

The Functions of Laryngeal Air Sacs in Primates: A New Hypothesis

Gwen Hewitt Ann MacLarnon Kate E. Jones

University of Surrey Roehampton, London, UK

Key Words

Air sacs • Primates • Hyperventilation • Vocalisations • Call rate •
Call duration • Allometry • Speech breathing • Resting breathing rate

Abstract

A possible function of laryngeal air sacs in apes and gibbons was investigated by examining the relationships between air sac distribution, call rate, call duration and body weight in a phylogenetic context. The results suggest that lack of sacs in the smaller gibbons and in humans is a derived feature. Call parameters in primates, such as rate and duration, scaled to resting breathing rate (and therefore to body weight) only in species without air sacs, which appear to modify these relationships. Apes and larger gibbons may be able to produce fast extended call sequences without the risk of hyperventilating because they can re-breathe exhaled air from their air sacs. Humans may have lost air sacs during their evolutionary history because they are able to modify their speech breathing patterns and so reduce any tendency to hyperventilate.

Copyright © 2002 S. Karger AG, Basel

Introduction

Many, but not all, primates have sac-like extensions of the larynx or other parts of the vocal tract called air sacs. These vary in size and configuration in different primate taxa. Only the large sacs of the apes, howler monkeys and cercopithecines are reasonably well known, while the air sacs in most other species of primates have not been a major area of research [1]. A maximum of four types of air sac (lateral ventricular, subhyoid, infraglottal and dorsal) have been identified, but no single source describes the morphology and summarises the distribution of all the types of air sac. The structure of the four sac types is illustrated in figure 1a–d,

KARGER

Fax +41 61 306 12 34
E-Mail karger@karger.ch
www.karger.com

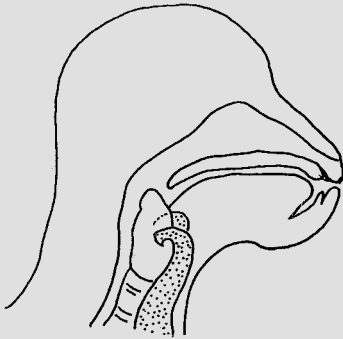
©2002 S. Karger AG, Basel
0015–5713/02/0733–0070\$18.50/0

Accessible online at:
www.karger.com/journals/fpr

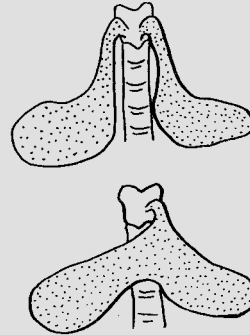
Dr. Gwen Hewitt, School of Life Sciences
University of Surrey Roehampton, West Hill
London, SW15 3SN (UK)
Tel. +44 20 8392 3524, Fax +44 20 8392 3527
E-Mail g.hewitt@roehampton.ac.uk

a Lateral ventricular sacs, e.g. *Pan troglodytes*

Mid-sagittal section of head and 3D sketch of larynx, trachea and air sacs [17–19]

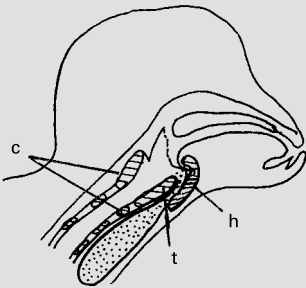


Ventral 3D sketch to show variation in sac development [16]



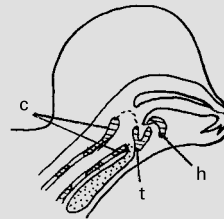
b Subhyoid sacs, e.g. *Cercopithecus* sp.

Mid-sagittal diagrammatic section of head [1]



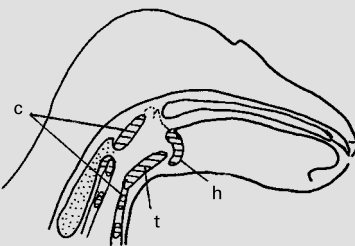
c Infraglottal sacs, e.g. *Callithrix* sp.

Mid-sagittal diagrammatic section of head [60]



d Dorsal sacs e.g. *Varecia variegata*

Mid-sagittal diagrammatic section of head [2, 11]



-  Air sacs
-  Bone and cartilage
- c = Cricoid cartilage
- h = Hyoid bone
- t = Thyroid cartilage

- a Paired lateral outgrowths from the ventricle, a recess in the larynx formed by the inferior thyro-arytenoid fold.
- b Unpaired, leave the pharynx just above the glottis, can extend ventrally to fill the cavity of the hyoid or beyond.
- c Single ventral infraglottal midline opening, extend forward between the cricoid and thyroid cartilages.
- d Single dorsal infraglottal opening, extend dorsally between the cricoid cartilage and the first tracheal ring and caudally between the trachea and the oesophagus.

Fig. 1. Four types of laryngeal air sac described in primates. 3D = Three-dimensional.

Table 1. A summary of the probable distribution of the four types of laryngeal air sac in primates

Sac type	Distribution	Source
Lateral ventricular	apes, <i>Alouatta</i> <i>Callicebus</i> and <i>Cebus</i> monkeys probably <i>Colobus</i> sp. and <i>Presbytis</i> sp.	2, 15, 55, 56 11 2, 11
Subhyoid	Old World monkeys, <i>Alouatta</i> and possibly in <i>Colobus</i> sp. <i>Cebus</i> , <i>Saguinus</i> and <i>Aotus trivirgatus</i>	1, 3, 11, 57–60, 62 2
Infraglottal	some, but not all, callitrichids	2, 15, 60, 61
Dorsal	<i>Indri</i> , <i>Varecia variegata</i> and <i>Microcebus murinus</i> <i>Ateles</i>	2, 45 2, 15, 60, 61

and table 1 summarises their probable distribution among primates, although this has not been documented comprehensively and authors do not always agree about the type of sac present in a particular taxon.

The function of the different types of air sac also remains uncertain though most authors assume that all air sacs modify vocalisations in one of three ways. The best supported suggestion is that the sacs of Old World monkeys help to amplify vocalisations, possibly by acting as resonance chambers [1–4]. For example, the intensity of the boom vocalisation of *Cercopithecus neglectus* was reduced when the air sac was punctured experimentally and male cercopithecines, which give loud calls, have larger sacs than the quieter females [1]. A second hypothesis that air sacs may help to increase the duration and alter the formant frequencies of vocalisations, enabling smaller animals to sound like larger ones [2, 5], has not been tested. Thirdly, other authors have suggested that the lateral air sacs in some species might have a more direct role in phonation as air passes in and out of sacs over a flexible vocal lip, producing sounds such as the boom of the siamang [6–8]. However, it is not clear if the air sacs in other gibbons and apes have a similar function.

It seems probable that the lateral ventricular and subhyoid sacs serve different purposes [3]. For example, Andrew [9] suggested in the 1960s that air sacs opening above the larynx (such as subhyoid sacs) can only function as resonators, unlike the air sacs that open within the ventricle. It is the function of the latter, especially the sacs of gibbons and apes, that is particularly unclear. Harrison [10], based on Negus [11], dismissed the idea of vocal functions for such sacs. He reasoned that the smaller gibbons lack air sacs, yet they are all renowned for their loud great calls and duets that can be heard over long distances in dense forest [10, 12]. Harrison [10] therefore concluded that ventricular air sacs in apes are unlikely to be necessary for the production of such vocalisations.

Both Harrison [10] and Starck and Schneider [2] explored and rejected three alternative functions for ventricular air sacs. Firstly, inflated air sacs are unlikely to stiffen the thorax in brachiators because some excellent brachiators such as gibbons lack air sacs while gorillas and chimps have them. Secondly, inflated air sacs must play only a limited role in visual social displays in most apes and gibbons because air sac inflation changes appearance markedly only in the siamang. Smaller

changes in appearance would not be sufficiently obvious to act as a visual signal when viewed at a distance in a forest canopy. Thirdly, air sacs are also unlikely to allow re-breathing of air so avoiding the necessity of taking a fresh breath during high levels of activity (as suggested by Negus [11]), because many highly active mammals do not have them. Additionally, air sac walls are not highly vascularised and would not give an appreciable oxygen supply [2].

Harrison [10] concluded that the large ventricular air sacs of apes are relatively functionless, and Kleinschmidt (1938, cited in Starck and Schneider [2]) even suggested that the development of air sacs is simply a by-product of high pressure in the airways during vocalisations. But, as Starck and Schneider [2] pointed out, reasonably well-developed sacs are found in fetuses and neonates, and these authors reasoned that air sacs in apes play some, as yet unclear, role in vocalisations. It also seems unlikely that the sacs of apes have no function because they can become seriously infected. Both captive and wild apes have been reported with 'air sacculitis' [13]. For example, an air sac infection in a free-ranging mountain gorilla was so severe that it was treated with antibiotics and the air sacs were surgically drained [14], and a captive bonobo had a similar problem [15]. Additionally, it seems strange that the lateral ventricular sacs of the apes are so large if they have no function. Those of the orang utan (*Pongo pygmaeus*) can extend to 6 litres in volume when fully inflated [2]. Gorillas (*Gorilla gorilla*), chimpanzees (*Pan troglodytes* and *P. paniscus*) and the siamang (*Hylobates syndactylus*) also have relatively large lateral ventricular sacs of paired origin [2, 6, 10, 11, 13, 15–20] (although they are variable in both size and in the relative development of the right and left sacs between individuals of a species [2, 16–19, 21]).

