

## Humming in bears: a peculiar sustained mammalian vocalization

Gustav PETERS, Megan OWEN and Lynn ROGERS

Peters G., Owen M. and Rogers L. 2007. Humming in bears: a peculiar sustained mammalian vocalization. *Acta Theriologica* 52: 379–389.

A peculiar sustained vocalization has long been known under various names in several bear species but not been studied in sufficient detail. Based on a critical survey of the relevant literature, analyses of tape recordings and pertinent own observations we tried to clarify the presence of this vocalization in the species of the Ursidae as well as its structural characteristics and specific mode of sound production. To avoid confusion with other vocalization types we introduce the term humming for it. Furthermore we discuss its communicatory and functional significance and formulate hypotheses as to its evolutionary origin against the background of acoustic communication signal repertoires known in the terrestrial Carnivora. Humming is present in all extant species of the Ursidae with the exception of the giant panda. It has similar structural characteristics and the same mode of sound production in all species. It is also known in adult bears but its occurrence is largely restricted to cubs. Humming is a synapomorphic vocalization type of the Ursidae which is not phylogenetically related to another vocalization type known in the terrestrial Carnivora. It is a rapid sequence of very short single sounds; long bouts of sustained exhalatory sound production are interrupted by very short inhalatory phases without sound. Both the sound and the body vibration accompanying its production are highly likely to be communication signals. Yet, controlled physiological experiments on bear mothers and cubs are still necessary to formulate and test specific hypotheses as to the communicatory function and adaptive significance of humming.

Zoologisches Forschungsmuseum Alexander Koenig, Adenauerallee 160, D-53113 Bonn, Germany, e-mail: g.peters.zfmk@uni-bonn.de (GP); Office of Giant Panda Conservation, CRES/San Diego Zoo, P.O. Box 120551, San Diego, CA 92112-0551, U.S.A. (MO); 145 West Conan Street, Ely, MN 55731, U.S.A. (LR)

*Key words:* acoustic communication, humming, phylogeny, Ursidae

### Introduction

With 8 extant species, the giant panda *Ailuropoda melanoleuca* (David, 1869), sun bear *Helarctos malayanus* (Raffles, 1821), sloth bear *Melursus ursinus* (Shaw, 1791), spectacled bear *Tremarctos ornatus* (F.G. Cuvier, 1825), Ameri-

can black bear *Ursus americanus* Pallas, 1780, brown bear *Ursus arctos* Linnaeus, 1758, polar bear *Ursus maritimus* Phipps, 1774, and Asiatic black bear *Ursus thibetanus* G. Cuvier, 1823, the bears (Ursidae) are a relatively small family in the suborder Caniformia of the order Carnivora (Wozencraft 2005). The origin of the family is thought to date back from the Eocene (Werdelin

1996, Bininda-Emonds *et al.* 1999). All species of the Ursidae are medium to large in size and largely solitary, have delayed implantation and give birth to highly altricial young in a den or a similarly secluded place (Ewer 1973, Rogers 1981, 1987, Ward and Kynaston 1995). Cubs of 7 of the 8 species of the Ursidae from a very early age on (the first day of life: Faust and Faust 1959) frequently produce a fairly loud vocalization for extended periods of time, somewhat like a fairly loud sustained monotonous hum or buzz. Especially in older cubs it is clearly audible at some distance from the den. This vocalization has long been known (Schneider 1933, Vlasák 1950) and has been identified by various names but it has hardly been described in a precise manner. Because of the persisting nomenclatorial looseness we suggest the unequivocal term “humming” in this regard. The term “humming” largely avoids confusion with other vocalization types of the terrestrial Carnivora and does not imply any functional connotation. In the general context of acoustic communication in mammals, the most remarkable characteristic of humming is its sustained production (usually for several minutes) at considerable loudness, with only very short and hardly noticeable interruptions.

Acoustic communication in the Ursidae is relatively poorly studied and not well understood (Pruitt and Burghardt 1977, Peters and Wozencraft 1989). With the exception of the giant panda (Peters 1982, 1985, Schaller *et al.*, 1985, Zhu Jing and Meng Zhibin 1987, Kleiman and Peters, 1990), there are very few publications (Wemmer *et al.* 1976, Peters 1978, 1984, Elowson 1989) dealing technically with specific vocalization types in any of the 7 other ursid species. Here we review the relevant literature on humming, present observations on sound production and describe its general structural features in cubs and adults of the Ursidae. Furthermore, we discuss its functional and motivational aspects and phylogenetic significance.

## Material and methods

The existing literature on humming is critically reviewed on the basis of live observations and audio record-

ings. These (original tape recordings or their copies on audio CD or cassette, from various sources, see Table 1) were available in cubs/juveniles of various ages and/or adults in the 6 following species: American black bear, Asiatic black bear, brown bear, sloth bear, spectacled bear, and sun bear. Not all age classes are documented on tape in all 6 species (Table 1). The sample of adult humming is much smaller than that in bear cubs. The proportion of recordings with a quality suitable for detailed bioacoustic analysis was small compared to the entirety of taped segments available for this study because: (1) sound recording conditions in the birthing dens are typically poor. (2) often there are 2 or more bear cubs in a litter producing humming at the same time which largely makes acoustic analysis impossible. Therefore this publication is no genuinely technical bioacoustic study with statistical treatment of measurement data; restrictions this situation imposes on the interpretation of our analyses are heeded.

Although recording equipment and conditions for the recordings analyzed in this study varied, comparability of the sound analyses and the significance of their results is hardly affected because bear humming has its main frequency components in the range below 2 kHz where most differences in the technical specifications of the various equipments used are of little importance. Sound analyses were done on a sound spectrograph MEDAV Spektro-3000, Version 4.4, 1996, with HANNING window in different frequency ranges (mostly 0–1 and 0–2 kHz) and FFT window lengths (mainly 128 and 256). Window overlap generally was 50%. Effective frequency and time resolution varied with the different analysis settings but the effect this has on the rough measurements of the few structural parameters analyzed is negligible. Calculation of repetition rate was done according to method B of Scoville and Gottlieb (1978), maximum amplitude frequencies were taken from power spectra. Spectrograms figured were done with window lengths 256 (Fig. 1a) or 128 (Fig. 1b, c) and different dynamic ranges. The taxonomy of the Ursidae and other taxa of the Carnivora adopted in this publication follow Wozencraft (2005).

