

Obwohl sich die Chromosomenzahlen zwischen europäischen und kleinasiatischen *Microspalax* stark unterscheiden, dürften die Karyotyp-Formen namentlich von *anatolicus* und *turcicus* verwandt sein. NF-Werte und Zahlen subakrozentrischer Chromosomen lassen nämlich vermuten, daß die Unterschiede durch Robertsonsche Fusionen bzw. Fissionen zustande gekommen sind.

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- Authors' addresses:* Dr. EVA GIAGIA, Zoological Laboratory, University of Patras, Patras, Greece;
Dr. IVO Savić and Dr. BOGOSAV SOLDATOVIĆ, Institute for Biological Research "Siniša Stanković", University of Belgrade, 142, 29th November St., 11060 Belgrade, Yugoslavia

A note on the vocal behaviour of the Giant panda, *Ailuropoda melanoleuca* (David, 1869)

By G. PETERS

*Department of Zoological Research, National Zoological Park, Smithsonian Institution,
Washington, D.C.*

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Abstract

The vocal repertoire of adult giant pandas as observed in the pair living at the National Zoo, Washington, D.C., was studied with the help of sound spectrographic analysis. Vocal activity in the ♂ and the ♀ is nearly exclusively restricted to pro-oestrus and oestrus period of the ♀. The vocal repertoire of the species consists of several vocal forms, the ♀ exhibiting more vocal types than the ♂. Most of the vocalizations form a graded system with at least one other form in the repertoire, one

vocalization seems to be discrete. With the exception of the vocal forms typical of agonistic behaviour, the functional significance of the other forms is hard to establish. The vocalization accounting for most of the vocal activity in the ♂ and the ♀ during the oestrus period of the ♀ is unlike any vocal form known in the Ursidae. It is structurally quite similar to a vocalization in the red panda (*Ailurus fulgens*) which is also its functional equivalent. Corresponding vocal forms are known in the Procyonidae.

Introduction

Since the discovery and first scientific description of the giant panda disagreement on the systematic position of this species has continued (for reviews see CHORN and HOFFMANN 1978; THENIUS 1979). For various reasons this little known species has remained appealing to zoologists and laymen alike.

With the recent policy of the government of the People's Republic of China to donate a pair of giant pandas to several major zoos in Europe, America and Japan, it has become possible to fill part of the gap in our knowledge of this species' behavioural biology. Detailed field studies of giant panda behaviour are lacking (a large-scale field project has begun [SCHALLER 1981]) and the data from captive animals have been rather fragmentary to date. Moreover, a detailed study of the vocal behaviour of this species in its natural habitat might be difficult, thus a study of this aspect of behaviour in captive animals is advantageous.

A few anecdotal reports on field observations of giant panda vocalizations were published by SHELDON (1937, 1975), SCHÄFER (1938) and SCHALLER (1981) and some notes on captive animals by SCHNEIDER (1939) and HAAS (1963). However, no structural details were presented. Good general accounts of the vocal behaviour of giant pandas in captivity were published by MORRIS and MORRIS (1966) and especially by KLEIMAN et al. (1979), the latter paper based on observations of the same two individuals that are dealt with here.

The object of this paper is to contribute to the knowledge of the giant panda's behaviour and to provide some additional characteristics to be considered in discussions of the systematic position of this species.

Material and methods

The vocal behaviour of the adult pair of giant pandas living at the National Zoological Park, Smithsonian Institution, Washington, D.C. was studied during spring and summer 1980. At the time of observation both animals were about 9 years old. Details on housing, maintenance, behaviour, and development of the two individuals have been published elsewhere (e.g. COLLINS and PAGE 1973; KLEIMAN 1974; MELUN 1975; KLEIMAN et al. 1979). From April 21st 1980 until June 2nd 1980 the two giant pandas were observed daily – mainly during their early morning activity period after 0700 hours. A total of 131 hours was spent observing the animals during which 20 reels (13 cm reels = 5 hours) of vocal activity were recorded on tape. After June 2nd sporadic observations of at least one hour each were made once or twice a week until July 15 and few tape recordings were made during these.