In contrast, humans are usually described as lacking air sacs, or having lost them during human evolution [6], and Harrison [10] proposed that the small sacculi extending from the human larynx might be vestigial air sacs. The pattern of evolution of air sacs in the Hominoidea has not been studied to date. However, if air sacs were lost during human evolution, then an examination of possible reasons for this loss (first considered by MacLarnon and Hewitt [22] in the context of the evolution of human speech and eloquently highlighted as an outstanding question by Fitch [23]) could help to illuminate the functions of air sacs in the other members of the Hominoidea.

MacLarnon and Hewitt [22] speculated that the loss of air sacs in humans may be related to the evolution of fine control of breathing required for speech. We are able to produce long phrases containing many syllables on single extended exhalations, each preceded by a rapid, deep inhalation. Apes and gibbons, in contrast, are not able to modify their quiet breathing cycle to this extent. They give their long, loud, varied call sequences on repeated cycles of inhalations and exhalations with one sound per air movement. In slower sequences, sounds may be made only on exhalations, but faster, louder sequences can involve sound production on both inhalations and exhalations.

Video observations recorded for the present study of the breathing patterns of other primates giving loud call sequences, and descriptions of calling breathing patterns by other authors, suggest that calling on repeated sequences of inhalations and exhalations is not restricted to gibbons and chimpanzees. It has also been observed in a number of strepsirrhines, such as the brown lemur [9], the ruffed lemur [pers. observation], the sifaka [9] and the indri [24]. Similarly, it has been de-

scribed in the night monkey [9], the titi monkey [25], in mangabeys [26], in the Mentawi langur [24] and in baboons and mandrills [9] and observed in a red howler monkey [pers. observation]. The majority of these species also have air sacs, but the pattern of movement of air in and out of the sacs during such call sequences is unknown. In fact, few studies have directly measured respiratory movements associated with naturally produced calls. One such study demonstrated that trills in squirrel monkeys involve repeated rapid, shallow inhalations and exhalations superimposed on a slightly extended exhalation [27]. However, trills in other species may not involve such vocalisation-correlated respiratory movements, for instance those of rhesus macaques may involve tongue and lip movements [28].

The very limited evidence indicates that air is breathed in and out from lateral ventricular sacs during extended vocalisation sequences in apes [3]. Most authors state that the sacs of apes are filled with expired air (e.g. Negus [11]) and radiological analyses in chimps, gorillas and orang-utans confirmed reports based on casual observations that air enters the air sacs during exhalation and leaves during inhalation in these species [6]. Sac inflation was also described as taking place on exhalations in the siamang [29]. It seems that air sacs in apes can either be filled and emptied on each breathing cycle, or they are filled on a series of exhalations until the sac is fully extended [3, 21]. This paper presents a preliminary examination of a speculative new hypothesis, that re-breathing expired air from air sacs has a function that is related to the production of the long, varied in/out vocalisation sequences, such as those of apes and gibbons (and perhaps of some other species?). That they might re-breathe air from their air sacs for reasons other than those of gaining an additional supply of oxygen does not seem to have been considered previously. Nor have possible relationships between the pattern of emptying and filling of sacs and breathing patterns during vocalisations been studied.

It might be expected that vocalisation parameters that are dependent on the rate of breathing should scale to body weight with negative allometry in primates, following the scaling pattern of resting breathing rate to body weight in mammals [30]. These could include the rate at which sequences of discrete, varied calls are given on a series of inhalations and exhalations (call rate). Conversely, the duration of calls given on an exhalation (call duration) might be expected to scale with positive allometry to body weight. That is, larger animals should call at a relatively slower rate where calls involve sequences of inhalations and exhalations and give relatively longer vocalisations on a single exhalation than smaller animals. The hypothesis to be tested here is that breathing air in and out of air sacs while calling could modify such relationships between call rate, call duration and body weight.

Neither the pattern of distribution and evolution of air sacs in relation to body size in primates nor the interrelationships between call parameters, body size and distribution of air sacs have been considered before. Three studies have shown that other parameters of calls, such as fundamental frequency, are constrained by body size in a range of primates, with larger species giving lower pitched calls [31–33]. Fitch and Hauser [5] also suggested that body size could affect the bandwidth, amplitude and duration of call sequences. Nobody has examined the relationship between call rate and body size in detail, although Zimmerman [34] did suggest that smaller nocturnal primates may call at a faster rate than larger ones. Therefore, the distribution of air sacs among primate species is explored here in relation to body size variation and vocalisation parameters. The main questions focus around the

distribution and pattern of evolution of air sacs in primates, particularly in the Hominoidea, the pattern of evolution of air sacs in relation to evolutionary changes in body weight, the scaling relationships between call duration, call rate and body weight in all primates and the possible role of air sacs in modifying these relationships.

Methods

Call Rate and Call Duration

In this preliminary study, data on adult call rates (the rate at which loud sequences of discrete units of sound are given on a series of inhalations and exhalations) and call duration (the length of individual calls given on a single, extended exhalation) were collated or calculated from quantitative data in published papers, or extracted by the analysis of suitable published spectrograms. The aim was to include only call sequences where the 'species' breathing patterns were described by the authors or observed personally in captive primates using video (31 species – identified in Appendix 1) but relatively few researchers have focused on relationships between breathing patterns and vocalisations in non-human primates. A number of compromises were therefore made in order to increase the data set. Data were included if the definitions for calls used in the published papers were derived from studies that reported breathing patterns in relation to calls or if breathing patterns had been described for related species (11 species). In other species (in particular, the nocturnal bushbabies, the macaques and the cercopithecines), spectrograms were analysed assuming that the pattern of call division into inhalations and exhalations was the same as for spectrograms with similar profiles from other species, or, on a similar basis, that the spectrogram represented a single exhalation.

Where several different call types were published, the most complex call sequences given by a species were analysed. These were mostly long-distance contact calls although alarm calls and other long sequences were also used if the species did not give loud contact calls or if high-quality spectrograms were not available for the latter (the call type analysed is detailed in Appendix 1). Only close calls of gorillas were included, because data on loud calls have not yet been published. Data on the breathing patterns of smaller nocturnal primates have not been reported in the literature. However, the spectrograms of their calls were analysed because tape recordings and sonograms of calls of African galagos made available by Paul Honess [pers. commun.] suggested that the calls could be interpreted as being given on repeated inhalation and exhalation sequences. The fastest rate of repetition of sounds within a 0.5-second period (the duration of some published spectrograms) was assessed if the call rate varied within a sequence. Average values for call rate and call duration were calculated where multiple data sets were available. The data sets used for the analyses are summarised in Appendix 1. They contain 55 species for call rate analyses and 36 species for duration analyses.

Air Sac Distribution

Data on the presence or absence of laryngeal air sacs were taken from the published literature. Species were categorised as possessing or lacking air sacs. The four main types of air sac were not distinguished in analyses because of the small sample size for each type and the lack of complete agreement about their distribution.

Body Weight

Mean species body weights were obtained from an unpublished data set collated by Martin and MacLarnon [pers. commun.], using data from wild-caught specimens where possible. Some gibbon body weights were taken from Geissman [35].

Resting Breathing Rate Estimates

Resting breathing rates of 25 species of primate were recorded by direct observation of available primates in zoos in London, Twycross, Paris and New York. Adult individuals were observed until their breathing rhythm could be identified. Activity levels were noted [1 = eyes shut, lying still possibly sleeping; 2 = eyes open, lying still or sitting with eyes closed; 3 = eyes open, sitting (included being groomed); 4 = as for 3 but individual moved during observation]. The number of cycles in 1 min was extrapolated from the number of in/out breathing cycles recorded in 10 s. Observations were repeated until at least 3 had been made at activity level 1. These were averaged for the individual. Observations were made from as many individuals of a species as were available, and mean levels were calculated for the species.

Analyses of Data Points from Closely Related Species

Data points from closely related species cannot necessarily be treated as independent points for statistical analyses because they may share associations among the characteristics of interest by descent from common ancestors rather than independent evolution [36]. However, the best method of controlling for such potential phylogenetic inertia is currently under debate [37, 38]. Therefore analyses were carried out on both the 'raw' species data and the phylogenetically independent contrasts derived from transformation of the species data using the comparative analysis by independent contrasts (CAIC) package [39]. Analyses by both methods are presented, and significance levels were only considered to be robust where their results are in agreement. A composite phylogeny for primate species with known branch lengths was used [40]. All variables were $\log_{10}$ transformed prior to analysis. Least-squares regression was used to estimate the relationship between call rate contrasts, call duration contrasts and body weight (forced through the origin for contrasts [41]). The adequacy of the contrast standardisation was checked prior to analysis by independent contrasts [41]. MacClade analysis (version 3.04) [42] (fig. 2) was used to map the distribution of air sacs in extant primate species onto the composite primate phylogeny [40].

