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ORIGINAL PAPER

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Mammalian ear specializations in arid habitats: structural and functional evidence from sand cat (*Felis margarita*)

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Abstract To test whether structural specializations of sand-cat ears are adaptations to their desert habitats we measured structural and acoustic features of their ears. The area of the external ear's pinna flange is similar to that of domestic cat. The dimensions of the ear canal are about twice domestic cat's, as is the volume of the middle-ear air space. The magnitude of the acoustic input-admittance at the tympanic membrane is about five times larger than that of domestic cat; both the middle-ear cavities and the ossicular chain contribute to the increase. Structure-based models suggest the acoustic admittance looking outward through the external ear is generally larger for sand cat than for domestic cat; the radiation power-efficiency is also larger in sand cat for frequencies below 2 kHz. Hearing sensitivity (estimated from measurements and model calculations) in sand cat is predicted to be about 8 dB greater than in domestic cat for frequencies below 2 kHz. Analysis of attenuation of sound in deserts implies that the increased sensitivity extends sand cat's hearing range beyond domestic cat by 0.4 km at 0.5 kHz. Thus, the structural specializations may provide habitat-specific survival value.

Keywords Adaptation · Comparative hearing · Sand cat · Sensory ecology

Abbreviations *TM* tympanic membrane

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Introduction

Some variations in ear structure among vertebrate species are thought to be influenced by adaptation to the species' environment. Well-studied examples are the unusually large auditory bullae in rodent species of the Gerbillinae (Old World) and Heteromyidae (New World) taxa, which live in deserts (e.g., Legouix and Wisner 1955; Webster 1962; Lay 1972). It has been proposed that this specialized ear structure increases hearing sensitivity for low frequencies and, as a consequence, the species are better able to survive in arid habitats. For example, Lay (1972) concluded from structural and functional measurements in gerbilline rodents that structural "[s]pecialization increases with increasing aridity... Auditory acuity for a wide range of low-frequency sounds augmented by auditory specialization is hence more advantageous here." (Lay 1972, p 41). In behavioral observations Lay (1974) reported that with gerbils (*Meriones libyca*) in a large enclosure with two owls, neither normal nor blinded adult gerbils were caught by the owls' strikes, whereas all juveniles (which had not developed adult-size bullae) were caught. From a physics-based model of a Mongolian gerbil middle ear (*M. unguiculatus*), Ravicz and Rosowski (1997) predicted that a loss in hearing sensitivity for low frequencies ($f < 2$ kHz) would result from reduction in middle-ear air volume (enclosed by the bony bulla). Thus, for some gerbillines from arid habitats the idea that enlarged auditory bullae (and therefore larger total middle-ear air volume) enhance low-frequency hearing and survival has both physiological and behavioral support.

This "adaptive" hypothesis was pursued vigorously in kangaroo rats (*Dipodomys merriami:* family Heteromyidae) by Webster and Webster (1984), who demonstrated that reduction of the middle-ear air volume reduced their behavioral hearing sensitivity for tones (Webster and Webster 1972) and made them more likely to be caught by owls and snakes, which generate

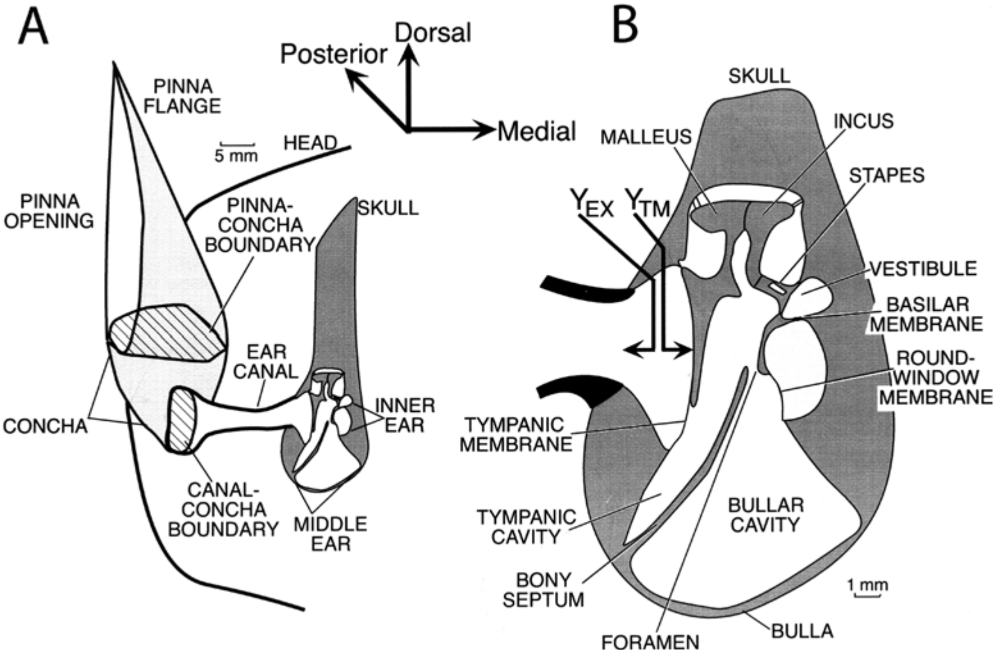

Fig. 1A, B. Schematic diagrams of the right ear of a domestic cat, viewed from an anterior location. **A** Airborne sound is transmitted to the inner ear via the external and middle ears. The external ear consists of the *pinna flange*, *concha*, and *ear canal*. The *cross-hatched areas* show the two-dimensional surfaces at the junctures of the pinna and concha, and the concha and ear canal. **B** Enlarged view of the middle and inner ears. (Black components on the *left* represent the medial portion of the cartilaginous ear canal.) The middle ear includes the *tympanic membrane* (TM), ossicles (*malleus*, *incus*, and *stapes*), and cavity air space. In the cat family, the middle-ear air space is enclosed by a prominent bony bulla and is divided into two distinct cavities (*tympanic cavity* and *bullar cavity*) by a bony septum. A foramen connects the two cavities. Acoustic quantities: Y_{TM} is the acoustic admittance just lateral to the TM ("looking" in the direction of the middle ear); Y_{EX} is the acoustic admittance at the same location, but looking out through the external ear

low-level, low-frequency sound during their attack strikes (Webster 1962). Apparently desert-dwelling rodents of two different families from different parts of the world have evolved similar structural specializations of their middle ears. The suggested coupling between aridity, hearing and species survival is that species living in desert habitats with sparse vegetation and little natural cover depend on increased hearing sensitivity to avoid predation (Webster and Plassman 1992).

Use of the comparative method to seek associations of one structural feature, e.g., large bulla volumes, to a functional specialization may be complicated by the occurrence of variation in other structures. For instance, both Lay (1972) and Webster and Webster (1975) found interspecies structural variations in the configuration of the tympanic-membrane ossicular-chain linkage that are correlated with species' habitats. Knowledge of the functional effects of these variations can help connect variations in structure to variations in hearing capabilities.

To test ecological and ethological influences on ear structure and function, we have chosen to focus on the cat family (Felidae), in which the same external- and middle-ear structures (Fig. 1) occur in all 36 modern species (Herrington 1985; Wozencraft 1989; Peake and Rosowski 1997; Huang et al. 2000a). The cartilaginous external ear (Fig. 1A) has three components: pinna flange, concha, and ear canal. At the medial end of the external ear canal (Fig. 1B), where sound signals reach the middle ear, the *output* admittance of the external ear is designated Y_{EX}. Measurements of Y_{EX} in domestic cat ears are well represented by a simple, structure-based, geometrical model (Rosowski et al. 1988; Fig. 11). The felid middle ear (Fig. 1B), with the usual mammalian arrangement of three ossicles in an enclosed air space, has a distinctive arrangement of its air space with a bony septum[1] that divides the space into the tympanic and bullar cavities. The two cavities are connected by a foramen in the septal wall. The effects of this arrangement on the middle ear's response to sound have been demonstrated in domestic cat (Møller 1965; Guinan and Peake 1967; Peake et al. 1992; Lynch et al. 1994) and several exotic species (Huang et al. 1997, 2000a). Features of the middle ear's acoustic response can be related to structural features. For instance, the dependence of the acoustic *input* admittance at the tympanic membrane, Y_{TM}, on experimental modification of the cavities has been explained by an anatomically based model in domestic cat and lion ears (Huang et al. 1997). The two admittances Y_{EX} and Y_{TM} are key factors in determining sound absorption by the ear.

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[1] The presence of a bony septum in the middle ear is one feature that divides Carnivora families into two suborders: the cat-like Feliformia *with* bony septa (hyenas, civets and genets, mongooses, felids) and the dog-like Caniformia *without* septa (dogs, bears, weasels, raccoons, seals, sea lions, walruses) (Hunt 1974; Neff 1991; Wozencraft 1993).

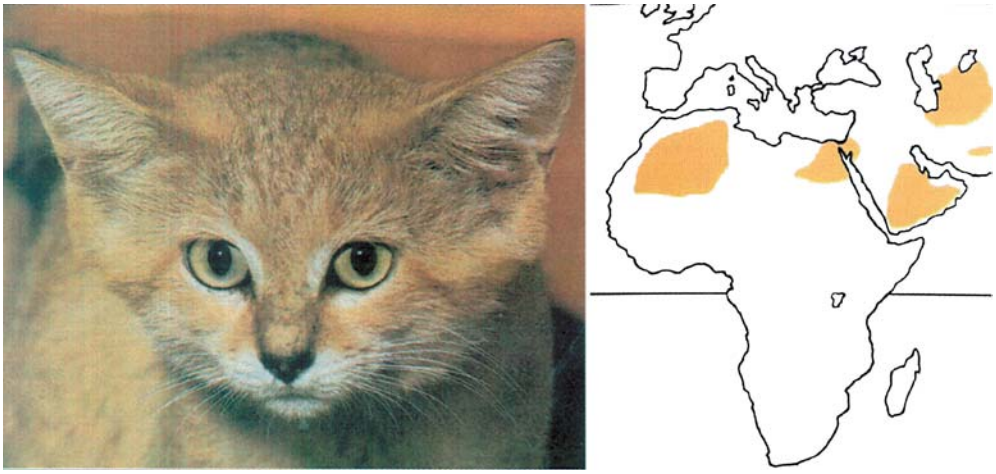

Fig. 2. Photograph of a sand cat (*Felis margarita*). The *map* shows habitat ranges in the Sahara, Arabian desert, trans-caspian deserts (Karakum and Kyzilkum) and Nushki desert of the western Pakistan-Afghanistan border. The range map is from Seidensticker and Lumpkin (1991, p 53). The photograph, credited to Tom McHugh, appears in Jackson (1987, p 114). Permission for use of the photo has been granted by Photo Researchers Inc

Only one felid species, the sand cat (*Felis margarita*), has a strong association with desert habitats (Ortolani and Caro 1996; Nowell and Jackson 1996, p 321) (see Fig. 2). Four subspecies have been identified from African and Asian deserts (Schauenberg 1974; Hemmer et al. 1976). Several structural features of the sand cat external and middle ear have been cited as unusual in size (Heim de Balzac 1936; Pocock 1938; Schauenberg 1974; Hemmer et al. 1976; Roberts 1977; Herrington 1985; Harrison and Bates 1991; Heptner and Sludskii 1992). The external ear (see Fig. 2) is described as "very large... set low and greatly inclined outward" (Heptner and Sludskii 1992, p 636). The three bony features of the external and middle ear in Fig. 3 are considered distinguishing features of the sand-cat skull by Schauenberg (1974). The bony ear canal (labeled 1 in Fig. 3) is unusually prominent; the region between the bullae (labeled 2) is unusually narrow, because of increased bullar width, and the anterior extreme of the bulla is further anterior than the jaw joint (labeled 3) as a consequence of the large length of the bullae. In fact, all bullar dimensions are unusually large (Pocock 1938; Heptner and Sludskii 1992). As sand cat has been identified as unusual in habitat and in ear structure, it is a promising candidate for testing the adaptive value of auditory specialization to habitat.

