

Acoustic communication in the genus *Lynx* (Mammalia: Felidae) — comparative survey and phylogenetic interpretation

Gustav Peters

Abstract. Based on observations in captive animals and sonographic analysis a description of acoustic signals in *Lynx lynx* and *L. rufus* is presented. Both species have the same signal types; very probably these are common to all species of the genus *Lynx*. Quantitative differences exist in certain structural characteristics of some vocalizations of *lynx* and *rufus*, like in the pitch of their mews. Their acoustic repertoire includes about 10 to 12 signal types, a repertoire size corresponding to that of other Felidae and species in other families of the terrestrial Carnivora. According to signal type and structural dimension, the extent of variability within the three basic structural dimensions (amplitude, frequency, time) is different in the various signal types. In some types quantitative differences in certain structural parameters differentiate functionally separate signals. In respect of signal types present and their structural characteristics the acoustic repertoire of the genus *Lynx* shows probable synapomorphies with that of species in the genus *Felis* s. l. No synapomorphic characters are shared with the acoustic repertoire of species in the genus *Panthera*.

Key words. Mammalia, Carnivora, Felidae, *Lynx lynx*, *L. rufus*, acoustic communication, phylogenetic relationships.

Introduction

Within the limits of the rather uniform felid habitus the 'lynx' type is distinguished by the following characters: tufted ears, short tail, long legs in relation to body length, and relatively small head (Werdelin 1981). However, there is no agreement as to whether all species having these characters share them due to a common ancestor, and thus which species ought to be included in the genus *Lynx* — if *Lynx* is recognized as a genus at all in the generally unstable generic classification of the Felidae. Moreover, the phylogenetic position of the lynxes within this family is unclear, and there is no commonly accepted view as to which forms of lynx represent well defined species. A comparison of a few fairly recent surveys, even different publications by the same authors, illustrates this situation (e. g. Corbet 1978, 1984, Corbet & Hill 1980, 1986, Honacki et al. 1982, Nowak & Paradiso 1983, Tumlinson 1987).

In a detailed comparative morphological study of the lynxes, including Pleistocene fossil material, Werdelin (1981) arrived at the conclusion that *Lynx canadensis* Kerr, 1792, *L. lynx* (Linnaeus, 1758), *L. pardinus* (Temminck, 1824), and *L. rufus* (Schreber, 1776) are well defined species and sufficiently differentiated from other felids to be included in a genus of their own. Despite over-all similarity with the lynxes the caracal (*Caracal caracal* [Schreber, 1776]) is not closely related with them.

Recent phylogenetic studies of the Felidae, based on chromosome banding patterns (Kral & Zima 1980, Gripenberg et al. 1982, Kratochvil 1982), immunological (Collier & O'Brien 1985) and morphological data (Herrington 1986) concurringly

put forward the interpretation that the lynxes are most closely related to the species of the genus *Panthera*. This view is in clear contrast to the concept of the phylogenetic position of the genus *Lynx* proposed by Hemmer (1978), using a large set of morphological, paleontological, physiological, karyological, and ethological data, or by Werdelin (1983) based on skull and dental morphology. Both authors argue that *Lynx* is most closely related to *Felis* s. str.

It is the aim of the present paper to present detailed technical information on vocalization in a felid genus for which nothing but anecdotal data has been published. The results of the analysis of the acoustic signals will then be discussed within the framework of the contradictory opinions on the phylogenetic relationships of the lynxes with the other species of the Felidae. As demonstrated earlier (e. g. Peters 1978, 1983, 1984a, Hemmer 1981) acoustic signals of felids as structurally well defined characters can yield useful clues in this respect.

Materials and methods

This study only deals with acoustic signals in *Lynx lynx* and *L. rufus*. No data are available for *L. pardinus* and only a short series of subdued mews was heard in an adult female of *L. canadensis* but could not be recorded. All observations drawn on and all tape recordings analyzed were done in captive animals in zoos or private animal parks. The scant published data on vocalization in lynxes will be discussed in the text where relevant. Detailed information on acoustic behaviour of wild lynxes is lacking.

Several sound types listed here are not documented on tape, others could not be recorded with a quality suitable for proper sonographic analysis. Signal types are only dealt with as far as unequivocal auditory identification was possible. Tables 1 and 2 list the material analyzed. Very few observations and recordings of acoustic communication in juveniles of both species

Table 1: Sonographic material analyzed in adult *Lynx lynx* and *L. rufus*.

species	signal type	no. analyzed (in no. of ♂)	no. analyzed (in no. of ♀)
<i>L. lynx</i>	mew	120 (4)	76 (1)
	purr		2 (2)
	yowl		8 (1)
	growl	2 (1)	
<i>L. rufus</i>	mew	7 (1)	35 (1)
	gurgle		2 (1)
	wah-wah		3 (1)
	yowl	3 (1)	
	growl		2 (1)

Table 2: Sonographic material analyzed in juvenile *Lynx lynx* and *L. rufus*.

species	age	signal type	no. analyzed	no. of individuals
<i>L. lynx</i>	4 days	mew	8	?
	1 month	mew	19	?
	3 months	mew	4	1 ♀
<i>L. rufus</i>	4½ months	mew	8	1
	10 months	purr	2	1 ♀, 1 ♂

could be made. Most recordings had to be done without the possibility to observe the animals while vocalizing. Therefore data on ontogeny of vocalization presented here are fragmentary.