Results

Observed and Estimated Resting Breathing Rates

The relationship between observed log resting breathing rate and log body weight was checked in 28 species using linear regression (fig. 3). A strong, negative relationship was found between log body weight and log resting breathing rate in these species, with a scaling slope almost identical to that in Stahl's formula ($r^2 = 0.8$, $b = -0.263$, $p = 0.0001$; breathing rate [cycles per second] = $53.5 \times \text{body weight [kg]}^{-0.26}$ [30]). Therefore Stahl's formula was used to calculate additional estimates of resting breathing rates from body weight in order to allow the vocalisations of more species to be included in the data sets. Surprisingly, given that it was not possible to be certain that the animals were resting, few observed breathing rates were higher than the estimated rate for that species. In the main, the observed values that fell below the regression line for estimated breathing rates were those for the same species that have been described previously as having observed basal metabolic rates that were lower than predicted [43]. They included prosimians

Fig. 2. Distribution of air sacs in primates mapped onto the primate phylogeny [40] with estimation of evolution of air sacs using MacClade analysis [42].

Editor's note: *Petterus*, used here as in Purvis' taxonomy, is more commonly called *Eulemur*.

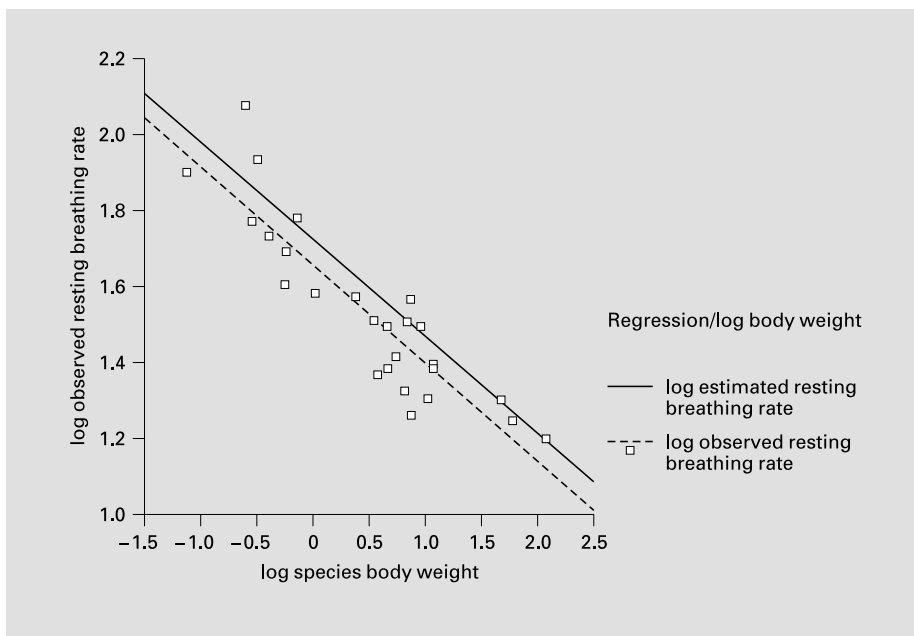


Fig. 3. Relationships of observed resting breathing rate and body weight.

(e.g. *Varecia variegata*) some callitrichids (e.g. *Callithrix jacchus*), *Aotus trivirgatus*, *Alouatta* sp. and *Colobus guereza*. This helps to confirm measurement of resting breathing rate by observation as a useful technique (fig. 2).

Distribution and Pattern of Evolution of Air Sacs in Primates

Air sacs appear to have evolved and been lost at several points during primate evolution. Figure 2a–d illustrates the distribution of air sacs in extant primates and the most probable evolutionary history of air sacs in the major primate groups as calculated by MacClade analysis. The possession of lateral ventricular air sacs is shown as the ancestral state for the Hominoidea and Colobinae and the lack of such sacs in the smaller gibbons and humans is shown as a derived feature. Repeat analyses using alternative phylogenies [35] gave the same results in 7 out of 8 cases. Gibbons with air sacs (the siamang, the concolor group and *H. hoolock*) split off from the main stem before the rest of the gibbons (the only exception was for a phylogeny in which the hoolock gibbon is placed with the lar group). Presence of subhyoid air sacs also appears to be an ancestral feature in cercopithecines. MacClade analysis identified the pattern of evolution of sacs in the Cebidae and Callitrichidae as ambiguous and the dorsal sacs of the Strepsirhini as having evolved a number of times.

Interpretation is problematic in all taxa because the soft tissue of air sacs leaves little trace in the fossil record, and therefore evolutionary directionality cannot be stated with certainty. Even the patterns identified in apes and humans must

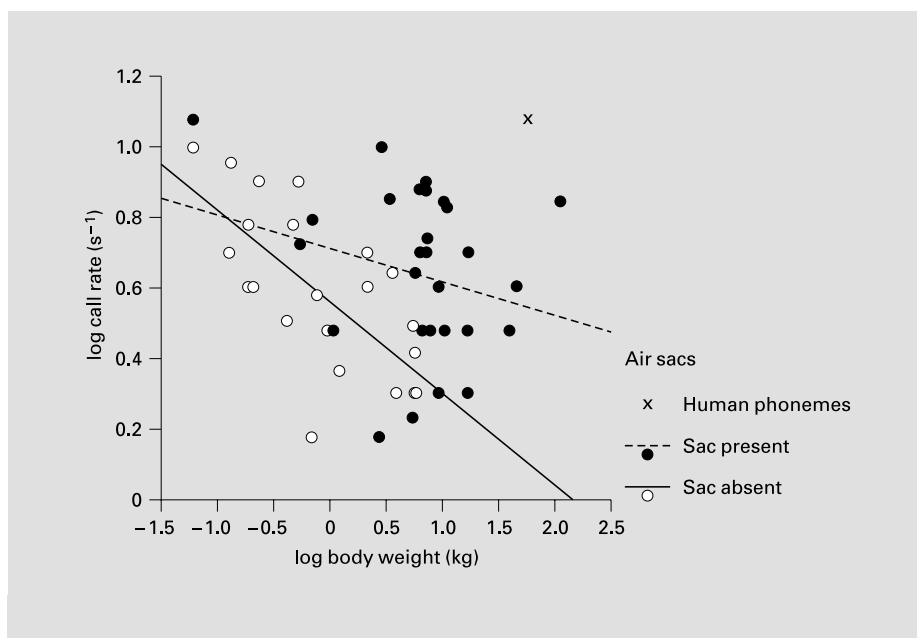


Fig. 4. Relationships of log call rate versus log body weight. Species data. 'Human phonemes' represents log fastest rate of phoneme production per second.

be considered preliminary until more precise descriptions of the morphology, relative size and positive reports of absence of sacs are available, both from more species and from more individuals of species. Consequently, the interpretation of the results of analyses of independent contrasts using CAIC discussed below can only be tentative, because CAIC relies on the phylogenetic patterning and uncertainty reduces its robustness.

Evolution of Air Sacs in Relation to Body Weight in Primates

The relationship between presence or absence of air sacs and body weight in primates was tested using the BRUNCH option of CAIC to examine whether evolution of air sacs was associated with a corresponding increase in body weight (or vice versa). Of 18 phylogenetically independent contrasts, or evolutionary points at which air sacs seem to have evolved or been lost, 14 show a positive association between the evolution of air sacs and an increase in body weight, or between the loss of air sacs and a decrease in body weight. A one-sample *t* test confirmed that evolution of air sacs was significantly associated with an increase in body weight or loss of sacs was associated with a reduction in body weight ($t = 2.72$, d.f. = 17, $p = 0.014$). The exceptions were the evolution of *Microcebus murinus*, *A. trivirgatus*, *Callicebus molloch* and *Homo sapiens*, the first 3 species having evolved sacs without an increase in body weight (2 negative contrasts and 1 zero contrast) and human evolution involved an increase in body weight and the loss of air sacs (negative contrast).

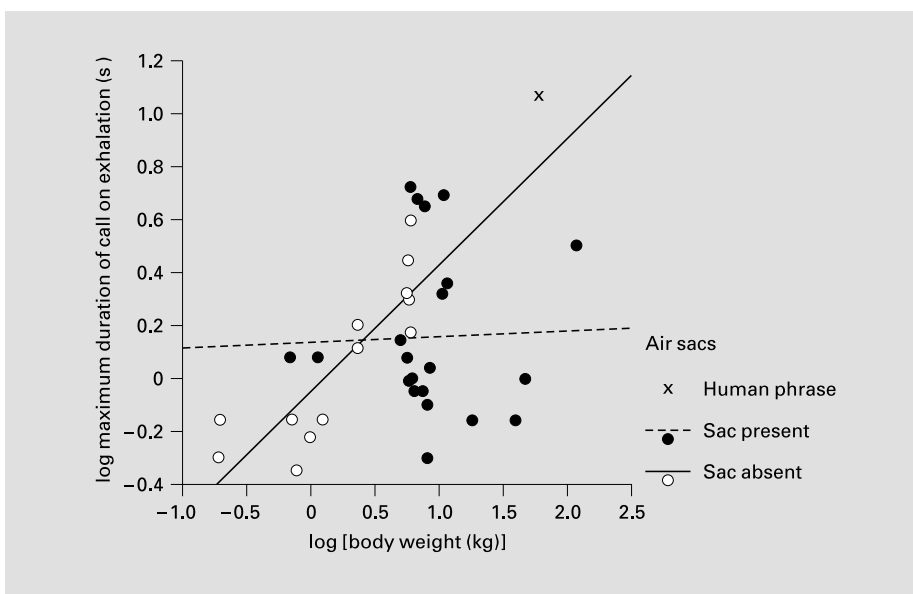


Fig. 5. Relationships of log maximum call duration versus log body weight. Species data. 'Human phrase' represents log mean duration of phrase on one exhalation.

