uses an FFT of 128 points which is quite discrete in time but not in frequency. The middle figure uses an FFT of 512 points which is a compromise between time and frequency resolution, and the bottom figure uses an FFT of 2048 points which gives better frequency resolution but poorer time resolution.

slid along the signal of interest. Assuming a transform of length 128 points, at the first point a power spectrum is generated by performing an FFT on that block of 128 points, and plotted with colour corresponding to intensity of each frequency. The transform then moves along to the next point, usually the start of the next block of 128 points. Without any overlap in the points covered by each transform the result is uneven. By specifying an overlap, the transform may only move along a few points before doing another FFT. By analysing some of the points more than once, and plotting power spectra at more regular intervals, the display can be made more smooth, though at the cost of computational speed. The higher the degree of overlap, the smoother the sonogram appears.

Windows

Another feature which can be altered in many analysis programs is the window. A variety of different types are listed such as Hamming, Hanning, Kaiser, Welch and Blackman. Rectangular is sometimes also listed, although this actually means that no window is used. When the transform is sliding along the waveform and takes a block of points, it has no memory of what the waveform did prior to the current block. If the first point in the block is high, it probably came from a smooth waveform which was reaching its peak in the previous block. However, to the transform, the block has started suddenly and gone from zero to a high value very quickly. The same effect can happen at the end of the transform. In a Fourier transform, a sudden step is the result of a large number of superimposed sine waves, and this is what the transform thinks has happened. The output from the transform is therefore wrong. On order to avoid these effects, the hard edges of the block are smoothed by applying a function which reduced those at the edge while leaving those in the middle of the transform unaffected. This is the window function (see Fig. 4). The various types are optimised to different requirements, but they all basically do the same job, so it is best to be consistent. The rectangular window basically multiplies all the amplitudes of the sample by 1, so does not actually smooth the block of points at all.

Aliasing

Aliasing is an important issue about sampling in either time-expanding bat detectors or playing signals into the computer. Sampling theory states that in order to accurately record a signal by sampling it, the sampling rate must be at least twice the maximum frequency in the signal being sampled (termed the Nyquist frequency). This is not usually a problem in time expanding detectors as the sampling rate is usually fixed, and is usually very high, at 450 kHz or so. This means that frequencies up to 225 kHz can be recorded, which are beyond most species and so high that any atmospheric attenuation would mean they are very weak. However, when recorded signals are played into the computer, the same principle applies as they are sampled by the sound card to convert them

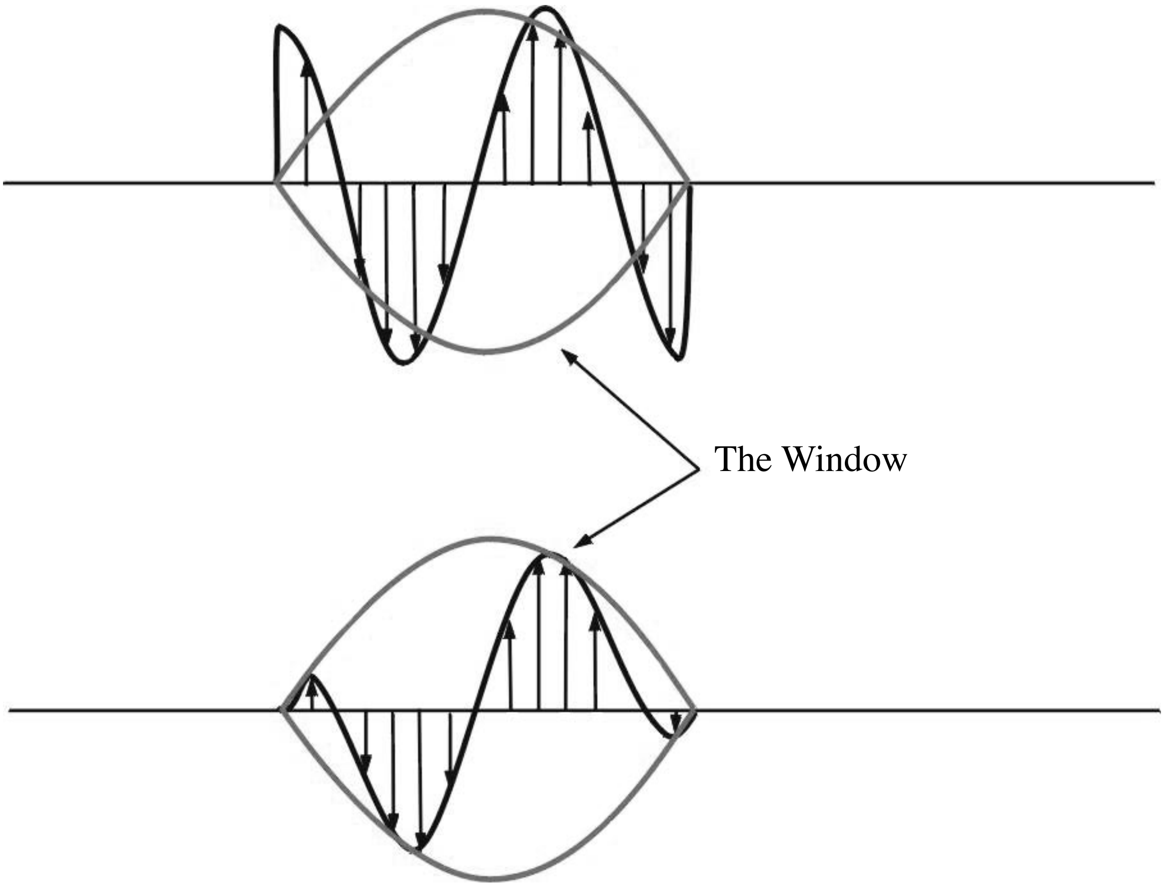

Fig. 4 : How a window function smoothes the waveform within the analysis window.

into digital format. The default sampling rates on most soundcards is 11 kHz, 22 kHz or 44 kHz. If a bat call that starts its call at 120 kHz and sweeps down to 20 kHz such as the call of *M. nattereri*, the time expanded recording would consist of a call that sweeps from 12 kHz down to 2 kHz. In order to encode this call properly, a sampling rate of 2 x 12 kHz = 24 kHz would be needed. If the soundcard is set to 22 kHz, aliasing will occur as the soundcards sampling rate is less than twice the maximum frequency being recorded. Rather than simply truncate the call at the upper frequency of 11 kHz, the "extra" 1 kHz becomes folded around the Nyquist frequency, and drops from 11 kHz to 10 kHz. This very peculiar effect means the Nyquist frequency acts like a mirror (Fig. 5). Even stranger effects can occur if harmonics are present. These become reflected in the Nyquist frequency and can overlap the original signal, but go from a low frequency to a high one producing a cross-shaped call like an "X". In order to avoid aliasing effects it is best to use a high sampling rate of 44 kHz until it is certain no hidden frequencies are present.

IDENTIFICATION OF SPECIES

Two main ways are used to identify bats to species or genus level. That of listening to the heterodyne output of a detector while observing the bat, and of making time-expanded recordings of the bats vocalisations before performing sound analysis on them. By listening to the bats, as well as watching them, it is possible to collect a large quantity of useful information and to tell what the frequency range of the bat is by scanning up and down the frequency dial until the highest and lowest frequencies are detected, as well as the peak frequency – the frequency at which the bat is loudest. The sound itself may give clues, whether it is a dry crackle, or the sound of a wet slap at a certain frequency, also the rhythm may be useful, as well as if the bat alternates two different call types. The human ear and brain is quite sophisticated in this respect and can pick out all kinds of subtleties in the signals. Seeing the bat may also give an idea of identification. Its size, shape of wing, foraging style may all help with identification. While all this may seem promising, the major problem with this form of identification, indeed with any identification of bats by bat detectors is that of

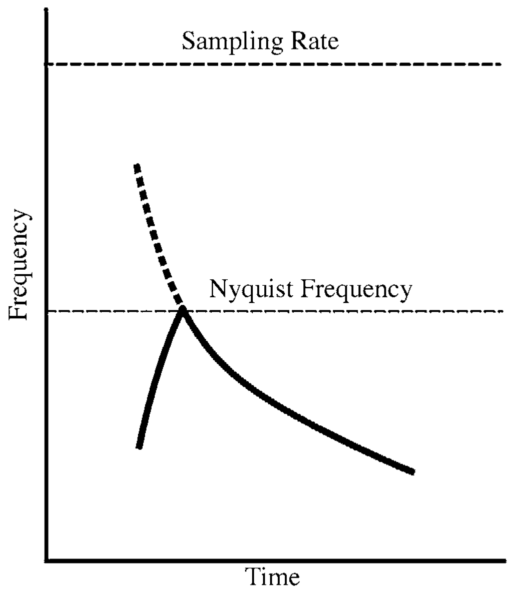

Fig. 5 : The effect of aliasing on a signal which has a frequency component above half of the sampling frequency. The top of the signal becomes reflected in the Nyquist frequency.

verification. Unless the bat has been tagged in some way or later captured, it is impossible to ever verify that the bat recorded was actually the species it was claimed to be. This makes it impossible to estimate the error rates in identification. An observer may be 100% accurate in their identifications, or 10%, it is impossible to know either way. It must then be asked as to whether a reliable record of "bat – species unknown" is better than a record where the bat species is claimed to be one species, but is actually wrong.

Time expanded recordings can be taken from bats of known species either at roosts or from bats which have been tagged, followed and recorded. The latter method is preferable, since the bats will be foraging rather than commuting and using the echolocation call structure more likely to be encountered in the field. A few studies have used this method, then used multivariate statistics to estimate how many times a call would be categorised correctly to species. For some species, this is quite an accurate way, but for others, there is a great deal of miss-classification. For example, Vaughan *et al.* (1997) found that only 70% of British bats using FM calls could be correctly classified to the correct species. The danger is also in taking the tabulated values of the call parameters and comparing them with library recordings without taking into account the variability of the tabulated values. For example, the following data is taken from Vaughan *et al.* (1997) and shows tabulated values for the duration, peak frequency and start frequency for *M. brandtii* (n=42 bats from 2 locations) and *M. mystacinus* (n=25 bats from 5 locations). The first table suggests the two species should be easily separable based on duration and start frequency.

Species	Duration	Peak F	Start F
M. brandtii	3.06	47.9	85.5
M. mystacinus	2.23	47.5	80.3

However, when the standard deviations and range of the data is shown, it can be seen that there is considerable overlap in the call structures.

Species	Duration	Peak F	Start F
M. brandtii	3.06 ± 0.83	47.9 ± 8.29	85.5 ± 13.3
	(1.50-5.00)	(38.0-78.4)	(59.2-123)
M. mystacinus	2.23 ± 0.92	47.5 ± 5.91	80.3 ± 21.1
	(0.30-4.00)	(38.8-65.2)	(56.0-102)

Comparison of recorded calls with a library of calls may be helpful in assisting with identification, as long as the library complies with the following criteria:

1. The library is from verified species identifications.
2. The library is statistically representative of the species.
3. The recording apparatus has no effect on the recording compared to the library.
4. The recording conditions have no effect on the recording compared to the library.
5. The analysis is conducted in the same way as the library.

However, once again there is the problem of verification. It will never be possible to know if the species recorded at a particular location was correctly identified. It is possible to reduce the risk of miss-classification, but only with the loss of identification to species level by grouping species with similar calls into an identification group. In Great Britain, it is possible to classify species to groups on the basis of echolocation call structure. These groups are:

1. *P. pygmaeus*
2. *P. pipistrellus, P. nathusii*
3. *N. noctula, N. leisleri, E. serotinus*
4. *M. brandtii, M. mystacinus, M. nattereri, M. daubentonii, M. bechsteinii, B. barbastellus.*
5. *P. auritus, P. austriacus*
6. *R. hipposideros*
7. *R. ferrumequinum.*

It is of course possible to subdivide these groups given extra information, such as if a bat from group 4 catches an insect from the water surface it is almost certainly a *M. daubentonii*, or if a bat from group 3 alternates two call types it is not *E. serotinus*. However, if it fails to alternate call types it does not mean it must be an *E. serotinus*, it could still be a *N. noctula* or *N. leisleri*. The identification between groups is likely to be close to 100% accurate. Some species have calls that are so characteristic that they are unlikely to be mistaken, others, such as *Myotis* species, have calls which are so similar they may need to be grouped into an FM group. Care must also be exercised when the bat is foraging in a different situation. *N. noctula* foraging in woodland glades or swarming at a roost sound very like *Myotis* species, so size and shape information is useful even when making time-expanded recordings. Whether such a strategy of allocating species into identifiable groups is adopted depends on how the survey defines what is a reliable identification.

Discriminant function analysis

The generation of a library allows the statistical interpretation of data on call characteristics. Simple statistics to compare between species can interpret intraspecific variability, but most often a library is used to assign a call from an unknown species of bat to particular species. At its simplest, a visual representation of a call in the form of a sonogram is compared to a reference call from a known species. Aside from any analytical differences in the generation of the sonogram of the unknown call and the known call, this makes no use of any statistical information about the call variability from the population rather than the individual. Such visual interpretation is often used as it is fast and requires no statistical methods. The major flaw in this method is that there is no estimation of the likelihood of the assignment to a particular species being correct. Some have claimed a high success rate of this method of identifying species (e.g. O'Farrell *et al*., 1999). However, objections stem from its lack of replication by other individuals and the lesser amount of training or experience by most who attempt to judge species identifications by the quality of the call alone.

The next level of analysis uses the mean and standard deviations of the library calls as a comparison index for the same parameters from the unknown call. Such an inspection can be visual or use some basic statistical processing. It is possible to construct a t-score (or Z score if the number of individuals per species in the library is over 30) which gives the probability of the chosen call parameter belonging to each species in the library. The consensus of probabilities for each parameter in turn can give the likelihood that the unknown bat belongs to each species. Such a technique does violate a number of statistical assumptions, not least it is a form of pseudo-replication and takes no account of the covariance between call parameters, but it does at least provide some indication of the likelihood that the unknown bat belongs to a particular species.

The most widely applied technique is discriminant function analysis. In this type of analysis, the parameters measured are evaluated for each species and an algorithm can be derived for allocating an unknown species to one of the species groups. Vaughan *et al*. (1996) used this technique on the echolocation calls of British bats and achieved very high correct classification using a cross-classification technique. Such analyses can be difficult to implement or interpret however. These data are likely to violate the assumption that covariance matrices are homogenous, meaning that the computationally easier Fishers linear discriminants cannot be used, but quadratic ones must be used instead. These data are also unlikely to be normal in multivariate space. This can be understood from the fact that different groups of bats have different call structures, so that bats using constant frequency calls such as *Rhinolophus*, will form a different cluster to *Myotis* since the covariance between different parameters of their calls will be different for the different groups. In practice these violations may not affect the overall ability of the discriminant function to allocate calls, the big disadvantage is whenever new calls are added to the library the discriminant function must be recalculated. While difficult to initially calculate, the discriminant functions can be easy to use in classifying an unknown bat. For a linear discriminant, the function will provide a constant and a series of coefficients for each measured parameter for each species. To classify an unknown bat, it is simply a case of taking the constant and summing up the products of the coefficients and values of each parameter. The value which is greatest indicates the likely species group to which the unknown bat belongs.

For example, consider a discriminant function between two species of *Myotis*.

$$C_{species1} = constant_{species1} + (c1_{species1} \text{ x } F_{min}) + (c2_{species1} \text{ x } F_{max}) + (c3_{species1} \text{ x duration})$$

$$C_{species2} = constant_{species2} + (c1_{species2} \text{ x } F_{min}) + (c2_{species2} \text{ x } F_{max}) + (c3_{species2} \text{ x duration})$$

Where:

C = the classification score

$constant_{species1}$ = the constant derived from the discriminant function for species 1.

$c1_{species1}$ = the classification coefficient for species 1 for parameter 1, in this case the minimum frequency.

Once the constants and coefficients are entered into a spreadsheet, only the call parameters from the unknown bat need to be entered, and the most likely species can be automatically calculated based on which species has the highest classification score.

For analyses where the covariance matrix is heterogenous, which is likely to apply to most analyses and can be tested using Box's M test (Mardia *et al*., 1994), these linear discriminants cannot be derived and a quadratic discriminant should be applied. Classification without using linear discriminants is less straightforward, one technique uses the Mahalanobis distance which is in effect the "distance" from the observation to each of the classified groups. The group to which it is nearest is the one to which it is classified. In practice, there may be little difference in classification based on linear or quadratic discriminants, and only verification through cross-classification or jackknifing will show differences. It should be noted however that if linear classification coefficients are derived for data which has a heterogenous covariance matrix, then there may be a bias in classification to species showing the greatest dispersion (Tabachnick & Fidell, 1996). In these cases, a suitable transformation of the predictors may solve the problem. Two factors that may improve the accuracy of classification are the use of priors and some degree of pre-processing or pre-classification. Priors indicate the prior probability that a bat belongs to a particular species group. By default, the priors are equal, that is, each bat has an equal probability of being assigned to each species before the analysis. Such an assumption may not be valid where a discriminant function is derived for all species in a particular country, but recordings are made in a region where only half those species are known to be present. The priors for those species not present will then be zero, and the chance of correct classification of the unknown bat will therefore be improved. This can of course turn into a circular argument in that the purpose of the analysis is to establish the range of species which may occur, but which are being excluded from the analysis because they do not occur.

Pre-classification may be of use when calls from the range of species to be discriminated fall into a number of discrete categories which are so clear as to have no need of discriminant function analysis. Such a division may occur between bats using FM calls and those using CF calls. The construction of two discriminant functions, one for each group, may improve the accuracy of the discrimination within each group, and may also help to alleviate the problem of heterogeneous covariance matrices.

RESUME

Les détecteurs d'ultrasons. Le rôle des détecteurs ultrasonores dans l'identification et l'étude du comportement des chauves-souris est présenté.

Les détecteurs d'ultrasons fonctionnent tous sur le principe de recevoir les écholocations grâce à des microphones sensibles aux ultrasons et de traiter électroniquement ces signaux. Les trois méthodes principales sont : l'hétérodynage, la division de fréquence, l'expansion de temps. Certains détecteurs n'utilisent qu'une méthode alors que d'autres permettent de sélectionner l'une ou l'autre. Chaque méthode est décrite et les avantages et inconvénients de chacune comparés selon les critères liés aux écholocations de chauves-souris.

Les logiciels d'analyse acoustique pour micro-ordinateurs deviennent de plus en plus abordables. L'influence des diverses techniques sur l'interprétation des signaux est présentée. L'analyse acoustique s'appuie généralement sur des enregistrements en expansion de temps. Une compréhension des fondements des techniques utilisées est essentielle à la bonne utilisation des logiciels d'analyse, la modification des divers paramètres pouvant influencer l'interprétation des signaux. Quelques-uns des principaux paramètres sont présentés.

Les problèmes associés à l'identification acoustique des chauves-souris sont discutés et quelques techniques permettant d'accroître les possibilités d'identification sont présentées.

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Acoustic variability, and identification possibilities for seven European bats of the genus *Myotis*

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Abstract. Seven European species of the genus *Myotis* (*M. myotis, M. daubentonii, M. bechsteinii, M. mystacinus, M. alcathoe, M. emarginatus, M. nattereri*) have been studied and recorded hunting in natural situations whilst noting their precise flight conditions at the moment of recording. The recordings were analysed using auditory criteria to classify them into 10 call types ; representative samples of each signal type were then digitally analysed to refine the classification. Three of these are specific, whereas the other seven may be used by several species (up to 5) in similar circumstances. Identification relies on a correlation between the call type and the prevailing environmental conditions, notably the distance to obstacles in front of the bat. This paper presents a method of evaluating these environmental conditions using signal intervals.

The results show that acoustic identification (without direct visual observation) of these *Myotis* species cannot be made reliably solely by means of the signal parameters. It is essential to put each signal in its context within a sequence (correlation between any variation in pulse repetition rate and possible accompanying variations in structure). Conclusions about species, or groups of species, can only be drawn after completing an analysis of all these factors.

Here some of the possible reasons why certain call types are used during the approach phase will be discussed. For example : an energy peak at the end of the signal could be useful in the discrimination of prey within foliage.

Key-words : Acoustic identification, acoustic variability, *Myotis* sp.

INTRODUCTION

Twenty years after the first publications by Ahlen (1981, 1990) which played a pioneering role, the acoustic identification of bats is still at the research stage. The extensive work undertaken since has highlighted many obstacles to the creation of reliable identification criteria. But these studies have not attempted to associate both the auditory and data-processing criteria to give reliable identification in the field. The subjectivity of auditory analysis is often quoted, although some of the criteria are simple to recognise and easily transmissible from one observer to another. In addition, the tools, recording methods, data-processing and computer signal analysis can each introduce some bias (Fenton *et al.*, 2001 ; White & Gehrt, 2001). Rather than fighting the shortcomings of two separate methods, they can be used in association to avoid the deficiencies in each.

One of the main difficulties encountered is that of intra-specific acoustic variability, because it produces significant inter-species overlap.

The difficulty is even greater with the *Myotis* species, which emit wideband FM signals of low intensity, complicating their analysis. Also, these species generally fly near to foliage, hence the signals vary much more within a short time period than those of high-flying species (i.e. distance changes between the calling bat and its flying environment are more significant). Variation in distance to obstacles is often cited as one of the main explanations for acoustic variability (Pye, 1980 ; Miller & Degn, 1981 ; Tupinier & Biraud, 1983-1984 ; Neuweiler, 1989 ; Rydell, 1990 ; Schumm *et al.*, 1991 ; Verboom *et al.*, 1999 ; Murray *et al.*, 2001).

The aim of the current study is to measure the acoustic variability of seven widespread European species of the genus *Myotis* (*M. myotis*, *M. daubentonii*, *M. bechsteinii*, *M. mystacinus*, *M. alcathoe*, *M. emarginatus*, *M. nattereri)*, in order to evaluate the possibility of their identification in the field. Signals of all seven species have been classified according to auditory and signal-analysis criteria. A link has then been established between these types of signals and the flight behaviour of the species at the precise time the calls were made. A relationship has been found between each signal type and the obstacle distance on the flight axis (by measurement of signal intervals).

EQUIPMENT AND TECHNIQUES

The results presented in this paper come from a programme on the acoustic identification of European

Chiroptera started in 1988 (Barataud, 1996, 2001). All of the species discussed here were recorded in the centre, west and south of France.

Each species was studied under normal flying conditions (hunting, transit) and in several types of habitat, from "in clutter" to "open". Individuals were fitted with luminescent capsules (Cyalume™) or followed after leaving their roost during their twilight hunting activities. The behaviour of the animal, its environment and its relation to obstacles were noted at the precise moment of sound recording.

The data was collected using two heterodyne/time expansion ultrasonic detectors (x 10 and x 20 ; 3 and 12 s memory) Pettersson D980 (Pettersson Elektronik AB™), and a Sony™ DAT TCD-D7 tape recorder.

A hundred or so sequences were recorded for each species, corresponding to a minimum of 2000 signals analysed.

Each expanded sequence (x 10) has been described using two methods :

Auditory analysis :

1) For each signal the criteria are : duration, frequency range, final frequency, intensity (approximate evaluation) and energy distribution during the course of the signal (presence and position of any audible energy peak).

2) For the complete sequence : estimation of any variation in rhythm and repetition rate correlated with any variation in audible signal structure, and the behaviour of the individual (distance to obstacles, etc).

Computer signal analysis (BatSound software, Pettersson Elektronik AB™) :

1) The criteria taken into account were : duration, frequency bandwidth, end frequency and frequency of maximum energy. Duration was measured on oscillograms ; bandwidth and end frequency on spectrograms, using 256, 512 or 1024 points according to pulse duration, and a Hanning window. Frequency of maximum energy is defined as the frequency with the most energy in the average spectrum. Because of the increased attenuation of higher frequencies in air, only the highest intensity signals were chosen in order to obtain the most accurate possible measurements of bandwidth and duration. Signals from juveniles were excluded from the analyses in order to avoid age-related variability (Jones & Kokurewicz, 1994).

2) For the complete sequence : estimation of any variation in rhythm and repetition rate by measurement of signal intervals on an oscillogram (taken from the end of one signal to the end of the next signal) ; correlated with any audible signal structure variation, and with the individual's behaviour (distance to obstacles, etc).

All of the signals (irrespective of species) were then regrouped by type in relation to their level of structural similarity. Then, for each species, the environmental conditions were examined with respect to each signal type and compared on an inter-specific basis to evaluate the overlap of "acoustic behaviour/flight behaviour".

In order to compare signal repetition rate within a sequence and behaviour (distance to obstacles and/or the individual's interest in its environment) in a standardised manner, measurements of signal interval were related with behaviour types noted in the field. The aim was to associate obstacle distance class with signal interval class in order to correlate these with types of acoustic structure.

The differences observed between species within the same acoustic type, and between the types have been compared statistically by the Student-Fisher t test.

RESULTS

Auditory analysis

At the end of the auditory analysis stage, the acoustic data could be regrouped into 10 types (Table 1) with sufficiently discriminating characteristics to allow classification by ear in the field. Each of these types is used by a bat in a fairly constant manner for particular flight circumstances ; any change in these flight events could result in another type being used. Signals during any transition between two types have intermediate characteristics ; for this reason they have not been included within the analysis. Although transition phases, when present, are very short (1 to 3 pulses in general).

Within the audible criteria, energy distribution appears to be particularly reliable, because of its ease of estimation and constancy under given conditions. Hence :

- 3 types show an energy peak at the end of the signal, giving a perfectly audible "explosive end" ;
- 2 types show a rapid intensity rise at the start of the signal, giving an "explosive start" ;
- 3 types, without a notable peak, show maximum energy towards the second half of the signal ;
- 2 types show a perfectly smooth audible structure, where the energy is distributed regularly along the whole signal length (Table 2).

Table 1 : Types of signals encountered and emitting species (from Barataud, 2002).

Tone	**Type**	**Abbreviation**	**Species**	**Confusion**	**Comments**
Myotis	*M. myotis*, open space	Open myo	*M. myotis/blythii/punicus*	Total between these 3 species	Small risk of confusion with *Eptesicus & Nyctalus* sp. near foliage ; take puse rate into account
	M. myotis, in clutter	Clutter myo	*M. myotis/blythii/punicus*	Total between these 3 species	Small risk of confusion with *Eptesicus & Nyctalus* sp. near foliage ; take puse rate into account
	Explosive end on high frequencies	EE on high freq.	*M. emarginatus*	Low risk	At a distance of 1-2 m from obstacles
			M. bechsteinii		Short sequence, in terminal approach of obstacle
	Explosive end on medium frequencies	EE on med. freq.	*M. daubentonii*	Total between these 2 species	In clutter or along edges, near foliage
			M. bechsteinii		
			M. myotis *M. mystacinus*	Low risk	Short sequence, in terminal approach of obstacle
			M. nattereri	Low risk	Short (and rare) sequence, mixed with EE on low freq
	Explosive end on low frequencies	EE on low freq.	*M. nattereri*	Impossible	All habitat types (variation of duration and rhythm only), except sometimes when flying in very open spaces
	Explosive start on high frequencies	ES on high freq.	*M. mystacinus* *M. emarginatus* *M. alcathoe*	High risk if short sequence	If sequence shows structure variation, with at least 1 signal with explosive end on high freq., then *M. emarginatus* If end freq > 40 kHz in semi-open : *M. alcathoe*
	Explosive start on medium frequencies	ES on med. freq.	*M. mystacinus* *M. daubentonii*	High risk exept pulse rate variation	*M. mystacinus* : 1-2 m from obstacle *M. daubentonii* : 2-3 m from obstacle
	daubentonii/bechsteinii along edges	Edge daub/bech	All “small *Myotis*” except *M. nattereri*	Total except if approach phase	Between 1-5 m from obstacle
	daubentonii in open space	Open daub	*M. daubentonii*	with *M. capacc.* & *M. dasycn.*?	More than 5 m from obstacle
	bechsteinii open space	Open bech	*M. bechsteinii*	Impossible	More than 5 m from obstacle

Table 2 : Energy distribution criteria : presence and position of an audible energy peak for each type decribed.

Type	Energy repartition			
	Explosive start	Expl.End	2nd half signal	Lack of energy peak
Open myotis			X	
Clutter myotis			X	
Expl. end high freq.		X		
Expl. end med. freq.		X		
Expl. end low freq.		X		
Expl. start high freq.	X			
Expl. start med. freq.	X			
Edge daub/ bech			X	
Open daub.				X
Open bech.				X

Other criteria, such as the end frequency and the frequency band, can only be evaluated approximately by ear, to give high, medium or low classes.

By combining these frequency criteria with the energy distribution, the ten signal types are much more distinct, requiring only minimal training for auditory recognition. Three types are specific, whereas the seven other types are used by several species (up to 5) in more or less similar circumstances. No significant differences have been noted for the 3 sibling species *M. myotis, M. blythii, M punicus,* but for the last two, only a limited number of sequences were available for examination.

Computer signal analysis

The results of the computer signal analysis undertaken on a sample of representative signals of each type are shown in Table 3.

The computer analysis provides precise measurements of the frequency criteria. It also allows confirmation of the auditory estimates. However, it does not always show a clear link with audible energy peaks (explosive start, explosive end), except for *M. nattereri* where the explosive end is always very clear and is generally easily seen on the oscillogram. This illustrates the need to combine computer-aided signal analysis with auditory analysis.

Table 3 : Average and standard deviations for measurements using analysis software ; for each signal type, the representative samples comprise characteristic signals from different sequences, irrespective of species.

Type	N. analysed signals	N. concerned species	Duration (ms)		Bandwidth (kHz)		End Frequency (kHz)		Freq. energy maximum (kHz)	
			mean value	S.D.	mean value	S.D.	mean value	S.D.	mean value	S.D.
Open myotis	20	1	**9,1**	0,7	**43,4**	4,7	**20,9**	1,2	**27,8**	1,7
Clutter myotis	20	1	**5,8**	1	**52,6**	13,5	**22,1**	1,9	**35,8**	5,4
Expl. End High freq.	32	2	**2,5**	0,3	**74,9**	13,3	**37,3**	4,3	**64**	8,4
Expl. End Med. freq.	61	5	**2,9**	1,1	**74,7**	13,4	**25,2**	5	**51**	7,4
Expl. End Low freq.	20	1	**4,1**	1,7	**105,3**	10,3	**13,7**	2,5	**54,5**	9,6
Expl. start High freq.	36	3	**3,3**	0,6	**86,1**	20,2	**37,5**	4,3	**70,3**	12,7
Expl. start Med. fréq.	27	2	**3**	0,4	**90,1**	12,3	**25**	3,6	**60,5**	6,3
Edge daub/bech	48	4	**3,6**	0,5	**54,9**	12,8	**28,9**	7,1	**51,2**	5,2
Open daub.	20	1	**5**	0,9	**47,3**	12,8	**30,6**	1,9	**49,1**	1,1
Open bech.	20	1	**10,7**	1,8	**69,1**	9,2	**21,8**	1,7	**42,5**	5,1

Table 4 : Statistical validity of differences between averages calculated for each acoustic type (Student-Fisher test t ; comparision of 2 observed averages).

Type	**N. analysed signals**	**Duration (ms)**		**Bandwidth (kHz)**		**End Frequency**		**Freq. energy maximum**	
		mean value		**mean value**		**mean value**		**mean value**	
Open myo	15	**9,1**	t = 10,616	**43,4**	t = 2,291	**20,9**	t = 1,858	**27,8**	t = 5,382
Clutter myo	20	**5,8**	ddl = 33	**52,6**	ddl = 33	**22,1**	ddl = 33	**35,8**	ddl = 33
EE high freq	32	**2,5**	t = 1,657	**74,9**	t = 0,081	**37,3**	t = 11,512	**64**	t = 7,713
EE med freq	61	**2,9**	ddl = 91	**74,7**	ddl = 91	**25,2**	ddl = 91	**51**	ddl = 91
EE high freq	32	**2,5**	t = 5,060	**74,9**	t = 8,643	**37,3**	t = 21,950	**64**	t = 3,728
EE low freq	20	**4,1**	ddl = 50	**105,3**	ddl = 50	**13,7**	ddl = 50	**54,5**	ddl = 50
EE med freq	61	**2,9**	t = 3,831	**74,7**	t = 9,383	**25,2**	t = 9,876	**51**	t = 1,735
EE low freq	20	**4,1**	ddl = 79	**105,3**	ddl = 79	**13,7**	ddl = 79	**54,5**	ddl = 79
ES high freq	36	**3,3**	t = 2,302	**86,1**	t = 0,933	**37,5**	t = 12,665	**70,3**	t = 3,627
ES med freq	27	**3**	ddl = 61	**90,1**	ddl = 61	**25**	ddl = 61	**60,5**	ddl = 61
Edge daub/bech	48	**3,6**	t = 7,272	**54,9**	t = 2,156	**28,9**	t = 1,012	**51,2**	t = 1,703
Open daub	20	**5**	ddl = 66	**47,3**	ddl = 66	**30,6**	ddl = 66	**49,1**	ddl = 66
Edge daub/bech	48	**3,6**	t = 24,269	**54,9**	t = 4,316	**28,9**	t = 4,378	**51,2**	t = 6,253
Open bech	20	**10,7**	ddl = 66	**69,1**	ddl = 66	**21,8**	ddl = 66	**42,5**	ddl = 66
Open daub	20	**5**	t = 12,478	**47,3**	t = 6,128	**30,6**	t = 14,875	**49,1**	t = 5,665
Open bech	20	**10,7**	ddl = 38	**69,1**	ddl = 38	**21,8**	ddl = 38	**42,5**	ddl = 38

significance threshold:
☐ Not significant
▢ p<0,05 (t =1,960)
■ p<0,001 (t =3,291)

Comparison between the types (Table 4) shows significant differences for the majority (78.1 %) of the comparisons undertaken (p<0.001 for 68.7 % comparisons).

Tables 5 to 9 show the inter-species variations within the same signal type. The species compared statistically pair by pair within each type (Table 5' to 9') show significant differences in 54.2 % of cases (p<0.001 for 26.5 % of comparisons).

The inter-species variation within each signal type remains much lower than the inter-type variability.

Spectrograms representative of each of the 10 types are given in Figures 1 to 10.

The 11th type (sinusoidal amplitude modulation) was initially chosen but then dropped (Fig. 11). Indeed certain signals show several amplitude peaks (from 3 to 10) on an oscillogram, often clearly heard by ear.

Table 5 : Species variation in measurements within the type “Explosive end on high frequencies.

EE on high freq	Number of signals analysed	**Duration (ms)**		**Bandwidth (kHz)**		**End Frequency**		**Freq. energy maximum**	
		mean value	**SD**	**mean value**	**SD**	**mean value**	**SD**	**mean value**	**SD**
M. emarginatus	20	**2,6**	0,17	**70,9**	13,5	**38,9**	4,7	**65,4**	9,6
M. bechsteinii	12	**2,4**	0,5	**81,7**	10,3	**34,6**	1	**61,8**	5,5

Table 5’ : Statistical validity of differences between averages calculated for each species within the type “Explosive end on high frequencies” (test t, Student-Fisher) ; ns : not significant.

EE on high freq	**Duration**	**Bandwidth**	**End Frequency**	**Freq. energy max.**
M. emarginatus ***M. bechsteinii***	p<0,05	p<0,02	p<0,01	ns

Table 6 : Species variation in measurements of the type “Explosive end on medium frequencies”.

	Number of signals analysed	**Duration (ms)**		**Bandwidth (kHz)**		**End Frequency**		**Freq. energy maximum**	
		mean value	**SD**	**mean value**	**SD**	**mean value**	**SD**	**mean value**	**SD**
M. mystacinus	12	**2,3**	0,4	**79**	12,8	**27,5**	2,9	**58,6**	8,4
M. myotis	12	**3,9**	0,7	**74,2**	9,4	**23,4**	5,7	**47,3**	6,1
M. daubentonii	12	**1,9**	0,2	**65,5**	5,4	**25,5**	1,7	**46,5**	3,5
M. bechsteinii	12	**2,2**	0,4	**68,1**	12	**31**	2,3	**49,9**	2,7
M. nattereri	13	**3,9**	1,2	**85,8**	15,2	**19,3**	0,9	**52,5**	7,8

Table 6’ : Statistical validity of differences between averages calculated for each species of the type “Explosive end on medium frequencies” (test t, Student-Fisher).

Duration	***M. daubentoni***	***M. bechsteini***	***M. mystacinus***	***M. myotis***	***M. nattereri***
M. daubentonii	-				
M. bechsteinii	p<0,05	-			
M. mystacinus	p<0,001	ns	-		
M. myotis	p<0,001	p<0,001	p<0,001	-	
M. nattereri	p<0,001	p<0,001	p<0,001	ns	-

Bandwidth	***M. daubentoni***	***M. bechsteini***	***M. mystacinus***	***M. myotis***	***M. nattereri***
M. daubentonii	-				
M. bechsteinii	ns	-			
M. mystacinus	p<0,01	p<0,05	-		
M. myotis	p<0,02	ns	ns	-	
M. nattereri	p<0,001	p<0,01	ns	p<0,05	-

End Frequency	***M. daubentoni***	***M. bechsteini***	***M. mystacinus***	***M.myotis***	***M. nattereri***
M. daubentonii	-				
M. bechsteinii	p<0,001	-			
M. mystacinus	p<0,05	p<0,01	-		
M. myotis	ns	p<0,001	p<0,05	-	
M. nattereri	p<0,001	p<0,001	p<0,001	p<0,02	-

Table 7 : Species variation in measurements within the type “Explosive start on high frequencies”.

ES on high freq	Number of signals analysed	**Duration (ms)**		**Bandwidth (kHz)**		**End Frequency**		**Freq. energy maximum**	
		mean value	**SD**	**mean value**	**SD**	**mean value**	**SD**	**mean value**	**SD**
M. mystacinus	12	**3,6**	0,3	**111,1**	5,3	**34,5**	2,4	**85,8**	7
M. alcathoe	12	**3,1**	0,3	**73,1**	5,2	**40,7**	3,7	**59,9**	2,9
M. emarginatus	12	**3,3**	0,9	**74**	15	**37,3**	4,2	**65,2**	6,9

Table 7’ : Statistical validity of differences between averages calculated for each species of the type “Explosive start on high frequencies” (test t, Student-Fisher).

Duration	***M. mystacinus***	***M. emarginatus***	***M. alcathoe***
M. mystacinus	-		
M. emarginatus	ns	-	
M. alcathoe	p<0,01	ns	-

Bandwidth	***M. mystacinus***	***M. emarginatus***	***M. alcathoe***
M. mystacinus	-		
M. emarginatus	p<0,001	-	
M. alcathoe	p<0,001	ns	-

End Frequency	***M. mystacinus***	***M. emarginatus***	***M. alcathoe***
M. mystacinus	-		
M. emarginatus	ns	-	
M. alcathoe	p<0,001	p<0,05	-

Freq. energy max.	***M. mystacinus***	***M. emarginatus***	***M. alcathoe***
M. mystacinus	-		
M. emarginatus	p<0,001	-	
M. alcathoe	p<0,001	p<0,02	-

Table 8 : Species variation in measurements within the type “Explosive start on medium frequencies”.

ES on med freq	Number of signals analysed	**Duration (ms)**		**Bandwidth (kHz)**		**End Frequency**		**Freq. energy maximum**	
		mean value	SD	**mean value**	**SD**	**mean value**	**SD**	**mean value**	**SD**
M. daubentonii	15	**2,7**	0,2	**93,6**	6,7	**25,6**	2,6	**61,1**	6,2
M. mystacinus	12	**3,4**	0,4	**85,6**	16,3	**24,5**	12,8	**60,5**	6,5

Table 8’ : Statistical validity of differences between averages calculated for each species of type “Explosive start on medium frequencies” (test t, Student-Fisher).

ES on med freq	**Duration**	**Bandwidth**	**End Frequency**	**Freq. energy max.**
M. daubentonii ***M. mystacinus***	p<0,001	ns	ns	ns

Table 9 : Species variation in measurements within the type “*daubentonii*/*bechsteinii* along edges”.

Edge daub/bech	Number of signals analysed	**Duration (ms)**		**Bandwidth (kHz)**		**End Frequency**		**Freq. energy maximum**	
		mean value	SD	**mean value**	**SD**	**mean value**	SD	**mean value**	**SD**
M. emarginatus	12	**3,7**	0,8	**53,9**	5,4	**35,3**	1,9	**55,2**	4,9
M. daubentonii	12	**3,3**	0,2	**53,9**	11,8	**26,9**	2,7	**51,9**	3,2
M. mystacinus	12	**3,8**	0,6	**51,5**	15,1	**29,5**	10,3	**50,3**	2,9
M. bechsteinii	12	**3,7**	0,3	**60,4**	15,8	**24**	4,6	**47,3**	6,1

Table 9’ : Statistical validity of differences between averages calculated for each species of the type “*daubentonii*/*bechsteinii* along edges” (test t, Student-Fisher).

Duration	***M. emarginatus***	***M. daubentoni***	***M. bechsteini***	***M. mystacinus***
M. emarginatus	-			
M. daubentonii	ns	-		
M. bechsteinii	ns	p<0,01	-	
M. mystacinus	ns	p<0,01	ns	-

Bandwidth	***M. emarginatus***	***M. daubentoni***	***M. bechsteini***	***M. mystacinus***
M. emarginatus	-			
M. daubentonii	ns	-		
M. bechsteinii	ns	ns	-	
M. mystacinus	ns	ns	ns	-

End Frequency	*M. emarginatus*	*M. daubentoni*	*M. bechsteini*	*M. mystacinus*
M. emarginatus	-			
M. daubentonii	p<0,001	-		
M. bechsteinii	p<0,001	ns	-	
M. mystacinus	ns	ns	ns	-

Freq. energy max.	*M. emarginatus*	*M. daubentoni*	*M. bechsteini*	*M. mystacinus*
M. emarginatus	-			
M. daubentonii	ns	-		
M. bechsteinii	p<0,01	p<0,05	-	
M. mystacinus	p<0,01	ns	ns	-

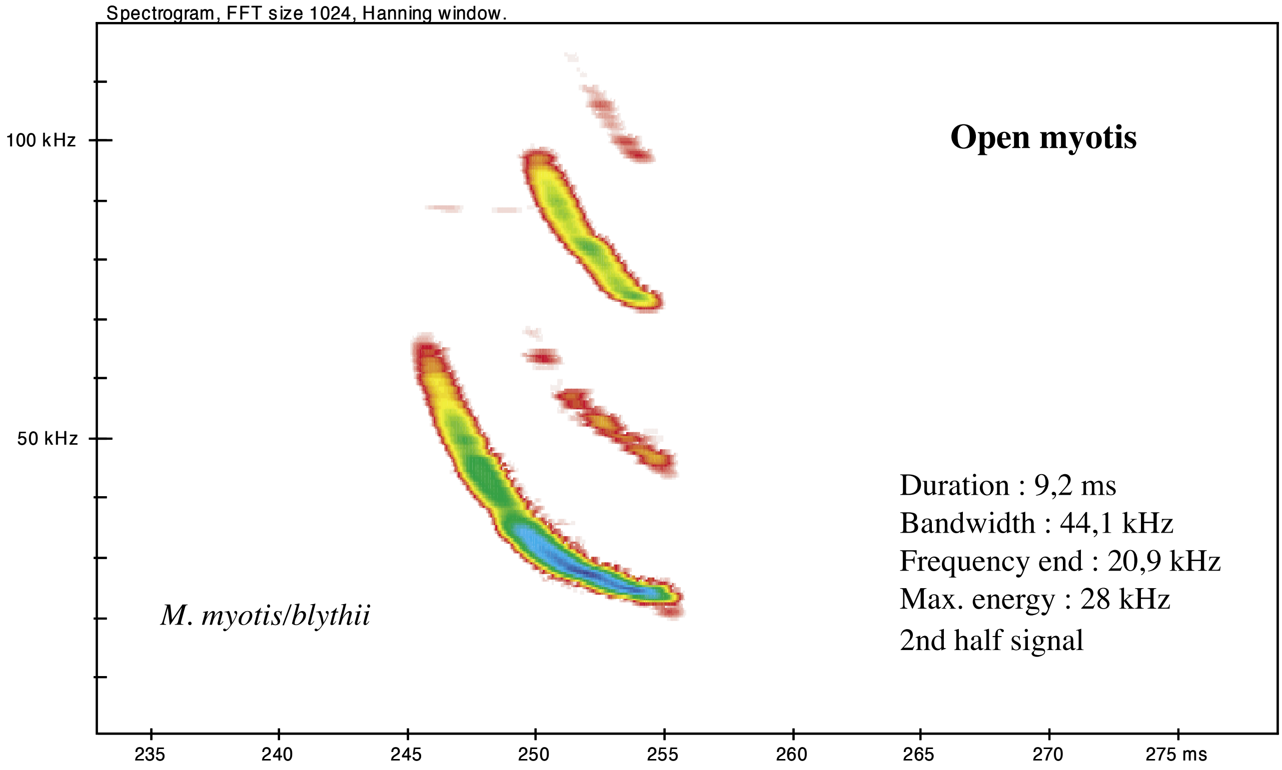


Fig. 1 : Spectrogram of the type : *M. myotis*, open space.

The signal has an audible "rolling" or "harsh" structure according to the number of peaks and their intensity. There may be several reasons for this phenomenon : recording effects (microphone sensitivity lobes, axis between the microphone and the calling animal, etc.) ; time delays between the signal emitted and echoes which overlap ; signal envelope modifications due to natural filters (maybe foliage), etc.

All of these effects are known as signal artifacts. However, this phenomenon has been observed quite consistently for certain species (*M. daubentonii, P. auritus*, and to a lesser extent *M. mystacinus* et *M. alcathoe* ...) regardless of flight zone and the animal's position with respect to the microphone, whereas it has never been noted for others, e.g. *M. bechsteinii*. Whilst it is known that artificial effects can create or amplify these artifacts (KALKO & SCHNITZLER, 1989 ; KAPTEYN, 1993), it may be possible that, in certain cases, amplitude modulation is an acoustic characteristic of a species. Something to investigate further... Given this uncertainty, it was excluded from the analysis, despite the possibility that in some cases of acoustic overlap it could provide a distinction between *M. bechsteinii* et *M. daubentonii.*

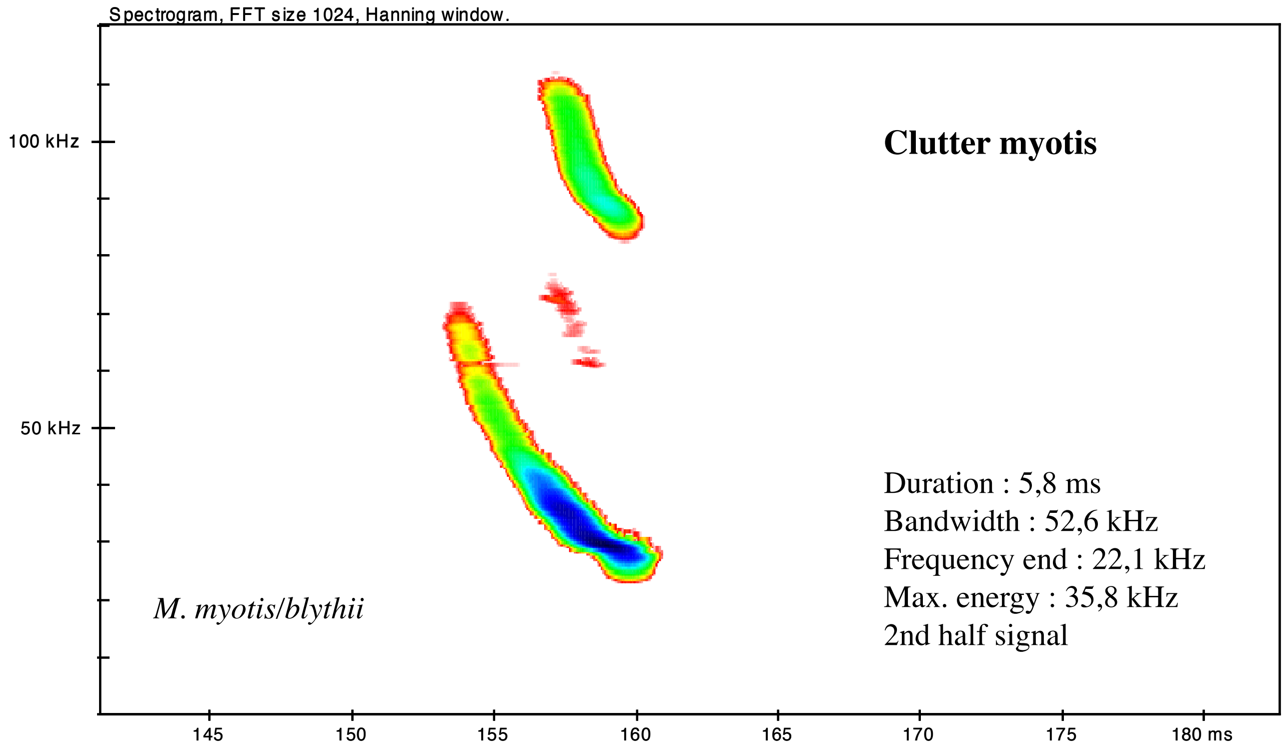


Fig. 2 : Spectrogram of the type : *M. myotis*, in clutter.