The recordings were made with a portable tape recorder UHER Report IC 4000 Automatic at 19 cm/s and a microphone SENNHEISER MKH 816. The tape recordings were analyzed on a sound spectrograph KAY Sonagraph model 7029 A in wide band setting (some also in narrow band) and shaping flat with different frequency ranges. In the range most often used (20–2000 Hz) the effective temporal resolution is 0.013 s and the effective frequency resolution 75 Hz in the wide band mode. A total of 262 sonagrams was evaluated, most of them comprising several vocalizations (cf. Fig. 5). Tape recordings of the vocal behaviour of these individuals from previous years were available for comparison. Data on their vocal behaviour during the 1981 oestrus period of the ♀ as well as that of the ♂ giant panda of the London Zoo which was at the National Zoo as a loan during this time were kindly provided by Dr. D. G. KLEIMAN and included in this paper.

The following statements on the vocal repertoire of the giant panda, structure of its vocalizations and functional context(s) are limited by the fact that the study was based on only two individuals of this species, one of either sex, (there are only relatively few data for the London ♂), living in captivity. Preliminary results of field observations of giant panda vocal behaviour are in full agreement with the data presented here (G. SCHALLER, in litt.).

All spectrograms figured are in wide band.

Results

The vocal repertoire of the giant panda

As stated by KLEIMAN et al. (1979) vocal activity in the ♂ and the ♀ is mainly restricted to the pro-oestrus and oestrus period of the ♀. Both individuals showed a significant increase in rate of vocalizing some days before the ♀'s peak heat on May 16, 1980, and a steady and relatively rapid decrease after that date. Both the increase and the decrease in rate of vocalizing stretched over a longer time in the ♂, the ♀ being highly vocal only during a few days around her peak heat. The vocal activity of both individuals very probably was affected by the procedures of electro-ejaculation and artificial insemination carried out on May 17 and 18 such that the decrease in rate of vocalizing observed was probably more rapid than normal. During the remainder of the observation period the animals vocalized only infrequently; generally there is little vocal activity in both individuals except during the oestrus period of the ♀.

In the ♀ two types of vocalization occurred nearly exclusively during the oestrus period; they were rarely heard at other times of the year. Thus in addition to other behavioural changes, the ♀'s oestrus was marked by a significant increase in rate of vocalizing and the occurrence of specific vocalizations, the bleat and the chirp (cf. KLEIMAN et al. 1979). In the ♂ one vocalization, the bleat, accounted for nearly all vocal activity, other vocalizations being uttered only occasionally. In 1981 the London ♂ did not perform any bleating and was less vocal than the National Zoo ♂.

The ♂'s repertoire comprised four vocal forms: honking, bleating, growling and squealing. The latter two vocalizations were not heard in the 1980 observation period but were identified on tape recordings from previous years. Honking (Fig. 1) (duration: 0.37–0.45 s; frequency range: 0.2–2 kHz, tonal, up to 4 harmonics, the fundamental has the highest amplitude) is a highly stereotyped short call of low to medium intensity with a rapid downfall in pitch towards its end. Usually it is produced in bouts with relatively regular intervals between the calls. Bleating (Figs. 2, 5) (duration: 0.06–2.8 s; frequency range: 0.18–5.4 kHz, up to 5 and more harmonics, the fundamental and the first harmonic usually have the highest amplitude) is a tonal call of medium intensity with a rapid