All recordings of acoustic signals in *L. lynx* were done with a portable tape recorder UHER 4200 Report Stereo and a microphone SENNHEISER MD 421-2. Most recordings of *L. rufus* were done with portable tape recorders UHER 4000 Report IC or NAGRA 4.2 with a microphone SENNHEISER MKH 816T. Recording speed generally was 19 cm/s, and recording was on one track only. Both microphones have a similar reasonably flat frequency response in the range from 100 Hz to 10 kHz, the frequency range of the vocalizations in the species studied. With very few exceptions the input level was controlled manually and usually not changed during a coherent bout of vocalization under fairly constant conditions.

Sonographic analysis was done on a VOICEPRINT Model 4691A in two modes for most signals: normal/WB (300 Hz) and normal/NB (50 Hz), to attain maximal temporal resp. frequency resolution. Measurements of structural details in the sonagrams were done with a calibrated plastic overlay, mainly in the type of sonagram allowing the more accurate measurement of the respective parameter. Because of the inherent frequency inaccuracy of the sonograph and additional measurement errors, frequency measurements are only given to the nearest 0.1 kHz, time measurements analogously to the nearest 0.01 s. Repetition rates are calculated according to method B as detailed by Scoville & Gottlieb (1978). Direct measurements of signal amplitude during recording were not made. Amplitude given in this paper represents the signals' loudness as perceived by the observer. No quantitative comparisons of amplitude of different sounds are possible because recording conditions were not standardized. The range and fidelity of structural details of an acoustic signal reproducible in a sonagram, among other factors are influenced by recording conditions and quality. This general qualification pertains to all structural data presented below, especially to frequency parameters. Limitations of sonographic analysis as described by e. g. Davis (1964), Watkins (1967), or Gaunt (1983) have to be borne in mind.

In this publication the terms 'acoustic signal' and 'vocalization' are used for any type of sound the animals produce, 'vocal' signals are generated by oscillations of the vocal chords, 'non-vocal' sounds in any other way. Acoustic signal types are defined primarily on the basis of their structural characteristics, including aspects on sound generating structures and mechanisms as far as available. Functionally different derivatives of the same basic structural pattern are regarded as the same vocalization type within this concept.

Results

In the following text the acoustic signals of *L. lynx* and *L. rufus* will be dealt with both together type by type. Only data in which the two species differ will be listed separately. Subsequently, the few available data on ontogeny of vocalization in the lynxes will be presented in the same style. Many signal types can be mixed; mixed vocalizations will only be mentioned and not be discussed in detail.

Mew (Figs. 1a—e, 2a—c, f)

General description: Mews in lynxes usually are relatively short, with little pitch-change during the call. Forms with a clearly disyllabic sound pattern like the domestic cat's meow are uncommon. In both species mews are very variable in respect of amplitude, tonality, and pitch, *rufus* mews usually being higher-pitched than those of *lynx*. Low-amplitude forms usually are more tonal and more variable in pitch than high-amplitude mews. The mew is the most commonly listed lynx vocalization in the literature, under various names though (Lindemann 1950, Reschke 1960, Kunc & Stehlik 1968, Matjuschkin 1978, Stehlik 1978, Heptner & Sludskij 1980, McCord & Cardoza 1982, Tumlinson 1987). Mews can be coupled and mixed with various other signal types.

Behavioural contexts and functional aspects: The wide range of mews occurs in various behavioural contexts and forms of different amplitude, duration, tonality, and/or pitch very likely have different functions. In females tonal and relatively low-amplitude mews of variable pitch are most common for a few weeks after their kittens have left the den. These forms are close contact calls. Main calling activity in both female and male lynxes is during the mating season in early spring (Ognev 1962, Bürger 1966, Wayre 1969, Stehlik 1978, 1983, Heptner & Sludskij 1980). Then the animals may utter series of mainly intense mews with fairly regular intervals between the calls (Tembrock 1968). These mews are long-distance signals and serve to bring the partners together for mating. In addition to the two forms mentioned the wide range of mews is further differentiated functionally. An exact structural definition of different functional variants requires more data than available at present.

Structure: Most lynx mews have a duration of 0.4–0.7 s, only few are longer than 1 s; in fairly regular series they may be repeated at intervals of about 0.7–2 s. The frequency range of *lynx* mews is mainly from 0.2–5 kHz, of *rufus* 0.6–6 kHz; main components in the former are 0.8–2 kHz (cf. Tembrock 1963), in the latter 1–2.5 kHz. In both species tonal mews have their highest energy either in the fundamental or in the first harmonic. Tonal forms of different pitch differ in the frequency range of the fundamental and/or relative energy of fundamental, first harmonic and higher harmonics. Many intense mews show rapid amplitude modulation; generally they are vocal sounds.