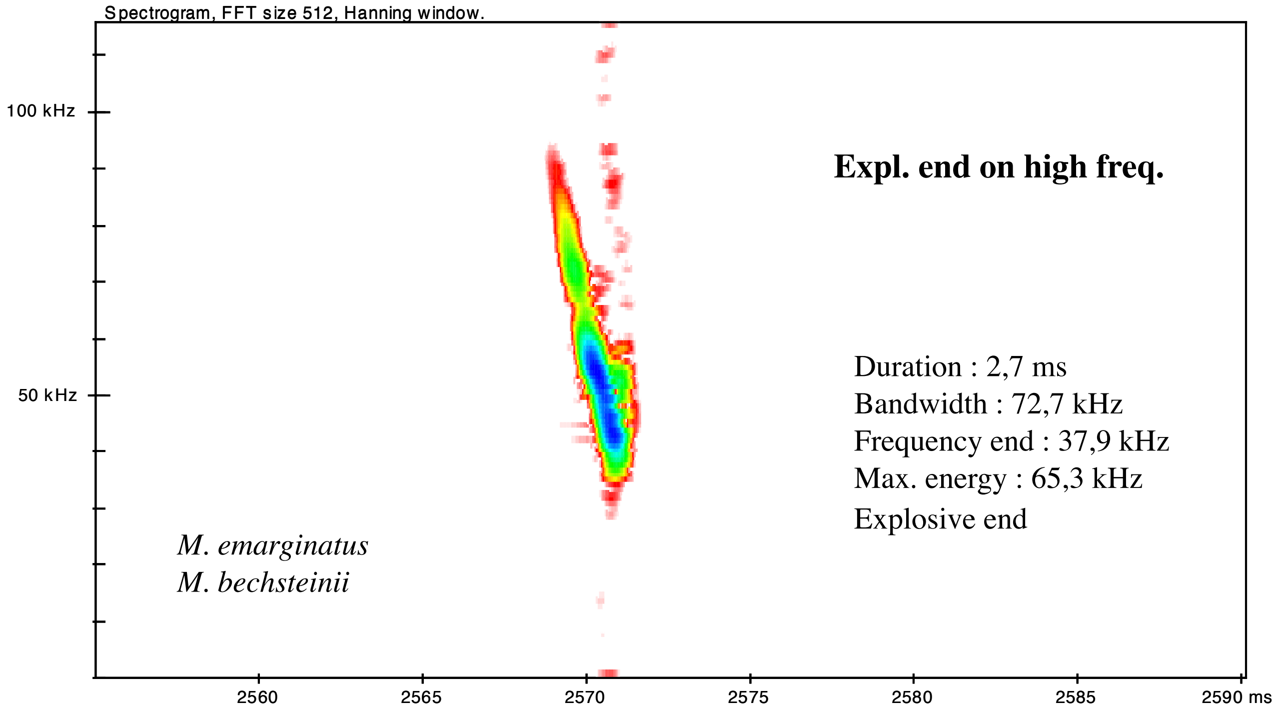
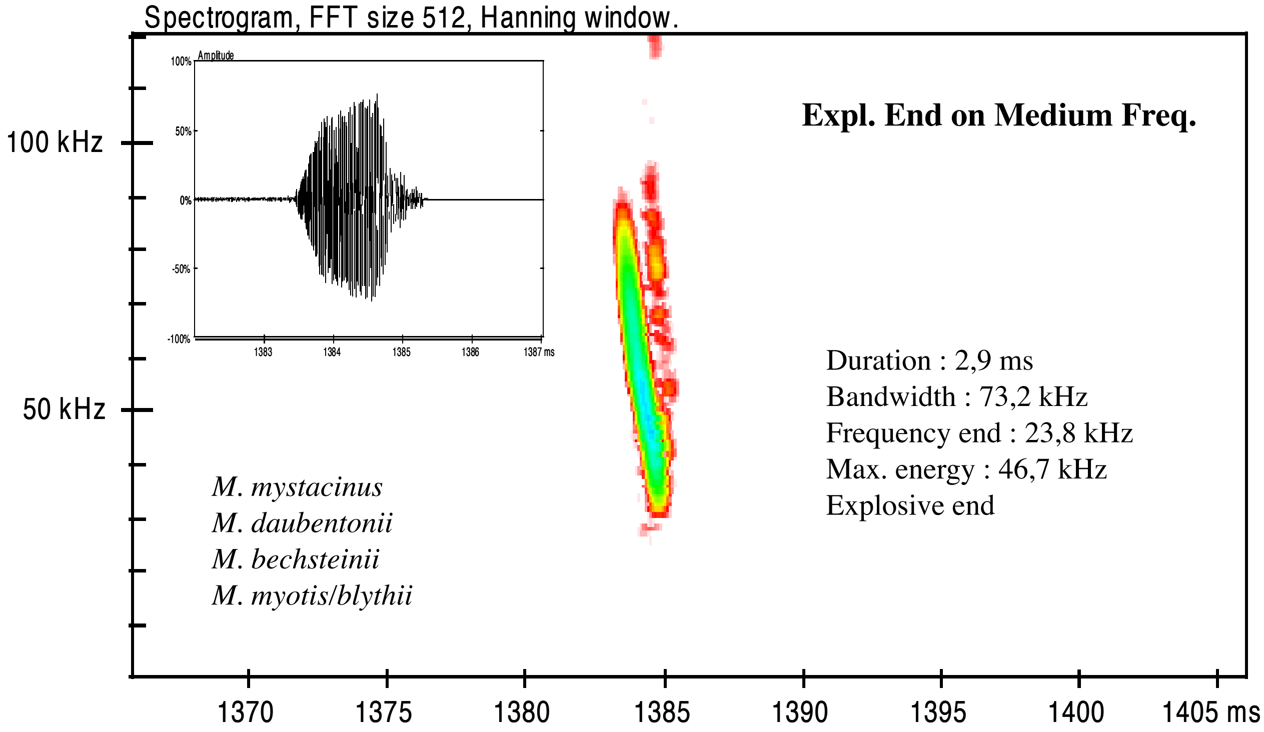


Fig. 3 : Spectrogram of the type : Explosive end on high frequencies.

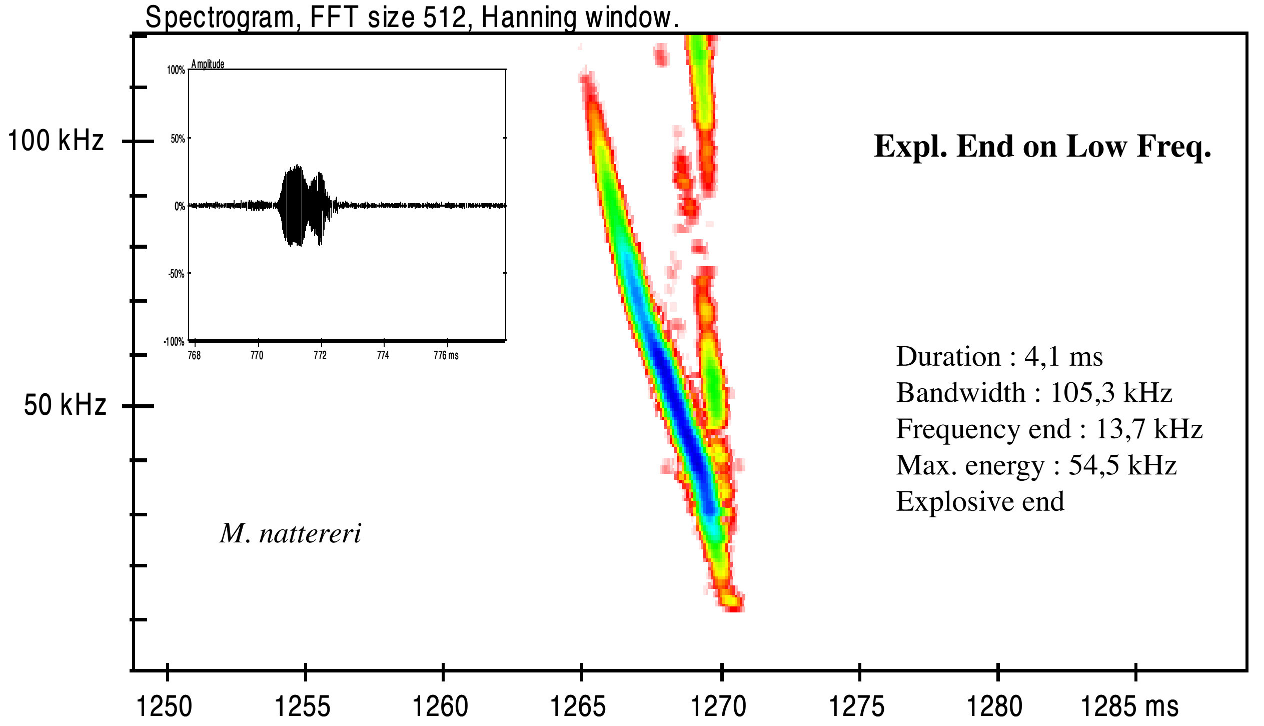

Spectrogram, FFT size 512, Hanning window.

Expl. End on Medium Freq.

Duration : 2,9 ms
Bandwidth : 73,2 kHz
Frequency end : 23,8 kHz
Max. energy : 46,7 kHz
Explosive end

M. mystacinus
M. daubentonii
M. bechsteinii
M. myotis/blythii

Fig. 4 : Spectrogram of the type : Explosive end on medium frequencies.


Spectrogram, FFT size 512, Hanning window.

Expl. End on Low Freq.

Duration : 4,1 ms
Bandwidth : 105,3 kHz
Frequency end : 13,7 kHz
Max. energy : 54,5 kHz
Explosive end

M. nattereri

Fig. 5 : Spectrogram of the type : Explosive end on low frequencies.

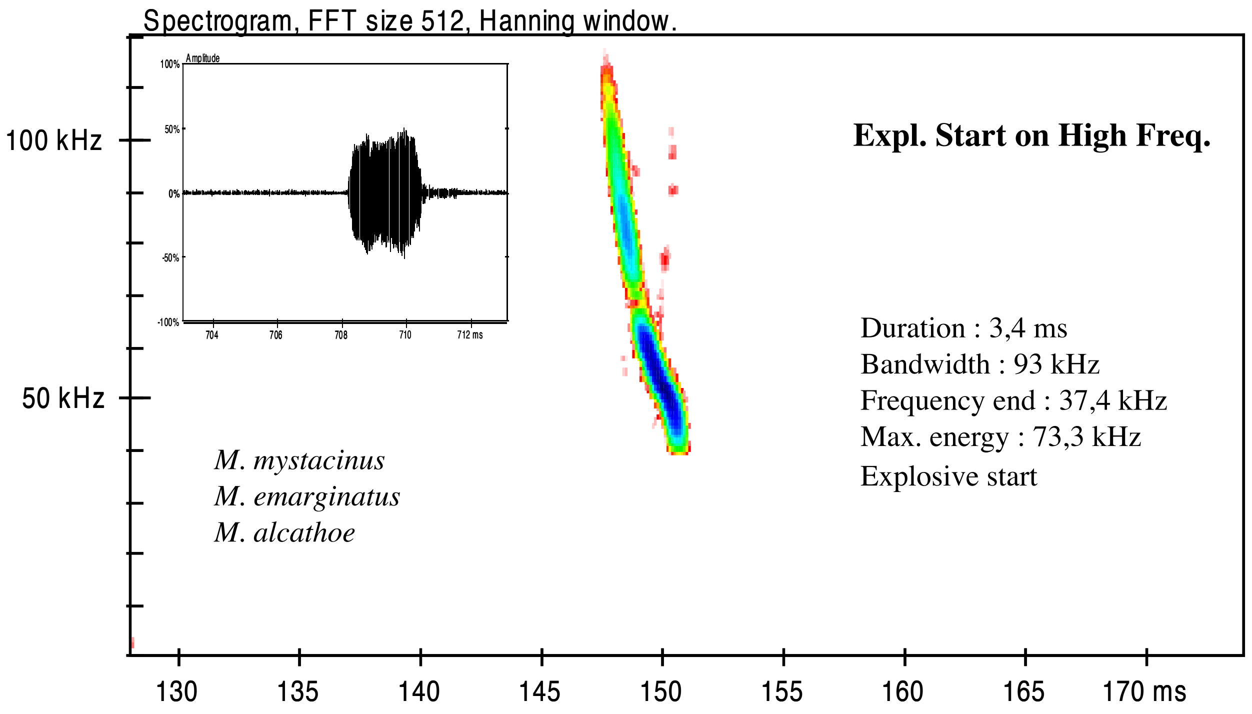


Fig. 6 : Spectrogram of the type : Explosive start on high frequencies.

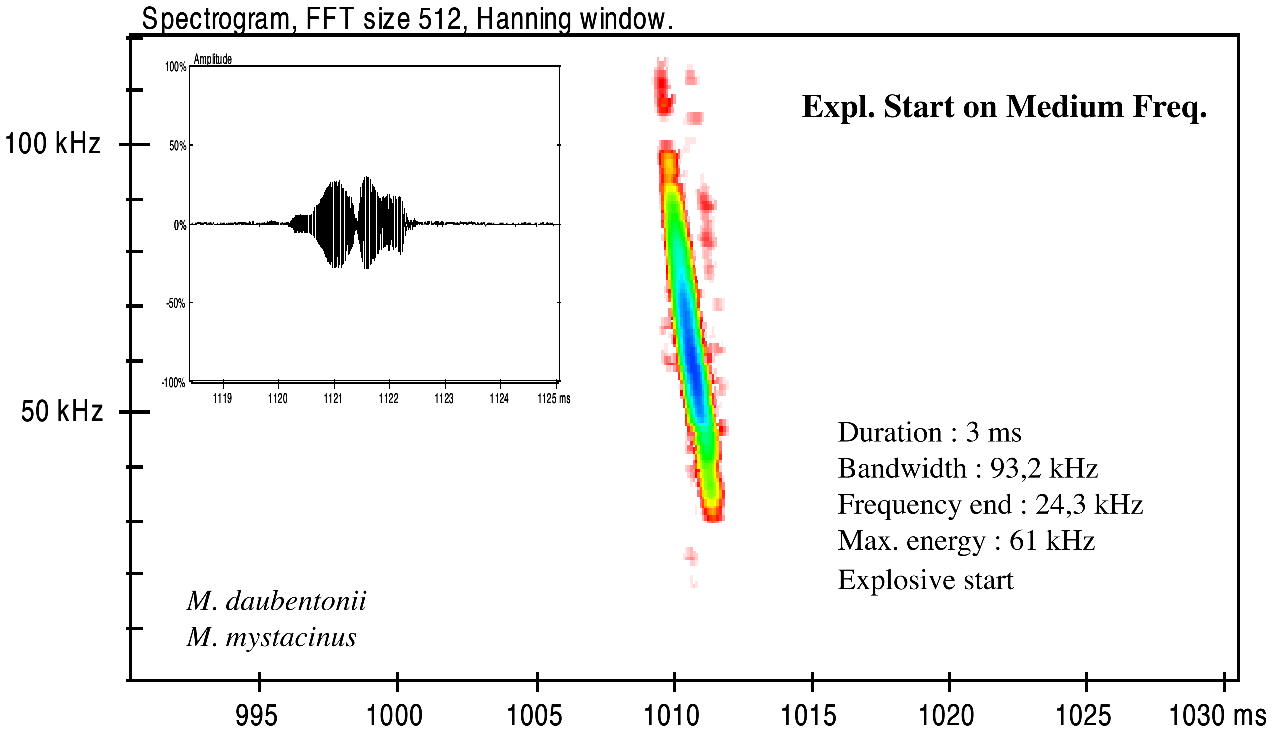


Fig. 7 : Spectrogram of the type : Explosive start on medium frequencies.

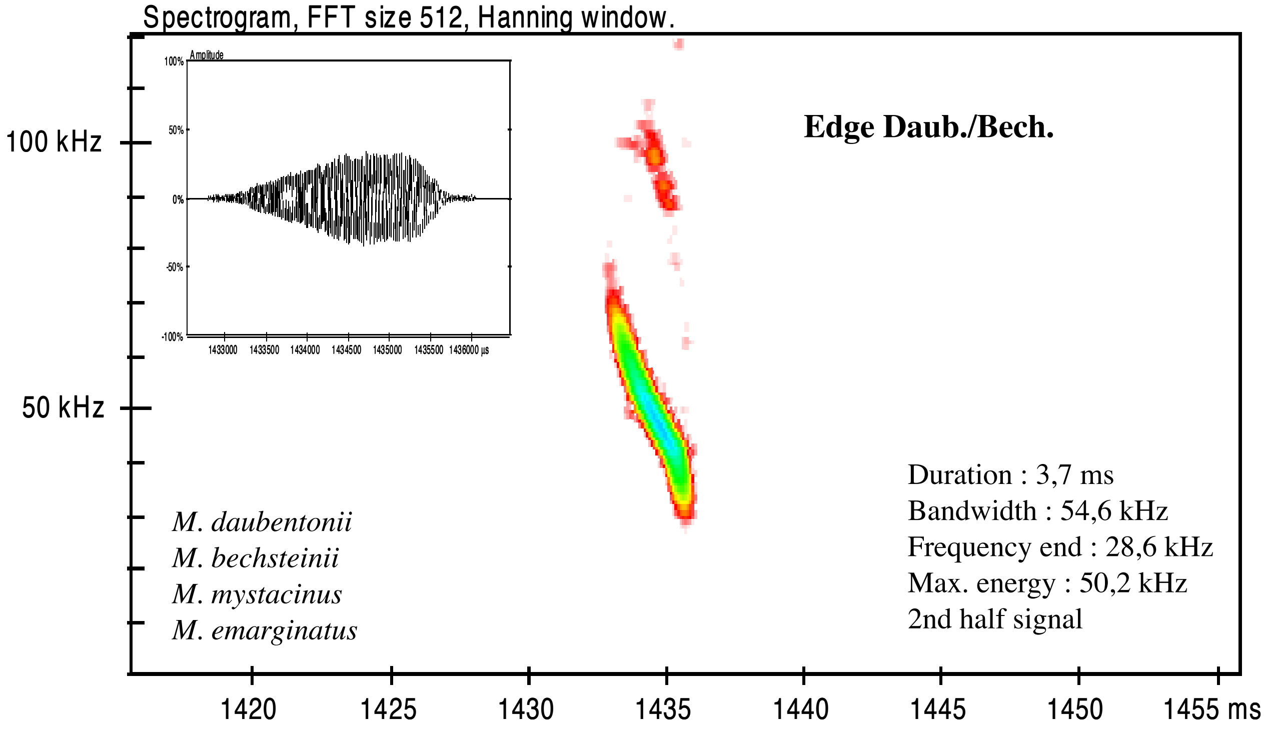


Fig. 8 : Spectrogram of the type : *daubentonii*/*bechsteinii* along edges.

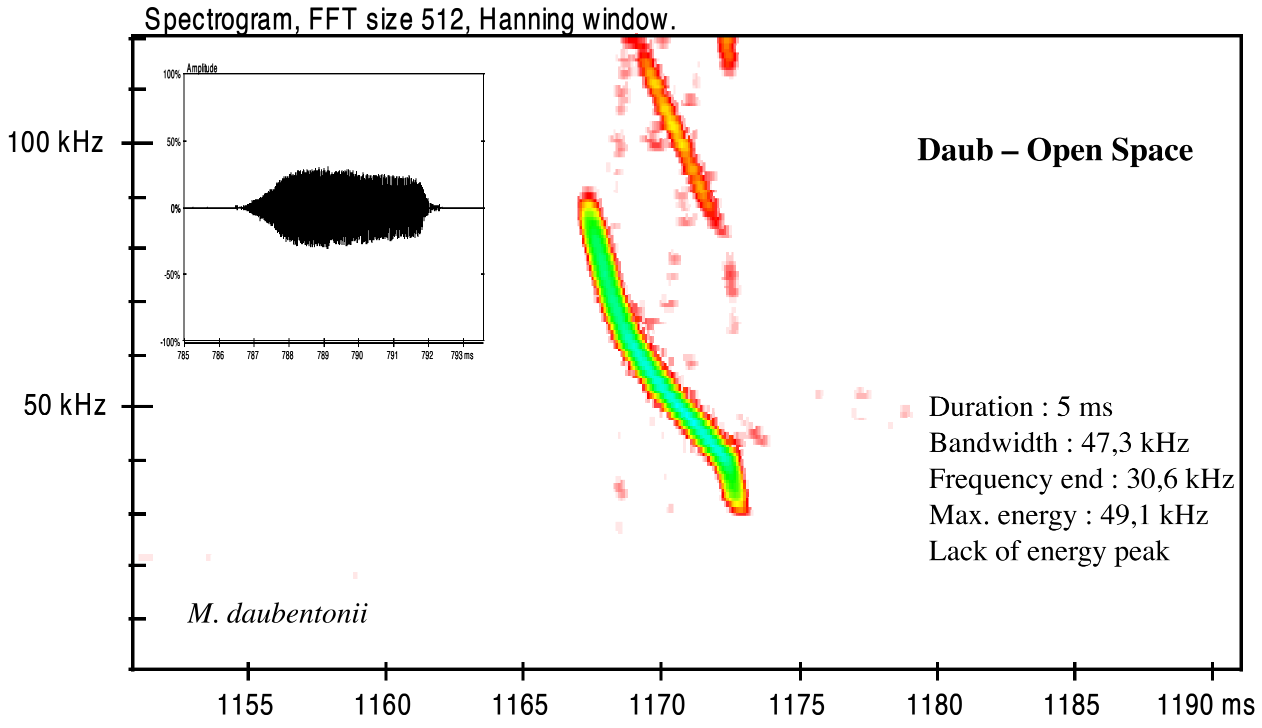


Fig. 9 : Spectrogram of the type : *daubentonii* in open spaces.

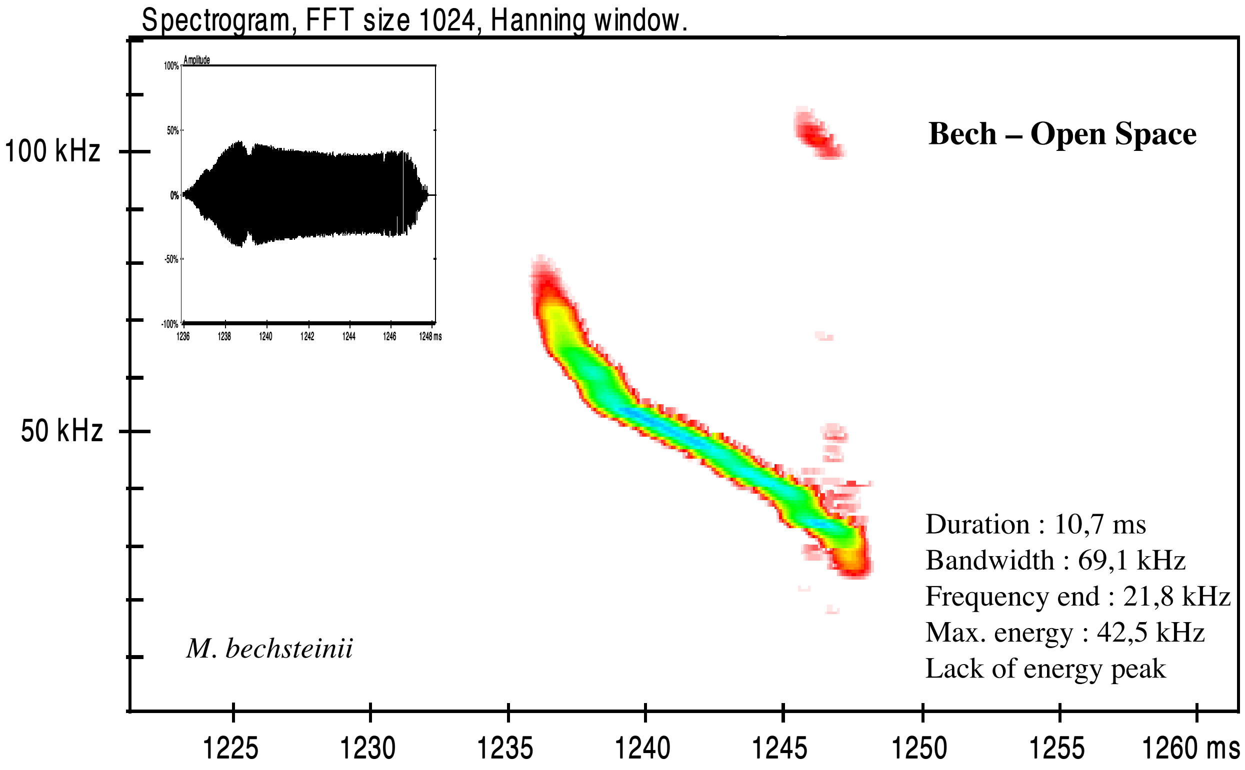


Fig. 10 : Spectrogram of the type : *bechsteinii* open space.

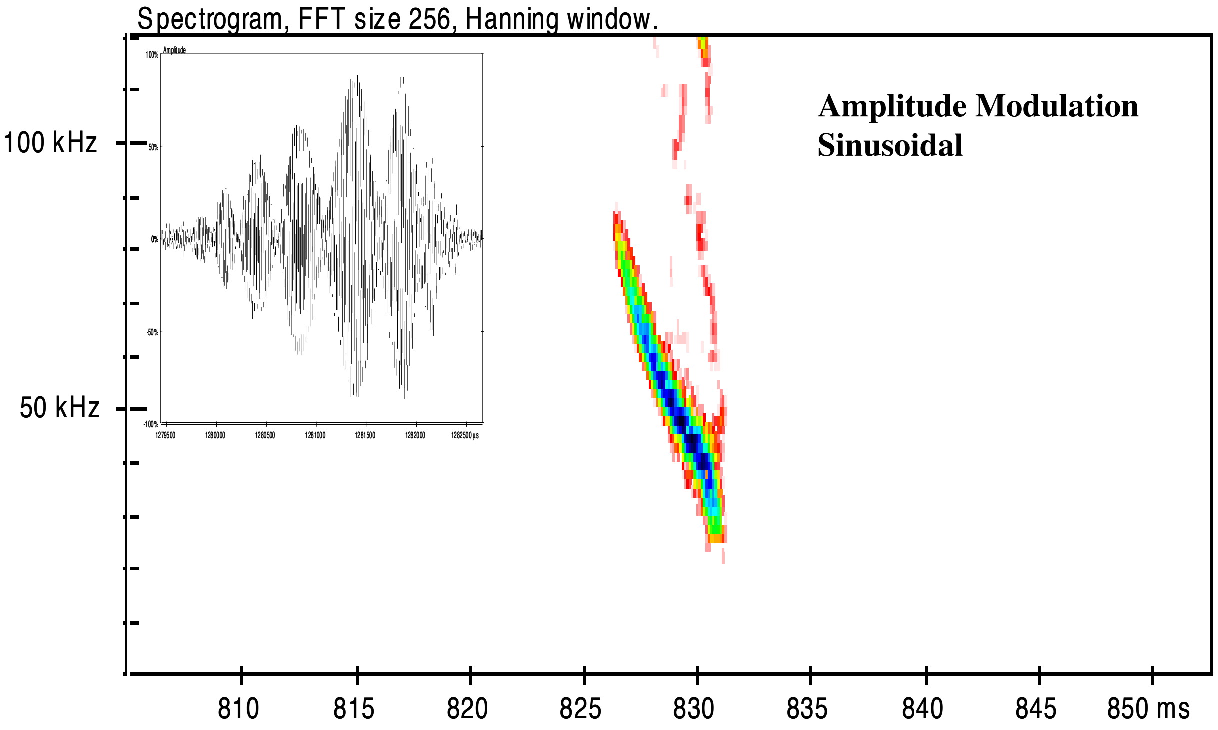


Fig. 11 : Spectrogram of the (type) : Amplitude modulation sinusoidal.

Figures 12 to 18 show the flight circumstances during which each of the seven species studied emit their various signal types. The biggest influence is that of the distance between the calling bat and the closest obstacles on the axis of emission. Although it also depends on the behaviour of the animal and its level of interest in the environment within its perception cone at that particular moment. Hence a *M. mystacinus* individual heard over meadow, far from any forest edges, could emit short signals of the type "explosive start on high frequency", if it is investigating tall grass, skimming the ground, looking for prey.

Taking into account the rhythm, notably the variation in pulse repetition rate within a sequence, allows interpretation not only of the clutter within the area, but also the behaviour of the animal and can provide a reliable identification when coupled with signal-structure criteria.

Rhythm consists of two main components:

- regularity: any variation of silent intervals between signals;
- pulse repetition rate (number of pulses per unit of time).

Interpretation of pulse repetition is very important in assessing flight habitat and type of activity (the faster the rhythm, the closer the obstacles or the more active the search for prey).

Three main rhythm types can be distinguished:

1) Cruising rhythm: no increase or **progressive** decrease in pulse repetition within a group of signals:
    a) slow and regular: shows an "active transit" (transit = the bat moves from one place to another). High probability of encountering prey or obstacles;
    b) slow and irregular: shows a "passive transit". The bat does not require much information, so saves energy, due to low prey density, no obstacles, well-known place, etc.;
    c) fast and regular: shows an active search for prey or obstacles;

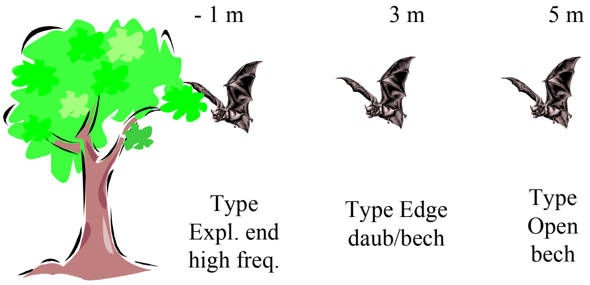


Fig. 12: Emission circumstances of each signal type in *M. bechsteinii*.

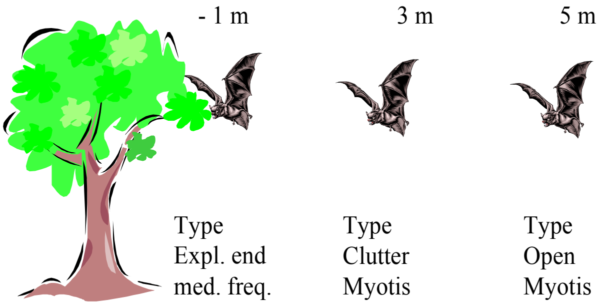


Fig. 13: Emission circumstances of each signal type in *M. myotis/blythii*.

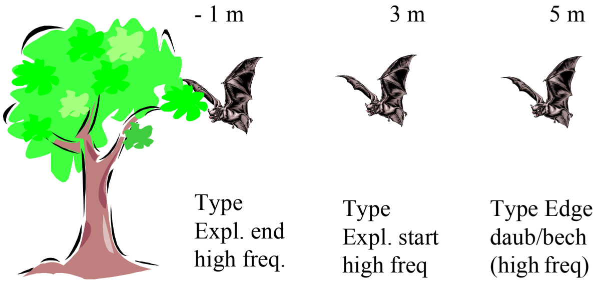


Fig. 14: Emission circumstances of each signal type in *M. emarginatus*.

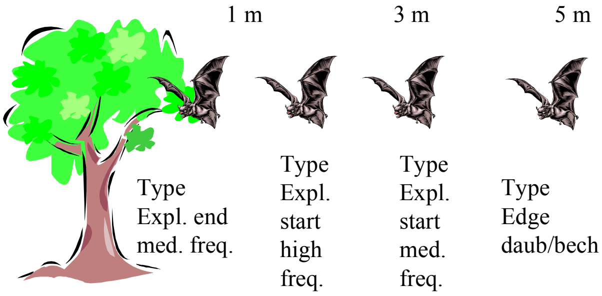


Fig. 15: Emission circumstances of each signal type in *M. mystacinus*.

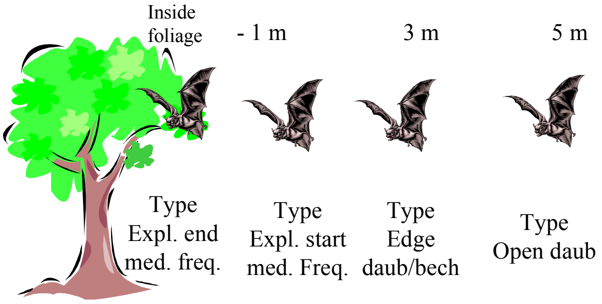


Fig. 16: Emission circumstances of each signal type in *M. daubentonii*.

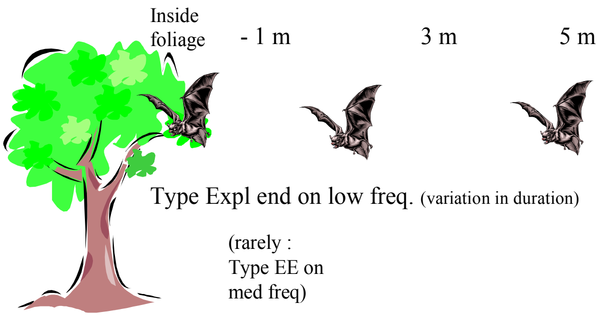


Fig. 17 : Emission circumstances of each signal type in *M. nattereri*.

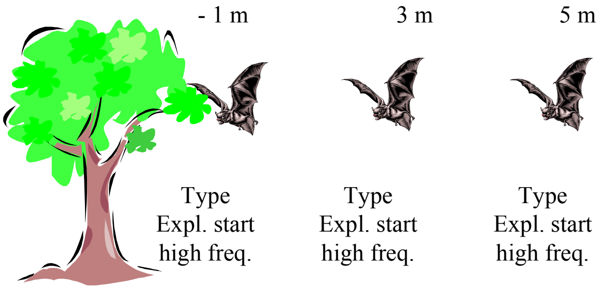


Fig. 18 : Emission circumstances of each signal type in *M. alcathoe*.

d) fast and irregular : unknown reason... Often used by foliage-dwelling species such as small species of *Myotis*. When flying close to vegetation, they sometimes emit pairs of signals. The bat may be searching for landmarks in the acoustic landscape, but possibly less actively than for the fast and regular rhythm.

2) Approach rhythm : shows a progressive increase of pulse repetition (or decrease when flying away from an obstacle) within a group of signals, after a cruising rhythm.

   Modification of pulse repetition indicates a change of distance between the bat and an object situated within its acoustic horizon. This variation is generally accompanied by changes in structure (bandwidth, appearance or disappearance of energy peak, maximum energy frequency), intensity and duration. All these parameters help to understand the bat behaviour.

   The approach phase is often a key element in the identification for species emitting steep FM signals.

3) Capture rhythm : shows a progressive increase in pulse repetition within a group of signals, after an approach rhythm. During the terminal approach, the rhythm is very fast (final “buzz”) and the structure of signals is stereotypical. It is not useful for species identification, but provides behavioural information (attempt to capture prey, e.g. active hunting behaviour).

A comparative evaluation of pulse repetition should be correlated with signal structure, flight conditions, species or group of species. It is thus a relative notion : the Noctule’s slow rhythm (high flying species) and the Pipistrelle’s slow rhythm (edge dwelling species) in their typical hunting habitat will not have the same absolute value of pulse repetition.

For species of the genus *Myotis*, a series of signal interval bands have been established from the data taken in the field. These correspond to distance bands between the calling bat and the closest obstacles.

On average, for the small *Myotis* species these are :

- 40 to 50 ms when at a distance of less than 1 m from obstacles ;
- 50 to 80 ms when at 1 to 3 m ;
- 80 to 100 ms when at 3 to 5 m ;
- 100 to 250 ms when more than 5 m.

Inter-specific differences do exist : in similar conditions *M. emarginatus* and *M. mystacinus* generally have a slightly faster rhythm compared with *M. daubentonii* and *M. bechsteinii*. But these variations are limited and the above correlations remain valid in most cases. These pulse repetition categories can be memorised from reference sequences, allowing a field identification method which combines the signal type and repetition rate, giving the best possible determination (Table 10).

For example, a signal sequence type “edge daub/bech” showing a cruising rhythm (regular and fairly slow : 80 to 100 ms interval) could correspond to 4 species (*M. daubentonii, M. bechsteinii, M. mystacinus* or *M. emarginatus*). However, if the next part of the same sequence includes an approach phase (reduction of some signal intervals to about 60 ms) and the structure becomes “ES on high freq.”, then only *M. mystacinus et M. emarginatus* remain as possibilities. If then, by chance, the approach sequence ends and the repetition rate increases so that intervals drop to 50 ms with the signal structure type becoming “EE on high frequency”, then it can only be *M. emarginatus*.

Therefore, it is no longer useful to describe the environment to support an identification, since the repetition rate best indicates the animal’s behaviour and flight situation.

This also allows distinctions to be made between *M. mystacinus, M. emarginatus* and *M. alcathoe*, which may use all 3 types of “ES on high freq.” signals, but under different circumstances (and therefore signal repetition rates).

Table 10 : Types of signals the most frequently used by each species in relation to the signal intervals.

	End of approach phase, or in clutter	Early approach phase, or near clutter	Semi-open environment	Open environment
	av. 40 to 50 ms (20 to 70 ms)	**av. 50 to 70 ms (50 to 80 ms)**	**av. 80 to 100 ms (60 to 120 ms)**	**120 to 250 ms**
M. myotis	EE on med freq	EE on med freq	Clutter myotis	Clutter/Open myotis
M. nattereri	EE on low freq	EE on low (med.) freq	EE on low freq	EE on low freq
M. bechsteinii	EE on high freq	EE on med freq	Edge daub/bech	Open bech
M. daubentonii	EE on med freq	ES on med freq	Edge daub/bech	Open daub
M. mystacinus	EE on med freq	ES on high freq	ES on high/med freq	Edge daub/bech
M. emarginatus	EE on high freq	ES on high freq	ES on high freq	Edge daub/bech
M. alcathoe	ES on high freq	ES on high freq	ES on high freq	ES on high freq

The possibility of identification is therefore often dependant on the number and nature of acoustic signal changes from one type to another (correlated with their respective repetition rates) within the same sequence (Table 10).

DISCUSSION

Different ultrasonic signal gathering and analysis techniques have been evaluated by PARSONS *et al.* (2000). Time expansion appears currently to be the most powerful method because the original signal is stored without the structure being modified. It also provides advantages in auditory analysis where the time expansion (x 10 or x 20) allows the listener to estimate details of frequency change and time-related energy factors.

The results presented show that within the genus *Myotis* (in so far as current techniques allow precise judgement) their sonar systems allow both large intra-specific variation and large inter-specific convergence. The latter is certainly due to similar constraints for each species, linked to habitat and hunting behaviour. Elsewhere RUEDI & MAYER (2001) have recently shown that, within this genus, environmental pressures could have produced somewhat surprising morphological and ecological similarities which can only have been the result of evolutionary convergence without any link to the species' phylogeny.

Except for some species where the type of emission remains very characteristic (such as *M. nattereri*), it is false to attribute a type of signal to a particular species within this genus. Only three signal types are specific, two of them (open daub & open bech) being used only under particular flight conditions which are not the most frequently encountered ones.

Discovery of this intra-specific variability could not have happened without hundreds of hours spent in the field following hunting bats, either tagged or after leaving their roosts. Records of species identification using ultrasonic detectors without sight of the animal, should be based on techniques which take into account this variability. The acoustic sequence coming from one animal can contain up to 3 or 4 types of signal. This confuses identification methods based on the analysis of only one signal in a sequence, selected by conventional or chance methods (VAUGHAN *et al.*, 1997 ; OBRIST *et al.*, in press). The work of VAUGHAN *et al.* shows that, for 4 of the species covered in this present study, the duration, final frequency and energy peak, appear to correspond to stereotypical behaviour (reorientation after release or leaving the roost). This is probably the reason that the successful classification rate for multivariate-analysis is only 12 % for *M. mystacinus*, 75 % for *M. daubentonii*, and 87 % for *M. nattereri*.

The fact that signal variability is related to environmental conditions is emphasised by SCHUMM *et al.* (1991) for *M. emarginatus,* SIEMERS & SCHNITZLER (2000) for *M. nattereri* and TUPINIER & BIRAUD (1983-84) for *M. daubentonii*. For this last species JONES & KOKUREWICZ (1994) have also found an age-related difference ; young bats, under a year old, emit at lower frequencies. On the other hand, MILLER & DEGN (1981) have found great similarities in the hunting environments (pond surfaces) throughout the season, with a low acoustic variability. WATERS & JONES (1995) studied *M. nattereri* signals in the laboratory and found that, on average, their frequency values were higher than those under the natural conditions seen here. This difference corresponds well to expected values for an animal which increases its "degree of interest" in an unfamiliar environment. KALKO & SCHNITZLER (1989) found great similarities between the emissions of *M. daubentonii* and those of *M. nattereri,* *M. emarginatus* and *M. mystacinus*. According to this study, sinusoidal amplitude modulation is only produced by interference between the signal and its delayed echo from a reflective surface. Some of the observations made within our study contradict the Kalko & Schnitzler hypothesis, notably the fact that some species produce this signal structure in environments where it appears difficult for a reflective surface to play such a role (except maybe the animals wings ?), i.e. flying at 1.5 m along a forest path, or in the middle of a meadow with long grass...). Furthermore, amplitude modulation appears often in certain species but has not been seen in others. It could be that many factors come together to explain this phenomenon, some related to behavioural artifacts, without excluding the animal itself as a possible source. Numerous species of birds (*Apus apus, Regulus regulus, Muscicapa striata, Turdus iliacus* ...) clearly emit sinusoidal amplitude modulated calls, probably with the aim of producing a specific signature. Although currently unknown, it would not be surprising if bats could do likewise. The solution to this problem requires the setting-up of a detailed experimental programme to fully evaluate the phenomenon.

Examining Table 10 shows that energy peaks only appear during the approach phase (except for *M. nattereri*). Also, an explosive end is often used towards the end of the approach phase, which seems to indicate that the presence of an energy peak at the signal end aids precise definition of objects close together within the depth of field. In their behavioural and acoustic study of *M. nattereri*, Siemens & Schnitzler (2000) have shown that this species, with its short signals and large bandwidth, is capable of locating prey situated only a few centimeters from vegetation. This is something that many species emitting a narrow bandwidth appear incapable of because of the overlap between the echo coming from the prey and that from the substrate.

A short signal with a very wide bandwidth may give better differentiation within a signal comprising of overlapping echoes, i.e. overlap between the low-frequency end of a prey echo and the high-frequency start of a background echo. It has been noted elsewhere (Table 3) that the widest frequency bands correspond to the types showing an energy peak, i.e. in different parts of the approach phase (Table 10). If this hypothesis is correct, it is possible that an energy peak at the start or end of a signal gives an additional benefit for this frequency differentiation. It could serve as a short and powerful time-base marker for interpreting small differences in distance by highlighting any slight offset in the overlaid echoes. The degree of offset in the echoes indicates to the bat a more or less accentuated relief. The fact that *M. nattereri* is the only species to always use an “explosive end”, whatever the type of habitat, could be interpreted as a specialist adaptation for hunting static and inaudible prey. The energy peak is situated at very low frequencies (15 to 20 kHz) reducing air attenuation effects for this part of the signal and its echo. This specialisation, if true, could also imply a more powerful ability of the bat to discriminate slight time delays between energy peaks.

It is also worth noting that for *M. nattereri*, of all the criteria measured, only the duration varies in a significant manner between very “open” areas and very “cluttered” ones. It’s use of the type “explosive end, medium frequency” remains somewhat anecdotal. Much rarer, and for unknown reasons, some individuals include one or two very high frequency calls in the middle of a sequence. All of this supports the hypothesis of a highly specialised signal structure.

It is interesting that all of these characteristics are present for another gleaning species, *Plecotus auritus*, which uses signals with a well-defined explosive start under all circumstances; but its bandwidth is much narrower (Barataud, 2002).

Of the other species, some will be more closely linked to passive location because of the motion of their prey and the noises produced. This was the conclusion of Staden & Schnitzler (1995) following their study of the capture phase of *M. bechsteinii*. Werner (1981) studied the reaction of tympanate moths perched on a substrate and subjected to ultrasonic signals. These signals provoked a significant reaction where the moths immediately became still and assumed a posture with their wings flattened against the substrate and their antennae against their body, thereby offering the flattest possible profile. For this behaviour to have evolved in prey, it must surely provide a benefit against predation. This confirms that, even if bats are in theory capable of resolving differences in depth of the order of 0.8 mm (Simmons *et al.,* 1974), nothing in the echo could allow a precise differentiation between a prey flattened against a surface and an irregularity on that surface.

Therefore, in general, a hunting bat should need either increased relief, or a stimulus linked to motion or noise from the prey, in order to trigger successful capture reactions. The fact that in their experiments Siemers & Schnitzler (2000) showed *M. nattereri* capable of capturing silent and motionless prey from substrates adds weight to the hypothesis that this species has a significant acoustic specialization. Furthermore, several dietary studies (Gregor & Bauerova, 1987; Shiel *et al.,* 1991; Beck, 1995; Swift, 1997) show at least 58 to 68 % gleaned prey, mainly Diptera (*Nematocera* et *Brachycera*). Some results for *M. emarginatus* (Krull *et al.,* 1991; Vaughan, 1997) appear to show similar characteristics.

With *Plecotus auritus*, a proportion of its diet of moths (Vaughan, 1997) are capable of hearing bat emissions (Barataud, 1990). This seems to indicate that it has some specialization to avoid the defence strategies of perching tympanate prey. Consequently, *Plecotus auritus* could be placed amongst the gleaning species, the equivalent of *B. barbastellus* (Barataud, 2004) within the aerial hawking bats.

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RÉSUMÉ

Variabilité acoustique et possibilité d'identification chez 7 espèces du genre *Myotis*. Sept espèces européennes du genre *Myotis* (*M. myotis, M. daubentonii, M. bechsteinii, M. mystacinus, M. alcathoe, M. emarginatus, M. nattereri*) sont étudiées et enregistrées dans des conditions naturelles de chasse, en notant de manière précise les conditions de vol au moment de l'enregistrement. L'ensemble des séquences sonores recueillies est analysé selon des critères d'appréciation auditive ; puis un nombre représentatif de signaux-types fait l'objet d'une analyse informatique pour préciser et compléter la classification des cris en 10 types acoustiques. Trois types sont spécifiques et les sept autres sont utilisés par plusieurs espèces (jusqu'à 5) dans des circonstances plus ou moins similaires. Les possibilités d'identification sont liées à la mise en corrélation du type acoustique, avec les conditions environnementales lors de l'émission, notamment la distance des obstacles situés en face du chiroptère. Nous proposons une méthode d'évaluation de ces conditions environnementales à travers la mesure des intervalles entre signaux.

Les résultats montrent que l'identification acoustique (sans recours à l'observation directe de l'animal) des espèces du genre *Myotis* ne peut pas être réalisée avec fiabilité par l'unique prise en compte de paramètres descriptifs des signaux. Il est indispensable de situer chaque signal dans son contexte au sein de la séquence (récurrence des signaux, et corrélation entre la variation éventuelle de cette récurrence et la variation possible de structure qui l'accompagne). Ce n'est qu'au terme de l'analyse de tous ces paramètres que l'on peut conclure sur l'espèce ou le groupe d'espèces.

Le déterminisme possible de certains types acoustiques utilisés au moment de la séquence d'approche est abordé. Un pic d'énergie en fin de signal pourrait s'avérer utile dans la discrimination de proies au sein du feuillage.

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First elements to recognise bats of French Guiana by theirs calls in the field

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Abstract. During a visit to French Guiana in Autumn 2001, 44 bat species from 3 different families: Emballonuridae, Phyllostomidae, Vespertilionidae, were captured and recorded.

Of the 465 recordings made (totalling about 6½ hours), only 80 or 90 have turned out to be usable for research on species identification criteria. Thus out of 44 species captured, only 31 species or groups of species have been characterised.

The initial data collected has enabled the differentiation of some species or the characterization of some families in a conclusive way. A number of acoustic convergences with European species allows some hypotheses to be made concerning hunting habitats and nutrition specificities.

Following these encouraging results, further studies are necessary to continue the research and to identify acoustically the 105 species of chiroptera found in French Guiana (and more widely within the American Neotropical Rainforest).

Key-words: Chiroptera, French Guiana, acoustic identification.

INTRODUCTION

In Europe, the acoustic recognition of chiroptera using ultrasonic bat detectors is widely known. It has been tested and developed within numerous studies (Ahlen, 1990, 1993a; Barataud, 1991, 1992, 1996; Briggs & King, 1998; Miller & Andersen, 1984; Pettersson, 1993a, b; Roue & Barataud, 1999; Tupinier, 1982, 1996; Tupinier & Mein, 1986; Walsh & Mayle, 1991).

Inventories and studies have been made over nearly 200 years (Sonnini, 1800; Bongers *et al.*, 2001; Brosset, 1967; Brosset & Charles-Dominique, 1990; Brosset *et al.*, 1995, 1996; Charles-Dominique *et al.*, 1981, 2001; Cockle, 1993; Cosson, 1992; Eisenberg, 1989; Emmons & Feer, 1997; Husson, 1962; Lim *et al.*, 1999; Masson & Cosson, 1992; Simmons & Voss, 1998; Simmons *et al.*, 2000), but the chiroptera of Guiana have never been the subject of bioacoustic study. On the other hand, many studies have been carried out in both Central and South America on the acoustic recognition of neotropical bats, of which some are present in French Guiana. Initial studies are particularly concerned with the laboratory analysis of ultrasonic calls. Owing to the different methods used (Arita & Fenton, 1997; Barclay *et al.*, 1981; Barclay, 1983; Wenstrup & Suthers, 1984; Ibanez *et al.*, 1999; Fenton, 1985, 2000; Fenton, *et al.*, 1992, 1998; Fleming *et al.*, 1977; Griffin *et al.*, 1960; Goudy-Trainor & Freeman, 2002; Kalko, 1995; Kalko *et al.*, 1996; Novick, 1963; Ochoa *et al.*, 2000; O'Farrell & Miller, 1997, 1999), the results obtained are difficult to compare and so precise conclusions are not possible.