Relationships between Call Rate, Call Duration, Air Sac Distribution and Body Weight

The relationships between call rate and duration and body weight were examined. Resting breathing rate scales with negative allometry to body weight in mammals [30] and call parameters that are dependent on breathing patterns such as call rate and duration would be expected to reflect this, call rate scaling negatively and call duration positively. Species data were plotted for log call rate against log body weight (fig. 4) and log call duration against log body weight (fig. 5). First, the relationships between log call rate, log call duration and log body weight were examined in the total samples using both species and independent contrast data. For call rate, a very weak, negative relationship with body weight was found with the species data, but this was not significant when 48 contrasts for call rate and body weight were analysed. For call duration data, positive (but weak) significant relationships with body weight were found in the analyses of both species and contrast data. These results are summarised in table 2.

The regression analyses for species and contrast data were repeated separating species with and without air sacs, because movement of air in and out of air sacs during call production could modify the relationships between call parameters and body weight. As can be seen in figure 3, smaller primates without air sacs call at a faster rate than the larger ones. A significant negative relationship was found between call rate and body weight in primates without air sacs using both species data and independent contrasts (table 3). No such relationship was found between call rate and body weight in primates with air sacs. All except 4 of the primate species

Table 2. Statistics for relationships between log call rate, log maximum call duration and log body weight

Statistic	Call rate/body weight (log/log)		Call duration/body weight (log/log)	
	species (n = 55)	contrasts (n = 48)	species (n = 36)	contrasts (n = 35)
<i>b</i>	-0.094	-0.195	0.189	0.370
<i>r</i>	-0.297	-0.237	0.367	0.476
<i>r</i> ²	-0.088	-0.056	0.135	0.226
<i>F</i>	-5.14	-2.72	5.29	9.64
d.f.	-1, 53	-1, 46	1, 34	1, 33
<i>p</i>	-0.028*	-0.105 n.s.	0.0277*	0.004**

* *p* < 0.05; ** *p* < 0.01.

Table 3. Statistics for relationships between log call rate and log body weight in primates with and without air sacs

Statistic	Primates without air sacs		Primates with air sacs	
	species (n = 24)	contrasts (n = 20)	species (n = 31)	contrasts (n = 28)
<i>b</i>	-0.264	-0.344	0.097	0.133
<i>r</i>	-0.712	-0.714	0.248	0.103
<i>r</i> ²	-0.508	-0.510	0.062	0.011
<i>F</i>	22.72	18.71	1.895	0.289
d.f.	-1, 22	1, 18	1, 29	1, 26
<i>p</i>	-0.0001**	-0.0004**	0.0277*	0.595 n.s.

* *p* < 0.05; ** *p* < 0.001.

Table 4. Statistics for relationships between log maximum call duration and log body weight in primates with and without air sacs

Statistic	Primates without air sacs		Primates with air sacs	
	species (n = 14)	contrasts (n = 14)	species (n = 22)	contrasts (n = 22)
<i>b</i>	0.480	0.306	0.021	0.478
<i>r</i>	0.865	0.588	0.032	0.442
<i>r</i> ²	0.747	0.346	0.001	0.195
<i>F</i>	35.57	6.34	0.02	4.85
d.f.	1, 12	1, 12	1, 20	1, 20
<i>p</i>	0.0001**	0.027*	0.888 n.s.	0.04*

* *p* < 0.05; ** *p* < 0.001.

with air sacs fall above the regression line for the primates without air sacs in figure 4, indicating that species with air sacs tend to call faster than would be predicted for sacless species of the same body weight.

Similar analyses of species data for call duration (fig. 5) indicated a positive, significant relationship with body weight in primates without air sacs, whichever method of analysis is used (table 4). The analyses of species data found no relationship between call duration and body weight in primates with air sacs whereas analysis of contrast data yielded a weak positive relationship. Primates with air sacs do not generally extend call duration beyond that which would be predicted from body weight. More data points for species with air sacs fall below the regression line for primates without air sacs in figure 4 than above it.

Differences between Primates with and without Air Sacs in Relative Call Rate and Relative Call Duration

The residuals for both independent contrasts and species data derived from the regression analyses of log call rate versus log body weight were compared for the species with and without air sacs using an independent t test. Analyses of both species data and independent contrast data showed that primate species with air sacs had significantly larger residuals, i.e. on average they call at a relatively faster rate than sacless species (species data, $t = 2.25$, $p = 0.029$, $p < 0.05$, and independent contrasts, $t = 3.43$, $p = 0.0008$, $p < 0.05$). Similar analyses were carried out on call duration data, where no significant differences between the residuals of primates with and without air sacs were found for either species or contrast data (species data, $t = 1.07$, $p = 0.285$, $p > 0.05$, and contrasts, $t = 0.507$, $p = 0.616$, $p > 0.05$).

Raw call rates in species with and without air sacs are very similar, averaging around 4 units per second. However, the mean call rate of primates with air sacs was almost 9 times their resting breathing rate, double the rate of species without air sacs. In contrast, all primates increased the duration of exhalations when calling to approximately twice that of a resting exhalation.

Discussion

Analyses of the most probable evolutionary history of air sacs in the Hominoidea, Colobinae and the Cercopithecinae (as calculated by MacClade analysis) indicate that the possession of air sacs is the ancestral state for these groups. The evidence about the presence of subhyoid sacs in the Old World monkeys and lateral ventricular sacs in apes and gibbons is relatively robust and, although there is some disagreement about sac type in the Colobinae, both *Presbytis* spp. and *Colobus* spp. have been described as possessing lateral ventricular sacs by some authors [2, 3, 11, 44]. Therefore, the fact that the different types of air sac were not distinguished in this analysis (because of uncertainty about sac embryology, morphology and distribution in primates as a whole) is perhaps less important here than in other primate groups. For example, all four sac types have been identified in New World primates (summarised in table 1).

The pattern of air sac evolution identified in the Hominoidea supports previous suggestions that the lack of such sacs in humans and the smaller gibbons is probably a derived feature [6, 10, 23]. This interpretation is consistent with the scanty

evidence about the size of fossil hylobatids, such as *Dendropithecus macinnesi*, which were probably of similar size to a siamang (10–11 kg [12]), implying that the evolution of smaller body size is a derived feature among gibbons.

The analysis of the relationship between the presence or absence of air sacs and body weight showed that the evolution of air sacs was associated with an increase in body weight and loss of air sacs with a decrease in body weight in all except 4 out of 18 evolutionary events. Humans were identified as one of the exceptions, a negative contrast suggesting that they lost air sacs though their body weight increased. As mentioned previously, this interpretation can only be speculative because the phylogeny used here was based on living species only and therefore evolutionary directionality cannot be stated with certainty. However, it would seem sensible that hypotheses concerning the functions of lateral ventricular air sacs in gibbons and apes should also account for the probable loss of air sacs in humans during their evolutionary history, despite their larger size.

It was hypothesised that re-breathing expired air from air sacs might in some way assist apes and gibbons in giving their long, loud, varied vocalisations, perhaps by modifying typical relationships between resting breathing rates (and body weight) and vocalisation parameters such as call rate and call duration. In order to examine this contention, the scaling patterns of call rate and call duration with body weight (and therefore with resting breathing rates) were explored. The predicted scaling patterns, based on the assumption that call parameters would be constrained by breathing rates, were only confirmed in species without air sacs. The results suggest that body size (and therefore breathing rates) could be imposing a constraint on call rate and call duration in these species, as has been reported for other parameters of calls such as fundamental frequency [31–33]. Call rates in primates without air sacs have a significant inverse relationship with body weight while call duration has a significant positive relationship with body weight. The present results show that these relationships are probably not an artefact resulting from the lack of independence of data points because results of the analyses of species' data and contrast data were in agreement. The relationships are also surprisingly strong (at least 50% of the variance shared) given the numerous assumptions that were made during the data collection about breathing patterns during calling and the varied functions of the calls analysed.

The prediction that the evolution of air sacs might uncouple the relationship between body size and call parameters was also supported. The call rates and call durations of species without air sacs do not fit the relationships established for primate species with air sacs. However, the results for call rate and call duration did not show the same pattern. Larger primates with air sacs achieve a similar mean absolute call rate to those without air sacs which tend to be smaller, despite the fact that the former are larger and call faster than would be expected for species of their body weight without air sacs. In contrast, the loss of relationship between call duration and body weight in primates with air sacs does not seem to be related to the fact that air sacs help to extend the maximum duration of calls on single exhalations. Most larger primates with air sacs give calls of shorter duration than expected for species without air sacs of similar body weight.

Air sacs therefore do not appear to allow most smaller primates to sound like larger ones by extending call duration as Fitch and Hauser [5] proposed. However, only the duration of calls on single, extended exhalations were analysed here. A

possible role of air sacs in extending the total length of call sequences given on series of inhalations and exhalations was not examined because of lack of suitable published data. Duration data were harder to find in the literature than call rate data, and further study of first hand data would be needed in order to draw firm conclusions. Additionally, the results for both call rate and call duration can only be considered as preliminary because the evidence about call rates and duration was derived from published sources rather than from first-hand data. More importantly, the assumptions about breathing patterns during calling and the involvement of air sacs in these calls need to be confirmed by simultaneous recordings of breathing patterns and calls.