Gurgle (Fig. 2d)

General description: In both species the gurgle is a short, atonal sound of low amplitude, fairly low and constant in pitch with short-phased rhythmical amplitude modulation. Often gurgles are coupled to or superimposed with mews. In *lynx* it was listed by Reschke (1960) and Tembrock (1970), in both species by Peters (1984b).

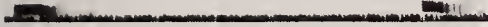
Behavioural contexts and functional aspects: Generally gurgles are close-range sounds and are most often heard in females with kittens, during courtship and mating, and friendly close-contact situations like greeting. In lynxes gurgles were observed in the first and last context listed. This acoustic signal probably has several functions, in females being an 'all is well' signal for her kittens, during greeting denoting appeasement or reassurance.

Structure: Gurgling probably is a vocal sound. Only two gurgles of a *rufus* female were available for analysis. Each is coupled to a short, faint mew, one preceding, the other following it. The frequency range is restricted to components below 1.3 kHz,

Figure 1: Acoustic signals of adult *Lynx lynx*. All sonagrams figured were analyzed on the same time basis and within the same frequency range. Therefore the one frequency and time axis shown is also applicable to the other sonagrams in the same figure. Sonagrams of the same vocalization(s) in different analysis modes have the same letter, e. g. a1 being the WB sonagram of the same sound that in the NB mode is figured in a2. This scheme is the same in all figures.

a.—c. Mews of low to medium intensity by a ♀. — d. One mew of low and the next of medium intensity by a ♂. — e. High intensity mews by the same ♂. — f.+g. Yowls of varying pitch by a ♀. — h. Purring by a ♀ (WB).

a1



a2



f1

b1



b2



c1



g1



c2



f2



d1



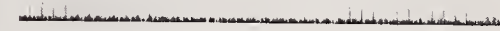
g2



d2



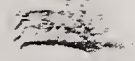
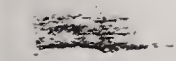
h



e1



e2



with main frequencies 0.2—0.6 kHz. One gurgle consists of 9, the other of 5 single pulses, duration is 0.32 resp. 0.16 s. Pulse repetition rate in both is about 27 pulses per s.

Purr (Fig. 1h)

General description: Purring in both lynx species is very similar to its well-known equivalent in the domestic cat. It is a continuous low-amplitude murmuring sound, like rolling 'rrrrr', produced during both in- and exhalation. In *lynx* it was listed by Reschke (1960) and Tembrock (1970), in both species by Peters (1981).

Behavioural contexts and functional aspects: Purring in *lynx* and *rufus* was observed in hand-reared animals snuggling up to people and in females while nursing or licking their kittens. The functional significance of this vocalization in the Felidae is still controversial (Leyhausen 1979). Like the gurgle it seems to function as an 'all is well' signal and a general friendly close-contact sound. Because of its very low amplitude it is only effective at very close range and body contact between sender and receiver may be important.

Structure: The exact mechanism of the production of purring in the Felidae is not yet established. Purring of two *lynx* females was available for analysis. The duration of this vocalization varies between less than 1 s to minutes on end. Frequency components present are from below 0.1 to about 7 kHz, with all major frequencies below 1 kHz. Pulses repeat at about 20 per s, indicative of a fundamental frequency of purring of around 20 Hz, being a little bit higher during expiration than during inspiration.

wah-wah (Fig. 2g)

General description: The term chosen for this sound type is onomatopoeic. In both species it is usually uttered in short bouts. A single wah is a muffled, short, atonal vocalization of low amplitude, sometimes with some tonal superimposition. Within a wah-wah bout the single sounds are relatively stereotyped and follow each other at fairly regular intervals. Forms of wah-wah fully mixed with another vocalization type are not known.

Behavioural contexts and functional aspects: The situations in which wah-wahs occur are diverse and allow no safe clue as to their function. Most often it was heard during close approaches by two animals or when a lynx was approached by a human observer. These contexts are equivalent to those in which wah-wah was observed in other felid species (Peters 1983). Most likely this sound represents an acoustic displacement activity. Its meaning to a conspecific receiver is not clear; it may include a slight threat.

Structure: Structures and processes involved in the production of this sound are not established, contribution by the vocal chords seems possible. One bout of wah-wah in a *rufus* female was available for analysis. It consists of 3 single sounds of about 0.1 s each within 0.9 s. The interval between the first and second wah is shorter than the next interval. Frequencies are fairly evenly distributed in the range from 0.3 — about 6.5 kHz. Slight structural differences between the wahs in this bout analyzed are probably due to their different tonal superimpositions.