An objective of this study was therefore to provide the deterministic elements for field workers familiar with the use of ultrasonic bat detectors (heterodyne and time expansion). The purpose is to attempt to gain reliable identification criteria for the acoustic recognition of bats in the field. The long-term aim is to produce a sonogram reference library. This requires a large number of recordings of neotropical species to cover, on one hand, the signal variability linked to the animal activity in relation to its natural environment and on the other hand, the possibility or not, of identification.

EQUIPMENT AND TECHNIQUES

The study zone of approximately 1 km^2 is situated close to the Nouragues (CNRS-UPS 656) site within the *Nouragues Nature Reserve* and in the heart of 100 000 hectares of primary tropical rain forest. The study zone varies in altitude between 92 m and 430 m. Primary rainforest is omnipresent in this site dominated by an inselberg. The forest provides a wide diversity of environments in spite of its overall apparent homogeneity: liana, bamboo, palms, chablis clearings, etc. (Oldeman, 1974). Most of the French Guiana bat species are found in this area, (Charles-Dominique *et al.*, 2001; Bongers *et al.*, 2001). Within the forest, the existence of an inselberg, caves and/or granite chaos' enables species with different ecological demands to be present. This is the case for underground dwelling species: *Lonchorhina inusitata*, *Phyllostomus latifolius*, *Pteronotus parnellii*, *P. personnatus* and *P. gymnonotus*; of which the last two species were not observed during the Nouragues site visit.

Six 12 m mist-nets were placed permanently in the canopy, and a further fifteen 12 m mist-nets erected in the forest and moved every other day. Using these, some 300 bats from 44 species were caught in five weeks.

After identifying each bat captured they were fitted with a chemiluminescent tag in accordance with proven methods (Buchler, 1976; Barataud, 1992). Owing to the dense nature of the environment (primary forest) and the numerous types of luminescent insects (Lampyridae, Elateridae, etc.), only about 15 % to 20 % of light-tagged animals were seen again. Where a bat was spotted again, its calls were recorded and its behaviour noted in detail. Given the problems encountered with light-tagging, additional recordings were made of bats during their release or when leaving roosts.

The bat detectors used in this study were: a Pettersson D.980 (frequency division, heterodyne, time expansion 3 or 12 seconds in memory); coupled with a tape-recorder Sony MZ – R 35, and a Pettersson D.200 (heterodyne). An Anabat II (frequency division using the zero-crossing principle) was used for comparison trials with the D.980. Despite the delicate electronic equipment, each detector resisted the quasi-extreme temperatures and high humidity, although they were stored in silica gel to help keep them dry.

The recordings were subsequently analysed using Pettersson Elektronics Batsound™ 3.1.0 software using the spectrogram set-up: Hanning window size 256 points or 512 points.

RESULTS

Of the 105 species in French Guiana, 72 are present in the Nouragues Nature Reserve. Among the 44 species captured during this study, only 31 species have been characterised (and another 7 species in March 2003 in a second stay). Indeed, amongst the 465 recordings made, amounting to about 6½ hours, only 90 of these have turned out to be relevant for characterising and differentiating between species or between groups of species.

A – Call structures

Several call structures are recognisable. This is the first step towards the acoustic recognition of bats in French Guiana by an observer in the field equipped with an ultrasonic bat detector. These different ultrasonic call structures appear to characterise some species or groups of species.

Recognition of call structures is the first step towards the acoustic identification of bats in French Guiana using an ultrasonic bat detector (O'Farrel, 1997; O'Farrel *et al.*, 1999; Leblanc, 2002). The different ultrasonic emission structures which appear to characterise some species, or groups of species, have been identified:

- Constant Frequency (for *Pteronotus parnelli*),
- Near Constant Frequency (for 5 species of Emballonuridae),
- Frequency Modulation with Constant Frequency tail (for the *Myotis* species and the *Eptesicus* species),
- Steep Frequency Modulated (for all of the Phyllostomidae species),
- Constant Frequency followed by a Parabolic Frequency Modulation (for *Rhynchonycteris naso* and the Noctilionidae species).

1. Constant Frequency (C. F.) – Figure 1

The structure shown in Figure 1 appears to characterise a single species: *Pteronotus parnelli* (Mormoopidae). The signals are comparable to the emissions of European Rhinolophidae. *Pteronotus parnelli* emitted a pure constant frequency signal at zero crossing between 53.2 and 59.1 kHz for 450 analysed signals in differents situations, e.g. hunting, exit from roost, etc.

2. Near Constant Frequency (Near C. F.) – Figure 2

This call structure is used by several species, all from the Emballonuridae family: *Saccopteryx* sp., *Peropteryx* sp., *Cormura brevirostris* (except *Rhynchonycteris naso*). Although there are slight differences, these signals are comparable with some European species, such as Noctules (*Nyctalus* sp.) and even the Barbastelle (*Barbastella barbastellus*).

However, it is possible to distinguish between these Emballonuridae calls. For example *Cormura brevirostris* emits a series of 3 signals with 3 different tones (resembling the first 3 notes of the old famous song "*Frère Jacques*"). (Fig. 3).

On the other hand, the *Saccopteryx* and the *Peropteryx* have two tone calls (Fig. 4).

3. Frequency Modulation with Constant Frequency tail (FM with C. F. tail) – Figure 5

This structure, shown in Figure 5, appears characteristic of the Vespertilionidae such as *Eptesicus* sp. These signals are similar to those of Serotines (*Eptesicus* sp.) and European Pipistrelles (*Pipistrellus* sp.). As no individuals were captured in flight, this remains to be confirmed.

4. Steep Frequency Modulated (Steep FM) – Figure 6

This structure (Fig. 6) appears the most commonly used by neotropical bats. All the Phyllostomidae emit Steep-

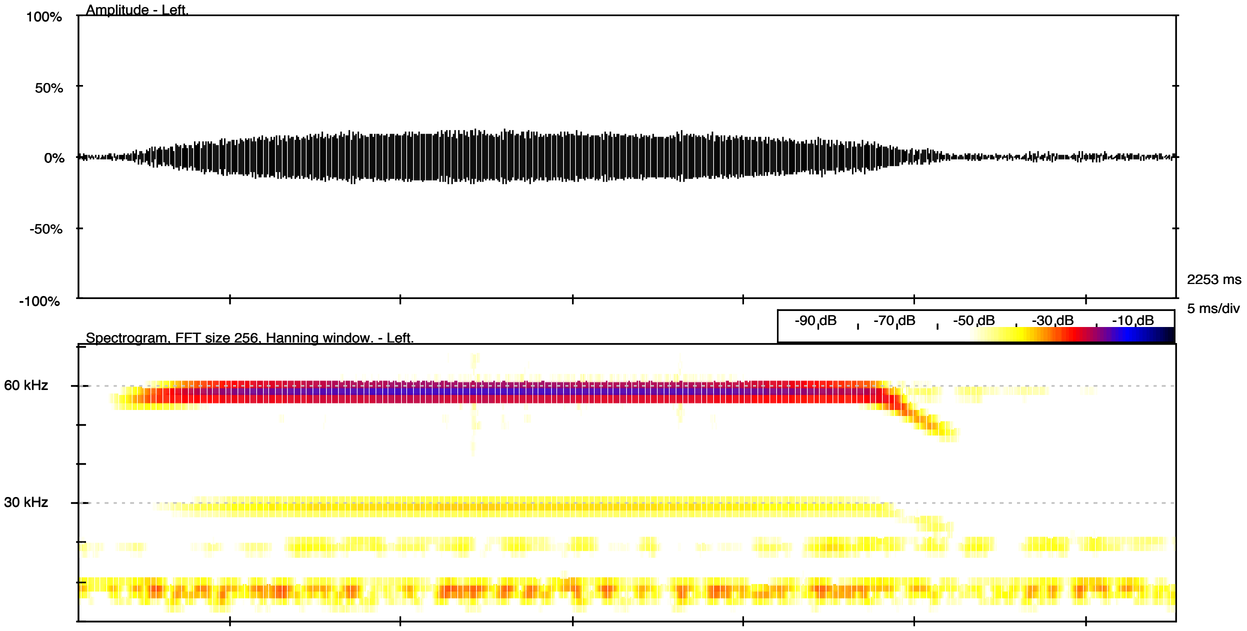

Fig. 1 : Call of *Pteronotus parnelli*.

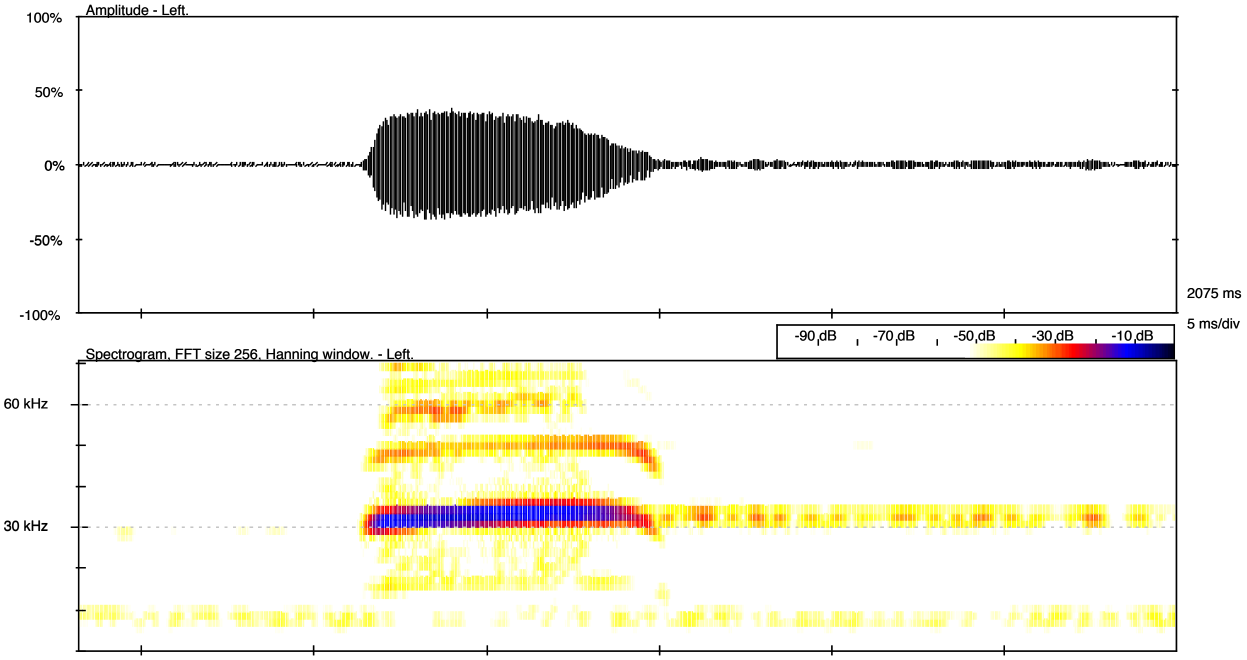

Fig. 2 : Call of *Cormura brevirostris*.

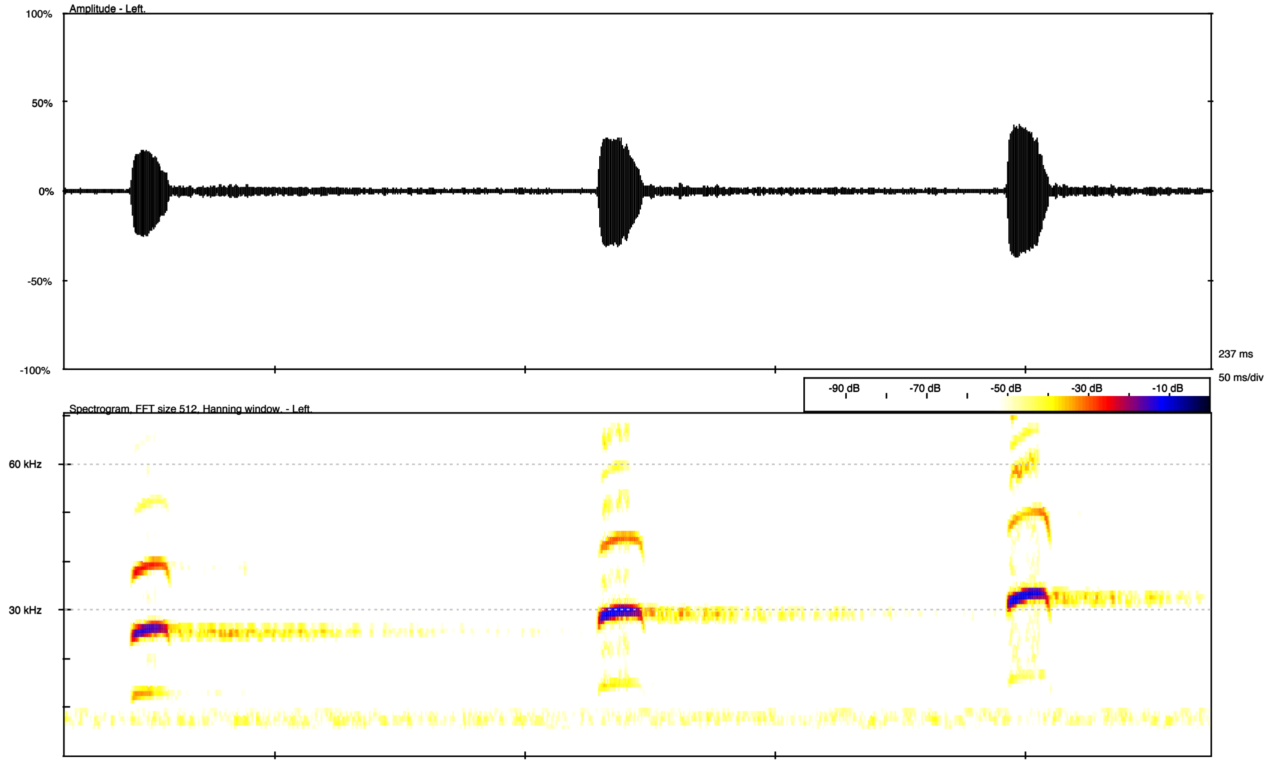

Fig. 3: Hunting sequence of *Cormura brevirostris*.

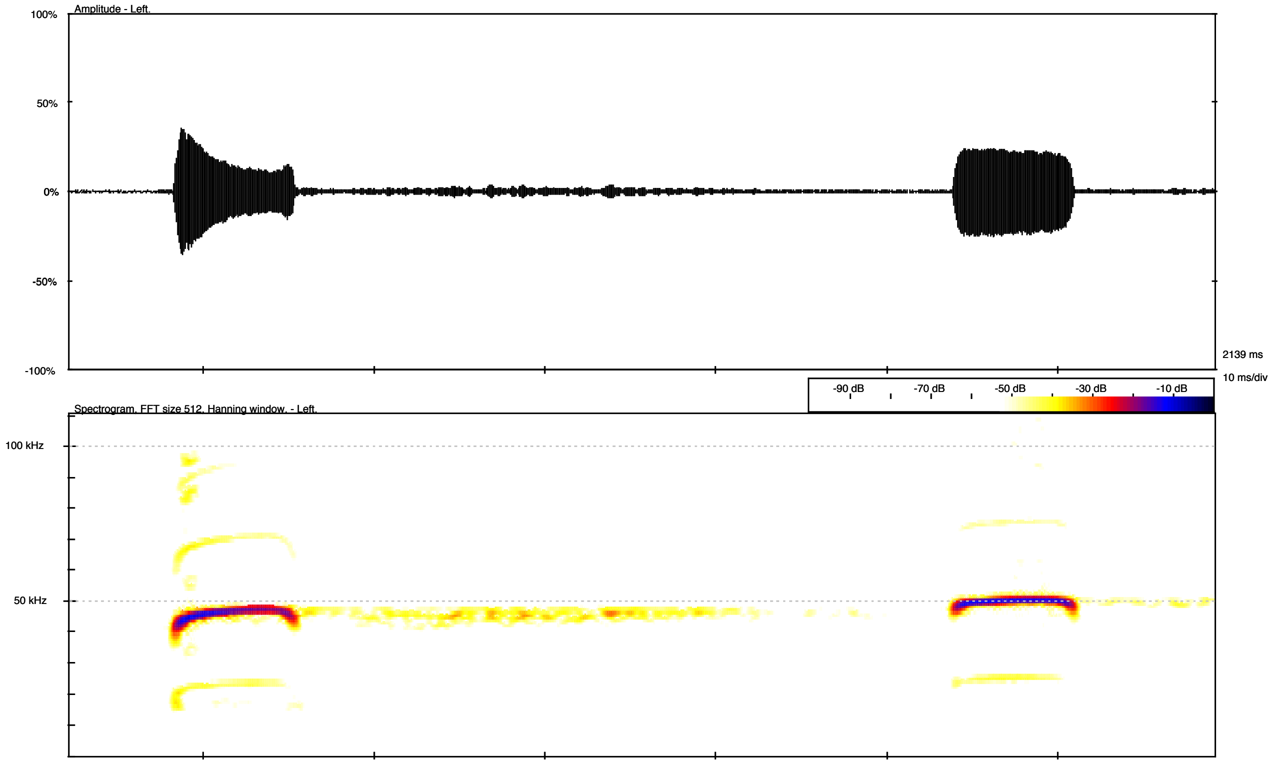

Fig. 4: Hunting sequence of *Saccopteryx leptura*.

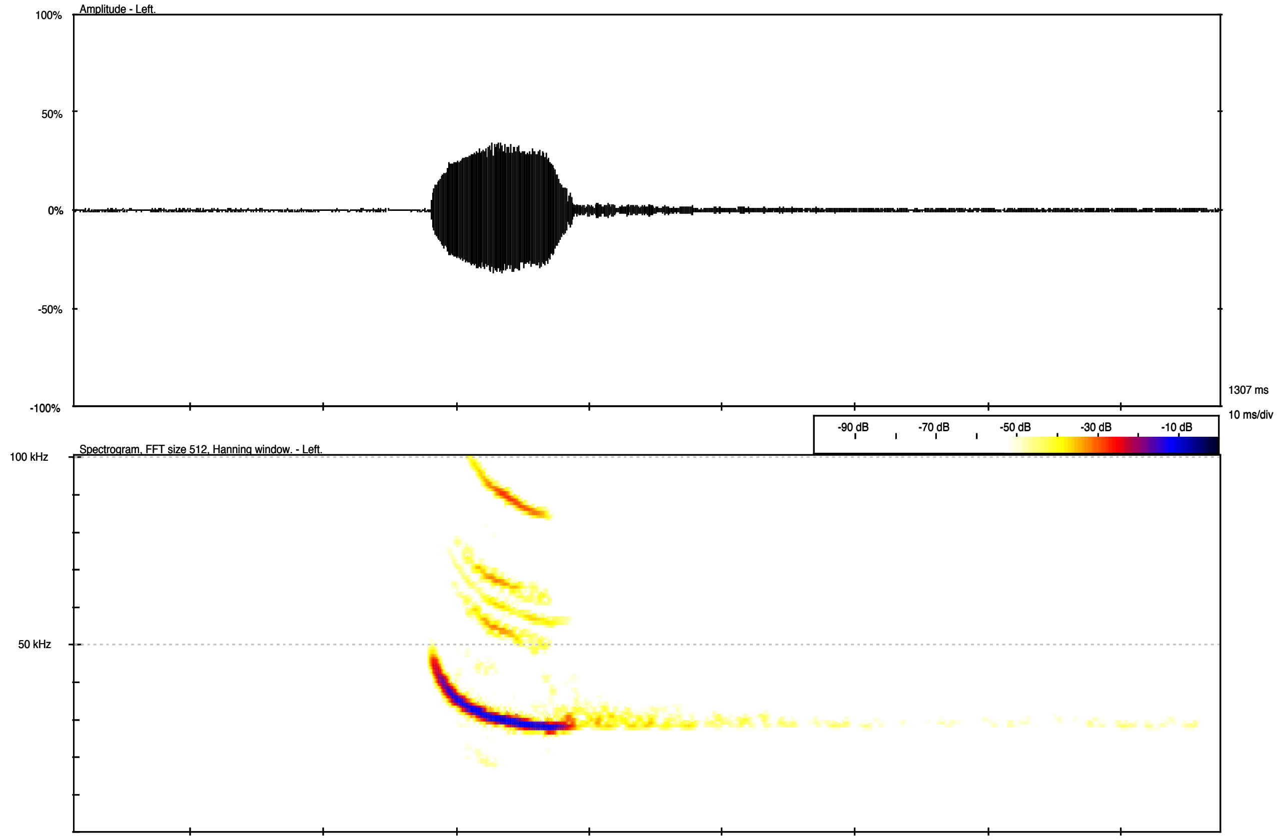

Fig. 5 : Call of *Eptesicus* sp.

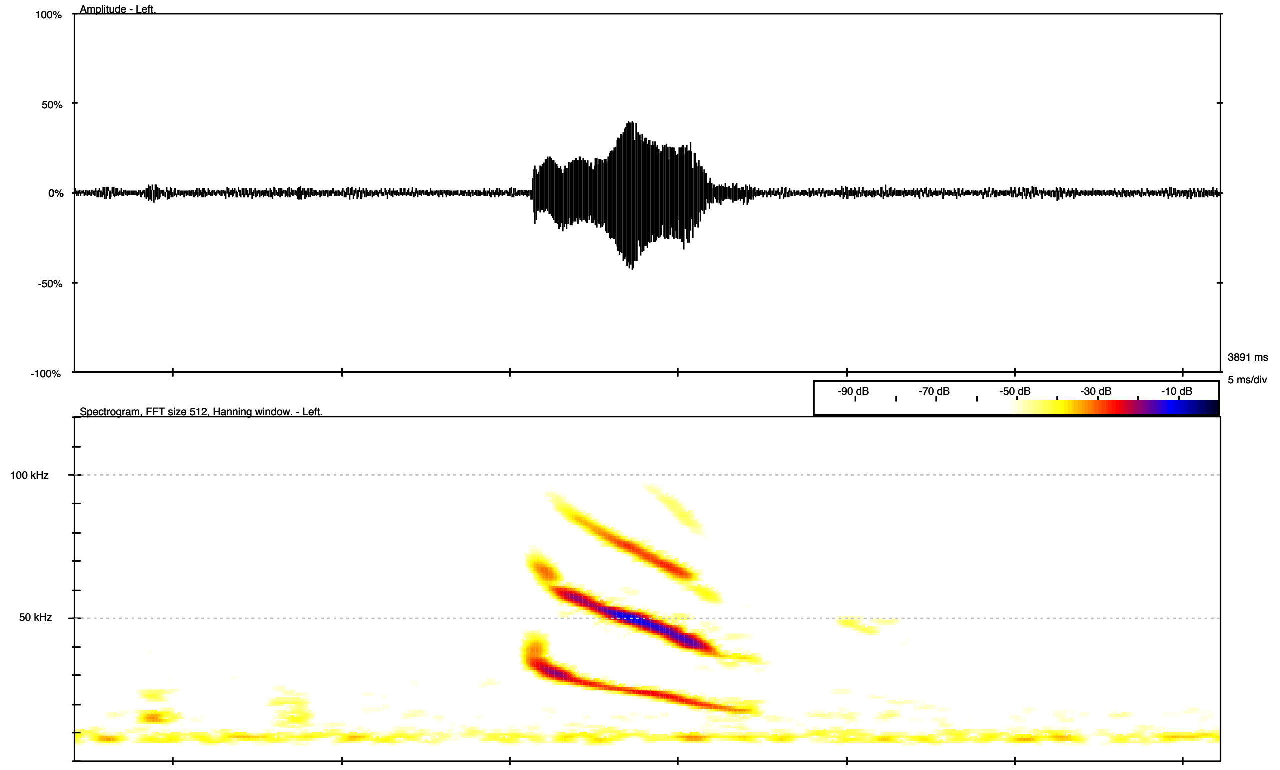

Fig. 6 : Call of *Phylloderma stenops*.

FM. These signals are comparable with European *Myotis* (*Myotis* sp.) but particularly European Long Eared bats (*Plecotus* sp.). To differentiate species within this family, which represents up to 60 % of bat populations in the rain forests, it is therefore necessary to resort to other distinctive criteria: explosive start, explosive end and energy peak.

5. Structures consisting of a Constant Frequency followed by a Parabolic Frequency Modulation (C. F. signal mixed with C. F.-FM signal) – Figure 7

This call structure (Fig. 7) appears characteristic of 3 species: *Rhynchonycteris naso* (Fig. 7), as well as *Noctilio leporinus* (Fig. 8) and *Noctilio albiventris* (Fig. 9). These latter were the two species not encountered in 2001 but found during a second visit in March 2003. None of the European species seem to use this type of signal structure.

B- Additional Acoustic Criteria

Once the emitted signal structure has been identified, it is then necessary to consider other distinctive characteristics especially for most of the Phyllostomidae where the call structure is almost always Steep FM: These additional criteria are:

- ES - explosive start (Fig. 10) (for many Phyllostomidae, cf. Table 1 – synopsis)
- EE - explosive end, (Fig. 11) (for *Anoura geoffroyi*)
- Energy peak (Fig. 12) (for all species)
- Sinusoïdal amplitude modulation (Fig. 13) (for *Noctilio albiventris*, like *Myotis daubentonii* in Europe).

Discrimination can be made between the sonar emissions for each species described can be obtained; a synopsis is given in Table 1.

The combination of several criteria estimated from the circumstances of emissions along with descriptive criteria of emitted signals are necessary to arrive at the determination of neotropical bats; as is also the case for the recognition of European bats. The technique used in this paper has allowed the sonic emissions of 38 species of bats in French Guiana to be described under different flight circumstances: mainly at release, in transit or whilst hunting. Around 20 species are relatively easily identified by simple acoustic recognition with high-performance bat detectors (used in heterodyne or time-expansion modes). This is the case for *Pteronotus parnelli, Rhynchonycteris naso, Noctilio leporinus, N. albiventris, Cormura brevirostris, Saccopteryx leptura, Peropteryx macrotis, P. trinitatis, Myotis riparius, Lionycteris spurelli, Ametrida centurio, Anoura geoffroyi*. For *Artibeus* or *Phyllostomus*, recording and computer analysis, rather than simple auditory means, is necessary for a reliable discrimination.

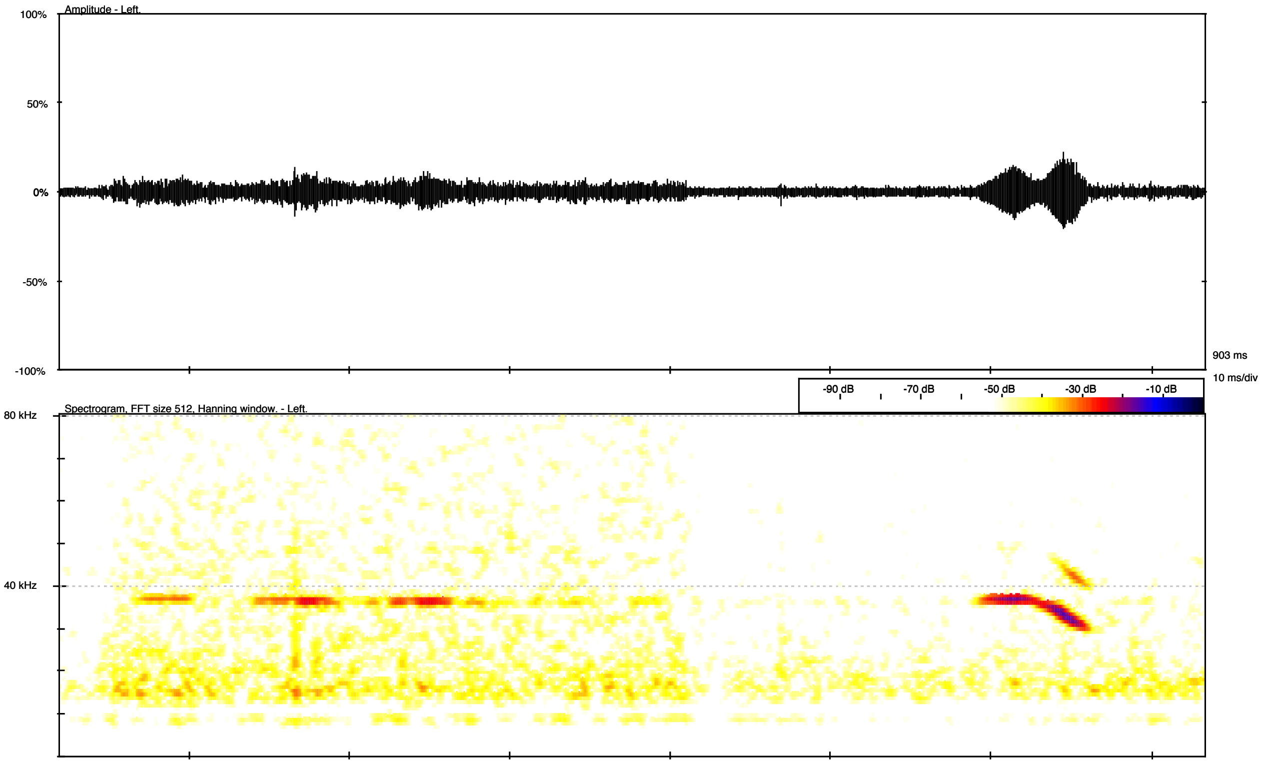

Fig. 7: Calls of *Rhynchonycteris naso*.

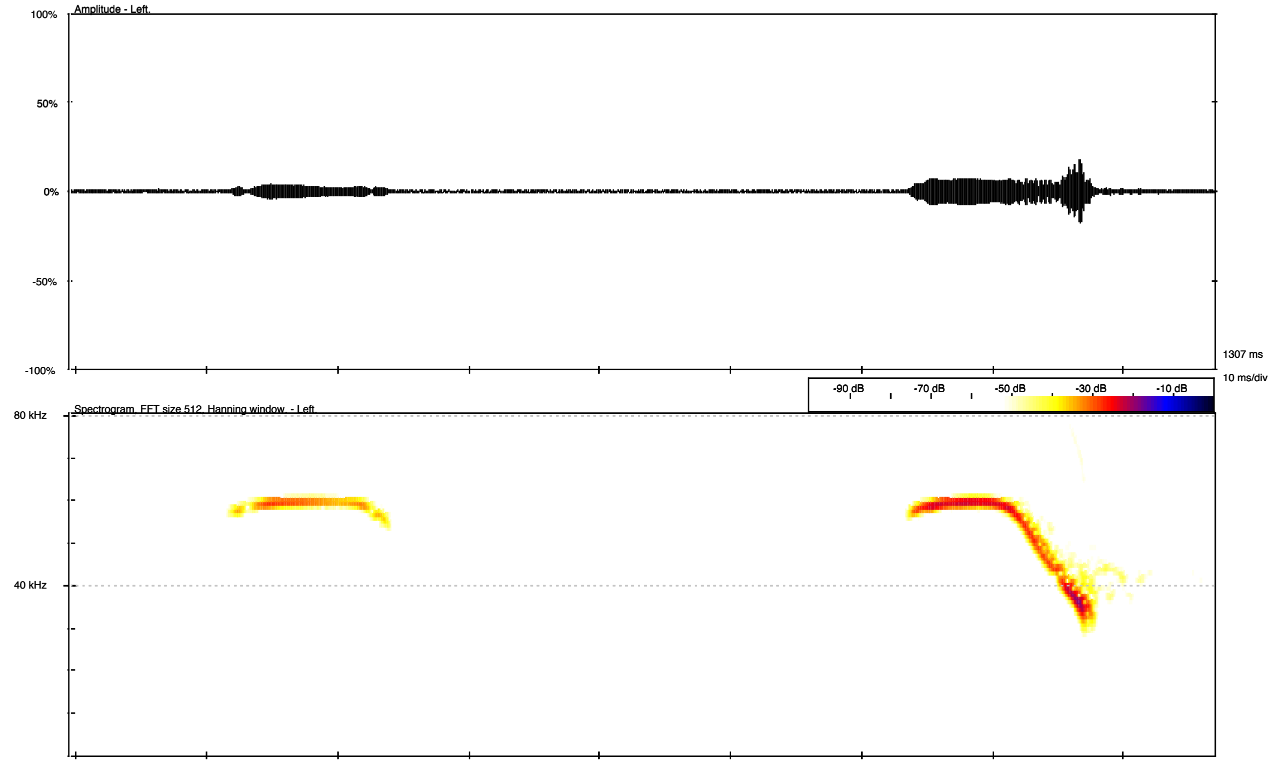

Fig. 8 : Calls of *Noctilio leporinus*.

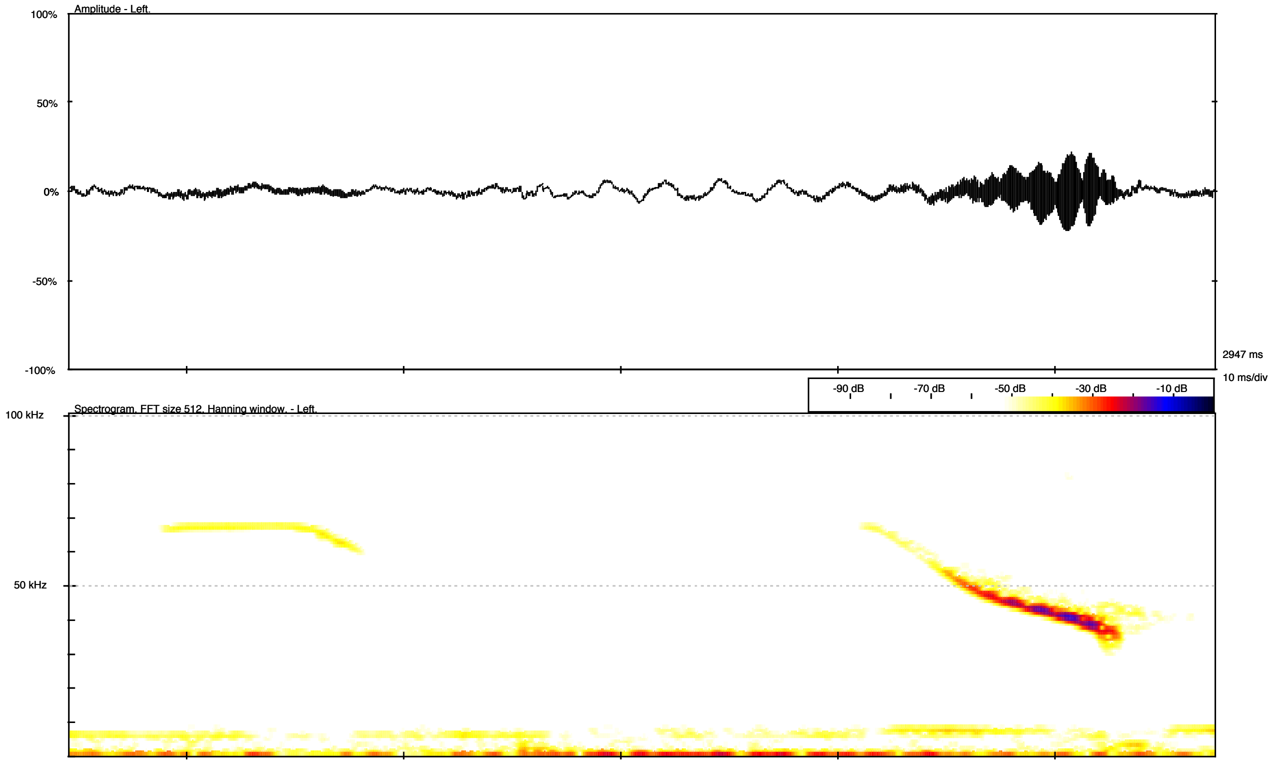

Fig. 9 : Calls of *Noctilio albiventris*.

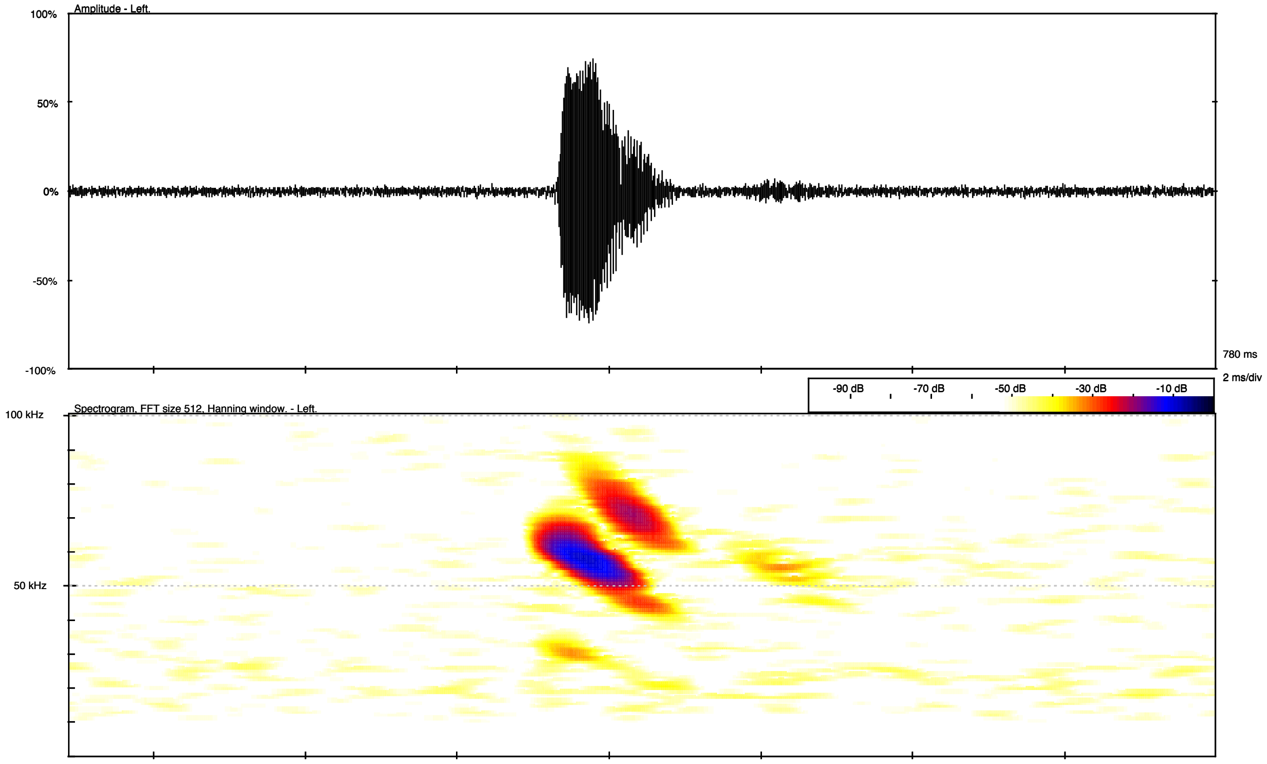

Fig. 10 : Oscillogram and spectogram of *Tonatia silvicola* showing an explosive start (ES).

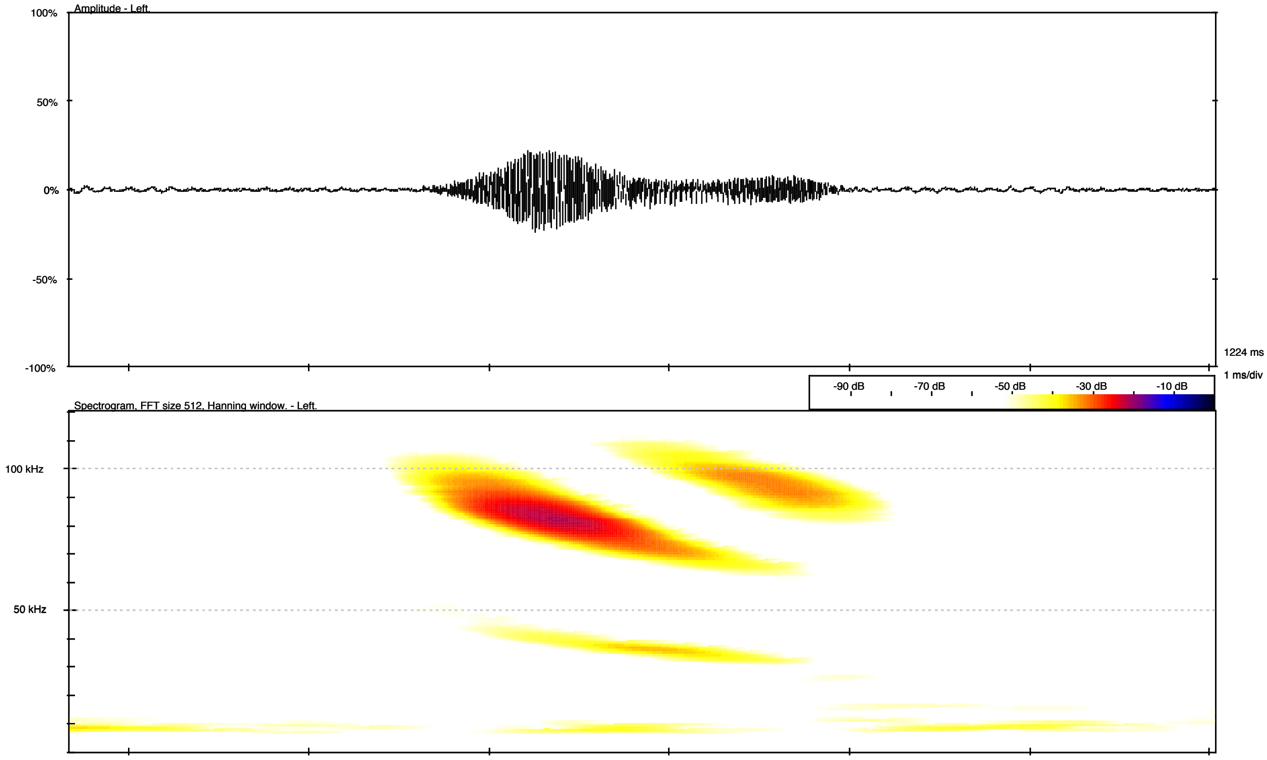

Fig. 11 : Oscillogram and spectogram of *Anoura geoffroyi* showing an explosive end (EE).

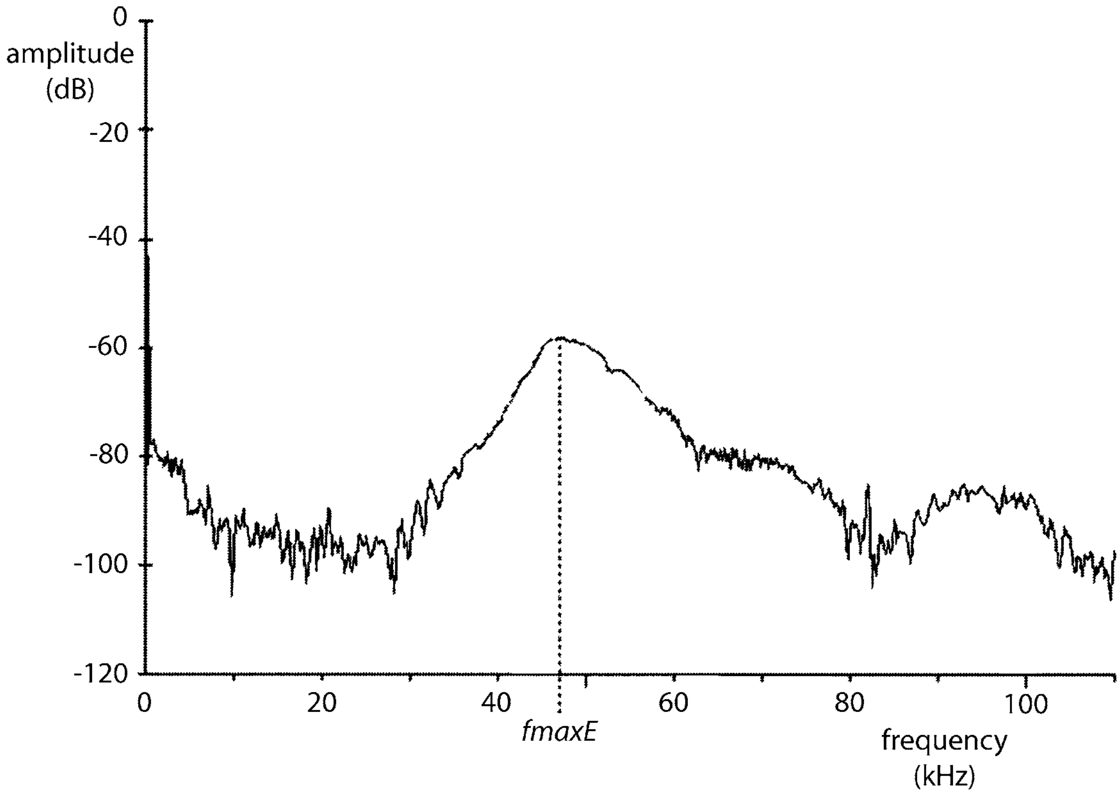

Fig. 12 : Measurement of Energy Peak ($f_{max}E$) of the signal's spectral density

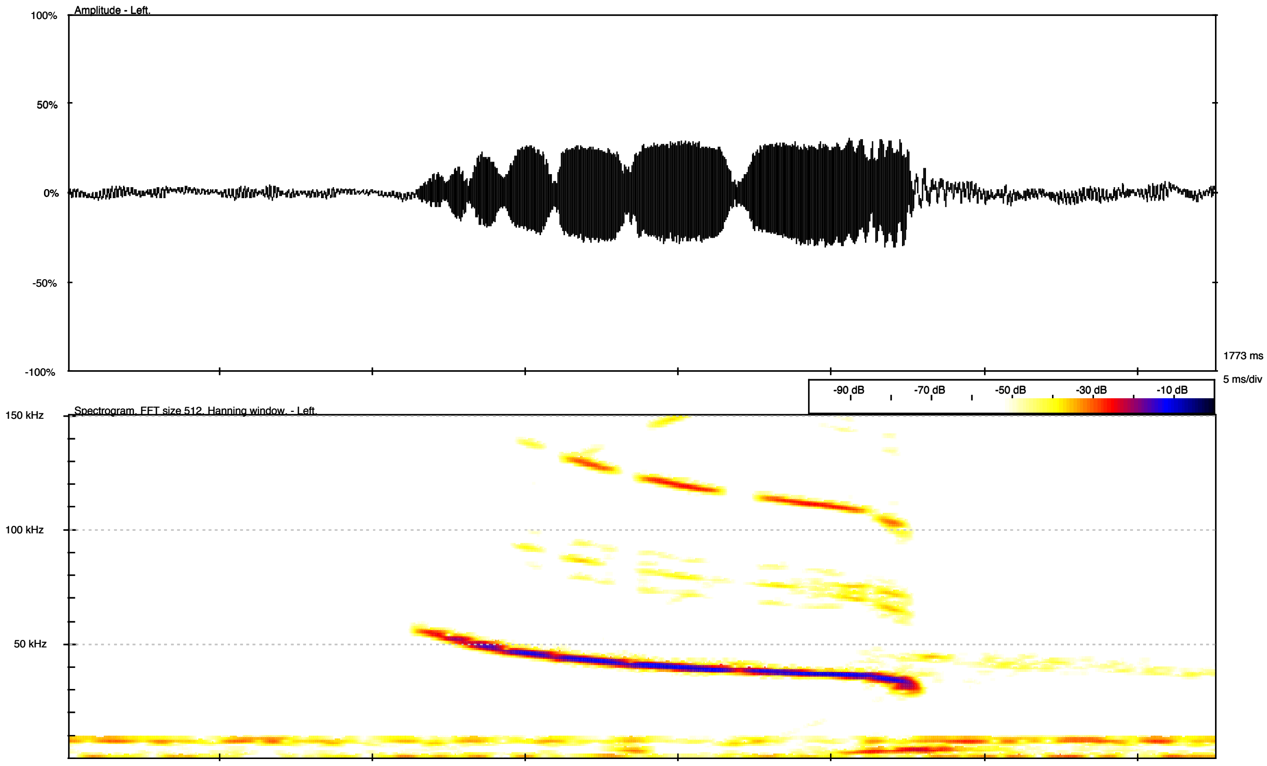

Fig. 13 : Call of *Noctilio albiventris* : Sinusoidal amplitude modulation visible in the oscillogram

Table 1: Synopsis Caracteristics of neotropical bats calls.