In this paper we report structural measurements of ears from sand-cat skulls together with structural and acoustic measurements in live sand-cat ears. We find the sand-cat ears quantitatively different in structure and acoustic function from others felids of similar size. To relate these results to sand-cat hearing, we compute the theoretical sound-collecting capability of sand-cat and domestic-cat ears as a function of sound frequency (Siebert 1973; Shaw 1988). The results show a substantial increase in sensitivity for sand-cat ears relative to domestic cat for frequencies below 2 kHz. We then seek a survival value for this hearing specialization in an arid environment. Sound propagation over ground in an open environment is a function of sound frequency, temperature distribution, relative humidity, and the ground's composition (Sutherland and Daigle 1997). In air, high audio frequencies are absorbed more than low frequencies, especially in a dry environment (Bass et al. 1995). From a description that includes three sound-attenuation processes we predict the advantage for the sand cat (relative to the domestic cat) in terms of extension of the distance over which a sound is audible.

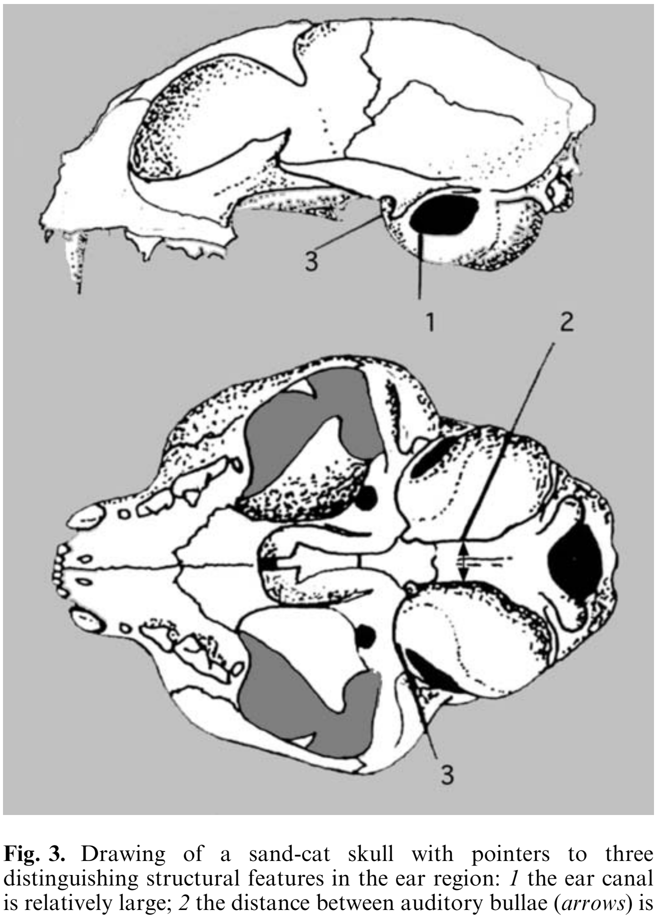

Fig. 3. Drawing of a sand-cat skull with pointers to three distinguishing structural features in the ear region: *1* the ear canal is relatively large; *2* the distance between auditory bullae (*arrows*) is relatively small; and *3* the auditory bullae extend anteriorly beyond the glenoid fossa. After Schauenberg (1974, p 956). The average sand cat skull length (83 mm) is not significantly different from domestic cat (81 mm; W.T. Peake and H.C. Peake, unpublished observations)

The survival benefits of the distance increase are considered as a possible driving force for the evolution of these specializations of the sand-cat ear for an extreme arid environment.

Materials and methods

Subjects

Measurements were made on 15 ears of 8 adult sand cats at The Living Desert (Palm Desert, Calif., USA) and one ear of an adult sand cat at the Cincinnati Zoo (Center for Research on Endangered Wildlife). Data from 5 live adult specimens of other species included in this report have not been described previously: one Arabian wildcat (*Felis silvestris tristami*) at The Living Desert; one Pallas's cat (*Otocolobus manul*) at the Cincinnati Zoo, one snow leopard (*Uncia uncia*), one caracal (*Caracal caracal*), and one leopard (*Panthera pardus*) at Carnivore Preservation Trust (Pittsboro, N.C., USA). All animals were healthy before and after the procedure; none had any history of middle-ear disease. Isoflurane (2–3%) anesthesia was delivered via tracheal intubation or a snout mask. Ears were screened for pathology by (1) examining the TM with an otoscope and (2) assessing variations in acoustic responses to controlled static pressures in the ear canal (i.e., tympanometry) (Margolis et al. 1978; Huang et al. 2000a, 2000b).

Acoustic measurements

We have reported (Huang et al. 2000a, 2000b, 2000c) a noninvasive method of measuring the middle-ear input admittance Y_{TM} – the ratio of the volume velocity of the TM to the sound pressure at the TM (Fig. 1B) – which characterizes the linear acoustic response at the input to the middle ear (Onchi 1961; Zwislocki 1962; Møller 1965). In brief, acoustic admittances were measured with an ear insert containing a calibrated acoustic source and microphone (modified Etymotic Research ER10C and eartip, Elk Grove Village, Ill., USA) sealed into the intact ear canal by injected earmold-impression material. The measurement location was within the ear canal about halfway between the TM and the canal-concha boundary (Fig. 1A). Admittances were corrected for the effect of the canal space between the probe and the TM with a uniform-tube approximation; the dimensions of this tube (length and cross-sectional area) were estimated acoustically (Keefe et al. 1992; Huang et al. 2000a, 2000b). Static air pressure in the canal was manipulated between –300 mm H_2O and +200 mm H_2O by a syringe and measured with a water-filled manometer. Measurements at different static pressures were used to assess the volume of the air space between the source and the TM. The method's frequency range of validity is 0.1–5 kHz; the main sources of error are biological noise, room noise, uncertainties in the canal dimensions, and non-uniform sound waves in the vicinity of the microphone (Huang et al. 2000b, 2000c). To describe Y_{TM} for the low-frequency region in which it is compliance-like, total acoustic compliance of the middle ear (C_{ME}) was computed as the average of $\mathrm{Im}\{Y_{\mathrm{TM}}(f)\}/(2\pi f)$ over ten frequencies between 0.12–0.34 kHz, where $\mathrm{Im}\{Y_{\mathrm{TM}}(f)\}$ denotes the imaginary part of the complex admittance.

Broad-band (0.1–5 kHz) middle-ear admittance data were accepted if (1) a proper seal was obtained in the ear canal, and (2) the response to controlled, static pressures was normal (Huang et al. 2000a). By "proper seal", we mean that the injected sealant reached the lateral face of the inserted eartip. By "normal response", we mean monotonic decreases in low-frequency admittance magnitude with increasing pressure magnitude in the canal, with a total decrease of at least 30% with middle-ear pressures of –300 mmH_2O. Low-frequency estimates of middle-ear admittance and compliance C_{ME} were also accepted from a few ears with a normal response to static pressure but a less than proper seal. Measurements were attempted in 16 sand cat ears. In 10 of these the methods permitted measurement of C_{ME}. (In at least two of the omitted ears the problem was due to a failure in the static pressure delivery and measurement system.) Broad-band admittance measurements were accepted from 8 of the 10 ears.

Structural measurements

We have compiled a museum-skull database that includes measurements of bullar and bony ear-canal dimensions from about 400 skulls of 34 felid species, and direct measurements of middle-ear cavity volumes from 16 skulls of five species (Peake and Rosowski 1997; Huang et al. 2000a; W.T. Peake and H.C. Peake, unpublished observations). A quantity $\tilde{N}$, related to the bony ear-canal cross-sectional area, was calculated as the product of the longest diameter of the oval bony canal and the largest diameter perpendicular to the longest diameter. A second quantity, $\hat{V}$, related to the middle-ear volume, was calculated from the product of the length, width and depth of the bony bulla. $\tilde{N}$ and $\hat{V}$ are over-estimates of the actual area and volume. To infer the actual volume, we use the result that, in 5 felid species of a broad range of body size, the total middle-ear cavity volume can be estimated as $V_{CAV} = 0.49\ \hat{V}^{0.96}$ (Huang et al. 2000a).

Species size was assessed by the skull length (L_S) defined as the midline distance from the anterior face of the upper incisors to the posterior edge of the occipital condyles, i.e., the condylobasilar length (Deblase and Martin 1981). The species' skull lengths used in this report are the intra-species means and standard errors from the museum skull database (Peake and Rosowski 1997; W.T. Peake and H.C. Peake, unpublished observations).

We use measurements of external-ear structures of the sand cat to constrain a model of external-ear acoustics (described in the next section). The area of the pinna flange was estimated from measurements in the anesthetized animals of lengths (a, b, and c) of the three sides of a triangle approximating the pinna-flange openings. The pinna area was calculated from the plane-geometry formula $A_p = [s(s-a)(s-b)(s-c)]^{1/2}$, where $s = (a+b+c)/2$. Earmold impression material was injected into the external ear to obtain molds of the concha and a portion of the canal. From one sand-cat ear, a mold was obtained that extended laterally to the pinna opening and medially approximately halfway down the canal; measurements on this mold with calipers determined the length of the horn-like portion (the concha plus pinna flange)[2].

The lengths and cross-sectional areas of the tube-like ear canals were estimated for each ear from a combination of the ear molds and the acoustic methods described in Huang et al. (2000b). The acoustic methods allowed us to determine the length and cross-sectional area of the ear-canal tube between the tip of the acoustic probe in the ear canal and the TM. The acoustically determined cross-sectional areas were consistent with measurements made from ear molds that extended into the ear canal. However, the acoustic length estimates do not account for the depth to which the probe tip is inserted into the canal. Measurements in each sand cat of the distance from the canal-concha border (at the lateral end of the canal) to the probe tip (the location of the acoustic measurements) were made from the extracted impression material and probe assemblies. In general the measurement location was about halfway down the canal. Total ear-canal length was estimated as the sum of the probe-tip insertion depth, estimated from the impressions, and the acoustically determined distance between the tip and the TM.

Acoustic model of the external ear

To estimate acoustic properties of the external ear (of sand cat and domestic cat) its structure was approximated by a model, in

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[2] The boundary between the horn-like concha and tube-like ear canal was clearly demarked by a narrowing and a sharp bend in the ear mold.

Table 1. Means and standard errors of measurements of dimensions of the ear region from skulls of sand cat and five other felid species of about the same size. In the bottom row, data for the somewhat larger wildcat (of Europe, Asia and Africa) are included. The quantity Bony Ear Canal "Area" $\tilde{N}$ is the product of the two ear-canal diameters and is therefore larger than the actual area. Similarly, Bullar "Volume" $\hat{V}$ is the product of length, depth and width of the bulla and over-estimates the actual volume. In the Normalized columns all values are divided by the domestic cat mean. The "Inferred Bullar Volume" is: $V_{INFERRED} = 0.49\ \hat{V}^{0.96}$ (Huang et al. 2000a)

Species	n	Skull length (mm)	Bony ear canal "area" $\tilde{N}$		Bullar "volume" $\hat{V}$		Inferred bullar volume (cm^3)	Septal foramen area (mm^2)
			(mm^2)	Normalized area	(cm^3)	Normalized volume		
Sand cat *Felis margarita*	6	82.6 ± 2.02	64.3 ± 2.86	2.2 ± 0.10	4.12 ± 0.12	2.18 ± 0.06	1.91	≈50
Domestic cat *F. silvestris catus*	15	81.3 ± 1.38	29.6 ± 0.88	1.0 ± 0.03	1.89 ± 0.08	1.00 ± 0.04	0.90	4.6 ± 0.2[a] (n = 7)
Kodkod *Oncifelis guigna*	9	79.3 ± 1.72	20.9 ± 0.90	0.7 ± 0.003	1.30 ± 0.13	0.69 ± 0.07	0.63	
Pallas's cat *Otocolobus manul*	10	80.8 ± 1.24	38.6 ± 0.79	1.3 ± 0.03	2.58 ± 0.11	1.36 ± 0.06	1.22	
Oncilla *Leopardus tigrinus*	11	82.1 ± 1.48	20.3 ± 1.38	0.7 ± 0.05	1.19 ± 0.10	0.63 ± 0.05	0.58	
Leopard cat *Prionailurus bengalensis*	10	82.3 ± 1.67	22.8 ± 0.28	0.8 ± 0.01	1.80 ± 0.13	0.95 ± 0.07	0.86	
Wildcat *F. silvestris*	10	89.5 ± 2.00	35.3 ± 1.42	1.2 ± 0.05	2.27 ± 0.13	1.20 ± 0.07	1.07	

[a] After Peake et al. (2001)

which the combination of the pinna flange and concha is an exponential horn and the ear canal is a tube of uniform cross-section. This configuration has been shown to represent sets of measurements of Y_{EX} for domestic cat (Rosowski et al. 1988; Fig. 11). The dimensions of each model's horn and tube were constrained by anatomical measurements of the external ear in the sand cats, and by published measurements for domestic cat (Rosowski et al. 1988, Table 1). Because acoustic power losses within the external ear can be significant (Keefe et al. 1994; Ravicz et al. 1996), the external ear model is based on equations that include representation of viscous and thermal losses (Egolf 1977). Such equations are available for uniform tubes, but not for horns, so the exponential horn was modeled as 40 concatenated uniform tubes of increasing diameter. To assess the adequacy of the model, we composed results averaged across frequency. The root-mean-square differences between the power-collection parameters (described below by Eqs. 1, 2, and 3) predicted by a 20- and 40-segment tube model were less than 2.5%, and were less than 7% between a 10- and 40-segment tube model. The model-based calculations of these power-collection parameters in the domestic cat are very similar to data-based calculations (Rosowski et al. 1988)[3]. A similar model has been shown to fit power-collection data in gerbil (Ravicz et al. 1996) and infant and adult humans (Keefe et al. 1994).

