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THE VOCAL REPERTOIRE OF *Graphiurus parvus*, AND COMPARISONS WITH OTHER SPECIES OF DORMICE

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ABSTRACT. A preliminary description of the vocal repertoire of *Graphiurus parvus* is presented together with a survey of published data on vocalization in other species of the Gliridae. All species studied have a relatively rich vocal repertoire with tonal and noisy vocalization types. *Graphiurus parvus* vocalizations can have frequency components in the range from about 1 kHz to well into the ultrasonic range above 20 kHz. Hypotheses on the homology of the various vocalization types of the Gliridae are hardly possible.

Key words: dormice, Africa, vocalization, behaviour.

Graphiurus parvus'UN VOKAL REPERTUARI VE DİĞER AĞAÇ FARESİ TÜRLERİNİNKİ İLE KARŞILAŞTIRILMASI

ÖZET. *Graphiurus parvus*'un vokal repertuarının bir ön tanımı, diğer Gliridae türlerinin vokalizasyonu ile ilgili yayınlardaki bilgilerle karşılaştırılarak verilmiştir. İncelenen tüm türler farklı vokalizasyon tipleri içeren oldukça zengin bir vokal repertuara sahiptir. *Graphiurus parvus*'un vokalizasyonlarının frekans bileşeni yaklaşık 1 kHz'den 20 kHz'in üstündeki ultrasonik seslere kadar uzanan bir dağılım gösterebilir. Gliridae türlerinde incelen bu vokalizasyon tiplerinin homolojisi üzerinde hipotezler sunmak henüz olası değildir.

Anahtar sözcükler: ağaç fareleri, Afrika, vokalizasyon, davranış.

INTRODUCTION

Eleven species of dormice occur in the Palaearctic Region, and another ten or so in Africa (Holden 1993). The African species all belong to the genus *Graphiurus*, a group of small to medium-sized dormice of mainly inconspicuous gray colour. Very little is known about their biology and behaviour (Webb & Skinner 1995). The same is true for our knowledge of their vocalization. An anecdotal statement by Kingdon (1974), "Young dormice grow rapidly and twitter shrilly", is about all that has been reported about the vocalization of *Graphiurus* so far.

The purpose of our study is to present a preliminary description of the vocal repertoire of *Graphiurus parvus* (True, 1893) and to outline a preliminary framework which may be used to compare its vocalization with that of other genera and species of Gliridae.

MATERIAL AND METHODS

Observations and sound recordings were made in a breeding colony of *Graphiurus parvus* of about 50 individuals kept in a cage (205 x 105 x 75 cm), furnished with nest boxes, tree branches and fresh twigs. The original individuals (1♂, 2 ♀♀) were obtained from the pet trade, with probable origin West Africa. Animals were fed with a variety of fruit, insect larvae and dry dog food. Sound recordings were made with portable tape recorders UHER Report 4200 and 6000 Universal at 19 cm/s and 9.5 cm/s recording speeds and SENNHEISER MD 441, ME 80 and ME 88 directional microphones. According to manufacturers' specifications this equipment allows sound recordings in a frequency range from about 50 Hz to 20 kHz. Because of the shyness of the animals all recordings were made with the microphone fixed on a tripod close to the animals' enclosure and a constant input level setting for one coherent recording session of one tape reel's length. This procedure constitutes a general drawback for recording quality. The animals being nocturnal and visibility of the vocalizing individual(s) in the cage being poor, detailed observation of the behavioural contexts in which vocalizations occurred was very limited.

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Sound analyses were made with a MEDAV Spektro 3000 sound spectrograph (software version 4.4, 1996) with various analysis settings. Settings are specified in the figured sonagrams. The Spektro 3000 has a built-in automatic antialiasing filter for recording analogue signals in a range up to 20 kHz. Vocalizations analyzed of other species of the Gliridae were made from commercially available CDs or cassettes and were obtained as copies on cassette from the animal sound archive of the Humboldt-University in Berlin. The original recordings had been made with various equipment and various recording settings, in all cases different from the one used in this study, thus somewhat qualifying the comparability of these analyses with those of our recordings of *Graphiurus parvus*.