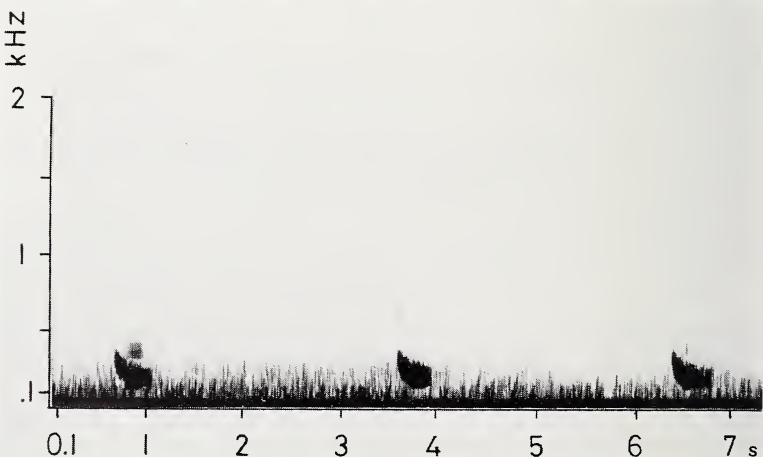


Fig. 1. Series of honks by the ♂ giant panda

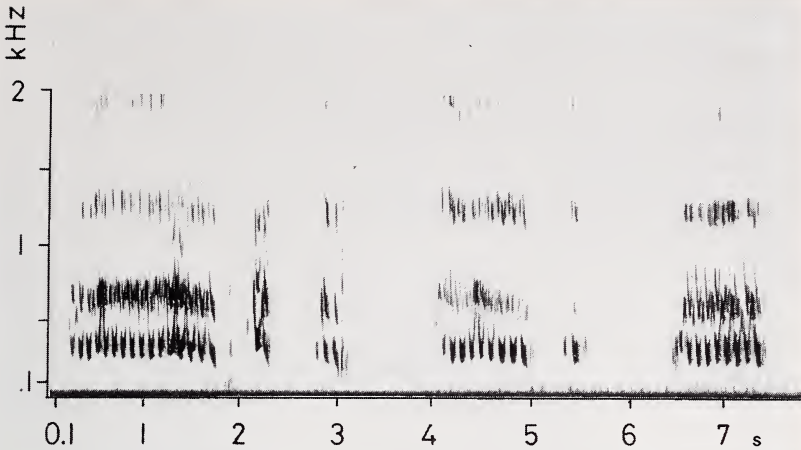


Fig. 2. Bleating by the δ . Note the high rate of vocalizing and the variable duration of the bleat, due to the number of phases of frequency modulation

frequency and amplitude modulation, its basic structural pattern being that of a twitter. The duration of the bleat varies according to the number of phases of regular frequency and amplitude modulation in the call. Compared with the size of the giant panda the bleat is rather high in pitch.

The vocal repertoire of the ♀ comprised more forms than that of the δ , including all types that were observed in the δ . In addition to bleating, honking, squealing and growling the ♀ articulates moans, barks and chirps; none of the latter three vocalizations was ever heard in the National Zoo δ during this study and in previous years (B. BINGHAM, J. BLOCK, F. DREHER, D. KLEIMAN, pers. comms.). KLEIMAN (in litt.), however, recorded moans from the London δ giant panda in April 1981.

Honking (Fig. 3) and bleating (Fig. 4) in the ♀ have the same basic structure as the equivalent vocalizations of the δ . Growling is a drawn-out, relatively low-pitched, noisy and pulsed vocalization (duration: 0.6–2.2 s; frequency range: 0.1 – above 8 kHz, with some tonal structure below 4 kHz and purely noisy in the upper range). These structural characteristics apply to this vocal type in the ♀ as well as in the London Zoo δ . Squealing (duration: 0.19–1.1 s; frequency range: 0.16–8 kHz, noisy beginning and end, tonal in the middle, the fundamental has the highest amplitude) is a short to medium-length, high-pitched piercing call of high intensity. The noisy beginning and end of the call are lower in pitch than its more tonal middle section which is rapidly frequency modulated. Its structure is similar in the δ and the ♀ ; the data given are of vocalizations recorded in previous years because it could not be recorded during the 1980 observation period. Chirping (Fig. 5) (duration: 0.08–0.99 s; frequency range: 0.14–8 kHz, up to 5 and more harmonics, the fundamental and sometimes the first harmonic have the highest energy) is a short to medium-length, high-pitched and tonal call of variable intensity with a rapid frequency modulation; generally it descends in pitch towards its end. The frequency modulation in the beginning of chirping is highly variable. In relation to the size of the giant panda chirping is remarkably high in pitch, even more so than bleating. Moans (Figs. 6, 7, 9) (duration: 0.13–2.46 s; frequency range: 0.08–4 kHz, rarely above this range, up to 10 harmonics, but usually less, the fundamental and the first two harmonics have the highest amplitude) usually are low- to medium-intensity calls of variable duration with a

relatively low pitch and little frequency modulation. Moans quite often are truncated in the beginning, thus forming one or several short starting elements in front of the main portion of the call (cf. Fig. 6) or a vocalization may just consist of one or several such fragmentary elements (cf. Fig. 7). The same structural characteristics were found in the moans of the London Zoo ♂ recorded by KLEIMAN in 1981. Barks (Figs. 6, 8) (duration: 0.13–0.29 s; frequency range: 0.06–6 kHz) are short, fairly tonal to totally noisy medium- to high-intensity vocalizations somewhat similar to the barking of a medium-sized dog.