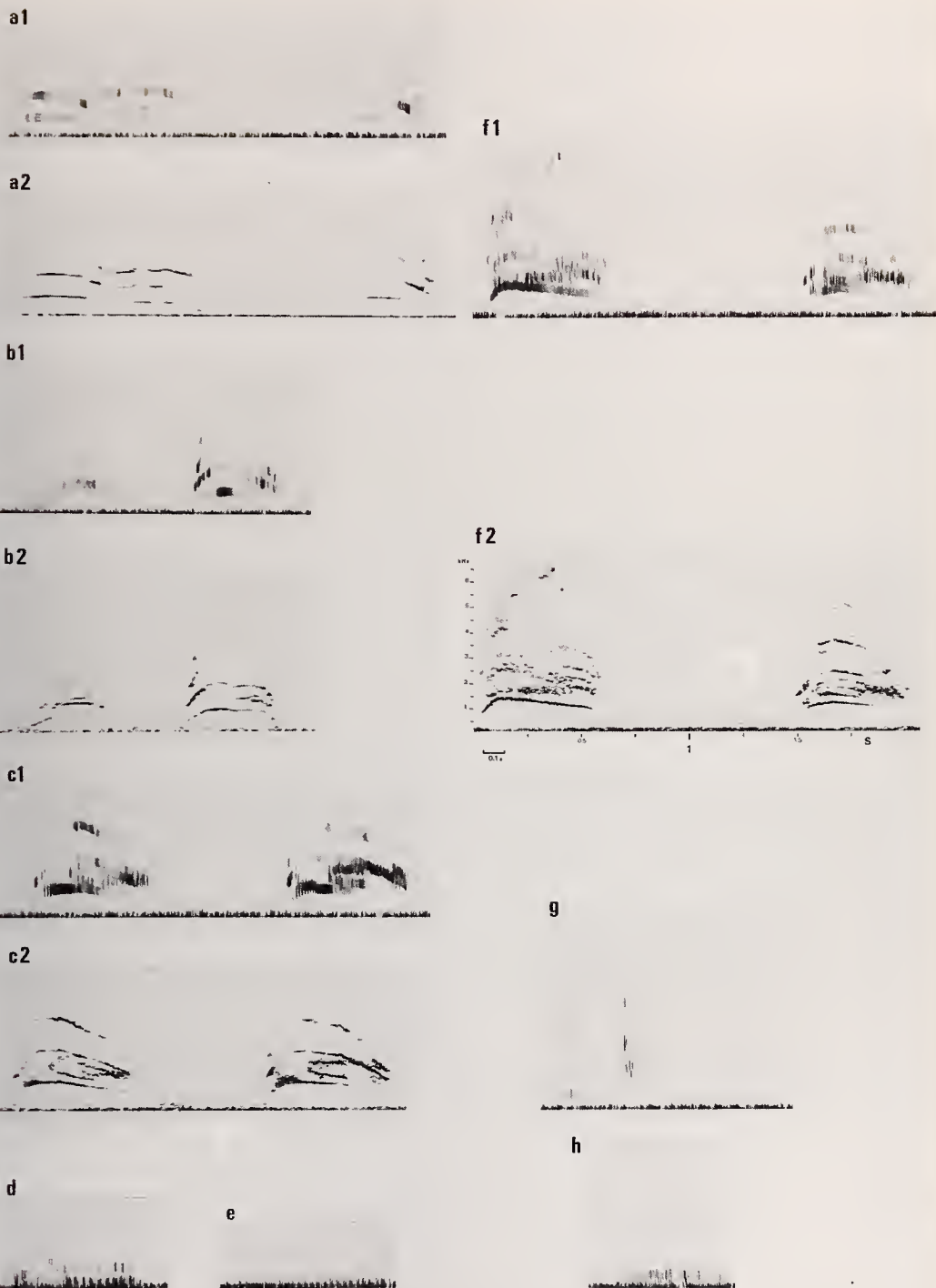


Figure 2: Acoustic signals of adult *Lynx rufus*. a. Mews of low intensity by a ♂. — b. + c. Mews of low and medium intensity by a ♀. The calls in c show rhythmical amplitude modulation. — d. A gurgle coupled to a faint preceding mew by a ♀ (WB). — e. Growling by a ♀ (WB). — f. Medium intensity mews by a ♀. — g. wah-wah by a ♀ (WB). — h. An exhalatory hiss by a ♀ (WB).

Spit

General description: The spit of lynxes is equivalent to spitting in the domestic cat and all other Felidae (Wemmer & Scow 1977). It is a very short, relatively intense, explosive burst of noise. Spits are rather stereotyped and cannot be mixed with other vocalization types. Quite often spits fade into a hiss.

Behavioural contexts and functional aspects: Spitting may occur during threatening behaviour and fights and is also used in interspecific threats, e. g. towards a human observer. It is an acoustic threat signal and denotes a defensive motivation in the sender.

