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Bill opening and sound spectrum in barnacle goose loud calls: individuals with 'wide mouths' have higher pitched voices

MARTINE HAUSBERGER*, JEFFREY M. BLACK† & JEAN-PIERRE RICHARD*
**Laboratoire d'Ethologie, URA CNRS no. 373, Université de Rennes 1, Campus de Beaulieu, F-35042 Rennes Cedex, France*
†The Wildfowl and Wetlands Trust, Slimbridge, Gloucester GL2 7BT, U.K.

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It is well known that vocal tract resonances are involved in sound production in mammals, but models of bird vocal production often assumed that their sounds are only source created (Greenwalt 1968). In large birds the source sound resonates off the sides of the long and curved trachea or within air sacs (Welty & Baptista 1988). Recently Nowicki (1987), who studied passerines with short rigid windpipes, showed that resonances are involved in bird song as well; however, the actual way resonances are produced is not yet well known. Several studies have shown that the tracheal length and diameter can influence the frequency spectrum of sounds (e.g. Warner 1972; Brakenbury 1978). As Nowicki & Marler (1988) emphasized, resonance in the trachea can vary with its length, and with the degree to which the open end is constricted or flared. This means that the degree of opening of the bill should influence the frequency of maximum amplitude of the sound produced. In the present study we test this hypothesis for barnacle goose, *Branta leucopsis*, loud calls. Observations of calling individuals have shown us that the same sounds are produced with different neck shapes (extended or S shape) which enables us to exclude neck shape from the possible sources of frequency spectrum variations.

The sounds made by birds are often complex and composed of a fundamental frequency plus a certain number of overtones. These elements are most often harmonics of this fundamental frequency. It is interesting that such elements can be differentially emphasized as is clearly the case in some songbirds such as chickadees, *Parus atricapillus* (Nowicki & Capranica 1986). We found the same phenomenon in barnacle goose loud calls, where such differential emphasis appears as a major factor in individuality. These calls had more or less the same fundamental frequency in the majority of birds but the amplitude spectrum varied greatly from one bird to another. No correlation could be found between the frequency of maximum amplitude and the age, weight or sex of the birds (unpublished data). We argue that such differential emphases of frequencies can be at least partially achieved through the degree of opening of the bill.

Barnacle goose loud calls can be heard from a long distance and are common in many social contexts. They are produced more often by males than females, but both sexes can produce them with similar sonographic structures. Each call is produced in an isolated way, although the calls may be repeated rapidly in a male–female duet (Hausberger & Black 1990). We consider only isolated loud calls here.

We observed individually ringed barnacle geese in a semi-captive flock at the Wildfowl and Wetlands Trust, Slimbridge, between 1 and 8 December 1989. The characteristics of the flock are described elsewhere (Black & Owen 1987). Forty birds of both sexes, aged between 1 and 10 years and with varied weights, were videotaped while they were calling. Videotapes were made within 5 m of the birds, which are very tame, using a Bauer sound-videocamera. Only recordings made while a bird held its head at an angle of 90° to the camera were kept for analysis. All birds were recorded in the same environment and over a very limited period in order to limit possible environmental effects.

Images of the birds' head profiles were used to measure the maximum angle of bill opening. The simultaneously recorded calls were analysed on an Amiga 2000 microcomputer programmed for sound analysis (Richard, in press). Sonagrams were carried out by a Fast Fourier Transform using 256 8-bit samples weighted by a Hanning window. In this case we used a sampling rate of 12 kHz which