All vocalizations mentioned so far in the ♂ and the ♀ can be clearly defined in their structural characteristics and thereby distinguished from one another. In the ♀ all call types with the exception of honking formed a graded system with at least one other type of vocalization. Intermediate vocal forms were especially frequent during peak oestrus. No

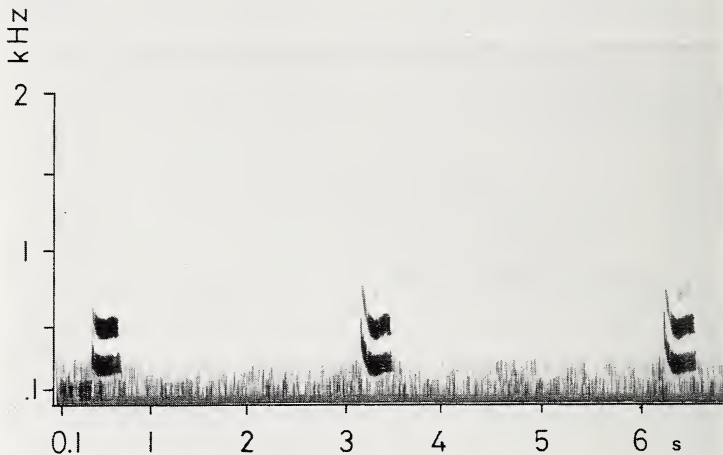


Fig. 3. Series of honks by the ♀ giant panda

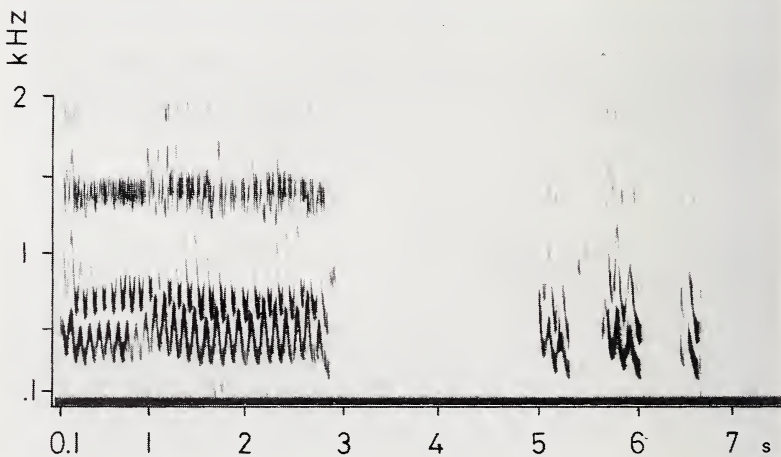


Fig. 4. Bleating by the ♀. This vocalization in the ♀ is structurally as variable as in the ♂

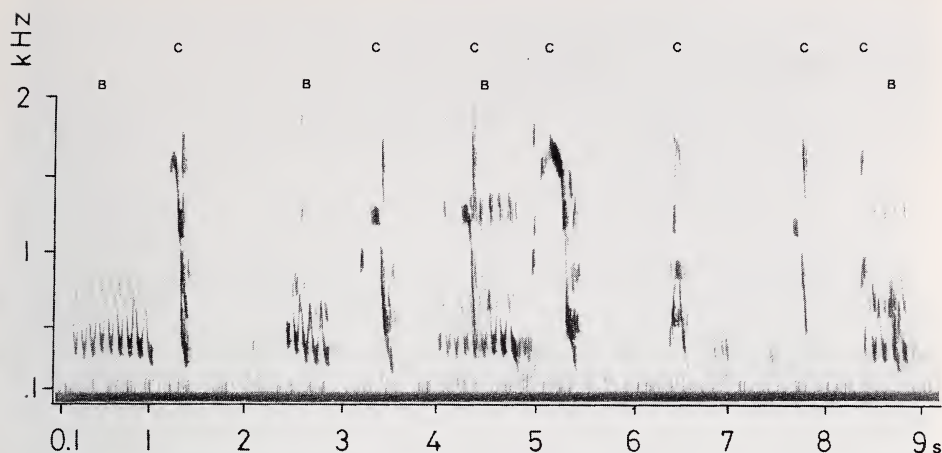


Fig. 5. Chirps (C) by the ♀ and bleats (B) by the ♂. The high rate of vocalizing in both sexes is typical of the peak oestrus of the ♀