Structure: The mechanism by which spitting is produced is not known, contribution by the vocal folds seems likely. No recordings of this vocalization in lynx were available for analysis. Because of the over-all similarity of this sound type in the Felidae it is safe to assume that its duration is about 0.01–0.02 s, and frequency components are fairly evenly distributed from about 0.1 — above 7 kHz, like in other felids.

Hiss (Fig. 2h)

General description: Lynx hissing is equivalent to the domestic cat's hiss; this type of vocalization is rather uniform in the Felidae. It is an atonal sound of variable duration, low to medium in intensity, usually produced during exhalation but sometimes also during inhalation. Mixed forms with other acoustic signal types are not known.

Behavioural contexts and functional aspects: Hissing may occur during agonistic close-range encounters like spitting. It is typical of an ambivalent motivation in the sender, denoting readiness to attack and/or defence resp. withdrawal.

Structure: It is not clear in which way hissing is produced and whether there are two different forms of this vocalization in the Felidae as argued by Reschke (1960). Only one poor recording of hissing in a *rufus* female was available for analysis, consisting of one inhalatory and two exhalatory hisses. Duration of the former is 0.3 s, of the two latter 0.3 s resp. 0.5 s. Frequencies are fairly evenly distributed in the range below 5 kHz, with the main components below 1 and between 2.5–3.5 kHz.

Growl (Fig. 2e)

General description: Like the other agonistic acoustic signals equivalent to growling in other felids. It is variable in duration, often prolonged, low in pitch and regularly pulsed, sounding like a deep rolling 'rrrr'. Growling may have a tonal component of variable pitch with frequency modulation, especially in mixed forms.

Behavioural contexts and functional aspects: Occurs in the same situations as spitting and hissing, denoting an aggressive motivation in the sender. Continued growling indicates readiness to attack.

Structure: Growling probably is a sound produced in the larynx. Based on the little recording material available for analysis, pure forms are restricted to the frequency range below 1 kHz. Growling is pulsed at a rate of about 50–60 pulses per s. Duration is variable, but usually this vocalization lasts for several seconds. In long forms that last for several respiratory cycles the short inhalatory phases are also 'noisy' but generally growling is an exhalatory sound.