## Earlier descriptions and behavioural context of humming

In the literature this bear sound has been mentioned under various terms, such as humming (Schneider 1933, Meyer-Holzappel 1957, Krott and Krott 1963, Tembrock 1968, 1996), keckering (Schaller *et al.* 1985), (low) trilling (Moss 1987), trilling (Elowson 1989), nursing call (Schaller *et al.* 1985), or (dull) purring (Schneider 1933, Jonkel and Cowan 1971, Pruitt and Burghardt 1977, Jordan and Burghardt 1986). As a major portion of the pertinent literature is in German (eg Schneider 1933, Vlasák 1950, Meyer-Holzappel 1957, Faust and Faust 1959, Dathe 1967, Linke 1991), the relevant terms used in it are also listed here: *Summen* – humming, *Schnurren* – purring, *Nuckern* (a newly coined onomatopoeic term, modeled on the German word *nuckeln* – to suck). Some of the terms used are inappropriate and/or misleading. Purring implies homology with felid purring which is not correct (Peters 2002). Trilling is inappropriate because it has repeatedly been used for a vo-

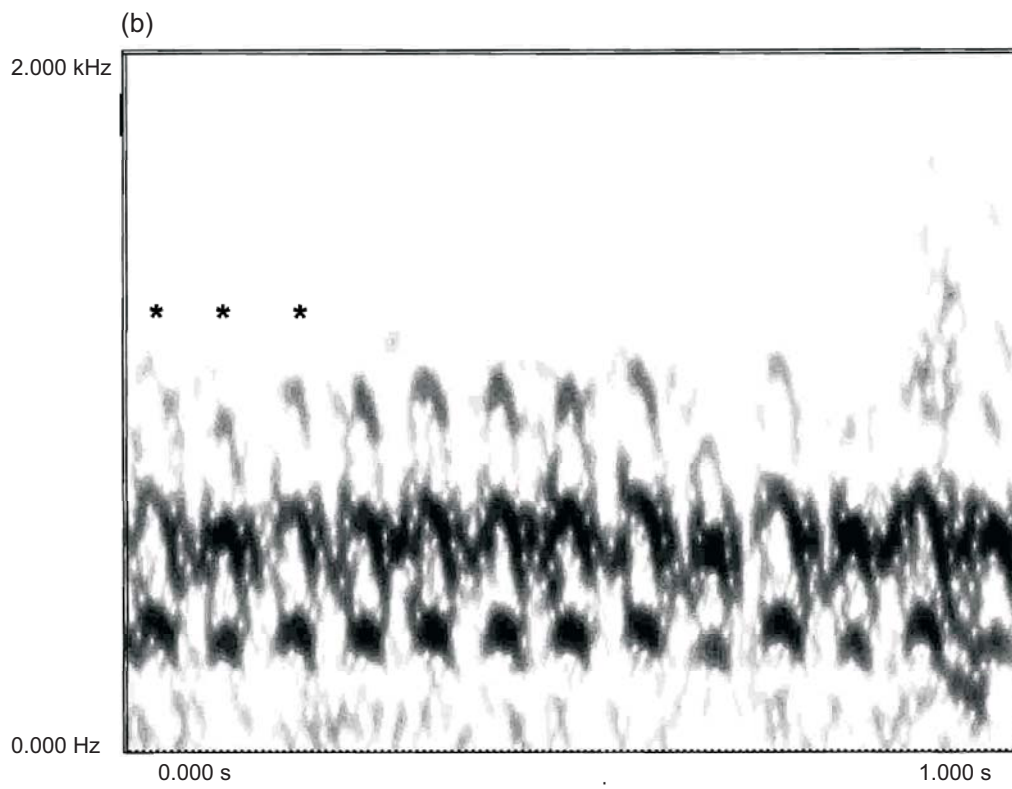
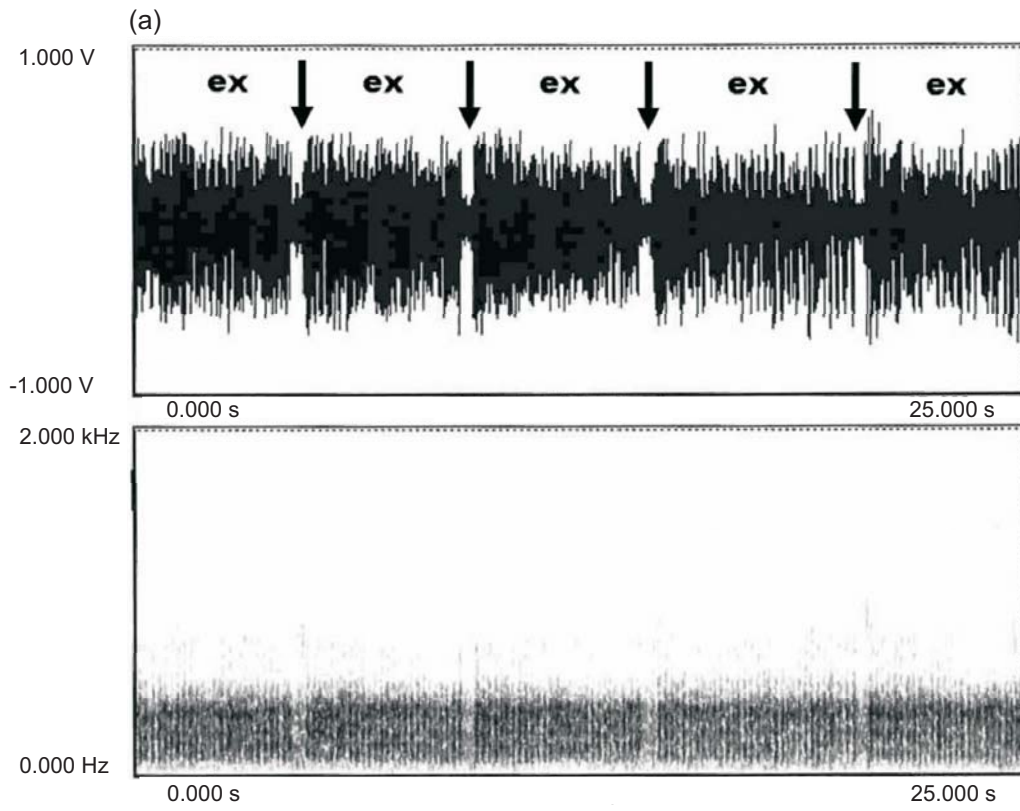
Table 1. Recordings of humming investigated in the different bear species. In a major portion of the recordings only a superficial inspection of general acoustic structure was possible. f – female, m – male, THUB – Tierstimmenarchiv der Humboldt-Universität zu Berlin, LR – Lynn Rogers, JG – John Gittleman, GP – Gustav Peters, ZFMK – Zoologisches Forschungsmuseum Alexander Koenig, Bonn.