However, given all these caveats, the results suggest that air sacs allow larger primates to call faster than similar-sized species without air sacs. Why this should be and therefore the functional role of air sacs can only be a matter of conjecture. One explanation for the latter could be that re-breathing exhaled air from lateral ventricular sacs during sequences of vocalisations in apes and some gibbons helps to prevent or reduce hyperventilation when calls are given on fast in/out sequences [22]. These long sequences of varied discrete sounds in apes and gibbons tend to be given at rates 10–15 times faster than their resting breathing rates (e.g. chimpanzees – pant hoot sequences up to 5 breath cycles per second, i.e. 300 cycles/min; resting breathing rate 20 cycles/min). Breathing in and out at this rate for even a short length of time, without an accompanying increase in energy expenditure, would be expected to result in hyperventilation. Certainly, it would cause seated humans, with similar or slightly lower resting breathing rates than chimpanzees, to hyperventilate and feel dizzy. Re-breathing air during vocalisations from air sacs filled with expired air could help to prevent larger apes hyperventilating. This could be viewed as equivalent to humans re-breathing exhaled air from a brown paper bag during a panic attack. Air sacs could be used as a reservoir, equivalent to the bag of bagpipes, which can be topped up by breathing into it at intervals that do not have to relate to the rate of sound production [G. Grimbale, pers. commun.] (a form of circular breathing?).

Loss of air sacs during the evolution of the smaller extant species of gibbon (less than 6 kg) can also be explained by this hypothesis. The reduction in body weight and related increase in resting breathing rate would allow them to call at higher rates for short periods without hyperventilating. Air sacs can be the site of infection, and their evolutionary loss would be an advantage.

An explanation is also needed for the loss of air sacs during human evolutionary history, despite their increase in body weight. Fitch [23] speculated that air sacs in other primates may play some role in loud calls but may not be required for relatively quiet human speech. It may be that in apes and gibbons, it is not just loud calls that require air sacs, but loud and varied calls given on fast sequences of inhalations and exhalations that could result in hyperventilation. Hyperventilation is normally not a problem for humans when speaking quietly. Enhanced speech breathing control enables humans to produce phrases equivalent to call sequences on single, extended exhalations rather than requiring cycles of inhalations and exhalations [22]. In addition, humans may have lost air sacs despite their increase in body weight, because they do not need to give such long, loud hyperventilation-inducing call sequences in order to communicate with others of their group at a distance. Quiet speech allows them to discuss the foraging pattern for a day and plan meetings in advance.

Of course, air sacs may not be the only way of reducing a tendency to hyperventilate. Other mechanisms could include physiological solutions to the problem such as development of the ability to withstand carbon dioxide levels fluctuating well outside the usual range or the undergoing of periods of apnoea after calling for any length of time. Physical exertion such as increased locomotor activity could also counteract a tendency to hyperventilate by using up oxygen and increasing carbon dioxide levels. This could be one function of the increase in brachiation activity during the fastest part of the calls of smaller gibbons, as described by a number of authors [29, 45–48, 50]. In contrast, apes and gibbons with large air sacs may be able to remain stationary while calling, only becoming active towards the later stages of long, loud, repeated call sequences when re-breathing exhaled air from air sacs is insufficient to counteract hyperventilation.

In conclusion, the proposed ‘reduction in ventilation’ hypothesis for the function of air sacs in apes and some gibbons is speculative. Much further study is needed in order to test the assumptions made in this paper and consideration also needs to be given to why larger primates with air sacs should call faster than expected. In addition, call parameters such as duration, amplitude, frequency and rate of unit production are interrelated and it is difficult to separate an amplification function for air sacs from a role in reducing hyperventilation. A smaller animal, which gives very loud sequences of sounds on a series of inhalations and exhalations, may be more likely to hyperventilate than an animal of similar size that calls more quietly (a possible explanation for the presence of air sacs in *Callicebus* and *Aotus*?). The relationships between all these parameters and the presence and absence of air sacs need to be investigated directly, particularly in gibbons and apes, in order to assess their relative importance. However, the evidence is at least congruent with the suggestion that air sacs may have evolved in some primate lineages to enable fast call sequences in larger-bodied species.

Acknowledgments

Data collection was funded by the University of Surrey Roehampton. The authors thank Paul Honess for generously providing his unpublished data and for time spent in discussion about the calls of nocturnal primates.

Appendix 1: Sources of Data for Analyses

Species	Species body weight kg	Resting breathing rate min ⁻¹	Fastest call rate s	Call rate ^a	Breathing pattern while calling	Call type ^b	Duration of/as			Sources of call duration data	P or A ^c	Sources of air sac data
							LC s ^d	RE s ^e	MRE ^f			
Allenopithecus												
Alouatta belzebuch	6.35	33.18	5	9.04	described observed	loud [63]					1	median-hyoid + lateral [2, 15, 56], could have 3 types, 1st, 2 + pharyngolaryngeal [55, 56], subhyoid/ventricular interconnect [11], differ between species and sexes [58, 61]
Alouatta palliata	6.55	32.89	3	5.47	described	loud [64]	4.8	0.9	5.1	[65]	1	median-hyoid not lateral [58], genus only [61]
Alouatta seniculus	5.85	34.2	–	–	inferred	–	5.3	0.9	5.6	[65]	1	genus only [61]
Aotus trivirgatus	0.73	58.1	6.2	6.4	described	threat [9, 66]	1.2	0.5	2.3	[9]	1	dorsal [15, 44], lateral large or subhyoid [2], large sacculles [11]
Ateles belzebuch	6.35	33.18	7.6	13.74	inferred	bark [9]	1.1	1.0	1.1	[9]	1	genus only – infraglottal dorsal/median [2, 15, 60, 61], no lateral sacs? [61]
Brachyteles arachnoides												
Cacajao											0	[61]
Callicebus moloch	1.09	52.33	3	3.44	described	loud, long graded sequences [25]	1.2	0.6	2.1	[25]	1	sacculles like ‘watch pockets’ [62]
Callimico goeldi	0.58	61.6	–	–	inferred	–	0.1	0.5	0.2	[9]	0?	small ventricular sacs [11, 61], incipient dilated hyoid [57] possible; not in other species [44]
Callithrix											0	median inferior [15], large sacculles in marmosets [10], no sac in this genus [57]
Cebuella pygmaea											0	no sacs [57]
Cebus capucinus	3.00	40.33	10	14.88	inferred	chirps [67]	–	–	–	–	1	often paired [2], ‘like apes’, lateral small ventricular sacs probable [11]; not all spp small paired [60]
Cercocebus albigena	7.35	31.98	8	15.01	described	whoop gobble [26]	–	–	–	–	1	subhyoid [59], largest [1], spp. subhyoid [15, 68], in both sexes but larger in males [68]
Cercocebus galeritus	7.85	31.8	3	5.66	described	whoop [26, 69]	0.5	1.0	0.5	[70]	1	subhyoid [59], vs. small, particularly in females [1]

<i>Cercocebus torquatus</i>	9.1	30.31	4	7.92	described	loud [70, 71]	–	–	–	1	subhyoid, medium-sized [11]
<i>Cercopithecus aethiops</i>										0?	possibly not or small [1, 62]
<i>Cercopithecus ascanius</i>	3.60	38.59	4.39	6.83		train of Ka calls [71, 72]	–	–	–	1	very small subhyoid [1, 60], in all spp. but size variation; look as if paired origin but different origin to apes [1]
<i>Cercopithecus campbelli</i>										0?	[70]
<i>Cercopithecus cephus</i>										1?	very small [1]
<i>Cercopithecus diana</i>	5.42	34.6	–	–			1.2	0.9	1.3	1	[68]
<i>Cercopithecus erythronis</i>										0?	very small [62]
<i>Cercopithecus hamlyni</i>										1?	[70]
<i>Cercopithecus lhoesti</i>										0?	[70]
<i>Cercopithecus mitis</i>	5.85	34.2	4.4	7.72		booms and barks [71]	–	–	–	1	subhyoid [59, 60]
<i>Cercopithecus mona</i>										0?	[70]
<i>Cercopithecus neglectus</i>	5.55	34.7	–	–		–	1.0	0.9	1.1	1	subhyoid [1, 59, 68]
<i>Cercopithecus nictitans</i>	5.40	35.62	1.65	2.78		loud calls [70, 71]	1.4	0.9	1.6	1	subhyoid [1, 60, 68]
<i>Cercopithecus pogonias</i>	2.67	41.47	1.5	2.17		booms and barks [70, 71]	–	–	–	1	subhyoid [1, 60]
<i>Cercopithecus solatus</i>										0?	[70]
<i>Cercopithecus wolffi</i>										1?	[70]
<i>Chiropotes</i>										0?	very small [44]
<i>Colobus badius</i>										0	[3]
<i>Colobus guereza</i>	9.15	30.15	2	3.98	inferred	roars [73]	–	–	–	1	subhyoid large in this sp. [3, 60], small ventricular sacs [11]
<i>Colobus polykomos</i>	9.15	30.21	2	3.97	described	roars [73]	–	–	–	1	median unpaired/paired lateral, males [2] large larynx, subhyoid but no lateral [3], small subhyoid, large lateral [11]
<i>Colobus satanas</i>					inferred					0	[3]

Appendix 1 (continued)