	SPECIES	Diet	Signal Structure	Signal Duration	Frequency : Max.	Min.	Max. Energy Peak (kHz)	Interval Duration	ES	EE	Rhythm	Tone	Signal Alternation
				(ms)	(kHz)			(ms)					
Mormoopidae	*Pteronotus parnelli*	I	*CF*	18.29 - 37.3	61	43.4	53.2 - 59.1	23 - 96	X	X	Slow	_	_
Emballonuridae	*Rynchonycteris naso*	I	*CF & CF-Steep FM*	7.37 - 63.7	39.1	30	35.4 - 39.1	43.6 - 229.3	X	X	Slow	_	2 signals
Noctilionidae	*Noctilio leporinus*	P	*CF & CF-Steep FM*	14.3 - 19.1	60.6	29.9	[37.2 - 45.6] [59.3 - 59.7]	47.6 - 178.7	X	√	Slow	_	2 signals
Noctilionidae	*Noctilio albiventris*	I	*CF & CF-Steep FM*	8.13 - 19.4	69.2	25.9	[35.2 - 38.6] [67.5 - 67.9]	38.3 - 120	X	X	Slow	_	2 signals
Emballonuridae	*Saccopteryx bilineata*	I	*Quasi-CF*	6,9 - 7,9	45	33	41,1 - 43,4	99,7 - 148,3	X	X		_	2 signals
Emballonuridae	*Saccopteryx leptura*	I	*Quasi-CF*	4.28 - 9.1	52.5	37	50.6 - 45.4	32 - 112	X	X	Slow	_	2 signals
Emballonuridae	*Cormura brevirostris*	I	*Quasi-CF*	5.2 - 11.6	26.5 - 34.9	20.4 - 29.8	[25.2 - 26.3] [28.6 - 30.9] [31.3 - 32.2]	36.7 - 219.5	X	X	Slow	_	3 signals
Emballonuridae	*Peropteryx trinitatis*	I	*Quasi-CF*	6.7 - 9.6	45.2 - 42.5	39.4 - 35	44.1 - 40.9	53 - 146	X	X	Slow	_	2 signals
Emballonuridae	*Peropteryx macrotis*	I	*Quasi-CF*	2.97 - 7.1	44.3	29.5	36.1 - 43.2	64.6 - 155	X	X	regular	_	_
Vespertilionidae	*Myotis riparius*	I	*FM -CF tail*	2.33 - 6.23	107.8	51.8	56.8 - 64.8	29 - 160	X	X		_	_
Vespertilionidae	*Eptesicus sp. ?*	I	*FM -CF tail*	6.95 - 12.17	48.4	26.6	28.6 - 30.9	130 - 205	X	X	Slow	_	_
Phyllostominae	*Mimon crenulatum*	I	*Steep FM & Quasi-CF*	1.24 - 1.74	80.5	56.9	63.6 - 64.3	51.3 - 156	√	X	Slow	_	_
Glossophaginae	*Lionycteris spurelli*	N	*Steep FM*	1.43 - 5.33	135.2	81	104.5 - 123.6	13.5 - 131	X	X	Slow	_	_
Stenodermatinae	*Ametrida centurio*	FN	*Steep FM*	0.83 - 4.54	127.4	58.9	73.8 - 91.1	74 - 103	X	X		European Myotis type	_
Glossophaginae	*Anoura geoffroyi*	N	*Short Steep FM*	0.96 - 4.38	108.2	28.7	48.8 - 89.8	22.4 - 181	X	√	Slow	nasal (Plecotus)	_
Stenodermatinae	*Artibeus lituratus*	FN	*Steep FM*	1.4 - 4.2	80.7	49.6	55.4 - 62.9	46 - 263	√	X	Slow	nasal (Plecotus)	_
Stenodermatinae	*Artibeus jamaicensis*	FN	*Steep FM*	2.42 - 5.62	70	38.5	45.6 - 59.3	46.7 - 162	√	X	Slow	nasal (Plecotus)	_
Stenodermatinae	*Artibeus gnomus*	F	*Steep FM*	2.81 - 3.2	101.8	52.7	64.8 - 70.9	103 - 195	√	X	Slow	nasal (Plecotus)	_
Stenodermatinae	*Artibeus obscurus*	FN	*Steep FM*	1.17 - 2.26	89.9	41.4	55 - 74.3	62.8 - 162	√	X	Slow	nasal (Plecotus)	_
Stenodermatinae	*Artibeus concolor*	F	*Steep FM*	4.01 - 7.33	105.6	31.9	37.5 - 90.4	89 - 143	√	X	Slow	nasal (Plecotus)	_

Phyllostominae	*Uroderma bilobatum*	F	*Steep FM*	1.79 - 2.58	97.1	62.1	81.3 - 82.5	27 - 136	√	X		nasal (Plecotus)	–
Phyllostominae	*Chiroderma trinitatum*	F	*Steep FM*	1.48 - 4	102.5	78.6	88.4 - 92	101.5 - 155	low - medium	X	Slow	nasal (Plecotus)	–
Phyllostominae	*Chiroderma villosum*	F	*Steep FM*	1.17 - 2.06	52.2 - 125.7	36 - 83.7	[41.6 - 44.1] - [81.8 - 98.6]	35 - 160	medium	X		nasal (Plecotus)	2 signals

Phyllostominae	*Phylloderma stenops*	IF	*Short Steep FM*	3.46 - 6.6	70.5	35	25.2 - 56.1	316 - 453	√	X	Slow	nasal (Plecotus)	–
Phyllostominae	*Phyllostomus discolor*	IN	*Short Steep FM*	2.06 - 2.5	89.6	62.9	73.4 - 79.3	48 - 117	√	X	Slow	nasal (Plecotus)	–
Phyllostominae	*Phyllostomus elongatus*	I	*Short Steep FM*	1.55 - 2.35	70	50	55.9 - 62.2	38 - 91	√	X		nasal (Plecotus)	–
Phyllostominae	*Phyllostomus latifolius*	I	*Short Steep FM*	1.41 - 1.52	67.4	54.1	56.3 - 56.5	290 - 310	√	X	Slow	nasal (Plecotus)	–
Phyllostominae	*Phyllostomus hastatus*	IF	*Short Steep FM*	1.53 - 2.56	56.3	37.5	43.2 - 47.7	37 - 81	√	X		nasal (Plecotus)	–
Phyllostominae	*Tonatia saurophila*	IC	*Short Steep FM*	1.65 - 2.75	43.4 - 86	31.4 - 75.4	40 - 79.3	131 - 134	√	X	Slow	nasal (Plecotus)	2 signals
Phyllostominae	*Tonatia schulzi*	I	*Short Steep FM*	0.75 - 2.2	66.4	50.5	55.9 - 57.5	24.5 - 72	√	X		nasal (Plecotus)	–
Phyllostominae	*Tonatia silvicola*	I	*Short Steep FM*	0.87 - 2.62	87.4	42.1	46.3 - 75.2	31 - 151	√	X		nasal (Plecotus)	–
Phyllostominae	*Platyrrhinus helleri*	F	*Short Steep FM*	1.42 - 1.86	110.4	86	92.7 - 98.8	26.3 - 79.4	√	X		nasal (Plecotus)	–
Phyllostominae	*Vampyressa brocki*	F	*Short Steep FM*	1.9 - 3.1	102.9	57.2	70.9 - 82.5	61.1 - 65.5	√	X		nasal (Plecotus)	–
Glossophaginae	*Lonchophylla thomasi*	NI	*Short Steep FM*	1.58 - 4.55	115.2	20.4	25.2 - 96.6	59 - 170	√	X	Slow	nasal (Plecotus)	–
Carolliinae	*Rhinophylla pumilio*	F	*Short Steep FM*	0.56 - 1.87	105.7	25.4	30.2 - 93.2	23 - 109	√	X		nasal (Plecotus)	–
Carolliinae	*Carollia perspicillata*	F	*Short Steep FM*	0.85 - 2.54	107.4	52.5	67.5 - 93.4	27 - 108	√	X		nasal (Plecotus)	–
Desmodontinae	*Desmodus rotundus*	S	*Short Steep FM*	1.6 - 4.6	89	42	54.7 - 79.5	27.8 - 137	√	X		nasal (Plecotus)	Harmonics
Desmodontinae	*Diaemus youngi*	S	*Short Steep FM*	1.45-3.46	65.4	35.5	47.2 - 51.8	33 - 108	√	X		nasal (Plecotus)	Harmonics

KEY:	I	insectivorous	C	Carnivorous	FM	Frequency Modulated	EE	Explosive End
	N	nectarivorous	S	Sanguivorous	CF	Constant Frequency	X	No/Non
	F	frugivorous			ES	Explosive Start	√	Yes/Oui

DISCUSSION

Compared with some of the vocal characteristics already known for some neotropical bat species, the results and observations of the study outlined largely corroborates previous research (Novick, 1963; Barclay, 1983; Wenstrup & Suthers, 1984; Kalko, 1995; O'Farrell & Miller, 1997).

Considering the results of echolocation calls of Emballonuridae bats from Panama (Barclay, 1983), it is evident that a knowledge of the emission circumstances is essential to understanding ultrasonic bat calls. In Barclay's study, bats were captured and then recorded in flight whilst in a cage, like Novick in 1963. Here, *Cormura brevirostris*, emitted one type of QCF signals or two alternating type of QCF signals. Whereas under natural conditions, when this bat is hunting, *Cormura brevirostris* emits three alternating QCF calls that are very characteristic of this species. However, if we consider Barclay's description, *Cormura brevirostris* could be confused with the *Saccopteryx* species.

The description of the call characteristics of *Rhynchonycteris naso* agree with those in the Kalko study. However, the bandwidth of calls is somewhat surprising. The calls recorded in the Natural Reserve of Nouragues are between 10 and 50 kHz lower than those in the Kalko and O'Farrell studies.

Furthermore Kalko, (1995) following the hypothesis of Barclay (1983), also provides the characteristics of one *Peropteryx* (*Peropteryx kappleri*). Here, their description of calls corresponds with our results for *Comura brevirostris*, i.e. QCF with three signals of different frequencies (cf. Table 1). Their results may have been influenced by the methods applied.

Bat identification using 3D night-vision goggles (Type Wild) may not be totally reliable, whereas the method employed in the current study enables a positive identification in the hand followed by chemiluminescent tagging.

In fact, it is very important to record a large number of calls in many different natural situations to know the entire range of possible calls for one bat species before it can be recognised with certainty. The Phyllostomidae are a good example of this as it is a large family, which are very numerous and emit calls with signals having the same basic structure (Steep FM).

During the study, only one Molossidae was caught, but this specimen is a unidentified *Molossops* sp. It was kept for the *Museum National d'Histoire Naturelle* and consequently was not released. Unfortunately, Molossidae are very difficult to catch with mist-nets.

The acoustic recognition of neotropical bats in the field is complementary to capture techniques with mist-nets and has the advantage of being able to observe animal behaviour without disturbance (Kunz & Brock, 1975; Kuenzi & Morrison, 1998; O'Farrell & Gannon, 1999; Watson, 1970; Zbinden, 1995). Habitat preferences may therefore be perceived differently depending on the technique used. As a result, recognition of the ultrasonic emissions of bats linked to their behaviour enables more to be known about species which, in some cases, are rarely captured and observed. Given this approach, it is hoped that the majority of insectivorous bats can be recognised and distinguished (Emballonuridae, Vespertilionidae, Molossidae, Noctilionidae). The most complex acoustic recognition relates to some members of the Phyllostomidae. In time, increasing the number of recordings of signal sequences emitted in different flight conditions should enable discriminating criteria to be established for each species.

CONCLUSIONS

The features of the study described include:

1. distinguish and determine bat species by acoustic observation, i.e. identification of calls in the field or from recordings;

2. observe their behavioural patterns linked with emitted signals.

The first step is recognition and definition of the different types of structures within the bat emissions. The next stage consists of linking visual observations with the acoustic information in order to describe the different types of ultrasonic calls emitted for each species related to their behaviour (hunting, transit, social calls, capture, approaching obstacles, etc) (Sherwin *et al.,* 2000).

The current study is incomplete owing to the large number of bat species present in French Guiana, only a third of which were recorded during the visit described here, coupled with the wide variation of calls emitted under different flight circumstances. However this introductory study has provided a good overall basis for future research.

List of species captured and recorded in 2001

Emballonuridae
(Rhynchonycteris naso)
Comura brevirostris
Peropteryx macrotis
Peropteryx trinitatis
Saccopteryx bilineata
Saccopteryx leptura
Mormoopidae
Pteronotus parnelli
Phyllostomidae
Lonchorina inusitata
Micronycteris megalotis
Micronycteris minuta

Micronycteris hirsuta
Micronycteris schmidtorum
Mimon crenulatum
Phylloderma stenops
Phyllostomus discolor
Phyllostomus elongatus
Phyllostomus hastatus
Phyllostomus latifolius
Tonatia saurophila
Tonatia schulzi
Tonatia silvicola
Glossophaginae
Anoura geoffroyi
Lionycteris spurelli
Lonchophylla thomasi
Carolliinae
Carollia perspicillata
Rhinophylla pumilio
Sternodermatinae
Ametrida centurio
Artibeus jamaicensis
Artibeus lituratus
Artibeus obscurus
Artibeus gnomus
Artibeus concolor
Chiroderma trinitatum
Chiroderma villosum
Mesophylla macconnelli
Platyrrhinus helleri
Uroderma bilobatum
Vampyressa brocki
Desmodontinae
Desmodus rotundus
Thyropteridae
Thyroptera tricolor
Thyroptera dicifera
Vespertilionidae
Myotis riparius
Eptesicus sp. ?
Molossidae
Molossops sp.?

RESUME

Premiers éléments sur l'identification acoustique des chiroptères de Guyane Française. Durant un séjour en Guyane Française en automne 2001, nous avons capturé et enregistré 44 espèces de chauves-souris de différentes familles : Emballonuridae, Phyllostomidae, Vespertilionidae.

Sur les 465 enregistrements effectués (soit 6h 30), seulement 80 à 90 enregistrements se sont avérés exploitables pour la recherche de critères d'identification des différentes espèces enregistrées. Ainsi sur les 44 espèces capturées, nous avons pu seulement caractériser 31 espèces ou groupes d'espèces.

Les premiers éléments recueillis permettent de différencier certaines espèces ou caractériser certaines familles de façon probante. Certaines convergences acoustiques avec des espèces européennes permettent de formuler des hypothèses sur les habitats de chasse ou les spécialisations alimentaires. Suite à ces résultats encourageants, des campagnes complémentaires sont donc indispensables pour poursuivre les recherches sur l'identification acoustique des 105 espèces de chiroptères présentes en Guyane française.

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The interactions between echolocating bats and their insect prey

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Abstract. This paper describes the complex acoustic relationship between predator and prey.

Many species of insect are known to have functional ears that are sensitive to ultrasound. High frequency signals provoke these insects to react in some way. This is generally accepted to be a defensive mechanism against insectivorous bats using ultrasonic location. Other insects can emit "clicks" in response to bat echolocation calls, which may "jam" bat sonar. Considering the orders of species exhibiting this defensive strategy, it is likely that 50 % of European moth species have the capability to evade predation by bats.

Insects are a known valuable source of nutrition for bats. This implies that bats have developed methods of overcoming the defence mechanisms of their prey. The structure of bat echolocation calls reflects their temporal and spatial resolution needs when foraging and navigating in their preferred environments. This is coupled with the physical constraints of bat biology, notably wing-related. Within the structure of bat echolocation calls, the call frequency, intensity, duration and pulse repetition frequency may affect the defensive reactions of insects.

The acoustic capabilities of some families of insects are reviewed and their influence on bat echolocation calls is discussed.

HEARING IN INSECTS

Many groups of insects are known to have functional ears which are sensitive to ultrasound. Species from the orders of Orthoptera, Neuroptera, Dictyoptera, Coleoptera, Diptera and Lepidoptera all show hearing abilities above sound frequencies of 20 kHz (Michelsen & Larsen, 1985 ; Yager & Hoy, 1986 ; Spangler, 1988a ; Robert *et al.*, 1992). In many of the species investigated, evasive action in flight can be elicited by an ultrasonic pulse train (Roeder, 1962 ; Miller, 1975 ; Nolen & Hoy, 1986 ; Yager *et al.*, 1990). This is generally accepted to be a defensive reaction to avoid predation by insectivorous bats which detect their prey by using ultrasonic sonar (Roeder, 1967a; Miller, 1984; Fullard, 1987a; Surlykke, 1988 ; Yager *et al.*, 1990).

Of all the groups investigated, more literature is available on nocturnal moths than any other order. The pioneering work of Kenneth Roeder in the 1960's, and early 1970's established a firm base of neuroethological data on the interactions between noctuid moths and the insectivorous bats which predate them (Treat, 1983). From this initial work, investigations spread to other families of Lepidoptera and other insect orders. This revealed that the ability to hear ultrasound has evolved independently at least eight times, three times in the Lepidoptera alone (Yager *et al.*, 1990). In moths, members of the superfamilies Noctuoidea, Notodontoidea, Geometroidea, Sphingoidea and Pyraloidea have all been shown to be sensitive to ultrasound (Roeder *et al.*, 1968 ; Roeder, 1974 ; Spangler & Takessian, 1983 ; Surlykke, 1984). Of these families, some members from the Noctuoidea, Notodontoidea and Sphingoidea have been shown to exhibit evasive flight manoeuvres on exposure to ultrasound (Fullard, 1988). If all the species from the above five families can be assumed to have similar hearing abilities and to exhibit defensive flight behaviour, then approximately 50 % of moth species occurring in Europe has some form of bat defense mechanism, including most of the Macrolepidoptera encountered (data from Kloet & Hincks, 1972). Considering that species of noctuids are seasonally often the most abundant family of moths (Hollyfield, 1993), there is a high probability that any moth encountered by a bat is going to possess some form of auditory system and associated defensive behaviour.

In certain Lepidoptera, ultrasound appears to be used for intraspecific communication. Examples have been identified in the Noctuidae (Surlykke & Gogala, 1986 ; Surlykke & Fullard, 1989), Arctiidae (Krasnoff & Yager, 1988) and Pyralidae (Gwynne & Edwards, 1986 ; Spangler, 1988b). It is believed that these functions are secondary changes to an auditory system which initially evolved in response to predation by echolocating bats (Fullard & Yack, 1993).

Some species of Arctiid moths emit clicks in response to hearing the echolocation calls of bats (Fullard *et al.* 1994). The clicks are produced by tymbal organs on modified thoracic episterna (Fullard, 1992). The function of the clicks is still unclear. They could be used to startle the bats, or jam their echolocation (Fullard *et al.* 1994), or to warn bats that they are unpalatable (Dunning *et al.* 1992; Acharya & Fenton, 1992).

In the choerocampine Hawkmoths, the acoustic detector is located in the distal lobe of the pilifer (Roeder, 1972). Its mode of action depends upon contact between the medial wall of the second palpal segment and the distal lobe of the pilifer. The medial wall serves as an acoustic interface and the distal lobe contains the sensory transducer. In the other families of Lepidoptera the acoustic detector is a tympanic membrane located in a recess on either side of the body. It can be found on the posterior margin of the metathorax in the Noctuoidea and Notodontoidea, and the first abdominal segment in the Pyraloidea and Geometroidea. Attached to the tympanic membrane are a variety of sensory cells, two in the Noctuoidea, one in the Notodontoidea and four in the Geometroidea and Pyraloidea (Eggers, 1919; Kennel & Eggers, 1933; Fullard, 1988). It is believed that the auditory system is an evolutionary development of the insect chordotonal system (Boyan, 1993), and analogs of components of the sensory system have been identified in atympanate moths (Yack & Fullard, 1990; 1993). In noctuids, stimulation of the sensory cells by ultrasound impinging on the tympanic membrane triggers a variety of escape behaviours, from negative phontaxis at low sound intensities (Roeder, 1967b), to complex unpredictable manoeuvres involving spirals, loops and dives at high sound intensities (Roeder, 1962; 1975a). It is generally accepted that these behaviours form a two-tier defense system aimed at taking the moth out of the flight path of a searching or feeding bat (Roeder, 1964). Roeder & Treat (1962) estimated a selective advantage of 44 % of reacting over non-reacting moths in real bat-moth interactions in the field. This led them to comment that “one might wonder how moths without means of evasion could have survived at all where predation by bats is a substantial hazard”.

It is obvious that whatever the exact figure, hearing in moths confers a very great selective advantage. But what of the other side of the equation? Moths are a very important food source to a number of bat species (Thompson, 1982; Jones, 1990; Robinson, 1990). Whether they are selectively taken is unclear due to the problems of estimating nocturnal invertebrate populations, but prey remains often indicate that large numbers of noctuid moths are taken by some species of bats. As noctuids are often sizable moths, they must represent a valuable food resource. The hearing abilities and frequency sensitivities of moths appears to be adapted to the call parameters of the main predatory bat species within their environment (Fullard, 1984a; 1987a; 1988; Surlykke, 1988). Selection may then act on the bat’s sonar system to make it acoustically less apparent to the moth. Various call parameter shifts have been proposed (Fenton & Fullard, 1979, 1981; Fenton, 1980; Pye, 1983; Surlykke, 1988), including altering the frequency, duration, intensity and repetition rate of the call, but none have been proven experimentally.

ECHOLOCATION SYSTEMS IN BATS

A wealth of literature is available on the various echolocation systems employed by bats. Most of the data is very species specific, and is often only applicable to the conditions under which the recordings were made or the experiments performed. General reviews of the theoretical requirements for the structure of bat calls can provide predictive information on how echolocation calls can be optimised for certain tasks using sonar theory. Useful accounts are given by Webster (1963); Pye (1980; 1983); Fenton (1980); Barclay (1988); Möhl (1988) and Neuweiler & Fenton (1988).

In general, the echolocation calls of Microchiropteran bats can be divided into two broad categories; frequency modulated (FM) calls and constant frequency (CF) calls. Frequency modulated calls start at a high frequency and sweep down through the frequency range. Constant frequency calls generally have longer durations than FM calls, and maintain the same frequency throughout the duration. Echolocation calls can be composites of the two types, or bats may alternate between types (Pye, 1980). The two types of call have different advantages for use in a sonar system. Frequency modulated calls provide accurate ranging since each frequency component can be accurately fixed in time. This leads to an accurate determination of pulse-echo interval not possible with constant frequency calls. The generally shorter duration of FM calls also means that a bat can approach a target more closely before pulse-echo overlap begins to degrade sonar performance. Constant frequency calls can potentially provide the bat with a greater sonar range due to the energy contained in the echo being concentrated into a narrow frequency band. This boosts the signal to noise ratio in the bat’s cochlea and allows a more distant target to be detected than an FM call with the same emitted intensity. An additional advantage of CF calls is that the longer duration allows the detection of amplitude modulations in the echo imparted by a moving prey item. This can be used by a foraging bat to discriminate between prey items and clutter (Schnitzler & Flieger, 1983; Schnitzler *et al.*, 1983).

In considering the structure of bat echolocation calls one must take into account the physical and physiological limitations of their generation and reception. The calls must meet certain criteria for effective spatial and temporal resolution of the target. The type of call will also be dependent on the foraging behaviour of the bat and the habitats utilised. This in turn is related to the wing loading and aspect ratio of the bat’s wing (Fenton, 1988). Thus to understand and resolve the role of moth audition in call design, one must also consider the constraints of physics, aerodynamics, neurological processing capabilities and energetics of the echolocation system. If any of these parameters are measurably shifted from what could be considered optimal for the bat, then a good case for selection acting on the call can be established.

SENSITIVITY OF THE MOTHS ACOUSTIC DETECTOR CELLS

In noctuid moths, three cells form the input into the tympanic nerve, two A cells and a B cell. The A1 cell is the most sensitive, with the A2 cell matching the response curve of the A1 cell but about 20 dB less sensitive (Roeder, 1964). There is no known mechanism by which the noctuid ear can differentiate frequency. The function of the B cell remains unclear, though a proprioceptive role (Roeder & Treat, 1957; Treat & Roeder, 1959; Payne *et al.*, 1966) and a sound receptive role (Lechtenberg, 1971) have been proposed. In electrophysiological recordings it can be identified by the large regular spike pattern which differentiates it from the smaller A cell spikes. The three axons leave the area of the tympanum together with a few motor axons and form the IIIN1b nerve (Treat, 1959) which runs over the inner surface of the metathoracic dorsoventral flight muscles to the pterothoracic ganglion (Roeder, 1966a). It is proposed that the action of two A cells with different degrees of sensitivity allows an extension of the dynamic range of the moth ear (Roeder, 1974). This would allow for the triggering of the two types of escape behaviour witnessed. The A1 cell would trigger negative phonotaxis at low sound intensities and the A2 (or A1 and A2 combined) would trigger the unpredictable random flight as a last ditch attempt at escape at high sound intensities (Roeder, 1966, 1967b, 1975b).

NEUROLOGICAL PROCESSING

It is with the aspect of neurological processing within the central nervous system that much of the recent work has been concentrated. Although many new techniques have become available, the results are often contradictory and reveal little about the underlying mode of action of decision making or the initiation of escape behaviour. Roeder (1969a) tentatively suggests that the effectors of these two types of behaviour can be divided into two efferent systems. The 'steering system' is made up of the motor neurone complex supplying the axillary and alar muscle group inserted directly on the wing bases and capable of changing the angle of attack and degree of wing extension on a differential basis (Roeder, 1967a). The second group is the 'drive system' consisting of the motor complex regulating the dorso-ventral and horizontal indirect flight muscles that power the wings as a unit. Differential responses in the two A1 cells on opposite sides of the body from a sound intensity gradient would cause a controlled alteration in the steering system. This would cause the moth to fly away from the source of ultrasound producing the negative phonotactic behaviour observed. Saturation of the A1 response and the initiation of the A2 response might bring about excessive feedback in the steering loop which may bring about erratic turns and spiralling, or it may cause complete or partial suppression of the drive system causing diving. While this explanation provides a useful conceptual framework, there is little evidence to suggest that any of it actually operates in this manner. Contributions from Surlykke & Miller (1982), Boyan & Fullard (1986; 1988), and Agee (1988), have begun to reveal some of the underlying processing operations needed to separate bat generated ultrasound from noise events, and to assess the direction and proximity of the foraging bat.

The A1 afferent projects into the metathoracic ganglion where it bifurcates (Boyan *et al.*, 1990). One branch ascends in the ventral intermediate tract to the brain, the other descends in the ventral intermediate tract into the abdominal neuromeres of the metathoracic ganglion. The projections of the A2 axon remain largely within the metathoracic ganglion. The axon bifurcates on the midline and directs arborisations dorsally to the dorsal intermediate and median dorsal tracts, and ventrally into the ring tract where the arborisations overlap those of the A1 cell (Paul, 1973; Surlykke & Miller, 1982; Boyan *et al.*, 1990). Orona & Agee (1988) state that there is a direct synaptic connection between the A2 cell and the motorneurones innervating the flight muscles. So far, fourteen auditory interneurones have been identified which have their cell bodies in the meso- or metathoracic neuromeres of the fused pterothoracic ganglion (Boyan & Fullard, 1986; Boyan *et al.*, 1990). Auditory interneurones have also been identified in the suboesophagal and procerebral ganglia (Roeder, 1969a; 1969b; 1973). Various functions of the characterised interneurones have been suggested, including noise filtering (Boyan & Fullard, 1988), pulse marking (Paul, 1974; Boyan & Miller, 1991) repeater functions (Boyan & Fullard, 1986) and higher functions of integrating auditory input with motor output sustaining flight (Roeder, 1975b; Orona & Agee, 1988; Boyan *et al.*, 1990).

ESCAPE BEHAVIOURS

The ultimate aim of all the complex interactions of the above factors is to produce an escape behaviour which will save the moth from being predated by bats. Experiments which use tethered moths, while providing useful results, can never really mimic actions in free flight conditions (Roeder, 1967b). Indeed, of the really important elements of any escape response ; reaction time, escape time and escape unpredictability, the first is the only one which can be accurately assessed under tethered conditions. Some attempts at free flight experiments have been conducted, most notably Roeder (1962) and Roeder & Treat (1962). These showed a variety of unclassifiable behaviours including loops, spirals, passive and power dives and dives that resulted in the moth reaching the ground and hiding. Ferro (1990) reports that dives and lateral turns occurred more frequently than spirals and vertical drops. Studies by Miller & Olesen (1979), and Miller (1984) on Lacewing evasive flight manoeuvres show how much useful information can be extracted from carefully controlled free flight experiments.

The direct influence on flight of auditory input from the A1 and A2 cells remains almost entirely unknown. Madsen & Miller (1987) and Miller & Madsen (1988) found that auditory input sufficient to excite both the A1 and A2 cells could augment the synaptic drive from the flight pattern generator causing the motor neurons supplying the dorsal longitudinal muscles to fire twice per cycle. The same sensory input could also inhibit spiking in the same motor neurones while the rhythmic drive from the pattern generator remained. A similar mechanism is proposed by Olesen & Miller (1979) to explain the diving behaviour of lacewings in response to ultrasound. They propose that the pattern generator is not affected by auditory input, but that the motor neurons supplying the flight muscles become uncoupled. In noctuids the variability in motor neurone response to the same stimulus could be responsible for what Roeder called the ‘evitability of behaviour’ (Roeder, 1975). Given that a stereotyped escape behaviour could be quickly learned by a predator, an unpredictable or ‘evitable’ behaviour could potentially have a greater survival value. This is predicted to be the functional significance of the highly variable escape manoeuvres witnessed when noctuid moths escape from foraging bats.

CALL PARAMETER SHIFTS BY BATS

It is possible to isolate four main parameters of the echolocation calls which are of interest. There is some evidence that each of these parameters has an effect on the way noctuid moths utilise the information as cues to initiate defensive behaviour. The parameters are :
i. Predominant call frequency.
ii. Call intensity.
iii. Call duration.
iv. Pulse repetition rate.

Predominant Call Frequency

Novick (1977) was the first to suggest that a bat might reduce its acoustic apparency by calling at frequencies above or below the moth’s most sensitive region. Fenton & Fullard (1979) described the detection distances theoretically possible using various frequencies either around the moth’s best frequency (syntonic), or outside it (allotonic). They found that for a typical nearctic moth, a bat could reduce its detection distance by up to 92 % by shifting its echolocation peak frequency from 30 kHz to 100 kHz (Fullard, 1987). While a higher frequency of call has increased spatial resolution, it has reduced range due to increased atmospheric attenuation (Griffin, 1971), doubly important since the bat has to receive an echo of the pulse. Lower frequencies, while being attenuated less, provide less spatial information as the acoustic reflectance of the target decreases rapidly as the wavelength of the sound becomes larger than the dimensions of the target (Pye, 1980 ; 1983). Jones (1992) found that there was a positive correlation between the peak frequency used by CF bats and the percentage of moths found in the diet. One of the possibilities is that moth hearing has been the selective drive in the evolution of higher echolocation call frequencies in Rhinolophid and Hipposiderid bats. Waters & Jones (1996) also found that higher call frequencies made bats less apparent to tympanate moths, although the longer durations of CF calls tended to counteract this effect (see below). The sharp tuning of moths to a best frequency in the range 20-40 kHz also opens up the possibility of using lower frequencies to avoid being detected. This seems to be a strategy used by *Tadarida teniotis* (Rydell & Arlettaz, 1994) and *Euderma maculatum* (Fullard & Dawson, 1997).

Call intensity

By reducing the emitted intensity of its echolocation call, a bat may reduce the distance that it becomes detected by the moth. Fullard (1987) calculates that a reduction of the pulse intensity from 100 dB SPL to 70 dB SPL at 10 cm from the bat’s mouth would result in a 90 % reduction in detection distance of the bat by the moth. This effect must be considered in the context of the moth receiving only the emitted pulse, while the bat has to receive the reflected pulse. The combined effect of the two factors of high frequency and low intensity have a complicated interplay when assessed in terms of atmospheric attenuation and reflective scattering, with implications for which party of the interaction detects the other first (Surlykke, 1988). Waters & Jones (1995) found that most bats call with intensities at 85-90 dB peSPL at 1 m, but that some moth specialists, such as *Plecotus auritus* use calls much lower in intensity at 68-77 dB peSPL. This allows them to avoid detection until much closer to their tympanate prey, although necessitating much larger ears to detect the quieter echos.

Call Duration

Adams (1971) has shown that the effectiveness of an ultrasound pulse in stimulating the sensory cells of the moth ear is dependent on the integral of stimulus power over the stimulus duration. What this essentially means is that the moth ear is less sensitive to short duration pulses than long duration ones when the amplitude is held constant. At the other end of the scale, long duration pulses may also be less apparent. This is due to the limited integration time of moths [c. 20 ms (Surlykke, 1988)] compared to 200 ms in most mammals (Dooling, 1980). Thus, a bat emitting a long constant frequency call should be able to integrate the total energy received from the echo. Since the response for a moth at durations of call longer than 20 ms depends only on the amplitude of the signal, the bat could gain an advantage by reducing the amplitude of its call but increasing the duration keeping the total emitted energy constant. Jones & Waters (2000) found that manipulating the duration of calls broadcast to moths could increase or reduce their apparency. Doubling the duration of a call meant that the moth could detect the call when it was 3 dB lower in amplitude than the unmanipulated call. This predicts that bats using short duration calls should be less detectable to moths. The duration effect counteracts the frequency effect for bats such as *Rhinolophus ferrumequinum*, which while using a high frequency call, also uses a long duration CF call, making it no more of less apparent than a normal FM bat.

Pulse Repetition Rate

Fullard (1984b) has reported that the tympanate arctiid moth, *Cycnia tenera* shows a maximal behavioural response to ultrasonic pulses when delivered at repetition rates of 30-50 Hz, typically emitted by bats during the early part of the terminal feeding buzz. At lower or higher rates the responsiveness is reduced. This indicates that the feeding buzz may have a function in initiating defense responses. This may serve to identify bats which are in their approach phase from bats in their search phase, or to differentiate bat calls from random noise in the environment. The encoding of information on pulse repetition rate appears to be regulated within the central nervous system (Boyan & Fullard, 1986, 1988).

CONCLUSIONS

It is clear that the auditory systems of insects have had a great influence on the design of bat echolocation calls. The calls of bats however have many other constraints that affect their overall design, and teasing out those which are due to insect auditory systems has been a difficult task. It is clear that bats which use high frequency, short duration, quiet calls should be more successful at capturing tympanate insects. Yet these call types have a large influence on bats flight behaviour, wing morphology and foraging habitat. Similarly, we would expect moths to have auditory systems adapted to the calls of bats which predate them most, and this is clearly not the case. One of the reasons for this is the bioacoustical limitations of building a receptor which is sensitive to low sound intensities and high frequencies. In addition, since bats using lower frequencies should not be able to detect smaller moths, it should be the case that larger moths will have auditory systems tuned to the lower frequencies of the bats that can detect them. This does seem to be the case (Surlykke & Filskov 1999), but of course pulls moths in the opposite direction from detecting bats which have high frequency calls.

The interactions between echolocating bats and tympanate insects is a fantastic system through which to view the evolution of a predator-prey system, and has by no means given up all its secrets yet.

RESUME

Interactions entre les chauves-souris et leurs insectes proies. Cet article décrit les relations acoustiques complexes entre prédateurs et proies.

De nombreuses espèces d’insectes disposent d’organes auditifs fonctionnels sensibles aux ultrasons. Les signaux émis en hautes fréquences provoquent diverses réactions chez ces insectes. On considère généralement qu’il s’agit d’un mécanisme de défense contre les chauves-souris insectivores qui utilisent des émissions ultrasonores. D’autres insectes peuvent émettre des « clics » en réponse à des écholocations de chiroptères, susceptibles de leurrer leur sonar. En prenant en compte les ordres d’insectes présentant cette stratégie de défense, on peut estimer que 50 % des lépidoptères hétérocères européens ont la capacité d’échapper aux chauves-souris.

Les insectes fournissent une importante source d’alimentation pour les chiroptères. Cela implique que les chauves-souris aient développé des méthodes de chasse pouvant surpasser les mécanismes de défense de leurs proies. La structure des écholocations des chauves-souris traduit leurs exigences en matière de résolution spatiale et temporelle liées à la chasse ou aux déplacements dans leurs habitats. Elle se plie par ailleurs aux contraintes physiques de la biologie des chiroptères, notamment en ce qui concerne les interférences du vol battu.

Au sein de la structure des signaux les paramètres de fréquence, d’intensité, de durée et de récurrence peuvent avoir un effet sur les réactions défensives des insectes.

Les capacités acoustiques de certaines familles d’insectes sont étudiées et leurs influences sur l’écholocation des chauves-souris discutées.

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Relationship of *Barbastella barbastellus* (Schreber, 1774) sonar with its habitat and prey

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Abstract. Barbastelles emit several kinds of sonar signal which are linked to behaviour or environmental conditions. The exception is the so-called 'alternation type', which is emitted in different habitats, without any correlated variation.

The diet of Barbastelle consists almost exclusively of small tympanate moths. Other bat species with a similar diet have developed acoustic adaptations against prey escape strategies, such as allotonic frequencies and whispering emissions.

This paper provides support for the hypothesis that Barbastelle sonar, with frequency and intensity alternation, is adapted to counteract the escape reaction of tympanate prey. This adaptation appears successful because Barbastelle's diet is the most specialised amongst European bats.

Key words : *Barbastella barbastellus*, sonar, tympanate moths, prey-predator relationship.

INTRODUCTION

Barbastella barbastellus is a species with wide variations in acoustic emissions (Barataud, 1996, 2002 ; Letard, 1999 ; Tupinier, 1996). This variability is far from unique within European species (Ahlén, 1981 ; Schumm *et al.* 1991 ; Siemers & Schnitzler, 2000 ; Tupinier & Biraud, 1983-84 ; Barataud, 2004). However, Barbastelle is the only European species to emit an alternating FM signal with a frequency shift under very varied flight conditions.

Within Europe, *B. barbastellus* undertakes most of its hunting along vertical and horizontal edges (hedges, woods/forests, forest tracks, canopy) in wooded vegetation (Sierro, 1997 ; Barataud, 1999).

Its hunting technique is the so-called 'aerial hawking strategy'. Its diet is without doubt the most specialised amongst European bat species : depending on the study area, Lepidoptera make up 99 % to 100 % of occurence, representing 73 % to 100 % by volume (Beck, 1995 ; Rydell *et al.*, 1996 ; Vaughan, 1997 ; Sierro & Arlettaz, 1997). Small Lepidoptera, comprising of numerous tympanate moths, seem to be particularly preferred by Barbastelle (Sierro & Arlettaz, 1997).

Can each acoustic type used by Barbastelle be related to the :

- behaviour of the species or an individual ?
- type of habitat frequented ?
- type of prey captured ?

With the aim of providing answers to these questions, this paper describes a study in which each signal type emitted by this species was analysed and correlated to circumstance and habitat.

EQUIPMENT AND METHOD

Numerous Barbastelle individuals were studied under normal flying conditions (hunting, transit) and in several types of habitat, from high 'clutter' to most 'open'. Individuals were fitted with luminescent capsules (Cyalume™) or followed after leaving their roost during their twilight hunting activities. The behaviour of the animal, its environment and its relation to obstacles were noted at the precise moment of sound recording.

Some acoustic sequences from the tympanate moths (Arctiidae) were also recorded.

The data was collected using two heterodyne/time expansion ultrasonic detectors (x10 and x20 ; 3 et 12 s memory) Pettersson D980 (Pettersson Elektronik AB™), and a Sony™ DAT TCD-D7 tape recorder.

Each expanded sequence (x10) has been described using two methods :

- **auditory analysis :**

  1) For each signal the criteria are : duration, frequency range, final frequency, intensity (approximate evaluation by class), energy distribution during the course of the signal (presence and position of any audible energy peak).

  2) For the complete sequence : estimation of any

rhythm or pulse rate variation, correlation between any variation in audible signal structure and the behaviour of the individual (distance to obstacles, etc).

- **computer analysis** (BatSound program, Pettersson Elektronik AB™):

  The criteria taken into account were: duration, frequency bandwidth, end frequency, frequency of maximum energy. Duration was measured on oscillograms; bandwidth and end frequency on spectrograms, using 256, 512 or 1024 points, according to pulse duration, and a Hanning window. Frequency of maximum energy is defined as the frequency with the most energy in the average spectrum. Because of the attenuation of high frequency signals passing through air, the highest intensity individual signals were chosen in order to obtain accurate measurements of bandwidth and duration.

RESULTS

Description of the different signal types used by *B. barbastellus*

• Alternating signals:

This type of emission consists of 2 types of signal, emitted alternatively and regularly (Fig. 1):

- Alt. Type 1 (Fig. 2): short signal (generally 2.2 to 2.5 ms) in a narrow frequency band (13 to 16 kHz); end frequency approximately 27 kHz with a maximum energy around 32 kHz. Medium intensity (in heterodyne, audible up to approx. 30m) and a generally explosive start when heard in time expansion (Barataud, 2002).
- Alt. Type 2 (Fig. 3): medium duration (mainly 3 to 4 ms, up to 6ms in ‘open’, frequency band generally lower than 20 kHz (sometimes the frequency band widens notably when obstacles are present; see also ‘transition signals’); end frequency of about 30 kHz with a maximum energy around 41 kHz. The start is generally progressive. When heard in time expansion, the intensity is weak (Type 1 is always more intense than Type 2 whatever the flight circumstances or the position of the observer with respect to the calling bat), sometimes when an individual moves away Type 2 diminishes to only just audible whereas Type 1 remains quite audible. This high amplitude variation cannot be explained only by frequency differences between the two types, with correlated differences of attenuation in the air.

The silent periods that separate the two types are asymmetric: about 55 to 57 ms between Type 1 and Type 2 and between 59 to 65 ms between Type 2 and Type 1. Very rarely (in a short sequence), Type 2 is not emitted.

• Transition signals (Fig. 4):

This type of signal is derived from Alternating Type 2, where the characteristics are modified under certain

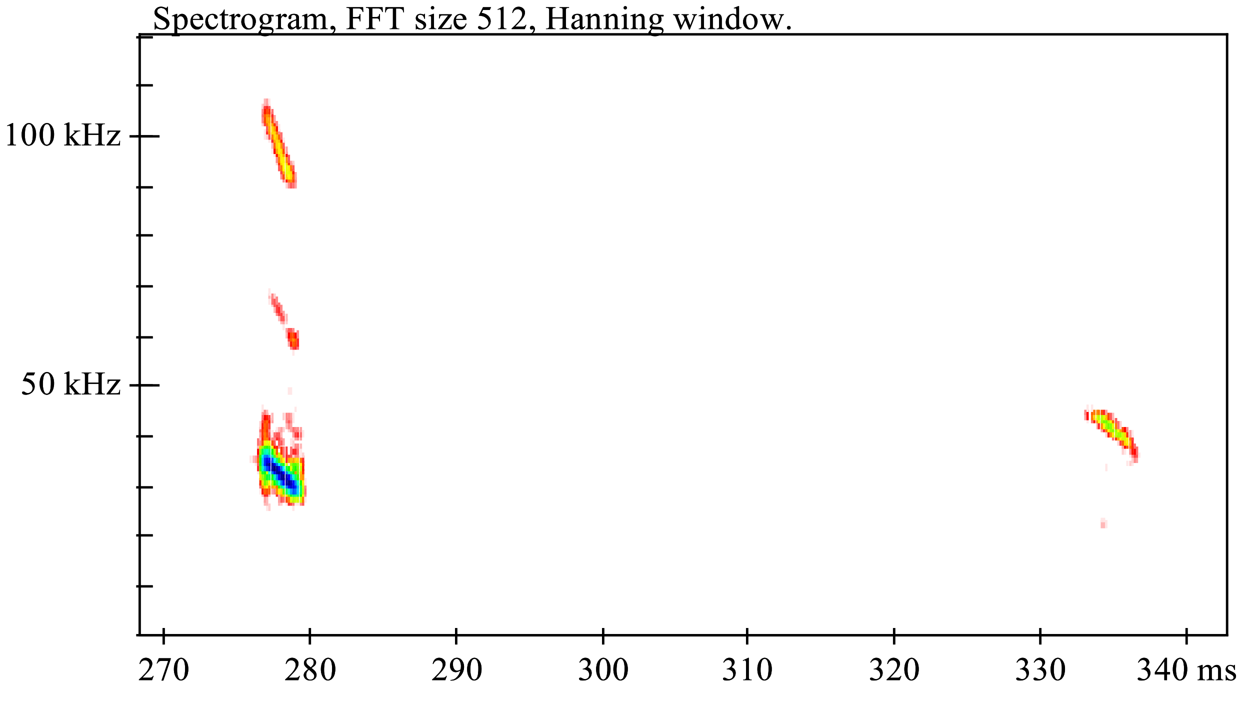
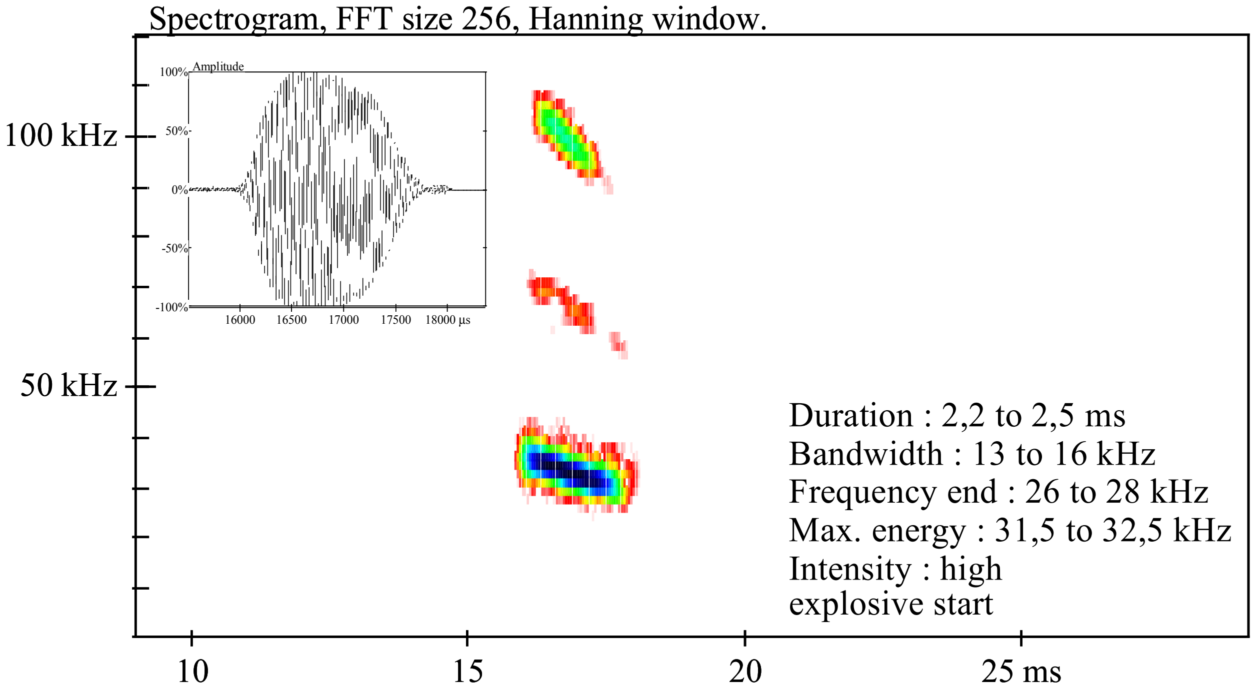
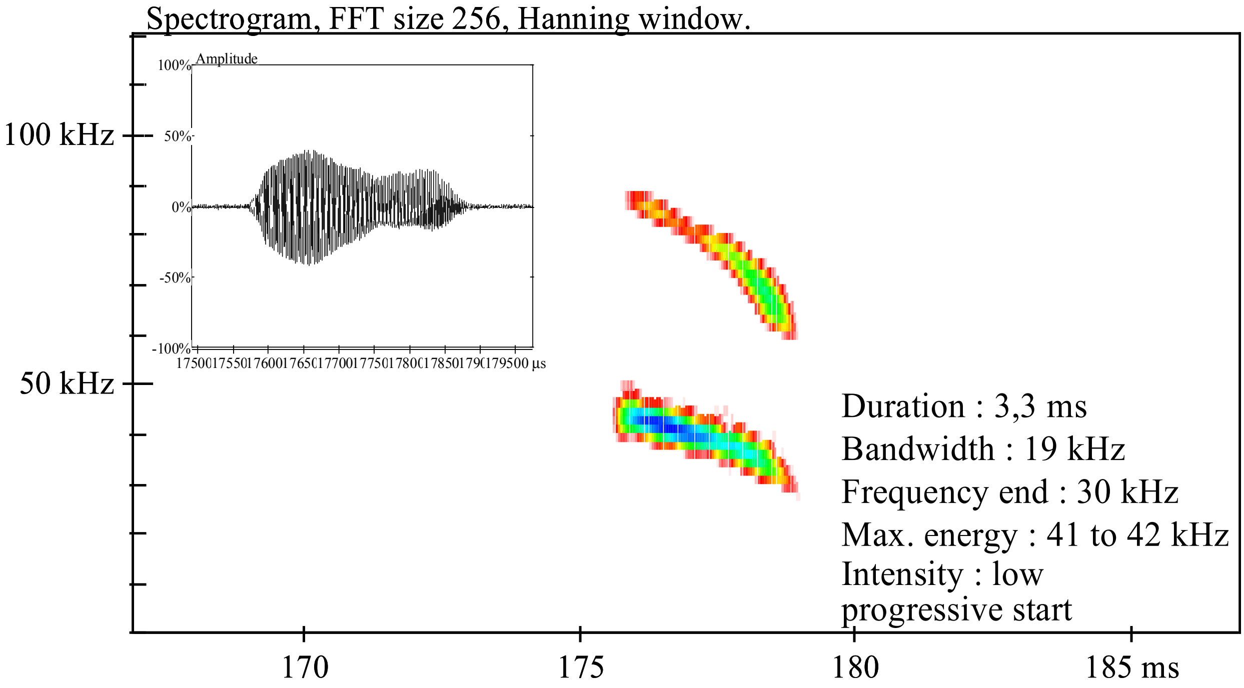


Fig. 1: *B. barbastellus:* “alternating signals”; two type shifted in frequency and intensity.


Spectrogram, FFT size 256, Hanning window.

Duration : 2,2 to 2,5 ms
Bandwidth : 13 to 16 kHz
Frequency end : 26 to 28 kHz
Max. energy : 31,5 to 32,5 kHz
Intensity : high
explosive start

Fig. 2: *B. barbastellus*: Alternating signals: Type 1.


Spectrogram, FFT size 256, Hanning window.

Duration : 3,3 ms
Bandwidth : 19 kHz
Frequency end : 30 kHz
Max. energy : 41 to 42 kHz
Intensity : low
progressive start

Fig. 3: *B. barbastellus*: Alternating signals: Type 2.