grading was found in the vocal repertoire of the National Zoo ♂, the London Zoo ♂ produced intermediate vocal forms between moaning and growling. Bleating, present in the repertoire of the ♂ and the ♀, formed a graded system with chirping and moaning which were not heard in the National Zoo ♂. In 1981 the London Zoo ♂ did not perform bleating during the observation period, therefore no statement as to the occurrence of intermediates between bleating and moaning in ♂♂ can be made at present.

Functional aspects of vocalization

With the exception of vocalizations emitted during agonistic behaviour (barking, growling, squealing) the functional significance of the giant panda's other vocal forms was difficult to establish. There was hardly any evidence as to consistent behavioural patterns associated with any other type of vocalization, either in the sender of the signal or its addressee. Growling and barking probably function as aggressive threats, and squealing may denote defensive threatening and/or submission. As squealing occurs when an animal is bitten it may also be an expression of pain. The nearly exclusive occurrence of chirping and bleating during the ♀'s oestrus period strongly suggests a functional correlation with physiological status. The ♂'s increased rate of bleating during this period also is probably related to the mating season, and the male rut, as well as the ♂'s attempts to approach the ♀. Bleating – among other functions – may also indicate appeasement and reassurance since the giant panda is a solitary animal in which the sexes rarely meet except for mating. Neither bleating nor chirping (in the ♀) probably function as long distance advertisement calls to attract a partner for mating nor help in mutual localization when animals alternately vocalize since the intensity of these calls seems insufficient to carry far in the dense vegetation of the giant panda's natural habitat. However, this needs experimental verification as to the relative absorption of the sound signal with increasing distance from the source under these conditions. Olfactory communication is probably the main method for bringing the partners together for mating, as indicated by the significant increase in scent marking activity of the ♀ during pro-oestrus and oestrus (KLEIMAN et al. 1979). The quantitative change in vocal activity observed during the oestrus period of the ♀ in these two

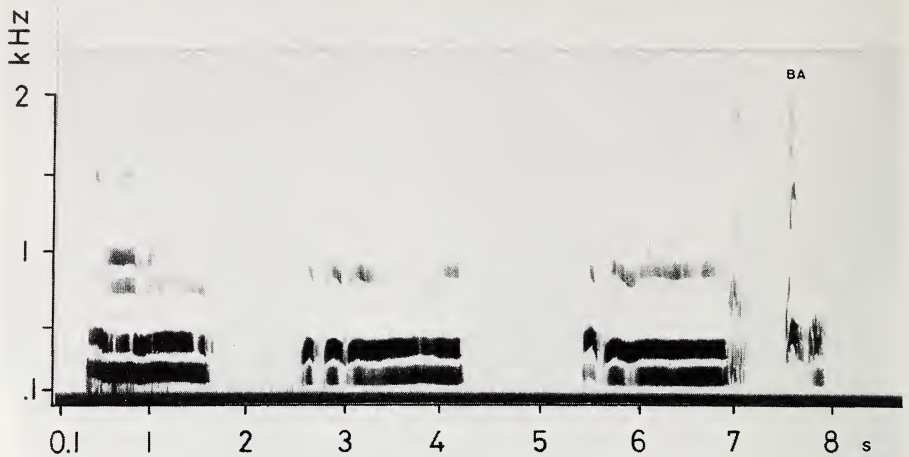


Fig. 6. A series of moans and a bark (BA) by the ♀. The beginning of the 2nd and 3rd moan are truncated, forming 2 resp. 1 short starting element(s)

individuals very probably was influenced by the fact that they are living in adjacent enclosures all year round with visual and olfactory contact between each other, a situation different from the wild.