Species	Species body weight kg	Resting breathing rate min ⁻¹	Fastest call rates	Call rate ^a	Breathing pattern while calling	Call type ^b	Duration of/as			Sources of call duration data	P or A ^c	Sources of air sac data
							LC s ^d	RE s ^e	MRE ^f			
<i>Erythrocebus patas</i>												
<i>Galago alleni</i>	0.25	76.92	8	6.15		alarm call [74]	–	–	–	–	0	galagos (no species) have large sacculles [10, 45]
<i>Galago granti</i>	0.13	90.2	5	3.33		[75]	–	–	–	–	0	probably no air sacs [45]
<i>Galago moholi</i>	0.21	80.12	4	3			–	–	–	–	0	probably no air sacs [45]
<i>Galago senegalensis</i>	0.19	82.38	3	2.18		[9, 76]	0.5	0.4	1.4	[9]	0	probably no air sacs [45]
<i>Galagoides demidoff</i>	0.07	108.91	10	5.51		[34, 74, 75]	–	–	–	–	0	probably no air sacs [45]
<i>Galagoides zanzibaricus</i>	0.14	89.3	9	6.05		[34]	–	–	–	–	0	probably no air sacs [45]
<i>Gorilla gorilla</i>	117.55	15.73	7	26.7		close calls [77]	3.2	2.1	1.6	[77]	1	paired, lateral [17]
<i>Homo sapiens</i>	60.00	18.0	–	–	described	–	12.0	1.7	7.2	[78]	0	possibly vestigial sacs [10]
<i>Hylobates agilis</i>	5.85	33.8	2	3.55	described	songs [29, 35, 79–81]	1.5	0.9	1.7	[29]	0	[12]
<i>Hylobates concolor</i>	7.55	31.63	3	5.69	described observed	songs [29, 53]	4.5	1.0	4.7	[52, 55, 82]	1	paired lateral, relatively small, in male only [15, 45, 52, 79, 82]
<i>Hylobates hoolock</i>	6.9	32.38	3	5.56	described	songs [29, 83, 84]	–	–	–	–	1	paired lateral [57], probably present in both sexes [15]
<i>Hylobates klossi</i>	5.8	33.88	2	3.54	described	songs [29, 51]	4.0	0.9	4.5	[29, 35]	0	[15]
<i>Hylobates lar</i>	5.6	34.2	2	3.51	described	[29, 53, 85, 86]	2.8	0.9	3.1	[53, 83]	0	[15]
<i>Hylobates moloch</i>	5.65	34.14	2	3.51	described	[29, 52]	2.0	0.9	2.2	[29, 52]	0	no sac [15, 17]
<i>Hylobates muelleri</i>	5.55	34.27	2	3.5	described	[24, 29]	2.0	0.9	2.3	[24, 79]	0	[15]
<i>Hylobates pileatus</i>	5.45	34.43	2	3.49	observed	[24, 29, 54]	2.1	0.9	2.4	observation 0	[15]	
<i>Hylobates syndactylus</i>	11.3	28.89	8	16.62	described observed	[15, 29, 54, 87]	2.3	1.1	2.2	[29, 51, 87]	1	paired lateral sacs [12, 20]
<i>Indri indri</i>	10.5	29.03	3	6.2	described	loud honk series [24, 88, 89]	5.0	1.0	4.8	[24, 88, 89]	1	dorsal median [2, 15], infraglottal median [60], large laryngotracheal [45]

<i>Lagothrix</i>	2.2	43.6	5	6.88	described	alarm barks [9, 90]	1.3	0.7	1.9	[91, 92]	0?	dorsal [15], most lemurs lack sacs [11], no sacculs in lemurs [10], no sacs [45]
<i>Lemur catta</i>	2.2	43.6	5	6.88	described	alarm barks [9, 90]	1.3	0.7	1.9	[91, 92]	0?	dorsal [15], most lemurs lack sacs [11], no sacculs in lemurs [10], no sacs [45]
<i>Leontopithecus rosalia</i>	0.56	62.2	5.3	5.11	observed	long loud calls [93]	–	–	–	–	1	unpaired median ventral [2], tamarins large sacculs [10], no sacs in genus [57]
<i>Macaca fascicularis</i>											1?	subhyoid [2], no sac [68]
<i>Macaca fuscata</i>	10.45	29.15	7	14.41		[70, 94, 95]	2.1	1.1	2.0	[95]	1	spp. subhyoid [15, 45]
<i>Macaca mulatta</i>	5.91	33.7	–	–	–	–	1.0	0.9	1.1	[9]	0?	may have very small sacs [15, 60]
<i>Macaca nemestrina</i>	7.76	31.8	–	–	–	–	0.8	1.0	0.8	[96]	1	yes, but unclear which sort [45]
<i>Macaca nigra</i>											1?	yes, but very small [68]
<i>Macaca radiata</i>											0	[68]
<i>Macaca sinica</i>											0	[68]
<i>Macaca sylvanus</i>											1	[68]
<i>Mandrillus sphinx</i>	16.43	26.3	3	6.84	described	segmented grunts [9]	–	–	–	–	1	genus, large lateral sacculs [11], large subhyoid [68]
<i>Microcebus murinus</i>	0.07	108.5	12	6.64		advertisement clicks [97]	–	–	–	–	1	dorsal, median [2], laryngotracheal [68]
<i>Miopithecus talapoin</i>											1	male, moderate size, no loud call [1]
<i>Nycticebus coucang</i>	0.68	59.2	1.5	1.52	described	loud threat [9]	0.7	0.5	1.4	[9]	0	no air sac and feeble development of ventricles [68]
<i>Otolemur crassicaudatus</i>	1.2	51.1	2.3	2.7		[9, 34]	0.7	0.6	1.2	[9]	0	no sac [45]
<i>Otolemur garnettii</i>	0.78	57.1	3.8	3.99		[34]	–	–	–	–	0	no sac [45]
<i>Nasalis larvatus</i>											1	[3]
<i>Pan paniscus</i>	39.1	20.7	3	8.69	described	high hoots, scream [98]	0.7	1.5	0.5	[98, 99]	1	lateral, paired [15, 21]
<i>Pan troglodytes</i>	45.9	19.83	4	12.1	described	pant hoot [47, 83, 100]	1.0	1.6	0.6	[83]	1	paired, lateral [2, 5], yes, but very variable [2, 21]
<i>Papio anubis</i>	17.13	25.9	5	11.58	described	grunt, bark [9, 26]	0.7	1.3	0.6	[26]	1	large subhyoid sac in genus [11, 101]
<i>Papio cynocephalus</i>	16.62	26.18	2	4.58	inferred	[26]	–	–	–	–	1	large subhyoid sac in genus [11, 101]

>

Appendix 1 (continued)

Species	Species body weight kg	Resting breathing rate min ⁻¹	Fastest call rate s	Call rate ^a	Breathing pattern while calling	Call type ^b	Duration of/as			Sources of call duration data	P or A ^c	Sources of air sac data
							LC s ^d	RE s ^e	MRE ^f			
<i>Papio hamadryas</i>	17.59	25.4	5	11.81	described	[9]	0.7	1.2	0.6	[9]	1	may not possess larger anterior median sac [101]
<i>Perodicticus potto</i>	0.95	54.17	3	3.32	described and inferred	[9, 34, 102]	0.6	0.6	1.1	[9]	0	no dorsal air sac and feeble development of ventricles [45]
<i>Pteropus fulvus</i>	2.2	43.64	4	5.5	described	grunt [9, 90]	1.6	0.7	2.4	[74]	0	no sac [45]
<i>Phaner furcifer</i>	0.42	67.04	3.2	2.86		[103]	–	–	–	–	0	no sac [45]
<i>Pithecia pithecia</i>											1	paired? [57]
<i>Presbytis entellus</i>											1	[44]
<i>Presbytis potenziani</i>	7.25	32.02	5	9.37	inferred	[24]	0.9	1.0	0.9	[24]	1	paired lateral? [2], both in a list of species [3], <i>P. entellus</i> large subhyoid [11]
<i>Procolobus verus</i>											0	[9]
<i>Presbytis</i> spp.											1?	probably in all members of genus [44]
<i>Propithecus verreauxi</i>	3.84	39	2	3.08	inferred	grunt [9]	–	–	–	–	0	no sac [45]
<i>Saguinus midas</i>	0.54	62.7	8	7.66	inferred	[66]	–	–	–	–	0	no sac [57], large saccules in tamarins [10]
<i>Saguinus oedipus</i>	0.48	64.82	6	5.55	described	[104]	–	–	–	–	0	no sac [57], large saccules in tamarins [10]
<i>Saimiri sciureus</i>	0.75	57.7	–	–	–	–	–	–	–	–	0	no sac [44]
<i>Tarsius spectrum</i>	0.2	81.99	6	4.39		[24]	0.7	0.4	2.0	[24]	0	no sac [57]
<i>Theropithecus gelada</i>											1	[68]
<i>Varecia variegata</i>	3.5	39.8	7.1	10.7	observed	loud [74, 105, 106]	–	–	–	–	1	dorsal, unpaired [2], infraglottal median [60], laryngotracheal [45]

^aCall rate as multiple of resting breathing rate.

^bCall type and sources of call rate data.

^cPresence or absence of air sacs.

^dDuration of longest call, s.

^eDuration of resting exhalation, s.

^fDuration as multiple of resting exhalation.