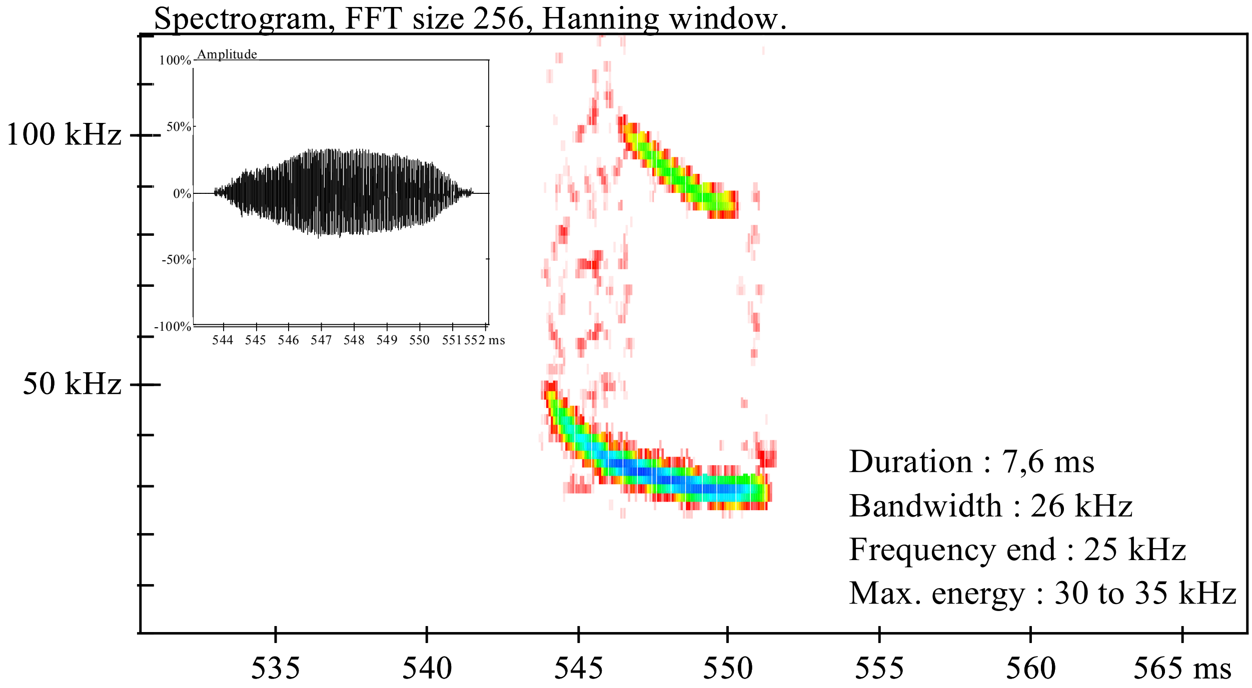


Fig. 4: *B. barbastellus:* “transition signals”; post-capture, pre-approach of obstacles.

circumstances; medium to long duration (7 to 8 ms), frequency band approximately 26kHz, end frequency approximately 25 kHz for a maximum energy between 30 and 35 kHz. Progressive start with no energy peak heard in time expansion.

- Terminal approach (Fig. 5):

Short duration (3 ms approx.), also derived from Alternating Type 2. Medium frequency band (30 kHz approx.); end frequency is around 29 kHz and the maximum energy extends from 35 to 40 kHz. The starts is always progressive, which is the only appreciable difference by ear to signals from the genus *Plecotus* in clutter (Fig. 6). In effect, the measurable parameters are very similar, as is the nasal sound quality (different from that of the genus *Myotis*); nevertheless, for *Plecotus* the start is always explosive.

- Encounter (Fig. 7):

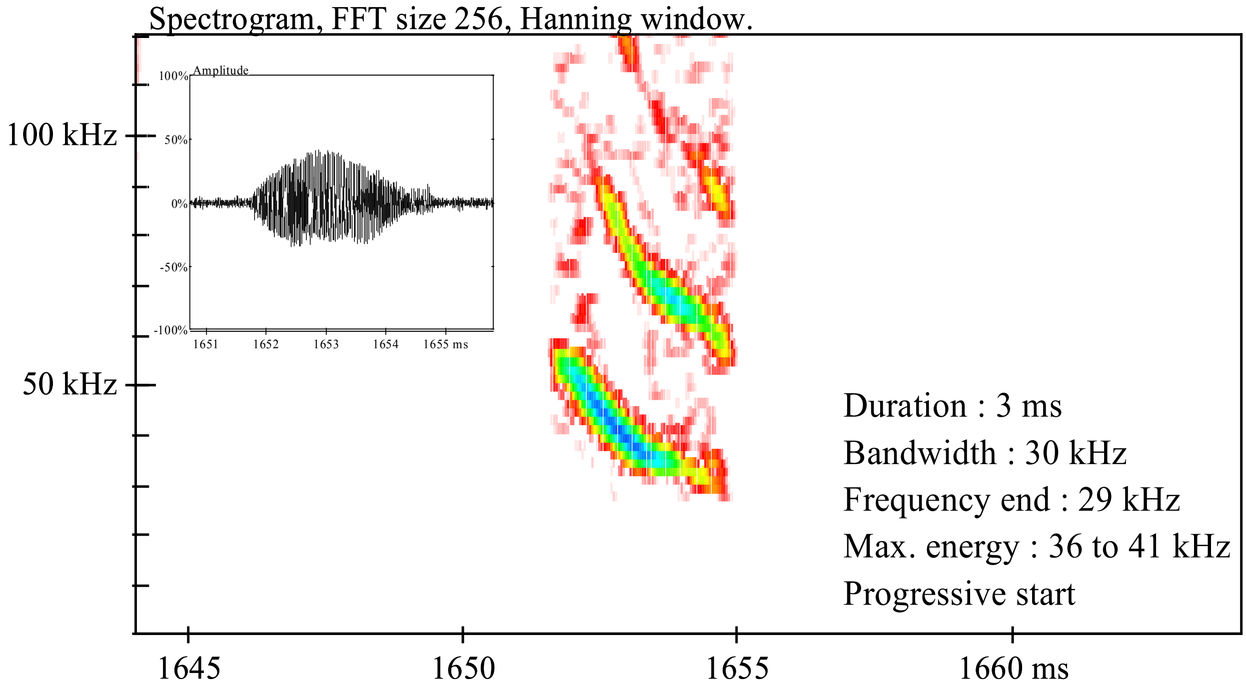
These long signals (6 to 9ms) are emitted in series, with a pulse rate of 20 Hz; one complete series can last up to 3s, with a distinct acceleration of pulse rate (together with a decreasing signal duration) in the last second. The end frequency is low (18 kHz), the frequency bandwidth remains medium (34 kHz) and the maximum energy is at 26 kHz. Energy distribution is very irregular: very weak during the first 2/3rds of the duration, rising rapidly towards the end.

- Territorial behaviour:

This acoustic behaviour comprises of two sorts of calls; echolocation signals and occasional social calls:

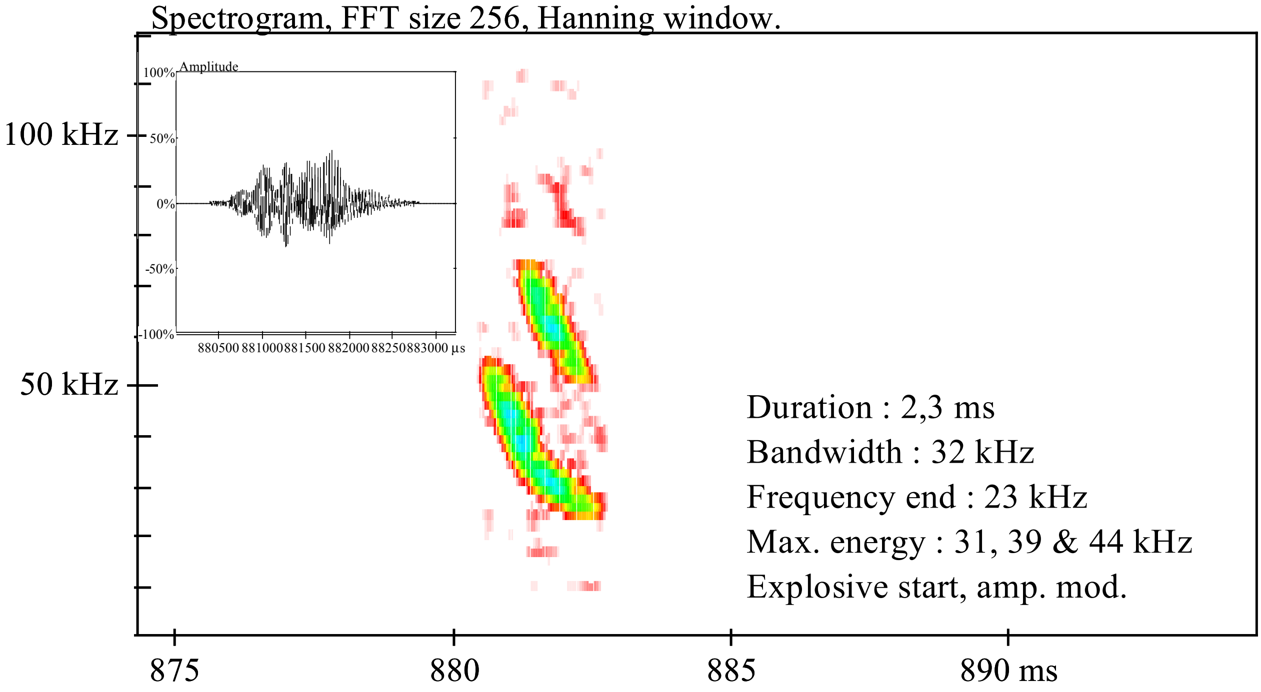
- The sonar signals (Fig. 8) are very different from the other types described above. The duration is approx. 6 to 7 ms, bandwidth approx. 55 kHz, with an end frequency of 18 to 22 kHz and a maximum energy at 34 kHz. These signals are very similar to those used by *M. myotis* in open and semi-open areas (Fig. 9), although the duration is higher for the latter. Differentiation is possible because of the rhythm (irregular for Barbastelle, regular for *M. myotis*), differences in the end frequency from one signal to another and the invariable presence of social calls with *B. barbastellus.*
- Social calls (Fig. 10) consist of two identical tones each with a duration of 11 to 12 ms, silent intervals of approx. 8ms; for an overall time of approx. 30ms. The intensity is high, the frequency band is approx. 30 kHz, the end frequency is 6 kHz and maximum energy occurs at 13kHz. This social call is very similar to that of *Pipistrellus kuhli* (Fig. 11), with two notable differences: *P. kuhli* has a higher end frequency (11 kHz minimum) and a distinctly shorter interval (2.5 ms) between the two tones, compared with approximately 8ms for *B. barbastellus.*

It should be noted that several types of Barbastelle emission are very similar to those used by three other genera (*Plecotus, Myotis, Pipistrellus*) and may be confused. However, the most common *B. barbastellus* type encountered is alternating which is very characteristic and does not overlap with any other European species.



Duration : 3 ms
Bandwidth : 30 kHz
Frequency end : 29 kHz
Max. energy : 36 to 41 kHz
Progressive start

Fig. 5: *B. barbastellus:* "Terminal approach"; approach of obstacles, or cluttered conditions.



Duration : 2,3 ms
Bandwidth : 32 kHz
Frequency end : 23 kHz
Max. energy : 31, 39 & 44 kHz
Explosive start, amp. mod.

Fig. 6: *P. auritus:* signal emitted near foliage (compare with Fig. 5).

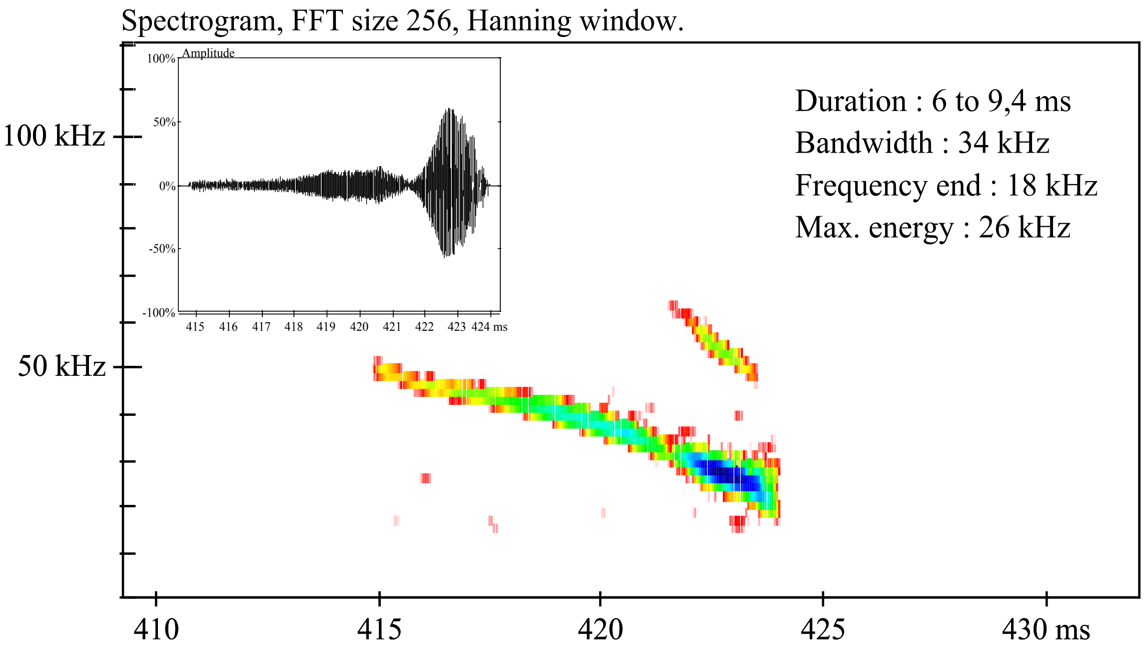


Fig. 7 : *B. barbastellus :* "Encounter signals".

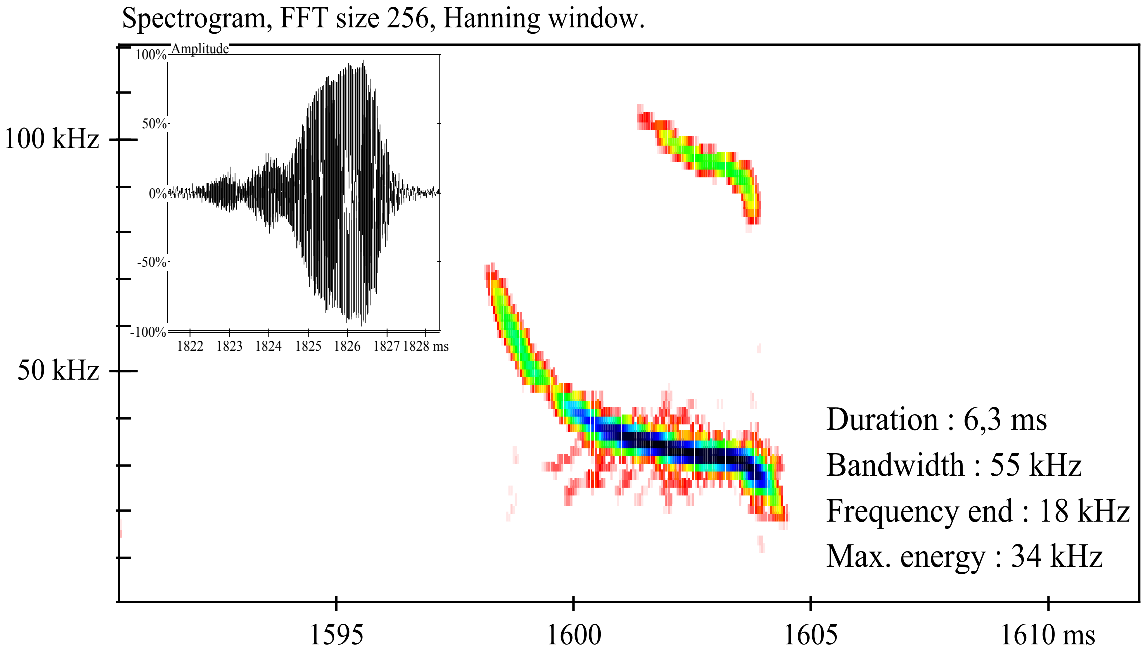


Fig. 8 : *B. barbastellus :* "Territorial behaviour" (associated with social calls, see Fig. 10).

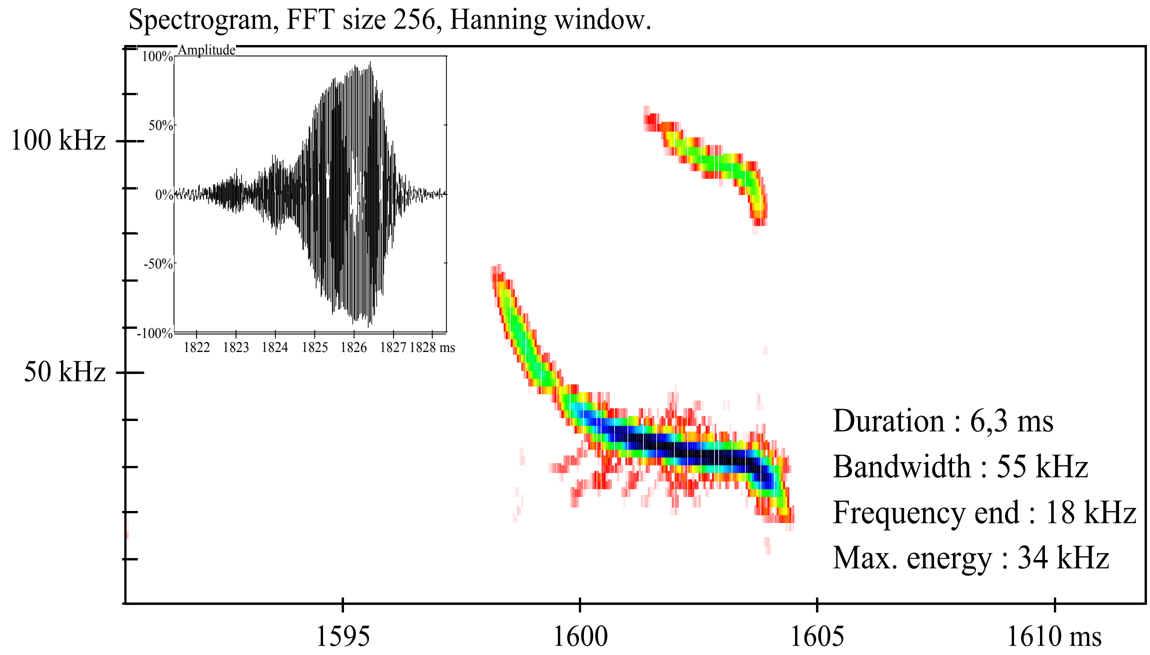


Fig. 9 : *M. myotis :* signal emitted in open (compared with Fig. 8).

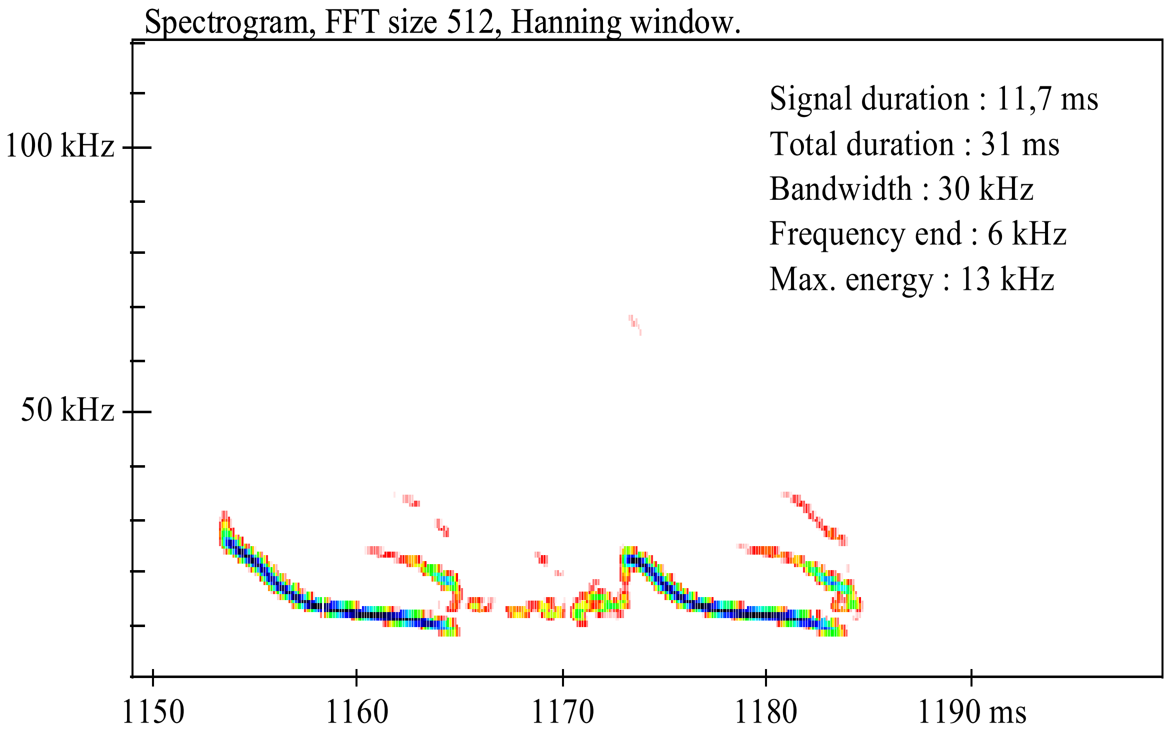


Fig. 10 : *B. barbastellus :* social calls (associated with “territorial signals”, see Fig. 8).

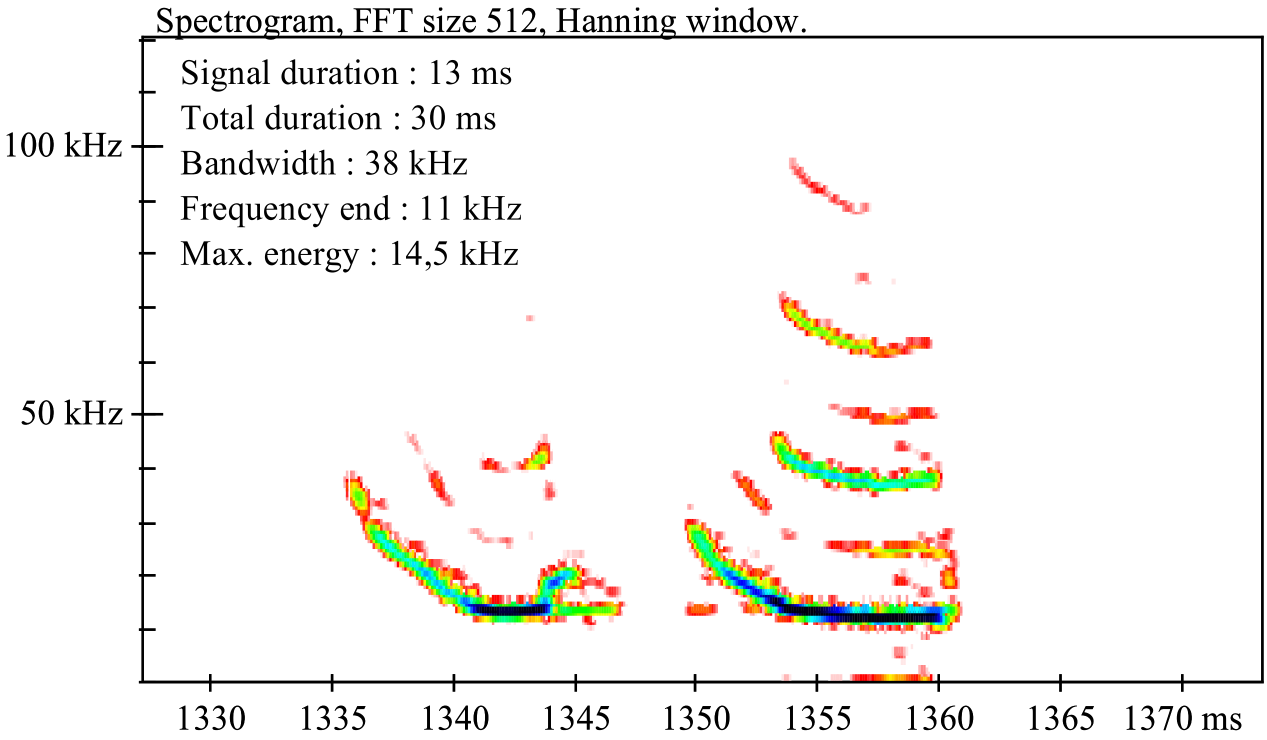


Fig. 11 : *P. kuhli :* social calls (compared with Fig. 10).

Emission circumstances for different signal types

- Alternating signals :

This very characteristic signal is used almost all of the time if the flight axis is not too cluttered (within different hunting environments and whilst in transit). This is why it is picked-up in very open areas (meadows, ponds, more that 20 m from wooded areas) but also along low or high hedgerows, forest edges, forest tracks/rides without overhead cover, covered woodland paths and within thinned plantations. Surprisingly, the signal repetition rate (18 to 20kHz) remains practically the same whether the animal is in an open area or less than 5 m from vegetation.

- Transition signals

This acoustic behaviour is not generally seen except with a very short duration. It is used between prey capture and the progressive return to alternating signals, or in obstacle pre-approach phase (1 to 3 m), excluding prey approach. Certain sequences show the passage between a capture and the type ‘alternating’, or between ‘alternating’ and approach to an obstacle. The transition signals are clearly derived from a Type 2 alternating : a progressive transformation with some signals providing intermediate stages.

- Terminal approach

This signal type is also found in relatively short sequences. It is used, for example, during the final approach to foliage, or when in dense understorey. It always corresponds to an immediate proximity to obstacles.

- Encounter

This signal type appears to be a rare acoustic behaviour, since it has only been found in two (end-of-July and end-of-August) of many hundreds of Barbastelle acoustic sequences. It corresponds to an encounter between two flying individuals and appears to have the characteristics of both a sonar signal (confirmed by the increased signal repetition rate when the bats are close) and a social signal (since it only appears to be emitted when two individuals meet).

- Territorial behaviour :

This association between some sonar signals and social calls has only been heard during May and from end-of-August to end-of-September. It always corresponds to an isolated individual making a routine pass along a line of trees or around a building surrounded by trees (sometimes lit), or likewise around a village square ; in several cases where a day-roost is situated nearby.

The behavioural association, the season and presence of social calls leads to the idea that this is a marking of territory by an individual (male in at least one case).

Concluding these descriptions; the different types of signals emitted by Barbastelle are linked to precise situations and behaviours, except for the alternating signals, which are made in diverse circumstances (transit, hunting) and environments (from open understorey to very open areas).

Comparison between alternating signals of *B. barbastellus* with *N. noctula*

Species of the genus *Nyctalus* also produce calls with alternating frequency and structure.

N. noctula, for example, emits short CF alternating signals at 18 to 20 kHz, and FM with CF tail of medium duration at 22 to 24 kHz (Fig. 14). But this alternation is never particularly regular, it changes in relation to variation in distance to obstacles and the bat's interest in its environment. In effect, when *N. noctula* is in transit, or hunting at high altitude in an area with poor prey numbers, it uses only CF signals (Fig. 12) which serve for finding possible obstacles at long distances. Conversely, when *N. noctula* is less than 10 m from trees or buildings, it emits only FM-CF tail (Fig. 13), increasing the bandwidth and reducing the duration as it approaches.

Its type of emission is therefore always dependent on its behaviour and flight environment, and alternating signals probably represent a compromise between two requirements when in rapid aerial hunting flight: finding possible distant obstacles (CF) and locating closer potential prey (FM-CF tail).

It has been seen that, for *B. barbastellus*, neither the flight environment nor the behaviour influence the evenness of alternation or the repetition rate, and have only a very small effect on structure (weak variation in bandwidth and duration of Type 2 in relation to obstacle distance). Therefore, this type of emission is largely unrelated to flight conditions and its constancy is probably related to another stable element of Barbastelle biology.

Hypothesis of the relationship between *B. barbastellus* alternating signals and its diet

The details of several prey capture sequences have been observed in order to confirm this hypothesis. It now appears that Barbastelle is the only known European species that always passes directly from the cruising phase to the capture phase without using a true approach phase (Fig. 15).

When approaching prey, Barbastelle continues to emit signals with a cruising repetition frequency (18 to 20 kHz). Regular alternation between two types of signals with very different characteristics (intensity, structure and frequency) has the capability of deceiving tympanate

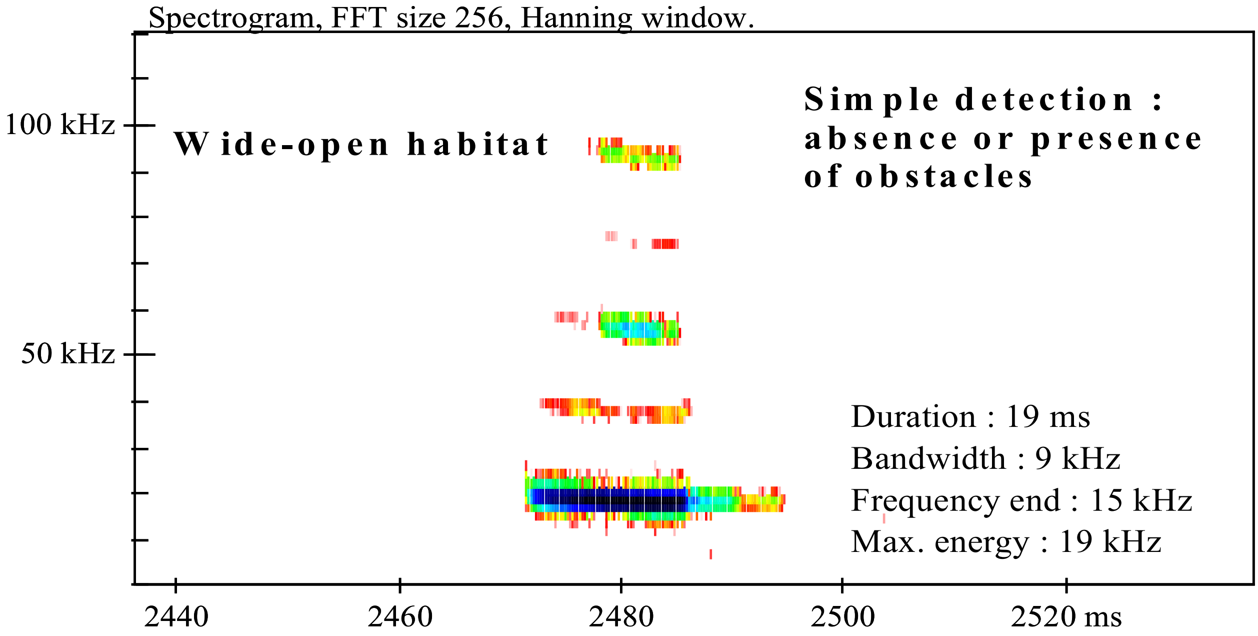


Fig. 12 *N. noctula*: quasi FC signals in open space.

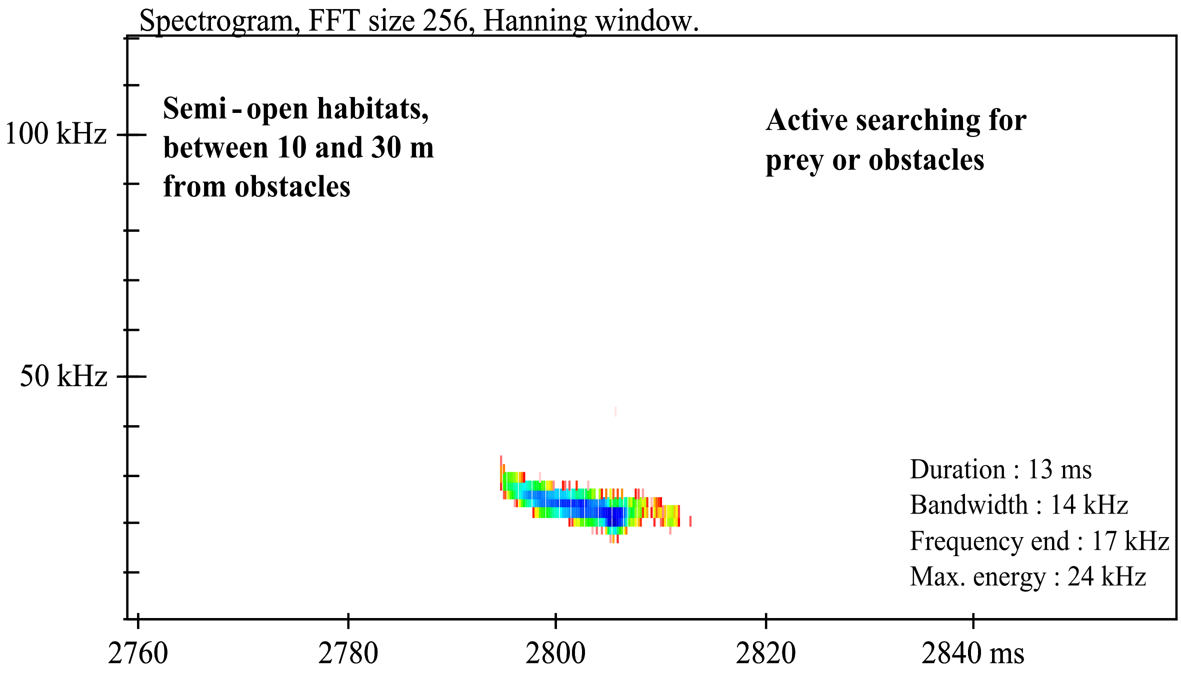


Fig. 13 *N. noctula* : FM/CF signals in semi-open space.

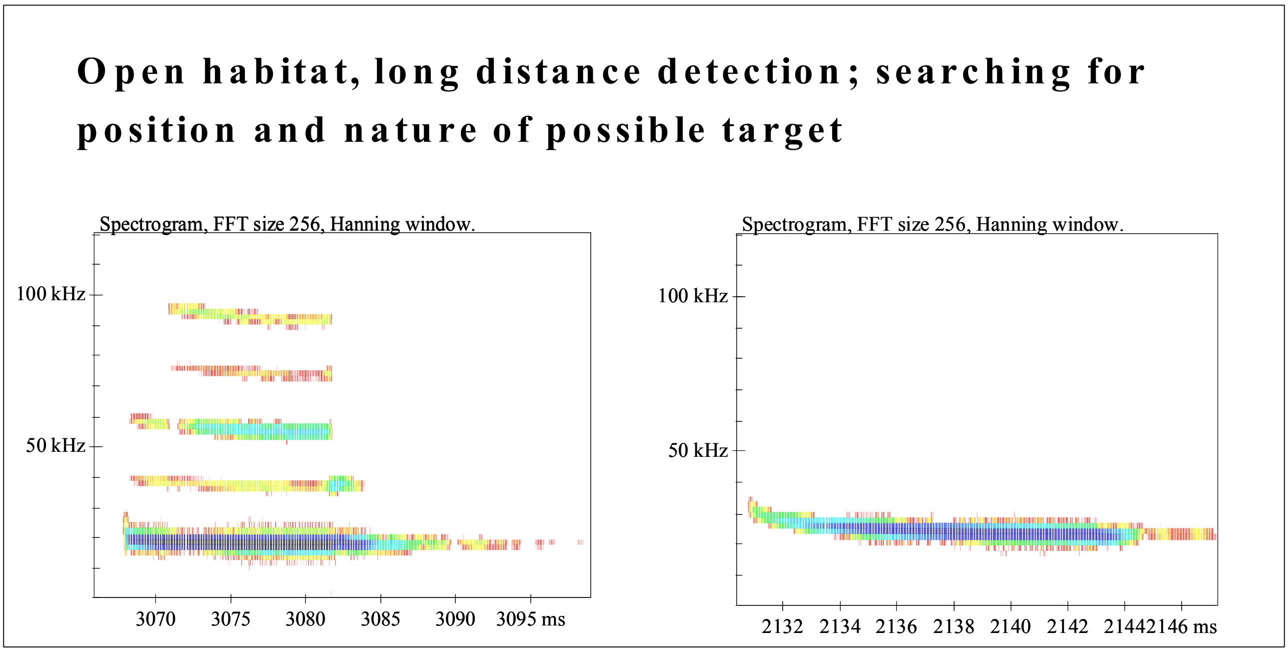


Fig. 14 : *N. noctula* : alternating signals ; hunting in open space.

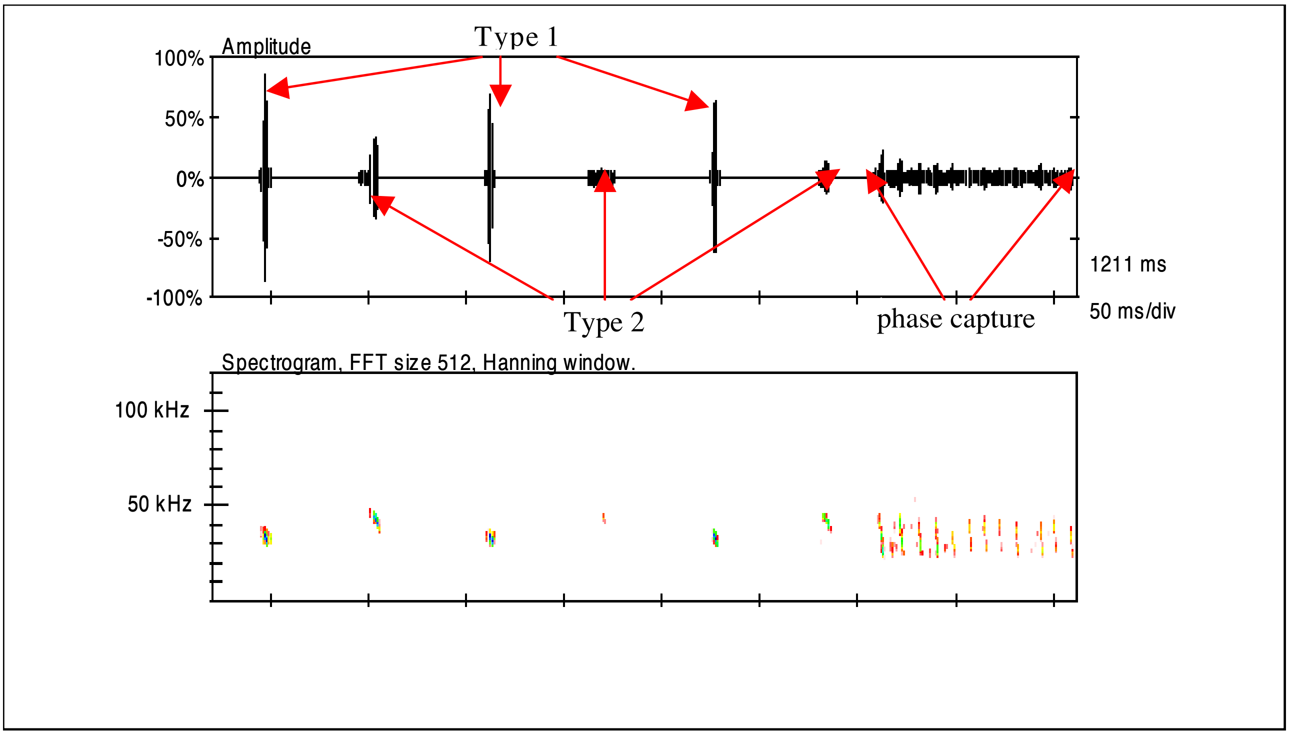


Fig. 15 : *B. barbastellus :* capture sequence of prey ; direct transition cruising phase (alternating signals) – capture phase, without approach phase.

prey. This alternation effectively mimics the presence of two bats at different distances, with sufficiently low repetition rates (9 to 10Hz for each signal type) so as not to provoke the prey's escape reaction.

Example of a tympanate moth emission

The emissions of a tympanate moth (*Setina aurita* – Arctiidae) were recorded in a known Barbastelle hunting area in the French Alps in July 1998.

These are double series of 3 to 6 tones (Fig. 16) generated by the rubbing movement of hardened and toothed parts at the thorax :abdomen junction. The tones in the first series have a duration of 0.4ms, a bandwidth going from 72 to 6 kHz and a maximum energy at 47 to 50 kHz. The tones in the second series last for 0.4ms, a bandwidth going from 86 to 7 kHz and a maximum energy at 55 kHz. An interval of 9 to 13 ms separates the two series. A sequence of two series, lasting from 17 to 22 ms, was repeated at a rhythm of one every 40 to 50 ms, sometimes with pauses of 100 to 130 ms.

DISCUSSION

Within the different Barbastelle acoustic types described herein, the alternation of signals has already been studied by Ahlén (1981) and Denzinger *et al.* (2001) ; the latter have also discussed the signal type termed in this paper 'terminal approach'. Konstantinov & Makarov (1981) have studied the echolocation system with animals held in the hand.

With respect to the descriptions, the results of this current study on alternating signals agrees with those of Ahlén (1981) and Denzinger *et al.* (2001). However, the latter's interpretation is based only on the characteristics of the two signal types, suggesting a better resolution of prey within a background of obstacles. It partly explains the difference in intensity between the two types by possible vertical movements of the animal's head, Type 1 then being emitted more towards the ground than Type 2.

Contacts have been made with Barbastelle hunting lower than or directly on the axis of the detector, the intensity differences between the two types were similar to those obtained in other positions. Therefore, while it is possible that vertical movements of the head play a role, it could prove to be a minor factor within the differences observed. There is a well-defined intensity difference at the emission source, produced by the emitting bat. The amplitude of this difference cannot be fully explained by flight environment factors.

Within Europe, Barbastelle is considered to be an 'edge' dwelling species (Ahlén, 1981 ; Sierro, 1997 ; Barataud, 1999). It mainly frequents forest edges, forest

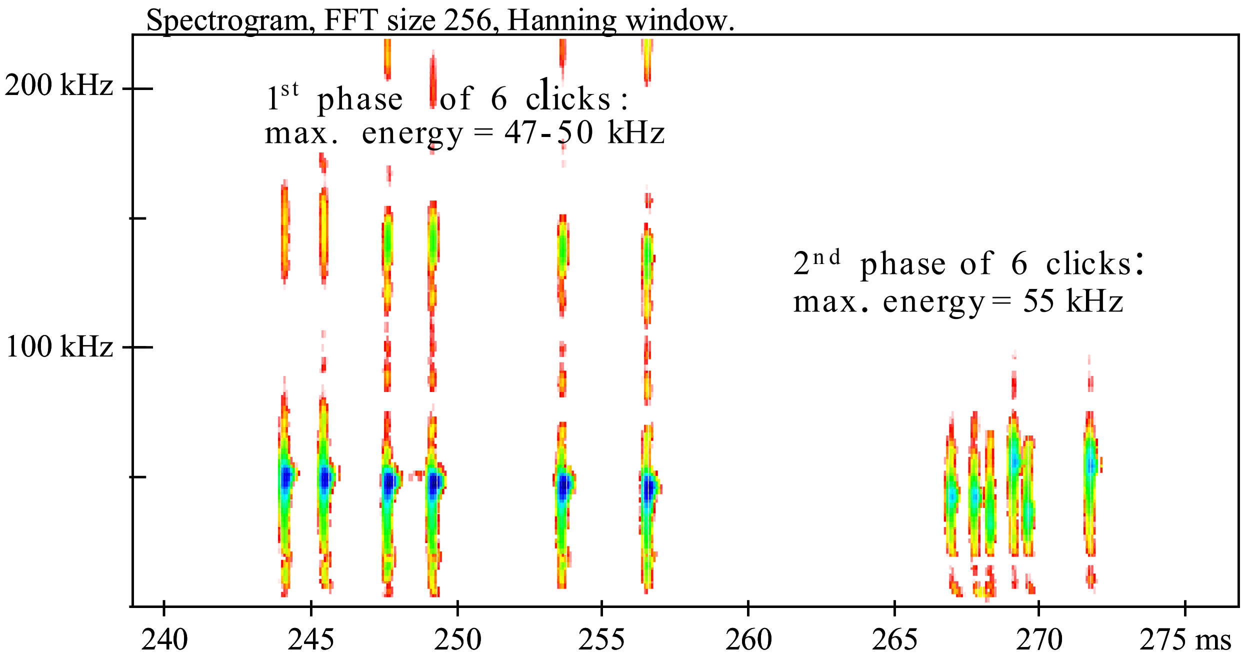


Fig. 16 : signals emitted by the tympanate moth *Setina aurita* - Arctiidae.

roads and tracks and horizontal edges above the canopy. Of the other bat species (*Pipistrellus* sp.*, Eptesicus* sp., *Miniopterus schreibersi*, etc.) which hunt under similar conditions, none emit similar signals.

All of the Barbastelle dietary studies (Beck, 1995 ; Rydell *et al.*, 1996 ; Sierro, 1997 ; Sierro & Arlettaz, 1997) note the major importance of moths (99 to 100 % present ; 73 to 100 % by volume) and in particular small species having a wing span of less than 30 mm (Sierro, 1997). Numerous families, and especially the smaller species of Lepidoptera (e.g. Arctiidae, Noctuidae, Pyralidae, Geometridae, Notodontidae, Sphyngidae, Lymantridae) and Neuroptera (Chrysopidae) have developed tympanate organs and sometimes specific emitter organs in response to their predation by bats. Within the latter group, the capacity to emit sounds is associated with the presence of thoracic glands with a repulsive taste. Bats rapidly learn to associate the unpleasant taste with the signals emitted before capture, and so no longer attempt pursuit. We have noted neththeless that specialized species (e.g. *Plecotus auritus*) by-pass this strategy, and only consume the abdomen of these preys, which is otherwise the most nutritive (Barataud, 1990).

For non-emitting tympanate species, detecting the bat's hunting sequence induces an escape reaction, which increases the survival rate by 40 % on average compared with deafened insects (Roeder, 1967). For bats which consume a large proportion of this type of prey, adaptations that reduce their sonar signals to a level practically inaudible by the insects are known. Species of the genus' *Rhinolophus* (Fenton & Fullard, 1979), et *Tadarida teniotis* (Rydell & Arlettaz, 1994) use allotonic frequency principles, by emitting above and below the frequency sensitivity bands of tympanate insects ; species of the *Plecotus* genus emit at very low intensities or hunt by sight at dusk (Barataud, 1990).

The auditory sensitivity of moths generally increases between 20 and 50 kHz (Pavey & Burwell, 1998). For the relatively larger species, such as *Noctua pronuba* et *Agrotis segetum*, the maximum sensitivity is between 15 and 25 kHz, showing an excellent adaptation to the frequencies used by large bats (*Nyctalus, Eptesicus*) which are their potential predator (Waters & Jones, 1996).

Barbastelle emits within the audible frequency range of its prey. Its adaptation is therefore based on principles other than allotonic frequencies.

According to Waters & Jones (1996), reduced signal intensity is an efficient means for a bat to counteract the defence strategies of tympanate prey. The moths will react to a minimum threshold corresponding to a critical distance between prey and predator. Signals of 2 ms, with an intensity less than 50 dB, can only be spotted by a moth at 10 to 15 cm (Fullard & Fenton, 1980). So Barbastelle uses two types of signals, one weak but the other having a much higher intensity. Its acoustic emissions, therefore, do not correspond completely to this strategy.

These two authors also indicate that decreasing the bats' signal duration lessens the ability of a tympanate prey to analyse the information that it contains. Barbastelle signals are short, especially Type 1 which are the most intense and therefore the most likely to provoke a reaction by the insect. This factor certainly plays a role in the choice of sonar type with respect to prey, but does not fully explain the high dietary specialization of this predator.

Finally, the progressive increase in signal rate, typical of an approach phase, is described by Roeder (1964) as triggering the escape reaction (or the defensive acoustic emissions of emitting moths) in tympanate prey. It is during this approach phase that the moth has the greatest chance of escape, during the capture phase it is already to late (Waters, 1996).

The signal rate of an approach phase for an edge species, such as *Pipistrellus kuhli*, is around 30 to 70 Hz (Waters, 1996). The lack of approach sequence in *B. barbastellus* allows it to approach within a critical distance of the prey. The use of cruising-type signals differentiated by intensity, structure and frequency, and with regular alternation, certainly avoid alerting the prey. Their nervous systems do not react to a signal repetition frequency of 9 kHz (corresponding to the apparently independent pulse rate analysis of the two signal types).

This hypothesis depends on the moth's sensory system being sufficiently advanced to distinguish between the two alternating signal types. It is probable that amongst the differences, intensity plays the most important role, whereas the variation in frequency and duration primarily provide Barbastelle with a better perception of its environment. This is emphasised by Denzinger *et al.* (2001); Type 1 could mainly be used in obstacle detection at medium distances (fairly low frequency, narrow bandwidth and high intensity) and Type 2 for the spatial location of close obstacles (higher frequency, slightly wider bandwidth). Hence, Type 1 represents a compromise between the need to investigate greater distances (higher intensity) and the need to delay as long as possible alerting the prey's sensory system (by minimising the duration). Likewise, Type 2 is a compromise between an intensity great enough to locate obstacles and prey sufficiently early but as low as possible to accentuate the differences with Type 1 signals.

For Barbastelle, the alternation of two signal types and the associated absence of an approach phase, can be shown to be a very sophisticated adaptation for the capture of tympanate prey. This particularly efficient strategy allows a highly specialised diet comprising 70 to 100 % small Lepidoptera, of which many are tympanate.