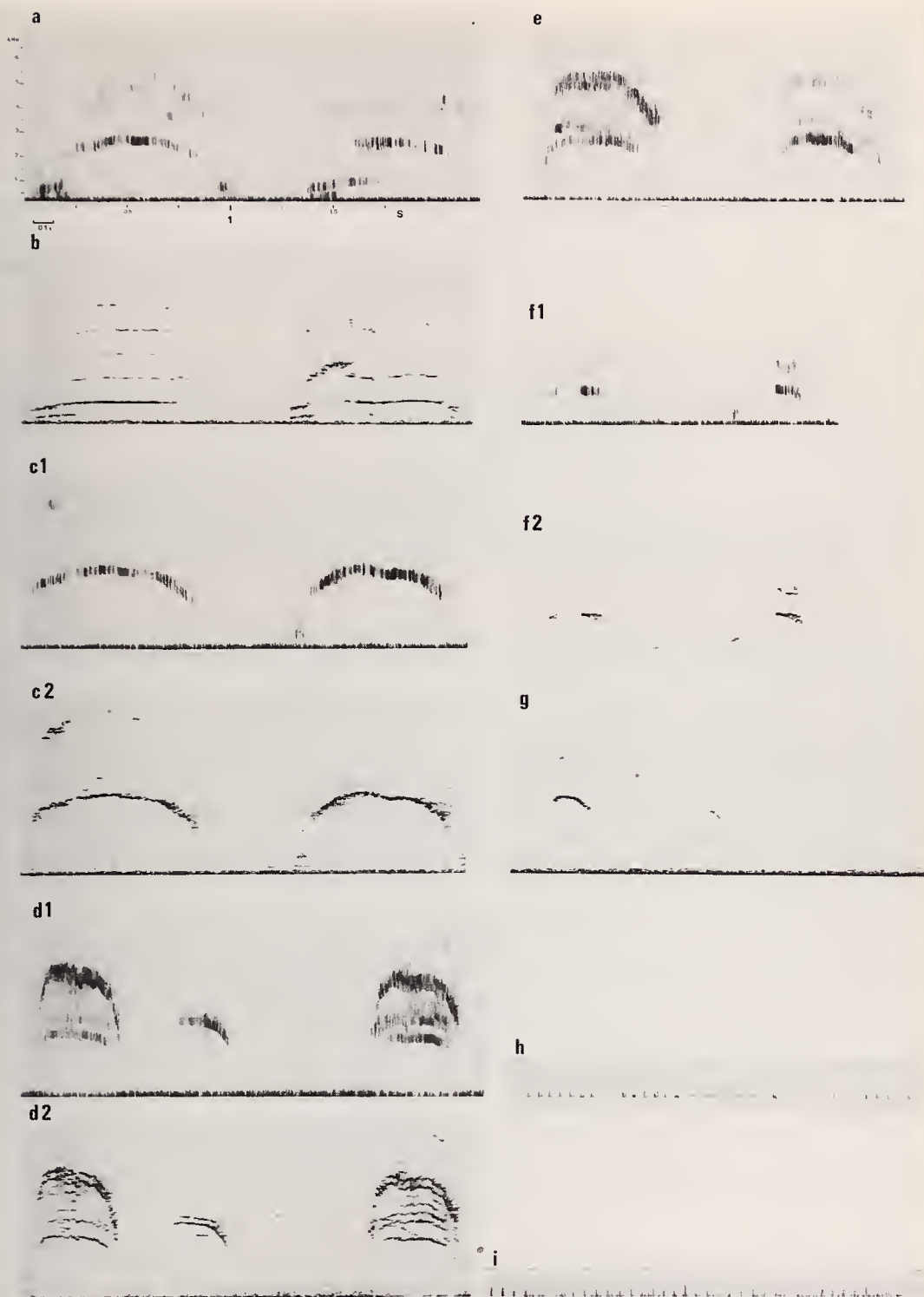


Figure 3: Acoustic signals of juvenile *Lynx lynx* and *L. rufus*. a.—c. Mews of different intensity and tonal quality by a 4-day-old *L. lynx*; a. (WB), b. (NB). — d.+e. Mews of different intensity and tonal quality by a juvenile *L. lynx* 1 month old; e. (WB). — f. Tonal mews by a juvenile *L. lynx* ♀ 3 months old. — g. Tonal mews by a juvenile *L. rufus* about 4½ months old (NB). — h.+i. Purring in *L. rufus* juveniles about 10 months old, h. a ♂, i. a ♀ (WB).

Yowl (Figs. 1f, g)

General description: In both species this is a vocalization of variable intensity, duration, pitch, and tonality, usually it is prolonged. Frequency modulation is common. Often it is mixed with growling. Yowling was also listed in *lynx* by Reschke (1960) and Tembrock (1970).

Behavioural contexts and functional aspects: Yowls were heard in various situations like females play-fighting with their kittens, being pestered by their kittens or a male and female lying close together expecting to be fed by their keeper. Probably yowling represents a mild to medium intensity threat. The functional significance of changes in pitch during the vocalization and changes in other structural parameters is not known.

Structure: Yowling is a vocal sound. Its duration may be less than 1 s, but usually is a few s. Normally it is produced during exhalation but perhaps can also be performed during short inhalatory phases between the exhalatory phases. Tonal forms resp. tonal sections of yowling have a frequency range from about 0.5–6 kHz with the main components between 0.8–2.2 kHz. Low growly forms are mainly restricted to the range below 1 kHz. With changing pitch main energy of the call is in the fundamental or first harmonic, the relative intensity of higher harmonics also varies.

Snort

General description: In both species the snort is a soft nasal exhalation of variable duration, usually sustained for a few seconds. It is hardly audible and it is not clear whether it constitutes an acoustic signal between conspecifics. Only Stehlik (1978) listed this sound in *lynx*; it is non-vocal.

Behavioural contexts and functional aspects: The situations in which this sound was observed correspond to those in which it was mentioned for Pallas' cat, *Felis manul* Pallas, 1776 by Heran (1967). Males and females produce it when threatening humans at close approach, accompanied by facial expressions and postures typical of felid threat behaviour (cf. Leyhausen 1979). Therefore, the snort may serve as an acoustic threat signal at very close range.

Structure: No structural details can be presented because no recordings were available for analysis. Probably a snort is similar to white noise with frequencies fairly evenly distributed over the whole analysis range.

Chatter

General description: Only observed in *lynx* and similar to the equivalent sound in the domestic cat described by Leyhausen (1979) as a smacking sound caused by rhythmical clashing of the jaws. It is not known whether the chatter represents an acoustic signal.

Behavioural contexts and functional aspects: Chattering in *lynx* occurred in situations like in the domestic cat when an animal is close to desirable prey that is out of its reach, e. g. behind a fence. It represents an acoustic displacement activity. In this respect it is probably similar to wah-wah. However, the latter very likely is an acoustic signal between conspecifics the meaning of which to the receiver is not yet clear.

Structure: No structural data are available for this non-vocal sound.

Ontogeny of vocalization

In both species recordings documenting ontogeny of vocalization and relevant observations are so scanty (Table 2) that the following text cannot present a proper analysis of this aspect of lynx vocalization. It is a cursory treatment of the data available. A relatively detailed description of ontogeny of vocalization in *lynx* is found in Lindemann (1955) but no structural data are presented. According to this publication distress calls, contact calls, purring, hissing and other sounds are already present by the end of the first month and in young *lynx* about 7 months old the acoustic repertoire is equivalent to that of adults. In this paper, only forms will be listed that were analyzed on the sonograph.