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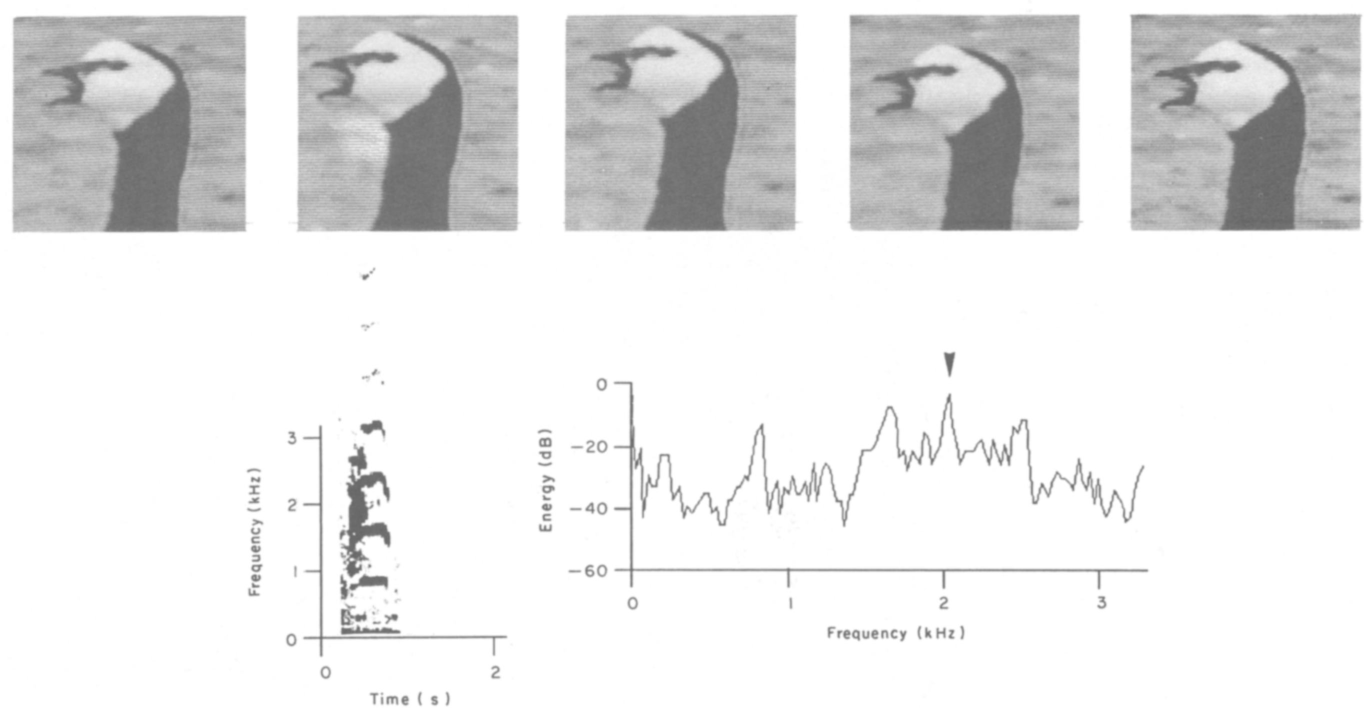
(a)



Frequency (kHz)
0
1
2
3
0
2
Time (s)
Energy (dB)
0
-20
-40
-60
0
1
2
3
Frequency (kHz)