Auditory performance in terms of sound-power absorption

To relate the acoustic quantities of the ear to the animal's hearing sensitivity, we focus on the sound-power-collection capability of the external and middle ear as described by their diffuse-field receiver cross-section A_{DF} (Shaw 1988; Rosowski et al. 1988, Rosowski 1991a, 1991b). A_{DF} is the ratio of power absorbed to the incident power *density* (i.e., power per unit area) in a diffuse field; a "diffuse sound field" is one in which equal power is incident from all directions. A_{DF}, then, is a measure of the sound-collecting ability of the ear averaged over all directions, and thereby removes the directional dependence of the ear as a receiver.

A_{DF} can be expressed as a product of three factors (Shaw 1988):

$$A_{DF} = \tfrac{\lambda^2}{4\pi} \quad \eta_R \quad \left[\tfrac{4\mathrm{Re}\{Y_{TM}\}\mathrm{Re}\{Y_{EX}\}}{|Y_{TM}+Y_{EX}|^2}\right]. \tag{1}$$

The rightmost factor has been called the power utilization ratio (PUR) (Rosowski et al. 1986; Rosowski 1991a). It describes the influence on power absorption of the admittances of the effective source (Y_{EX}) and the load (Y_{TM}) at the external-middle ear boundary:

$$PUR = \left[\frac{4\mathrm{Re}\{Y_{TM}\}\mathrm{Re}\{Y_{EX}\}}{|Y_{TM} + Y_{EX}|^2}\right], \tag{2}$$

where Y_{TM} is the measured middle-ear input admittance, Y_{EX} is the external-ear model's output admittance and $\mathrm{Re}\{Y\}$ is the "real part" of the complex admittance Y computed from the product of its magnitude $|Y|$ and the cosine of its angle $\angle Y$. Y_{TM} and Y_{EX} are designated "matched" if they have the same magnitude and their angles are equal but opposite in sign (i.e., when Y_{TM} and Y_{EX} are complex conjugates). For the matched condition, PUR has its maximum value of 1.

The middle factor on the right side of Eq. 1, η_{R}, is the radiation efficiency (Shaw 1988), which is a measure of the external ear's effectiveness in *radiating* sound power outward:

$$\eta_R = \frac{\text{Power radiated at the pinna flange}}{\text{Power input at the canal end}}. \tag{3}$$

The power input can be expressed in terms of P_{IN}, the sound pressure at the narrow end of the external-ear model as

$$\text{Power input} = |P_{IN}|^2 \mathrm{Re}\{Y_{EX}\}. \tag{4}$$

The power radiated from the pinna flange is

$$\text{Power radiated} = |P_{OUT}|^2 \mathrm{Re}\{Y_{RAD}\}. \tag{5}$$

where P_{OUT} and Y_{RAD} are evaluated at the pinna flange. The radiation admittance Y_{RAD} is approximated by an expression for the radiation admittance from the end of a round tube (Beranek 1986, p 123). If the external ear were lossless, $\eta_{\mathrm{R}} = 1$.

If the two impedances are matched ($PUR = 1$), and there is no acoustic power lost in passage through the external ear ($\eta_{\mathrm{R}} = 1$), only the first term on the right of Eq. 1 is important. This term is called the maximum receiver cross-section:

$$A_{DF}^{Max} = \frac{\lambda^2}{4\pi} = \frac{c^2}{4\pi f^2}. \tag{6}$$

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[3] The model-based estimates of Y_{EX}, A_{DF}, power-utilization ratio (PUR) and η_{R} (as defined in Eqs. 1, 2, and 3) in domestic cat are nearly identical to those based on mean measurements at frequencies below 1–2 kHz. At higher frequencies, the differences between the model predictions and measurements are within the range of differences observed between the ears of different individuals (Rosowski et al. 1988; J.J. Rosowski, unpublished observations).

Table 2. Dimensions of the cartilaginous external-ear components for sand cat and domestic cat. The domestic cat values are from Rosowski et al. (1988, Table I, p 1699). For sand cats the length of the canal was estimated from a combination of caliper measurements of ear molds and acoustic measurements (see Materials and methods). Values are mean ± SEM

Species	Pinna flange area (cm^2)	Cartilaginous ear canal cross-section (mm^2)	Ear canal length (mm)
Sand cat *Felis margarita*	14.4 ± 0.94 ($n = 8$)	59.2 ± 3.3 ($n = 8$)	28.3 ± 0.85 ($n = 8$)
Domestic cat *F. silvestris catus*	12.7 ± 2.06 ($n = 2$)	19 ± 0.82 ($n = 6$)	14.2 ± 0.57 ($n = 6$)

The dependence of A_{DF}^{Max} on the wavelength of the sound λ, the propagation velocity of sound c, and sound frequency f (where $\lambda = c/f$) is a consequence of the wave nature of sound (Shaw 1988).

Results

Structural measurements

Ear dimensions from skulls

To determine quantitative descriptions of the unique structural features of sand-cat ears, we measured museum skulls. Table 1 includes measurements of sand cat with those of six other species of about the same size (including domestic cat and five exotic species). Note that for five of the other species in this sample the size measure, skull length, differs from that of sand cat by less than 4%. Dimensions for the somewhat larger "wildcat" are included because they provide comparisons to a closely related species (Hemmer et al. 1976; Johnson and O'Brien 1997; Bininda-Emonds et al. 1999).

Comparisons are most easily made of the "normalized" areas and volumes. The bony ear-canal "area" $\tilde{N}$ in sand cat is 2.2 times larger than domestic cat and substantially larger than all the other species including the (larger) wild cat. A Student's *t*-test comparing the sand-cat mean with the species that is closest in normalized area, Pallas's cat, yields a probability that the two means are equal of well below 0.1%; clearly the area of the sand cat's bony ear canal is significantly larger than the others. For the bullar "Volume" $\hat{V}$ the normalized results show similarly large differences between sand cat and the others. For the species closest in "volume", Pallas's cat, the probability that the two means are equal is again well below 0.1%. These results provide quantitative support for the numerous reports in the literature of relatively large sand-cat ear canals and bullae.

The volume parameter $\hat{V}$ is related to the total volume of the divided middle-ear air space, where the bony septum divides the total into two air spaces. Although the orientation of the septum in sand cat has been described as unusual (Pocock 1938; Herrington 1985; Heptner and Sludskii 1992), we will not consider this feature in this paper. The septal foramen that connects the two portions of the divided middle-ear air space (Fig. 1B) has not been described previously in sand cat. In our observations of museum skulls we noted that the sand-cat foramen, when viewed through the ear canal, has a distinctive triangular shape, which is a consequence of the septum's dorsal edge gradually separating from the petrous bone over a few millimeters of its postero-medial end. From our drawings of this configuration we estimate the foramen's area (right-hand column of Table 1) to be about ten times larger than measurements of this area in domestic cat, the only species of this collection for which we have accurate measurements.

In summary, three bony structures of the ear – the bony ear canal, the auditory bulla, and the septal foramen – are distinctly larger in sand cat than in domestic cat and other exotic species of similar skull size.

Cartilaginous external-ear dimensions

Dimensions of the sand-cat and domestic-cat external ear are compared in Table 2; our pinna flange measurements are similar to the sand-cat pinna height estimates of 64 mm that are found in the literature (Pocock 1951; Heptner and Sludskii 1992). The mean pinna-flange areas are not significantly different, in contradiction to common sand-cat descriptions such as "ears very large" (Heptner and Sludskii 1992, p 636).[4] In contrast, the mean cross-sectional area at the mid-point of the cartilaginous ear canal (Fig. 1A) in sand cat is about three times larger than that of domestic cat. This factor is larger than the factor-of-two ratio of *bony* ear-canal areas between these species (Table 1).

In addition to ear-canal cross-sectional area, the length of the sand-cat ear canal is about twice that of domestic cat. These data show that the sand cat's external ear canal is large compared with that of domestic cat, whereas the lateral pinna-flange size is similar to that of domestic cat.

Acoustic results

Connection to hearing capabilities

A goal of this paper is to relate the structural and acoustic measurements of sand-cat ears to their influence on hearing sensitivity. The approach, which

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[4] In contrast to the subjective statements of relative pinna size in the literature, measurements of "ear height" (Heptner and Sludskii 1992, Table 16, p 462 and Table 39, p 646; Pocock 1951, tables on pp 65 and 145) do not show a significant difference between sand cat and the somewhat larger wildcat. Thus, while the sand-cat pinna may be relatively large compared to other cats, in terms of absolute size the sand-cat pinna is not different from that of less specialized close relatives.

evaluates the ear's ability to absorb acoustic power, uses knowledge only of acoustic properties of the middle and external ears. In the following three sections we present: (1) measurements of acoustic input admittance at the TM (Y_{TM}) and analysis of this quantity in terms of structural components; (2) analysis of a structural model of the external ear that allows computation of the output admittance of the external ear Y_{EX}, the admittance seen looking out from the TM through the external ear (see Fig. 1B), and the efficiency of outward radiation η_{R} (see Eq. 2); and (3) from Y_{TM}, Y_{EX}, and η_{R} we compute the diffuse-field absorption-cross-section A_{DF}, a measure of sound-power collection capability of the external-middle ear combination (Shaw 1988), for sand cat and domestic cat. Domestic cat is used for comparisons because it is the only felid for which the necessary acoustic data exist. Domestic cats are thought to be derived from the wildcat (*F. silvestris lybica*) over the last 10,000 years, and there are numerous reports of interbreeding (Zeuner 1963). Sand cat is thought to be closely related to wildcat (e.g., Heptner and Sludskii 1992, p 456). Thus, sand cat and domestic cat may have had a common ancestor in the late Pleistocene and their comparison forms a good test of a hearing specialization in association with extreme dry habitat.

Middle-ear input admittance, Y_{TM}

Admittance measurements: comparison to domestic cat The acoustic input admittances at the TM Y_{TM} measured in eight sand-cat ears are plotted versus frequency in Fig. 4. Also plotted are the mean and range of Y_{TM} measured in six domestic cat ears by Lynch et al. (1994). (The domestic cat is the only other felid species with measurements for more than a few ears.) The admittance magnitudes in the two species clearly differ, whereas the angles are similar in many respects. For frequencies less than 0.5 kHz admittances for both species are compliance-like (i.e., the magnitudes are proportional to frequency and the angles are near 0.25 periods), but the sand-cat admittance is greater in magnitude by about a factor of 5. Between 0.5 kHz and 3 kHz, the magnitudes in both species flatten off, and the angle falls toward zero (past zero in two of the sand cats). In this middle-frequency range the magnitude of the admittance in sand cat is still larger than domestic cat by about a factor of 5. The larger inter-ear variation in the sand-cat admittance at frequencies above 1000 Hz may result from increased errors in our measurements at higher frequencies (Huang et al. 2000b, 2000c).