Outside Europe, other species notably the family Emballonurida also emit alternating signals. *Coleura sechellensis* in the Seychelles alternates two signals, whereas *Cormura brevirostris* in French Guyana uses three signals. It would be interesting to establish whether their diet is similarly specialised on tympanate prey.

ACKNOWLEDGEMENTS

Thanks to Pascal and Sylvie Gosa, and Philippe Jourde who helped in the collection of sequences. Frédéric Leblanc and Philippe Favre for the data on *Cormura brevirostris* and *Coleura sechellensis*. Yves Tupinier for all his advice concerning computer-aided analysis and its interpretation. Bob Hussey and Jo Wilson for the translation of this manuscript into English.

RÉSUMÉ

Relations entre le sonar de la barbastelle et ses habitats et proies. La barbastelle utilise plusieurs types de signaux sonar ou cris sociaux, qui sont liés à son milieu de vol ou son comportement. Seul un type d'émission, appelé « alternance », ne subit pas de variation en rapport avec le contexte environnemental.

Le régime alimentaire de la barbastelle est presque exclusivement constitué de petits lépidoptères, dont beaucoup sont tympanés. Les autres espèces de chiroptères ayant adopté un régime similaire ont développé des adaptations acoustiques contre la stratégie de leurs proies, comme les fréquences « allotoniques » et une très faible intensité d'émissions.

Les résultats présentés supportent l'hypothèse que le sonar de la barbastelle, alternant des signaux décalés en fréquence et en intensité, est parfaitement adapté à un retardement maximal de la réaction de fuite d'une proie tympanée.

Cette adaptation semble très efficace puisque la barbastelle présente le régime alimentaire le plus spécialisé parmi les chiroptères européens.

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Social calls and vocal activity of the brown long-eared bat *Plecotus auritus* in SW Poland

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Abstract. Social calls of the brown long-eared bat *Plecotus auritus* were studied at swarming sites (hibernacula), in the city park and in summer colonies at a church attic in the SW Poland in 1999-2001. The sounds were recorded with Pettersson detector D980 and D240x connected to the SONY Digital Audio Tape-corder TCD D-8. An analysis of about 870 calls resulted in six basic types of *P. auritus* social calls. Most of the signals were performed during songflight display, but some calls were emitted when perched (e.g. on tree trunks or branches, or from rock walls underground). The main signal type was a typical FM call at about 13-15 kHz and call parameters vary from one observation place to another. Bats often performed displays of rhythmic and rapid sequences of two, three or more (up to tens of) single calls one after another ('staccato buzzes'). Another series of sounds consisted of a several specific signals, in which an undulating part is followed by a short falling FM sweep. V-shape signals were emitted while two or more bats are chasing one after another. Most of the social calls were noted at swarming sites in spring (March, April) and in autumn (September, October), but in spring the vocalization was ten times higher and much more diversified. This diversified vocalizations probably play a special role during the mating season of this species during spring and autumn swarming. In the summer colonies bats emitted mainly sequences of several single FM calls when they were emerging from or entering the roost site. These calls differ from the social calls recorded at swarming sites.

Key words: *Plecotus auritus*, social calls, vocalization, vocal activity, swarming, mating period.

INTRODUCTION

Numerous European bat species produce characteristic social calls, often containing lower frequencies than are used in their echolocation calls. Male pipistrelle bats *Pipistrellus pipistrellus* and *P. pygmaeus*, particoloured bat *Vespertilio murinus*, Leisler's bat *Nyctalus leisleri,* Nathusius' pipistrelles *P. nathusii* perform a songflight display where a male flies around its shelter or on their territory on circle or ellipsoid pathways, intensively vocalizing at the same time (Sosnovtzeva, 1974; Ahlen, 1981; 1990; Lundberg & Gerell, 1986; Lundberg, 1989; Weid, 1988; Helversen & Helversen, 1994; Limpens & Roschen, 1995; Barlow & Jones, 1996; Szkudlarek & Paszkiewicz, 2000). Some of them (*Nyctalus leisleri, Pipistrellus nathusii*) additionally produce social calls from specific sites, like a tree or from the openings of their mating roosts, too. Male Noctule bats *Nyctalus noctula* typically vocalize only while sitting at the entrances to their roosts (Ahlen, 1981, 1990; Lundberg, 1989; Weid, 1994; Limpens & Roschen, 1995; Zingg, 1990). For many species signals function in advertisement by males during the mating period (Sosnovtzeva, 1974; Lundberg, 1989; Furmankiewicz, 2003). But often there is not sufficient evidence to establish the functions of all these calls and which sex emits them, since some species of bats are known to produce social calls similar to advertisement sound beyond the mating period (e.g. *Pipistrellus pipistrellus, P. pygmaeus and P. nathusii*) and social calls for Noctule bat female, similar to the advertisement call of male were described (Barlow & Jones, 1997; Helversen, 1989). Hence another function of the vocalization in the mating and pre-mating period is expected. Barlow & Jones (1997) suggest that the social calls of *P. pipistrellus* and *P. pygmaeus* play a rule during the defence of a food patch. But during the mating period the vocalizations are emitted at a higher repetition rate, and could then be important for males to attract females and additionally to repel rival males.

The social vocalization of the brown long-eared bat *Plecotus auritus* was described by several authors, but in most cases they were only typical single FM calls (Ahlen, 1981; 1990; Dzenaevich & Sobolevski, 1988; Limpens & Roschen, 1995; Barataud, 1996; Szkudlarek & Paszkiewicz, 2000). In this paper I distinguish different social calls and attempt to connect these calls with different behaviour and show the differences between three observation places in SW Poland. To develop our knowledge about vocalizations of this species I also describe seasonal changes in vocal activity of brown long-eared bat during autumn and spring swarming. If swarming of bats plays specific mating function, as it is suggested (Fenton, 1969; Thomas *et al.,* 1979; Parsons *et al.,* 2003), the social vocalization in this time should be connected with mating behaviour and therefore should be more diversified and different from vocalization in non-mating places (e. g. maternity roosts, foraging places).

MATERIAL AND METHODS

The study was carried out during 1999-2002 in south-west Poland at three swarming sites of the brown long-eared bat: the city park in Wrocław (called Szczytnicki Park) and two abandoned mining shafts in the Sudetic Mountains – in Stolec and in Gontowa Mount by Sokolec. Szczytnicki Park in Wrocław is situated at 120 m a.s.l. It is the largest park in the city (area about 1 km^2), transformed from an ash-alder forest. A study plot of ca. 0.3 km^2 was established, where the strong vocalization of brown long-eared bat was observed. Recordings were made here at park clearings and in semi-open or closed areas, mostly in conifer plantations. The mine in Stolec is at 367 m a.s.l. It is 500 m long and inside the mine there are big halls and corridors (from 3 to 10 m high). The space in front of the entrance is partly enclosed by young deciduous and coniferous trees and bushes. The recordings were carried out inside the mine, in a big hall of the height of about 10 m and outside, near the entrance. The mine in Gontowa is at 670 m a.s.l. in a spruce forest. It is 750 m long, and 3 m high corridors end with two high halls. Surrounding entrance are spruces trees, with some open spaces. The recordings were made only outside the mine, in front of its opening. Additionally, the social calls of the bats in a maternity roost of *P. auritus* were investigated, in order to compare them to vocalization at swarming sites. The maternity roost is placed in a small village in the Sudetic Mts. (Krajanów), at the church attic, where the sounds were recorded in September 2001 (Fig. 1).

Social calls were recorded by using ultrasonic detectors (Pettersson D 240 x and D 980 models) connected to a digital audio tape recorder (SONY™ TCD-D 100 model). The microphones of these detectors probably have different frequency responses, so will give different frequency representations of the same call. But there was no bias in which equipment was used at which site, so any between site differences in frequency are not caused by different detectors. In order to describe the social calls, the time expansion system was used and the calls were recorded in early spring (from the middle of March to the middle of April) from 1999 to 2002 at the swarming sites, and in September 2001 in the maternity roost.

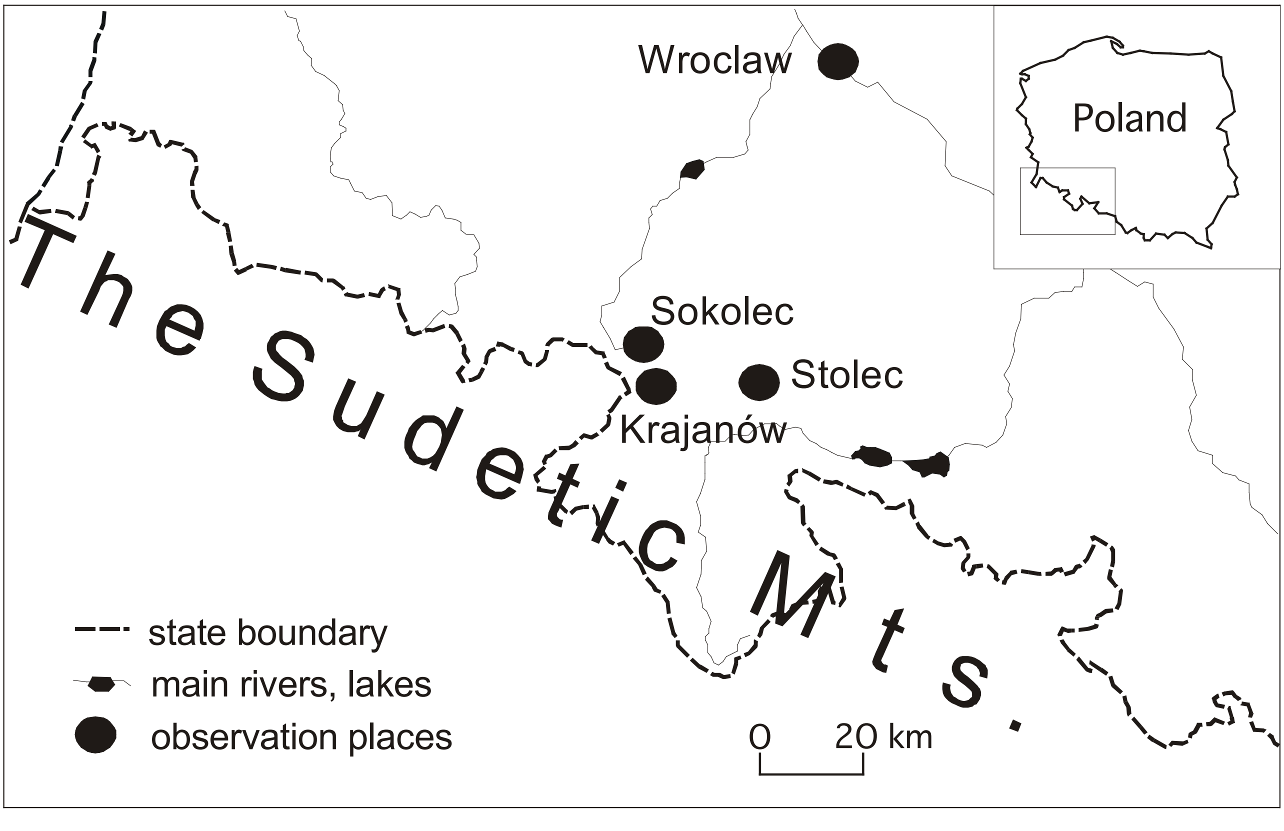

Fig. 1: Study area with marked observation places: Szczytnicki Park in Wrocław, mine in Stolec, mine in Gontowa Mount by Sokolec, Krajanów.

Additionally, the behaviour during the performance of different calls was observed. The following parameters of sounds were measured: pulse length in ms, pulse interval in ms, peaks of maximal sound pressure in the power spectrum in kHz, minimum and maximum frequency in kHz (frequency range) for fundamental sweep, number of harmonics and repetition rate (pulses per second). The majority of signals had two or three peaks of energy in the power spectrum, so all of them were measured and presented in the order of appearance (peak 1, 2 and 3). This order was followed because of switching the peaks between particular signals from the first – highest to the second or third – highest, which could be caused by the angle between the bats and the microphone during recording (Waters, 2001).

In order to determine the vocal activity of bats, a heterodyne system was used and observations were conducted once a week, from 1st March to 30th April and from 15th August to 30th October in 2000-2001. Recordings near the mines were carried out from sunset to sunrise, every hour, for 15 minutes during the whole night, inside and outside the mine in Stolec (15 min inside and 15 min outside it) and at the mine in Gontowa (only on the outside, near the entrance). In Szczytnicki Park, three 30-min transects were performed: first at sunset, and then two and four hours after sunset. The number and types of calls were used to measure vocal activity and the mean number of calls per hour or per night was calculated.

Sound analysis was done with the computer program Cool Edit Pro version 1.2a (Johnston, 2000). The value of frequency peaks in power spectrum was measured in a Blackman-Harris window with FFT size 2048. This window has a broad frequency band but low sidelobes, which makes it easier to pick out the major frequency component and the high FFT size gives more accurate results in establishing frequency. The figures of power spectra are taken from Cool Edit (Blackman-Harris 1024 window) and the spectrograms were made in BatSound 1.2 (Pettersson Elektronik, Uppsala, Sweden).

RESULTS

1. Description of social calls of brown long-eared bat *Plecotus auritus*

The brown long-eared bat emitted social calls at swarming sites (hibernacual and city park) and in the maternity roost. At swarming sites the social calls were produced during songflight display, performed from several up to a dozen or so meters above the ground, and when the bats were perched from one site on a rock wall, tree trunk or on a tree branch. In the maternity roost specific social calls were emitted inside the church attic, when the bats were leaving and entering the roost at night or dawn. In order to describe different social calls of *P. auritus* 871 time expanded signals were analised. Five basic types of calls at swarming sites (1-5) and one type in maternity roost were distinguished (6): 1) single calls, 2) double calls, 3) long and rapid series of single calls, 4) V-shape calls, 5) undulating calls, 6) series of single calls. Sound parameters are given in Table 1.

1.1. Single calls recorded at swarming sites

Single calls were emitted during flight, from several up to a dozen or so meters above the ground, and when the bat was sitting on a rock wall, tree trunk or on a tree branch. During flight, bats often seemed to perform a songflight display, flying along a circular or ellipsoid pathway, or on straight flights. They emitted frequency modulated calls (FM), ending with a short narrowband part (Fig. 2), sweeping from about 65 kHz to 5.5 kHz and heard as strong smacks. The maximum number of harmonics was 5. Single calls recorded at the different swarming sites differ significantly one from another in particular parameters (Tab.1 and 2). The shortest calls were recorded inside the mine in Stolec, and the longest in Szczytnicki Park and at the mine in Gontowa (Tab. 1, Fig. 4). The length of 60-70% of calls recorded in flight outside the mine in Stolec, Gontowa and in Szczytnicki Park were between 7-9 ms (Fig. 4 B, C, E). The highest frequencies for peaks in the power spectrum were noted for the sounds from Szczytnicki Park.

Single calls recorded at the mine in Stolec

The calls were emitted inside and outside the mine, near the entrance. Sometimes two individuals were heard simultaneously. The vocalizing bats seemed to appear rapidly at the mining shaft and afterwards disappeared, probably in the mine. Underground, they emitted single calls from one site too, sitting high (up to several meters) on rock walls. Only sounds in flight were analysed, because the sample size of calls emitted when resting was too small. The fundamental sweeps between about 65 kHz to 7 kHz (Tab. 1). Most of the calls show the first peak in the power spectrum, on average at 14-15 kHz. About 80-88 % of calls have the second peak at about 20-21 kHz, and 30-45 % the third peak at about 23 kHz (Tab. 1, Fig. 2 B, C). The first peak was the highest for about 45 % calls and the second was the highest for the next 40 %. The signals had generally two or three harmonics (Tab. 1). The calls emitted outside the mine were on average longer (about 7.4 ms long) in comparison to the underground calls (6.5 ms long). They had the first and second peak of a slightly higher frequency and were emitted at a higher and more regular repetition rate – about 5.6 pulses per second outside, to 5.0 pulses per second inside the mine (Tab.1, Fig. 4-5 A-B). These differences are statistically significant (Tab. 2). Generally the calls from Stolec differ from the sounds recorded at other places (Tab. 2).

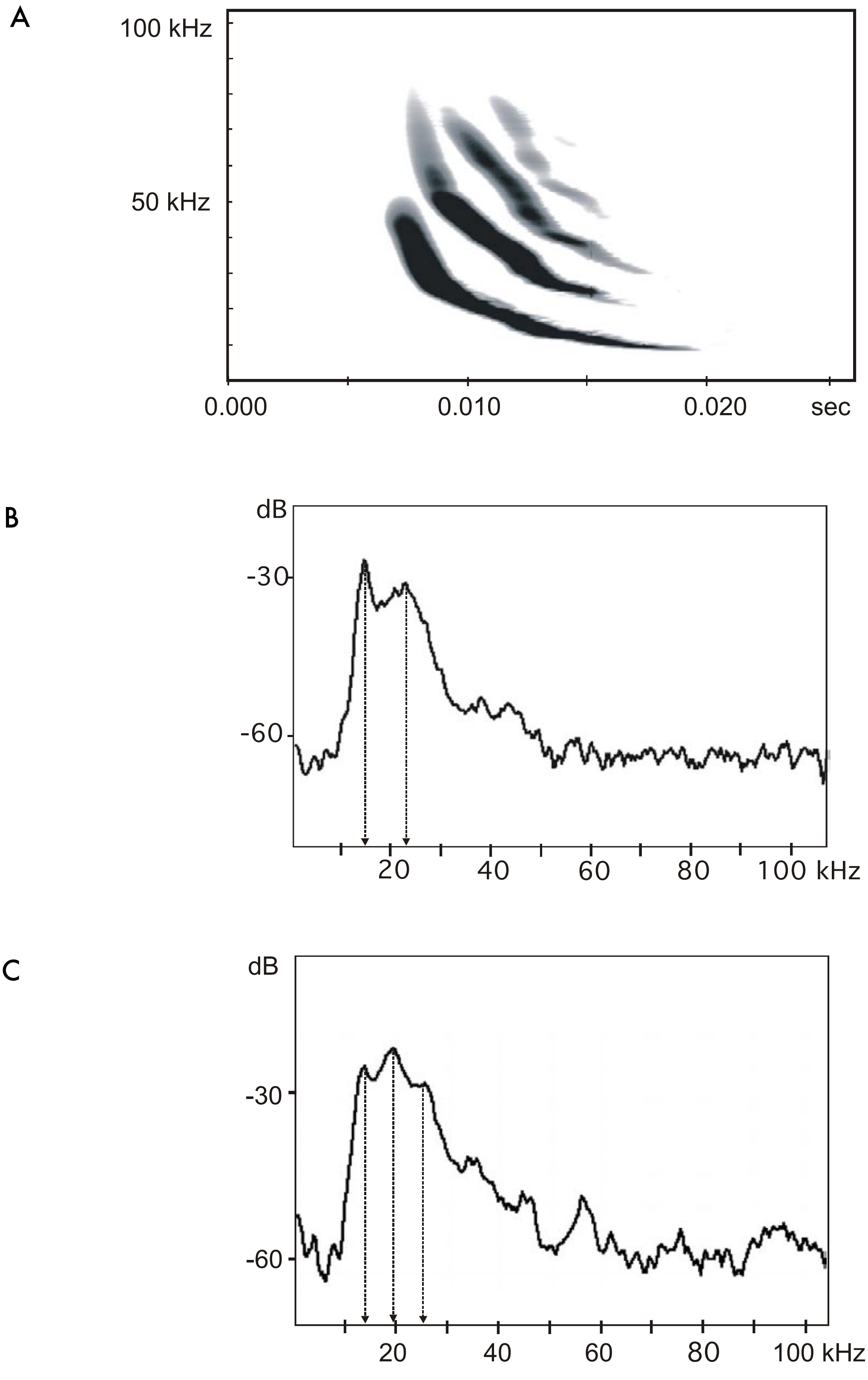

Fig. 2: Single social call of *Plecotus auritus* emitted during songflight display: A. spectrogram (call recorded in the Szczytnicki Park in spring), B, C. two examples of the power spectrum with two and three peaks (calls recorded inside the Stolec mine in spring).

Single calls recorded at the mine in Gontowa Mt. by Sokolec

The bats circled to about 50-100 m around the mine and performed calls mostly during songflight displays, within a dozen or so meters in front of the entrance, only sometimes vocalizing from perches. The songflight displays were performed irregularly. No calls were heard inside the mine. The single calls emitted during flights were 8.1 ms long and most of them showed two, sometimes three peaks in power spectrum. The highest peak in the power spectrum fell at about 14 kHz (for 64 % of calls), at 21 kHz (15 %) or at 24 kHz (21 %) (Tab. 1). Most of the pulse intervals were between 270 and 290 ms, so the repetition rate was relatively low – about 3.6 pulses per second (Fig. 5, Tab. 1). The calls differed significantly from those recorded in other observation sites, but the differences were smaller in comparison to signals from Szczytnicki Park (Tab. 2).

Single calls recorded in Szczytnicki Park in Wrocław

The single calls were performed mostly in flight, but also from tree trunks or branches. Bats performing songflight displays were observed yearly in spring in the same places of the park, mostly in the conifer plantations, circling and vocalizing with irregular pauses. Sometimes two chasing and vocalizing individuals were seen. The single calls emitted during songflight were longer than signals when perched from one site (8.3 ms and 6.6 ms, respectively) (Tab. 1 and 2, Fig. 4). Most had two or three peaks of energy (in order of appearance): the first at about 13.7-14.4 kHz, the second at 19.2-22.5 kHz and the third at about 22.6-27.0 kHz, but the highest value characterised the calls in flight (Tab. 1 and 2). For about 60 % of calls the frequency of best listening occurred at the first peak and for about 30 % at second peak. The calls produced from tree trunks or branches were much more regular but of a slower repetition rate (3.1 pulses per second), whereas calls during flights were emitted rather irregularly but with a higher repetition rate (5.3 pulses per second) (Tab. 1 and 2, Fig. 5 C-D). All calls emitted when perched from one site had two harmonics, and calls in flight from 1 to 5 harmonics.

1.2. Series of singles calls emitted in the maternity roost

Single calls in the maternity roost were emitted in short or long series of calls, inside the church attic, when the bats were leaving and entering the roost at night or dawn. Bats of both sexes were present in the roost and the calls were produced by males and females, as well. These series resembled trills or series of soft smacks and consisted of several up to a dozen or so single calls (Fig. 3 A-B), produced about 20 times per second (Tab. 1, Fig. 5 G). The pulses were FM-sweeps running from about 67 kHz to 7.4 kHz in average 9.4 ms (Tab. 1, Fig. 4 G). The last part of signal had a narrowband character. Most of the calls had two peaks in the power spectrum: the first at about 17 kHz and the second at about 23.6 kHz. Only 26 % of signals showed the third peak at about 27 kHz (Tab. 1, Fig. 3 C). The first peak was the highest in 84 % of all signals, and the second had the frequency of best listening for the next 12 %. Only 4 % of calls had the highest peak frequency at about 27 kHz. Often the second and the third and sometimes the fourth harmonic were observed. The signals from the maternity roost are significantly different from the single calls emitted at the swarming sites of the brown long-eared bat (Tab. 1 and 2).

1.3. Double calls at swarming sites

Double signals were emitted during flights and from one site, sometimes inserted between single calls. Sometimes bats emitted triple calls. They consist of two (or three) single calls rapidly following each other with the interval of about 50 ms (Tab. 1). They were recorded mostly in Szczytnicki Park and inside the mine in Stolec. The sounds in Stolec were significantly shorter (about 7.1 ms to 8.2 ms in Szczytnicki Park) and their first peak in power spectrum fell at higher frequencies (15.3 kHz to 13.5 kHz in Szczytnicki Park) (Tab. 1 and 2). This peak was the highest for most the calls. The second peak frequency occurred at about 21-22 kHz, and sometimes the third at about 25-27 kHz (Tab. 1).

1.4. Long and rapid series of single calls at swarming sites

Such calls were observed mostly inside the mine in Stolec during songflight displays, when bats flew trough the mine or when bats were sitting on the rock walls. Sometimes these calls were performed during hovering flights when bats hovered in front of the rock wall. This kind of calls differed significantly from single calls described in part 3.1.1. The single signals in series were longer (Kruskal-Wallis test, $\chi^2=17.9$, $P<0.001$), were emitted faster (Kruskal-Wallis test, $\chi^2=64.8$, $P<0.001$) and the first frequency peak reached higher frequency (Kruskal-Wallis test, $\chi^2=45.0$, $P<0.001$) (Tab. 1, Fig. 5 A, 6 B, D). The single FM signals running from 50 kHz to 9.6 kHz, following rapidly and regularly each other in long series consisting of several up to dozens (about 70-100) of calls, which could last from about 1 sec to about 5 sec (Fig. 6 A). Without detectors the sounds which we perceived resembled a series of distant gunshots or 'staccato buzzes'. The pulse length and interval analysis were made together for all these series (Fig. 6 C, D), as few sequences from hovering bats were recorded. However it seems that there are differences between series performed during these two types of behaviour (Tab. 1). The calls in series in normal straight flight lasted about 6.6 ms and were on average shorter at about 4 ms (Kruskal-Wallis test, $\chi^2=15.4$, $P<0.001$) (Tab. 1), and were emitted much faster, at about 20 pulses per second (Kruskal-Wallis test, $\chi^2=6.1$, $P<0.05$). While hovering, most intervals between pulses lasted for 70 ms and hence

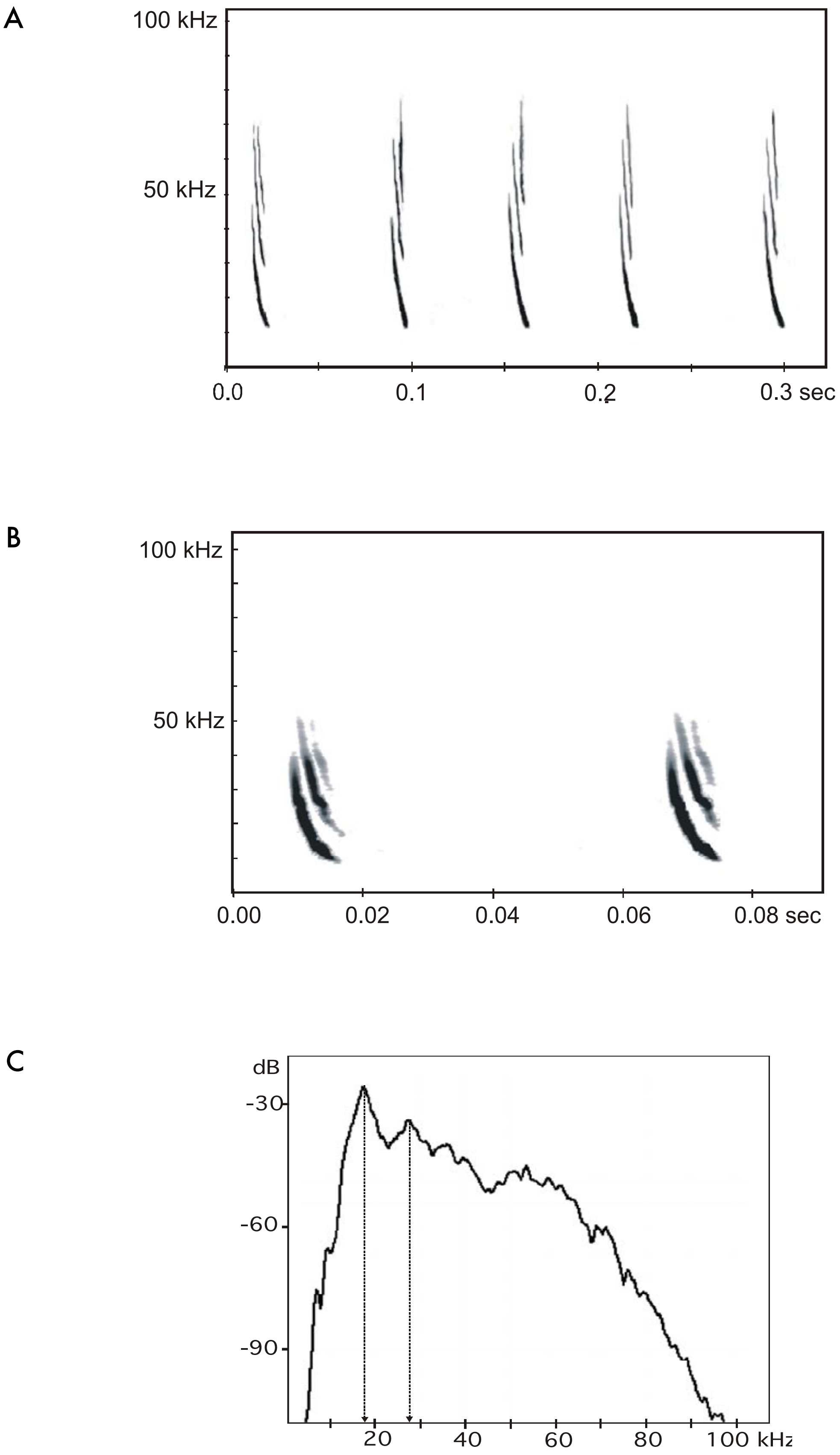

Fig. 3: Single social calls of *Plecotus auritus* recorded in the maternity roost (Krajanów, the Sudetic Mts.): A. spectrogram of series of single calls, B. spectrogram of two calls from series, C. the power spectrum of these calls showing two peaks of energy and a very weak third peak.

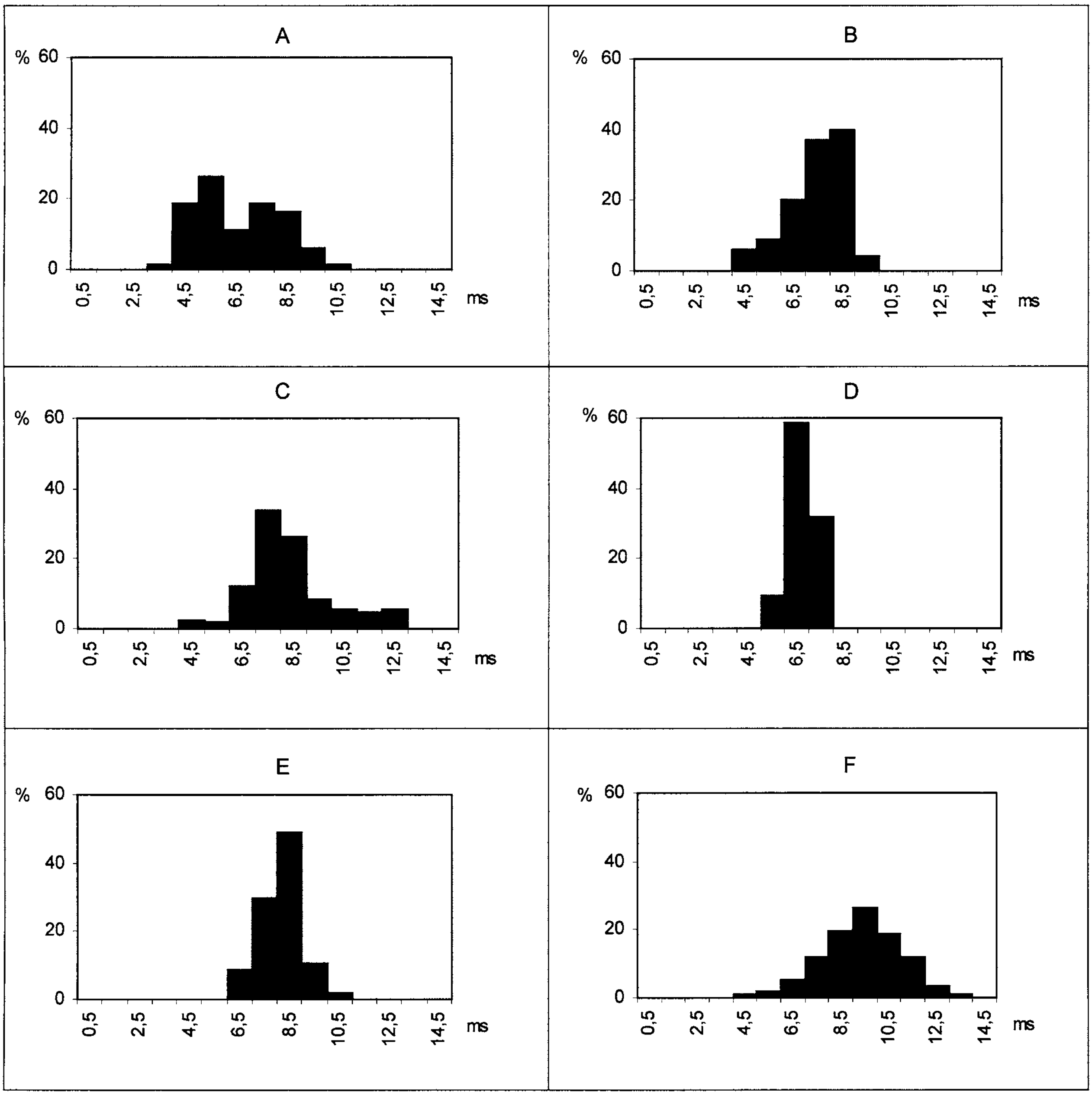

Fig. 4: Pulse length analysis for single calls of *Plecotus auritus* recorded in spring in years 1999-2002: A. in flight inside the mine in Stolec, B. in flight outside the mine in Stolec, C. in flight in the Szczytnicki Park, D. from one site in the Szczytnicki Park, E. in flight outside the mine in Sokolec, F. in flight in the maternity roost (church attic in Krajanów). On X-axis the middle of succeeding sections are marked.

the repetition rate was 14.3 pulses per second (Tab. 1). The first peak of energy in all calls fell at about 16.4-17.0 kHz and for most signals it was the maximal sound pressure. There is no difference in this case between the two types of series. The second peak was produced at about 22.3 kHz in signals in straight flight and at a significantly lower frequency of 19.0 kHz in hovering (Kruskal-Wallis test, $\chi^2=8.9$, $P<0.01$). The third peak fell only sometimes at about 21-25 kHz and was higher in series in straight flight (Kruskal-Wallis test, $\chi^2=5.7$, $P<0.05$) (Fig. 6 B). Two harmonics were observed in calls during hovering and generally one fundamental harmonic in straight flight (Tab. 1).

1.5. V-shape calls at swarming sites

These signals were produce during chases of one or more individuals in a long fast series of several up to dozen or so signals. Most of the calls were recorded underground.

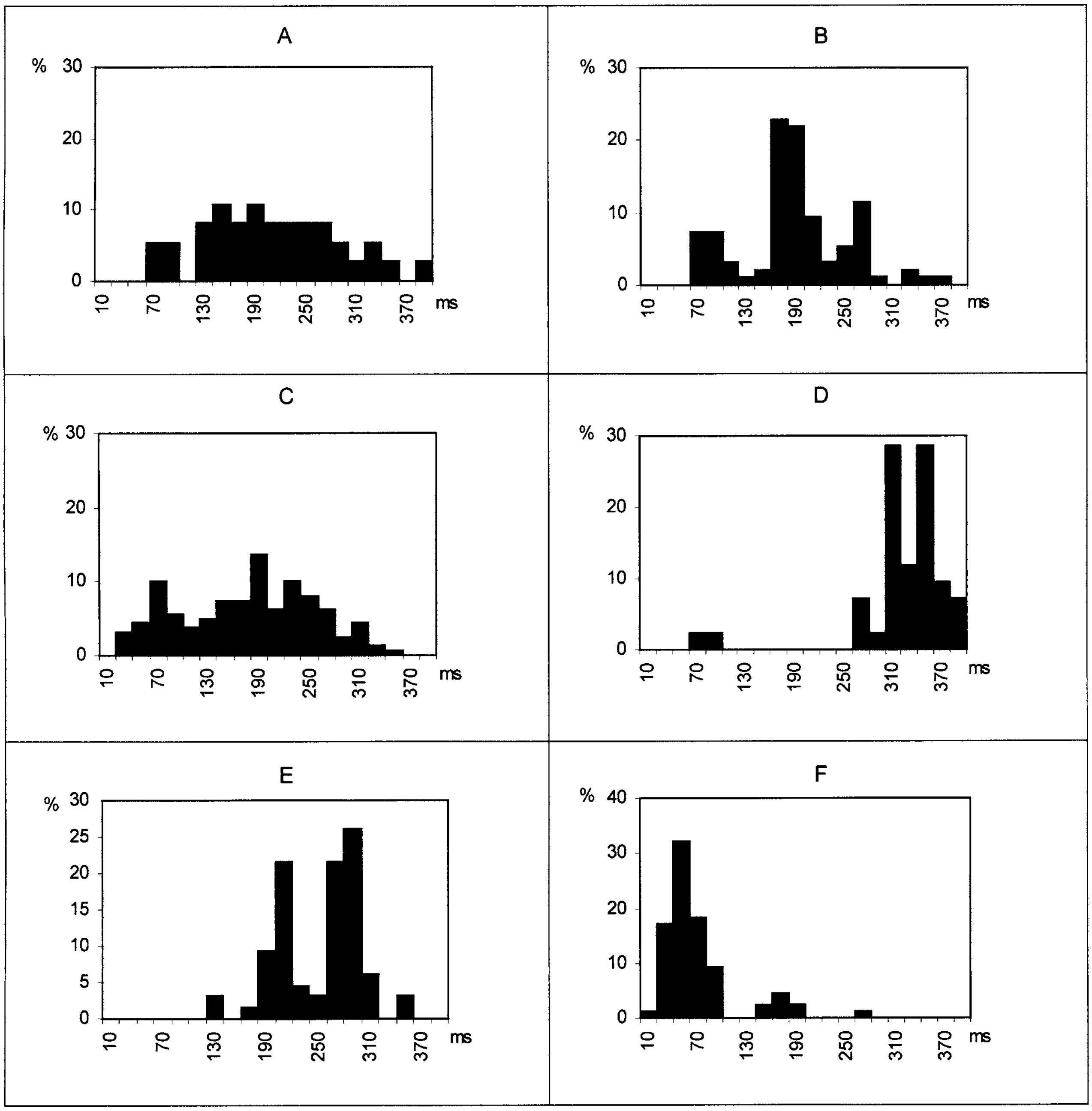

Fig. 5: Pulse interval analysis for single calls of *Plecotus auritus* recorded in spring in years 1999-2002: A. in flight inside the mine in Stolec, B. in flight outside the mine in Stolec, C. in flight in the Szczytnicki Park, D. from one site in the Szczytnicki Park, E. in flight outside the mine in Sokolec, F. in flight in the maternity roost (church attic in Krajanów). On X-axis the middle of succeeding sections are marked.

They resembled long series of whirrs or buzzes. Individual pulses were FM-sweeps only about 3.3 ms long (Table 1, Fig. 7 A, B, D). Calls had a weaker 0.5 ms long "vertical" element just over the main FM-sweep and therefore resembled a letter V. The modulation of the main elements started from maximum 139.5 kHz and swept to 9.6 kHz. Most of the calls showed two or three peaks in the power spectrum. In order of appearance there were: the first peak at about 22 kHz, the second at 37 kHz and the third at 52 kHz (Tab. 1, Fig. 7 C). In most cases the first peak contained most energy. The vertical elements were emitted at higher frequencies, from about 41.3 to 159.6 kHz (minimal and maximal measured values). All V-shape calls had only one fundamental harmonic. The mean inter-pulse interval was 43.4 ms, but most of the intervals had a peak at 30-50 ms, which

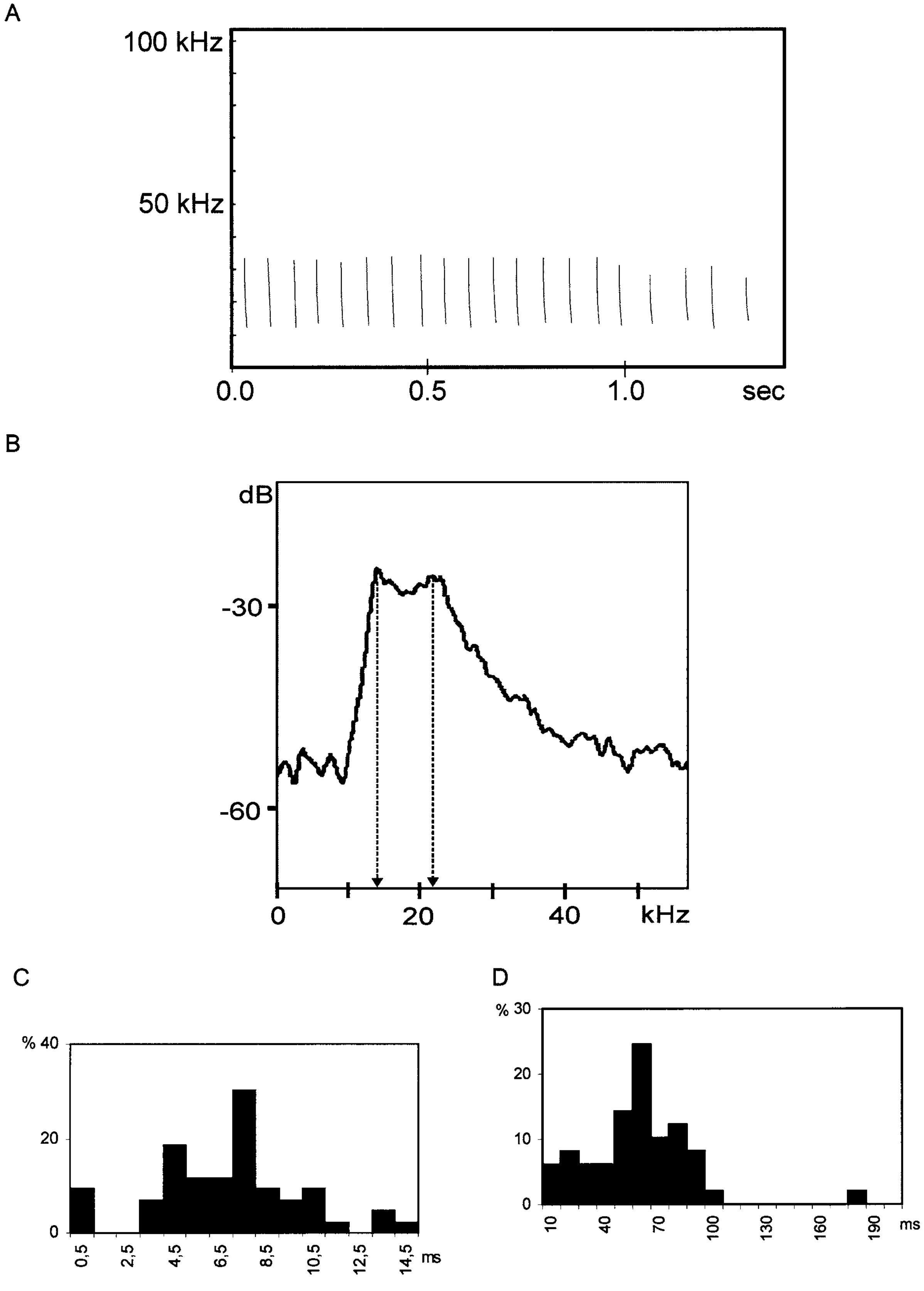

Fig. 6: Long series of single calls of *Plecotus auritus* emitted inside the mine in Stolec (record from March 2001): A. spectrogram (schematic diagram), B. the power spectrum of single call from series showing two peaks, C. pulse length analysis, D. pulse interval analysis.

corresponded with very high repetition rate 25 pulses per second (Tab. 1, Fig. 7 E).

1.6. Series of undulating calls at swarming sites

The series of undulating signals were observed in spring inside the mine in Stolec. They were emitted during songflight displays and from the rock walls, too. On heterodyne detectors or without detectors they resembled melodious trills. Series comprised 2 to 7 signals (Fig. 8 A). Each signal had a very steep main FM part, sweeping from about 71 to 11 kHz in 2.6 ms (min – 1.7, max – 4.2, SD ± 0.6). It was preceded by a longer, about 7.9 ms undulating part, at a very high frequency range (68.6-24.2 kHz) (Tab. 1). The undulating element of the

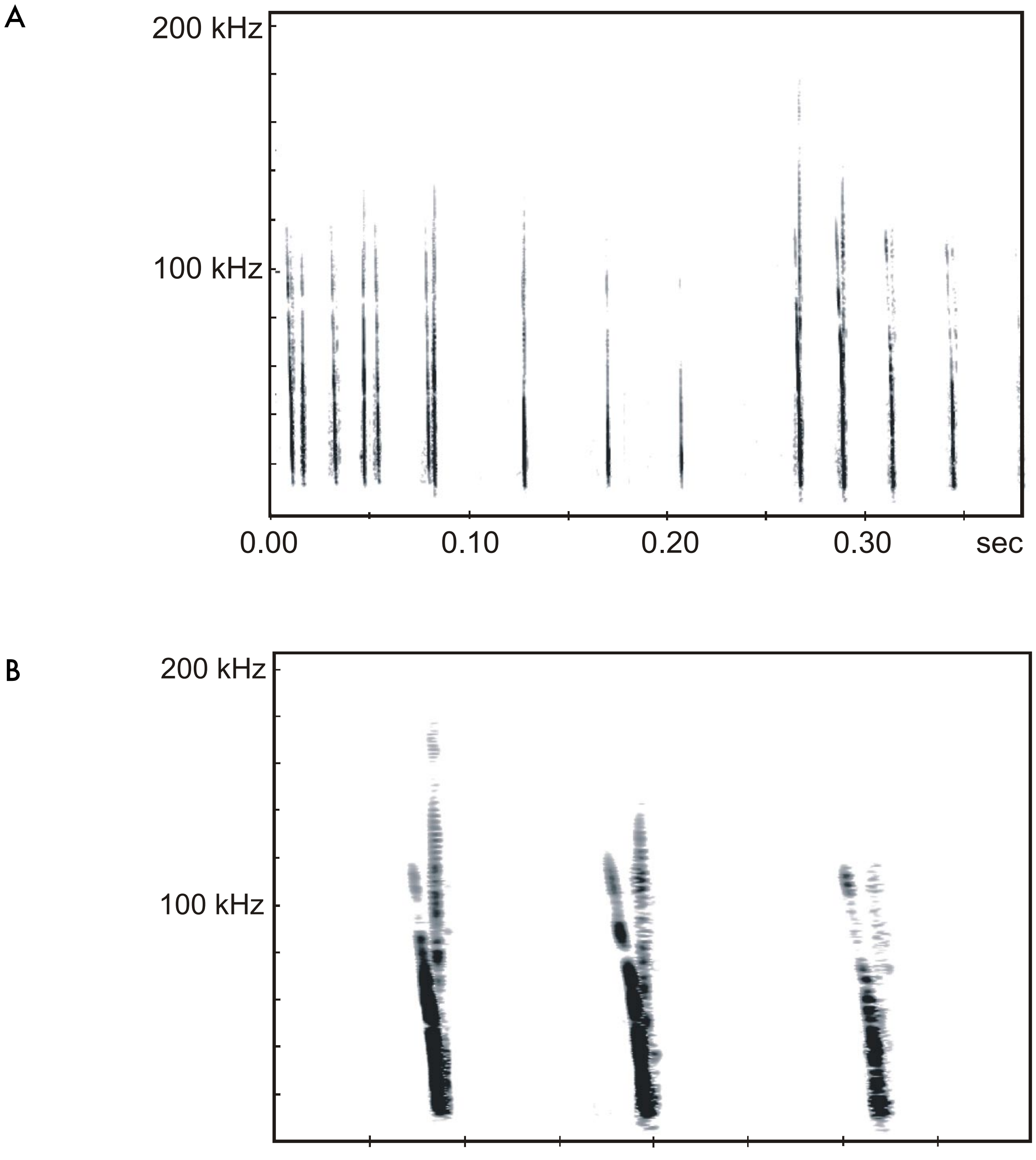

Fig. 7 A-B : Series of V-shape calls of *Plecotus auritus* emitted during chases of two or more bats (inside the Stolec mine, March 2001) : A. series of calls, B. single calls.