As the taxonomy of the genus *Graphiurus* still requires revision (Holden 1993), voucher specimens have been deposited for further study in the collection of the Museum Alexander Koenig, Bonn.

RESULTS

In *Graphiurus parvus* we were able to preliminarily distinguish 4 to 6 sound types (see Tables 1, 2). Until now we have only named them tentatively because we would like to avoid the use of a term already established for a vocalization of other species of the Gliridae (or other sciurognath rodents) without evidence that phylogenetically it is the same type of vocalization in *Graphiurus*. The terms used (Tables 1, 2) refer to specific structural characters of the sounds and/or their impression to the human listener. It is highly likely that more sound types exist in this species than we could observe until now. The structural characters of the vocalization types as established on the basis of our recordings is shown in Table 2. A few of the sound types show a wide range of structural variability, the others are relatively stereotyped. However, our sample of recordings is highly unlikely to cover the whole range of structural variability of each vocalization type listed in this species. The repertoire comprises discrete vocalization types and others that very probably belong to graded systems. Tonal, noisy or intermediate and click-like vocalizations are documented and may have frequency components in the range from about 0.3 kHz to > 20 kHz but most are limited to only a specific portion of this range. The rapid-down sweep is classified as '(tonal)' (see Table 2) because the frequency band is modulated over such a wide frequency range so rapidly that the human auditory impression is that of a click-like sound. Due to the lack of appropriate recording equipment we could not check for the presence of purely ultrasonic vocalizations. It is established, though, that all glirid species studied in this respect so far can hear well in the ultrasonic range (Kahmann & Ostermann 1951; Schleidt 1952). Considering the fact that some vocalization types nearly cover the complete frequency range from below 0.5 kHz to about 20 kHz and the species' small size, it is noteworthy that other vocalization types are largely restricted to the range below 1 kHz. All tonal vocalization types are frequency modulated, some of them with very rapid modulation. With the possible exception of one vocalization type modulation patterns in the different types documented so far are fairly stereotyped: either down-sweeps or v-shaped or inverted v-shaped. Nearly all vocalization types documented are primarily uttered serially, sometimes in rapid volleys. The majority of the vocalization types is short (< 50 ms), interval duration between the sounds in bouts can vary but can also be fairly regular and often very short (< 100 ms). Intensity of the calls, their rate of emission and/or number per calling bout seems to increase with increasing motivation. It is not clear yet whether in sound types with variable tonality/noisyness tonality decreases with increasing intensity. The interpretation of the structure of the vocalization type 'rapid-down sweep' constitutes a problem in as far as frequency components as high as nearly 40 kHz are traceable in the sound spectrograms (checked by analysis of original recordings played back at half speed) although the technical specifications of the recording equipment used ought to rule out that such high frequencies are registered. Moreover, two frequency bands exist which are not harmonically related (see Fig. 1 h). The cause of these two phenomena is still unsettled, a recording/analysis artifact cannot be excluded.

Data on behavioural contexts and possible functions of the various sound types in *Graphiurus parvus* (see Table 1) are still limited because of the difficult conditions for close and lasting detailed observation of the situations in which vocalization occurred and the behaviour of vocalizing and other individuals. Most of the vocalizations we recorded seemed to occur in the context of agonistic behaviour. Friendly close contact situations like females with dependent young or a male courting a female are likely to be accompanied by vocalization types which we may be missing in our recordings as well as possible long distance calls.

Table 1. Vocal repertoire of *Graphiurus parvus*: Classification of vocalization types based on physical structural characteristics.