Another obvious difference between the domestic cat and sand cat Y_{TM} is the sharp notch in magnitude (marked by the arrow in Fig. 4) and the rapid angle change that occurs in the domestic cat data near 4 kHz. In fact, the lack of this notch is a qualitative *difference* between the sand-cat admittance and those measured in other felid species (Huang et al. 2000a; Fig. 4). The magnitude notch and associated angle change in Y_{TM} result from the divided middle-ear cavity and the connecting foramen (Huang et al. 1997), structural features which sand cat shares with other felids (Fig. 1B). It is possible that a notch occurs in sand cat's admittance magnitude at a frequency above 5 kHz, the high-frequency limit of the measurement method. The larger area of the foramen in sand cat (Table 1) would theoretically increase the notch's frequency (Huang et al. 2000a, Eqs. 7 and 15); however, the increase of cavity volumes would *de*crease it. Thus, the reason for the absence of this feature in the sand-cat measurements is not clear. Measurements in post-mortem sand-cat ears of the acoustic admittance of the cavities over a wide frequency range with cavity modifications (as in Huang et al. 1997) would settle this issue.

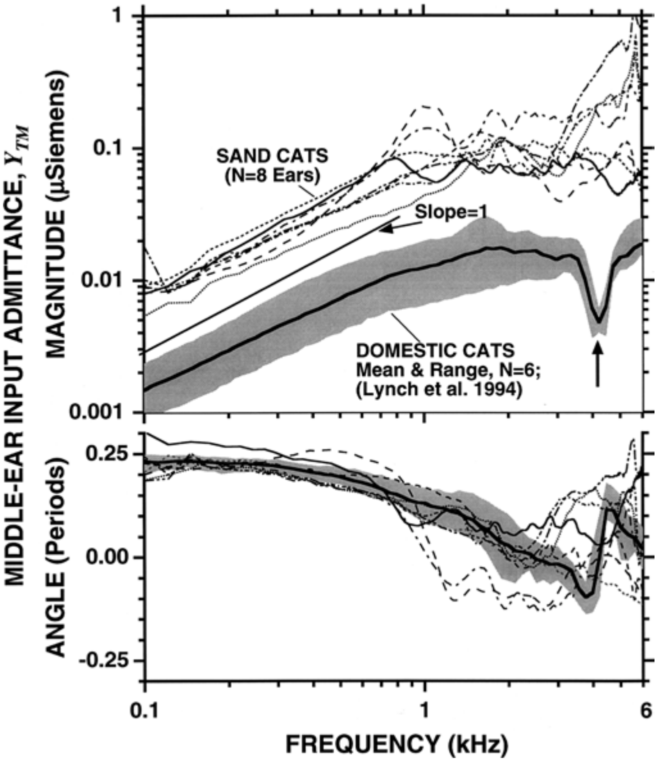


Fig. 4. Measurements of acoustic input admittance at the TM (Y_{TM}) of sand cats ($n=8$) and domestic cats ($n=6$). Each of the *thinner data curves* represents measurements from one sand-cat ear. Admittances were measured in the intact ear canal and corrected for the space between the probe and the TM via a uniform-tube transformation. For domestic cats the *shaded region* shows the range of admittances measured and the *thick line* is the mean (from Lynch et al. 1994, Fig. 12). The *vertical arrow* indicates the "notch" in the $|Y_{\mathrm{TM}}|$ in the domestic cats. The *thin straight line* labeled *Slope = 1* indicates a magnitude that is proportional to frequency. Acoustic admittance magnitude units: $1\ \mu\mathrm{S} = 1/(\mathrm{mks\ M}\Omega) = 10^{-6}\ \mathrm{m}^3/(\mathrm{Pa\text{-}s})$. Angles are plotted in periods ($1\ \mathrm{period} = 2\pi\ \mathrm{radians} = 360°$)

Low-frequency admittance: comparisons across felid species For low frequencies ($f < 0.5$ kHz) comparisons and analysis of the admittance are simplified (Huang et al.

2000a, p 456), because the admittances are compliance-like and each can be described by one number, the compliance. From measurements of Y_{TM}, we compute (see Materials and methods) the acoustic compliance of the middle ear, C_{ME}, which is not frequency dependent (Fig. 5A). C_{ME} is a measure of the low-frequency responsiveness of the middle ear, representing the volume displacement of the TM per unit sound pressure at the TM. We can compare measured compliance from sand cat ears with measurements from 11 other felid species in Fig. 5A, where compliance is plotted versus species size. If we ignore the sand cat, there is a general increase in net compliance with species' skull size (Huang et al. 2000a). The sand cat's C_{ME} is not only substantially larger than that of other cats of similar body size, it is comparable to that found in the largest species: mountain lion (M), leopard (Le), jaguar (J) and tiger (T).

Low-frequency admittance: structural analysis What structures contribute to sand cat's large middle-ear compliance? To interpret this acoustic difference in terms of structural features, it is helpful to recognize that the measured admittance Y_{TM} is determined by two admittances involving distinct structures. The cavity admittance Y_{CAV} is determined by the acoustic properties of the middle-ear cavities and foramen; the contribution of the TM and the ossicular chain is designated Y_{TOC}. Because the TM and the ossicular chain are driven by the pressure difference across the TM, these admittances are related as

$$1/Y_{TM} = 1/Y_{TOC} + 1/Y_{CAV} \tag{7}$$

(e.g., Peake et al. 1992, pp 246–247). In terms of the compliances Eq. 7 becomes

$$1/C_{ME} = 1/C_{TOC} + 1/C_{CAV} \tag{8}$$

in which the compliance of the middle-ear cavity C_{CAV} is determined by the total volume of the middle-ear air space. Although C_{TOC} cannot be directly measured noninvasively, we can solve Eqn. 8 for C_{TOC} based on the measured C_{ME} (Fig. 5A) and estimates of C_{CAV} determined by the total bullar volume inferred from our skull measurements (see Huang et al. 2000a, Table 1); the results of this computation for sand cat and other felid species are plotted in Fig. 5B. Unlike C_{ME} the values of C_{TOC} have no systematic dependence on species size. However, the sand cat's C_{TOC} value is large, about three times the average of all of the other species. (The sand cat's large C_{TOC} may not be unique among cats; the inferred C_{TOC} in one Pallas's cat ear nearly equals the mean sand cat C_{TOC}.)

The important conclusion here is that the large compliance (and low-frequency admittance magnitude) of the sand-cat middle ear is a consequence of *both* an enlarged middle-ear air space, *and* an unusually compliant TM and ossicular chain.

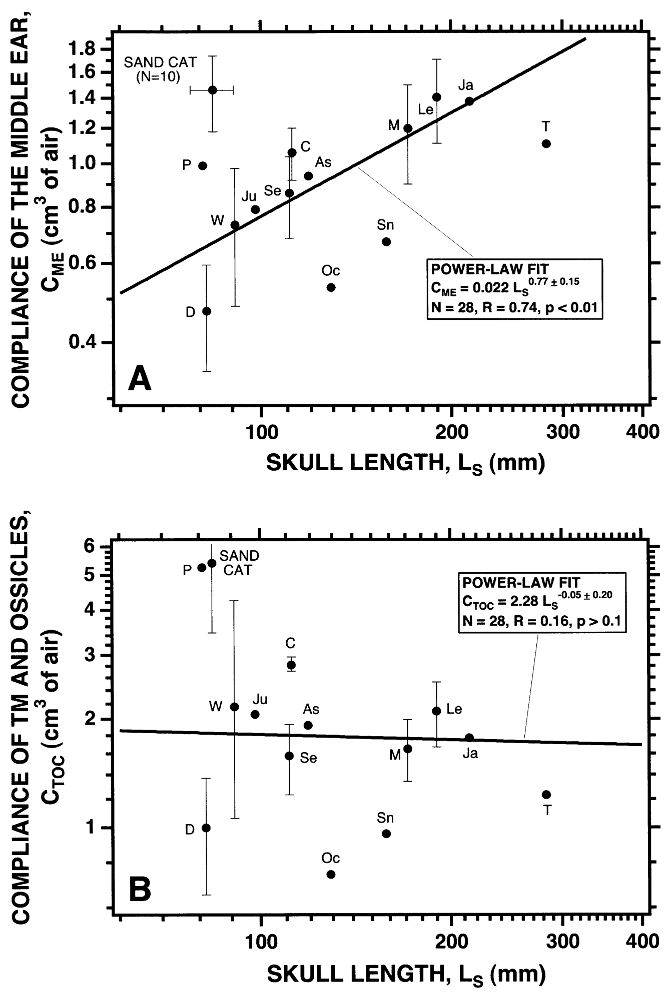


Fig. 5A, B. Acoustic compliances of the sand cat's middle ear compared with size trends for the family. In both plots, compliances (*C*) are expressed as equivalent air volumes *CK*, where *K* is the adiabotic bulk modulus of air. **A** Net acoustic compliance of the middle ear, C_{ME}. Values were computed as $\mathrm{Im}\{Y_{TM}(f)\}/(2\pi f)$ averaged over ten frequencies between 0.12 kHz and 0.34 kHz, where $\mathrm{Im}\{Y_{TM}\}$ denotes the imaginary part of the measured input admittance. Each point represents a mean of ears (of one species) in which acoustic measurements were made. The *vertical error bars* represent standard deviations of our samples. The *horizontal error bar* (±8%) represents the average coefficient of variation (SD/mean) in skull-length measurements for all species plotted. The domestic cat measurements used in this figure are those of Huang et al. (2000a) ($n=4$), which were obtained with the same techniques used in all other species. They differ somewhat from those of Lynch et al. (1994) in Fig. 4. **B** Inferred acoustic compliances of the TM, ossicles and the cochlea, C_{TOC}. These values were computed as $(1/C_{TOC}) = (1/C_{ME}) - (1/C_{CAV})$, where C_{CAV} is the average compliance of the middle-ear cavity for each species (Table 1; see also Huang et al. 2000a, Table 1). The *vertical bars* represent ranges of values computed by pairing means ± SDs from **A** with means ± deviations in the C_{CAV} measurements. The power laws are least-squares fits to the log-log data, excluding the sand cat data. *R* is the correlation coefficient; *p* is the probability that the slope of the line is zero (Rohlf and Sokal 1969, p 225). The data are from 10 sand cats and 28 individuals of 13 other cat species: *D* domestic cat ($n=4$), *W* wildcat (*F. silvestris*, $n=3$), *P* Pallas's cat (*Otocolobus manul*), *Ju* jungle cat (*F. chaus*), *Se* serval (*Leptailurus serval*, $n=2$), *C* caracal (*Caracal caracal*, $n=4$), *Oc* ocelot (*Leopardus pardalis*), *As* Asian golden cat (*Catopuma temminckii*), *Sn* snow leopard (*Uncia uncia*), *M* mountain lion (*Puma concolor*, $n=4$), *Le* leopard (*Panthera pardus*, $n=4$), *Ja* jaguar (*P. onca*), *T* tiger (*P. tigris*)

External ear

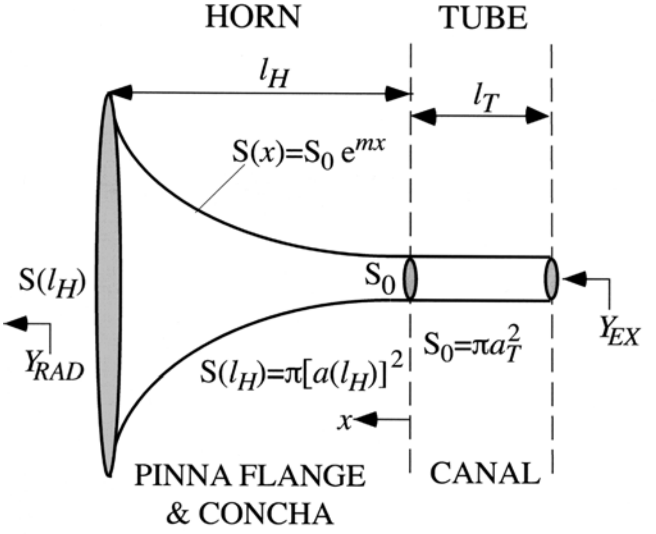
Output admittance of the external ear The acoustic admittance Y_{EX}, which can be measured by determining the admittance looking out through the external ear from just lateral to the TM to the outside, is the output admittance of the external ear as it delivers sound to the middle ear. Measurements of Y_{EX} have been made on excised ears of domestic cats and a simple structural model has been shown to represent the main features of the measurements (Rosowski et al. 1988). As no measurements of this quantity for sand-cat ears have been made, we analyze a similar structural model, comprised of a uniform, cylindrical, rigid-walled tube joined to a rigid-walled exponential horn. The dimensions for each species' model are constrained by the anatomical measurements (Table 2) as illustrated in Fig. 6. The most important differences in the dimensions of the two models are in the radius and length of the uniform tube that represents the ear canal, with a canal radius a_T of 2.5 mm and 4.3 mm in the domestic cat and sand cat, respectively, and a length l_T of 14.5 mm and 28.3 mm, respectively. The horn length l_H and the pinna-flange radius a(l_H) are similar in the two models. The horn flare constant *m,* which describes the change in cross-sectional area of the horn $S(x)$ with distance from the horn's origin at the canal-concha border, is a little smaller in the sand cat, which produces a slightly more gradual flare.