Species	Subfamily	Age class, age	Sex	Individuals (n)	ID recording analyzed
<i>Helarctos malayanus</i>	Ursinae	cub, 5 days	?	1	cassette copy THUB D28
		cub, 15 days	?	1	cassette copy THUB S1358(?)
		15 days			
		juvenile, about 1 year	m	1	cassette copy THUB S1267
		juvenile?	?	1	cassette copy THUB S688
		adult	f	1	cassette copy THUB S678, THUB S1138
<i>Melursus ursinus</i>	Ursinae	adult	f	1	cassette copy THUB S1395
<i>Tremarctos ornatus</i>	Tremarctinae	cub, < 4 weeks	?	1	cassette copy THUB S1420
<i>Ursus americanus</i>	Ursinae	cub, 6–8 weeks	?	2	audio CD copy LR track 15
		cub, ~ 2 months	?	4	original JG JG 4/720
		cub, ~ 2–3 months	?	2	audio CD copy LR track 12
<i>Ursus arctos</i>	Ursinae	cub, 4.5 months	m	1	original GP ZFMK M85/1/933
<i>Ursus thibetanus</i>	Ursinae	cub, 2 months	f	1	original GP ZFMK 71/498

calization type in the spectacled bear (Eck 1969, Peters 1984, Elowson 1989) which is different from humming. Nursing call is misrepresentative because the occurrence of humming is neither restricted to nursing cubs, nor to cubs in the context of nursing (Kilham and Gray 2002). In its earliest detailed description Schneider (1933) contended that young bear cubs produce it while they are nursing, ie actually drinking from a teat, and that only at an older age is it uttered in other contexts. Moss (1987), who observed a mother-reared spectacled bear cub at the age of 6–7 months, remarked "... [the cub] would only trill while actually suckling." Yet, in discussing this vocalization on the basis of their close observations of bear cubs during artificial rearing from an early age, other authors (Vlasák 1950, Faust and Faust 1959, Volf 1963, Dathe 1966, 1967, Steinemann 1966, Linke 1991) clearly stated that the cubs usually do not nurse in a strict sense, ie drink from the nursing bottle,

while they produce this sound. Instead they often utter it for extended periods while they suck on the nipple, but rarely while they actually drink from it, and then again regularly after long nursing bouts (Linke 1991). Cubs may also produce this sound for extended periods in various behavioural situations like sucking on some part of their own body, that of their human keeper or a companion animal, an object, or just lying or sleeping relaxed without sucking (Linke 1991, Krott and Krott 1963, Kilham and Gray 2002).

There are very few observations of an adult wild bear producing humming. For example, one of us (L.R.) heard a wild adult American black bear (probably 4 years old) producing it when it first licked and then consumed a warmed piece of beef fat given to it. In captive adult bears humming usually occurs while the animals suck on parts of their own body or of that of another co-habiting bear, a behaviour not known to occur in wild bears.