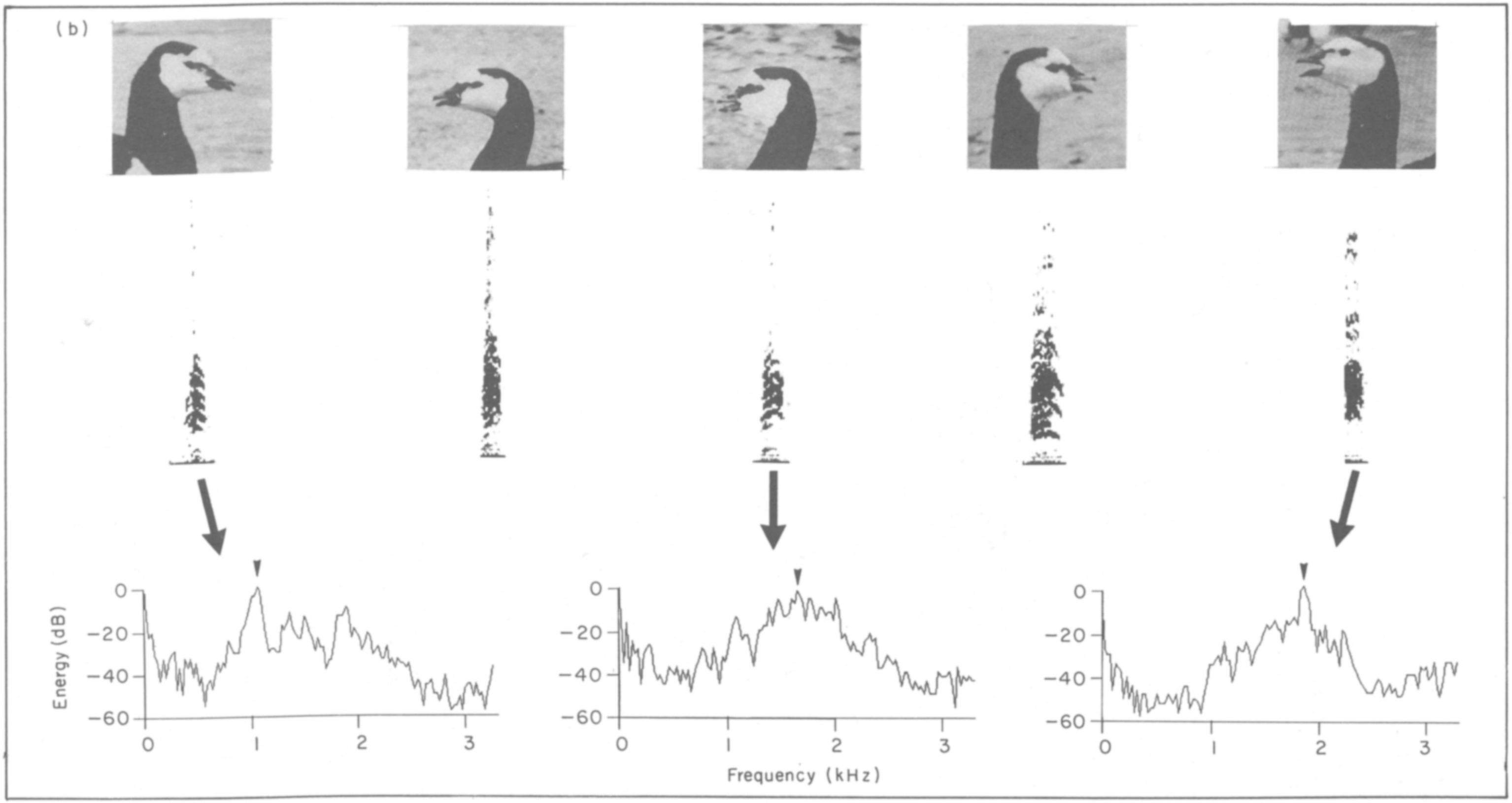


Figure 1. (a) The bill opening profiles and corresponding sonagrams and amplitude spectra of five loud calls of bird number 1. The dark triangle points to the peak frequency of the amplitude spectra. (b) The bill opening profiles and corresponding sonagrams and amplitude spectra of the loud calls of different geese. The arrows link particular sonagrams with three amplitude spectra.

produced a band width of 6 kHz with a frequency resolution of 51 Hz. The interval of 128 samples between successive FFT yielded a time resolution of 10·6 ms. The amplitude spectra were the average of all successive FFT analyses for each call thus limiting the frequency modulation. All the measurements were calculated directly by the computer, thus enabling the precise frequency corresponding to the peak of maximum amplitude to be calculated.

We used 200 (2–15 per bird) measurable bill profiles and the simultaneous calls. The peak amplitude spectrum was consistent within individuals (e.g. bird 1: $N=15$ calls, $\bar{X}\pm\text{SD}=2025\pm25$ Hz). Birds were equally consistent in how wide they opened their bills (e.g. bird 1: $\bar{X}\pm\text{SD}=21\pm1°$, Fig. 1a). There was, however, more variability between individuals for both measurements (peak amplitude range from 970 to 2225 Hz: $N=40$ birds, $\bar{X}\pm\text{SD}=1632\pm240$ Hz; angles between 4 and 21°: $\bar{X}\pm\text{SD}=12{\cdot}7\pm4{\cdot}3°$; Fig. 1b). The peak of amplitude from the calls for the entire sample ($N=40$ birds) was highly correlated with the corresponding measurements of the bill openings; those birds that open their bill widely emphasize higher frequencies (Spearman rank correlation, $r_S=0{\cdot}80$, $P<0{\cdot}001$).

The results are therefore consistent with our hypothesis that there should be a correlation between the degree of opening of the bill and the frequency of maximum amplitude. Of course, the peak of maximum energy is only an elementary measure and the energy distribution along the frequency spectrum is complex, which could also explain why the correlation is not perfect. Given the conditions of recordings, which were identical for all birds, the results cannot be explained by environmental effects. In particular, the closeness to which the birds can be approached and recorded allowed us to avoid phenomena such as ground absorption or other factors of degradation. Although we did not use measurements of sound pressure levels in this study, observations show that they do not depend on the degree of opening of the bill: two geese can be equally loud and open their bills very differently.

The most likely explanation for our results is that resonances are involved in the production of such sounds. Sound radiation pattern could also be involved, but because we made all the recordings at the same angle to the birds' heads and at a very small distance, this appears to us as rather unlikely. As Nowicki & Marler (1988) suggested, the degree to which the mouth is open can certainly modify the resonances in the trachea. Other structures can also be involved: for example, on examination of the videotapes it was obvious that different geese held their tongues in different ways when calling, while a given bird always put it the same way (Fig. 1). We could not measure this precisely but it can certainly also influence the resonances in the trachea. Resonances might be a very widespread phenomenon in sound production, both in songbirds and non-songbirds (Nowicki 1987). It is, however, unusual that differential emphases of frequencies play a major role in individual distinctiveness as appears to be the case in barnacle geese.

We have yet to discover why certain geese open their bills widely while others do not. Only ontogenetic and genetic studies will give us an answer.

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