From these model representations of the external ears, assuming rigid walls, and a description of the acoustic properties of the enclosed air (Egolf 1977), we have calculated the admittance Y_{EX} (Fig. 7). The features of Y_{EX} in the two species are generally similar, but the sand cat $|Y_{EX}|$ is larger than domestic cat for both low frequencies ($f < 1$ kHz) and high ($f > 3$ kHz), and the magnitude minimum (with the associated rapid angle change) occurs at a lower frequency in the sand cat (2 kHz) than in the domestic cat (near 3 kHz).

To interpret these comparisons in terms of structural features we use approximations for low- and high-frequency regions. For frequencies below the $|Y_{EX}|$ minimum the two admittances are mass-like (i.e., the magnitudes are inversely proportional to frequency and the angles are about –0.25 periods). Rosowski et al. (1988) demonstrated that the mass-dominated admittance observed at low frequencies in domestic-cat ears is heavily influenced by the acoustic mass of the ear-canal tube, i.e.,

$$\left|Y_{EX}^{\text{low frequency}}\right| \approx \frac{1}{2\pi f M_{EC}} = \frac{\pi a_T^2}{2\pi f \rho_0 l_T} = \frac{a_T^2}{2frho_0 l_T}, \qquad (9)$$

where M_{EC} is the acoustic mass of the ear canal, and ρ_0 is the density of air. Therefore, differences in the magnitude of the two admittances at low frequencies should depend primarily on the differences in the length l_T and radius a_T of the ear-canal tube. As the factor-of-two increase in length of the sand-cat canal is more than balanced by the factor-of-three increase in the square of its radius, Equation 9 implies that the sand cat $|Y_{EX}|$ should be 1.5 times greater in magnitude than that in the domestic cat, which is close to the factor of 1.8 from the exact analysis of the model plotted in Fig. 7. The difference between the prediction of Eq. 9 and the model arises from the contribution of the horns to the radiation admittances.



	PinnaFlange Radius $a(l_H)$	Horn Length l_H	Horn-Flare Constant m	Canal Radius a_T	Canal Length l_T
SAND CAT	21.5 mm	40 mm	0.080 mm^{-1}	4.3 mm	28.3 mm
DOMESTIC CAT	20	44.7	0.093 mm-1	2.5	14.5

Fig. 6. Model of external-ear geometry used to predict Y_{EX} and η_R. The model consists of rigid walls containing an air-filled tube of circular cross section and variable radius. Its two sections are a tube of uniform radius a_T and cross-section S_0 (the ear canal) concatenated with an exponential horn of varying cross section $S(x)$ (concha and pinna flange) terminated by a free-space radiation admittance Y_{RAD}. The description of sound propagation in the tube includes representation of viscous forces and heat transfer. For the sand-cat model, the dimensions shown were determined from (1) acoustic estimates of the canal diameter and length, (2) measurements of ear molds made of the concha and canal, and (3) measurements of the pinna-flange opening. For domestic cat, the model dimensions are from Rosowski et al. (1988, Table I)

At frequencies above the magnitude minimum, Y_{EX} is more conductance-like and begins to approximate the characteristic admittance of the ear canal ($Y_0 = \pi a_T^2/\rho_0 c$) (see Fig. 7), which is directly proportional to the cross-sectional area of the canal ($Y_0 = 0.15$ μS and 0.047 μS for sand cat and domestic cat, respectively). This approximation predicts that at high frequencies the two admittances should differ by a factor of 3, which agrees roughly with Fig. 7.

Radiation efficiency, η_R The diffuse-field receiver cross-section A_{DF} depends on the "*radiation efficiency*" of the external ear η_R (defined in Eq. 3). The results of calculations of this efficiency for sand-cat and domestic-cat

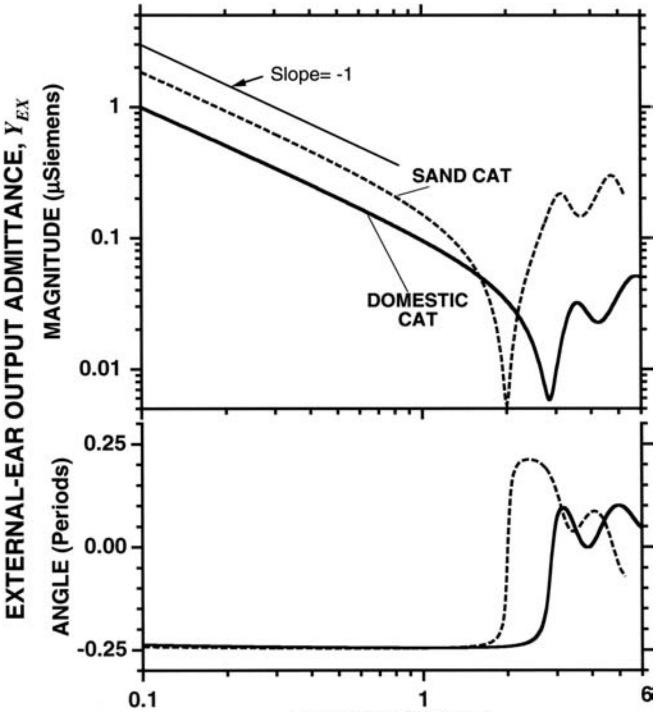


Fig. 7. Magnitude and angle of the output admittance of the external ear Y_{EX} computed from the rigid-walled external-ear models of Fig. 6 assuming plane-wave propagation. The thin straight line labeled *Slope = –1* indicates a magnitude that is inversely proportional to frequency. The model estimates of Y_{EX} in the domestic cat are nearly identical to the model predictions illustrated in Fig. 11 of Rosowski et al. (1988), except that the tube-wall losses (e.g., Egolf 1977) included in the present model smooth the rapid changes in admittance magnitude and angle that occur at frequencies above 2 kHz

models are plotted in Fig. 8. The calculations show that for frequencies above 3 kHz the external-ear models radiate sounds with $\eta_{\mathrm{R}} \approx 1$, meaning that only a small fraction of the power that enters the narrow end of the external ear is dissipated before it radiates into the environment. At lower frequencies, however, neither of the external ears acts as a "lossless" sound radiator. In this low-frequency range η_{R} in both species is proportional to $f^{1.6}$ and the sand cat η_{R} is about a factor of 3 larger than that of the domestic cat. The main structural feature that contributes to the larger η_{R} in the sand cat is the larger radius of the ear canal, which reduces losses from viscosity and heat transfer (Egolf 1977).

Power collection by the external and middle ear

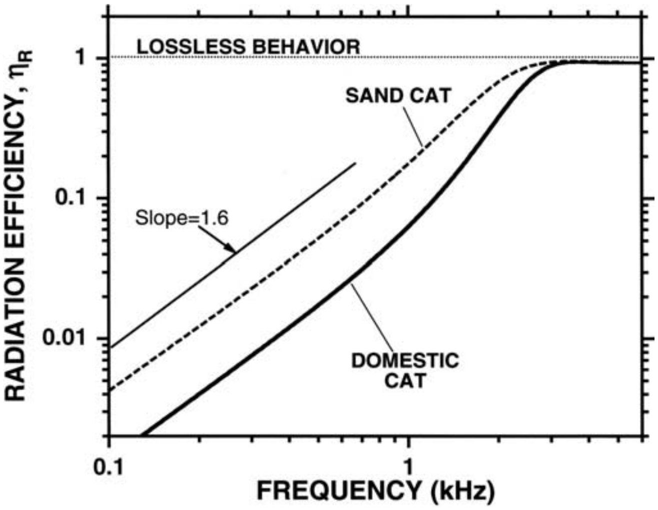


Fig. 8. The radiation efficiency η_{R} calculated from the external-ear models (Fig. 6) of sand cat and domestic cat using Eq. 3. The efficiency is a measure of how well the external ear acts as a radiator of sound power. The thin straight line labeled *Slope = 1.6* indicates the shape of a function that is proportional to $f^{1.6}$

Power-utilization ratio The effect of the "match" between admittances Y_{TM} and Y_{EX} on power absorption is described by the PUR (Eq. 2), which is plotted in Fig. 9 for sand-cat and domestic-cat ears. For frequencies above 3 kHz, where Y_{TM} and Y_{EX} are relatively independent of frequency and of about zero angle (except for the "foramen" notch in the domestic cat Y_{TM}), the computed PUR is close to the "matched" condition in that PUR is > 0.5. As frequency decreases below 3 kHz, PUR decreases such that it is less than 10% below 1 kHz. This decrease results because Y_{TM} and Y_{EX} are grossly mismatched in this frequency range in both species (while Y_{TM} and Y_{EX} are of opposite angle, they are of greatly different magnitudes). Between 0.5 kHz and 2 kHz, the PUR in sand cat is larger than that in domestic cat by a factor of 2–5.

Computation and comparison of A_{DF} The diffuse-field receiver cross-sections A_{DF} calculated from PUR and the radiation efficiency η_{R} (Eq. 1) are plotted in Fig. 10. Both functions have peaks near 3 kHz, where both A_{DF}s are close to the IDEAL limit ($A_{DF}^{Max} = \lambda^2/(4\pi)$). For frequencies below the peak, both A_{DF}s decrease at a rate of about 2.5 orders of magnitude for a decade of frequency, i.e., proportionally to $f^{2.5}$. The sand-cat A_{DF} starts its low-frequency roll-off at a lower frequency; at frequencies below 2 kHz, the sand-cat A_{DF} is five to ten times larger than that of domestic cat. This result indicates that the sand-cat external/middle ear combination is superior to domestic cat's in absorbing sound power from the environment at frequencies below 2 kHz. (As the diffuse-field condition involves all directions for the received sound, variations in sensitivity with direction are not represented in this assessment.)

Analysis: low-frequency values of A_{DF} Which acoustic quantities are primary contributors to the difference in A_{DF} between sand cat and domestic cat at low frequencies? First, we make two approximations that are appropriate for low frequencies (i.e., $f < 0.8$ kHz). (1) For this frequency range the exponential horns are operating below "cutoff frequency" (see, for example, Kinsler et al.