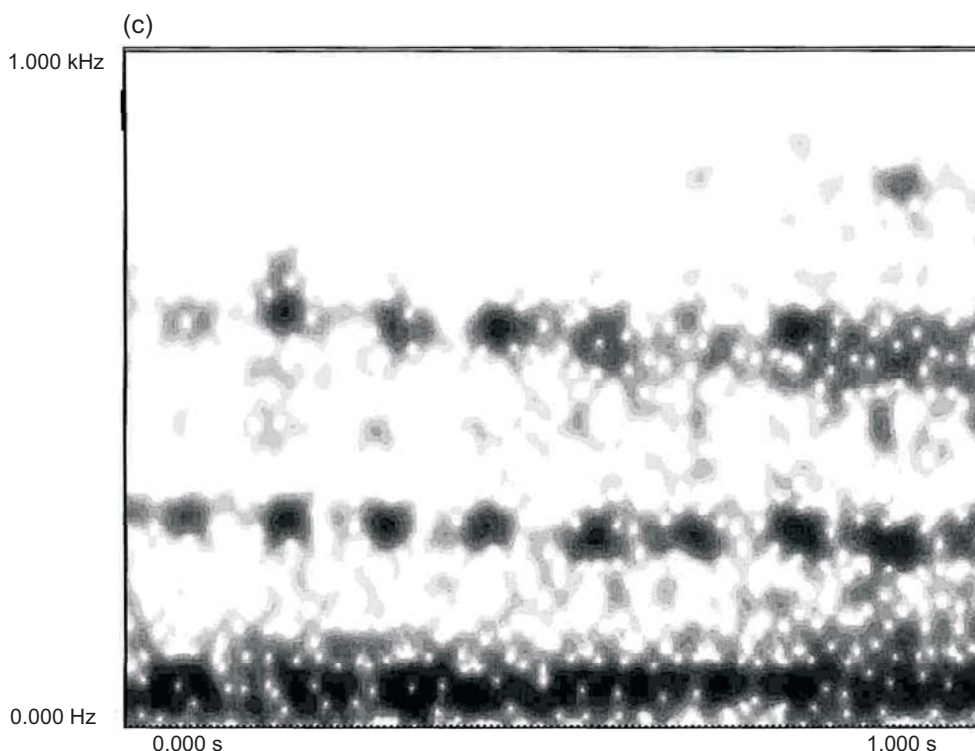


Fig. 1. (a) A coherent stretch of 25 seconds of humming in a European brown bear cub, 4 months old (top: oscillogram; bottom: spectrogram; both have the same time axis), consisting of 5 exhalatory sounds (marked 'ex', first and last one truncated) and 4 short inhalations (marked with an arrow, duration less than 0.4 s each) during which sound production is interrupted (particularly obvious in the oscillogram). This example illustrates the unusually long continuous sound production in this ursid vocalization with only very short interruptions during which the animals inhale. (b) Spectrogram of humming of juvenile American black bears (age probably 2–3 months) to show the fine structure of the single sounds (the first 3 each marked with an asterisk \*); time axis: 1 second, frequency axis 0 – 2 kHz. More than one individual is likely to vocalize most of the time but the predominantly tonal structure of the single sounds is visible (fundamental frequency, first and second harmonic present). Single sounds are repeated at a rate of about 12 per s. (c) Spectrogram of humming of a juvenile Asiatic black bear (age about 2 months); time axis: 1 second, frequency axis: 0 – 1 kHz. At times another cub is humming simultaneously. The predominantly tonal structure of the single sounds is discernible above the low frequency background noise; their repetition rate is about 10 per s.

## Results

### Sound production and structural characteristics

A few temporal structural parameters of humming are listed in Table 2. Its structure is relatively stereotyped in all species that have it, at least based on acoustic measurements in cubs. Due to sample size limitations possible structural changes of humming during ontogeny, interspecific differences in structure or other aspects of variability of this vocalization cannot be properly addressed.

For a typical example of humming in a cub of any of the 7 ursid species that have this vocalization these characters can be summarized as follows: Sustained exhalatory sound production of very short and rapidly repeated single sounds at considerable loudness with short interruptions only (duration: < 0.5 s, often considerably shorter) during which the animals inhale; duration of coherent vocalization phases between inhalations about 3.5 seconds on average, rarely up to 10 seconds and more. Assuming a resting respiratory rate of about 30 breaths per minute for a cub of approximately 8 kg body weight (about 3–4 months old) (cf. Lindstedt and



Table 2. Measurements of temporal structural parameters of humming in juveniles and adults of the species of the Ursidae. For parameters in which the number of accurate measurements is  $\leq 4$  an approximate value (~) only is given, for those which could not be measured properly due to poor recording quality './.' is entered. m – months; w – weeks.

Species	Age class/age	Duration coherent exhalatory sound production (marked 'ex' in Fig. 1a) range (s)	<i>n</i>	Duration inhalation (marked with arrow in Fig. 1a) range (s)	<i>n</i>	Duration single sounds (see Fig. 1b) range (s)	<i>n</i>	Repetition rate single sounds (see Fig. 1b) range (1/s)	<i>n</i> single sounds/in <i>n</i> sequences
<i>Helarctos malayanus</i>	juv	0.73–3.56	20	0.22–0.85	18	~ 0.07		7.6–12.4	14/3
<i>Melursus ursinus</i>	ad	./.		./.		./.		~ 14.7	10/2
<i>Tremarctos ornatus</i>	juv, < 4 w	~ 3.6		~ 0.37		~ 0.05		~ 9.7	
<i>Ursus americanus</i>	juv, ~ 2 m	0.8–11.7	42	0.17–0.6	42	~ 0.06	14	9.8–13.5	33/5
<i>Ursus a. arctos</i>	juv, 4.5 m	3.2–6.0	19	0.2–0.4	8	0.03–0.06	28	14.0–15.3	27/5
<i>Ursus thibetanus</i>	juv, 2 m	2.1–4.2	9	0.2–0.4	9	~ 0.07		9.5–10.3	12/2

Schaeffer 2002), coherent humming of more than 3–4 seconds duration is longer than a 'normal' resting exhalation phase and its ongoing production is likely to have physiological costs. The structure of the single sounds shows a different degree of tonality from largely tonal to considerable noisy superimposition, with variable frequency modulation (Fig. 1b). The main frequency range of ursid humming is  $< 2$  kHz or even lower. On average, frequencies with the highest amplitude are  $< 0.5$  kHz; usually they are in the fundamental or in the first harmonic. The duration of single sounds is  $< 0.1$  s, their repetition rate is at about 9–15 sounds per second, the rapid repetition gives the impression of a coherent sound. Occasionally repetition rate is slower at about 5–6 per second. The production of humming may start off as a series of clearly separate single sounds, uttered at an increasingly accelerating repetition rate, before reaching its typical slurred form. Alternatively, monotonous continuous humming may gradually decay into a sequence of separate single sounds with variably extended intervals before the animal ceases to vocalize.

## Discussion

### Structural characteristics of humming

The only technical measurements published so far of structural features of humming in any ursid species are for a juvenile spectacled bear (Elowson 1989): mean duration of one coherent humming period ( $5.33 \pm 3.65$  s), mean peak frequency of the single sounds ( $375 \pm 104$  Hz). A figured sound spectrogram points at a repetition rate of about 15 single sounds per second. These measurements agree relatively well with the analyses presented here (see Table 2). The statement "..... one instance of a trill by the cub that was 16 seconds long (all on one breath!)" provides additional structural information. Uninterrupted exhalatory sound production of similar duration is known to occur occasionally in humming of the other bear species included in this study. An oscillogram of humming of a brown bear cub figured by Tembrock (1968) suggests a repetition rate of about 12 single sounds per second, which is also in the range of the measurements for this parameter found in this study, as

are estimates of repetition rate (10 single sounds per second) and of duration of continuous sound production periods (approximately 4 seconds) in humming of polar bear and brown bear cubs mentioned by Schneider (1933). Therefore it is assumed that the basic structural characteristics of humming of polar bears, the only species of the Ursidae for which no pertinent recordings were available for analysis in this study, closely agree with the fairly uniform basic structure found in the other bear species. Because of the specific mode of sound production and structural characteristics in these 7 bear species it is very likely that they share the same ancestral vocalization type, ie that they are homologous.

#### **Motivational basis and communicative function of humming**

The most widely-held notion regarding the motivational basis for the production of humming in bear cubs, juveniles, and adults is that it signals comfort or contentment (Schneider 1933, Krott and Krott 1963, Jonkel and Cowan 1971, Moss 1987, Linke 1991, Kilham and Gray 2002). The behavioural contexts in which this vocalization can be observed strongly support this interpretation. Nevertheless, as all potential addressees are very close to the vocalizing individual the fact that this vocalization is so relatively loud and sustained calls for an explanation. Why signal comfort or contentment so loudly, for so long, with the risk of being detected by potential predators and very likely physiological costs? This is even more astonishing as bear mothers in the den always remain alert enough to provide for their cubs' needs instantly whenever distress or hunger are signaled vocally (L. Rogers, pers. obs.).