Moaning may denote a slightly aggressive threat. Its structural affinity to barking and the fact that both vocalizations quite often occur in the very same behavioural context support this view. Moreover, the increasing aggressiveness of the ♀, signified by lunges towards the ♂, was accompanied by the occurrence of intermediate forms of moans and barks and – with more aggressive behaviour – a progressive replacement of the former by

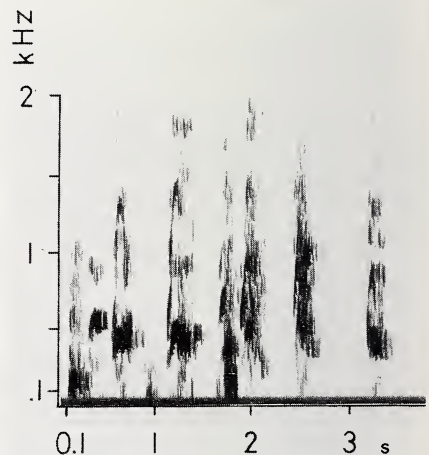
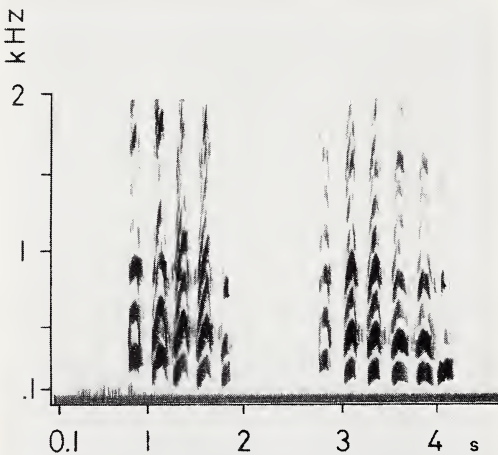


Fig. 7 (left). Two fully truncated moans by the ♀, split into 5 resp. 6 short elements. – Fig. 8 (right). A series of noisy barks by the ♀. In highly agonistic contexts barks are uttered in bouts in rapid succession

the latter. The structural relationship between growling and moaning and their occurrence in the same behavioural situations supports the functional interpretation of moaning given above. The situations in which honking was observed in both individuals gave no unequivocal hint as to the function of this vocalization. The ♂ occasionally honked when he was locked in his den and appeared to want to be released to his main cage. Several times the ♂ and the ♀ uttered bouts of honks when they were resting or even seemed to be sleeping. On the other hand, the ♂ performed a long series of honks on seeing the zoo's veterinarian after the first electro-ejaculation had been performed on him. Among other functions honking may probably denote frustration. Of the different vocal forms of *Ailuropoda* observed and analyzed in this study honking is the most highly stereotyped call structurally, not showing any grading with other vocal types and usually is produced in relatively regular sequences even though no intra-specific communicatory function is obvious as it was never heard during interactions between the animals.

In only a few cases the occurrence of intermediate type vocalizations, i.e. the phenomenon of grading, in the ♀ (and in the London ♂ in 1981) seemed to be correlated with motivational changes inferred from changes in the ♀'s behaviour in her interaction with the ♂. The increase in aggressive threat behaviour accompanied by the occurrence of moan/bark intermediates has already been mentioned. However, the highest incidence of vocal grading in the ♀ was observed during long bouts of vocalizing which were accompanied by the ♀ masturbating (rubbing the genital region with a forepaw). During masturbation she mainly performed bleat/chirp/(moan) intermediates without any changes in behaviour nor any interaction with the ♂. In 1981 the London Zoo ♂ performed moan/growl intermediates during agonistic interactions with the ♀ as did the ♀ in these situations.