References

- 1 Gautier JP: Etude morphologique et fonctionnelle des annexes extra-laryngées des Cercopithecinae: liaison avec les cris d'espacement. *Biol Gabon* 1971;7:230–267.
- 2 Starck D, Schneider R: Respirationsorgane; in Hofer H, Schultz AH, Starck D (eds): *Primatologia*. Basel, Karger, 1960, vol III/2.
- 3 Hill WCO, Booth AH: Voice and larynx in African and Asiatic Colobidae. *J Bombay Nat Hist Soc* 1957;54:309–321.
- 4 Brown CH: Auditory localization and primate auditory behaviour; in Snowdon CT, Brown CH, Petersen MR (eds): *Primate Communication*. Cambridge, Cambridge University Press, 1982, pp 144–164.
- 5 Fitch WT, Hauser MD: Vocal production in nonhuman primates: Acoustics, physiology, and functional constraints on 'honest' advertisement. *J Comp Psychol* 1995;37:191–219.
- 6 Fink BR, Frederickson EL: Laryngeal 'preadaptation' to articulated language; in Chivers DJ, Joysey KA (eds): *Advances in Primatology*. London, Academic Press, 1978, pp 93–95.
- 7 Marshall J, Marshall F: Gibbons and their territorial songs. *Science* 1976;193:235–237.
- 8 Brown CH, Cannito MP: Modes of vocal variation in Sykes monkey (*Cercopithecus albogularis*) squeals. *J Comp Psychol* 1995;109:398–415.
- 9 Andrew RJ: The origin and evolution of the calls and facial expressions of the primates. *Behaviour* 1963;20:1–109.
- 10 Harrison DFN: *The Anatomy and Physiology of the Mammalian Larynx*. Cambridge, Cambridge University Press, 1995.
- 11 Negus VE: *The Comparative Anatomy and Physiology of the Larynx*. London, William Heinemann Medical Books, 1949.
- 12 Tuttle RH: *Apes of the World: Their Social Behaviour, Communication, Mentality and Ecology*. Park Ridge, Noyes Publications, 1986.
- 13 Guilloid NB, McClure HM: Air sac infection in the orang-utan (*Pongo pygmaeus*); in Noback C, Montagna W (eds): *Recent Advances in Primatology*. New York, Karger, 1969.
- 14 Hastings BE: The veterinary management of a laryngeal air sac infection in a free-ranging mountain gorilla. *J Med Primatol* 1991;20:361–364.
- 15 Rietschel W, Kleeschulte E: Beitrag zur Erkrankung der Kehlsäcke (Sacci laryngis) beim Bonobo (*Pan paniscus*). *Tierärztl Prax* 1989;17:323–326.
- 16 Avril C: Kehlkopf und Kehlsack des Schimpansen, *Pan troglodytes*. *Morphol Jahrb* 1963;105:74–129.
- 17 Jordan J: Studies on the structure of the organ of voice and vocalizations in the chimpanzee. *Folia Morphol (Warsz)* 1971;30:97–126.
- 18 Jordan J: Studies on the structure of the organ of voice and vocalisation in chimpanzees. Part 2. *Folia Morphol (Warsz)* 1971;30:222–248.
- 19 Jordan J: Studies on the structure of the organs of voice and vocalisations in chimpanzees. Part 3. *Folia Morphol (Warsz)* 1971;30:323–340.
- 20 Tembrock G: Sound production of *Hylobates* and *Symphalangus*; in Rumbaugh DM (ed): *Gibbon and Siamang*. Basel, Karger, 1974, pp 176–205.
- 21 Kelemen G: Anatomy of the larynx and the anatomical basis of vocal performance; in Bourne GH (ed): *The Chimpanzee*. Basel, Karger, 1969, vol 1: *Anatomy behaviour and diseases of chimpanzees*, pp 35–186.
- 22 MacLarnon AM, Hewitt GP: The evolution of human speech: The role of enhanced breathing control. *Am J Phys Anthropol* 1999;109:341–363.
- 23 Fitch WT: The evolution of speech: A comparative review. *Trends Cogn Sci* 2000;47:258–267.
- 24 Haimoff EH: Convergence in the duetting of monogamous Old World primates. *J Hum Evol* 1986;15:51–59.
- 25 Robinson JG: An analysis of the organization of vocal communication in the titi monkey *Callicebus moloch*. *Z Tierpsychol* 1979;49:381–405.
- 26 Waser PM: The evolution of male loud calls among mangabeys and baboons; in Snowdon CT, Brown CH, Petersen MR (eds): *Primate Communication*. Cambridge, Cambridge University Press, 1982, pp 117–143.
- 27 Häusler U: Vocalization-correlated respiratory movements in the squirrel monkey. *J Acoust Soc Am* 2000;108:1443–1450.
- 28 Hauser MD, Evans CS, Marler P: The role of articulation in the production of the rhesus monkey, *Macaca mulatta*, vocalisations. *Anim Behav* 1993;45:423–433.
- 29 Haimoff EH: Acoustic and organizational features of gibbon songs; in Preuschoft H, Chivers DJ, Brockleman WY, Creel N (eds): *The Lesser Apes: Evolution and Behavioural Biology*. Edinburgh, Edinburgh University Press, 1984, pp 333–353.
- 30 Stahl WR: Scaling of respiratory variables in mammals. *J Appl Physiol* 1967;22:453–460.

- 31 Gouzoules H, Gouzoules S: Body size effects on the acoustic structure of pigtail macaque (*Macaca nemestrina*) screams. *Ethology* 1990;85:324–334.
- 32 Hauser MD: The evolution of nonhuman primate vocalizations: Effects of phylogeny, body weight and social context. *Am Nat* 1993;142:528–542.
- 33 Mitani JC, Stult J: The evolution of nonhuman primate loud calls: Acoustic adaptation for long-distance transmission. *Primates* 1998;39:171–182.
- 34 Zimmermann E: Differentiation of vocalizations in bushbabies (Galaginae, Prosimiae, Primates) and the significance for assessing phylogenetic relationships. *J Zool Syst Evol Res* 1990;28:217–239.
- 35 Geissmann T. Evolution of Communication in Gibbons; PhD thesis, Universität Zürich, 1993.
- 36 Felsenstein J: Phylogenies and the comparative method. *Am Nat* 1995;125:1–15.
- 37 Price T: Correlated evolution and independent contrasts. *Philos Trans R Soc Lond (Biol)* 1997; 352:519–529.
- 38 Losos JB: Uncertainty in the reconstruction of ancestral character states and limitations on the use of phylogenetic comparative methods. *Anim Behav* 2000;58:1319–1324.
- 39 Purvis A, Rambaut A: Comparative analysis by independent contrasts (CAIC): An Apple Macintosh application for analysing comparative data. *Comput Appl Biosci* 1995;11:247–251.
- 40 Purvis A: A composite estimate of primate phylogeny. *Philos Trans R Soc Lond (Biol)* 1995;348: 405–421.
- 41 Garland T, Harvey PH, Ives AR: Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Syst Biol* 1992;41:18–32.
- 42 Maddison WP, Maddison DR: MacClade: Analysis of phylogeny and character evolution, version 3.0. Sunderland, Sinauer, 1992.
- 43 Ross C: Basal metabolic rate, body weight and diet in Primates: An evaluation of the evidence. *Folia Primatol* 1992;58:7–23.
- 44 Hill WCO: Primate Comparative Anatomy and Taxonomy: Cebidae. Edinburgh, Edinburgh University Press, 1960, vol 4.
- 45 Hill WCO: Primate Comparative Anatomy and Taxonomy: Strepsirhini. Edinburgh, Edinburgh University Press, 1953, vol 1.
- 46 Tenaza R: Songs, choruses and countersinging of Kloss' gibbons (*Hylobates klossi*) in Siberut Island, Indonesia. *Z Tierpsychol* 1976;40:37–52.
- 47 Kappeler MK: Vocal bouts and territorial maintenance in the Moloch gibbon; in Preuschoft H, Chivers DJ, Brockleman WY, Creel N (eds): *The Lesser Apes: Evolutionary and Behavioural Biology*. Edinburgh, Edinburgh University Press, 1984, pp 376–389.
- 48 Mitani JC: Gibbon song duets and intergroup spacing. *Behaviour* 1985;92:59–96.
- 49 Raemaekers JJ, Raemaekers PM: Field playback of loud calls to gibbons (*Hylobates lar*): Territorial, sex-specific and species-specific responses. *Anim Behav* 1985;33:481–493.
- 50 Chivers DJ: Communication within and between family groups of siamangs (*Symphalangus syndactylus*). *Behaviour* 1976;57:116–135.
- 51 Haimoff EH: Video analysis of siamang (*Hylobates syndactylus*) songs. *Behaviour* 1981;76:128.
- 52 Deputte BL: Duetting in male and female songs of the white-cheeked gibbon (*Hylobates concolor leucogenys*); in Snowdon CT, Brown CH, Petersen MR (eds): *Primate Communication*. Cambridge, Cambridge University Press, 1982, pp 67–93.
- 53 Haimoff EH, Yang XJ, He SJ, Chen N: Preliminary observations of wild black-crested gibbons (*Hylobates concolor concolor*) in Yunnan Province, People's Republic of China. *Primates* 1987; 28:319–335.
- 54 Geissmann T: Female capped gibbon (*Hylobates pileatus* Gray 1891) sings male song. *J Hum Evol* 1983;12:667–671.
- 55 Schon MA: On the mechanism of modulating the volume of the voice in howling monkeys. *Acta Otolaryngol (Stockh)* 1970;70:443–447.
- 56 Schon MA: The anatomy of the resonating mechanism in howling monkeys. *Folia Primatol* 1971; 15:117–132.
- 57 Hill WCO: Primate Comparative Anatomy and Taxonomy: Platyrrhini. Edinburgh, Edinburgh University Press, 1957, vol 3.
- 58 Kelemen G, Sade J: The vocal organ of the howling monkey (*Alouatta palliata*). *J Morphol* 1960; 107:123–140.
- 59 Andrew RJ: Trends apparent in the evolution of vocalization in the Old World monkeys and apes. Symposium 10: *The Primates*. London, Zoological Society of London, 1963.
- 60 Schon Ybarra MA: A comparative approach to the non-human primate vocal tract: Implications for sound production; in Zimmermann E, et al (eds): *Current Topics in Primate Vocal Communication*. New York, Plenum Press, 1995, pp 185–198.
- 61 Hill WCO: Primate Comparative Anatomy and Taxonomy: Cebidae, Part B. Edinburgh, Edinburgh University Press, 1962, vol 5.