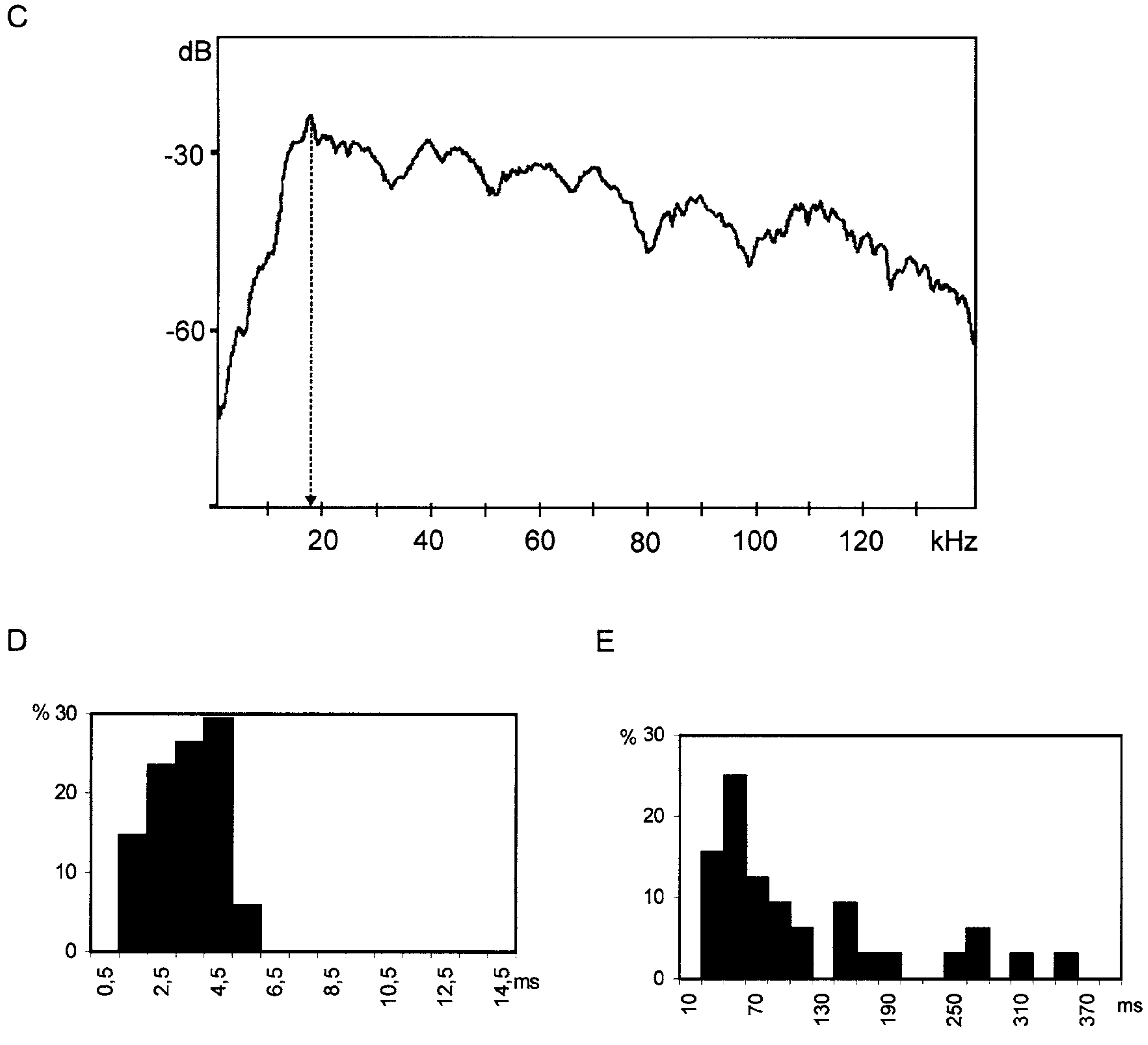

Fig. 7 C-E: Series of V-shape calls of *Plecotus auritus* emitted during chases of two or more bats (inside the Stolec mine, March 2001): C. the power spectrum (several peaks are shown, the highest at about 17 kHz), D. pulse length analysis, E. pulse interval analysis.

first signal in a series was as a rule longer and consisted of a soaring part, next a falling one and then again a soaring one (Fig. 8 A). The second call had generally only one soaring part which was repeated only once or not at all in the next signals in series. Often the undulating element was connected with the main one, so the whole call was long – see Fig. 8 C, where pulse lengths are clearly divided in two groups. The first group represents pulse lengths without an undulating part (lasted an average 2.6 ms), and the second group showed signals with this element (lasted on average 10-13 ms). Most of the calls had two, sometimes three peak frequencies in power spectrum, at about 20 kHz, above 30 kHz and above 40 kHz (Tab. 1, Fig. 8 B). For most calls the first peak was that of highest energy. The peaks for modulated parts fell at about 47 and 50 kHz (Tab. 1). Often a second harmonic, and occasionally a third, were observed. The intervals between particular signals were very short. In pulse interval analysis two peaks were observed, at 15-17 ms and at 25-27 ms, which corresponds with a very high repetition rate – about 45 pulses per second (Tab. 1, Fig. 8 D).

Two undulating signals were emitted at higher frequencies, not audible for human ears: frequency range 25.1 to 63.1 kHz, with frequency peak in power spectrum at 38 and at 50 kHz and average duration 14.3 ms ± 10.1 (min 3.3, max 36.4 ms) (Fig. 9). They were recorded between typical single calls of the brown long-eared bat inside the mine in Stolec and in Szczytnicki Park. In Table 1 only parameters of the 'low-frequency' undulating calls are given.

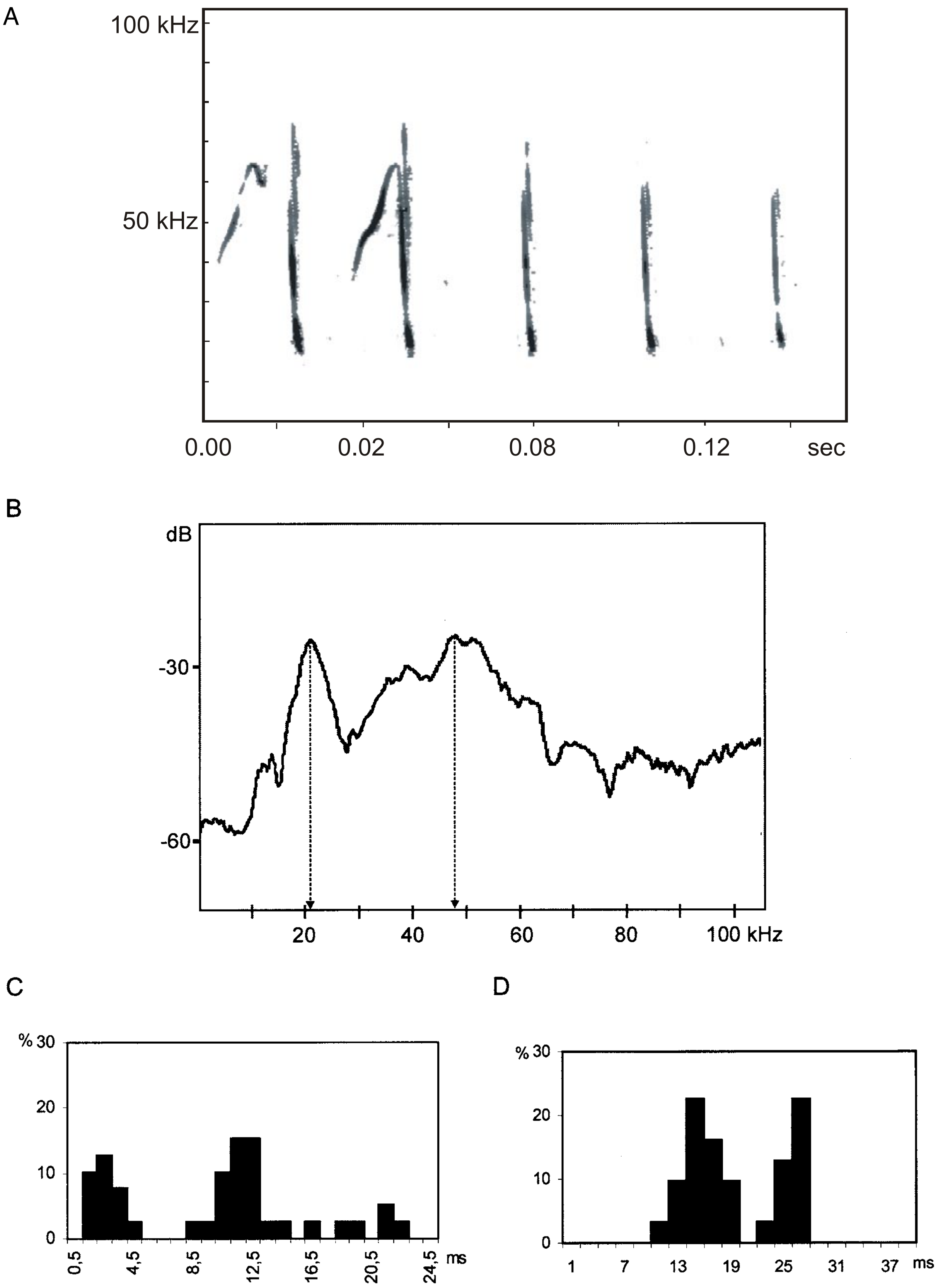

Fig. 8: Undulating calls of *Plecotus auritus* emitted from the rock wall inside the mine in Stolec (record from March 2001): A. spectrogram, B. the power spectrum with two main peaks and the third weaker between them, C. pulse length analysis, D. pulse interval analysis.

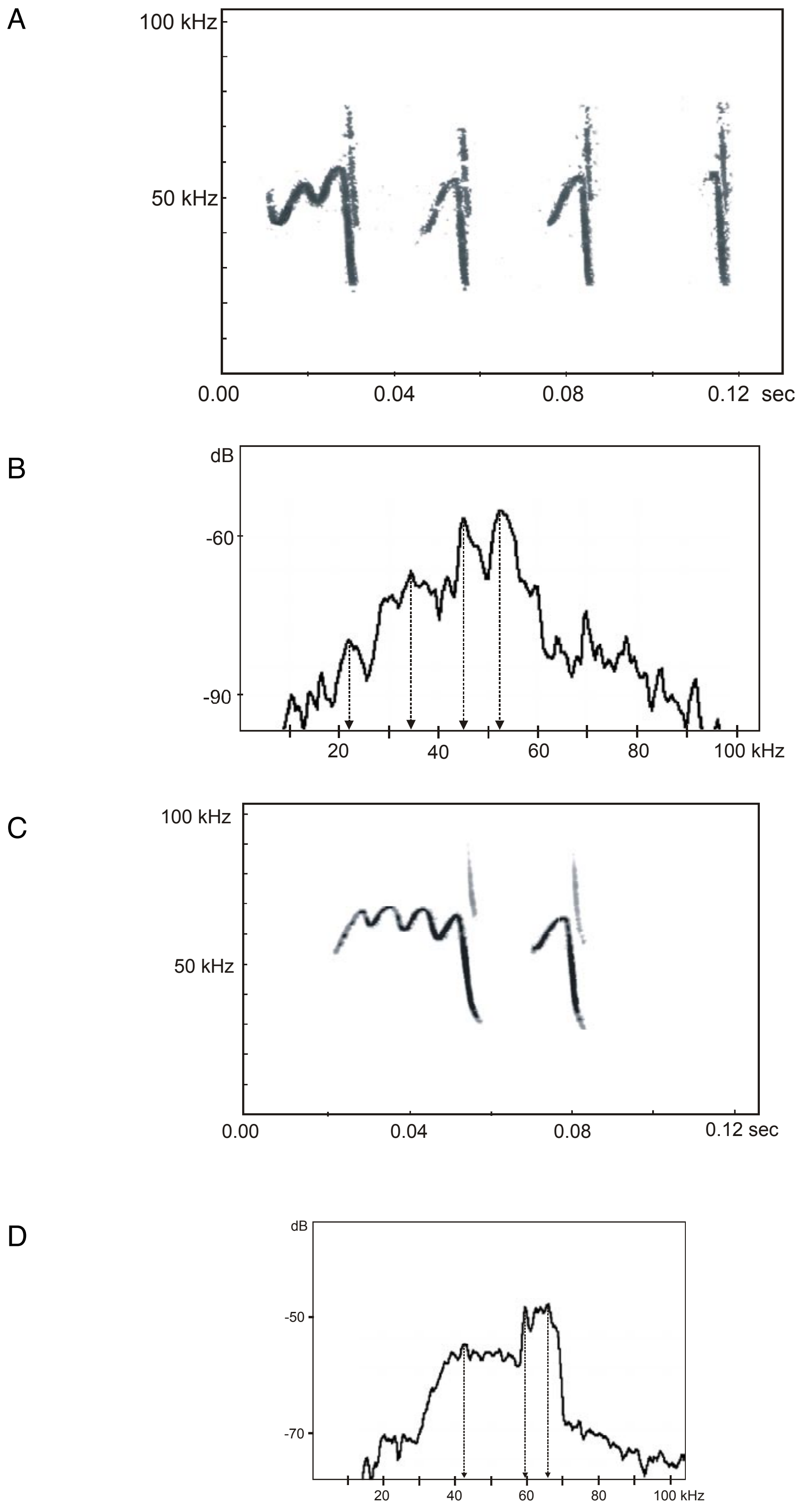

Fig. 9: Undulating calls emitted at higher frequencies, not audible for human ears (see text), recorded in spring 2000 in the Szczytnicki Park (A, B) and inside the mine in Stolec (C,D). A, C. spectrograms; B, D. the power spectra (the highest peaks are shown above 40 and 60 kHz).

Table 1: Parameters of different social calls of the brown long-eared bat *Plecotus auritus*, recorded at the swarming sites and in the maternity roost of this species. For length, interval length and peaks of energy in power spectra mean value and for frequency range the minimum and maximum value are given. N – number of measured calls, SD – standard deviation, * - in number of harmonics was given together with the first fundamental

Type of calls and observation site	N	Pulse length (min-max) [ms]	Peak 1 (min-max) [kHz]	Peak 2 (min-max) [kHz]	Peak 3 (min-max) [kHz]	Frequency range [kHz]	N harmonics– mode (min-max) *	Interval length (min-max) [ms]	Repetition rate (from peaks of interval length, ms) $[s^{-1}]$
MINE IN STOLEC									
Single calls emitted during flight, inside the mine	80	**6.5** ± 1.7 3.4–10.6	**14.1** 12.2–17.1	**19.6** 15.1–26.1	**22.7** 18.0–29.1	7.0–65.0	2 1–4	**234.0** ± 111.0 70.0–593.1	**5.0** 130–270
Single calls emitted during flight, outside the mine	116	**7.4** ± 1.1 4.0–9.9	**14.7** 12.5–23.5	**20.7** 15.7–27.1	**23.0** 20.7–26.4	6.7–55.6	2 1–3	**188.2** ± 65.4 60.5–365.2	**5.6** 170–190
Double calls, first and second signal	24 (48)	**7.1** ± 1.0 4.6–9.6	**15.3** 12.1–22.5	**21.3** 16.7–26.8	sporadically at ca. 25.0	6.9–61.4	2 1–3	**44.9** ± 1.4 6.7–70.4	
Long series of single calls during straight flight	41	**6.6** ± 1.8 3.5–9.9	**17.0** 13.5–24.0	**22.3** 15.2–27.2	**24.7** 21.3 – 33.8	8.8–44.9	1 1–2	**48.0** ± 20.8 6.2–91.0	**20.0** 50
Long series of single calls during hovering	14	**10.4** ± 2.0 5.5–14.6	**16.4** 14.6–19.1	**19.0** 16.5–23.0	**21.2** 19.4–23.3	8.9–44.6	2	**93.0** ± 7.1 11.4–284.0	**14.3** 70
V-shape calls	34	**3.3** ± 1.0 1.5–5.1	**21.9** 14.6–28.8	**36.8** 18.0–48.3	**51.9** 25.5–72.8	9.6–139.5	1	**43.4** ± 48.2 3.7–170.0	**25.0** 30–50
Series of undulating calls – the whole signal	41	**10.5** ± 7.2 1.7–36.4	**19.5** 12.7–22.62	**34.6** 16.7–49.8	**44.2** 20.0–52.9	10.7–71.3	2 1–3	**19.6** ± 5.3	**45.0** 15–17
Series of undulating calls – modulated part	28	**7.9** ± 5.5 3.7–31.5	**47.1** 22.0–54.6	**49.9** 32.1–63.5		24.2–68.6	1	11.7–27.5	and 25–27
MINE IN GONTOWA									
Single calls emitted during flight	47	**8.1** ± 0.8 6.1–10.0	**14.3** 12.5–21.3	**20.9** 15.7–24.4	**24.3** 21.3–28.0	6.1–46.9	2 1–3	**255.4** ± 56.9 121.0–499.3	**3.6** 270–290
SZCZYTNICKI PARK IN WROCŁAW									
Single calls emitted during flight	280	**8.3** ± 1.7 4.1–12.9	**14.4** 11.8–28.4	**22.5** 11.8–39.7	**27.0** 18.0–53.7	5.5–63.5	2 1–5	**187.7** ± 99.2 27.6–626.8	**5.3** 180
Single calls emitted from one site	53	**6.6** ± 0.6 5.3–7.8	**13.7** 12.3–14.6	**19.2** 14.6–24.0	**22.6** 19.1–25.9	6.9–47.5	2	**362.8** ± 105.5 651–634.8	**3.1** 310–330
Double calls, first and second signal	21 (42)	**8.2** ± 1.4 5.6–10.1	**13.5** 12.3–14.6	**21.9** 15.2–32.1	**26.1** 19.4–31.1	6.9–52.1	2 2–3	**50.6** ± 12.7 33.1–76.4	
KRAJANÓW – MATERNITY ROOST									
Series of single calls emitted during flight	118	**9.4** ± 1.7 4.5–13.7	**16.8** 12.3–22.0	**23.6** 14.8–40.9	**26.9** 17.7–39.1	7.4–67.0	2 1–4	**104.4** ± 136.0 75.0–710.5	**20.0** 30–70

Table 2 : Differences between single social calls of the brown long-eared bat *Plecotus auritus*, recorded at the four observation places, estimated from the Mann-Whitney^{MW} test and the Kruskal-Wallis test ^{KW}. Significance level: NS – not significant, ^{a} = P =0.06; * = P<0.05; ** = P<0.01; *** = P< 0.001.

Parameter **Observation place**	**length**	**peak 1**	**peak 2**	**peak 3**	**minimum frequency**	**maximum frequency**	**number of harmonics**	**pulse interval**
Stolec – Gontowa (calls outside the mines)^{MW}	***	***	NS	**	***	***	^{a}	***
Stolec – Szczytnicki Park (calls during flight)^{MW}	***	***	**	***	***	*	***	NS
Stolec (inside the mine) – Stolec (outside the mine)^{KW}	**	***	*	NS	*	NS	***	*
Gontowa – Szczytnicki Park (calls during flight)^{MW}	NS	NS	*	*	NS	**	***	***
Szczytnicki Park: calls during flight – calls from one site ^{KW}	***	NS	***	***	***	NS	***	***
Double calls in Stolec – double calls in Szczytnicki Park ^{MW}	***	***	NS	NS	***	**	NS	NS
Krajanów – Stolec (calls inside the mine)^{MW}	***	***	***	***	***	***	NS	***
Krajanów – Stolec (calls outside the mine)^{MW}	***	***	*	***	NS	***	**	***
Krajanów – Gontowa ^{MW}	***	***	NS	**	***	***	NS	***
Krajanów – Szczytnicki Park (calls during flight)^{MW}	***	***	NS	*	***	***	***	***

2. Quantitative differences in emitting different type of calls

In Stolec a higher level of vocalization was noted underground than outside the mine (Wilcoxon test, Z = -2,99, P < 0.01) (Fig. 10A). The single calls were produced most often and similar numbers of them were noted inside and outside the mine (Wilcoxon test, Z = -0.29, NS). Other signal types were scarcer, but they were emitted mostly underground (Wilcoxon test for all these calls, P<0.001). The calls emitted from one site (rock wall) were put into one category. They were observed only inside the mine (Wilcoxon test Z = -5.23, P<0.001) (Fig. 10A). At the mine in Gontowa and in Szczytnicki Park, again the single calls were most often emitted, and the remaining kinds of sounds were underrepresented (Fig. 10B, C). At mine in Gontowa, the vocalization of the brown long-eared bat was observed only outside the mine, near the entrance. In Szczytnicki Park, bats flew and vocalized at the same places and along similar flight routes each year.

3. Seasonal changes in vocal activity of brown long-eared bat *Plecotus auritus* at the swarming sites

The highest vocal activity (measured as the mean number of all types of calls) in the three observation places was noted in early spring, from March until mid April. In Szczytnicki Park and at the mine in Stolec, calling began in the first half of March, then increased and reached maximum levels at the end of March and beginning of April. At the end of April no or few social calls were noted. At the mine in Gontowa, the activity began three weeks later – in the fourth week of March, and therefore lasted shorter, to the third week of April, but the peak

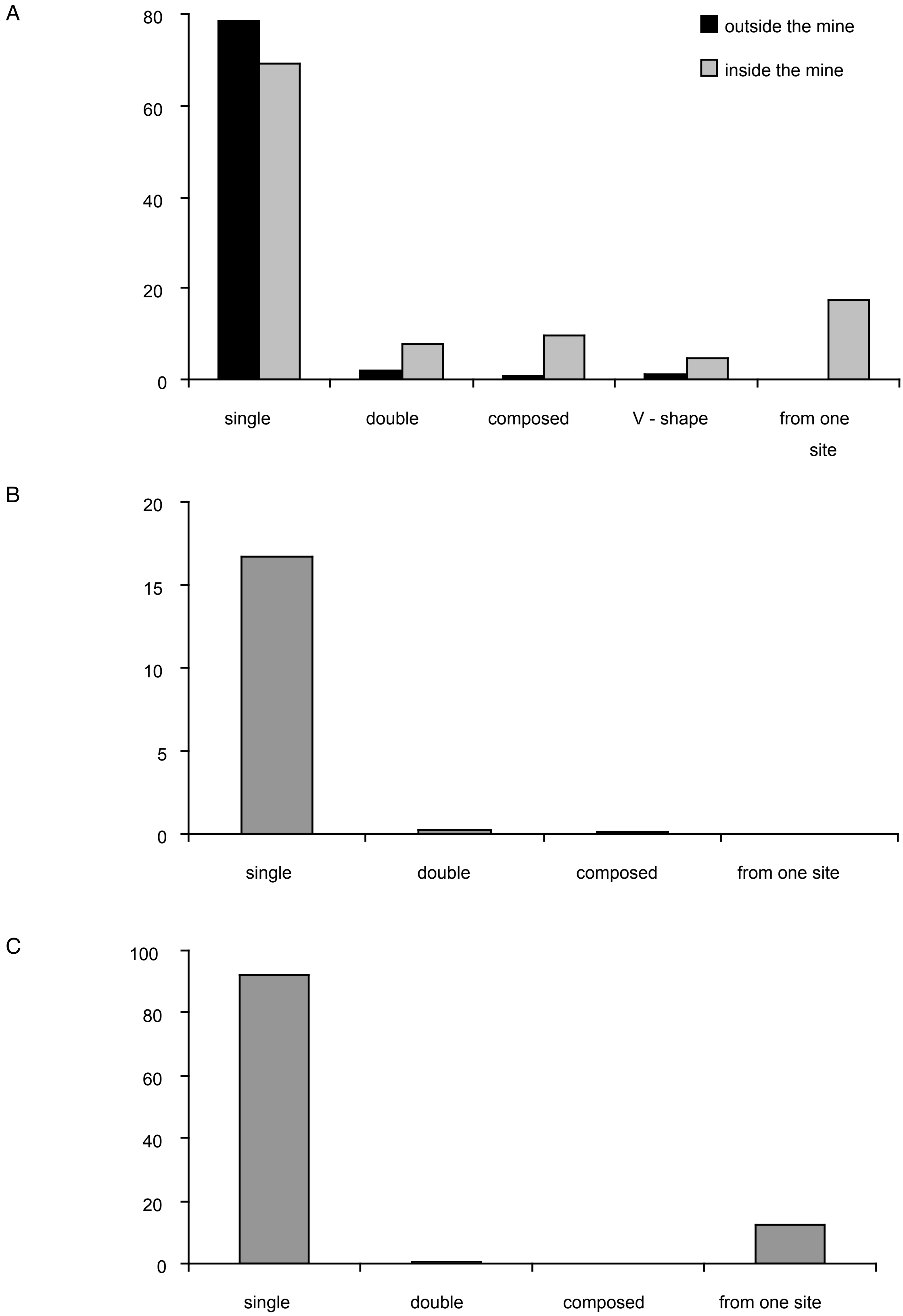

Fig. 10: Differences in emitting different types of social calls of *Plecotus auritus* in two spring seasons 2000-2001: A. outside and inside the mine in Stolec, B. outside the mine in Sokolec, C. the Park Szczytnicki in Wrocław ("composed calls" mean: long series of single calls and of an undulating calls). Significance level in vocalization inside and outside the mine in Stolec: NS = not significant, *** = P<0.001.

was reached at the same time as in the other places. The highest vocal activity was noted at the mine in Stolec and the lowest at the mine in Gontowa. The autumn activity was ten times lower than in spring, and relatively few calls were recorded. In summer, no swarming and vocalizing bats were observed in the mines and in the city park (Fig. 11).

DISCUSSION

1. Variability and function of social calls

So far, social vocalization of the brown long-eared bat has been described by several authors, but the sound parameters have been given only for typical single social calls and other types of signals have only sometimes been mentioned (Ahlen, 1981, 1990; Dzenaevich & Sobolevski, 1988; Limpens & Roschen, 1995; Barataud, 1996; Szkudlarek & Paszkiewicz, 2000). This study shows that the social vocalization of the brown long-eared bat is much more diversified, even within the typical single social calls. Such variation in vocalization could have several explanations. First, the signals were recorded in slightly different habitats, in open and semi-open spaces in Szczytnicki Park and near the mine in Gontowa, in contrast with the almost closed habitat near the mine in Stolec and at the specific underground site. In all of these localities, the sounds produced by bats could be distorted (Bradbury & Vehrencamp, 1998). Additionally, given the directionality of many bat sounds, the angles between bat's mouth and the microphone and the equipment will affect the signal characteristics (Waters, 2001; Bradbury & Vehrencamp, 1998). But the statistically significant differences in some call parameters suggests that variability in vocalization is not a result of recording conditions or sound distortion. The type of habitat could influenced signal parameters only if the social calls are partly used in echolocation. The echolocation of bats changed according to the habitat structure (e. g. Barataud, 1996) so we can predict changes in social call parameters. In more open spaces, when sound has to travel futher, lower frequencies and longer calls should be used. The comparison of single calls recorded at three swarming sites only partly support this assumption. In Szczytnicki Park, where recordings were made mostly in more open habitat, the calls are longer, but their peak frequencies are not lower. Therefore, between sites differences could be explained by interpopulational or geographical variability, because bats from different local populations were recorded. Such geographical variability is often described in case of birds' songs (Thielcke, 1969; Mundinger, 1982) or even bats' echolocation (Jones & Kokurewicz, 1994; Boughman, 1997; Barclay *et al.*, 1999; Law *et al.*, 2002).

Another explanation of the signals' variability is the function the sounds could have. Bats use the social calls for communication between individuals, including mother-young recognition (Jones, 2000), territoriality or social interaction during mating period. It is interesting to speculate on what messages such signals encode and if we can predict behavioural responses to particular call types. We could expect that the diversified calls

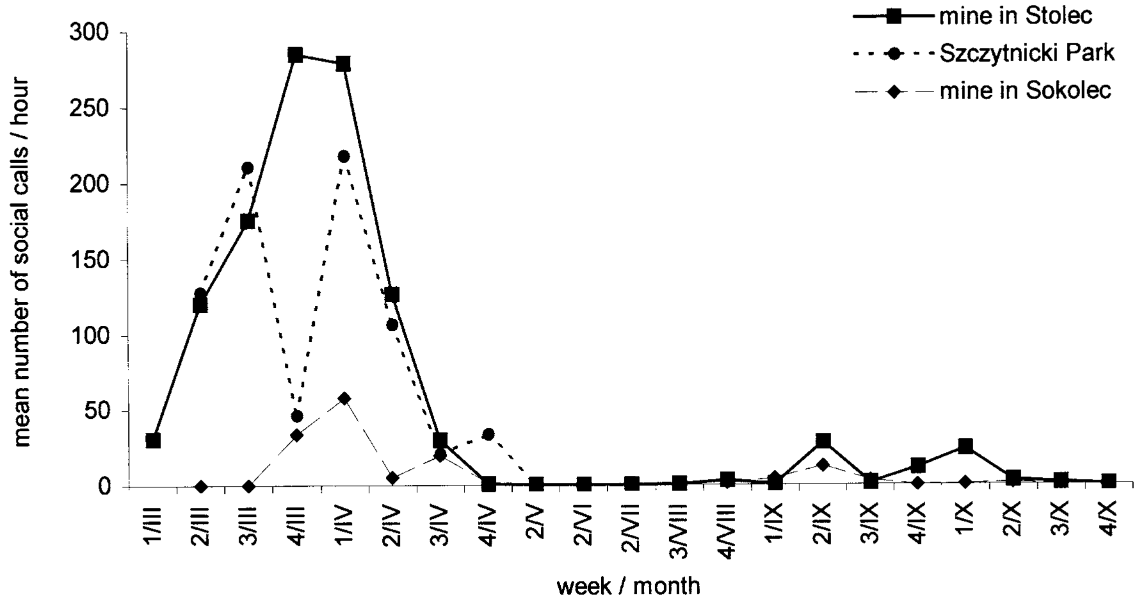

Fig. 11 : Seasonal changes in vocal activity of the brown long-eared bat *Plecotus auritus* at swarming sites of this species in years 2000-2001.

can define sex, age, affiliation to a social group, or even individual identity (Jones *et al.*, 1992; Jones & Kokurewicz, 1994; Master *et al.*, 1995; Boughman, 1997). In social calls, when animals communicate with others, such variability and information value seems to be greater than in echolocation calls (Fenton, 1977, 1994). These factors could explain the use of several types of social signals by the swarming long-eared bats, and sometimes a great variability within a particular type of call. This kind of variability is observed in a wide range of almost all parameters, for example the "category" of single calls includes short and long pulses (from 4 to 9.9 ms) and the first peak in the power spectrum changes from about 12 kHz to max 28 kHz. It could be caused by measuring the parameters of signals which are produced by a different individuals and in various situations. Dzenaevich & Sobolevski, (1988) described single social calls of *Plecotus auritus* in various states. When a male was alone in the acoustic room, it emitted 12-20 ms long signals sliding from 36 kHz to 6 kHz with the highest sound pressure at 16 kHz for the first harmonic, and 32 kHz for the second harmonic. When additionally a female resided in the room, the male produced shorter FM calls about 3-9 ms long, with a start and end frequency at 28-26 kHz and 8-6 kHz, respectively. The peaks in the power spectrum for the first and second harmonics were at 14 and 28 kHz, respectively. But when there was another male around, the first male twice emitted much longer calls to 32 ms including in the last 20 ms CF part.

Different types of social calls of the brown long-eared should have different functions, which was suggested or described in case of other bat species (e.g. Fenton, 1977; Weid, 1994; Kozhurina, 1996; Zahn & Dippel, 1997; Pfalzer & Kusch, 2003). The lowest frequency peaks were noted in single calls, in comparison to other types of signals, therefore they may travel further. Such calls are better propagated over long distances and probably their functions are associated with attracting the receiver's attention to the sender. We could predict that at shorter distances the vocalization might be more diversified, because vocalizing bats could use higher frequencies and their sounds should contain additional information, for example about sex and intentions, according to sound changes and performance (Weid, 1994; Kozhurina, 1996). Two undulating calls of *P. auritus* (Fig. 9) were produced on higher frequencies inaudible for human ears. It could be a "higher version" of the undulating audible sounds, produced for other tasks or in other situations. Changes in undulating signals (called "W-note") were observed for *Myotis myotis*. During copulations the bats switched frequency of maximum sound pressure to the higher one (Zahn & Dippel, 1997).

Important factors worth consideration are the time of vocalization, its function and the sex of the bat which emits it. So far, the majority of social calls (excluding the vocal interaction between mother and offspring) have been considered as produced during mating seasons by males to attract females, or to show aggression to repel other males (Sosnovtzeva, 1974; Lundberg & Gerell, 1986; Lundberg, 1989; Weid, 1988, 1994). The diversified vocalization and high vocal activity of brown long-eared bat at the swarming sites in spring play probably important mating function. Copulations of this species take place in the late autumn and early spring, so these times are considered its mating period (Moffat, 1922; Stebbings, 1966, 1970). Calls characteristic for these periods were not observed beyond these places, for example at foraging areas. And the social calls from the maternity roost are significantly different and probably used in order to communicate the bats which are entering and leaving the colony. We could suppose that most of these calls, according to the data obtained for males in another bat species, are produced by males probably to attract females. Indeed, in spring many males are netted at the swarming sites and they were observed vocalizing (Furmankiewicz, 2002 and unpublished). In case of the mine in Stolec, the highest and most diversified vocal activity of the brown long-eared bat was observed inside the mine. Probably the big halls and corridors create better conditions for sound propagation, and the underground place could be a specific swarming and mating site for this species. Bats could arrive at the mine to meet potential mates and occupy rather temporary mating sites on rock walls, from which they vocalize. In the city park in Wrocław, the bats flew and vocalized at the same places and along similar flying routes every year, which resembled the territorial behaviour described for example in case of the Noctule and Pipistrelle. But probably the brown long-eared bat is not territorial, because the netting data showed two or three males present in one site (Furmankiewicz, unpublished). Such places within tree-covered areas could be small swarming sites as there is no other bigger underground swarming site in the vicinity.

2. Differences in vocal activity between swarming sites

The differences in level, time of onset and duration of activity between the three swarming sites is probably a result of the size of the population which visits them and the distribution of the population on a greater area. For example, the highest number of bats was noted at the mine in Stolec and the lowest at the mine in Gontowa (Furmankiewicz, 2002). Climatic variations should be considered, too. In the mountains (the mine in Gontowa), the activity began three weeks later. In Stolec and in Wrocław, early spring begins in the second half of March, whereas in Gontowa low temperatures – below 0°C, last longer, thus early spring begins later, between 10th and 20th March.

CONCLUSION

Social vocalization of brown long-eared bat at swarming sites is very diversified and bats perform different types of social calls in different situations. Such vocal activity was not observed in foraging sites or in maternity roosts of this species. Additionally, bats visit swarming sites very frequently and most males have distended caudae epididymides indicating their ability to copulations (Furmankiewicz *et al.*, in prep). It supports the hypothesis that swarming of brown long-eared bat is connected with mating behaviour.

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RESUME

Cris sociaux et activité vocale chez l'oreillard roux *Plecotus auritus* dans le sud-ouest de la Pologne. Les cris sociaux de l'oreillard roux *Plecotus auritus* ont été étudiés dans des sites d'hibernation, dans un parc urbain et dans une colonie estivale située dans le grenier d'une maison du sud de la Pologne de 1999 à 2001. Les sons ont été enregistrés avec des détecteurs ultrasonores D980 et D240X connectés à un enregistreur numérique DAT SONY TCD D-8. Plusieurs types de cris sociaux ont été différenciés. La plupart sont émis durant des phases de vol mais quelques-uns sont émis posés (tronc d'arbre ou branche, mur de pierre d'un souterrain). L'émission principale consiste en un signal isolé en FM, émis à environ 13-15 kHz et les paramètres varient d'un site d'observation à un autre. Les chauves-souris émettent souvent des séquences rythmées et rapides de deux, trois ou plus (jusqu'à dix) signaux isolés les uns après les autres. D'autres séries d'émissions consistent en plusieurs signaux très particuliers, caractérisés par une oscillation à double ascension, suivie d'une FM abrupte. Des signaux en V sont émis alors que deux ou plus de deux chauves-souris se poursuivent. La plupart des cris sociaux ont été notés dans les sites de vols sociaux en essaim au printemps (mars-avril) et en automne (septembre-octobre). Les vocalisations vernales sont dix fois plus abondantes et bien plus diversifiées. Ces émissions jouent probablement un rôle durant la période d'accouplement de cette espèce au printemps et à l'automne. Dans les colonies estivales, les chauves-souris émettent principalement des séquences rapides de plusieurs signaux FM isolés quand elles émergent ou rentrent dans le gîte.

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Line counting and point counting of foraging bats in Estonia, a comparison

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Abstract. In mid-summer 2001 line counting (LC) and point counting (PC) of foraging bats were carried out in 8 bat monitoring stations in Estonia. Heterodyne ultrasound detectors, the Pettersson Elektronik AB D200 and D240 were used, in combination with visual observation. A total of 31 km of routes and 72 five-minute points were studied, covering typical foraging habitats of bats in the countryside and in small towns. Over 90 % of bats were identified to the species level. Both methods gave similar results, but PC was relatively more efficient for *Myotis dasycneme*, *Myotis daubentonii* and *Nyctalus noctula*, and especially, for *Plecotus auritus*. With both methods *Eptesicus nilssoni* was most numerous species. Next in numbers were *Pipistrellus nathusii*, *Myotis daubentonii*, *Nyctalus noctula* and *Myotis dasycneme*. Other species were less numerous. Total cumulative indices (for all bat species together) were 721 inds/100 km in LC, and 197 inds/100 points in PC.

INTRODUCTION

During the past decades special methods have been used to count foraging bats using ultrasound detectors. Of these methods line counting (LC) and point counting (PC) were most common (Ahlén, 1981 ; Jüdes, 1989 ; Masing, 1994 ; Boonman, 1996 ; de Wijs, 1999). Using heterodyne detectors many bat species can be identified by their echolocation calls on spot (Ahlén, 1981, 1987). Some of the bats not recognized in field can be identified later, e.g. using time expansion system, sound recording equipment and sound analysis program (Pettersson, 1999).

Recently a powerful route counting method (RCM) was described in which heterodyne detectors were used. In RCM line counting and point counting were not separated (Masing *et al.*, 1998). This is similar to the lines-and-points method used in the Netherlands in the 1990s (De Wijs, 1999). In 2000-2001 an improved version of the route counting method (RCM-2) was developed in Estonia in which line counting and point counting were separated (Masing *et al.*, 2002).

The present paper compares the results of line counting and point counting carried out in the same sites, at the same time and by the same observers.

METHODS

Description of RCM-2

RCM-2 includes the following aspects : 1. line counting (LC) and point counting (PC) are separated (Fig. 1) ; 2. bats are recorded and their species identified using a sensitive heterodyne detector and visual observation ; 3. during search phase the frequency is held constantly on 30 kHz that enables to notice all boreal bat species except *Pipistrellus pygmaeus/mediterraneus* ; when the bat is heard, its best listening frequency and other sound characters are checked for species identification ; 4. bat counting starts 1-1.5 hours after sunset depending on light conditions ; 5. only suitable weather conditions (temperature at least +10ºC, no rain, no strong wind) are recommended for counting bats in the purpose of monitoring their populations ; 6. in LC route length is between 3-5 km, while bats (maximum number of every species heard or seen) are counted per 50 m segments of the route ; 7. in PC bats are counted in nine 5-min waiting points, situated either on or near the LC route, in three points in each main habitat type (edge of water-body, forest or park, buildings with trees) ; 8. the counting is completed during 2.5-3 hours (including 45 min for nine PC waiting points) ; 9. the results of LC and PC are given in inds/10 km (or inds/100 km) and inds/100 points, respectively ; 10. to characterize bat populations in a larger area the results of several routes are summarized (Masing *et al.*, 2002).

Fieldwork done in 2001

In mid-summer 2001 line counting (LC) and point counting (PC) of foraging bats were carried out in 8 bat monitoring stations in Estonia (Masing *et al.*, 2002). In this work heterodyne ultrasound detectors, the Pettersson Elektronik AB D200 and D240, were used in combination with visual observation. A total of 31 km

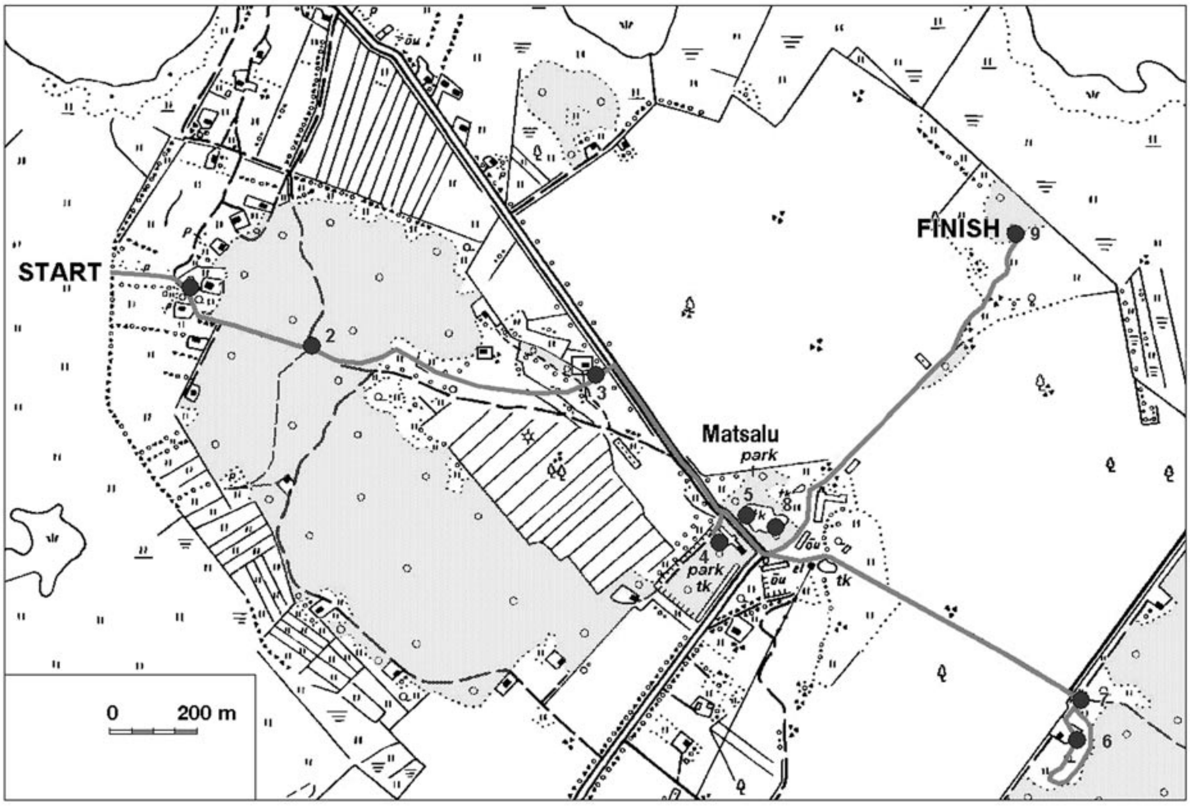

Fig. 1: A map of Matsalu showing a line counting route passing through several habitats (the line) and the points of point counting situated in three main habitat types (dots).

of routes and 72 five-minute points were studied during 22 hours, covering typical foraging habitats of bats in the countryside and in small towns. Bat species were mostly identified using heterodyne system and visual observation in combination. In some cases, especially when several bats were heard at one spot, the time expansion system of D240 was used to make a recording for further species identification using BatSound program. It should be mentioned that counting sites often represented the best foraging habitats of bats in the area.

The following persons participated in fieldwork: Vello Keppart (Jõgeva), Kaja Lotman (Matsalu, Penijõe), Lauri Lutsar (Räpina, Värska) & Matti Masing (Kuressaare, Loode, Matsalu, Tooma, Jõgeva, Värska).

RESULTS

Because counting sites often represented the best foraging habitats of bats in the area, it was possible in this study to record ten species of bat out of eleven species found in Estonia, some of which are considered rare. *Myotis brandtii* and *Myotis mystacinus* were not separated in this study, but according to the present knowledge the first species is more numerous in Estonia compared to the second species.

Comparison of the results of line counting and point counting

The results of PC characterize certain habitat types while the results of LC apply to the whole landscape where the counting route passes.

Using LC the following cumulative indices were received, concerning all 8 stations (inds/100 km): En - 299, Pn - 167, Md - 102, Nn - 36, Mds - 25, Pp - 19, Mb/m - 13, Vm - 8, Pa - 3, Mn - 3 and Csp - 46 (Fig. 2). Using PC the following cumulative indices were received (inds/100 points): En - 64.0, Pn - 40.3, Md - 36.8, Nn - 14.2, Mds -12.2, Pa - 4.2, Mb/m - 2.8, Pp - 2.1, Vm - 1.4 and Csp - 18.7 (Fig. 3).

The total cumulative indices (for all bat species together) were 721 inds/100 km in LC, and 197 inds/100 points in PC. Using sensitive and accurate heterodyne detectors in combination with visual observation the experienced observers were able to identify 93.6% of bats in LC and 90.5% of bats in PC from the total number of bats

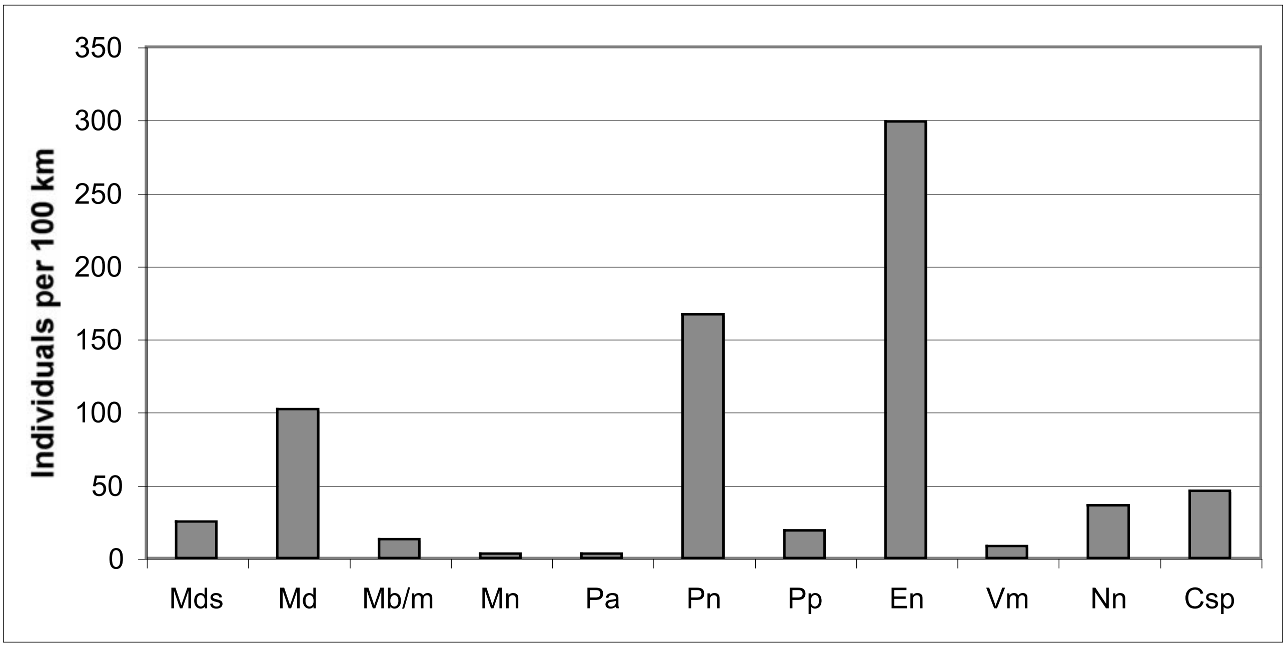

Fig. 2: Results of line counting of foraging bats on monitoring routes in Estonia in mid-summer 2001. Cumulative data from eight routes with total length of 31 km. Species' names are abbreviated.

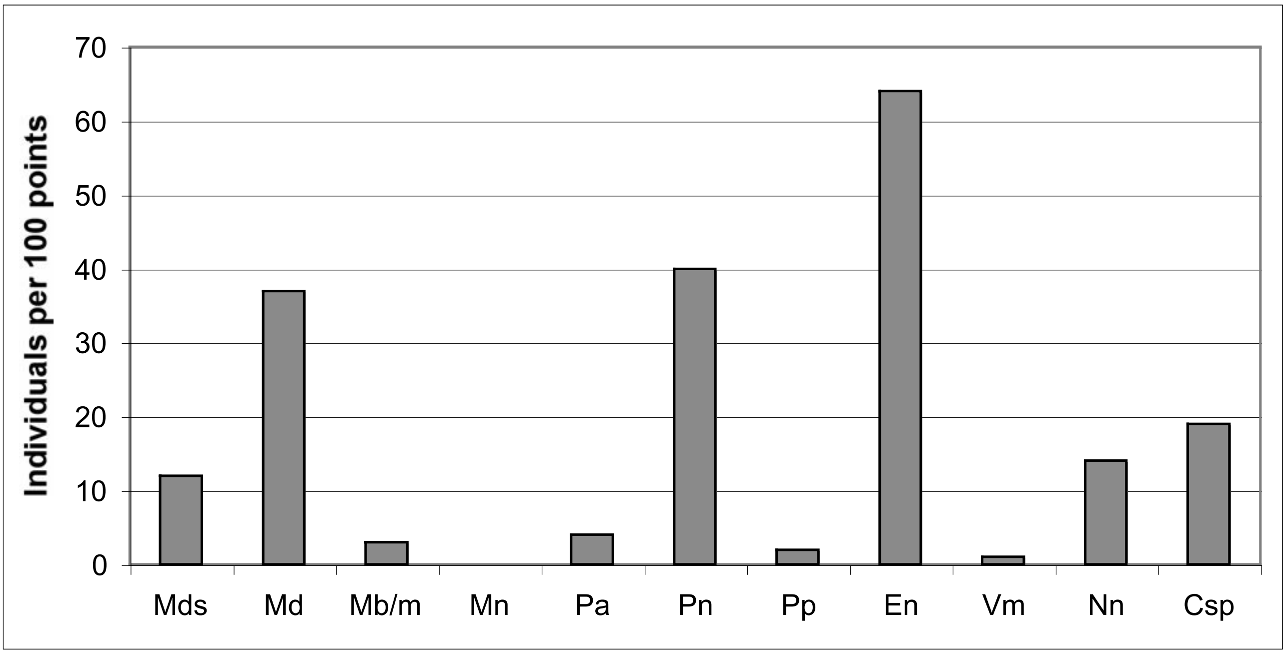

Fig. 3: Results of point counting of foraging bats on monitoring routes in Estonia in mid-summer 2001. Cumulative data from 72 five-minute points, with 24 points representing each main habitat type: 1) edge of water-body, 2) forest or park and 3) buildings with trees. Species' names are abbreviated.