Mew (Figs. 3a—g)

General description: Mews of juveniles in both species are similar to domestic cat kitten mews but usually shorter. They are variable in intensity, pitch, duration, and tonality, lower intensity forms normally being more tonal and higher in pitch. The latter forms can be considerably higher in pitch than equivalent sounds in domestic cat kittens. Like in adults, disyllabic forms of mews in young lynxes are uncommon. With age mews change their pitch and the rate of occurrence of different forms changes.

Behavioural contexts and functional aspects: The situations in which mews occur also change with age. In young kittens they are most common in distress, e. g. if the animals are hungry, cold, or feel pain. In such situations mews usually are high-amplitude and relatively atonal. Later when the kittens start to leave the den low-intensity mews of mainly tonal character serve as close contact calls with the mother and siblings. However, high-intensity forms are still present and are uttered in situations of distress, e. g. when a kitten is separated from its siblings and mother. So, like in adults variation in certain structural parameters differentiates functionally different mews, and mews may change their function during ontogeny.

Structure: Mews are vocal sounds. Basically these calls of juveniles resemble those of adults. In juveniles their frequency components are in a higher range as obvious in a comparison of the figures presented. The pitch of *rufus* mews usually is higher than that of *lynx* kittens of the same age. Frequency modulation in juvenile mews is more pronounced than in adults. The main energy in mew distress calls of *lynx* kittens is in a lower frequency range during the first days after birth than during further development, and only then drops continuously. This phenomenon is also known in other felids (Peters 1978).

Purr (Figs. 3h, i)

General description: The purring of juveniles is similar to that of adults.

Behavioural contexts and functional aspects: The examples of purring in *rufus* observed were heard while the juveniles that had been hand-reared snuggled up to humans. In kittens purring very probably is an acoustic signal of contentment.

Structure: Fully equivalent in all respects to purring in adults. It is interesting to note that in certain structural characters of purring like pulse repetition rate (i. e. fundamental frequency) there seems to be no or hardly any ontogenetical change.

Table 3: Acoustic repertoire of the genus *Lynx* (observation listed only if not documented on tape).

signal type	documented in			observed in	
	<i>lynx</i>	<i>rufus</i>		<i>lynx</i>	<i>rufus</i>
mew	+	+			
gurgle		+		+	
purr	+	+			
wah-wah		+		+	
spit				+	+
hiss		+		+	
growl	+	+			
yowl	+	+			
(snort)*				+	+
(chatter)*				+	

* may be no acoustic signal

Discussion

Published data on vocalization in the genus *Lynx* give no reliable information as to the existence of other types of acoustic signals in these species than those described here. Nevertheless, few additional types may be present. Like in other felids, courtship and/or mating are likely to be accompanied by specific vocalizations and the signal repertoire during agonistic behaviour may be even more diverse. Therefore, 10–12 signal types seems to be a good estimate for the repertoire size in lynxes; this is in agreement with other species of the Felidae. Similar to most terrestrial carnivores some types structurally are quite stereotyped whereas others show large variability and form graded systems with other types. Within the same type variation within certain parameters may separate functionally different sounds.

The mew, spit, hiss, and growl (and possibly other additional agonistic signal types) are common to all Felidae. The other signal types present in the genus *Lynx* are only shared with certain felid taxa.

The gurgle is established in a large number of felids and very probably is common to all but 6 species of this family. These species have an acoustic signal type that structurally is similar and functionally equivalent to the gurgle. This is prusten in *Neofelis nebulosa* (Griffith, 1821), *Panthera onca* (Linnaeus, 1758), *P. tigris* (Linnaeus, 1758), and *P. uncia* (Schreber, 1775) and puffing in *P. leo* (Linnaeus, 1758) and *P. pardus* (Linnaeus, 1758) (Peters 1978, 1984a, b). The felid species for which the relevant vocalization is not yet documented are all likely to produce the gurgle, none is likely to have prusten or puffing. In having the gurgle *Lynx* is clearly differentiated from the felid group including *Neofelis* and *Panthera*.

The long-standing question which felids are able to purr and which are not (Pocock 1917, Peters 1981) is not yet answered definitively. In the felid classification detailed in Honacki et al. (1982) purring is established in the genera *Acinonyx*, *Felis*, and *Lynx*. There are no such structural details based on modern sound analysis techniques in *Neofelis* and *Panthera*.

The wah-wah sound is a peculiar felid vocalization which in addition to the lynxes is only documented in *Felis concolor* Linnaeus, 1771 (Peters 1978) and *Lynx caracal* (Schreber, 1776) (Peters 1983). In addition, it is known in *F. yagouaroundi* E. Geoffroy, 1803 (pers. obs.) and *F. aurata* Temminck, 1827, *F. serval* Schreber, 1776, and *F. temmincki* Vigors and Horsfield, 1827 (B. A. Leyhausen, pers. comm.). Based on observations of felid acoustic communication for more than 15 years, it seems fairly safe to state that wah-wah is highly unlikely to be present in considerably more felid species than listed here. There is not the slightest evidence for its occurrence in *Neofelis* or *Panthera*.