Schaller *et al.* (1985) suggested that the communicative function of humming is to signal the lethargic female to release milk and retain her body position. A similar view was expressed by Moss (1987) and Tembrock (1996), the latter also stating that the vibrations accompanying the production of this sound may be important for the bear mother. These hypotheses are based on the assumption that the production of this sound in bear cubs is closely connected with

their trying to nurse or actually nursing. If the detailed observations of the occurrence of humming in hand-reared bear cubs that usually it is not produced during actual nutritional nursing but most often after satiated cubs have stopped nursing (eg Vlasák 1950, Faust and Faust 1959, Linke 1991) are also true for mother-reared bear cubs, this would be difficult to integrate with these functional interpretations, especially those of Schaller *et al.* (1985). A somewhat related interpretation of the effect of this vocalization of cubs on the nursing female bear is that it is a tactile signal and/or an acoustical signal which has a relaxing effect on her and thus strengthens the mother-young bond. As such it could constitute an instance of a "tonic" communication signal (Schleidt 1973) which fosters or causes a long-term effect in the addressee.

There is growing evidence in humans and various non-human mammals that induced muscle vibrations can have effects on various physiological parameters, eg modulate release of hormones (Gosselink *et al.* 2004). It is conceivable that vibrations of the lips/cheeks which are highly likely to accompany humming of bear cubs have such effects being transmitted to the mother through the teat on which the cub sucks. It may also be that humming is not (solely) addressed at the mother, but that it represents autocommunication (the act of producing a signal which has a meaning to its sender itself) with a relaxing, soothing effect on the vocalizing animal. This could explain the relatively common observation of bear cubs and juveniles humming while they are on their own. Testible hypotheses as to the functional significance of humming in bear mother-cub communication – whether as an acoustic or a tactile signal – require controlled (playback) experiments with measurements of physiological parameters in the mother and the cubs.

#### **The evolution of humming**

There are sufficient data on the vocal behaviour of giant pandas (Peters 1982, 1985, Schaller *et al.* 1985, Zhu Jing and Meng Zhibin 1987, Kleiman and Peters 1990) to strongly suggest that adults do not have humming (Schaller *et al.*

1985). Observations of vocalizations in a few wild (X. Zhu, pers. comm.) and numerous captive-born cubs (R. Swaisgood, pers. comm.) have as yet yielded no evidence as well that they produce humming.

The fact that the giant panda is the only extant ursid species which does not hum calls for explanation. Based on the phylogeny of the superfamily Arctoidea (Vrana *et al.* 1994, Flynn and Nedbal 1998, Bininda-Emonds *et al.* 1999, Flynn *et al.* 2000, Yu *et al.* 2004b, Fulton and Strobeck 2007) and the phylogeny of the Ursidae (Thenius 1959, Kitchener 1994, Bininda-Emonds *et al.* 1999, Waits *et al.* 1999, Bininda-Emonds 2004, Hunt 2004, Waits 2004, Yu *et al.* 2004a), the presence of humming in all extant Ursidae with the exception of the giant panda may be explained by one of the following alternative hypotheses: (1) Humming is a vocalization type the Ursidae share with other Arctoidea. It was lost in the giant panda only or one of its direct ancestors. (2) It evolved in the early stem line of the Ursidae before the branch leading to the giant panda split off and then was lost later in this branch but was retained during later ursid evolution subsequent to this split-up. (3) It evolved in the ursid stem line only after the ancestor of the giant panda had branched off from it but before the split into the Tremarctinae and Ursinae occurred. (4) It evolved independently in the stem lines of these 2 subfamilies after they split. (5) It evolved independently in each respective ancestor of all extant species in these 2 subfamilies.

A well-grounded discussion of hypothesis (1) is only possible on the basis of a careful evaluation of acoustic signal repertoires of species in all the other extant families of the superfamily Arctoidea [Mephitidae, Mustelidae, Procyonidae (and red panda), Phocidae, Otariidae, Odobenidae], and in the superfamily Cynoidea (family Canidae) (McKenna and Bell 1997) as its most closely related group (Hunt 1996, Bininda-Emonds *et al.* 1999, Yu *et al.* 2004b). To the best of our knowledge very few vocalization types have been described so far in the relevant carnivore clades which are somewhat similar to humming of ursids in sound production and structure (and, as a less conclusive criterion, general behavioural context of occurrence) and hence could

be reasonably taken into account as perhaps sharing the same ancestral vocalization type with this ursid vocalization. Possible candidate vocalization types in the Procyonidae are the nursing mew of ringtails *Bassariscus astutus* (Willey and Richards 1981) (as already implied by Schaller *et al.* 1985), the churr and/or the purr of raccoons *Procyon lotor* (Sieber 1984), and the (quiet) chitter of coatis *Nasua narica* (Kaufmann 1962, Smith 1980). At the present state of knowledge, though, there is no substantial data for any of these vocalizations to support a well-founded hypothesis that it shares the same ancestral vocalization type with humming of ursids. The same is true for vocalizations in the subfamilies Lutrinae, Melinae, and Mustelinae, based on comprehensive surveys of acoustic communication in the Mustelidae like Gossow (1970), Farley *et al.* (1987), Wong *et al.* (1999), and the references evaluated by these authors. Likewise, no vocalization type has been documented so far in any species of the Phocidae, Otariidae and Odobenidae (cf. Winn and Schneider 1977, Dudzinski *et al.* 2002, Frankel 2002, Tyack and Miller 2002) for which this hypothesis would be tenable. The same is true of the species of the Canidae for which acoustic communication repertoires are well studied (cf. Tembrock 1976a, b, Fox and Cohen 1977, Lehner 1978, Brady 1981, Newton-Fisher *et al.* 1993, Schasburger 1993, Wilden 1997, Volodin *et al.* 2001, Robbins and McCreery 2003). Thus, data available do not support hypothesis (1).