Discussion

It is not known whether the vocal repertoire of the giant panda presented here is complete. D. G. KLEIMAN (pers. comm.) and G. SCHALLER (pers. comm. through KLEIMAN) heard explosive breaths and jaw clapping which may constitute vocal signals and perhaps there are further vocal types in this species not observed until now. However, if the differences

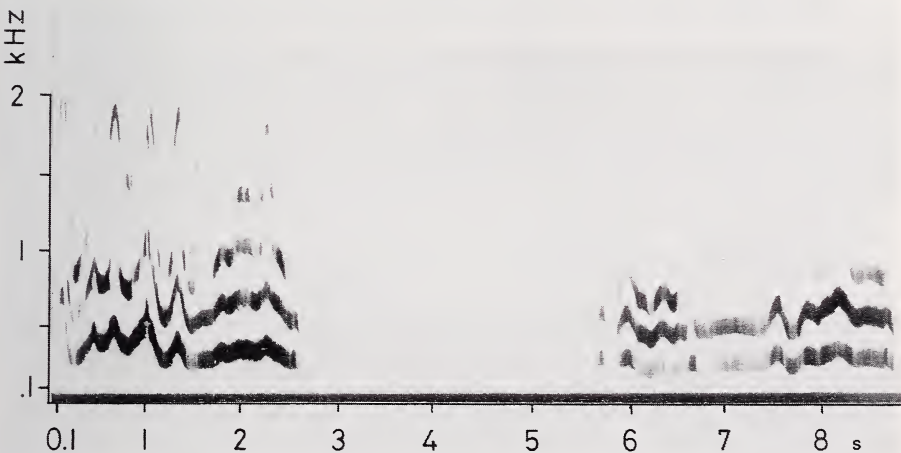


Fig. 9. Two intermediate moans by the ♀ with significant frequency modulation and relatively high in pitch. The beginning of the 1st call structurally represents a transition to bleating

in the vocal repertoire found in these two individuals (and the London Zoo ♂) are species-typical, it would suggest a significant sex-specific difference in the vocal repertoire of *Ailuropoda*, the ♀ having more forms than the ♂. In most mammals the species-specific vocal repertoire is genetically fixed (PETERS 1978a; EHRET 1980) and thus not influenced by captivity.

To my knowledge comparisons of vocalizations between mammalian families have not been evaluated as taxonomic evidence and therefore the phylogenetic significance of differences or conformities in vocalizations at this taxonomic level is not yet established. In the Pinnipedia STIRLING and WARNEKE (1971) and TRILLMICH and MAJLUF (1981) argued that the intermediate position of *Arctocephalus pusillus* between the two sub-families Arctocephalinae and Otariinae of the family Otariidae is also evident in the vocal repertoire of this species. In birds the significance of vocalization above the generic level has been questioned (THORPE 1961; THIELCKE 1964; LANYON 1969). Nevertheless, the available data of vocalization of the giant panda (with vocalizations assumed to be genetically fixed behavior characteristics) should be incorporated in the discussions of the systematic position of this species.

In no bear species (Ursidae) studied so far (PETERS 1978b; JORDAN 1979) has a vocalization like bleating, a predominant form in *Ailuropoda*, been described, whereas the twitter call of the red panda (*Ailurus fulgens*) represents the same structural pattern as the giant panda's bleat and appears to be functionally equivalent to it (ROBERTS and KESSLER 1979; ROBERTS 1981). Similar vocalizations in corresponding functional contexts are known in procyonid species like the ringtail (*Bassariscus astutus*) (WILLEY and RICHARDS 1981) and juvenile raccoons (*Procyon lotor*) (personal observations). Vocal forms with a basic structural pattern of a twitter call in the relevant functional contexts are quite uncommon in the Carnivora (personal observations), therefore this similarity is striking. Although no conclusive arguments can be made without more details on ursid, procyonid and *Ailurus* vocalizations, some comments can be made.

It seems doubtful that the conformity in *Ailuropoda*, *Ailurus* and procyonid twitter/bleat vocalizations is a result of convergent evolution. Nor are these forms likely to represent symplesiomorphic characteristics. A convergence would imply the adaptive significance of this structural pattern in the vocalizations of *Ailuropoda*, *Ailurus* and procyonids as opposed to the different phylogenesis of the functionally equivalent vocalizations in other carnivores and especially in the Ursidae. On the other hand, to argue that the twitter/bleat pattern is a symplesiomorphic character requires an explanation why this supposedly original structural pattern was retained in some species (especially in those mentioned here) but not in the majority of carnivore species known so far in this respect and specifically not in the Ursidae. Moreover, the bleating and chirping of *Ailuropoda* (the latter is also not known in any ursid species) are extremely high in pitch compared with the species' size, for which there is no plausible explanation, either functional or anatomical. According to DAVIS (1964) the larynx of the giant panda resembles that of the Ursidae.