The yowl is only mentioned in very few technical studies of felid acoustic communication like Reschke (1960) and McKinley (1981). Lynxes share this sound type with *Felis*, it is not known in *Neofelis* or *Panthera*.

Even if the snort and the chatter do not represent acoustic signals the presence of this typical behaviour in the various species of the Felidae seems to be relevant. In addition to the lynxes, snorting is only documented in the manul (Heran 1967). There is, however, some indication that it may also occur in other *Felis* (B. A. Leyhausen, pers. comm.). A definitive statement requires more detailed data and analyses. No behavioural pattern similar to snorting in lynxes was ever observed in *Neofelis* or *Panthera*. The only other felids in which chattering is known belong to the genus *Felis*, and again nothing similar is documented in *Neofelis* or *Panthera*.

Of the vocalizations in the genus *Lynx* not common to all Felidae, none is shared with *Neofelis* and/or *Panthera*. Moreover, acoustic signal types peculiar to species of the latter two genera (Peters 1978) are not present in *Lynx*.

According to signal type, conformities of *Lynx* with other felids are diverse. Where they are present with only a few species these are mainly in the genus *Felis* s. str. The wah-wah sound shows correspondence with species like the puma, African golden cat or jaguarundi.

Phylograms of the Felidae presented by Collier & O'Brien (1985) and Herrington (1986) both place *Lynx* and *Panthera* as closely related, sharing a direct common ancestor. As hypotheses, these phylograms must be testable within the set of vocalization data presented here. It is not argued that vocalization data are definitive evidence for the construction of phylogenetic trees but that if the phylograms presented by the above mentioned authors are correct the vocalization data ought to fit in without inconsistencies.

Several felid acoustic signals not common to all species of this family can be discussed within this framework. If *Lynx* and *Panthera* share a direct common ancestor and *Neofelis* branched off considerably earlier — before other species like the puma and cheetah (Collier & O'Brien 1985) — the presence of prusten in the clouded leopard but not in lynxes needs to be explained. *Lynx* shares its relevant vocalization, the gurgle, with all other Felidae except *Neofelis* and *Panthera*. Unless it is argued that these sound types evolved convergently in the felids several times the distribution of prusten, puffing and gurgling clearly contradicts a close phylogenetic relationship of *Lynx* and *Panthera*. Within the Felidae the gurgle is regarded as a plesiomorph vocalization type, prusten and puffing are apomorph. Another apomorph acoustic signal type is the wah-wah. Lynxes share this characteristic with various species, none of them belonging to the genus *Panthera*. Yowling is also not

documented in any *Panthera* but several *Felis*. Even if they are no communicatory signals the snort and the chatter as typical behaviour patterns of lynxes similarly are also present in some *Felis* but in no *Panthera*.

The vocalization data presented clearly show that *Lynx* and *Panthera* are not closely related but the lynxes show more affinities to species of the genus *Felis* s. l. A substantiated statement on the phylogenetic tree of the Felidae ought to be based on ample data from various fields of evidence. The time given for the split between *Lynx* and *Panthera*, 2 million years B. P., (Collier & O'Brien 1985) 'is a time at which there are already several species of *Lynx* closely related to if not identical with the modern species' (Werdelin in litt.).

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Zusammenfassung

Das Lautrepertoire von *Lynx lynx* und *L. rufus* ist aufgrund von Beobachtungen an Zootieren und sonographischen Analysen beschrieben. Beide Arten besitzen dieselben Lauttypen, die sie sehr wahrscheinlich auch mit den anderen Arten der Gattung *Lynx* gemeinsam haben. In einigen Strukturmerkmalen bestimmter Lautformen existieren zwischen *L. lynx* und *L. rufus* quantitative Unterschiede, so etwa in der Tonhöhe ihrer Mauzer. Ihr Repertoire umfaßt wie bei anderen Feliden und auch Arten aus anderen Familien der landlebenden Carnivora ungefähr 10—12 Lauttypen. Der Umfang struktureller Varianz in den drei Grundparametern (Amplitude, Frequenz, Zeit) ist in den einzelnen Lauttypen je nach Parameter verschieden. Quantitative Unterschiede in bestimmten Strukturmerkmalen trennen innerhalb einzelner Lauttypen Signale unterschiedlicher Bedeutung. Die Gattung *Lynx* weist in der Zusammensetzung ihres Lautrepertoires und der Struktur einzelner Lauttypen wahrscheinlich synapomorphe Ähnlichkeiten mit Arten der Gattung *Felis* s. l. auf, mit Arten der Gattung *Panthera* bestehen keine derartigen Merkmalsübereinstimmungen.

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Dr. Gustav Peters, Zoologisches Forschungsinstitut und Museum Alexander Koenig, Adenauerallee 150—164, D-5300 Bonn 1, Germany (FRG).

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