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POWER CAPABILITIES OF THE AVIAN SOUND-PRODUCING SYSTEM

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SUMMARY

1. The vocal performance of different species of songbird was compared by measuring the maximum total sound power produced during normal song. This varied from 10 mW/Kg body weight in the linnet *Acanthus cannabina* and the whitethroat *Sylvia communis* to 870 mW/Kg in the song-thrush *Turdus philomelos*.
2. In comparison, the performance of the chicken *Gallus domesticus* during crowing was approximately 60 mW/Kg.
3. There was some evidence that performance was related to size in the songbirds as a group, the smaller bird being less effective than the larger.
4. Differences in performance are discussed in relation to the presence or absence of intrinsic muscles in the syrinx and to possible effects of scale on the efficiency of the fundamental sound-producing process.

INTRODUCTION

The structure and function of the syrinx in birds have received growing consideration in recent years (Greenewalt, 1968; Chamberlain, Gross, Cornwell & Mosby, 1968; Stein, 1968; Harris, Gross & Robeson, 1969; Warner, 1972; Gaunt, Stein & Gaunt, 1973; Youngren, Peek & Phillips, 1974; Lockner & Youngren, 1976; Gaunt, Gaunt & Hector, 1976; Gaunt & Gaunt, 1977; Brackenbury, 1978*a*). A beginning has also been made on the study of the energetics of sound production (Brackenbury, 1977; 1978*b*). From the point of view of communication between birds, the ability to extract the maximum amount of sound energy from the biological apparatus available must clearly have been of great selective value during the evolution of voice production. This, one imagines, applied particularly to those species of songbird which maintain a concentrated vocal output during the breeding season, often in the face of severe competition from rival birds. In many cases sounds must be transmitted over very large distances compared to the physical size of the animals producing them. They must also be sufficiently powerful to carry above the ambient noise level due to both climatic and biotic factors in the environment.

The present paper examines the sound power produced by a variety of British species of songbird. An attempt is made to determine whether any general relationships can be found between performance and size. Corresponding data on the chicken are used for comparison.

METHODS

Sound power output was estimated using a simplified version of the method described by Brackenbury (1978*b*). Sound pressure levels were measured using a Brüel & Kjaer 4161 1" omnidirectional microphone attached to the sound level meter of a Nagra IV SJ recorder. Values were assessed visually from the displacement of the meter needle with the instrument set for fast response. Some inaccuracy due to the lag of the needle was inevitable, particularly during the quicker songs. During recordings of chicken sounds in the laboratory the meter was checked against a Brüel & Kjaer precision sound level meter and showed an error of approximately ± 1 dB. It was however impracticable to carry out similar checks in the field. All field measurements were made under the following conditions: the bird was in full song, at a known distance from the microphone and with the beak facing the microphone. When one or more of these conditions were absent the reading was discarded. In successful cases only the maximum level achieved throughout the song was noted. Distance was then measured using a rule and a length of string. In most cases the subject was within 5–10 m of the microphone and sound intensity could be assessed with an estimated error of ± 2 dB. The intensity maxima were all adjusted to a standard distance of 1 m using the inverse square rule. Maximum total sound power output was then calculated for each bird using the method described elsewhere (Brackenbury, 1978*b*). This method assumes that sound energy is radiated uniformly over a solid angle of π radians in front of the bird. The error involved in this assumption is not known although in the case of human speech it has been shown to be small (Sacia, 1925; Olson, 1957).

RESULTS

Table 1 shows the following data for the chicken and seventeen species of songbird: body weight (B.W.), maximum instantaneous sound pressure level (S.P.L.) achieved during song, estimated maximum total sound power output (I) in mW and estimated maximum unit sound power output (I/B.W.) in mW/Kg. Data for body weights were kindly supplied by Dr C. Thorne of the Department of Biochemistry, Cambridge University. The most obvious conclusion to be drawn from the table is that the largest birds produce the greatest amount of sound power. This is only to be expected since the ultimate source of power is the respiratory muscles and larger birds possess larger and more powerful muscles. The data in column 4 however, show that on a weight-for-weight basis the performance of the chicken *Gallus domesticus*, which produces the most sound, is approximately only 7% that of its nearest rival the thrush *Turdus philomelos*. The scaled values in column 4 can be used as an indication of relative efficiency of sound production in the different species if it is assumed that each bird exerts proportionally the same amount of effort compared to its size during singing. Whilst it is clear that in general the poorest performances come from the smaller birds the presence of outstanding exceptions such as the wren *Troglodytes troglodytes* and the blackbird *Turdus merula* make it impossible to say from these data alone that there is a definite correlation between size and efficiency within the songbirds as a group.