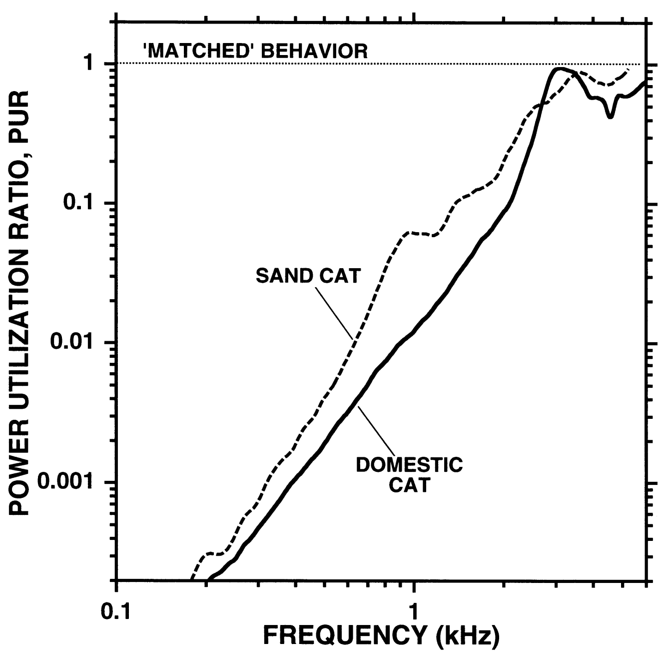


Fig. 9. Power utilization ratio *PUR* versus frequency for the sand cat and domestic cat. For each species PUR was calculated with Eq. 2 and the mean measured Y_{TM} from Fig. 4 and the model-derived values of Y_{EX} from Fig. 7. The *dotted horizontal line* indicates PUR = 1 when Y_{EX} and Y_{TM} are "matched". PUR is a measure of power flow across the boundary of the external and middle ear; if PUR = 1, all of the power available is delivered to the middle ear

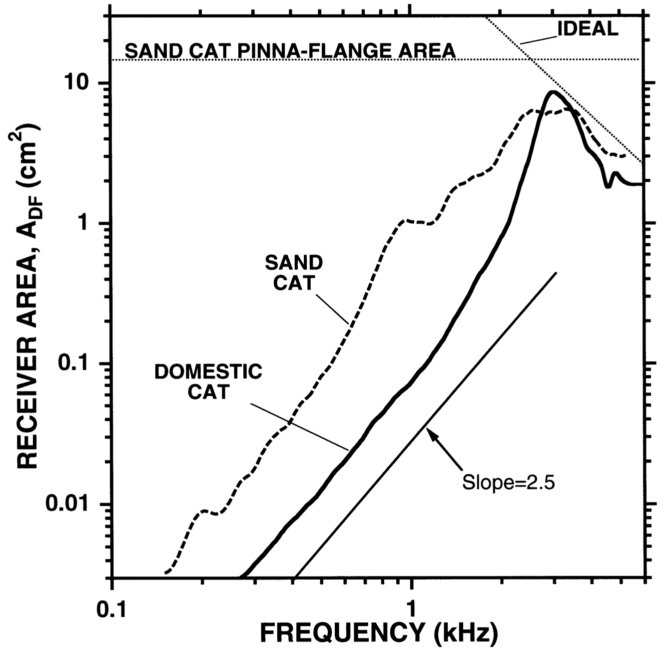


Fig. 10. Diffuse-field power absorption (cross-section) A_{DF} for the sand cat and domestic cat. The curves were computed with Eq. 1 from results in Figs. 4, 7 and 8. The downward sloping dotted line labeled *Ideal* is $A_{DF}^{MAX} = \lambda^2/4\pi$. The *horizontal dotted line* marks the area of the sand-cat's pinna-flange opening. The upward sloping thin line labeled *Slope* = *2.5*, illustrates the shape of a function that is proportional to $f^{2.5}$. A_{DF} is a measure of the sound-collecting ability of the cats' external and middle ear

1982, p 375), so waves do not propagate in the horn. In this case the radiation efficiency can be approximated by the ratio of the acoustic resistance R_{RAD}, the real part of the acoustic impedance associated with radiation from the pinna flange, and the acoustic resistance looking into the external ear from the TM R_{EX}; i.e.,

$$\eta_R(f<0.8\ kHz) \approx \frac{R_{RAD}}{R_{EX}} = \frac{\mathrm{Re}\{Y_{RAD}\}}{|Y_{RAD}|^2}\,\frac{|Y_{EX}|^2}{\mathrm{Re}\{Y_{EX}\}}. \tag{10}$$

(2) Figures 4 and 7 demonstrate that for frequencies $f < 0.8$ kHz, $|Y_{EX}|$ is at least twice the mean $|Y_{TM}|$ so the factor (PUR) is simplified, such that

$$PUR(f<0.8\ kHz) \approx \frac{4\mathrm{Re}\{Y_{EX}\}\mathrm{Re}\{Y_{TM}\}}{|Y_{EX}|^2}. \tag{11}$$

With these approximations (Eqs. 10 and 11) Eq. 1 yields:

$$A_{DF}(f<0.8\ kHz) \approx \frac{\lambda^2}{\pi}\frac{\mathrm{Re}\{Y_{RAD}\}}{|Y_{RAD}|^2}\mathrm{Re}\{Y_{TM}\}, \tag{12}$$

in which A_{DF} depends only on the radiation admittance at the pinna end of the horn and the real part of the middle-ear input admittance, Y_{TM}. Because Y_{RAD} depends only on the pinna radius, which is essentially identical in sand cat and domestic cat, the interspecies differences in A_{DF} below 0.8 kHz (Fig. 10) result primarily from differences in the real part of the middle-ear input admittance Y_{TM}. (Note that as long as the areas of the pinna opening are the same, the details of the external-ear structure, and how those details contribute to Y_{EX} and η_R, have little effect on A_{DF} for low frequencies.) In summary, the increased power collection by the sand-cat ear relative to domestic cat at frequencies below 0.8 kHz is a consequence of the relatively larger real part of the admittance of its middle ear, where $\mathrm{Re}\{Y_{TM}\} = |Y_{TM}|\cos(\angle Y_{TM})$. As the mean angles of the admittance, $\angle Y_{TM}$, of the two species are nearly identical in this low-frequency region (Fig. 4), the $\mathrm{Re}\{Y_{TM}\}$ for sand cat is roughly five times larger than for domestic cat, because of the larger magnitude of the admittance, $|Y_{TM}|$, for sand cat (Fig. 4).

Discussion

Organization

The following sections argue that the structural specializations of the sand cat ear favor survival in an arid habitat. Steps in the argument are as follows: (1) summarize sand cat's structural specializations and relate them to hearing sensitivity through the diffuse-field sound-absorption cross-section A_{DF}; (2) transform this hearing advantage to an increase in hearing range (distance), taking into account properties of acoustic propagation in desert air; (3) connect the increased range to behavior beneficial to the sand cat; and (4) speculate about the evolutionary sequence that led to the development of sand cats.

Structural specializations and hearing consequences

External ear

The size of the sand-cat pinna flange, which is often referred to as *size of the ear*, is not significantly different from that of domestic cat. [The common perception that the pinna is unusually large may result from a relatively lateral placement of the pinnae on the head (Fig. 2)]. However, the sand-cat cartilaginous external-ear canal is of larger diameter and length compared to domestic cat and other cats of its size (Tables 1 and 2). The combined acoustic effect of these features is that the magnitude of the output admittance of the external ear $|Y_{\mathrm{EX}}|$ is generally larger for sand cat (Fig. 7).

The increased length of the ear canal in sand cat contributes to the more lateral placement of the external ears on the sand-cat head (Pocock 1951; Heptner and Sludskii 1992). The increased canal length may produce an increase in the inter-aural time-of-arrival difference between sounds from the same source, and thereby increase the accuracy of the sand cats' localization of sound sources in space (Heffner and Heffner 1992; Brown 1994).

Middle ear

The relatively large TMs (implied by the large bony ear-canals) and bullae of sand cat (Tables 1 and 2) contribute to the relatively large input admittance of the middle ear $|Y_{\mathrm{TM}}|$ (Figs. 4, 5A, B), as do components of the ossicular-chain and cochlea (Fig. 5B). The combined effect is an increase in the power input to the middle ear for a given sound pressure at the TM, which is a principal cause of a similar sized increase in the power absorbed by the external and middle ear (Fig. 10).

Another structural specialization is that the foramen in the bony septum is very large in sand cat (Table 2). This feature might be related to the absence of a notch in the sand cat middle-ear admittance magnitude $|Y_{\mathrm{TM}}|$ (Fig. 4), but we have no direct evidence about the acoustic consequences of this structural feature. A large foramen in the septum separating the middle-ear cavities would have the benefit of increasing the frequency of the middle-ear notch without compromising the increase in the mechanical strength of the bullar wall provided by the septum.

Sound absorption from a diffuse field and hearing sensitivity

Sand-cat ears are expected to absorb five to ten times more low-frequency acoustic power from a diffuse sound field than domestic-cat ears (Fig. 10). How might this difference affect sand cats' auditory sensitivity relative to domestic cat?

It has been proposed that the auditory system's threshold for detection of tones is determined by the sound power absorbed by the ear, and that variations in hearing sensitivity with frequency are a consequence of variations of the peripheral ear's effectiveness in coupling sound power from the external sound field into the system (Khanna and Tonndorf 1969; Rosowski et al. 1986; Rosowski 1994). Evidence from a few mammalian species is roughly consistent with this idea (Rosowski et al. 1986, Fig. 10; Rosowski 1991a, 1991b; Ravicz et al. 1996). If we assume that the cochleas and central auditory systems of sand cat and domestic cat are equally sensitive to sound power, and that the middle ears are equally efficient in transmitting power from TM to inner ear (assumptions required in the absence of physiological data), then differences in A_{DF}, a measure of the efficacy of sound coupling into the middle ear, will determine the difference in behavioral sensitivity between these two species. Subject to these assumptions, we can use our computations of A_{DF} to estimate the differences in the threshold sound pressures between sand cat and domestic cat. For example, the curves in Fig. 10 show that at 0.5 kHz the ratio R of sand-cat A_{DF} to domestic-cat A_{DF} is 0.08/0.0126 cm^2 or $R = 6.3$. To express this power ratio R in decibels we take $10\log_{10}R$ yielding 8.0 dB, which we call $\Delta H(0.5\ \mathrm{kHz})$, the interspecies difference in hearing sensitivity at 0.5 kHz. The same process applied to other frequencies yields $\Delta H(1\ \mathrm{kHz}) = 11.5$ dB, $\Delta H(2\ \mathrm{kHz}) = 6.1$ dB, and $\Delta H(4\ \mathrm{kHz}) = 1.3$ dB. This simple transformation expresses the sensitivity differences in terms of the logarithmic decibel scale commonly used in assessing hearing sensitivity, where the sand cat is suggested to be 8.0 dB, 11.5 dB, 6.1 dB, and 1.5 dB more sensitive than the domestic cat to tones of 0.5 kHz, 1 kHz, 2 kHz, and 4 kHz, respectively.

Measurements of hearing sensitivity for tones are often summarized by plots of threshold level (the minimum sound pressure level – in dB SPL – in the sound field required to produce a behavioral response) versus tone frequency. Comparison of features of these *audiograms* has been a primary approach in the comparative study of hearing (Fay 1988, 1994; Heffner and Heffner 2001). A combination of the A_{DF} measurements and values for the sound power at the TM at threshold can produce a diffuse-field audiogram. Previous studies have demonstrated that the domestic cat audiogram can be well approximated by the diffuse-field sound pressure required to produce 1.6×10^{-18} W of sound power at the TM[5] With our assumptions concerning the comparable

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[5] Rosowski (1991a) demonstrated a match between measured auditory thresholds as a function of frequency in domestic cat and a diffuse-field power level of 4×10^{-19} W at the entrance to the *inne*r ear. That paper suggested that the power-transfer efficiency of the cat middle ear was about 25%, implying that the threshold power level at the domestic cat TM is four times higher, or 1.6×10^{-18} W. (Rosowski 1991a).

sensitivity of the inner ears, we can compute predicted thresholds for the two species (Fig. 11).

The domestic cat curve in Fig. 11 is generally similar to domestic-cat audiograms obtained with sound fields approximating uniform plane waves, in that as frequency increases the threshold SPL decreases to a minimum between 1 kHz and 10 kHz and the value of the minimum is around –20 dB SPL (Fay 1988, pp 47–50). While the shape of the predicted sand-cat threshold curve is similar, the larger low-frequency A_{DF} in sand cat leads to a prediction of a 5- to 10-dB increase in sensitivity (decrease in threshold) at frequencies below 2 kHz. The magnitude of this threshold decrease at 0.5, 1, 2 and 4 kHz is identical to the ΔH values computed from the A_{DF} curves of Fig. 10.

Sound propagation in arid habitats

Although the increased hearing sensitivity of about 8 ± 3 dB for the sand cat for $f < 2$ kHz (Fig. 11) is a relatively small change by some standards, its consequences could be especially important in a desert habitat. To assess this possibility we describe the propagation of sound over the ground from a source in an acoustic environment approximating a desert.

Though numerous mechanisms affect sound propagation in a natural environment (see, for example, Sutherland and Daigle 1997), we consider three that are ubiquitous, important, and relatively simple to describe. Each mechanism introduces a decrease in sound pressure (i.e., attenuation) as sound propagates away from a source, as illustrated in Fig. 12. We use the net effect of these three mechanisms to provide an approximation to a particular ecological situation.