Vocalization type	General description	Senders	Behavioural contexts	Motivation of sender	Function(s)	Comments
twitter	rapid regular series of very short tonal twittering sounds	ad. ♂♂, ♀♀(?)Juv.(?)	non-aggressive close-range situations	friendly	appeasement reassurance	
chirp	high-pitched, faint, very short tonal sounds with varying frequency modulation, sometimes in short, rapid series	ad. Juv. (?)	?	?	?	several structurally different chirp types documented which may have different functions
kecker/shriek	usually volleys of short explosive sounds of varying noisyness and pitch, calls sometimes extended	ad.+juv. ♂♂ + ♀♀	agonistic interactions	aggressive? defensive?	aggressive?, defensive? threat	kecker and shriek represent a sound continuum varying in several structural parameters
rapid down-sweep	barely audible very faint and short sounds	ad.+juv.(?)	?	?	?	structure of vocalization type not yet fully clear

Table 2. Vocal repertoire of *Graphiurus parvus*: Structural characteristics of vocalization types.

	Vocalization type					
Structural characteristic	twitter	chirp variant 1	chirp variant 2	chirp variant 3	kecker/shriek	rapid down-sweep
Duration [ms]	50-60	40	15	3 - >250	15-20	
Interval duration [ms]	30-60		~160	120-160	variable	80-20
Repetition rate [1/s]	~12		<12	<6	<16	<10
Frequency range [kHz]	0.75-3.25	10.5-14.6	8-12	4 - >20	1 - >20	12 - >20
Frequency distribution	tonal	tonal	tonal	tonal	rather tonal to fully noisy	(tonal)
Number of harmonics	<4	1	1	<4	variable	1?
FM[a]/shape	+/ inverted v	+/ inverted v	+/ v shaped	+/ v shaped		+/ rapid down-sweep
AM[b]/rate [Hz]					+/700-1000	
Frequency range of fundamental[kHz]	0.75-1.1	10.5-14.6	8-12	4.5 - >20	< 2	12 - >20
"Spectral slope"[c]	f0,f1,f2,f3			f0,f1,f2 or f1,f0,f2		variable
Frequency of maximum intensity [kHz]	~ 0.97	13.3	9	12-13	1-1.5	15-19
Main variable structural parameters	number of single sounds in sequence		number of single sounds in sequence, FM	number of single sounds in sequence, FM	duration, tonality, number of single sounds in volley	
Calls per sequence	1 - > 30		1 – 3	1 – 4	variable	2 - > 15
N[d]	78	1	11	7	91	42
Comments			sequences not always regular, calls in pairs or triplets	sequences not always regular	call structure highly variable	sequences not always fully regular

[a] FM - regular frequency modulation; [b] AM - regular amplitude modulation; [c] - intensity ranking of fundamental and higher harmonics in descending order of intensity (f0 - fundamental frequency, f1 – first harmonic, f2 - second harmonic, etc.); [d] - number of single sounds analyzed.