DISCUSSION

It has been suggested (Gaunt *et al.* 1973, 1976; Brackenbury, 1977, 1978*a*, *b*) that one of the major factors influencing the efficiency of sound production in birds may be the presence or absence of intrinsic muscles in the syrinx. These may be capable of altering the configuration of the syrinx and of regulating the airflow through the syrinx in a way most favourable to the effective coupling between the airstream and the tympaniform membranes. Several pairs of these muscles are present in the passerine syrinx (Warner, 1972) but they are absent in the chicken and this may be one reason for the relatively poor performance of the latter in comparison with many of the species in Table 1. This consideration however, cannot account for the performance of especially the smaller birds in Table 1, which is even poorer than that of the chicken. It is possible that the physical mechanism of sound production in the syrinx may be inherently affected by scale in a way which operates to the disadvantage of relatively small birds. Data on more species must be obtained, however, before scaling arguments can be accurately employed.

Table 1. *Estimated maximum root-mean-square values of sound pressure level (S.P.L.) in dB w.r.t.*

(2×10^{-4} dynes cm^{-2}, power (I) in mW and unit power (I/Body weight) during normal song in different species of songbird. Sound pressure measurements were made using a Brüel & Kjaer type 4161 1" omnidirectional microphone connected to the sound level meter of a Nagra IV SJ tape-recorder. Levels were adjusted to a distance of 1 m from source using the inverse square rule. Sound power output was calculated according to the method described in Brackenbury (1978*b*).)

Species	B.W. (g)	S.P.L. (dB)	I (mW)	$I.Kg^{-1}$
Gallus domesticus	3500	105	200	57
Turdus philomelos	69	100	60	870
Troglodytes troglodytes	10	90	6	600
Erithacus rubecula	20	90	6	300
Sylvia atricapilla	18	88	4	220
Turdus merula	96	87	3	30
Fringella coelebs	22	86	3	135
Locustella naevia	12	85	2	165
Emberiza citrinella	28	85	2	70
Phylloscopus collybita	9	80	0·6	65
Sylvia curruca	12	80	0·6	50
Acrocephalus schoenobaenus	11	80	0·6	55
Parus ater	9	78	0·4	45
Emberiza schoeniclus	20	78	0·4	20
Phylloscopus trochilus	8	77	0·3	40
Regulus regulus	6	75	0·2	35
Acanthus cannabina	19	75	0·2	10
Sylvia communis	15	74	0·15	10

Nevertheless it is possible to identify in crude terms some of the major features of the sound-production mechanism through which possible scale effects might be thought to operate and upon which future experimental, morphological and theoretical investigation might concentrate. The mechanical efficiency of sound-production can be defined as the ration of sound power radiated from the mouth to the fluid power generated within the vocal/respiratory tract by the action of the air sacs (Brackenbury, 1977). These powers can be expressed respectively as:

$$r_A \dot{x}^2 \quad \text{and} \quad (R_{aw}+R'_{aw})\dot{V}^2,$$

where r_A is the acoustic radiation resistance of the external air, R_{aw} is the respiratory (non-vocal) airflow resistance at the flow rate $\dot{V}$, R'_{aw} is the increase in airflow resistance at the time of vocalization due to the motion of the tympaniform membranes, $\dot{x}$ is the root-mean-square (r.m.s.) acoustic air particle velocity and $\dot{V}$ is the volume flow rate of air from the air sacs. The mechanical quantities r_A and $\dot{x}$ will have the dimensions of Kg s^{-1} and m s^{-1} respectively whilst R_{aw} and $\dot{V}$, as is the normal practice in respiratory physiology, will have the dimensions of Kg m^{-4} s^{-1} and m^3 s^{-1} respectively. During crowing in the chicken R'_{aw} is approximately 5–6 times R_{aw} (Brackenbury, 1977). Also bearing in mind that $\dot{x}$ is proportional to the velocity of vibration of the tympaniform membranes, $\dot{x}_m$, and that $\dot{x}_m = 2\pi f x_m$, where f and x_m are the frequency and amplitude of the membrane vibration respectively, the efficiency as defined above can be expressed in the approximate form

$$e \propto (r_A f^2 x_m^2 / R'_{aw} \dot{V}^2).$$

The possible scale-dependency of e will therefore be determined *inter alia* by the scale-dependency of the individual factors in this expression. These are difficult questions, the answers to which depend on a fuller understanding of the fundamental sound-producing process than is at present available. This understanding will come from further investigation of the mechano-aero-acoustic and morphometric properties of the syrinx.

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