Although the data on vocalizations presented here cannot offer any conclusive evidence as to the phylogenetic position of the giant panda, they are, however, inconsistent with the view published by THENIUS (1979) that *Ailuropoda* is an early offshoot of the Ursidae (deserving family rank because of its many peculiar characteristics) and is not related to the red panda (considered the sole species of the sub-family Ailurinae in the Procyonidae), more so with the view of CHORN and HOFFMANN (1978) that the giant panda is a species belonging to the family Ursidae.

Note added in proof: One ♂ was heard to chirp in a recent study in China (KLEIMAN in litt.). Thus, ♂♂ and ♀♀ seem to have the same basic vocal repertoire but differ in the frequency of use of the different vocalizations.

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Zusammenfassung

Beobachtungen zum Lautgebungsverhalten des Großen Panda, *Ailuropoda melanoleuca* (David, 1869)

Das Lautgebungsverhalten des Paares Großer Pandas im National Zoological Park, Washington, D.C., wurde zwischen 15. April und 15. Juli 1980 131 h lang beobachtet. Die Lautäußerungen wurden auf Tonband aufgezeichnet und lautspektrographisch ausgewertet. Tonbandaufnahmen vom Lautgebungsverhalten dieser beiden Individuen aus den vorhergehenden Jahren lagen zum Vergleich vor.

Bei ♂ und ♀ ist die lautliche Aktivität im wesentlichen auf die Hitzeperiode des ♀ beschränkt, wo beide Tiere sehr lautfreudig sind. Während der übrigen Zeit des Jahres äußern sie nur sporadisch Laute. ♀ und ♂ haben mehrere strukturell eindeutig definierte Lautformen, die jedoch bis auf einen Lauttyp jeweils mit zumindest einer anderen Lautform ein Kontinuum vielfältiger Übergangslaute bilden. Das ♀ besitzt ein reichhaltigeres Lautrepertoire als das ♂; anhand der bisherigen Beobachtungen ist allerdings keine Aussage möglich, ob schon alle Lautformen dieser Art erfaßt sind.

Die Funktion der einzelnen Lauttypen ist bis auf diejenigen, die für agonistische Verhaltenszusammenhänge charakteristisch sind, nur ungefähr zu bestimmen. Da beim ♀ zwei Lautformen nahezu ausschließlich während ihrer Hitzeperiode auftreten, dürfte ihr physiologischer Zustand dafür mit auslösend sein.

Einige Lauttypen des Großen Panda sind angesichts der Körpergröße der Art von ganz ungewöhnlich hellem Klang. Strukturell zeigt eine dieser Lautformen deutliche Übereinstimmungen mit einem auch funktional entsprechenden Laut von Procyoniden und dem Kleinen Panda (*Ailurus fulgens*), bei Ursiden sind keine derartigen Lautäußerungen bekannt. Im Hinblick auf das Problem der stammesgeschichtlichen Ableitung von *Ailuropoda* erscheint dies als ein Hinweis, Beziehungen dieser Art zu den Ursiden neu zu interpretieren.

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Author's address: DR. GUSTAV PETERS, Zoologisches Forschungsinstitut und Museum Alexander Koenig, Adenauerallee 150–164, D–5300 Bonn 1

***Trichinella spiralis* in walruses from the Thule district, North Greenland, and possible routes of transmission**

E. W. BORN, B. CLAUSEN and Sv. AA. HENRIKSEN

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Abstract

Examined samples of muscle tissue from 126 Atlantic walruses, *Odobenus rosmarus rosmarus* (L.), collected in the Thule district, North Greenland (1975, 77 and 78), for *Trichinella spiralis*.

Two adult males were found to be infected with *Trichinella spiralis* (prevalence of 1.6%).

It is suggested that the walrus in the Thule district contracts trichinosis from scavenging on carcasses of polar bears or/and sled dogs.

Introduction

The parasite *Trichinella spiralis* in the walrus (*Odobenus rosmarus* Linnaeus) is a potential threat to the Inuit health. An epidemic disease in 1947 among the Inuit of central West Greenland was caused by the eating of trichinous walrus meat (THORBORG et al. 1948; ROTH 1949). Since then, trichinous walruses have been reported from different arctic areas

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