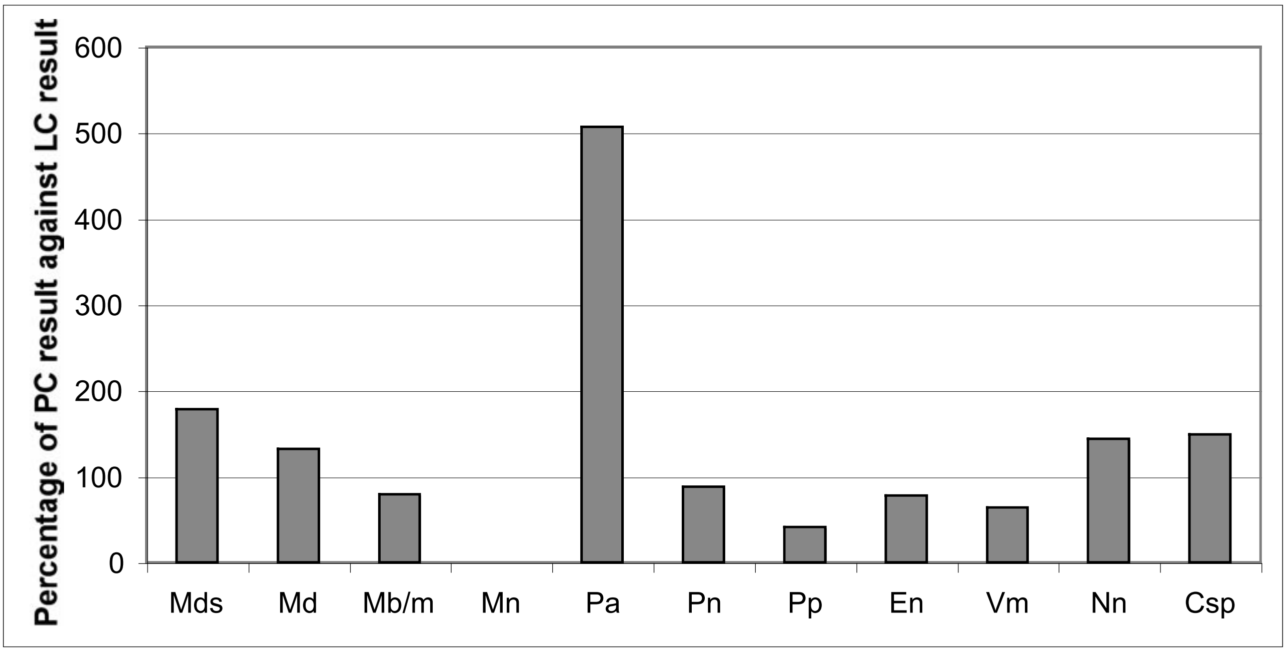

Fig. 4: Comparison of the results of line counting (LC) and point counting (PC) received from the same sites. Cumulative data from 8 monitoring stations in Estonia. LC result is 100 %. Computed from Fig. 2 & 3. Species' names are abbreviated.

encountered on 8 bat counting routes in Estonia in 2001 (computed from Figs 2 & 3).

Generally, PC is slightly more effective in detecting bats, if the counting points are well chosen. In 2001 point counting gave slightly higher values for three species (Md, Mds, Nn), compared to line counting. In *Plecotus auritus* PC gave even five times higher values compared to LC, indicating that PC is much more efficient for detecting this quiet species (Fig. 4). It is easier to hear the sounds of quiet species at points because the observer is not moving.

Abbreviations: En: *Eptesicus nilssonii*; Mb/m: *Myotis brandtii/mystacinus*; Md: *Myotis daubentonii*; Mds: *Myotis dasycneme*; Mn: *Myotis nattereri*; Nn: *Nyctalus noctula*; Pa: *Plecotus auritus*; Pn: *Pipistrellus nathusii*; Pp: *Pipistrellus pipistrellus* (45 kHz); Vm: *Vespertilio murinus*; Csp: *Chiroptera* species.

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RÉSUMÉ

Ligne de transect et points d'écoute pour dénombrer les chauves-souris en activités de chasse en Estonie: une comparaison. A la mi-automne 2001 des lignes de transect (LC) et des points d'écoute (PC) de chauves-souris en activité de chasse ont été menés dans 8 stations de suivi des chauves-souris en Estonie. Des détecteurs ultrasonores hétérodyne Pettersson D200 et D240 ont été utilisés en combinaison avec des observations visuelles. Un total de 31 km de transects et 72 points d'écoute de 5 mn ont été étudiés, couvrant les habitats typiques de chasse des chauves-souris dans la campagne et dans des villages. Plus de 90 % des chauves-souris ont été identifiées au niveau spécifique. Les deux méthodes ont donné des résultats similaires mais les points d'écoute ont été relativement plus efficaces pour repérer *Myotis dasycneme*, *Myotis daubentonii*, *Nyctalus noctula* et tout particulièrement *Plecotus auritus*. Par les deux méthodes, *Eptesicus nilssonii* apparaît comme l'espèce la plus abondante. Viennent ensuite *Pipistrellus nathusii*, *Myotis daubentonii*, *Nyctalus noctula* et *Myotis dasycneme*. Les autres espèces sont moins abondantes. Les indices totaux cumulés (toutes espèces confondues) sont de 721 individus/100 km et de 197 individus/100 points d'écoute.

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Methods in surveying advertisement calling *Vespertilio murinus* L., 1758, and notes on its fall distribution in Europe

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Abstract. When concerning *V. murinus* we have some knowledge of the species original habitats. This species is originally associated to the steppe regions of Southeastern Europe. During fall it moved to mountainous regions where it carried out its display flight. During recent times this species is associated to agricultural regions during summer. During fall it inhabits cities in which the display flight is carried out near tall buildings.

The species is often difficult to detect during summer. Ahlén writes that this is the European bat species with highest variation in its echolocating calls. Typically the species forage above lakes, often far from the lake shore. Detection by terrestrial bat workers is therefore difficult. However, the display flight during fall is easily detected both with or without the aid of an ultrasound device. The use of cities and their activity period during night makes this species easy to detect during fall. However, when comparing the location of the cities in which the bat has been found during fall with its general distribution in Europe, it becomes quite obvious that fieldwork during fall by bat workers is rather low.

This article gives some information of the species history and geography, as well as how the species is easiest detected during fall. The objective of this article is to encourage people to search for this bat in their own cities throughout Europe.

INTRODUCTION

Vespertilio murinus is believed to have its original distribution in the steppe regions of Southeastern Europe. During fall this species has its mating season. It is presumed it migrated from the steppes to the mountains where it carried out its characteristic display flight in front of cliffs to attract females for mating.

Later this species has adapted to human changes of the landscape. The steppe is replaced with agriculture. The mountainous areas are replaced by cities, and the cliffs are replaced by tall buildings such as churches, industrial compounds and tall apartment buildings.

The objective of this article is to inform of how the species is easiest detected and which areas of Europe which might prove to be the most interesting. General information has been included as it is important to understand the species distribution and ecology, which in turn is important when planning field work during fall. Information without references, included in this article, is the authors temporary results mainly based on a behavioral study at Romsås in Oslo which was initiated in 1993.

Earlier distribution

The original foraging habitat seems to be open areas such as the steppes of South-East Europe (e.g. Pucek, 1981). It is, however, difficult to obtain reliable information concerning which steppes it has been recorded at. Unfortunately, mostly old sources are to be found. Mentioned areas are mainly in southeastern Europe, north of the Black Sea and the Caspian Sea. In these areas it has been found at the Chernozem steppes which lies near the Ural mountains, where the species has also been found. Furthermore, it has been recorded at the Volga-Ural steppes, the Baraba steppes, the Don steppes and the Kirgishian steppes north of the Caspian Sea at the foot of the Ural mountains (Ognev, 1928).

Presumed changes in distribution and habitat preference :

- Steppes / Agricultural land
- Mountain areas / Cities
- Cliffs / Tall buildings

Present distribution

Today *V. murinus* has a wide distribution throughout Europe and Asia. To the west it is found at the Jura mountains in Switzerland and the Rhine valley in Germany (Stutz & Haffner, 1984 ; Kock & Schwarting, 1990), north to Stavanger (Gjerde, 1994b), Oslo (Gjerde, 1995a) and Falun-Gävle (Ahlén, 1986), eastwards through Polen, Belarussia, the Ukraine, Azerbaijan, northern Iran and Afghanistan. In Russia it is found south of the 55-60°N meridian, east to Manchuria and the Ussuri-region in eastern Siberia (Wallin, 1969 ; Rydell & Baagøe, 1994 ; Kierus & Gjerde, 1997 ; Baagøe, *in press*).

In Europe the species has a patchy distribution and is rare throughout most of its range. However, it seems to be common in southern Scandinavia from Drammen to the west, to Gävle in the northeast and Sjælland to the south (Ahlén, 1986 ; Baagøe, 1986 ; Gjerde, 1993, 1995b). On the Danish island of Sjælland over 200 maternity colonies have been found (Baagøe, 1996). The species' European stronghold outside Scandinavia seems to be at Neuchâtel in Switzerland (Blant & Jaberg, 1995) and central and eastern Poland (Pucek, 1981 ; Rachwald & Nowakowski, 1994).

Outside the species general European range it has been found in central and southern England (e.g. Corbet & Harris, 1991), Belgium and the Netherlands (Content & Gompel, 1990 ; Lina, 1984 ; 1990) the Faeroe Islands (Baagøe & Bloch, 1994), North Sea oil rigs (Stansfield, 1966, Rydell & Baagøe, 1994) and central Scandinavia (Tjernberg, 1924 ; Gjerde, 1994a). Observations the past ten years in the Netherlands (e.g. Jansen & Noort, *in prep.*) and England (e.g. Anonymous, 2002) suggest the species might be more common then presviously believed in the west. This might be due to the species have increased its distribution, or that the species ecology make it difficult to detect.

Summer habitat

V. murinus is an opportunistic hunter. It hasn't specialized on foraging a selective group of insects, but rather hunts what ever is available. It forages on swarming insects which are 3-10 mm in size (Petrusenko & Sologor, 1981 ; Bauerová & Ruprecht, 1989 ; Rydell, 1992a ; Jaberg *et al.*, 1998). Chironomidae and Trichoptera contain much of its diet, but it also feeds on Aphidoiea and Nauroptera.

Steppes

Today it seems *V. murinus* prefer agricultural lowland areas (Baagøe, 1986 ; Gjerde, 1995a). Most likely the flat agricultural areas function as some sort of substitute for the steppes.

Lakes and rivers

Wetlands seem to be the most important foraging habitat. Especially lakes are chosen where they forage far from the shore (Patlyakevich, 1980 ; Bauerová & Ruprecht, 1989 ; Rydell, 1992a ; Gjerde, 1993 ; Jaberg *et al.*, 1998). Foraging in open spaces make it vulnerable for wind, and calm nights are important for a successful hunt (Jaberg *et al.*, 1998). It may also forage above marshy forest, adjoining parks and open marshes (Bauer, 1954 ; Gjerde, 1993 ; Jaberg *et al.*, 1998).

Forests

In Central Europe the species seem to be most common at higher altitudes (1000 m.a.s.l.) covered with forest (Schaefer, 1974 ; Tress & Tress, 1988 ; Cervený & Bürger, 1989). However, it has been recorded at 1800 m in the Alps (Ognev, 1928) and at 3050 m.a.s.l. in the western Himalayas (Ryberg, 1947).

In Sweden and Norway it may forage in forest areas (Ahlén & Gerell, 1989 ; Ahlén 1990 ; Gundersen & Mauritzen, 1998). From Polen it has been found foraging Aphidoidea above city parks (Bauerová & Ruprecht, 1989).

Cities

In urban areas during late summer and fall it hunts for beetles and moths in which it finds around bluish white street lamps (Baagøe, 1986 ; Ahlén, 1990 ; Kock & Schwarting, 1990 ; Rydell, 1992a, b ; Rydell & Baagøe, 1994).

Migration and movement

The species have been found to make quite extensive movements, but no evidence of a typical migration have been presented. However, evidence of regional movements between seasons have been presented. On Sjælland in Denmark the species is found in the agricultural areas exclusively during summer, and in the city of København during fall (Bauer, 1954 ; 1955 ; Baagøe, 1986). Such regional movements according to the season has also been found in the Oslo area. Here *V. murinus* is found near tall buildings during fall and in wetland and agricultural areas outside Oslo during summer (Gjerde, 1993 ; 1995a ; Krog, 1995).

Accidental observations far outside its normal range show they may move over long distances. It has been found as far north as Pajala (67°07'N) and Luleå (65°35'N) in Sweden (Tjernberg, 1924 ; Lönnberg, 1929) and on North Sea oil rigs (Stansfield, 1966 ; Rydell & Baagøe, 1994). Longest recorded movement has been made of a young male banded in Estonia on 29 July 1988. It was recovered in Austria on 13 November the same year. It had moved at least 1440 km (Masing, 1989). Long distance movements has also been recorded from individuals marked in Belarussia and the Ukraine. They include distances of 360, 800 and 850 km (Kurskov, 1961 ; Strelkov, 1969).

During 1993 to 1996 Ingemar Ahlén studied bat migration along the Swedish coast of Skåne, Blekinge and Öland (Ahlén, 1997). At Ottenby two *V. murinus* were observed as they broke loose from a group of five before crossing the open sea. At Falsterbo one individual was observed as it left the coast in a southeastern direction. It was seen during the evening at a height of 10 meters. However, Ahlén does not mention when during the fall these observations are made.

Fig. 1 : Cities in which advertisement calling males have been observed. Cities with only fall or winter observations are in parenthesis.

Norway	Sweden	Denmark	Germany	Poland	Netherlands	England
Vagsøy	(Pajala)	Kobenhavn	Lübeck	Bialystok	(Hague)	Southampton
(Kristiansand)	Lulea?	Roskilde	Hamburg	(Warszawa)	(Haarlem)	
Horten	Falun	Hillerod	(Mannheim)	(Poznan)		
Holmestrand	Gävle	Helsingor	(Walldorf)			
Drammen	Herräng	(Fredricia)	(Heidelberg)			
Oslo	Karlstad	(Dronninglund)	(Wiesloch)			
Moss	Örebro	Aarhus	(Karlsruhe)			
Fredrikstad	Västeras	(Randers)				
Halden	Uppsala	(Aalborg)				
	Stockholm	(Samso)				
	Jönköbing					
	Göteborg					
	Lund					
	Malmö					
	Borgholm					

Display flight

Habitat

The species do perform their display flight at natural cliffs (Ahlén, 1981 ; Weid, 1988 ; Gjerde, 1995b), which also is believed to be its original habitat. Today typical display flight habitats are tall buildings, usually at least 9 stories tall. Such buildings may be tall apartment buildings, silos, hospitals, churches, industrial buildings (Fig. 1).

In some areas of Norway (Fredrikstad, Drammen, Lørenskog) it has also been heard at villa residential areas, but this is not typical for the species (Hardeng, 1992 ; Gjerde, 1995b). The author has also observed the species' display flight above deciduous trees in a park in Southampton during April 1995.

Activity

The species seem to tolerate a wide range of temperatures. Individuals have been observed in display flight just after a heavy snow fall when the entire landscape is white and air temperature is 0°C. Also at temperatures as high as 14°C it is active (higher night temperatures then this have not been measured during fall within the areas field work has been carried out). However, optimal temperatures seem to be above 6-8°C.

Rain seems to have some influence. However, drizzling or dripping rain seem to have little impact on its activity.

It is presumed that wind speed has a high influence on bat activity since it cools the bat, reduces the sound range of its cries, and increases flight energy when flying against heavy wind. Wind probably has least importance at high temperatures during the peak of the season as the bats seem to be active the entire night.

Flight height does vary much depending on the bats activity and the surrounding terrain. Generally they seem to fly at 10-20 meters height (5-9 stories up).

The activity period during night seems to be at its highest from 1,5 hours after sunset and the following 3-4 hours. The complexity of parameters effecting activity of advertisement calling *V. murinus* is still not fully appreciated. Temperature is important, but is not important alone. It is not uncommon for bats to be active at -1 to 5°C. However, the number of individual males are much lower. Furthermore, at optimal weather conditions such as no wind, precipitation and 10-14°C the bats might be absent entirely, even during high season. This does suggest there must be other important factors than weather which influence their behavioral activity. This makes it necessary to visit each site a number of times before it may be confirmed if the species is present. No less than three (preferably more) visits during optimal conditions (wheather and timing) should be carried out. If possible, supporting methods should be carried out where the public is asked for observations. Using posters, newspapers, contacting locals etc. can prove to be quite effective. Never describe the sound of advertisement calling males to the public. Let people describe the sound they hear themselves, assuring you of a more reliable identification.

Sound

The advertisement calls are easily recognizable, and is audible to the normal ear. It resembles a metallic ticking sound. The peak frequency is at 14.4 kHz and may also be heard when using a detector. The use of an ultrasound detector may increase the detectability by perhaps 10 percent. However, this has not been tested, and is so far based on subjective experience during field work. Our ear is much more effective in detecting the direction and strength of the advertisement calls. I therefore recommend not to use the detector for checking advertisement calls, but rather have it continuously tuned at 25 kHz to detect any foraging activity.

However, using an ultrasound detector tuned at 14 kHz might prove to be useful when surveying advertisement calling males by car since noise from the vehicle reduces our ear as an effective hearing aid.

The advertisement calls are audible at a distance of 80-100 meters (Leif Gjerde, pers. comm.).

Phenology

Display flight are normally carried out during mild evenings from the end of September to the beginning of November. During favorable conditions males have been heard as early as 11 September, or as late as 14 December in Oslo (Leif Gjerde, pers. com.) and the end of December in København (Baagøe in press). Ryberg (1947) writes that the display flight may be heard during spring. However, only documented spring observation is made in Southampton in 1995 (Leif Gjerde, pers. comm.). The peak of activity seems to be all October and the beginning of November, a period of 5 weeks.

Hibernation

V. murinus hibernate in tall buildings, the same localities as they use during fall (Ryberg, 1947; Spitzenberger, 1984; Ahlén, 1986; Baagøe, 1986; in press). It has also been found hibernating in caves and mines in a.o. the Rarau-Suceava cave in Romania. Such localities are, however, rarely used and always in small numbers (e.g. Strelkov, 1969; Khabilov, 1980; Cervený & Bürger, 1989; Valenciuc, 1989). In Poland it has also been found in a fortification in Poznan (Dzieciolowski *et al.*, 1998).

Mapping advertisement calling males

Timing

The species may start its display flight as soon as it becomes dark. However, it is recommended to start the survey from 1.5 hours after sunset since some studies indicate the species may forage during the first hour.

Looking for potential localities

Building structures should be mapped by first checking with the local taxi drivers, police stations and fire departments. These have usually a fairly good knowledge of the local situation. Own observations may add or correct the information on potential sites.

All pipes, churches, silos, tall apartment buildings, fortress', industrial buildings or similar buildings with a height of at least a 9 story building should be checked. Localities not exceeding this height may also be checked. Whenever possible, natural habitats, such as cliffs, should be surveyed as well.

Checking localities

Each potential locality should be visited at least three separate evenings during optimal conditions. Each location should be visited for the time it takes to walk around a cluster of buildings, and for at least five minutes. Even if the species is recorded at a locality it is important to survey the site three times. This enables you to check the reliabililty of your method.

A locality is defined as a single or cluster of tall buildings which is outside the reach of a neighboring territory. For practical reasons a distance of 100-150 meters have been used in combination with landscape features.

I do not recommend the use of headphones since the advertisement calls should be heard directly by your ears. The detectors loudspeaker will reveal any foraging bats when tuned at 25 kHz.

We need your help

Any information or observations of advertisement calling males are appreciated. Also any publications concerning *V. murinus* is appreciated.

The author is working on a program to study the behavior and ecology of advertisement calling *V. murinus*. Little information is known of this species' distribution in Europe during fall. Therefore, we need your help to visit and investigate potential localities in European cities during October.

It is recommended to contact the author prior to the fieldwork so more specific advice may be given.

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RÉSUMÉ

Méthode de recherche accoustique de *Vespertilio murinus* L., 1758 et note sur sa distribution automnale

en Europe. Nous possédons quelques informations sur l'habitat initial de la Sérotine bicolore *V. murinus*. Originellement, cette espèce est associée aux régions steppiques du sud-est de l'Europe. En automne, elle se déplace vers les régions montagneuses où elle pratique son vol territorial. Cette espèce s'est récemment adaptée aux régions agricoles en été. A l'automne, elle fréquente alors les villes, dans lesquelles le vol territorial est effectué à proximité d'immeubles élevés.

Cette espèce est souvent délicate à détecter en été. Ahlén écrit que c'est l'espèce européenne dotée de la plus grande variabilité dans ses écholocations. Classiquement, elle s'alimente au-dessus des lacs, souvent loin des berges. La détection à partir des rives est souvent problématique. Cependant, les signaux émis lors des vols territoriaux automnaux sont facilement repérables au détecteur ou à l'oreille. La fréquentation des villes et les habitudes nocturnes du chiroptère le rendent facilement détectable à cette saison. Cela dit, en comparant l'aire de répartition de l'espèce en Europe avec la localisation des villes dans lesquelles l'espèce a été observée en automne, il apparaît clairement que l'activité automnale des chiroptérologues est relativement faible. Cet article apporte quelques informations sur l'histoire et la distribution de la Sérotine bicolore et présente la technique la plus aisée pour repérer l'espèce en automne. L'objectif de ce travail est d'encourager les naturalistes européens à rechercher cette espèce dans leurs propres villes.

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Posters et résumés de présentation

Experience with bat counting in Tartu, Estonia

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Abstract

From June till September 2001 and from April till July 2002 a new modification of the route counting method (RCM-2) was implemented to count foraging bats on two routes (3.6 km and 4.7 km) at Raadi in Tartu. The Pettersson D200 heterodyne detector was used. The task was to identify bats, estimate their numbers and determine the value of different habitats for foraging bats. Two sub-methods of RCM-2, including line counting (LC) and point counting (PC), were used simultaneously (Masing *et al.*, 2002).

By September 2001 the following preliminary results were received. First, LC and PC gave similar results. Second, 6 species of bat were observed foraging at River Emajõgi, 5 species were recorded in the streets and around houses, and 4 species were recorded in parks. Third, a total of eight species were recorded on the routes in Tartu (*M. daubentonii, M. dasycneme, P. auritus, P. nathusii, P. pipistrellus, E. nilssonii, V. murinus* and *N. noctula*). Fourth, the largest numbers of foraging bats were found either near or over River Emajõgi, especially in the vicinity of old trees.

Method

For monitoring bats I used the Improved Route Counting Method (RCM-2). This is the improved version of Route Counting Method (RCM – Masing *et al.*, 1988).

RCM-2 uses two different methods:

a) the detector-line-counting (DLC, LC) (Ahlén, 1981; Boonman, 1996; Masing *et al.*, 2000).

   In 3-5 km route all bats heard (with detector) are registered, divided in 50 metres sectors. Results are given for 10 km.

b) the detector-point-counting (DPC, PC) (Ahlén, 1981; Boonman, 1996; Masing *et al.*, 2000).

   There are 9 counting points in three main habitats. In each point all bats heard in 5 minutes are registered. The results are given for 100 counting points.

Bat detectors used are Pettersson Elektronik D-200 and D-240 .

Some of bats are recorded with D-240 time expansion program and species determining was re-checked later with the Pettersson BatSound™ program.

The bat counting took place in Southern Estonia, in the northern part of Tartu.

Two counting routes were 8,4 km together and shared three different habitats:

1) Street habitat (43 % of the whole distance) consists of streets and areas between houses.

2) Park habitat (49 % of the whole distance) consists of parks and cemeteries.

3) Shore habitat (8 %) consists of shores of lakes and rivers.

Counting time is from April till August 2002, with frequency at least once in a month in both counting routes.

Temperatures fluctuated a lot. There was 6ºC in the beginning of monitor and 3ºC in the end of route in April and in August the temperatures were 19ºC and 18ºC accordingly.

Results

Line-counting method

6 species were found:
- *Myotis daubentonii* 5 %
- *Plecotus auritus* 7 %
- *Pipistrellus nathusii* 15 %
- *Pipistrellus pipistrellus* 10 %
- *Eptesicus nilssonii* 58 %
- *Nyctalus noctula* 5 %

The most numerous species with Line-Counting Method in different habitats:
1. Street habitat: *Eptesicus nilssonii*, *Pipistrellus nathusii*, *Plecotus auritus*
2. Park habitat: *Eptesicus nilssonii*, *Plecotus auritus*, *Pipistrellus nathusii*
3. Shore habitat: *Eptesicus nilssonii*, *Pipistrellus pipistrellus*, *Pipistrellus nathusii*

Point-counting method

7 species were found:

- *Myotis dasycneme* 4 %
- *Myotis daubentonii* 19 %
- *Plecotus auritus* 7 %
- *Pipistrellus nathusii* 16 %
- *Pipistrellus pipistrellus* 4 %
- *Eptesicus nilssonii* 44 %
- *Nyctalus noctula* 6 %

The most numerous species with Point-Counting Method in different habitats:

1. Street habitat: *Eptesicus nilssonii*, *Pipistrellus nathusii*, *Nyctalus noctula*
2. Park habitat: *Eptesicus nilssonii*, *Plecotus auritus*, *Nyctalus noctula/Pipistrellus nathusii*
3. Shore habitat: *Eptesicus nilssonii*, *Myotis daubentonii*, *Pipistrellus nathusii*

Comparison of Species in the Lake and in the River with Point-Counting Method, given for 100 points (Fig. 1a, 1b)

Fig. 1a: Shore habitat: species of the Lake.

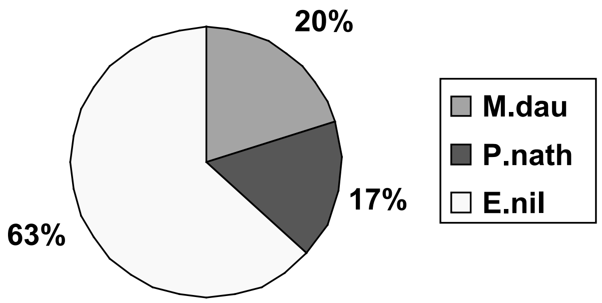
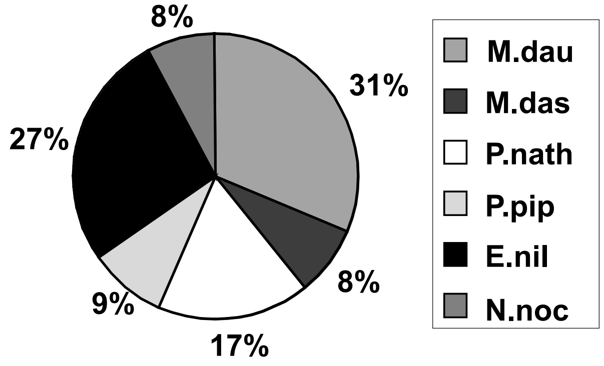


Fig. 1b: Shore habitat: species of the River.



Comparison of line-counting method and point-counting method (Fig. 2)

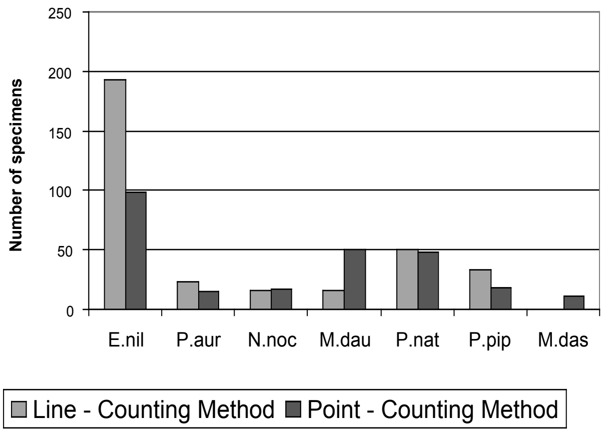


Fig. 2: Comparison of Line-Counting and Point-Counting Methods.

Number of species in different habitats

	Line-Counting Method	**Point-Counting Method**
Street habitat	4	3
Park habitat	6	5
Shore habitat	5	6

Résumé

Expérience de dénombrement des chauves-souris à Tartu, Estonie. De juin à septembre 2001 et d'avril à juillet 2002, une nouvelle modification de la méthode de dénombrement sur transect (RCM-2) a été mise en œuvre pour dénombrer les chauves-souris en activité de chasse le long de deux lignes d'échantillonnage (3,6 km et 4,7 km) à Raadi, Tartu, Estonie. Un détecteur hétérodyne Pettersson D200 a été utilisé pour identifier les chiroptères, estimer leurs effectifs et déterminer la valeur des différents habitats pour les chauves-souris en activité de chasse. Deux sous-techniques de la méthode RCM-2, concernant la mise en œuvre de transects continus (LC) et de points d'écoute (PC), ont été utilisées simultanément (Masing *et al.*, 2002).

En septembre 2001, les résultats préliminaires suivants ont été obtenus. Les LC et PC donnent des résultats similaires. Six espèces de chauves-souris en chasse ont été contactées sur la rivière Emajõgi, 5 espèces dans les rues et autours des villages et 4 espèces dans les parcs. Huit espèces ont été détectées au total le long des lignes d'échantillonnage à Tartu (*M. daubentonii, M. dasycneme, P. auritus, P. nathusii, P. pipistrellus, E. nilssonii, V. murinus* and *N. noctula*). Enfin, le plus grand nombre de chauves-souris en chasse a été obtenu près ou sur la rivière Emajõgi, notamment à proximité de vieux arbres.

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Significance of water bodies for insectivorous bats in a semi-humid tropical forest in the Yucatan Peninsula, Mexico

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Abstract

The region of the Calakmul Biosphere Reserve is characterized by a dry season during which water is restricted to natural rain collectors called locally “aguadas”. These conditions offer the opportunity to determine the importance of “aguadas” as open areas and water sources for bats. During the dry season of 2002, we compared species richness and activity of insectivorous bats in “aguadas”, forest gaps and continuous forest (control) in the Calakmul region. We called a unit a combination “aguada”-gap-control, and four of these units were established. The mean distance between each element of a unit was 100 m. We realized five samplings of each unit from March to May. For a given unit, sampling was simultaneous, and lasted for 1.5 h using the ANABAT II system. We evaluated bat activity with the acoustic activity index (AAI) proposed by MILLER (2001). For both species richness and AAI, we found a striking difference between “aguadas”, gaps and controls. Species richness (N) and AAI were significantly higher in “aguadas” (N=10 ; AAI=120), followed by gaps (N=4 ; AAI=22), and finally controls (N=1 ; AAI=1). These differences might be due to the differential disponibility of insects, though it remains to be demonstrated. Our results highlight the importance of “aguadas” in areas where water is discretely distributed over the landscape.

Résumé

Importance des points d’eau pour les chauves-souris insectivores en forêt tropicale semi-humide de la péninsule du Yucatan, Mexique. Le climat de la réserve de la biosphère de Calakmul se caractérise par une saison sèche durant laquelle la ressource en eau se limite à des bassins naturels de collecte d’eau pluviale appelés localement « aguadas ». Ces conditions permettent de déterminer l’importance des « aguadas » en tant qu’espace ouvert et de point d’eau pour les chauves-souris. Durant la saison sèche de 2002, nous avons comparé la richesse spécifique et l’activité des chauves-souris insectivores dans les aguadas, les ouvertures forestières et les massifs forestiers (zone témoin) de la région de Calakmul. Nous qualifions d’unité la combinaison aguadas-ouverture forestière-zone témoin. Quatre de ces unités ont été définies. La distance moyenne entre deux éléments d’une unité est de 100 m. Nous avons réalisé cinq échantillonnages sur chaque unité de mars à mai. Pour une unité donnée, les échantillonnages sont simultanés et durent 1h30 en utilisant le système ANABAT II. Nous évaluons la richesse spécifique (N) et l’index d’activité acoustique (AAI) proposé par MILLER (2001). N et AAI sont tous deux significativement plus élevés dans les aguadas (N=10 ; AAI=120), suivi des ouvertures forestières (N=4 ; AAI=22) et finalement des massifs forestiers servant de zones témoin (N=1 ; AAI=1). Ces différences pourraient être dues à des variations de disponibilité en insectes, bien que cela reste à démontrer. Nos résultats soulignent l’importance des « aguadas » dans des zones où l’eau est inégalement répartie dans le paysage.

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Active assessment of the occurrence and distribution of Geoffroy's bats *(Myotis emarginatus)* using a spectrum of survey methods

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Abstract

The distribution and especially regional and local occurrence of Geoffroy's bat *(Myotis emarginatus)* in its Eurasian range is not known well enough to effectively protect the species. Different survey methods such as visual inspection of attics and lofts, netting on flight paths and in hunting habitats, bat detector survey in hunting habitat, tracking back flight paths and locating swarming bats, radio-tracking, and their effectiveness to reveal the species occurrence in different european regions are discussed. Characteristics enabling identification and assessment of the Geoffroy's bats bat with the help of bat detectors are described. A practical approach to assessment of the Geoffroy's bats occurrence is proposed.

Résumé

Détermination de la présence et de la répartition du murin à oreilles échancrées *Myotis emarginatus* par l'utilisation d'un panel de techniques de prospection. La répartition et tout particulièrement la présence régionale et locale du murin à oreilles échancrées *Myotis emarginatus* dans son aire eurasiatique n'est pas suffisamment connue pour protéger efficacement l'espèce. Les différentes techniques de recherche (prospection visuelle des greniers et des dessous de toit; capture au filet sur les corridors de déplacement et les terrains de chasse; remontée à rebours le long des voies de déplacements et localisation des vols sociaux en essaim; radio-traking) ainsi que leur efficacité pour détecter la présence de l'espèce dans différentes régions européennes sont commentées. Les caractéristiques permettant l'identification et l'étude du murin à oreilles échancrées à l'aide de détecteurs d'ultrasons sont décrites. Une approche pratique de recherche du Murin à oreilles échancrées est proposée.

Novel Training for the Identification of Bats Using Heterodyne Detectors

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Abstract

The National Bat Monitoring Programme was established in the United Kingdom in 1995 to establish a framework for bat population monitoring in response to the 1991 European Bats Agreement.

The programme uses trained volunteers to carry out field surveys using a range of methods including emergence counts, hibernacula counts and random transects using a bat detector, across all four countries of the UK.

Training of volunteers has focussed on work with heterodyne bat detectors for the field survey work. Innovative training has been devised using techniques to enhance the sonic memory by providing reference points that can be used to compare bat calls. To maximise the use of hearing as a tool, the bat calls heard through a heterodyne detector are broken down into 4 elements; repetition rate, rhythm, tonal quality and pitch. Using recordings of typical calls from four UK species targeted by the NBMP, in combination with artificially generated sounds, we demonstrate how these four elements and their relationships can be used to help understand what the bat is doing in the field and identify the likely species or group.

The training is presented in the form of an interactive workshop that employs audio and visual methods and is

targeted to geographic areas where new volunteers are needed to achieve full UK coverage. Recruitment and training is combined to provide volunteers with the skills necessary to carry out NBMP surveys. To date 78 full Bat Detector Workshops have been run with the help of many local Bat Groups and other organisations. Through these sessions the NBMP has reached over 1000 people. In evaluations completed by a sample of participants, a variety of reasons were given for attendance of the workshops but 100 % of respondents felt that their original objectives had been achieved through this style of training.

Over the first five-year phase this strategy of recruitment, engagement and implementation has enabled the NBMP to collect data from a wide geographical range. The focus of the training programme is now shifting towards consolidation and investing in volunteers and Bat Groups that have contributed considerable time and effort to the NBMP. The gradual introduction of broadband detectors now available as a cheap and robust technology for volunteers will require a new strategy and new set of educational resources.

Résumé

Nouvelle technique de formation pour identifier les chauves-souris grâce à l'utilisation de détecteurs ultrasonores hétérodynes. Le Programme National de Suivi des Chauves-souris (NBMP) a été lancé en 1995 au Royaume-Uni pour constituer le cadre d'un suivi des populations de chauves-souris répondant aux recommandations de l'Accord Européen sur la Protection des Chauves-souris de 1991.

Le programme s'appuie sur un réseau de bénévoles formés, qui réalisent des prospections de terrain dans tout le pays, en mettant en œuvre une gamme de techniques comprenant des comptages en sortie de gîtes, des dénombrements dans les gîtes d'hibernation et des transects aléatoires.

La formation des bénévoles a été axée sur l'utilisation de détecteurs hétérodynes pour réaliser les prospections de terrain. Une technique innovante de formation a été conçue pour développer la mémoire auditive des participants en fournissant des sons de référence, permettant une comparaison avec les signaux de chauves-souris. Pour maximiser l'écoute en tant qu'outil de prospection, les émissions de chauves-souris sont analysés selon quatre paramètres : récurrence, rythme, qualité tonale, hauteur. En utilisant des sons typiques des 4 espèces de chauves-souris visées par le NBMP, combinés avec des sons artificiels, nous démontrons comment ces quatre éléments et leurs relations peuvent être utilisés pour comprendre ce que fait la chauve-souris et l'identifier au niveau du groupe ou de l'espèce.

La formation se présente sous forme d'ateliers interactifs utilisant des éléments sonores et visuels. Ils sont organisés dans des régions où de nouveaux bénévoles sont nécessaires pour obtenir une bonne couverture de prospection. Le recrutement et la formation des bénévoles vise à leur offrir les connaissances nécessaires à la réalisation des suivis du NBMP. Le programme national de suivi repose, grâce à ces sessions, sur plus de 1000 personnes. Dans les évaluations effectuées sur un panel de participants, il apparaît que diverses raisons ont motivé les bénévoles à s'impliquer mais 100 % des correspondants indiquent que ce type de formation a répondu à leur attente initiale.

Sur les 5 premières années, cette stratégie de recrutement, d'engagement et d'amélioration du réseau de suivi a permis au NBMP de collecter des données sur une vaste surface géographique. L'objet des séances de formations s'oriente désormais vers la consolidation du réseau des bénévoles et des groupes chiroptères locaux qui ont consacré un temps et une énergie considérable au NBMP. L'arrivée progressive de détecteurs à large bande désormais robustes et plus abordables financièrement nécessitera la mise en œuvre de nouvelles stratégies et de nouveaux outils de formation.

Myotis alcathoe's echolocation. Comparative description and identification possibilities

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Abstract

Myotis alcathoe was described from Greece as a new species to science in 2001 (Helversen *et al.*). According to Helversen *et al.*, *Myotis alcathoe* has the highest-frequency echolocation calls of all the European *Myotis* species.

Ruedi *et al.* (2002) recently confirmed that the Alcathoe's bat also occurs in France. Acoustic material collected from Charente-Maritime in various flight conditions is described and compared with calls of closely related species. Key criteria for acoustic identification are proposed and identification possibilities according to bat environment are discussed.

Résumé

Echolocation du murin d'Alcathoe *Myotis alcathoe*. Description comparative et possibilités d'identification. Le murin d'Alcathoe a été décrit de Grèce en tant que nouvelle espèce pour la science en 2001 (Helversen *et al.*). Selon Helversen *et al.*, de tous les murins d'Europe, c'est *Myotis alcathoe* qui émet les signaux les plus élevés en fréquence. Ruedi *et al.* (2002) ont confirmé la présence du murin d'Alcathoe en France. Les séquences sonores collectées en Charente-Maritime dans diverses conditions de vol sont décrites et comparées avec celles des espèces proches. Des critères déterminants pour l'identification acoustique sont proposés et les possibilités d'identification discutées en fonction de l'environnement de la chauve-souris.

Active assessment of the occurrence and distribution of natterer's bats (*Myotis nattereri*) using bat detectors and other survey methods

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Abstract

The distribution and especially regional and local occurrence of Natterer's bat (*Myotis nattereri*) in its Eurasian range, as well as roost and feeding habitat preferences are not known well enough to effectively protect the species. Different survey methods, e.g. visual inspection of attics and lofts, netting on flight paths and in hunting habitats, bat detector survey in hunting habitat, tracking back flight paths and locating swarming bats, and their effectiveness to reveal the species occurrence and its roost and feeding habitat preferences are discussed. Characteristics enabling identification and assessment of the Natterer's bat with the help of bat detectors are described. A practical approach to assessment of the Natterer's bats occurrence is proposed.

Résumé

Détermination de la présence et de la répartition du Murin de Natterer *Myotis nattereri* par l'utilisation de détecteurs d'ultrasons et d'autres techniques de prospection. La répartition et la présence régionale et locale du murin de Natterer *Myotis nattereri* dans son aire eurasiatique ainsi que ses exigences quant aux gîtes et aux habitats de chasse ne sont pas suffisamment connues pour protéger efficacement l'espèce. Les différentes techniques de recherche (prospection visuelle des greniers et des dessous de toit ; capture au filet sur les corridors de déplacement et les terrains de chasse ; recherche au détecteur d'ultrasons sur les terrains de chasse ; remontée à rebours le long des voies de déplacement et localisation des vols sociaux en essaim) ainsi que leur efficacité pour détecter la présence de l'espèce et des préférences en matière de gîtes et de terrain de chasse sont commentées. Les caractéristiques permettant l'identification et l'étude du murin de Natterer à l'aide de détecteurs d'ultrasons sont décrites. Une approche pratique de recherche du murin à oreilles échancrées est proposée.

Bioacoustics as an essential complementary inventory tool for bat conservation planning in the French overseas territories: the case of New Caledonia

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Abstract

Amongst the overseas territories administered by France 8 present altogether a remarkably diverse chiropterofauna of 132 species which is still poorly known. The French Overseas Territories Bat Conservation Group (French Mammal Society, SFEPM) prepares a strategy to preserve these species and their habitats. The recent developments in bioacoustics have allowed elsewhere to make considerable contributions to the knowledge of species distribution and ecology, and at the light of our first results gathered in New Caledonia, this discipline is ought to become a major tool for the conservation planning of bat species in these regions. We present here partial bioacoustic results of a 4 months survey of bats in New Caledonia, emphasizing on the rediscovery of the endemic *Chalinolobus neocaledonicus* and the confirmation of *Miniopterus robustior* as the world most restricted bent-winged bat. A reference call library was established (with help of Yves Tupinier) with hand released individuals, and compared with bat calls emitted in open space around a known roost. On New Caledonia main island, we found that *C. neocaledonicus* calls are hyperbolic FM with a maximum of energy (Emax) around 33-36 kHz (N=156), while miniopterine bats emit above 50 kHz. Amongst these bent-winged bats, *M. robustior* restricted to Lifou and Mare islands could be discriminated with a lower Emax at 42-45 kHz.

Résumé

La bioacoustique en tant qu'outil essentiel d'inventaire complémentaire pour la conservation des chauves-souris dans les départements et territoires français d'outre-mer : le cas de la Nouvelle Calédonie. Parmi les territoires d'outre-mer administrés par la France, huit ont une faune chiroptérologique remarquablement diversifiée, composée au total de 132 espèces, encore largement méconnues. Le Groupe Chiroptères d'Outre-Mer de la Société Française pour l'Etude et la Protection des Mammifères (SFEPM) élabore une stratégie de conservation de ces espèces et de leurs habitats. Les progrès récents en bioacoustique ont permis ailleurs d'accroître considérablement les connaissances sur la distribution des espèces et leur écologie. A la lumière de nos travaux préliminaires en Nouvelle-Calédonie, la bioacoustique apparaît comme un outil majeur pour la conservation des chauves-souris de ces régions. Nous présentons les résultats bioacoustiques partiels d'une prospection chiroptérologique de quatre mois en Nouvelle Calédonie, en mettant en exergue la redécouverte de l'espèce endémique *Chalinolobus neocaledonicus* et en confirmant *Miniopterus robustior* en tant que minioptère le plus localisé au monde. Une collection de sons de référence a été constituée avec Yves Tupinier, à partir d'animaux relâchés après capture, et comparée à des signaux émis en milieu ouvert autour de gîtes connus. Sur l'île principale de Nouvelle-Calédonie, nous avons découvert que les émissions de *C. neocaledonicus* se présentent sous forme de FM hyperbolique avec un pic d'énergie située entre 33-36 kHz (N= 156) alors que les minioptérinés émettent au-delà de 50 kHz. Parmi ces minioptères, *M. robustior*, localisé aux îles de Lifou et de Maré, se caractérise par des émissions dont le pic d'énergie est plus bas, entre 42-45 kHz.

Habitat use and conservation issues of bats of Bangladesh

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Abstract

Study is based on the direct field observation and collection of data on bats from hilly and mangrove forests and plain woodland in the rural and urban areas for a several years. Sixteen species of bats have so far been reported and recorded from Bangladesh. Of these, habitats and conservation issues were studied on Fruit bats (*Pteropus giganteus*) and *Taphozous* sp. false vampire (*Megaderma lyra*), yellow bats *Scotophilus* sp. and *Pipistrellus* sp.

Fruit bats are colonized more in the open woodlands habitats in the plain and few in botanical garden of the urban areas. The change of habitats is noticed with climatic changes, seasonality and food abundance. Some habitats have been eliminated from the district towns by the destruction of habitats because of the increasing human population, commercial expansion and cutting of roosting trees. *Mangifera indica, Ficus bengalensis*, *Albizea* sp.*, Eucalyptus* sp.*, Bambusa* sp. etc. are being used as roosting habitats of Fruit bats. False vampires are usually roosted in small colonies in the unused buildings left by Hundu Jamindars (Land lords and administrators) and in some ruin temples, buildings and rarely in the old large trees.

The rest of the other species of bats find their roosting habitats in tree holes, compact tree trunks, palm trees, the ground holes of hills, crevice and furrow of buildings, etc.

Lack of awareness about the biology and value of bats, destruction of habitats, shortage of food, agrochemical use in tree fruits, environmental degradation are the major issues for conservation of bats in Bangladesh.

Résumé

Utilisation de l'habitat et problèmes de conservation des chauves-souris au Bangladesh. Cette étude est basée sur plusieurs années d'observations de terrain et de collectes de données relatives aux chauves-souris des mangroves, des forêts collinéennes et de plaines des zones rurales et urbaines du Bangladesh. Seize espèces de chiroptères ont été répertoriées au Bangladesh. Les problématiques d'habitats et de conservation ont été étudiées pour *Pteropus giganteus*, *Megaderma lyra, Taphozous* sp., *Scotophilus* sp. et *Pipistrellus* sp.

Les chauves-souris frugivores colonisent préférentiellement les boisements ouverts de plaine et quelques jardins botaniques des zones urbaines. Des changements d'habitats sont notés en relation avec les changements climatiques, les saisons et la disponibilité trophique. Certains habitats ont disparu à proximité des grandes zones urbaines du fait de la pression anthropique et de nombreux arbres-gîtes qui ont été abattus.

Mangifera indica, Ficus bengalensis, *Albizea* sp., *Eucalyptus* sp., *Bambusa* sp., etc. sont utilisés comme gîte par les chauves-souris frugivores. Les faux vampires *Megaderma lyra* forment généralement de petites colonies dans les bâtiments abandonnés, dans certains temples en ruine et, plus rarement, dans de grands et vieux arbres.

Les autres espèces établissent leurs gîtes dans les troncs d'arbres, les palmiers, les cavités souterraines, les crevasses et les disjointements de bâtiments, etc.

Le manque de connaissances au sujet de la biologie et de la valeur patrimoniale des chauves-souris, la destruction des habitats, les pénuries alimentaires, l'utilisation de produits phytosanitaires dans la production de fruits, la dégradation environnementale sont les principales problématiques pour la conservation des chiroptères au Bangladesh.

Implementation of the point counting method to monitor foraging bats in Estonia

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Abstract

From August till September 2001 and from April till July 2002 the point counting method (PC) was used to count foraging bats in a countryside landscape at Melliste and Poka in southern Tartumaa. The Pettersson D200 heterodyne detector was used to record bats. The task was to identify bats, estimate their numbers and compare the results of 5- and 10-minute counting periods. Two main habitats (edges of lakes with trees ; and forest edges, sometimes in the vicinity of buildings) were chosen for the counts, six points in each habitat. The counts were carried out twice a month, always with suitable weather. The counting result was presented as maximum number of animals of each species recorded per 100 points (Masing, Lutsar & Lotman, 2002).

By September 2001 the following preliminary results were received. First, considerably more animals and more species were foraging near the water (four species and 111 animals per 100 points) compared to the sites away from the water (one species and 14 animals). Second, the 10-minute counting period gave a slightly larger number of animals (n = 72) per 100 points, but the same number of species (four) compared to the 5-minute counting period (n = 60 animals).

Résumé

Amélioration de la technique de point d'écoute pour étudier les chauves-souris en activité de chasse en Estonie. D'août à septembre 2001 et d'avril à juillet 2002 la méthode des points d'écoute a été utilisée pour dénombrer les chauves-souris en activité de chasse dans un paysage de campagne à Melliste et Poka, en Tartumaa méridional. Un détecteur hétérodyne Pettersson D200 a été utilisé pour enregistrer les chauves-souris. La tâche a consisté à identifier les chauves-souris, estimer leur nombre et comparer les résultats obtenus sur des périodes de 5 ou 10 mn Six points d'écoute ont été réalisés dans les deux habitats principaux (berge arborée de lacs ; lisière forestière, parfois à proximité de bâtiments). Les comptages ont été réalisés deux fois par mois par conditions climatiques favorables. Le résultat de comptage correspond au chiffre maximum obtenu par espèce sur 100 points (Masing, Lutsar & Lotman, 2002).

En septembre 2001, les résultats préliminaires suivants ont été obtenus : l'abondance d'individus en activité de chasse et la diversité d'espèces maximales sont enregistrées près de l'eau (4 espèces et 11 individus pour 100 points) alors qu'on obtient 1 espèce et 14 animaux à l'écart des points d'eau ; les points d'écoute de 10 mn permettent d'obtenir un peu plus de contacts d'animaux (n=72 contre 60) mais le même nombre d'espèces que les points d'écoute de 5 min (n=4).