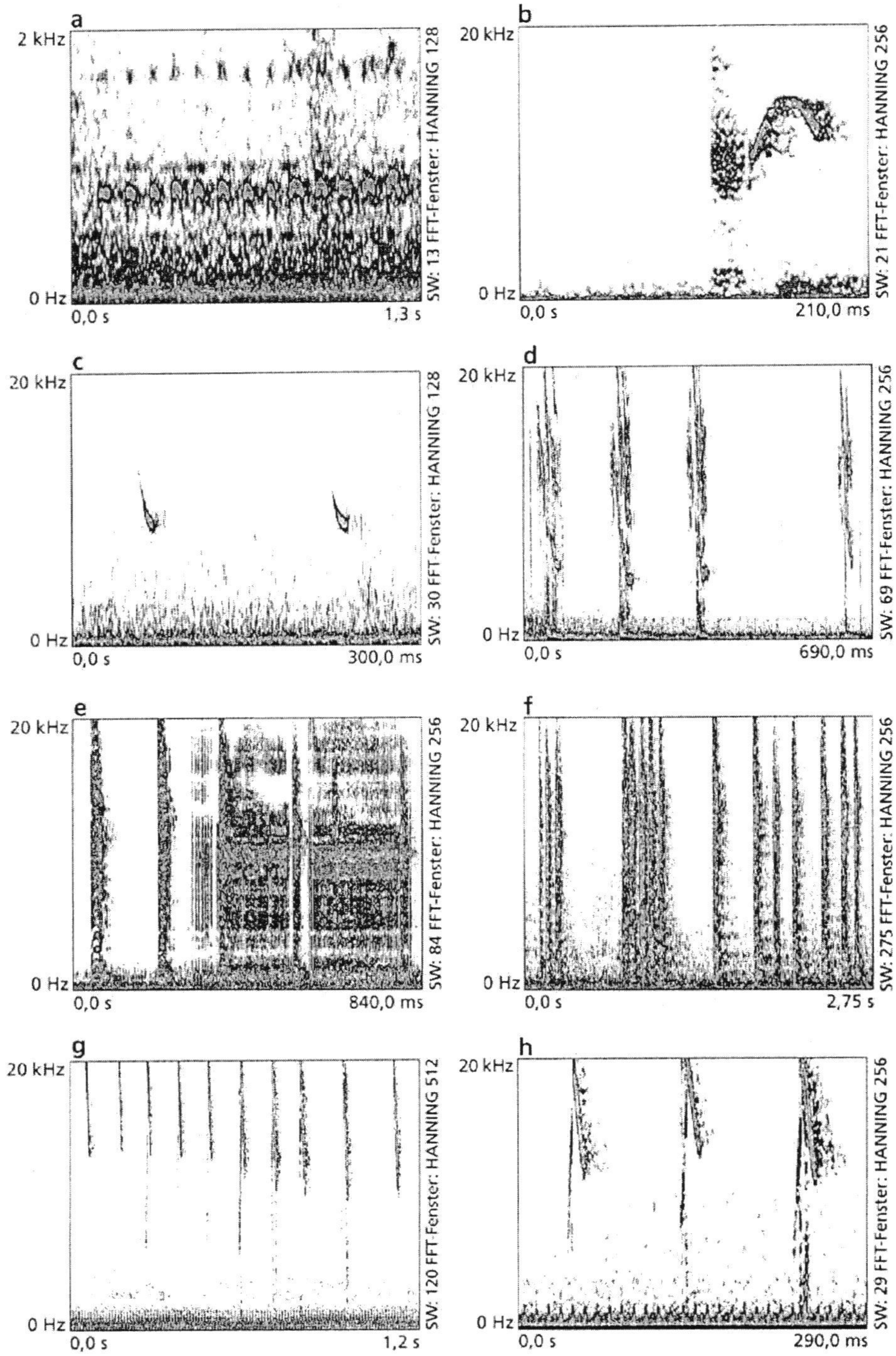

Fig. 1. Sound spectrograms of vocalization types of *Graphiurus parvus*. Note legends of frequency and time axes because these are significantly different for some sound types. Analysis settings for each sonagram are given on the right side of its frame. The structural differences between the three chirp variants are obvious. a - twitter; b - chirp, variant 1 (noise directly preceding the chirp); c - chirp, variant 2, two single calls; d - chirp, variant 3, a volley of four single sounds; e, f - kecker/shriek, two volleys of sounds of variable structure (e.g. in respect of tonality, duration, AM); g, h - rapid down-sweep - volleys of several single sounds, their peculiar structure mentioned in the text is clearly visible in h.

COMPARISONS AND DISCUSSION

Information on vocalization of *Dryomys, Eliomys, Glis* and *Muscardinus* is based on the scattered published literature - much of it non-technical - and our sound spectrographic analyses of recordings made available by colleagues and published on commercially available CDs or cassettes. The data base for the different genera is unequally extensive, uneven and far from being complete and therefore not fully appropriate for a comprehensive comparison as to each vocalization type documented in the different genera. Table 3 tries to summarize our own data and the available published information drawn from the following sources in the respective genera: *Dryomys* (Schreitmüller 1952; Konstantinov & Movchan 1985), *Eliomys* (Konstantinov & Movchan 1985; Baudoin 1982; Baudoin et al. 1984), *Glis* (Konstantinov & Movchan 1985; Koenig 1960; Schulze 1970), *Muscardinus* (Konstantinov & Movchan 1985; Schulze 1970; Zippelius & Goethe 1951). The only previous attempt at a comparative survey of vocalization in several glirid species based on sound spectrographic analyses was published by Konstantinov & Movchan (1985). For various reasons it is not possible to interpret their data and the redrawn sonagrams figured unequivocally.