As humming is present in fairly uniform structure and mode of production in 7 of the 8 extant species of the Ursidae, the most parsimonious phylogenetic explanation is that it evolved in the direct stem line of the Ursidae, either before (hypothesis 2) or after the branch leading to the giant panda split off (hypothesis 3). Currently it is not possible to corroborate or reject one of these 2 alternative hypotheses unequivocally. Hypothesis (4) is less likely to be correct because the independent evolution in the Tremarctinae and the Ursinae of a vocalization of the particular structure and mode of sound production of humming is an improbable event. The same argument is even more true for hypothesis (5) of a multiple parallel evolution of such a vo-



calization type in all species of these 2 ursid subfamilies.

Ideally a reasonable hypothesis as to the phylogenetic origin of humming in the Ursidae ought to be supported by plausible ideas of a scenario in which its evolution would have been of selective advantage. All living ursid species in the subfamilies Tremarctinae and Ursinae are the product of a relatively recent Plio-Pleistocene radiation that took place on the northern continents (Hunt 1996, 2004, Spady *et al.* 2007). Marked seasonal differences in the availability of food may have led to the evolution of winter dormancy in this radiation. Because of their nutritional adaptation to bamboo giant pandas respectively their ancestors have not experienced such differences in the availability of food (Schaller *et al.* 1985). Unlike in the other taxa of the arctoid carnivores with winter dormancy, cubs in the temperate zone bear species are born after delayed implantation while their mother is in dormancy (Garshelis 2004). This is a unique feature in mammals in the context of which the evolution of humming as an auditory and/or tactile signal of the cubs may have been a selective advantage in communicating the message of 'wellbeing' (or another) to a dormant mother over fairly long periods of time. Although giving birth while in dormancy was later lost in the tropical bear species in the Old World (sloth bear, sun bear) and New World (spectacled bear), respectively their ancestors, they retained delayed implantation, the highly altricial state of the young at birth and other plesiomorph reproductive characteristics of the Ursinae and Tremarctinae (Spady *et al.* 2007), and humming (Ewer 1973, Garshelis 2004). The last is an indication that it is highly likely to be an important communicatory signal. To date, though, there are insufficient data from which to construct an irrefutable scenario which would comprehensively describe its phylogenetic origin, adaptive significance, and communicatory function. These aspects beg further study and discussion.

Acknowledgements: Our special thanks are due to K.-H. Frommolt for placing the copies of all pertinent ursid vocalization recordings in "Tierstimmenarchiv der Humboldt-Universität zu Berlin" (THUB) at our disposal and to J. L. Gittleman for kindly doing so with his recordings of American black bear vocalizations. G. P. sincerely thanks D. G.

Kleiman for making possible several stays at the National Zoo, Smithsonian Institution, for the study of giant panda vocalization. Grants were provided within the Smithsonian Scholarly Studies Program "Analysis of Animal Communication" and by the Friends of the National Zoo (FONZ). Sincere thanks are also due to the directors, curators and carnivore keepers in the many zoos in Europe and the US where with their kind permission and assistance the observations and recording of ursid acoustic communication behaviour were possible. K. Linke, Rostock Zoo, generously shared her knowledge on bear humming with us. We are very grateful to an anonymous referee, L. Kolter, and especially to D. G. Kleiman for helpful comments on the manuscript from which it greatly benefited.

## References

- Bininda-Emonds O. R. P. 2004. The phylogenetic position of the giant panda (*Ailuropoda melanoleuca*): a historical consensus through supertree analysis. [In: Giant pandas – biology and conservation. D. G. Lindburg and K. Baragona, eds]. University of California Press, Berkeley, CA: 11–35.
- Bininda-Emonds O. R. P., Gittleman J. L. and Purvis A. 1999. Building large trees by combining phylogenetic information: a complete phylogeny of the extant Carnivora (Mammalia). *Biological Reviews* 74: 143–175.
- Brady C. A. 1981. The vocal repertoires of the bush dog (*Speothos venaticus*), crab-eating fox (*Cerdocyon thous*), and maned wolf (*Chrysocyon brachyurus*). *Animal Behaviour* 29: 649–669.
- Dathe H. 1966. Einige Bemerkungen zur Zucht des Malaienbären, *Helarctos malayanus* (Raffl.). *Der Zoologische Garten (N.F.)* 32: 193–198.
- Dathe H. 1967. Bemerkungen zur Aufzucht von Brillenbären, *Tremarctos ornatus* (Cuv.), im Tierpark Berlin. *Der Zoologische Garten (N.F.)* 34: 105–133.
- Dudzinski A., Thomas J. A. and Douaze E. 2002. Communication. [In: Encyclopedia of marine mammals. W. F. Perrin B. Würsig and J. G. M. Thewissen, eds]. Academic Press, San Diego: 248–268.
- Eck S. 1969. Über das Verhalten eines im Dresdner Zoologischen Garten aufgezogenen Brillenbären (*Tremarctos ornatus* [Cuv.]). *Der Zoologische Garten (N.F.)* 37: 81–92.
- Elowson A. M. 1989. Mother/cub vocal communication in the captive spectacled bear (*Tremarctos ornatus*). [In: Proceedings of the first international symposium on the spectacled bear. M. Rosenthal, ed.]. Lincoln Park Zoo, Chicago: 131–155.
- Ewer R. F. 1973. The carnivores. Weidenfeld and Nicolson, London: 1–494.
- Farley S. D., Lehner P. N., Clark T. and Trost C. 1987. Vocalizations of the Siberian ferret (*Mustela eversmanni*) and comparisons with other mustelids. *Journal of Mammalogy* 68: 413–416.
- Faust R. and Faust I. 1959. Bericht über Aufzucht und Entwicklung eines isolierten Eisbären, *Thalarctos maritimus* (Phipps). *Der Zoologische Garten (N.F.)* 25: 143–165.