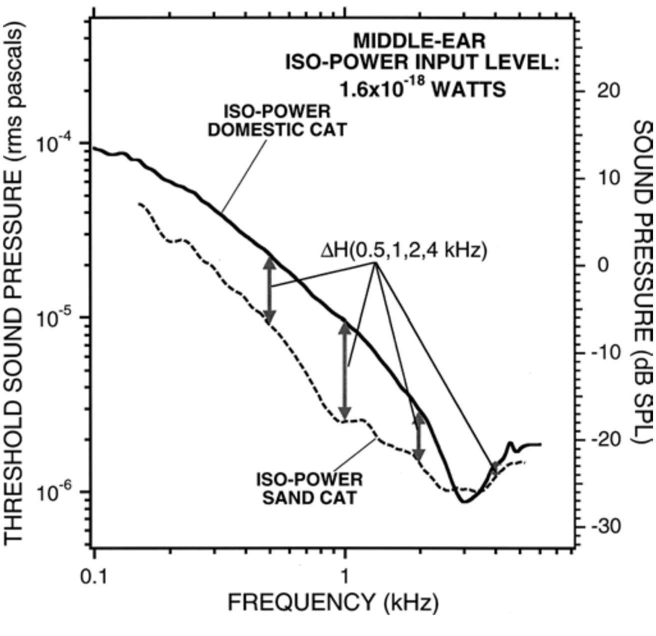

Fig. 11. Inferred behavioral thresholds for tones with diffuse field stimulation computed for sand cat and domestic cat. The two lines are iso-power contours that yield a constant power input to the middle ear of 1.6 fW (fem to watts). The *vertical gray arrows* mark the differences in threshold ΔH at 0.5 kHz, 1 kHz, 2 kHz, and 4 kHz of 8 dB, 11.5 dB, 6 dB, and 1.3 dB, respectively. The contours were computed from the estimates of A_{DF} (Fig. 10) assuming that the middle and inner ears of the sand and domestic cat are equivalent in sound power transmission and sensitivity

One attenuation mechanism results from the sound wave's spreading out in three dimensions; the effect is that sound-pressure amplitude is proportional to the inverse of the distance from the source in a frequency independent manner. This "geometrical spreading" mechanism is designated A_{GS} in Fig. 12, which shows an attenuation of 60 dB between locations 1 m and 1 km from the source.

A second attenuation mechanism, atmospheric absorption A_{AA}, which is a consequence of sound energy's being absorbed by (primarily) oxygen molecules, introduces a decrease in sound pressure that is exponential with distance; that is, the SPL decreases a fixed number of decibels per meter. Extensive measurements and theory have led to a rather complete description of the dependence of A_{AA} on frequency and relative humidity (RH) (Bass et al. 1995). Three features are of primary interest: (1) A_{AA} generally increases with frequency (e.g., in Fig. 12 at $D = 1$ km, A_{AA} for 4 kHz and RH = 90% (about 20 dB) is larger than for 0.5 kHz (about 3 dB)); (2) dependence on RH is substantial and complicated; for $f = 0.5$ kHz and RH between 10% and 100% variation with RH is negligible, but at 4 kHz, with increasing humidity, A_{AA} decreases from 109 dB km^{-1} at 10% RH to 20 dB km^{-1} at 90% RH. (For RH less than 10% the effects of humidity variations are large and opposite in direction, which is an additional complication. We have, therefore, not included extreme, low humidity conditions.); (3) the dependence of A_{AA} on relative humidity also complicates the effect of temperature on absorption (Sutherland and Daigle 1997). In the simple case of constant water content, A_{AA} increases and RH goes down as temperature increases. The plotted examples of A_{AA} show that with an ambient temperature of 20°C and RH of 10% atmospheric attenuation at 0.5 kHz is very small compared to 4 kHz. To extend the description of RH dependence to an intermediate frequency, for 2 kHz A_{AA} at 1 km is 9 dB for RH = 90% and 45 dB for RH = 10%, a less dramatic difference than at 4 kHz, but still a substantial RH dependence.

A third mechanism is the loss associated with propagation over ground that interacts acoustically with the propagating wave in the air. In theory, the *ground effect* term A_{GE} is dependent on the acoustic properties of the ground, sound frequency, and the heights of the source and receiver above the ground (Sutherland and Daigle 1997, pp 343–353). To include this term in Fig. 12 we use measurements made over a 1.1-km distance in open grassland (Parkin and Scholes 1965). These results show that the ground effect, though significant, is relatively small (i.e., less that 25 dB) even for a distance of a 1 km or more, because

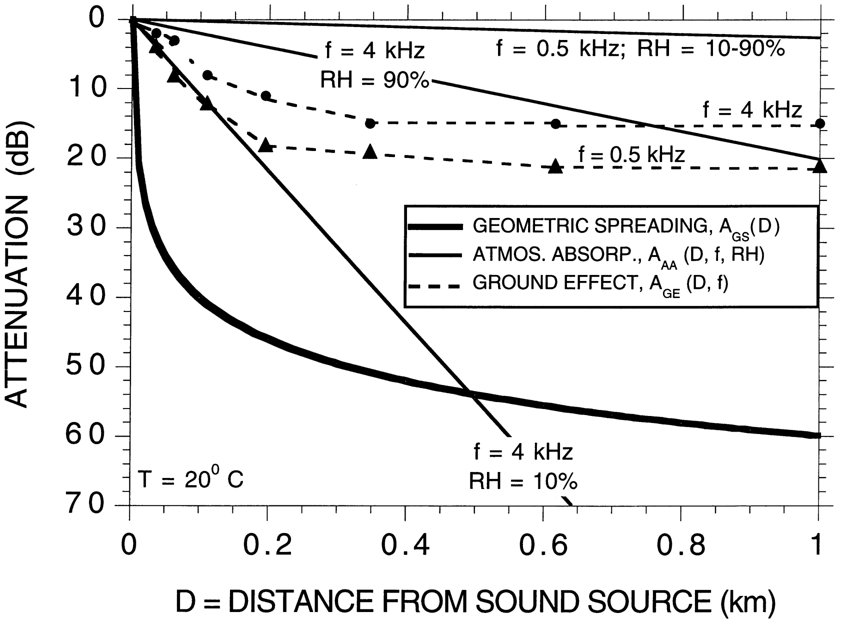

Fig. 12. Mechanisms of sound attenuation with distance from a non-directional source. Sound attenuation (plotted downward) versus distance D from a sound source. The reference level is 0 dB at a distance of 1 m from the source ($D = 0.001$ km). Attenuation due to *geometric spreading* of sound A_{GS} (*thick solid curve*) is proportional to distance from the source and independent of frequency f or relative humidity (RH). Attenuation due to *atmospheric absorption* A_{AA} (*thin solid curves*) has a dependence on RH that varies with frequency: at 0.5 kHz, A_{AA} is small and independent of RH (for RH between 10% and 90%); but at 4 kHz, A_{AA} is much larger at 10% RH than at 90% RH (Sutherland and Daigle 1997, Fig. 1). Attenuation due to *ground effect* A_{GE} (*dashed curves*) varies with frequency but is independent of RH: at 0.5 kHz, A_{GE} (measured over open flat grassland) is slightly larger than at 4 kHz (Parkin and Scholes 1965, Fig. 3; no wind, no inversion condition, microphones 1.5 m above ground)

A_{GE} does not increase much with distance beyond the first 0.3 km.

If now we compare these three mechanisms of atmospheric attenuation, we see that for short distances from the source (i.e., less than 0.2 km), geometric spreading is the dominant effect in reducing sound level. For larger distances, the ground effect adds 18 ± 4 dB, and for relatively high frequencies (i.e., 4 kHz) atmospheric attenuation adds appreciably and is the dominant mechanism *for low humidities*. Note that in this description the effect of a desert habitat is included *only* in the atmospheric absorption term, where low RH produces a large attenuation for higher audio frequencies. Although it is conceivable that the acoustic properties of a desert surface are unique and therefore the ground effect would be different from the measurements used here, available data on acoustic properties of sand do not suggest a substantial difference (e.g., Sutherland and Daigle 1997, Table 2).

The next step is to use this description of sound attenuation to relate hearing sensitivity to distance. With the effect of the three attenuation mechanisms added together to give the total attenuation A_T versus distance (Fig. 13) for a RH (20%) representative of deserts at night (Griffiths and Soliman 1972), the result shows that low-frequency sound (0.5 kHz in the plot) is attenuated less than higher frequency sound (4 kHz) with 2 kHz in between. Because of the large value of A_{AA} for 4 kHz the net attenuation at that frequency is larger and increases more rapidly for $D > 0.1$ km.

With this description of the distance dependence of sound level, we can assess the effect of an increase in sensitivity on the distance over which a sound source can be detected (“earshot”). Assume a “point” sound source at $D = 0$ emits a tone at either 0.5 kHz, 2 kHz, or 4 kHz at a level just audible to a domestic cat located near $D = 0.5$ km. Because we predict that the sand cat’s hearing is more sensitive, these sounds should be above threshold to a sand cat by the amount indicated by the vertical lines labeled ΔH. Therefore, the sound level at the sand cat’s ear could be reduced (by 8 dB at 0.5 kHz, 6.1 dB at 2 kHz, and 1.3 dB at 4 kHz) and still remain audible. The reduction in level could be accomplished by moving the sand cat further away from the source by the amount indicated by the horizontal lines labeled ΔD (Fig. 13). This increase in earshot is approximately 0.4 km at 0.5 kHz, 0.2 km at 2 kHz, and 0.03 km at 4 kHz. Note that there are two reasons for the small ΔD at 4 kHz. One is that ΔH is smaller; the other is that the slope of the attenuation curve is larger for the higher frequency; even if ΔH were 8 dB at 4 kHz, ΔD would be less than 0.1 km. Because attenuation increases with distance so rapidly for high-frequency sound (in low RH), a moderate increase in either the receiver’s sensitivity (or the source’s output level) produces a relatively small increase in earshot.

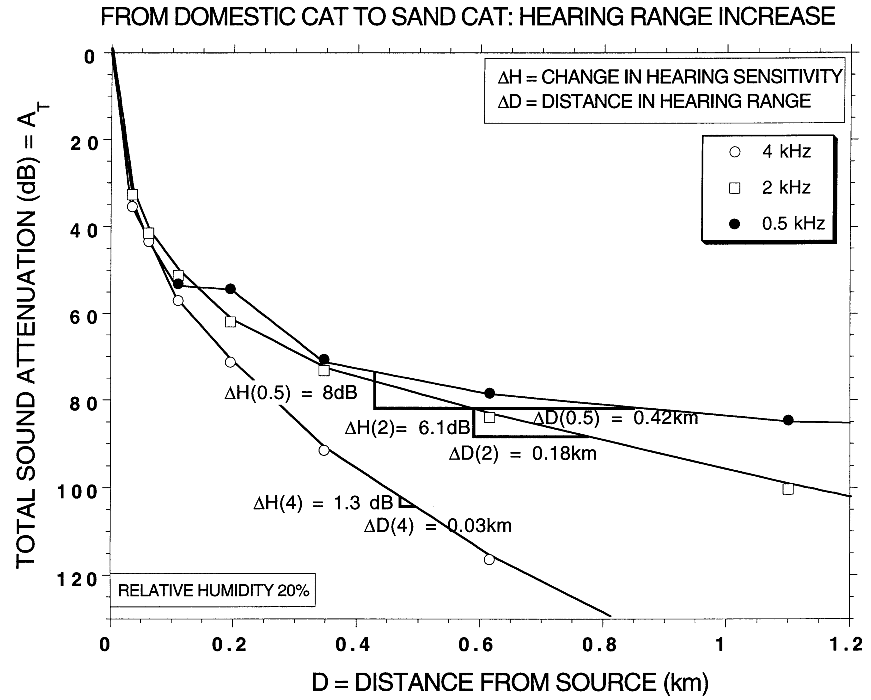

Fig. 13. Total sound attenuation $A_T = A_{GS} + A_{AA} + A_{GE}$ (plotted downward) versus distance *D* from a sound source for low- (0.5 kHz), mid- (2 kHz), and high-frequency (4 kHz) sounds at a RH of 20% (typical of deserts at night). Attached to each curve are (1) a *vertical line* of length ΔH showing the increased sensitivity of the sand cat ear relative to the domestic cat ear at that frequency (from Fig. 11) and (2) a *horizontal line* projected from the vertical ΔH line to the curve, which shows the increase in hearing range for sand cat ΔD resulting from the increase in sensitivity

Ethology: habitat and hearing in sand cat behavior

Other features of desert habitats also influence transmission and reception of acoustic signals. The sparseness of vegetation that defines "desert" removes the large attenuation effect that trees can have in scattering sound (e.g., Embleton 1963; Price et al. 1988). In addition, the absence of trees removes noise generated by wind that would mask reception of sound signals (see Bradbury and Vehrencamp 1998, Fig. 3.5). A mechanism that enhances sound propagation over the ground surface is refraction caused by temperature increases with altitude ("temperature inversions"), which channel the sound near the surface (Larom et al. 1997a, 1997b). The effectiveness of this mechanism changes with atmospheric conditions; its greatest effect is at night when the ground is relatively cool[6] As sand cats are primarily nocturnal this enhancement mechanism could be important to them. These physical mechanisms generally improve the possibilities for long distance sound communication in deserts.