- 62 Hill WCO: Primate Comparative Anatomy and Taxonomy: Catarrhini, Cercopithecoidea. Edinburgh, Edinburgh University Press, 1966, vol 6.
- 63 Whitehead JM: Vocially mediated reciprocity between neighbouring groups of mantled howler monkeys (*Alouatta palliata palliata*). Anim Behav 1987;35:1615–1627.
- 64 Baldwin JD, Baldwin JI: Vocalizations of howler monkeys (*Alouatta palliata*) in Southwestern Panama. Folia Primatol 1976;26:81–108.
- 65 Sekulic R, Chivers DJ: The significance of call duration in howler monkeys. Int J Primatol 1986; 7:183–190.
- 66 Oppenheimer JR: Communication in New World monkeys; in Sebeok TA (ed): How Animals Communicate. Bloomington, Indiana University Press, 1977, pp 851–889.
- 67 Robinson JG: Syntactic structures in the vocalizations of wedge-capped capuchin monkeys (*Cebus olivaceus*). Behaviour 1984;90:46–79.
- 68 Hill WCO: Primate Comparative Anatomy and Taxonomy: Cynopithecinae. Edinburgh, Edinburgh University Press, 1974, vol 7.
- 69 Gust DA: A brief report on the social behavior of the crested mangabey (*Cercocebus galeritus galeritus*) with a comparison to the sooty mangabey (*C. torquatus atys*). Primates 1994;35:375–383.
- 70 Gautier JP, Gautier A: Communication in Old World monkeys; in Sebeok TA (ed): How Animals Communicate. Bloomington, Indiana University Press, 1977, pp 890–964.
- 71 Gautier JP: Interspecific affinities among guenons as deduced from vocalizations; in Gautier-Hion A, Bourlière F, Gautier JP, Kingdon J (eds): A Primate Radiation: Evolutionary Biology of the African Guenons. Cambridge, Cambridge University Press, 1988, pp 196–226.
- 72 Marler P: A comparison of vocalizations of red-tailed monkeys and blue monkeys, *Cercopithecus ascanius* and *C. mitis* in Uganda. Z Tierpsychol 1973;33:223–247.
- 73 Oates JF, Trocco TF: Taxonomy and phylogeny of black and white colobus monkeys: Inference from analysis of loud-call variation. Folia Primatol 1983;40:80–113.
- 74 Macedonia JM, Stanger KF: Phylogeny of the Lemnidae revisited – Evidence from communication signals. Folia Primatol 1994;63:1–43.
- 75 Honess P. Speciation among Galagos (Primates, Galagidae) in Tanzanian Forests; PhD thesis, Brookes University, Oxford, 1996.
- 76 Zimmermann E, Bearder SK, Doyle GA, Andersson AB: Variations in vocal patterns of Senegal and South African lesser bushbabies and their implications for taxonomic relationships. Folia Primatol 1988;51:87–105.
- 77 Harcourt AH, Stewart KJ, Hauser M: Functions of wild gorilla close calls. 1. Repertoire, context, and interspecific comparison. Behaviour 1993;124:89–122.
- 78 Winkworth AL, Davis PJ, Ellis E, Adams RD: Variability and consistency in speech breathing during reading: Lung volumes, speech intensity and linguistic factors. J Speech Hear Res 1994;37:535–556.
- 79 Gittins SP: The vocal repertoire and song of the agile gibbon; in Preuschoft H, Chivers DJ, Brockleman WY, Creel N (eds): The Lesser Apes: Evolutionary and Behavioural Biology. Edinburgh, Edinburgh University Press, 1984, pp 354–375.
- 80 Mitani J: Species discrimination of male song in gibbons. J Comp Psychol 1987;13:413–423.
- 81 Mitani J, Marler P: A phonological analysis of male gibbon singing behaviour. Behaviour 1989; 109:20–45.
- 82 Schilling D: Song bouts and duetting in the concolor gibbon; in Preuschoft H, Chivers DJ, Brockleman WY, Creel N (eds): The Lesser Apes: Evolutionary and Behavioural Biology. Edinburgh, Edinburgh University Press, 1984, pp 390–403.
- 83 Marler P, Tenaza R: Signalling behaviour of apes with special reference to vocalizations; in Sebeok TA (ed): How Animals Communicate. Bloomington, Indiana University Press, 1977, pp 965–1033.
- 84 Gittins SP, Tilson RL: Notes on the ecology and behaviour of the hoolock gibbon; in Preuschoft H, Chivers DJ, Brockleman WY, Creel N (eds): The Lesser Apes: Evolutionary and Behavioural Biology. Edinburgh, Edinburgh University Press, 1984, pp 258–266.
- 85 Raemaekers JJ, Raemaekers PM, Haimoff EH: Loud calls of the gibbon (*Hylobates lar*): Repertoire, organisation and context. Behaviour 1984;91:146–189.
- 86 Raemaekers JJ, Raemaekers PM: The ooa duet of the gibbon (*Hylobates lar*) – A group call which triggers other groups to respond in kind. Folia Primatol 1984;42:209–215.
- 87 Haimoff EH: Occurrence of anti-resonance in the song of the siamang (*Hylobates syndactylus*). J Comp Psychol 1983;5:249–256.
- 88 Pollock JI: The song of the indris (*Indris indris*): Natural history, form and function. Int J Primatol 1986;7:225–264.
- 89 Thalmann U, Geissmann T, Simona A, Mutschler T: The indris of Anjanaharibe-Sud, Northeastern Madagascar. Int J Primatol 1993;14:357–381.
- 90 Paillette M, Petter JJ: Vocal repertoire of *Lemur fulvus albifrons*; in Chivers DJ, Herbert J (eds): Recent Advances in Primatology. London, Academic Press, 1978, vol 1: Behaviour, pp 831–834.

- 91 Macedonia JM: Individuality in a contact call of a ringtailed lemur (*Lemur catta*). J Comp Psychol 1986;11:163–179.
- 92 Macedonia JM: The vocal repertoire of the ringtailed lemur (*Lemur catta*). Folia Primatol 1993; 61:186–217.
- 93 Snowdon C, Hodun A, Rosenberger A, Coimbra-Filho A: Long-call structure and its relation to taxonomy in lion tamarins. J Comp Psychol 1986;11:253–262.
- 94 Itani J: Vocal communication of the wild Japanese monkey. Primates 1963;4:11–66.
- 95 Green S: Variation in vocal pattern with social situation on the Japanese monkey (*Macaca fus-cata*): A field study; in Rosenblum LA (ed): Primate Behaviour: Developments in Field and Laboratory Research. New York, Academic Press, 1975, pp 1–102.
- 96 West R, Larson CR: Laryngeal and respiratory activity during vocalization in macaque monkeys. J Voice 1993;7:54–68.
- 97 Zimmermann E, Lerch C: The complex acoustic design of an advertisement call in male mouse lemurs (*Microcebus murinus*) and sources of variation. Ethology 1993;93:211–224.
- 98 Mitani JC, Gros-louis J: Species and sex differences in the screams of chimpanzees and bonobos. Int J Primatol 1995;16:393–411.
- 99 Hohmann G, Fruth B: Structure and use of distance calls in wild bonobos (*Pan paniscus*). Int J Primatol 1994;15:767–782.
- 100 Clark AP, Wrangham RW: Acoustic analysis of wild chimpanzee pant hoots: Do Kibale forest chimpanzees have an acoustically distinct arrival pant hoot? J Comp Psychol 1993;31:99–109.
- 101 Hill WCO: Primate Comparative Anatomy and Taxonomy: Cynopithecinae. Edinburgh, Edinburgh University Press, 1970, vol 8.
- 102 Charles-Dominique P: Ecology and Behaviour of Nocturnal Primates. London, Duckworth, 1977.
- 103 Niauxat M, Molin D: Hearing and vocalisation in a Malagasy lemur (*Phaner furcifer*); in Chivers DJ, Herbert J (eds): Recent Advances in Primatology. London, Academic Press, 1978, vol 1: Behaviour, pp 821–825.
- 104 Snowdon CT: Communication as social interaction: Its importance in ontogeny and adult behaviour; in Todt D, Goedekeking P, Symmes D (eds): Primate Vocal Communication. Berlin, Springer, 1988, pp 108–122.
- 105 Macedonia JM, Taylor LL: Subspecific divergence in a loud call of the ruffed lemur (*Varecia variegata*). J Comp Psychol 1985;9:295–304.
- 106 Macedonia JM, Evans CS: Variation among mammalian alarm call systems and the problem of meaning in animal signals. Ethology 1993;93:177–197.