- Flynn J. J. and Nedbal M. A. 1998. Phylogeny of the Carnivora (Mammalia): Congruence vs incompatibility among multiple data sets. *Molecular Phylogenetics and Evolution* 9: 414–426.
- Flynn J. J., Nedbal M., Dragoo J. and Honeycutt R. 2000. Whence the red panda? *Molecular Phylogenetics and Evolution* 17: 190–199.
- Fox M. W. and Cohen J. A. 1977. Canid communication. [In: How animals communicate. Th. A. Sebeok, ed]. Indiana University Press, Bloomington: 728–748.
- Frankel A. S. 2002. Sound production. [In: Encyclopedia of marine mammals. W. F. Perrin B. Würsig and J. G. M. Thewissen, eds]. Academic Press, San Diego: 1126–1138.
- Fulton T. L. and Strobeck C. 2007. Novel phylogeny of the raccoon family (Procyonidae: Carnivora) based on nuclear and mitochondrial DNA evidence. *Molecular Phylogenetics and Evolution* 43: 1171–1177.
- Garshelis D. L. 2004. Variation in ursid life histories. [In: Giant pandas – biology and conservation. D. G. Lindburg and K. Baragona, eds]. University of California Press, Berkeley, CA: 53–73.
- Gosselink K. L., Roy R. R., Zhong H., Grindeland R. E., Bigbee A. J. and Edgerton V. R. 2004. Vibration-induced activation of muscle afferents modulates bioassayable growth hormone release. *Journal of Applied Physiology* 96: 2097–2102.
- Gossow H. 1970. Vergleichende Verhaltensstudien an Marderartigen. I. Über Lautäußerungen und zum Beuteverhalten. *Zeitschrift für Tierpsychologie* 27: 405–480.
- Hunt R. M. Jr 1996. Biogeography of the order Carnivora. [In: Carnivore behavior, ecology, and evolution. Vol. 2. J. L. Gittleman, ed]. Cornell University Press, Ithaca: 485–541.
- Hunt R. M. Jr 2004. A paleontologist's perspective on the origin and relationships of the giant panda. [In: Giant pandas – biology and conservation. D. G. Lindburg and K. Baragona, eds]. University of California Press, Berkeley, CA: 45–52.
- Jonkel C. J. and Cowan I. McT. 1971. The black bear in the spruce-fir forest. *Wildlife Monographs* 27: 1–57.
- Jordan R. H. and Burghardt G. M. 1986. Employing an ethogram to detect reactivity of black bears (*Ursus americanus*) to the presence of humans. *Ethology* 73: 89–115.
- Kaufmann J. H. 1962. Ecology and social behavior of the coati, *Nasua narica*, on Barro Colorado Island, Panama. *University of California Publications in Zoology* 60: 95–222.
- Kilham B. and Gray E. 2002. Among the bears – raising orphan cubs in the wild. Henry Holt and Company, New York: 1–289.
- Kitchener A. 1994. A review of the evolution, systematics, functional morphology, distribution and status of the Ursidae. *International Zoo News* 41 (No. 245): 4–24.
- Kleiman D. and Peters G. 1990. Auditory communication in the giant panda: motivation and function. [In: Giant panda. Proceedings of the 2nd international symposium on giant panda. S. Asakura and S. Nakagawa, eds]. Tokyo Zoological Park Society, Tokyo: 107–122.
- Krott P. and Krott G. 1963. Zum Verhalten des Braunbären (*Ursus arctos* L. 1758) in den Alpen. *Zeitschrift für Tierpsychologie* 20: 160–206.
- Lehner P. N. 1978. Coyote vocalizations: a lexicon and comparisons with other canids. *Animal Behaviour* 26: 712–722.
- Lindstedt S. L. and Schaeffer P. J. 2002. Use of allometry in predicting anatomical and physiological parameters of mammals. *Laboratory Animals* 36: 1–19.
- Linke K. 1991. Handaufzucht eines Eisbären (*Thalarctos maritimus*) im Zoologischen Garten Rostock. *Jahresbericht 1990 des Zoologischen Garten Rostock*: 36–44.
- McKenna M. C. and Bell S. K. 1997. Classification of mammals above the species level. Columbia University Press, New York: 1–631.
- Meyer-Holzappel M. 1957. Das Verhalten der Bären (Ursidae). Walter de Gruyter, Berlin, *Handbuch der Zoologie* 10 (17): 1–28.
- Moss S. P. 1987. Analysis of the vocal communication between a captive mother and cub spectacled bear (*Tremarctos ornatus*). [In: International studbook for the spectacled bear *Tremarctos ornatus* (F. Cuvier, 1825). D. L. Weinhardt, ed]. Lincoln Park Zoo, Chicago: 73–91.
- Newton-Fisher N., Harris S., White P. and Jones G. 1993. Structure and functions of red fox *Vulpes vulpes* vocalizations. *Bioacoustics* 5: 1–31.
- Peters G. 1978. Einige Beobachtungen zur Lautgebung der Bären – Bioakustische Untersuchungen im Zoologischen Garten. *Zeitschrift des Kölner Zoo* 21: 45–51.
- Peters G. 1982. A note on the vocal behaviour of the giant panda, *Ailuropoda melanoleuca* (David, 1869). *Zeitschrift für Säugetierkunde* 47: 236–246.
- Peters G. 1984. On the structure of friendly close range vocalizations in terrestrial carnivores (Mammalia: Carnivora: Fissipedia). *Zeitschrift für Säugetierkunde* 49: 157–182.
- Peters G. 1985. A comparative survey of vocalization in the giant panda (*Ailuropoda melanoleuca*, David, 1869). *Bongo* 10: 197–208.
- Peters G. 2002. Purring and similar vocalizations in mammals. *Mammal Review* 32: 245–271.
- Peters G. and Wozencraft W. C. 1989. Acoustic communication by fissioned carnivores. [In: Carnivore behavior, ecology, and evolution. J. L. Gittleman, ed.]. Cornell University Press, Ithaca: 14–56.
- Pruitt C. H. and Burghardt G. M. 1977. Communication in terrestrial carnivores: Mustelidae, Procyonidae, and Ursidae. [In: How animals communicate. Th. A. Sebeok, ed]. Indiana University Press, Bloomington: 767–793.
- Robbins R. L. and McCreery E. K. 2003. African wild dog pup vocalizations with special reference to Morton's model. *Behaviour* 140: 333–351.
- Rogers L. L. 1981. A bear in its lair. *Natural History* 90(10): 64–70.
- Rogers L. L. 1987. Effects of food supply and kinship on social behavior, movements, and population growth of black bears in northeastern Minnesota. *Wildlife Monographs* 97: 1–72.