Biological requirements in desert habitats determine the *importance* of long-distance sound reception. Low vegetation density leads to relatively low density of small prey animals, such as the seed-eating gerbils and jerboas that are common sand cat prey (Heptner and Sludskii 1992, p 657; Roberts 1977, p 143). As a consequence sand cats must range over relatively large territories to find prey; 16 km^2 has been estimated as a coverage area in Israel (Abbadi 1993) and "tens of square kilometers" comprise an individual's territory in the transcaspian deserts (Heptner and Sludskii 1992, p 658). For the closely related black-footed cat (*F. nigripes*) of South Africa, extensive behavioral observations have established nightly travel of 10 km (Sliwa 1999). The large distances involved generate a *need* for long-distance sound reception.

What specific behavioral situations might involve long distance reception? Although observations of sand-cat behavior in native habitats are generally anecdotal, they do cover the sand cat range including the western Sahara (Dragesco-Joffé 1993), Israel (Mendelssohn 1989; Abbadi 1993), the Arabian peninsula (Gasparetti et al. 1985), western Pakistan (Roberts 1977), and central Asia (Heptner and Sludskii 1992)[7] . Because sand cats are primarily active at night, the principal method for sensing prey, predators, and conspecifics at a distance is probably hearing. Thus, detection of important events such as activity of gerbils or wolves, and vocalizations of conspecifics, e.g., as territorial markers, estrus announcements, or a mother's message to her den-bound kittens of her impending delivery of food (Sliwa 1994, 1999), depend on the adequacy of sound propagation. In all of these situations, enhanced detection sensitivity for sounds over large distance would improve sand cat survival. Sand cat vocalizations, which are described as "barks" (e.g., Hemmer 1974), apparently have less-prominent high-

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[6] Larom et al. (1997b, p 428) propose that these "atmospheric fluctuations have exerted a selective pressure on the calling behavior of... lions [which] roar almost exclusively at night.".

[7] Methods of data collection included radio collaring four specimens in a difficult geographical situation (Mendelssohn 1989; Abbadi 1993), collecting observations from local human inhabitants (Dragesco-Joffé 1993), and analyzing feces and stomach contents of collected specimens (see Heptner and Sludskii 1992, p 657).

frequency content than that of a more standard high-intensity felid "mew";[8] the latter is regarded as a common long-distance signal for Felidae (Peters 1987, p 318). These considerations, together with our quantitative analysis of sound attenuation over the desert surface, support the adaptive contribution of low-frequency sound reception for sand cats.

In addition to sound *detection*, a second basic perceptual feature in hearing of paramount importance in sand cat's ethology is identification of the location (or, at least, direction) of the sound source (Brown 1994; Naguib and Wiley 2001). This "sound localization" ability depends to a great extent on detection of differences in the sounds at the two ears (i.e., binaural differences) (Heffner and Heffner 1988; May and Huang 1996; Populin and Yin 1998). One cue, which depends on the distance between the ears, is the interaural time-difference for sounds coming from off the midline. The placement of sand cats' pinna flanges toward the side of the head that with relatively long ear canals, could increase the interaural time differences and thereby improve sand cats' accuracy in pinpointing the location of sound sources. Enhancement of this key perceptual capability could provide benefits beyond the "earshot extension" that results from increased hearing sensitivity.

Ears, habitats and evolution; connections and tests thereof

An interpretation of sand cat evidence

Our results demonstrate that the external ear canals and auditory bullae of sand cats are unusually large, and our acoustic measurements demonstrate that sand-cat middle ears respond to a given sound pressure level with substantially larger motion ($|Y_{\mathrm{TM}}|$ is larger) and increased power absorption compared to domestic cat. With our theoretical estimation of the external ear's output admittance Y_{EX} and radiation efficiency η_{R} we predict (with some assumptions) that sand-cat hearing has increased sensitivity relative to domestic cat and (by inference) also to closely related exotic cats such as Eurasian/African wildcat (*F. silvestris*). We have shown that an expected ethological effect of this specialization is a substantial increase in range for detection of low-frequency sounds in the desert habitat (Fig. 13). An evolutionary scenario might be that in the Pliocene, when modern felid species were evolving (Johnson and O'Brien 1997), ancestral cats came to inhabit more arid habitats and those that happened to have larger ear canals and bullae were better able to thrive because of extended earshot at low frequencies. This advantage enhanced detection of prey, predators and conspecifics thereby favoring survival of the phenotype that became *F. margarita*. This picture suggests two complementary conclusions (or corollaries): (1) the structural changes that improve low-frequency hearing sensitivity are *not adaptive* in other habitats, perhaps because long-distance communication is not effective in habitats with denser vegetation; and (2) structural changes (hypothetical) that improve high-frequency hearing sensitivity are not adaptive in the desert, because in low humidity "atmosphere absorption" at high frequencies is so large that hearing range is not significantly increased (Fig. 13).

Alternative interpretations, of course, may involve entirely different sequences of "causes"; we consider examples of two kinds. First, suppose that the shortening of the facial part of the skull in sand cats (Heptner and Sludskii 1992, p 642) was adaptive through enhancing the force of the canine teeth's "aimed lethal bite" (a distinguishing felid behavior; Ewer 1973, p 5) through reduction of the lever arm from jaw joint to canines, and thereby made these predators more successful in quickly immobilizing prey (e.g., jerboas) before they jump away. In this picture the increase in size of the cranium (Heptner and Sludskii 1992, p 642) would also contribute to bite strength through provision of a larger area for attachment of jaw-closing muscles. These adaptive alterations (or distortions) of the configuration of the skull might be coupled (e.g., through a genetically controlled growth pattern) to an increase in bony ear-canal size and bullar dimensions. In this scenario the change in ear configuration is entirely a side effect of jaw adaptation for predation, i.e., the ear changes are non-adaptive (as with the spandrels of San Marco; Gould and Lewontin 1979).

In a second kind of alternative, the changes in ear configuration are adaptive, but not through improvements in hearing sensitivity. In this case, the lowering of the pinnae to a more lateral position might improve accuracy of sound-source localization (as suggested above) and the changes in ear canal and bullar size might then be changes associated with rearrangement of the numerous muscles that control pinna movement and attach to the skull in the ear region. In this case the structural change would be adaptive to hearing, but not through increased sensitivity.

The important point here is that our results can be consistent with many hypotheses. Exclusions of particular hypotheses require well-designed tests.

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[8] In preliminary analysis of 17 recorded sand cat bark-like vocalizations (recorded in a zoo; G. Peters, personal communication), W.T. Peake and K.N. O'Connor (unpublished observations) found fundamental frequencies of around 0.66 ± 0.02 kHz (mean and standard error) and harmonics whose magnitudes are more than 25 dB below the fundamental component. These bark-like vocalizations have a duration of 210 ± 11 ms. A similar analysis of 30 bob-cat "mews" (also recorded by G. Peters, unpublished communication) yielded significantly higher fundamental frequencies, more prominent higher harmonics and longer durations (O'Connor 2001).

Tests of key ideas

Habitat ear-structure coupling If the properties of acoustic propagation in dry air encourage improvements in low-frequency hearing sensitivity for sand cat, they might have similar effects in other species, especially closely related species. According to Ortolani and Caro (1996, Appendix 4.2) sand cat is the only felid species found exclusively in desert habitats. Five other species, somewhat less selective in that they inhabit both 'desert' and 'grassland' habitats, are: (1) black-footed cat (*F. nigripes*) of open, dry regions around the Kalahari Desert of southern Africa; (2) Pallas's cat (*Otocolobus manul*) of the steppes of central Asia; (3) caracal (*Caracal caracal*) of deserts and grasslands of Africa and Asia; (4) cheetah (*Acinonyx jubatus*), and (5) lion (*Panthera leo*) both now found mainly in savannas and deserts of Africa. If dry air and an open habitat encourage large bullae and ear canals, one might expect to see them in these other species. In fact, measurements of museum skulls show that black-footed cat and Pallas's cat have bony ear-canal areas $\tilde{N}$ and bullar volumes $\hat{V}$ that are substantially ($>33\%$) above the allometric fit for the whole family (W.T. Peake and H.C. Peake, unpublished observations) (see Table 1 for Pallas's cat data). These structural features might result from the same mechanisms working in species whose usual habitat is not as open and dry as sand cat's, and whose structural specialization is less extreme. Results for the other three species differ: caracal and lion show smaller, but significant positive deviations ($>15\%$) from the family allometric fit for $\tilde{N}$ and $\hat{V}$, but cheetah is marginally *below* the family trends for both measures. Thus, the coupling of structural variations of the ear with habitat is not evident in all the species that live in similar habitats. A convenient explanation for cheetah as an exception is that it is unique among felids (Seidensticker and Lumpkin 1991, p 21) in body structure (long legs, slender body, small head), activity pattern (diurnal rather than nocturnal) and predation style (running rather than stalking). Hearing sensitivity may be less important to a diurnal, running hunter.

To extend the search for similar auditory specializations in other desert-living Carnivora, we need consider only the one other species considered to inhabit desert exclusively, the fennec fox (*Vulpes zerda*) (Ortolani and Caro 1996). This small canid shares with sand cat and black-footed cat a non-ear specialization, coverage of the footpads with long hair. The fennec has dramatically large pinnae and bullae (Heim de Balsac 1936; Ewer 1973). The bullar enlargement could be parallel evolution of fennec and sand cat to the same Saharan habitats. Physiological measurements of effects of bullar-volume variation on hearing sensitivity would be one kind of test. Tests of hearing thresholds for fennec compared to related non-desert species would also be relevant. Although several domestic dog breeds have been tested (Heffner 1983), no exotic canid species are represented in Fay's (1988) compendium.

For other mammalian orders, the subjective evidence of Heim de Balsac (1936) supports the occurrence of enlarged bullae in Sahara-dwelling species of all orders that are represented there. Whether the argument for increased hearing sensitivity would be supported in these taxa requires new evidence.

Ear acoustics Our specific conclusions, based on analysis of the external-ear acoustic model, can be tested; for instance, is the radiation efficiency of the sand-cat external ear substantially larger than domestic cat, as indicated by Fig. 8? Tests could be made with post-mortem sand-cat materials (Rosowski et al. 1988).

Acoustic power absorption and hearing thresholds Whether sand cat hearing is more sensitive than domestic cats (or wildcat) could be tested in anesthetized specimens with evoked potentials recording (Walsh and McGee 1986, Walsh et al. 2001), or by behavioral tests on captive specimens (e.g., Heffner and Heffner 2001). As the hypothesis implies unusually low thresholds the tests would require careful control of ambient noise that might mask the test tones.

Sound propagation in habitats A purely acoustic test could determine whether sound propagation in a real sand-cat habitat has the properties presented in terms of humidity and frequency dependence. It is possible that other effects make this theory inaccurate for real habitats.

Range extension for sand-cat relevant signals Sand cat vocalizations regarded as long-distance signals (G. Peters, personal communication) may have spectra with strong components only at low frequencies; they have been described as quite loud (Jackson 1987). The propagation of such vocalizations in a desert habitat could be compared to that of the "mew" of a wildcat (also found in deserts), to test whether adaptations in vocalization are consistent with the range-extension idea.

Survival benefits: prey capture Do unusual hearing capabilities contribute to sand cats' success in hunting? One can imagine locations where sand cats could be radio-collared and monitored in a way that allows assessment of hunting success (see Sliwa 1999). Then some sand cats could have their hearing modified (reversibly) by insertion of an appropriately "tailored" earplug that removed the sand cats' enhanced sensitivity. Comparisons could test whether the earplugs had an effect on prey capture. Control observations could use earplugs that were tactually comparable but acoustically transparent.

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