Table 3. Preliminary comparative survey of vocalization in dormice (Gliridae). Classification of vocalization types is provisional as is the number of sound types listed for a specific genus/species. Only presence of the specific vocalization type is listed; generally, the data basis is too poor to make a definitive statement that a specific vocalization type is absent from a species' repertoire.

Vocalization type	Genus				
	Dryomys	*Eliomys*	*Glis*	*Graphiurus*	*Muscardinus*
twitter	+		+	+	
chirp			+	+	
kecker/shriek	+	+	+[2]	+	+
churr			+		
hissing	+				
rapid down-sweep				+	
whistle	+	+	+		+
tooth-chatter			+		
buzz (juvenile)			+		
other[1]	+	+	+		+

[1] - one or several additional vocalizations described in a genus or species which cannot be classified within the present scheme on the basis of the data presented in the literature; [2] - Krystufek, pers. comm.; + - vocalization type present or highly likely to be present.

Based on the available data the acoustic signal repertoires of all have about the same size. Vocalizations of *Graphiurus parvus* differ from those of the Palaearctic genera of the Gliridae with probably only few shared vocalization characters/types. The same holds true for a comparison of the repertoires of *Dryomys, Eliomys, Muscardinus*, and *Glis*, though. Konstantinov & Movchan (1985), on the other hand, classify all vocalization types they observed in these four genera as belonging to the same two basic categories, each of them again divided into two sub-categories. Their classification, however, is rather rough in being based on very few general structural characters only and no statement is made as to whether these categories comprise phylogenetically related sounds in the different genera. An equivalent situation is true of *Eliomys quercinus*, the glirid species for which the most detailed technical study of its acoustic communication (including data on its ontogeny) is published (Baudoin 1982; Baudoin et al. 1984). Based on physical structural characteristics, the repertoire comprises three general classes of vocalization types, which the authors further subdivide into 6 or 7 call categories.

With the likely exception of the kecker/shriek (see Table 3), it is not possible yet at present on the basis of the available data to establish whether there are vocalization types common to the family Gliridae or some of its genera which may be homologous, being either synapomorphic or plesiomorphic characters. It is possible that a more comprehensive intergeneric comparison will reveal that certain genera of the Gliridae or each of them has peculiar vocalization types. The difficulties in exactly classifying some of the vocalization types described in *Dryomys, Eliomys*, and *Muscardinus* within the scheme adopted in Table 3 and the limited and non-uniform data basis in these taxa cannot be taken as evidence at the present state of knowledge that these genera and *Graphiurus* have a smaller vocalization repertoire than *Glis*.

Auditory threshold curves have been published for three glirid species: *Glis glis, Dryomys nitedula* (Konstantinov & Movchan 1985) and *Eliomys quercinus* (Baudoin et al. 1984). No particularly detailed interpretation can be based on the curves of the former two species but they agree in showing fairly uniform hearing sensivity without significant maxima and/or minima in the frequency range from < 1 kHz to about 35 kHz. At higher frequencies hearing sensitivity drops off drastically (Konstantinov & Movchan 1985). The upper hearing limit of the garden dormouse is between 36 and 45 kHz (Baudoin et al. 1984). *Eliomys quercinus* has two peaks of about equal best sensitivity between 1 - 2 kHz and between 16 - 28 kHz, corresponding well with the main frequency ranges of different adult and juvenile vocalization types (Baudoin 1982; Baudoin et al. 1984). A similar situation may be true of *Graphiurus*, as some of the species' vocalization types are largely restricted to the low frequency range < 1 kHz and others to the higher range > 16 kHz.

Technical data on vocalization in *Dryomys*, *Eliomys*, *Muscardinus* (Boratynski et al. 1999) and *Glirulus* (Minato & Hikada 1999) were presented at the "Fourth International Conference on Dormice" in Edirne and considerably improve our knowledge of vocalization in the Gliridae. It is essential to consider our provisional sound classifications and the survey presented in Table 3 together with this new but yet unpublished data.

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