- Schaller G. B., Hu Jinchu Pan Wenshi and Zhu Jing 1985. The giant pandas of Wolong. University of Chicago Press, Chicago: 1–298.
- Schassburger R. M. 1993. Vocal communication in the timber wolf *Canis lupus*, Linnaeus – structure, motivation, and ontogeny. *Advances in Ethology* 30: 1–84.
- Schleidt W. M. 1973. Tonic communication: continual effects of discrete signs in animal communication systems. *Journal of Theoretical Biology* 42: 359–386.
- Schneider K. M. 1933. Zur Jugendentwicklung eines Eisbären. II. Aus dem Verhalten: Lage, Bewegung, Saugen, stimmliche Äußerung. *Der Zoologische Garten (N.F.)* 6: 224–237.
- Scoville R. and Gottlieb G. 1978. The calculation of repetition rate in avian vocalizations. *Animal Behaviour* 26: 962–963.
- Sieber O. J. 1984. Vocal communication in raccoons (*Procyon lotor*). *Behaviour* 90: 80–113.
- Smith H. J. 1980. Behavior of the coati (*Nasua narica*) in captivity. *Carnivore* 3: 88–136.
- Spady T. J., Lindburg D. G. and Durrant B. S. 2007. Evolution of reproductive seasonality in bears. *Mammal Review* 37: 21–53.
- Steinemann P. 1966. Künstliche Aufzucht eines Eisbären. *Der Zoologische Garten (N.F.)* 32: 129–145.
- Tembrock G. 1968. Land mammals. [In: *Animal communication*. Th. A. Sebeok, ed]. Indiana University Press, Bloomington: 338–404.
- Tembrock G. 1976a. Die Lautgebung der Caniden – eine vergleichende Untersuchung. *Milu* 4: 1–44.
- Tembrock G. 1976b. Canid vocalizations. *Behavioural Processes* 1: 57–75.
- Tembrock G. 1996. Akustische Kommunikation bei Säugtieren – die Stimmen der Säugetiere und ihre Bedeutung. *Wissenschaftliche Buchgesellschaft, Darmstadt*: 1–181.
- Thenius E. 1959. Ursidenphylogenie und Biostratigraphie. *Zeitschrift für Säugetierkunde* 24: 78–84.
- Tyack P. L. and Miller E. H. 2002. Vocal anatomy, acoustic communication and echolocation. [In: *Marine mammal biology – an evolutionary approach*. A. R. Hoelzel, ed]. Blackwell Publishing, Oxford: 142–184.
- Vlasák J. 1950. Über künstliche Aufzucht eines Eisbären, *Thalartos maritimus* Phipps. *Der Zoologische Garten (N.F.)* 16: 159–179.
- Volf J. 1963. Einige Bemerkungen zur Aufzucht von Eisbären (*Thalartos maritimus*) in Gefangenschaft. *Der Zoologische Garten (N.F.)* 28: 97–108.
- Volodin I., Volodina E. and Isaeva I. 2001. The dhole *Cuon alpinus* vocal repertoire in captivity. *Zoologicheskii Zhurnal* 80: 1252–1267. [In Russian with English summary]
- Vrana P. B., Milinkovitch M. C., Powell J. R. and Wheeler W. C. 1994. Higher level relationships of the arctoid Carnivora based on sequence data and ‘total evidence’. *Molecular Phylogenetics and Evolution* 3: 47–58.
- Waits L. P. 2004. Phylogenetic placement of the giant panda based on molecular data. [In: *Giant pandas – biology and conservation*. D. G. Lindburg and K. Baragona, eds]. University of California Press, Berkeley, CA: 36–37.
- Waits L., Sullivan J., O’Brien S. and Ward R. 1999. Rapid radiation events in the family Ursidae indicated by likelihood phylogenetic estimation from multiple fragments of mtDNA. *Molecular Phylogenetics and Evolution* 13: 82–92.
- Ward P. and Kynaston S. 1995. *Bears of the world*. Blandford, London: 1–191.
- Wemmer C., von Ebers M. and Scow K. 1976. An analysis of the chuffing vocalization in the Polar bear (*Ursus maritimus*). *Journal of Zoology, London* 180: 425–439.
- Werdelin L. 1996. Carnivoran ecomorphology: a phylogenetic perspective. [In: *Carnivore behavior, ecology, and evolution*. vol. 2. J.L. Gittleman, ed]. Cornell University Press, Ithaca: 582–624.
- Wilden I. 1997. Phonetische Variabilität in der Lautgebung Afrikanischer Wildhunde (*Lycan pictus*) und deren frühe Ontogenese. *Shaker Verlag, Aachen*: 1–135.
- Wiley R. and Richards R. 1981. Vocalizations of the ringtail (*Bassariscus astutus*). *Southwestern Naturalist* 26: 23–30.
- Winn H. E. and Schneider J. 1977. Communication in sireniens, sea otters, and pinnipeds. [In: *How animals communicate*. Th. A. Sebeok, ed]. Indiana University Press, Bloomington: 809–840.
- Wong J., Stewart P. D. and Macdonald D. W. 1999. Vocal repertoire of the European badger (*Meles meles*): structure, context, and function. *Journal of Mammalogy* 80: 570–588.
- Wozencraft W. C. 2005. Order Carnivora. [In: *Mammal species of the world – a taxonomic and geographic reference*. 3rd ed. vol. 1. D. E. Wilson and D. M. Reeder, eds]. The Johns Hopkins University Press, Baltimore: 532–628.
- Yu L., Li Q., Ryder O.A. and Zhang Y. 2004a. Phylogeny of the bears (Ursidae) based on nuclear and mitochondrial genes. *Molecular Phylogenetics and Evolution* 32: 480–494.
- Yu L., Li Q., Ryder O.A. and Zhang Y. 2004b. Phylogenetic relationships within mammalian order Carnivora indicated by sequences of two nuclear DNA genes. *Molecular Phylogenetics and Evolution* 33: 694–705.
- Zhu Jing and Meng Zhibin 1987. On the vocal behavior during the estrous period of the giant panda *Ailuropoda melanoleuca*. *Acta Zoologica Sinica* 33: 283–292. [In Chinese with English summary]

Received 10 January 2007, accepted 21 June 2007.

Associate editor was Krzysztof Schmidt.

